INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

University of Alberta

SYSTEMATIC STUDIES OF THE TROPICAL GENUS *LEUCOLOMA* BRID. (DICRANACEAE, BRYOPSIDA)

by

Catherine La Farge - England ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy

in

Plant Systematics
Department of Botany

Edmonton, Alberta
Spring 1997

National Library of Canada
Acquisitions and Bibliographic Services
395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada
Acquisitions et services bibliographiques
395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

0-612-21587-3

University of Alberta

Library Release Form

Name of Author: Catherine La Farge - England

Title of Thesis: Systematic Studies of the Tropical Genus *Leucoloma* Brid.
(Dicranaceae, Bryopsida)

Degree: Doctor of Philosophy

Year This Degree Granted: 1997

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly, or scientific purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

Catherine La Farge-England

51068 Range Road 223
Sherwood Park, Alberta
T8C 1G9

Date: March 25, 1997

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Systematic Studies of the Tropical Genus *Leucoloma* Brid. (Dicranaceae, Bryopsida) by Catherine La Farge - England in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Plant Systematics.

Dale H. Vitt

Dale H. Vitt (Supervisor)

George E. Ball

D A Craig

Douglas A. Craig

J S Nelson

Joseph S. Nelson

William R. Buck

William R. Buck

Date: March 24/1997

For

John, Jennifer, Margaret,

and

Anne and Edward

Abstract

Leucoloma Brid., a pantropical genus with a center of diversity in Madagascar is the second most species rich moss genus in the region. From an initial 134 accepted species, I accept 112 species for the genus; five new species are described; new synonymy is proposed; a revision of the Afro-Madagascan species of subgenus *Leucoloma* is made; and typification of the revised species or synonymised species is included. A reassessment of the species groups distinguished 14 infrageneric taxa that were used for a phylogenetic analysis of the genus. The cladistic analysis resulted in a single most parsimonious tree that provides an evolutionary hypothesis of the infrageneric relationships. Character evolution is examined within the genus and comparisons with general trends in mosses are made. *Leucoloma* is a morphologically diverse genus, that is supported as a monophyletic taxon, based on 60 characters used for the cladistic analysis. The results provide data for a new proposed infrageneric classification. The distribution and diversity of the infrageneric taxa are examined. There is a clear distribution pattern that features the highest species richness in Madagascar and includes both plesiomorphic and apomorphic taxa. Nearly half of the species are endemic to Madagascar and the surrounding islands; a region that has been designated as "the greatest priority for conservation and biological inventory on earth". *Leucoloma* is primarily an epiphytic genus that is restricted to the rainforests of tropical regions. The high proportion of endemics in the Madagascan rainforests, makes it one of the most threatened moss genera of the region. The study of *Leucoloma* specimens stimulated a re-examination of the terms used for growth form, branching pattern, and perichaetial position in mosses. These terms used for the structural organization in Bryopsida, are reviewed, classified, and redefined. Growth form is differentiated from life form. Direction of growth does not necessarily infer perichaetial position. Pseudo-pleurocarpy is simply a prostrate acrocarp. Cladocarpy is distinguished from acrocarpy or pleurocarpy, based on subperichaetial primordia, juvenile leaf development, and position of perichaetium.

Acknowledgements

Without the continued support and encouragement of my resilient professor, Dale H. Vitt, this work would not have been possible. I am ever appreciative of the many discussions we have had, particularly on pleurocarpy and cladocarpy; a controversy which will no doubt be on going. Many thanks for allowing me to pursue this subject in detail and for never giving up the "faith" in my ability to bring this endeavor to fruition.

I would like to thank Marshall Crosby (Missouri Botanical Garden, MO) for initially suggesting the revision of *Leucoloma*. It is truly a remarkably diverse genus which has warranted every ounce of effort. The Missouri Botanical Garden's Madagascar program headed by Pete Lowry (Natural History Museum in Paris, PC) has proven to be a critical link between the field collections and the data analysis in the lab. Without the strong collaborative efforts of the Garden's staff with the Madagascan government, the collecting excursions would have been extremely difficult. I am most indebted to Robert Magill (MO), who shared his many years of experience of in tropical bryology, and provided the opportunity to join him on field excursions to Tanzania and Madagascar on two occasions. He was also instructive in answering a number of bibliographic and nomenclatural queries on the African material. The Tropicos program designed by Bob has been particularly useful in dealing with the vast number of names in *Leucoloma*. Without a similar type of program, the manipulation of the nomenclatural data would be daunting. I would also like to thank Tamas Pócs (EGR) for his continuous generosity during the two field excursions to Tanzania and Madagascar (especially the Hungarian sausages and paté). His field experience in the tropics was an invaluable asset to the success of our trips. We were most appreciative of the physical support provided by the local porters in both Tanzania and Madagascar, making the collecting efforts far more effective.

The dedicated and conscientious effort made by my defense committee, George E. Ball, Douglas A. Craig, Joseph S. Nelson (all from the Department of Biological Sciences), and William R. Buck (New York Botanical Garden) to thoroughly review this lengthy thesis is greatly appreciated. I would like to thank Hélène Bischler (PC) for her hospitality in the grand archives of the Cryptogamic Herbarium at the Natural History Museum in Paris. Access to photo copying of critical material from the herbaria of Bescherelle, Cardot, Thériot, and Renauld proved to be of great value. I would also like to thank Jan-Peter Frahm (Bonn) for helpful insights on various aspects of the Dicranaceae, and David Cass (University of Alberta) for his generosity with his microtome, SEM preparations, and exquisite microscopes for photographic purposes. Lars Hedenäs (Stockholm) and Efrain De Luna (Mexico City) contributed constructive criticism on the growth form manuscript. Dan Norris (Washington) and Timo Koponen (Helsinki) made helpful comments on a manuscript included in the thesis, as series *Holomitrioidea*. George Braybrook of the Scanning Electron Microscope Lab (Department of Earth and Atmospheric Sciences, University of Alberta) provided the essential expertise for the micrographs and was extremely generous with his computer experience that saved many hours of frustration with the production of the figures. I am most grateful to the large number of curators and private collectors who have loaned their specimens for an extended period of time to allow me to pursue the breadth of the revision. Without their generosity and patience this project would not have been possible.

I would like to acknowledge the financial support provided to me by a Queen Elizabeth II Doctoral Scholarship, Alberta Heritage Scholarship Fund. This research has also been supported by the Natural Sciences and Engineering Research Council of Canada (Grant A-6390 to Dale H. Vitt), and a National Geographic Society Research Grant to Robert Magill (MO), for which I am grateful.

There is no doubt that the one who had to suffer the details of the thesis the most and tolerate the wild enthusiasm of the more exuberant moments was mon cher ami and colleague, Bernard Goffinet. Without his attentive ear for the grandest to most trivial thoughts about mosses, this project would never have been as enjoyable - avec mes plus sincères remerciements.

There can be no way to express my deepest gratitude to my family, John, Jennifer, and Margaret who have supported me throughout the seemingly unending stages of my learning process. I am especially appreciative of their encouragement during the most difficult moments.

Table of Contents

List of Tables

List of Figures

Chapter I

INTRODUCTION

Bryophytes are a pervasive, yet largely unstudied, component of the epiphytic biomass in tropical montane rainforests. The role of epiphytic bryophytes includes humus accumulation, rainfall interception and retention, as well as trapping and provision of nutrients that modify the physical habitat for successive epiphytes (i.e., orchids, ferns; pers. observ.). Increasing rates of forest destruction threaten these rich epiphytic floras in tropical rainforests (Campbell 1990). An urgent need for concentrated research on the biodiversity of rapidly disappearing tropical ecosystems has been emphasized by the Earth Summit in São Paulo, Brazil in 1992. The Convention on Biological Diversity was one of five important documents that resulted from the Earth Summit, that emphasized the need to protect the world's biological diversity as one of the most critical resources for man. Systematic research is essential as the foundation for medical, ecological, evolutionary, floristic, and phytogeographic research, yet the current monetary support for systematic research has lagged behind other disciplines (Wilson 1985, 1988, Steussy 1993).

Madagascar has been designated "the greatest priority for conservation and biological inventory on Earth" (Campbell 1990). Leroy (1978) emphasized the unique species richness of its flora by the preservation of primitive Gondwanaland elements, recent speciation events (e.g. Baobabs and Didieraceae), and recent introductions by long distance dispersal. The destructive paleoclimatic changes that impoverished Africa's flora, had minimal effect on Madagascar's flora (Raven and Axelrod 1974). The moss flora of Madagascar has been estimated at 1065 species (Kis 1985). The second largest moss genus of Madagascar is *Leucoloma* of the Dicranaceae. It forms one of the most conspicuous epiphytic elements of the eastern montane and elfin rainforests that are severely threatened.

The current research is a systematic revision of the epiphytic, pantropical genus *Leucoloma*. It is estimated to be the largest genus of the Dicranaceae subfamily

Dicranoideae in the Bryopsida, with 134 accepted species names (Wijk et al. 1964, 1969, Crosby and Magill 1994, Crosby et al. 1992). A re-evaluation of the enumeration of species and grouping of the species is made. A phylogenetic analysis of the previously circumscribed and new infrageneric taxa is made with respect to its sister taxa *Dicranum*, *Dicranoloma*, and *Sclerodontium*. A new classification is proposed and a biogeographical analysis is made of the infrageneric taxa.

From the examination of characters used in the taxonomic revision and the phylogenetic analysis of *Leucoloma*, a detailed study was made of the terminology applied to growth form, branching patterns and perichaetial position in mosses. A review of the current use of terms and modifications of the definitions are proposed for future systematic studies.

Bibliography

Campbell, D.G. 1990. Rates of botanical exploration in Asia and Latin America; similarities and dissimilarities with Africa. Proceedings of the twelfth plenary meeting of AEFAT. Hamburg, September 4-10, 1988. Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg 23 a: 155-168.

Crosby, M.R. & R.E. Magill. 1994. Index of mosses. Monographs in Systematic Botany from the Missouri Botanical Garden 50: 1-87.

Crosby, M.R., R.E. Magill, & C.R. Bauer. 1992. Index of mosses. Monographs in Systematic Botany from the Missouri Botanical Garden. 42: 1-646.

Kis, G. 1985. Mosses of southeast tropical Africa. An annotated list with distributional data. Vácrátót, Hungary, Institute of Ecology and Botany of the Hungarian Academy of Sciences.

Leroy, J.-F. 1978. Composition, origin and affinities of the madagascan vascular flora. Annals of the Missouri Botanical Garden 65: 535-589.

Raven, P.H. & D.I. Axelrod 1974. Angiosperm biogeography and past continental movements. Annals of the Missouri Botanical Garden 61: 539-673.

Steussy, T.F. 1993. The role of creative monography in the biodiversity crisis. Taxon 42: 313-321.

Wijk, R. van der, W.D. Margadant, & P.A. Florschutz. 1964. Index Muscorum 3: 287-299. Bureau for Plant Taxonomy and Nomenclature, Utrecht.

______, ______ & ______. 1969. Index Muscorum 5: 759-761. Bureau for Plant Taxonomy and Nomenclature, Utrecht.

Wilson, E.O. 1985. Time to revive systematics. Science 230: 4731.

______. 1988. The biological diversity crisis: A challenge to science. Acta Universitatis Upsaliensis Symbolae Botanicae Upsalienses 28: 5-12.

Chapter II

A SYNOPSIS OF THE TROPICAL MOSS GENUS *LEUCOLOMA* BRID. (DICRANACEAE, BRYOPSIDA)

Historical Background

The genus *Leucoloma* Brid. was originally described in 1827 as a monotypic genus, with *Hypnum bifidum* as the basionym for the type species. The generic name is based on two Greek root words: *leuco-* refers to white and *--loma-* to border. Besides the differentiated hyaline border, the distinguishing characters for *Leucoloma* were 1) the single peristome of 16 teeth, bifid to the base; 2) a symmetrical capsule without an annulus; 3) presumed dioicous sexual condition (male plants not seen); 4) "axillary" female gametangia, with about 12 archegonia with paraphyses; 5) a long slender habit, moderately branched; 6) leaves costate, narrow, with subquadrate cell areolation; and 7) capsule erect, oblong, with a short seta, operculum "subulatum". The distribution was described as southern within the tropics, on trees, and perennial (Bridel 1827, pp. 218-219).

Initially, Bridel (1801) had classified the type species in the diplolepideous, pleurocarpous genus *Hypnum*, even though the haplolepideous, acrocarpous genus *Dicranum* Hedw. had been described (Hedwig 1782, 1801). *Dicranum* is a closely related genus to *Leucoloma*. The placement of the type material in *Hypnum* was not without some doubt:

> "Genus incertum cum vere Hypni nomine instructum inuenerim et praecedentibus affine videntur, inter Hypna reliqui." (Bridel 1801, p. 52)

In 1827, following the generic description of *Leucoloma*, Bridel commented that the lateral sporophytes were similar to those of *Trichostomum*. He recognised that the perichaetia are initially terminal, and become displaced laterally by subapical innovations:

"An reipsa fructus lateralis sit aut tantum pseudolateralis (in quodam quasi

> caulis nodulo axillarem Schwaegrichen dicit) videant autoptae. Si fructus autem primordio terminalis, tantum ex innovatione hypogynaea axillaris videntur, genus istud, haud invita natura, ad Trichostomum iterum revocandum erit." (Bridel 1827, p. 219)

Thus, he placed *Leucoloma* within the pleurocarpous genera, not recognising it as a prostrate acrocarp. This misinterpretation has been prevalent in the literature (see La Farge-England 1996 for review, Chapter IV).

Within the same year Schwaegrichen expanded *Leucoloma* to include 3 species, although one of the species, *L. angustifolium* Schwaegr., is currently considered conspecific with *L. bifidum* (Brid.) Brid. (Schwaegrichen 1827). In *Synopsis Muscorum Frondosorum*, Mueller (1848) followed the Bridel's classification (Bridel 1826, 1827), based primarily on acrocarpous versus pleurocarpous taxa. He moved *Leucoloma* from the pleurocarpous taxa and classified it as a section within his broad concept of the acrocarpous genus *Dicranum*. He included five sections within *Dicranum*: *Dicranum, Campylopus, Leucoloma, Oncophorus,* and *Orthodicranum*. The first four have been accepted as independent genera and the last has been treated at the generic or subgeneric rank by various authors (Bruch, Schimper, and Gümbel 1835-1855, Brotherus 1924, Dixon 1932, Nyholm 1954, Peterson 1979, Crum and Anderson 1980, Crosby and Magill 1981, Vitt 1984). Mueller placed 7 species in *Dicranum* sect. *Leucoloma*, including *Dicranum sieberianum* that is presently placed in a distinct genus, *Sclerodontium* Schwaegr. (Table II.1).

Mitten (1859) proposed a new classification of mosses based on peristome structure in his East Indian flora. This differed from the Bridel-Schimper classification that used cladocarpy, acrocarpy, and pleurocarpy as the primary categories, with cleistocarpy (capsule with operculum absent), stegocarpy (capsule with operculum), and schistocarpy (capsule with longitudinal slits) as secondary categories. Mitten considered cleistocarpy an unnatural group, because the taxa occurred in a number of independent lineages. He retained the divisions of schistocarpi and stegocarpi as natural groups. The critical departure from previous classifications was the introduction of "Arthrodonti" and "Nematodonti" subdivisions within the suborder Stegocarpi. *Leucoloma* was classified within the arthrodontous mosses in the Dicranaceae, following Mueller's interpretation of *Leucoloma*'s affiliation with *Dicranum*. Two species of *Leucoloma* were treated in his flora (Mitten 1859).

In a floristic treatment of neotropical material, Mitten placed a single species in Bridel's genus *Leucoloma* and described a new genus *Poecilophyllum* with 9 species (Mitten 1869; Table II.1). Eight of the nine species belong to the current concept of *Leucoloma*, whereas the other belongs to the genus *Dicranoloma* (Ren.) Ren. He differentiated *Poecilophyllum* and *Leucoloma* by the length of the seta, the shape of the capsule, and cucullate versus mitrate calyptrae. Mitten was the first to use sporophytic characters to distinguish taxa within the present-day concept of *Leucoloma*.

In a moss flora of Réunion and the other East African islands, Bescherelle accepted *Leucoloma* at a generic rank, following Jaeger and Sauerbeck (1872). He did not use Mitten's neotropical genus, *Poecilophyllum*. Bescherelle described 5 sections within *Leucoloma*, establishing the first subgeneric classification of the genus (Bescherelle 1878, Table II.1).

In Renauld's regional flora of Madagascar, the Mascarenes and the Comoros the generic concept of *Leucoloma* was expanded and subdivided into 3 subgenera: *Dicnemoloma*, *Dicranoloma*, and *Euleucoloma* (Renauld 1898). The essential characters for delimiting *L.* subgenus *Dicnemoloma* were 1) juxtacostal cells occupying most of the lamina and descending along the margins to the base; 2) membranaceous cells restricted to the inner basal portion of the leaf; 3) hyaline margin narrow, but conspicuous; 4) peristome split to the middle, "nonunquam ad apicem in cruribus duobus fissi"; 5) operculum obliquely rostrate; 6) calyptra smooth, diminutive; and 7) capsule arcuate. *Leucoloma* subg. *Dicranoloma* was based on plants with 1) dicranoid habit; 2) non differentiated juxtacostal cells; 3) hyaline margin; 4) asymmetric, arcuate capsule; 5) "pro more" curved, operculum; and 6) a cucullate calyptra. *Leucoloma* subgenus *Euleucoloma* was based on 1) thick-walled, minute, quadrate-rounded to shortly oblong, juxtacostal cells that formed differentiated bands, tapered in the basal region; 2) elongate interior cells, narrowly linear, thick-walled, smooth, appearing membranaceous in the lower 1/2 of the leaf; 3) extremely narrow, hyaline marginal cells; 4) symmetric, erect capsules; 5) "recterostratum" operculum; and 6) calyptra with "latere fissa" to basally many lobed, often scabrous apically. This subgenus was a synopsis of 42 species, and represents the present-day concept of *Leucoloma*. The former 2 subgenera have been retained as distinct taxa to the present, although their rank has changed.

Renauld expanded and refined the classification within *Leucoloma* subg. *Euleucoloma* into sections, subsections, and series, using Bescherelle's original infrageneric taxa of *Leucoloma* (Renauld 1898, Table II.1). Renauld included all of Bescherelle's sections as subsections within a section, *L.* sect. *Transmutantia*, and excluded *L.* sect. *Prinodontoidea* Besch. from the genus. Renauld described two new subsections, *Holomitrioidea* and *Pseudocaespitulosa*, within *Leucoloma* section *Transmutantia*. Section *Transmutantia* represented the most diverse section, with 23 species from the East African islands. Renauld described *L.* sect. *Vittata* with 14 species, that included subsection *Euvittata* and a monotypic subsection *Subvittata*. The former subsection was further subdivided into two series: *Obscura* and *Distincta*. A third new section was described based on 5 species, *Leucoloma* sect. *Attenuata*. These taxa within *L.* subg. *Euleucoloma* have been the foundation for the classification of *Leucoloma*, with only slight modifications to present. In addition to the systematic value, Renauld's regional study provides critical information on collectors and locality data, that is otherwise lacking on the type specimens.

Paris (1900) classified the subgeneric rank of *Dicnemoloma* and *Dicranoloma* as sections within *Leucoloma*. No justification was given at the time. In *Die Natürlichen Pflanzenfamilien*, Brotherus (1901) based his classification of *Leucoloma* on the synopsis by Renauld (1898). Brotherus described a new monotypic subsection *Semivittata* within section *Vittata*. The new subsection was differentiated by 1) plants robust as in *Dicranum*, 2) leaves with long acuminate subulate apices, 3) inner cells at mid leaf forming a band, 4) alar cells inflated or scalariform, and 5) a long seta. Renauld (1901) transferred the subgenera *Dicnemoloma* and *Dicranoloma* from *Leucoloma*, and raised their rank to genus. The characters he used to delineate the 3 genera are outlined in Table II.2. The essential characters were based on laminal cell architecture and the sporophyte. The subgenus *Euleucoloma* formed the new, refined concept of *Leucoloma*. As well, he renamed and changed the rank of the 3 sections to subgenera: *Taeniodictyon, Sphenodictyon,* and *Syncratodictyon*. A synopsis of his character analysis is presented in Table II.3. His reassessment of *Leucoloma* did not include an enumeration of species.

In the Flora of Java, Fleischer (1902-1923), based his systematic arrangement on Mitten's (1859) system of classification and Philibert's peristome analyses (translation by Taylor 1962). The mosses were primarily classified as "Nematodontei" or "Arthrodontei", with the latter subdivided into 3 classes: Haplolepideae Phil., Heterolepideae Phil., and Diplolepideae Phil. *Leucoloma* was classified within the Haplolepideae, which were distinguished by peristomes with "a single row of external plates" (translation by Taylor 1962). The three diagnostic characters that Fleischer used to separate *Leucoloma* from other dicranaceous genera were: 1) hyaline or colored alar cells, 2) capsules without stomata, and 3) leaves with a hyaline border. Using the cellular patterns of the peristome in the classification of mosses was a major contribution to the understanding of genealogical relationships. The concept of haplolepideous and diplolepideous has not always been well understood. A common misconception was that the terms referred to single versus double peristomes, respectively (Edwards 1984). A number of diplolepideous mosses have a single row of teeth as the result of reduction; as well some haplolepideous mosses have residual exostomes. Thus caution must be used in determining what the number of cells plates refer to. (For a comprehensive review of the difference between haplolepideous and diplolepideous and Diplolepideae, Haplolepideae, and Heterolepideae see Edwards 1984).

Renauld (1909) produced a monograph of *Leucoloma*, based primarily on detailed histological characters of the gametophyte and basic morphological characters of the sporophyte. He refined the generic definitions of *Dicnemoloma, Dicranoloma,* and *Leucoloma,* with laminal cell architecture, stem and costal anatomy, and sporophytic characters. It is curious that he did not use the presence or absence of stomates in his analysis, as Fleischer (1902-1923) had for distinguishing *Dicranoloma.*

Renauld modified his 1898 classification primarily by elevating the ranks of the taxa. The subsections were changed to sections and placed in new subgenera, within the restricted concept of *Leucoloma* (Renauld 1898, 1901, 1909; Table II.1). The synopsis of the genus delineated 114 species in 10 sections and 3 subgenera (Renauld 1909, pp.42-44); an additional 3 species were treated in the supplement (Renauld 1909), that resulted in 117 species enumerated for *Leucoloma.* Renauld moved *Leucoloma* sect. *Semivittata* Broth. from *L.* subg. *Euleucoloma* (= *Taeniodictyon* Ren.) to *L.* subg. *Syncratodictyon.* Renauld's comprehensive monograph of the genus also included a summary of the geographical distribution of the taxa.

The most recent synopsis of the genus enumerated 105 species for *Leucoloma* [1] and followed Renauld's latest classification (Brotherus 1924). Brotherus included 10 new species in the classification, and excluded 20 species that occur in Renauld's classification. Three species (*L. renauldii, L. tenerum,* and *L. cruegerianum*) are listed twice: once in *L.* section *Dicranoidea* and once in *L.* section *Subvittata.* It is assumed this was a printing error. Renauld (1909) had placed them in the former section. A single species, *L. limbatulum* was reclassified from section *Dicranoidea* to section *Subvittata.* Since Brotherus (1924), a new monotypic section was described by Potier de la Varde (1950), *L.* section *Rhacomitrioidea.* In summary, *Leucoloma* consisted of 3 subgenera, with two further subdivided into sections. Subgenus *Taeniodictyon* had 3 sections, and subgenus *Syncratodictyon* included a total of 8 sections (Table. II.1). Renauld's 1909 classification of *Leucoloma* has remained unmodified to present.

The most prolific period for newly described species or those transferred to the

---

[1] Although three species were listed twice, the enumeration of the 105 species is correct (Brotherus 1924, p. 14).

genus was between 1900 and 1910, when there was an expansion rate averaging more than 16 species per year (Table II.4). Prior to this period, the average expansion rate was less than 5 per year and after 1911, the rate fell to less than 2 per year. This interval coincides with Brotherus' transfer of numerous species from *Dicranum* to *Leucoloma*, which was based on Renauld's 1898 classification (Brotherus 1901). It appears that Renauld's 1901 publication of *Dicranoloma* and *Dicnemoloma* as separate genera was not followed immediately, for 11 species were described in *Leucoloma* that belong to *Dicranoloma* between 1902 and 1906, whereas since 1906 two new species were erroneously classified.

The synoptic classifications of *Leucoloma* show the initial 70 years as a gradual broadening of the concept of the genus (Table II.5). Within the next 6 years the numbers of species more than doubled (85 to 176 spp.). Renauld's monograph of the genus reduced the number of species considered "true" *Leucoloma* by 1/3. If one compares the number of species enumerated by Brotherus (1901) in *Leucoloma* subgenus *Euleucoloma*, 95 spp., to the monograph by Renauld (1909), 117 spp., one can see that the "modern day" concept of *Leucoloma* shows a steady increase in species. There was a decrease of 12 species between Renauld (1909) and Brotherus (1924), although the actual difference is 30 species if novelties and exclusions are considered. During the last 70 years a modest number of new species has been added to the genus. With over 280 names applied to the genus, excluding names transferred to other genera, 134 species are accepted for the genus (*fide* Wijk et al. 1964, 1969; Crosby and Magill 1994, Crosby et al. 1992). Early authors described geographical species. Thus, a previously unknown species from a new region was presumed to be new to science. Mueller and Kindberg were particularly adept at this (Schofield 1985). As a result, part of the inflation is due to superfluous names from the tropics. Inflated species numbers have been predicted for exotic moss genera, and are expected to decrease by 30 to 50 % of the number of species (Frahm 1991, Gradstein and Pocs 1989, Magill 1982, Reese 1987, Touw 1974). The following synopsis re-evaluates the enumeration of species for the genus, with a revision of the Afro-Madagascan species of subgenus *Leucoloma* and subgenus *Syncratodictyon* section *Holomitrioidea*.

Materials and Methods

Specimens

The material used for the synopsis of *Leucoloma* is based on specimens from the following herbaria: ALTA, B, BISH, BM, BP, BR, CANM, CATHUP, CBG, E, EGR, F, FH, G, GRO, HBG, H, HIRO, JE, KEW, L, LAF, LD, M, MAUR, MELU, MEXU, MICH, MO, NMW, NSW, NY, PDA, PMA, PRE, QCA, RO, S, SRGH, STR, U, UBC, UPS, W, Z, and the private herbaria of Jean Louis De Sloover, G. Een, J.-P. Frahm, K. Mägdefrau, Fr. M. Onraedt, R. Redfearn, A. Schäfer-Verwimp, and Z. Soldan (Vitt et al. 1985). Revisions of tropical genera commonly require loans from a large number of herbaria, for one problem is to obtain an adequate number of specimens for each taxon. Prior to the species re-evaluation, 30 out of 134 (22%) accepted species of *Index Muscorum* were known only from type material, and two lacked any type material. Heterogenic material sent as duplicates or syntypes of the original type material, or mixed type material can create problematic concepts of species or subspecific taxa. Therefore, as much type material as possible has been examined for the species level revision.

Nomenclature

The systematic revision of *Leucoloma* has included an assessment of 283 specific or infraspecific names, excluding those names that have been transferred to other genera (e.g., *Dicranoloma, Sclerodontium, Rutenbergia*). Many of the early expeditions made isolated collections in the exotic territories; novel species were described simply because they were from new tropical regions (Reese 1987, Touw 1974, Frahm 1991). A summary of the nomenclatural novelties and current synonymy of 112 valid names in *Leucoloma* is presented (Table II.6). Species insufficiently known are included at the end of the table. *Nomina nuda* and *nomina invalida* are listed in Table II.7, and excluded names in Table II.8. Typification of the subgeneric taxa and the species are made in the current revision of subgenus *Leucoloma* and of subgenus *Syncratodictyon*. The species level revision is restricted to the Afro-Madagascan species of subgenus *Leucoloma* and the species of section *Holomitrioidea*. A preliminary species level revision of subgenus *Syncratodictyon*, with nomenclatural novelties and synonymy, is summarised in Table II.9.

For type citation the protologue information is enclosed in quotation marks. Additional critical information (e.g, in the beginning of the article or on the type specimen) was included but not put in quotations. Duplicates of lectotypes are designated as isotypes; and duplicates of syntypes are designated as isosyntypes.

Fieldwork

For many regions of the world, the collections of *Leucoloma* have been limited to a few excursions in the late 1800's and early 1900's. Many of these expeditions did not include a bryologist. Label data providing any extensive habitat or locality information were often lacking. To build on the treatment by Renauld (1909), an excursion was made in 1990 to Tanzania and Madagascar with support from the National Geographic Society and The Missouri Botanical Garden. Specimens were collected at two main localities in Tanzania: Kilimanjaro and the Nguru Mts. As many different populations as possible were sampled of each species within a given locality. The objective was to obtain the broadest range of morphological expression of each taxon. *Leucoloma* species were abundant and especially numerous in the Nguru Mts. In Madagascar two main regions were collected: the central east coast - Andasibe and the north east at the forest reserve of Marojezy. The original collection is deposited in ALTA, with duplicates in MO and TANA. The main objective was to gain some understanding of the diversity of habitats in which *Leucoloma* occurs, as well as an understanding of substrate, growth form, and exposure. A detailed ecological study of microhabitat was beyond the scope of the project.

Measurements

Observations were made with the aid of a Zeiss compound microscope and a Wild M-5 dissecting microscope. Specimens were hydrated and representative structures were mounted for measurement or drawing. An inset micrometer was used to measure cell length and width, as well as the leaf width and border. Seta, capsule, and leaf length were measured under the dissecting scope with a "minitool" ruler to the closest 0.1 mm. Ranges are given for the characters measured. Measurements given in parentheses are rare and outside of the common range.

Illustrations

Drawings were made by means of a camera lucida on the Zeiss compound or Wild M5 dissecting microscope. The line drawings include a single scale bar, that represents a different measurement for each magnification used. A list of the structures drawn at each magnification is provided in each drawing, with its respective measurement for the scale bar. The leaves were drawn at two scales, with the smaller scale to show leaf shape variation. The large scale leaf drawing is provided to show the details of the juxtacostal bands, leaf border, and acumen. Stippling of the juxtacostal bands of the larger leaves indicates the papillose regions. Laminal cells were drawn to indicate lumen shape, not ornamentation. Laminal transverse sections are illustrated to show variation of the costa and leaf cell ornamentation. Characters that remain constant for a section are not illustrated for each taxon (e.g., a mitrate calyptra).

Scanning electron micrographs

Scanning electron micrographs were provided for several of the key characters differentiating sections within *Leucoloma* and for differentiating closely related or commonly confused species. Standard preparation of herbarium material was followed: Material was placed in teflon capsules and hydrated for 10 minutes in boiling distilled H_2O, placed in OsO_4 for 30 minutes, rinsed in distilled H_2O for 30 minutes, followed by dehydration series of 25%, 50%, 75%, overnight, 90%, 95%, 100% of 95% ETOH, 100%, 100% of 98% ETOH, followed by an amyl acetate series of 25%, 50%, 75%, 100%. The material was critical point dried, then mounted on doubled sided sticky tape on a stub. The specimen was gilded with two coatings of 10 nanometres of gold using a Nanotech Sputtercoater. Scanning and photography was done using a Cambridge 250 Stereoscan and Jeol JSM 6301 FXV electron microscope at 5-20 KV. Exceptions to the normal preparation of bryophyte material included the following.

SEMs of leaf cross sections were obtained by 1) hydration material in distilled H_2O; 2) blotted for removal of excess H_2O; 3) freeze drying the specimens in liquid nitrogen; 4) fracturing the lamina; 5) mounting the specimens as above; 6) and scanning the material in a cryostage. Sporophyte material was scanned with no preparation, except for mounting on the stubs and gilding of the material. In the case where it was critical to use type material, the specimen was scanned without any preparation to prevent damage to the material.

Mapping

The revised species are mapped from the specimens of the herbaria cited above, if the number of specimens was limited (less than 20). Given a large number of specimens, selected specimens from each different political region (i.e., province) were mapped. Numerous specimens from localities of close proximity may result in a discrepancy between the number of dots on a map versus the number of specimens cited. Specimens lacking adequate locality data have not been mapped, unless they represent the only available material. A number of specimens have early Malgache names used by the French colonists that were not found in the gazetteer for Madagascar, Réunion, and the Comoros (Office of Geography, Department of the Interior, Washington, D.C., 1955). Numerous duplicate place names in Madagasacar add to the difficulty in mapping the specimens.

Habitat

A compilation of the habitat data, including substrate, exposure, elevation, and forest type was noted from available label information. Height above forest floor was noted for all specimens the author collected.

Distribution

A general summary of the distribution is given for each species. Longitude and latitude are given for known localities to the nearest minute. For localities where detailed maps existed, coordinates are given to the nearest second.

Floristic Treatments

Regional treatments with descriptions, keys, and illustrations of taxa have been limited for the tropics, although continuing projects including bryophytes have mandates to correct this: Flora North America, Flora Neotropica, Bryologia Africana, Flora Australia, Flora of Papua New Guinea, and the Chinese Flora project. These treatments will provide an assessment of biodiversity with current species concepts, nomenclature, and distribution patterns. It is critical to have descriptions, keys, illustrations and current bibliography of original literature in order to identify material from a given region.

The regional nature of floras or species lists have some obvious disadvantages compared with monographs. Synonymy with taxa outside the area of study is often not considered. The generic descriptions are commonly based only on the species within the study region. Some advantages of these treatments are the description of variation at the specific level. A species within a restricted region may express a plasticity not found in another region; therefore, detailed regional studies contribute valuable data on specific variation.

Taxonomic Concepts

Species

The binomial system of nomenclature was devised by Linnaeus (1753). The origin of this system was based on phenetic similarity of organisms. The theory of evolution was presented by Darwin (1859) in the *Origin of Species*, which opposed the prevailing creationist viewpoint, that all species were static entities. Darwin discussed the theory of evolution, descent from a common ancestor, based on his world travels, observations, and discussions with colleagues. Darwin presented the concept, that organisms change through time as a result of natural selection (survival of the fittest) by environmental factors or competition with other organisms.

A definition of a species that can be applied to all organisms has remained elusive, and a perpetual, central question for biologists (Donoghue 1985, Mishler and Brandon 1987). The definition has been amended through time, as different disciplines have developed research techniques: phenetics (based on overall similarity, including homoplasies and homologies), reproductive biology and genetics (biological species, dependent on interbreeding compatibility, gene exchange, and isolating mechanisms that prevent gene exchange), ecology (ecotypes, species which are separated by the microhabitat, e.g., altitude, substrate, exposure, etc.), evolutionists (all plesiomorphic and apomorphic characters, homoplasy and homology differentiated), and phylogenetists (monophyly, apomorphic characters).

In a review of species definitions, Mishler and Budd (1990) differentiated four major types: 1) biological, based on interbreeding capability; 2) phenetic, based on overall similarities morphological, ecological, behavioral, or genetic; 3) evolutionary or ecological, still centered on interbreeding capability, or in asexual species overall similarity as the basis for species delineation; 4) phylogenetic, based on monophyly or shared derived characters. Although the phylogenetic species definition has gained increasing support, a review of evolutionary processes that result in a speciation event has questioned the strict requirement of monophyly for the definition of a species (Olmstead 1995, Donoghue 1985). Olmstead (1995) has proposed a distinction between "apospecies" and "plesiospecies". Apospecies are defined by uniquely derived character(s), whereas, plesiospecies lack any uniquely derived character(s). If divergent, satellite populations develop a new attribute, distinct from the main population that results in a speciation event, then the remaining populations of the progenitor species will be defined by plesiomorphic characters rather than any autapomorphies. This makes the latter a paraphyletic group, that with time may evolve its own unique evolutionary history through extinction and selection on these populations.

In a survey on the use of species concepts in botanical monographs, McDade (1995) stated that different definitions would be "expected to vary considerably" in different lineages (e.g, ferns, lichens, bryophytes). Mishler and Donoghue (1982) argued for a pluralistic species definition, based on the variation of discontinuities between organisms. They advocated that different processes produce and maintain lineages in any particular taxon (i.e., a sexual species may be dependent on phenology versus an asexual species may have microhabitat constraints). Morphological, genetic, and ecological data may indicate different relationships of the taxa. A morphological species may contain populations that are genetically or ecologically distinct (cryptic species), or two morphologically distinct species may lack any reproductive barriers (hybridization). The genus *Quercus*, in which hybridization between species has been shown to be extensive, is a classical example of speciation that lacks reproductive isolation (Burger 1975). Clausen, Keck, and Hiesey (1940) in their classical research on ecotypes have shown how speciation can take place in response to ecological factors. Initially considered evolutionary relics, isozyme analyses on populations of bryophytes have shown as much genetic variation in bryophyte species as in vascular plants (cf. Wyatt 1985, de Vries 1983). Therefore, a morphologically uniform species may have considerable cryptic genetic variation between the populations of its range. As well, in bryophytes distinct morphological species have been shown to hybridize based on isozyme data, negating any reproductive barriers (Wyatt et al. 1992). The factors that maintain a species in any particular group of organisms may differ. Species are organic and are constantly responding to internal and external factors.

Two primary tasks of the systematist are grouping and ranking of taxa. The former task is to gather the empirical data of organisms (morphological and anatomical, ontogenetic, physiological, ecological, genetic, biogeographical, etc.) in order to establish a natural system of relationships. Morphology remains the initial data base investigated for most organisms. Discontinuity in morphological features is used to distinguish the species of *Leucoloma*. The value of the morphology to distinguish species has been emphasized by Burger (1975):

> "The Linnaean or classical species concept of readily recognized and morphologically defined species has served as a practical and efficient system for retrieval in most flowering plants. There are very few groups where morphological correlations as a basis of taxonomy have failed to identify meaningful taxa. Even in those cases where intermediates and hybridization are known, the classical concepts have often continued to be useful and meaningful"

Whether a genetic, phyletic, or ecological species definition is to be applied, the selection of individuals to be tested cannot escape an initial morphological assessment.

Species defined by a morphology provide a testable hypothesis of relationship based on similarites or dissimilarites between individuals. The taxa are grouped and ranked, based on unique characters or a unique combination of characters (Nixon and Wheeler 1990). These features of the species are proposed as hypothetical homologues, that share a common ancestry. With the completion of a revision of the morphological species, a phylogenetic analysis will be applied to establish an evolutionary relationship and test the support for the morphological species.

Subspecies

The subspecies rank is a geographically separated group of populations (for the most part). Respective subspecies have isolated gene pools, that can result in divergent evolutionary histories. At the subspecies level of divergence, these populations may potentially still have gene exchange.

Variety

The variety rank is used for variation within a given locality or geographic region that results from ecological modification (altitude, xerophytism, light conditions, niche availability). Varieties typically exhibit gradation in character expression.

Morphological Characters

The characters that were significant for the taxonomic analysis are reviewed below. Characters used for the phylogenetic analysis and their polarity are treated in the cladistic section on evolution (see Chapter III).

Color

The range of color observed within *Leucoloma* is from a glaucous green, which is characteristic of subsection *Albescentia* (e.g., *L. humbertii*) to a brown, commonly found in section *Dichelymoidea* and section *Leucoloma* (e.g., *L. dichelymoides*, *L. holstii*), with a spectrum of pale yellow-green, green, olive-green, dark green, to dark brown-green. The true copper tones of *Dicranum* and *Dicranoloma* are lacking in *Leucoloma*. The variation of color within *Leucoloma* may have some correlation with habitat. Field collections by the author suggest that exposure to sunlight can modify the coloration (e.g., green to yellow-green). *Leucoloma* species of wet habitats tend to have dark green coloration (e.g., seeps, within the stream beds or splash zones). Those specimens found in more exposed habitats have a lighter range of color (e.g., forest clearings, low elfin forests). A number of specimens of *Campylopus* have been misidentified as *Leucoloma*. In addition to obvious morphological differences (e.g., costal anatomy, lack of differentiated border), *Campylopus* has a distinctive, bright, pink-orange, red color of the stem and rhizoids not found in *Leucoloma*. A biochemical basis for the difference in coloration has not been investigated.

Representative species from each section of *Leucoloma* were tested with a 2% KOH solution (Zander 1993) for a color reaction. A positive yellow color reaction indicates the presence of phenolic compounds with one or no hydroxyl groups (Zander 1993). A single taxon, series *Holomitrioidea*, produced a strong orange-brown color reaction in the non-chlorophyllose basal cells in all species.

Life and Growth form

The distinction of life form versus growth form is extensively reviewed in Chapter IV. The life forms of *Leucoloma* species include dense to loose turfs or gregarious stems. The growth form of the individuals varies from short, long or tall stems, that are erect, ascending, downwardly out-spreading or pendent. Erect short or tall turfs is the predominant life form for the species of subgenus *Syncratodictyon*. Within subgenus *Leucoloma* the species form colonies of short to long gregarious stems, loose turfs, or pendants.

Transitional growth forms have been observed within a population. *Leucoloma sanctae-mariae* has young stems that grow perpendicular to the vertical tree trunk surface. With an increase in length, mature stems grow in a downward, outspreading direction, in response to gravity and phototropism. Horikawa and Ando (1952) defined pendent bryophytes as "shoots (that) hang down from their bases on substratum". The pendent *Leucoloma* species are attached from a single point at the base of the stem. In the Madagascan elfin forests, *Leucoloma dichelymoides* forms ramicolous populations consisting of both erect and pendent stems.

Branching

Both sympodial and monopodial branching is found in *Leucoloma* (see Chapter IV for definitions of the two patterns). The branching pattern can be taxonomically useful at the species level. Sympodial branches in *Leucoloma* are formed typically by 1-3 (5) subapical innovations, that result in distally ramose stems. These branches are of the same hierarchy as the supporting axis (i.e., a chain of 1° branches or a chain of 2° branches). *Leucoloma sanctae-mariae* is characterized by two subapical innovations that form the primary modules of the sympodial branching pattern. *Leucoloma albocinctum* commonly develops a single subapical innovation to form a chain of primary modules (Fig.II.1).

Monopodial branches in *Leucoloma* are scattered, lateral branches, that are unassociated with terminal gametangia (e.g., *L. dichelymoides*). The branches are subsidiary modules of a different hierarchy than the supporting axis (i.e., 2° branches on 1° axes or 3° branches on 2° axes). In *Leucoloma* both monopodial or sympodial branches are often fragile and easily detached. This provides the predominantly dioicous genus a potential means of vegetative propagation. Fragile branches have been observed in a number of genera within the Calymperaceae and Dicranaceae (e.g., *Leucophanes*, Salazar Allen 1985; *Campylopus*, Frahm 1983; *Dicranum*, Newton and Mishler 1994). Recent studies on the regenerative ability of mosses versus establishment by spore germination suggest that gametophytic fragments readily develop new shoots (Miles and Longton, 1990).

Dormant branch primordia occur in a spiral arrangement along the stem. They are typically pale, naked, non-protruding, circular regions on the axis at regular intervals. Branch primordia at various stages of development have been observed 1) non-protruding; 2) protruding, but lacking juvenile leaf development; or 3) branch innovations with juvenile leaf development. The direction of maturation is varied along a stem. *Leucoloma humbertii* shows a basipetal development in response to the production of terminal gametangia. *Leucoloma dichelymoides* develops acropetal monopodial branches on its pendent stems. The developmental sequence of primordia in *Leucoloma madagascariense* is irregular. (For a more extensive discussion on branching patterns see Chapter IV).

Perichaetial position

Leucoloma is an acrocarpous genus, although initially classified as a pleurocarp (Bridel 1827). The genus is dioicous, although two autoicous specimens have been found (*L. zuluense*: *Crosby & Crosby 13184* MO and *La Farge-England 5321* ALTA). Most of the specimens examined have been female, with male plants often not seen for a given species. This gametangial imbalance has been observed often in dioicous mosses, and usually typifies a "general rarity" of sporophytes for a species (Longton 1990).

The perigonia are yellow-tan, flask shaped and clustered with paraphyses. They are terminal on the main axis, and may develop additional perigonia on short, subapical, lateral branches. The subsidiary perigonia are often smaller and numerous (3). A profusion of perigonia occurs by further subapical branching and terminal perigonia production. This clustered production of perigonia has been seen in other orders (e.g., Orthotrichales, pers. comm. B. Goffinet). The abundant production of perigonia increases the number of male gametes for potential dispersion and sexual reproduction. Odu (1981) examined the phenology of four species of tropical mosses and reviewed the factors that effect gametangia development. He found that there was an annual cycle that followed the rainy and dry seasons. His observations indicate a correspondence between the rainy season with gametangia production, and the dry season with spore dispersal.

Stems

The length of stems are short (0.5 cm) to long (to 20 cm). The stems are either round or slightly elliptic in cross section. The older portions of the stem are usually blackened and distally red. In a study on the conducting tissue of bryophytes, Kawai (1979) classified *Leucoloma* as having 3 types of differentiated tissues, based on two species (*L. molle* and *L. okamurae*). Kawai distinguished a differentiated central strand, cortex, and epidermis. The following treatment does not differentiate between the epidermis and outer cortical cells. Hand sections of the stems show an outer cortex of 2-6 layers, thick-walled and red-brown; an inner cortex of large lumened cells, red-orange to yellow; and a differentiated central strand of smaller lumened cells, or lacking. Transverse sections of stems of subgenus *Syncratodictyon* are round, whereas the stems of subgenus *Leucoloma* are elliptic in section (Fig.II.2)

Rhizoids

Koponen (1982) and Crundwell (1979) reviewed the systematic significance of rhizoids in mosses. The rhizoids in *Leucoloma* are large, relatively unbranched, smooth, and red-brown. The development of the rhizoids is predominantly from initials on the stem or branch at the base. Additional scattered, solitary rhizoids occur along the stem near the leaf insertion (e.g., section *Dichelymoidea*). Solitary rhizoids also develop from alar cells (e.g., species of section *Subvittata*). *Leucoloma*, "as a rule", does not produce stem tomentum in contrast to *Dicranum* and *Dicranoloma*. Rare exceptions have been observed in *Leucoloma humbertii* (*La Farge-England 6324* ALTA) and *L. sanctae-mariae*, (*La Farge-England 6284* ALTA), although the production was restricted a small portion of the stem. Rhizoid organography within the Dicranales is often specialized and systematically informative. Within the subfamily Campylopoideae, rhizoids have been found on the adaxial surface of the costa in *Dicranodontium* and *Atractylocarpus* (Frahm 1991). In all other genera of subfamily Campylopoideae with leaf bearing rhizoids, the rhizoids develop on the abaxial surface of the costa. Rhizoids develop from nematogenous laminal cells within the Dicnemonaceae, and are a critical synapomorphy for that family (Allen 1987). *Mesotus* which has recently been transferred to the Dicranaceae, also has rhizoids from nematogenous laminal cells (Allen 1987).

Axillary hairs

The axillary hairs are fragile, hyaline, uniseriate, 5-6 cells long, with 1-2 hairs per leaf axil. They are restricted to the distal portion of the stem. Significant variation is not evident.

Leaves

The habit of the leaves in *Leucoloma* ranges from erect-spreading to squarrose and are contorted, crisped, spirally twisted, secund, or flexuose. Often the bases are squarrose with distally "bowed" or erect-spreading apices (e.g.,. section *Obscura* and section *Attenuata*). Subsection *Albescentia* usually has leaves with erect-spreading bases and secund to slightly falcate-secund leaves. Series *Holomitrioidea*, series *Contorta*, and subsection *Caespitulosa* have distinctly contorted leaf sets. Spirally twisted leaves are commonly found in section *Leucoloma*. A flexuose habit is typical of section *Dicranoidea* and section *Subvittata*.

The leaf shape within *Leucoloma* varies from narrowly lanceolate, lanceolate, ovate-lanceolate, ovate, elliptic-lanceolate to obovate (Fig.II.3). The term lanceolate has had several applications in botany (Stearn 1983). Lanceolate is used in the present study to refer to leaves with more or less parallel margins which taper at the ends. Leaf length ranges from 0.6 mm (*L. grimmioides*) to 20.0 mm (*L. humbertii*). Leaf width ranges from 0.2 (*L. grimmioides*) to 1.8 mm (*L. fontinaloides*).

The distal leaf forms a long or short acumen, that varies from setaceous to acuminate, with truncate, obtuse or rounded, apiculate, or tapered apices. The distal acumen is either flat, terete, caniculate, or subtubulose.

Margins

The leaf margins are plane and entire, with distal margins subentire, crenulate from the projection of papillae, or serrulate (or with small serrations). The margins are bordered by a band of hyaline cells, 2.5-60.0 µm wide, rarely is the hyaline border lacking (e.g., *L. subchrysobasilare*, *L. onraedtii*). The differentiated hyaline margin is broadest mid leaf, and either gradually tapered toward the leaf base (e.g., section *Leucoloma*) or abruptly tapered in the basal region (e.g., subsection *Albescentia*). The measurements for border width were taken at the broadest expression. The hyaline border is either restricted to the lower 1/2-1/3 of the leaf in series *Holomitrioidea*, series *Contorta*, subsection *Serrata*, or extends to the apical region (subgenus *Leucoloma*, subgenus *Syncratodictyon* subsection *Albescentia*, section *Dicranoidea*). In subsection *Albescentia* the margin can be slighlty undulate (e.g., *L. cruegerianum*, *L. albulum*), with the cell lumen slightly irregular.

Costa

The costa varies from subpercurrent to excurrent. This variation can be found within a single species of *Leucoloma* (e.g., *L. schelpei*) or it can have a restricted expression within species (e.g., excurrent - *L. tuberculosum*, subpercurrent - *L. chrysobasilare*).

The costal anatomy of *Leucoloma* was studied by Renauld (1909). He concluded that it was uniform within *Leucoloma* and *Sclerodontium* (as *Dicnemoloma*), and varied within *Dicranoloma*. The current research has shown that there is variability within *Leucoloma*. It has taxomomic significance at the species and infrageneric level (Fig.III.4). The guide cells (eurycysts or deuters) form a central layer in cross-section of (3)-4-(8) cells. Species with a large number of guide cells belong to section *Dicranoidea*. This layer is sandwiched by two stereid bands that vary in thickness from 1-6 cells. In some taxa the stereid bands are replaced with substereid cells (e.g., series *Serrata*). There is no differentiation of the adaxial or abaxial epidermal layer, as in some species of *Dicranum*. Typically, the guide cells have an oblique orientation, and have a single bistratose layer in transition to the laminal cells. The bistratose row is either lacking or consists of up to 6 (9) bi- or multistratose rows of cells. The amplification of this region, or lack of it, is usually consistent within a taxon (*L. crosbyi* vs. *L. grandidieri*, *L. madagascariense* vs. *L. bifidum*). Subgenus *Syncratodictyon* has the greatest variability of costal anatomy. Lateral doubling of the guide cells is common in section *Dicranoidea* and subsection *Serrata*.

Laminal cells

The leaf lamina consists of five differentiated cell types. Differences from the terms used by Renauld are presented below.

Renauld (1909)	(present study)
internes	juxtacostal
intermédiaires/membraneuses	interior/basal

cellules marginales	marginal
oreillettes	alar

The juxtacostal cells are differentiated, chlorophyllose, mostly papillose, with the lumen shape angular or rounded, oblong to elongate, quadrate to rectangular, or irregularly shaped, sinuose, porose or not. The measurements for the cells were from one cell lumen wall to the corresponding lumen in the adjacent cell. The descriptions refer to the cell lumen, not the actual cell, since the variation is in the lumen shape. The juxtacostal cells in *Leucoloma* are either sharply differentiated from the interior and basal cells (e.g., subgenus *Leucoloma* and series *Holomitrioidea*); sharply defined laterally, but gradually merging with basal cells (subsection *Albescentia*); or have a gradual transition laterally and basally with the interior and basal cells (series *Teretia*, series *Contorta*, and section *Dicranoidea*).

Renauld (1901) differentiated the three genera *Leucoloma*, *Dicranoloma* and *Dicnemoloma* by cell architecture. He described *Dicranoloma* with cells uniform from the costa to the differentiated border. *Leucoloma* was defined as having two types: "internes" and the "intermédiaires/ menbraneuses" between the costa and differentiated border. *Sclerodontium* (as *Dicnemoloma*) was defined as laminal cells chlorophyllose, that descend along the margin to the base, with a membraneous tissue restricted to the basal interior region. In general his observations are accurate, although there are exceptions. Within *Dicranum* and *Dicranoloma sensu* Renauld, there are species which develop shorter juxtacostal cells that gradually lengthen marginally, a character of species in *Leucoloma* subgenus *Syncratodictyon*. There are also species within *Leucoloma* series *Contorta* and series *Holomitrioidea* that form a membraneous, basal interior as found in *Sclerodontium*. In series *Holomitrioidea* the boundary is sharp between the chlorophyllose cell and the membraneous cells. The chlorophyllose cells descend along the costa, rather than the margin as in *Sclerodontium*.

The interior cells occupy the leaf lamina between the juxtacostal cells and the marginal cells. These cells are smooth, thick-walled, porose or not, and are generally elongate to linear. They are either restricted to the basal region of the leaf or they extend upward along the hyaline border, tapered distally.

One distinction between *Leucoloma* versus *Dicranum* and *Dicranoloma* is the size of the laminal cells. *Leucoloma* has cells that have a maximum width of < 12 (rarely 14) µm, whereas the other genera have cells that are > 14 µm.

The marginal cells form a distinct hyaline border. These cells are extremely long (often > 150 µm long), narrow (mostly 2.5 µm wide), and thick-walled. The cell lumen is reduced to an almost imperceptible line, visible with the compound microscope.

Papillae

Papillae are diverse in *Leucoloma* and their absence or presence have been used to differentiate *Dicranoloma* from *Leucoloma*, respectively (e.g., Gangulee 1971, Magill 1981). Papillose leaf cells also occur in some species of *Dicranum* and *Dicranoloma*, and species with smooth leaf cells occur in *Leucoloma* (e.g., *L. subsecundifolium*, *L. entabiense*). The diversity of papillae is more elaborate within *Leucoloma* than in related genera (Fig.II.5).

Papillae are restricted to the differentiated juxtacostal cells. The development can be predominantly restricted to the abaxial surface (e.g., section *Subvittata*, section *Leucoloma*, subsection *Albescentia*), or there is equal development on both surfaces of the papillose cells (e.g., section *Obscura*, section *Attenuata*, subsection *Acuminata*, series *Serrata*, and series *Holomitrioidea*). The ornamented cells are unipapillose (subsection *Albescentia*, e.g., *L. rehmannii*) or pluripapillose (e.g., section *Leucoloma*, series *Holomitrioidea*, series *Contorta*), and develop over the cell lumen or the cell wall. In subsection *Seriata* the papillae are arranged in a seriate row on the cell lumen (*L. sprengelianum*). As well, in series *Holomitrioidea* distinct rows are formed over the cell walls by the papillae. Each cell develops two marginal rows of papillae, that coalesce with the papillae of the adjacent cell (Fig.II.74). This type of papillae development also occurs in *Racomitrium aquaticum* and *Mesotus celatus*, although it has not been previously reported for the Dicranales.

In subsection *Albescentia* the distal leaf cells develop strongly projecting, hooked papillae, that are similar to the papillae in *Sclerodontium*. Within section *Dichelymoidea* the papillae form distinct transverse rows (e.g., *L. tuberculosum*), creating a corrugated abaxial surface (Fig.II.5 e,f). The extremely dense papillae of section *Attenuata* form a rugose surface in several species (e.g., *L. grandidieri*, Fig.II.5.c). It is superficially similar to a corrugated surface, but differs by having a smooth, transversely "buckled" surface in profile.

The papillae are simple to multifid, acute to rounded. The papillae toward the base of the leaf tend to be less prominent than the distal papillae. In subgenus *Syncratodictyon*, there is a gradual transition from the papillose cells to the smooth interior or basal cells.

In transverse section, the wall thickenings are extremely variable. In subgenus *Syncratodictyon* the abaxial and adaxial cell wall thickness is thinner than the lumen. An exception is in section *Dicranoidea*, where the basal cells often have thicker adaxial-abaxial cell walls than the anticlinal walls. In subgenus *Leucoloma*, the cells have a pyramid or subquadrate shaped lumen in transverse section. Often the adaxial surface has bulging walls over the anticlinal walls in some species, as in *Dicranum brevifolium* (Peterson 1979).

Alar cells

The alar cells are sharply differentiated and unistratose within *Leucoloma*. The color range is from a deep red-brown to orange-brown, or hyaline. The marginal rows have a tendency to lose the coloration and be longer and thinner walled in subgenus *Leucoloma*. The cells are either scalariform (i.e., cells with longitudinally thickened walls), bulging with longitudinally thickened walls, evenly and modestly thickened walls, or thin-walled and inflated (Fig.II.2). The species of subgenus *Syncratodictyon* have typically inflated, thin-walled or bulging, longitudinally thickened cell walls. Within section *Dichelymoidea*, section *Subvittata*, section *Attenuata*, and section *Obscura* the alar cells have longitudinally thick-walled cells, that are not bulging, but flat. Section *Dicranoidea* typically has evenly thickened walls, that are slightly bulging.

The alar region is best developed in section *Dichelymoidea*. Species within the section have convolute to clasping alar regions. Auriculate alar regions are common in subgenus *Syncratodictyon*. The size, cell type, and orientation of the alar region are taxonomically valuable attributes.

Perichaetial Leaves

The perichaetial leaves have bases similar in width to the stem leaves, but differ by abruptly contracted acumina. The bases are clasping to convolute around the perichaetium. The distal portion of the leaves is commonly setaceous, stiffly erect to somewhat flexuose. Similar types of perichaetial leaves can be found in *Dicranum* (Peterson 1979).

The cell differentiation is slightly different than that of the stem leaves. The differentiated juxtacostal cells are confined to the acumen. The basal portion of the leaf is colored yellow to orange-brown. The cells are typically enlarged and are either porose with longitudinally thickened walls or thin walled. The alar region is not differentiated.

Within the perichaetium there is a cluster of archegonia and paraphyses. The archegonia are uniform for the genus. The neck is especially elongate in proportion to the venter. This shape of archegonia is found in *Dicranum* and *Dicranoloma*. The overall length of the archegonium, 0.6-1.2 mm,varies within the genus, but the proportion does not change.

Vegetative propagation

Vegetative propagation is an viable alternative to sexual reproduction for many dioicous species (Longton 1990), that results in clonal organisms. Environmental stress can induce the production of diaspores in mosses to provide a means of continued reproduction (e.g., *Tayloria hornschuchii*, La Farge-England and Vitt 1985). Deposits of gemmae in diaspore soil banks provide a "dormant" phase of the life cycle, when growing conditions are unfavourable (During & ter Horst 1983). Unspecialized moss fragments also have a regenerative capacity to initiate protonematal development (Newton and Mishler 1994). Within high arctic peat deposits (La Farge-England et al.

1990) and temperate peat deposits (Clymo & Duckett 1986) regeneration of moss fragments has been observed. In vitro growth experiments by Pringsheim in 1876 and 1878 has shown that diploid gametophytic material can be induced to develop from sporophytic tissue (Parihar 1961). Thus the regenerative capacity of moss cells to grow and reproduce vegetatively appears to be extensive.

Within Musci a number of specialized structures have been developed to disperse propagules (e.g., gemmae stalks of *Aulacomnium*; rhizoidal tubers - *Bryum*; leaf gemmae - *Tortula*; propagula - *Pohlia*; caducous leaves, fragile leaf apices - *Macromitrium*, *Leucoloma*, *Dicranum*; specialized branches - *Dicranum*). *Leucoloma* exhibits several specialized modes of vegetative propagation (e.g., *Leucoloma talazaccii* and *L. cuneifolium* have fragile leaf apices; *L. hostii*, as well as other members of subgenus *Leucoloma*, has fragile lateral branches). If one compares the lateral branches of *L. dichelymoidea* and *L. holstii*, there is a difference at the point of attachment. *Leucoloma holstii* has a constriction at the attachment point, whereas a constriction is lacking in *L. dichelymoidea*. This constriction may facilitate the fragile nature of the lateral branches. Caducous leaves are often found in species of section *Subvittata* (*e.g.*, *L. chrysobasilare*, *L. molle*).

Sporophytes

Sporophytic material is rare in specimens of *Leucoloma*. The sporophytes in *Leucoloma* are terminal and mono- or polysetous. The capsules lack stomata and an annulus. The shape ranges from subglobose to short cylindric, erect and symmetrical in subgenus *Leucoloma* to cylindric to long cylindric, erect, symmetrical or slightly asymmetric in subgenus *Syncratodictyon* (Fig.II.6). Within subgenus *Leucoloma* the capsules are immersed to shortly exserted, with short, stout opaque, tan to red-brown setae in young material. In transverse section of the setae, a single layer, the outer periclinal wall, is thickened, in contrast to the anticlinal walls of the epidermis (Fig.II.7). The setae are slightly twisted to the right (as viewed from the base). In subgenus *Syncratodictyon* the capsules are long exserted, with long, slender, translucent, red setae. In transverse section of the setae there are several layers of differentiated, thick-walled, outer cortical cells (Fig.II.7). These cells have exocentric lumina (see Chapter III, phylogenetic characters for discussion, with respect to other genera). A central strand is present in all setae.

The peristome is a reduced form of that of the Dicranaceae. It is characterized as follows: haplolepideous with 2:3 (to rarely 4) cell pattern, 16 bifid (rarely trifid) teeth, split 1/2-3/4 of the tooth length, distally truncate or filiform (Fig.II.8). The peristome on opened capsules tend to have recurved bases below the rim of the capsule with the apices appressed towards the center or are reduced and erect. The PPL, or outer surface of the peristome, is vertically pitted-striate, striate, roughened to papillose, or smooth at the base. The mid-tooth varies from transverse, papillose ridges, papillose, or smooth, with the distal tooth papillose or roughened. The ornamentation of the peristome is a valuable character at the species level. The degree of thickening on the PPL versus IPL surface varies among the taxa. The development of the strong trabeculae on the PPL versus IPL surface is another source of variation. As well, a single example of a fused OPL, PPL, and IPL cell remnants have been observed, with a (4):2:3(4), pattern (Fig.II.9). Within the haplolepideae, this has also been noted for the Seligeriaceae (Edwards 1979). Edwards (1979) enumerated a number of taxa within the Haplolepideae that have partially thickened OPL layers, fused or free of the PPL-IPL layers (ie. *Dicranella heteromalla*). Preperistomial thickening has been observed in *Holomitriopsis*, Leucobryaceae (Newton and Robinson 1994). The extent of this variation within the Haplolepideae is in need of further study.

The basal width of the peristome tooth is between 35-96 (108) µm and the length 0.16-0.70 mm long. The opercula are rostrate, erect or obliquely oriented. Within subgenus *Leucoloma*, section *Obscura* and section *Attenuata* the operculum can be reduced to conic, erect. The calyptrae in subgenus *Leucoloma* are lobate, mitrate. The calyptrae cover the operculum and uppermost portion of the capsule. Within subgenus *Syncratodictyon* the calyptrae are entire, cucullate and typically cover more than 1/2 the capsule. The spores are granulose, with a consistent size range 18-31 µm.

The outer spore wall ranges in thickness from 2.5-5.0 µm wide.

Ecology

Leucoloma is a predominantly epiphytic genus, that grows on sapling or tree trunks, buttresses, roots, lianas, decaying wood (logs or stumps), nodes of bamboo, or rarely on other mosses, and has been collected as an epiphyll in tropical rainforests. As well, species are terricolous or saxicolous along streambeds and on seepage cliffs. The collections made by the author in Tanzania and Madagascar were predominantly within 2 m of the forest floor. Rarely were the populations observed above this height. A recent study of the canopy bryophytes in Costa Rica listed two species from the inner crowns of montane forest trees 12-22 m above the forest floor (Sillett et al. 1995).

The species of subgenus *Syncratodictyon* often grow close to the forest floor (e.g., on rocks, fallen logs, aerial or exposed roots, or at the base of tree trunks). Species of subgenus *Leucoloma* commonly grow on tree trunks and pendent species of section *Dichelymoidea* grow on branches. The elevational range of the genus is broad, sea level to 2800 m. The forest types include coastal lowland, submontane, montane, upper montane, and elfin rainforests (Gradstein and Frahm 1987). The exposure ranges from full shade of the montane forests to partial shade of clearings, to the more exposed habitats of the stunted elfin forests on ridges. *Leucoloma* grows in both primary and secondary growth forests. A comparison of species richness from collections around Andasibe, Province Tamatave, Madagascar, indicates primary forests have a more diverse *Leucoloma* flora (12 spp. opposed to 6 spp.). All of the species that occurred in the secondary forests were present in the primary forest. *Leucoloma* was commonly found with orchid bulbs growing within the turfs, indicating that it may provide an important microhabitat for the establishment of successive vascular plants.

Taxonomic Treatment of *Leucoloma*

The following taxonomic treatment includes: 1) a key to the bordered genera of the Dicranaceae, 2) a key to the infrageneric taxa of *Leucoloma*; 3) a key to the species of series *Holomitrioidea*; 4) a key to the Afro-Madagascan species of subgenus *Leucoloma*; and 5) each taxon, including the generic, infrageneric and specific levels, is typified and followed by the current accepted synonymy. New infrageneric taxa are described and arranged systematically in accordance with the results of the phylogenetic analysis (see Chapter III). Species are listed alphabetically within each infrageneric taxon.

A KEY TO BORDERED GENERA OF THE DICRANACEAE

1\. Differentiated border tinged with cells short, smooth, porose ..... ***Mesotus*** Mitt.

1\. Differentiated border hyaline with cells extremely linear smooth, non-porose ... 2

2\. Stems with tomentum; laminal cells lacking three distinct types; basal cells ≥ 14µm; stomata present; annulus present .... ***Dicranum*** Hedw. and ***Dicranoloma*** Ren.
(see Norris and Koponen 1990 for generic delimitation debate)

2\. Stems lacking tomentum; laminal cells of three distinct types; basal cells ≤ 14 µm; stomata lacking; annulus absent 3

3\. Capsules arcuate; peristome split in distal ½ of tooth, with broad base 96-120 µm; leaves with hair points or fragile swollen leaf tips .... ***Sclerodontium*** Schwaegr.

3\. Capsules erect; peristome split ¾ of tooth length, with narrow base 35-96 µm; leaves lacking hair points or fragile swollen leaf tips .... ***Leucoloma*** Brid.

KEY TO THE INFRAGENERIC TAXA OF *LEUCOLOMA* AND AFRO-MADAGASCAN SPECIES OF SUBGENUS *LEUCOLOMA*

1\. Leaves with juxtacostal bands sharply defined; alar region mostly intermediate to enlarged, (6)10-40 cells wide; alar cells with longitudinally thick-walled cells, flat, not bulging or inflated; sporophytes immersed, emergent, or shortly exserted; setae tan, opaque, < 3 mm long; capsules globose, ovoid to short cylindric
.... (subgenus *Leucoloma*, p. 64) . 2

1. Leaves with juxtacostal bands with a gradual transition to basal and interior cells; alar region intermediate to reduced (3-20 cells wide); alar cells with thin-walled and inflated, equally thickened and flat, or longitudinally thick-walled cells and bulging; sporophytes exserted to long exserted; setae red, translucent, > 4 mm long; capsules short to long cylindric . . . . (subgenus *Syncratodictyon*, p. 43) . 25

2. Papillae developed equally on adaxial and abaxial surface of differentiated juxtacostal cells; or with scattered, less prominent adaxial papillae and prominent abaxial papillae 3
2. Papillae not developed equally on adaxial and abaxial surface of differentiated juxtacostal cells, adaxial surface smooth with a few papillae present restricted to the distal lamina along the costa and abaxial papillae 5

3. Surface of differentiated juxtacostal cells pluripapillose, with papillae dense, equally developed on adaxial and abaxial surface of differentiated juxtacostal cells; juxtacostal bands opaque, rugose or smooth 4
3. Surface of differentiated juxtacostal cells unipapillose, with scattered adaxial papillae and prominent abaxial papillae; juxtacostal bands not opaque, corrugated . . . . (section *Dichelymoidea*, p. 140) . 21

4. Juxtacostal bands tapered toward the costa, smooth or rugose; alar region intermediate to enlarged; alar cells with a pronounced, oblique orientation to the basal cells . . . . (section *Attenuata*, p. 122) . 15
4. Juxtacostal bands parallel to costa, smooth; alar region small to intermediate; alar cells obliquely oriented to the basal cells . . . . (section *Obscura*, p. 113) . 19

SECTION *LEUCOLOMA* AND SECTION *SUBVITTATA* (REN.) REN.

5. Leaves with extremely narrow hyaline margins, 1-3 (5) cells wide, < 7µm wide (rarely 12 µm) 6
5. Leaves with narrow to broad hyaline margins, > 3 cells wide, > 7 µm wide (mostly

12-64 µm) 9

6. Plants medium sized; leaves falcate-secund, with a more or less stout acumen . . . . *L. subchrysobasilare* (p. 102)

6. Plants small to medium sized; leaves crisped or erect-spreading, with flexuose to spirally twisted fine acumen 7

7. Plants to 3 cm tall; juxtacostal cells dense, small, quadrate, 5-7 µm wide; juxtacostal bands reaching the alar region, sharply defined; leaves short, 1.5-2.5 mm, lanceolate to ovate-lanceolate . . . . *L. subbiplicatum* (p. 99)

7. Plants to 10 cm tall; juxtacostal cells thick-walled, oblong to elongate, 5-10 µm wide; juxtacostal bands ending above the alar region, grading into basal cells; leaves mostly > 2.5 mm long, ovate to ovate-lanceolate 8

8. Leaves crisped, 2.5-4.0 mm long, ovate-lanceolate to lanceolate; hyaline margin 2.5-12.0 µm wide, or lacking; costa subpercurrent . . . . *L. gracilescens* (p. 82)

8. Leaves crisped or erect-spreading, 2-3 mm long, ovate to ovate-lanceolate; hyaline margin 2.5-7.2 µm wide or lacking; costa subpercurrent to excurrent . . . . *L. lepervancheri* (p. 87)

9. Leaves 5-8 mm long, with alar region vertically oriented to basal cells; inner basal cells porose, with 1-4 rows of isodiametric cells between the basal cells and alar region; proximal leaves caducous . . (section *Subvittata*) . *L. chrysobasilare* (p. 66)

9. Leaves 1.8-6.0 mm long, with alar region oriented at a slight angle to the basal cells; inner basal cells porose or not, lacking rows of isodiametric cells between the basal cells and alar region; proximal leaves non-caducous 10

10. Leaves large, 0.8-1.2 mm wide, 4.5-6.0 mm long, distally entire; costa excurrent; alar region large, 26-33 cells wide . . . . *L. procerum* (p. 94)

10. Leaves small to medium, 0.35-0.84 mm wide, 2-5 mm long (if broad to 0.95 mm,

then short to 3.5 mm long), distally serrulate; costa subpercurrent or excurrent; alar region small, 13-17 cells wide 11

11. Juxtacostal cells thick-walled, mostly oblong to elongate, 5-10 µm wide; basal and interior cells porose to non-porose . . . . *L. zuluense* (p. 106)
11. Juxtacostal cells dense, quadrate to oblong, 5-7 µm wide; basal and interior cells non-porose 12

12. Leaves flexuose, not strongly crisped 13
12. Leaves spirally twisted, strongly crisped, ... 14

13. Costa subpercurrent; leaves radially arranged, densely or more distally arranged along the stem; juxtacostal bands narrower, 1/2-2/3 basal leaf width *L. bifidum* (p. 76)
13. Costa long excurrent; leaves somewhat complanate and densely arranged along stem; juxtacostal bands broad, 3/4 of basal leaf width . . . *L. madagascariense* (p. 90)

14. Leaves 1.8-3.0 mm long; hyaline margin 17-36 µm; PPL basal surface of peristome pitted-striate . . . . *L. holstii* (p. 84)
14. Leaves 2.5-4.0 mm long; hyaline margin (17) 24-64 µm; PPL basal surface of peristome smooth . . . . *L. schelpei* (p. 97)

SECTION *ATTENUATA* REN.

15. Juxtacostal bands dorsally smooth, narrow; leaves slender, caducous proximally with alar region fragile below; leaf apices often fragile, inner basal cells rhomboidal to elongate, non-porose to porose . . . . *L. talazacii* (p. 136)
15. Juxtacostal bands dorsally rugose or not, broad to narrow; leaves broad to slender, not distinctly caducous with alar region not fragile below; leaf apices not fragile; inner basal cells elongate to linear, often strongly porose 16

16. Plants robust 17

16. Plants medium to small 18

17. Leaves non-crisped or incurved; juxtacostal bands dorsally smooth; transverse section of costa with 2-9 rows of bi- to multistratose cells in transition to laminal cells . . . . **L. crosbyi** (p. 123)

17. Leaves slightly crisped and incurved; juxtacostal bands dorsally rugose; transverse section of costa with 1-3 bistratose transitional cells to laminal cells . . . . **L. grandidieri** (p. 126)

18. Plants with juxtacostal bands abruptly tapered to the costa, mostly ending well above the base of the leaf; juxtacostal bands broad, dorsally non-rugose, and irregularly tapered toward base . . . . **L. membranaceum** (p. 130)

18. Plants with juxtacostal bands gradually tapered to the costa, mostly reaching the very base of the leaf; juxtacostal bands narrow, or if broad then dorsally rugose, and more or less evenly tapered toward base . . . . **L. seychellense** (p. 132)

SECTION *OBSCURA* (REN.) REN.

19. Leaves with sharply defined broad hyaline margin, 48-77 µm wide; acumen tapered to long fine point . . . . **L. sanctae-mariae** (p. 116)

19. Leaves with narrow hyaline margin, < 30 µm wide; acumen tapered to a stout or more slender apex 20

20. Leaves squarrose to widespreading or patent; apex more slender . . . . **L. thraustum** (p. 116)

20. Leaves strongly squarrose; apex stout, opaque, terete . . . . . . **L. thuretii** (p. 120)

SECTION *DICHELYMOIDEA* BESCH.

21. Plants slender, delicate with lanceolate to ovate-lanceolate leaves; apices filiform; leaves distantly arranged on pendent stems . . . . **L. dichelymoides** (p. 141)

21. Plants medium to robust, with broadly ovate, elliptic-ovate lanceolate to ovate-

lanceolate leaves; apices abruptly acuminate, short or more gradually tapered; leaves densely arranged on stems 22

22. Leaves broad 0.9-1.8 mm wide; papillose juxtacostal cells restricted to the upper lamina . . . . *L. fontinaloides* (p. 145)
22. Leaves narrower 0.5-1.3 mm wide; papillose juxtacostal cells that extend to the basal region or mid-leaf 23

23. Leaves with strongly corrugated, abaxial surfaces; papillae sharply prominent, acute to multifid . . . . *L. tuberculosum* (p. 158)
23. Leaves with moderately corrugated, abaxial surfaces; papillae less prominent . 24

24. Plants small; leaves slightly crisped; hyaline margin broad, 14-48 µm; plants restricted to Réunion . . . . *L. mafatense* (p. 149)
24. Plants medium to large; leaves crisped, spirally twisted; hyaline margin narrow, 7-12 µm; plants of Madagascar . . . . *L. ochrobasilare* (p. 151)

SUBGENUS *SYNCRATODICTYON* REN.

25. Upper cells opaque or not, with a gradual transition to the smooth, membranous basal cells; abaxial and adaxial papillae variable 26
25. Upper cells opaque, sharply differentiated from smooth, linear, membranous basal cells; abaxial and adaxial papillae biseriate at cell margins; in transverse section a distinctive lack of thickening (or "depression") over cell lumen, with thickening over interlumenal wall . . . . (series *Holomitrioidea*, p. 48) . 33

26. Distal cells equally papillose on both surfaces, or smooth; distal abaxial papillae low, dense, not hooked toward apex 27
26. Distal cells unipapillose or pluripapillose, uniseriate on abaxial surface, or smooth, adaxial papillae scattered long upper costa, few if any; distal abaxial papillae commonly hooked toward apex . . . . (section *Caespitulosa*, p. 45) . 31

27. Alar region intermediate, 10 to 20 cells wide ...... **section *Dicranoidea*** (p. 43)
27. Alar region reduced, 3 to 9 cells wide 28

28. Papillae dense, biseriate at the margins of the cell, with a depression centered over cell lumen in transverse section; leaf apices long and gradually acuminate; hyaline margin extending to apex, or ending just below apex . **subsection *Acuminata*** (p. 49)
28. Papillae dense, formed over cell lumen, with a lack of distinctive depression lumen; leaf apices apiculate or not, distally contracted to a long flattened, strap-like or ligulate acumen; hyaline margin restricted to the lower 1/2-2/3 of leaf length 29

29. Upper margins crenulate, formed by projecting papillae; alar cells thin-walled inflated, hyaline; apices often apiculate .... **series *Contorta*** (p. 63)
29. Upper margins serrate, formed from short laminal cells; alar cells bulging with slightly thickened longitudinal walls and red-brown, or thin-walled and hyaline; apices serrate not apiculate .... (**subsection *Serrata***, p. 49) . 30

30. Distal acumen somewhat flattened, long, and slender; distal laminal cells with papillae evenly developed on abaxial and adaxial surfaces; stem with central strand .... **series *Serrata*** (p. 50)
30. Distal acumen terete, stout, long or short; distal laminal cells with papillae evenly developed on abaxial and adaxial surfaces, or smooth; stem lacking central strand .... **series *Teretia*** (p. 50)

31. Distal laminal cells pluripapillose on abaxial surface; papillae distinctly uniseriate; juxtacostal cells with irregular or sinuose walls .... **subsection *Seriata*** (p. 45)
31.Distal laminal cells unipapillose on abaxial surface; papillae not distinctly uniseriate; juxtacostal cells more or less quadrate or rectangular 32

32. Papillae centered on the cell, not forming distinct pairs between cells in surface view; hyaline margin undulate .... **subsection *Albescentia*** (p. 47)

32. Papillae formed in pairs, the distal end of one cell and the proximal end of the cell above it in surface view; hyaline margin not undulate **subsection *Caespitulosa*** (p. 46)

SERIES *HOLOMITRIOIDEA* (REN.) REN.

33. Leaf apices fragile; lower chlorophyllose cells with isodiametric lumina . . . . **L. *cuneifolium*** (p. 55)

33. Leaf apices intact; lower chlorophyllose cells with oblong to elongate lumina . 34

34. Foliose stems robust; leaf apices rounded; chlorophyllose cells strongly sinuose . . . . **L. *marojeziense*** (p. 60)

34. Foliose stems slender to small; leaf apices with pellucid points; chlorophyllose cells irregularly sinuose 35

35. Leaves 1.5-2.5 mm long, patent to squarrose; apices falcate to circinate when wet; foliose stem 1.5-2.5 mm wide, when wet . . . . **L. *circinale*** (p. 52)

35. Leaves 0.6-1.5 mm long, erect-spreading to patent; apices erect to falcate when wet; foliose stem 0.5-1.0 mm wide, when wet . . . . **L. *grimmioides*** (p. 58)

Leucoloma Brid., Bryol. Univer. 2: 218. 1827, ***nom. cons.***

Type: *Leucoloma bifidum* (Brid.) Brid.

Walkeria Hornsch., Flora 8: (Ergbl. 2): 21. 1825, *nom. rejic.*

Type: *Trichostomum leucoloma* Brid. (G! lectotype seen).

Macrodon Arnott, Mem. Soc. Linn Paris 5: 290. 1827, *nom. rejic.*

Type: *Macrodon aubertii* Arnott.

Dicranum sect. *Leucoloma* (Brid.) C. Muell., Syn. 1: 352. 1848, *in synon.*

Type: *Leucoloma bifidum* (Brid.) Brid.

Poecilophyllum Mitt., J. Linn. Soc. Bot. 12: 92. 1869, *in synon.*

Lectotype: *Poecilophyllum serrulatum* (Brid.) Mitt. (lectotype chosen here!).

Nomenclatural Notes: *Leucoloma* has been conserved against a number of other generic names that were described during the same year or before: *Sclerodontium* (Schwaegrichen 1824), *Walkeria* (Hornschuch 1825), *Macrodon* (Arnott 1827). A list of 29 names for *Nomina conservanda* was compiled by Cardot in 1914 and presented to the "nom du Bureau Permanent et des Commissions de nomenclature" at the 5th International Botanical Congress in Cambridge, England 1930 (Briquet 1930). The list had been prepared for the Congress in 1915, but due to World War I, the Congress did not meet between 1910 and 1930. The reasons for conserving a particular name were not indicated by Cardot, only the proposed list was submitted. I presume the conservation of *Leucoloma* as a valid generic name was based on its historical use, reflected in the size of the genus and the recently published monograph (Renauld 1909), and floristic treatments (e.g., Renauld & Cardot 1915).

Species that are included in the present concept of *Sclerodontium* have been placed in the *Dicranum* sect. *Leucoloma* (Mueller 1849), *Leucoloma* (Mitten 1856, Jaeger & Sauerbeck 1872) or *Leucoloma* subg. *Dicnemoloma* (Renauld 1898). Renauld discussed the placement of 2 species (*L. clavinerve* and *Dicranum sieberianum*) in his new subgenus *Dicnemoloma* without officially synonymizing *Sclerodontium* with *Leucoloma*. Renauld refined the generic concept of *Leucoloma*, that excluded the subgenera *Dicnemoloma* and *Dicranoloma* from the genus (Renauld 1901), without any mention of the genus *Sclerodontium*. In 1909, he justified his use of *Leucoloma* by stating that bryologists had adopted Bridel's genus, and that the older synonyms are only of secondary interest (Renauld 1909). Cardot (1910) recognized the need for conserving *Leucoloma* against *Sclerodontium*, and therefore it was included in the proposed list. In a recent historical review of conserved names in mosses, *Leucoloma* was listed as a proposed name in 1910 and accepted as a conserved name in 1932 (Magill 1993).

The type species of *Walkeria*, *Trichostomum leucoloma*, is a synonym of *Leucoloma sanctae-mariae*, not *Leucoloma bifidum* as originally proposed. Therefore *Walkeria* is synonymised with *Leucoloma* here, based on a different rationale than proposed initially.

The type of *Macrodon* is *Macrodon aubertii*, a homotypic synonym of *Hypnum* *bifidum*, and thus is designated as *nomen illegitimum inclusum species prior*. Bridel (1827) justified the use of *Leucoloma* against *Macrodon* in the supplement to *Bryologia Universa*:

> *Piget nomen genericum a clar. Arnott excogitatum recipere non potuisse; at nostrum jam anno antiquius, types et graphio evulgatum abolere non possumus.*

Plants minute to robust, 0.5-20 cm tall, in compact to loose tufts or as gregarious stems. Stems erect, prostrate, downwardly outspreading to pendent, red, blackened below, non-tomentous, with or without central strand, branches mostly fragile, sympodial branching by subapical innovations and monopodial branching by lateral innovations unassociated with the gametangia. Axillary hairs hyaline, uniseriate, in the upper leaf axils only, 4-5 cells. Rhizoids smooth, red brown, restricted to the base of branch or stem, rarely solitary at the base of leaf or on alar cells. Leaves lanceolate, ovate-lanceolate, elliptic-lanceolate, ovate to rarely obovate; habit squarrose, falcate secund, contorted, spirally twisted, or flexuous; apices acuminate, truncate, or rounded, rarely apiculate, fragile or not. Margins plane, entire basally, often subentire, serrulate or serrate distally, hyaline border 2.5-65.0 µm wide, rarely lacking. Costa subpercurrent to excurrent, translucent, smooth or with few low abaxial teeth; in transverse section with two stereid bands, 1-5 layers of stereids, with a central layer of 4-6 (8) guide cells, with a 1-8 bistratose rows of cells in transition to the laminal cells or lacking. Laminal cells differentiated into three types: juxtacostal or upper, basal and interior, and marginal. Juxtacostal cells 5-10 (12) µm wide, oblate, quadrate to elongate, sinuose, angular or rounded, often thick-walled, chlorophyllose, uni- to pluripapillose, with abaxial papillae simple to multifid, low to prominent, coalescent or distinct, in distinct rows or not, rarely smooth, adaxial surface smooth, with scattered papillae or a few along the costa, or papillose as the abaxial surface. Basal and interior cells 5-12 µm wide, elongate to linear, porose or not, thick-walled, tinged, smoot. Marginal cells 2.5 µm wide to 288 µm long, narrowly linear, smooth, hyaline. Alar cells longitudinally thick-walled to thin-walled, inflated, bulging or flat, decurrent or not, auriculate or not, hyaline or red-brown with marginal cells hyaline.

Dioicous, rarely autoicous. Perichaetia terminal, acrocarpous; perichaetial leaves clasping, with differentiated bases broad, orange-brown, mostly abruptly contracted to a long setaceous acumen; archegonia red-brown, 10-40 per perichaetium, necks elongated , 0.6-1.5 mm long, with numerous paraphyses. Perigonia terminal; perigonial leaves with strongly concave bases, ovate to elliptic-ovate, abruptly tapered to a long or short acumen; antheridia flask-shaped, tan, stalked.

Sporophyte mono- or polysetous. Seta short to long, tan and opaque or red and translucent, smooth, slightly twisted to the right, with central strand; capsules immersed or exserted, ovoid, short to long cylindric, erect, symmetric to slightly asymmetric, stomates lacking, annulus undifferentiated. Operculum conic to rostrate, erect or oblique. Peristome haplolepideous, peristomial formula: OPL:PPL:IPL-(4):2:3(4); teeth 16, 35-96 µm wide at base, 0.2-0.6 mm long, red-brown, asymmetrically bifid (rarely trifid) split 1/2 to 3/4 to the base or perforate, or simple, lanceolate, filiform distally to lanceolate with truncated, obtuse apices; PPL: pitted striolate, papillose or smooth at base, mid portion distally papillose, transversely striate, or smooth; IPL: smooth or papillose. Trabeculae thickening variable: IPL trabeculae more pronounced than PPL or IPL and PPL trabeculae equally pronounced. Calyptra mitrate or cucullate, lobate or entire, distally roughened. Spores small, 18-24 µm, unicellular, finely granulose.

Habitat: Species of *Leucoloma* are predominantly epiphytic on tree trunks and saplings, ramicolous, lignicolous, as well humicolous, saxicolous, or terricolous. The specimens examined ranged from sea level to 2800 m, from lowland to upper montane and elfin rainforests, or drier heath forests and dry deciduous forests of western Madagascar (White, 1983).

Distribution: *Leucoloma* is pantropical, in tropical to subtropical regions: Subsaharan Africa, from the west to east and to the southern tip of Africa, Madagascar and the East African islands, the Indian subcontinent, Nepal to Sri Lanka, southeast Asia through Melanesia, north to Japan, and south to Australia, Hawaii to the South Pacific

Ocean islands, Mexico to Brazil, and the Caribbean.

Subgenus *Syncratodictyon* Ren., Rev. Bryol. Lichénol. 28: 86. 1901.

Lectotype: *L. sinuosum* (Brid.) Jaeg. (lectotype chosen here!).

Section *Transmutantia* Ren., Prod. Fl. Bryol. Madag. 72. 1898, *nom. illeg. incl. sect. prior.*

Plants erect to ascending, glaucous-green, green, black-green, or yellow-green. Stems mostly round in transverse section, with or without differentiated central strand. Leaves 0.6-20 mm long, minute to robust, obovate, elliptic-lanceolate, ovate-lanceolate, or lanceolate, flexuose, falcate secund, crispate or contorted. Costa smooth or with low abaxial teeth, subpercurrent to excurrent; in transverse section guides 4-8, lateral doubling or not, abaxial and adaxial stereid bands in 1-5 layers. Juxtacostal bands with a gradual transition into the basal cells or with sharply defined upper-basal cells. Alar cells hyaline, inflated, thin-walled or red-brown with evenly thickened walls or bulging with slightly, longitudinally thickened walls; alar region small to intermediate, 3-20 cells wide, 2-8 cells long. Dioicous.

Sporophyte mono-or polysetous. Seta > 4 mm long, slender, red, smooth, translucent; in transverse section with 2 or more thick-walled outer cortical cells. Capsules exserted, ovoid or short to long cylindric, symmetric or slightly asymmetric at base, tan, brown, to black-brown, epidermal cells in transverse section with the long axis parallel or perpendicular to capsule wall. Operculum rostrate, oblique. Peristome 16 teeth, 0.15-0.6 mm long, reduced or not. Calyptra cucullate, not lobed at base.

Leucoloma* Section *Dicranoidea Besch., Ann. Sci. Nat. Bot. sér. 6, 9: 315. 1878.

Lectotype: *L. sinuosum* (Brid.) Jaeg. (lectotype chosen here!).

Subsection *Dicranoidea* (Besch.) Ren., Prodr. Fl. Bryol. Madag. 81. 1898.

Lectotype: *L. sinuosum* (Brid.) Jaeg. (lectotype chosen here!).

Subsection *Semivittata* Broth., Nat. Pflanzenfam. 1(3): 324. 1901.

Type: *Leucoloma secundifolium* Mitt.

Section *Semivittata* (Broth.) Broth., Nat. Pflanzenfam. (ed. 2) 10: 211. 1924.

Type: *Leucoloma secundifolium* Mitt.

Nomenclatural notes: In Bescherelle's circumscription of section *Dicranoidea*, *Leucoloma sinuosum* was included as one of the original species and is chosen as the type species for the section, here! *Trichostomum longifolium* Brid. is the earliest name for the material and thus it is conspecific with *L. longifolium* (Brid.) Wijk et Marg.

Leaves ovate-lanceolate, flexuose, upper margins serrate. Costa with low teeth on abaxial surface. Juxtacostal cells papillose distally on adaxial and abaxial surface or smooth. Leaf base with one to several isodiametric transitional cells between the elongate basal cells and differentiated alar cells. Alar cells thin-walled, inflated or quadrate with cell walls evenly thickened; alar region intermediate, 10-19 cells wide. Capsules in transverse section with the long axis of the exothecial cells perpendicular or parallel to capsule wall. Peristome teeth well developed, 0.5-0.6 mm long.

Section *Dicranoidea*: 11 species

L. allorgei Thér.
L. boivinianum Besch.
L. charrieri Thér. & P. Varde
L. entabiense (Magill) La Farge-England
L. humbertii P. Varde
L. incrassatum Thér.
L. latifolium Broth. & P. Varde
L. longifolium (Brid.) Wijk & Marg.
L. onraedtii (Biz.) La Farge-England
L. rutenbergii (Geh.) Wright
  L. rutenbergii var. *abbreviatum* Ren.
  L. rutenbergii var. *elatum* Ren.
  L. rutenbergii var. *porosis* Thér.

L. rutenbergii var. *perrotii* Ren.
L. secundifolium Mitt.

Leucoloma **Section** ***Caespitulosa*** Besch., Ann. Sci. Nat. Bot. sér. 6, 9: 312. 1878.
Lectotype: *Leucoloma caespitulans* (C. Muell.) Jaeg. (lectotype chosen here!).

Section *Albescentia* Besch., Ann. Sci. Nat. Bot. sér. 6, 9: 313. 1878. **Lectotype:** *Leucoloma sinuosulum* C. Muell. *ex* Besch. (lectotype chosen here!).

Section *Pseudocaespitulosa* (Ren.) Ren., Suppl. Prodr. Fl. Bryol. Madag. 11. 1909. **Lectotype:** *Leucoloma ambreanum* Ren. & Card. (lectotype chosen here!).

Plants erect tufts. Leaves flexuose, commonly falcate secund, contorted or spirally twisted distally, acumen caniculate or subtubulose. Costa abaxial surface serrulate or entire. Juxtacostal cells with abaxial surface unipapillose, or papillae in a uniseriate row, gradual transition into smooth basal cells or interior cells laterally. Alar cells thin-walled, inflated; alar region reduced, 3-9 cells wide. Capsules long exserted, cylindric to long cylindric, symmetric or slightly asymmetric at base. Peristome 16 teeth, reduced, 0.15-0.4 mm long.

Leucoloma **Subsection** ***Seriata*** La Farge-England ***subsect. nov.***
Type: *Leucoloma sprengelianum* (C. Muell.) Jaeg.

Caulis sine filo centrale. Cellulae juxtacostales abaxiales papillae unipapillosae vel uniserialis distale, uniseriatae ad basim, humiles, multifidae, lumena irregularia vel sinuosa. Capsulae cylindricae, erectae, cum peristomae deminutae, < 0.4 mm longae.

Stem without central strand. Leaves flexuose, falcate secund distal acumen, unistratose, subtubulose. Juxtacostal cells differentiated with irregular or sinuóse lumen, abaxial surface of upper cells unipapillose or papillae uniseriate, papillae uniseriate basally, abaxial papillae low, multifid. Capsules cylindric, erect, symmetric to slightly asymmetric at base. Peristome 16 teeth, reduced, <0.4 mm long; PPL pitted striate to just below apex, papillose at apex; IPL smooth with papillae forming on the trabeculae.

Subsection *Seriata*: 6 species

L. okamurae Broth.
L. mariei Besch.
L. mosenii Broth.
L. scaberulum E. Bartr.
L. sprengelianum (C. Muell.) Jaeg.
L. zeyheri (C. Muell.) Kindb.

Leucoloma* Subsection *Caespitulosa (Besch.) Ren., Prodr. Fl. Bryol. Madag. 72. 1898.
Lectotype: *Leucoloma caespitulans* (C. Muell.) Jaeg. (lectotype chosen here!).

Subsection *Pseudocaespitulosa* Ren., Prodr. Fl. Bryol. Madag. 75. 1898.
Lectotype: *Leucoloma ambreanum* Ren. & Card., (lectotype chosen here!).

Stem with central strand. Leaves contorted, unistratose distally, caniculate; hyaline margin ending below the apex, not undulate. Juxtacostal cells with abaxial papillae, unipapillose, paired between the base of one cell and the top of the adjacent cell, distally hooked toward apex. Basal cells short to short elongate, < 3:1, length: width ratio. Peristome 16 teeth, reduced, 0.2 mm long, truncate to obtuse distally, deep ruby red; peristomial formula OPL:PPL:IPL (4):2:3(4); PPL finely pitted or papillose, IPL smooth.

Subsection *Caespitulosa*: 4 species

L. amblyacron C. Muell. ex Besch.

L. ambreanum Ren. & Card. in Ren.

L. caespitulans (C. Muell.) Jaeg.

L. subcaespitulans Besch.

Leucoloma* Subsection *Albescentia (Besch.) Ren., Prodr. Fl. Bryol. Madag. 77. 1898. **Lectotype:** *Leucoloma sinuosulum* C. Muell. *ex* Besch. (lectotype chosen here!).

Stem with or without central strand. Leaves often falcate secund, distally spirally twisted or contorted, unistratose distally, caniculate; hyaline margin extending to the apex or just below, commonly undulate. Juxtacostal cells quadrate, rectangular or oblong, variously angled, not oblate, with abaxial, prominent stellate papillae, unipapillose, distal papillae hooked toward apex, papillae centered over cell lumen. Alar cells thin-walled, inflated. Capsules cylindric, erect, symmetric or slightly asymmetric at base. Peristome 16 teeth, red, reduced, 0.20-0.35 mm long; PPL pitted striate at base or smooth, with the mid region transversely striate, with apices papillose or transversely striate; IPL is smooth.

Subsection *Albescentia*: 24 species

L. albo-cinctum Ren. & Card. in Ren.

  L. albo-cinctum var. *subelimbatum* Ren. in Levier

L. asperrimum (C. Muell.) Kindb.

L. brevioperculatum Dix.

L. brotheri Ren.

L. candidulum C. Muell. ex Besch.

L. candidum Broth. in Voeltzk.

L. cirrosulum Ren.

L. cruegerianum (C. Muell.) Jaeg.

L. decaryi Thér.

  L. decaryi var. *comorense* Thér.

L. delicatulum Ren.

L. isleanum Besch. in Par.

L. isleanum var. *subtortile* Ren.

L. itatiaiense Broth.

L. pallidulum Thér.

L. perrieri Thér.

L. persecundum C. Muell. ex Besch.

L. persecundum var. *perrotii* Ren.

L. pumilum Wright

L. pusillum Card. in Grand.

L. scabricuspis Broth.

L. schwaneckeanum (Hampe) Broth.

L. sinuosulum C. Muell. ex Besch.

L. subimmarginatum (C. Muell.) Jaeg.

L. syrrhopodontoides Broth.

L. theriotii Ren. & Card.

L. villaumei Thér.

Leucoloma **Section** ***Holomitrioidea*** (Ren.) Ren., Essai Leucoloma 28. 1909.

Basionym: Subsection *Holomitrioidea* Ren., Prodr. Fl. Bryol. Madag. 74. 1898.

Type: *Leucoloma cuneifolium* (Hampe ex C. Muell. et Geh.) Wright

Section *Rhacomitrioidea* P. Varde, Rev. Bryol. Lichénol. 19: 150-152. 1950, *synon. nov.* **Type:** *Leucoloma grimmioides* P. Varde

<u>Leaves</u> obovate, elliptic-lanceolate, or lanceolate, flexuose or crispate, or spirally twisted distally, acumen flattened or terete; upper margins entire or serrate. <u>Costa</u> with abaxial surface smooth. <u>Juxtacostal cells</u> commonly oblate, papillose distally on adaxial and abaxial surface or smooth. Leaf base lacking rows of

isodiametric cells between basal and alar cells. Alar cells thin-walled, inflated or bulging with longitudinally thickened walls; alar region reduced, 3-9 cells wide. Capsules in transverse section with the long axis of the exothecial cells parallel to capsule wall. Peristome 16 teeth, reduced, < 0.4 mm long.

Leucoloma* Subsection *Acuminata La Farge-England ***subsect. nov.***

Type: *Leucoloma tenerum* Mitt.

Caules densis foliis, folia longa acuminata, flexuosa vel cripata distale; cellulae alaris cum parietibus tenuibus, hyalinis vel rufae fuscae, protuberantes. Cellulae juxtacostales papillosae densissimiae utrinque super interlumena parietes in sectione tranversale.

Stems densely foliate; leaves long acuminate, flexuose to crisped distally; alar cells hyaline and thin-walled or red-brown, bulging, and slightly thick-walled. Juxtacostal cells with papillae, evenly developed on adaxial and abaxial surface, dense, developed over the interlumenal cell wall in transverse section. Transition from juxtacostal to basal interior or basal cells gradual. Alar cells thin-walled, hyaline or red brown, bulging, slightly longitudinally.

Subsection *Acuminata*: 4 species

L. cameruniae Par. ex La Farge-England *ined.*
L. malabarense Besch. ex Ren. & Card.
L. siamense Broth.
L. tenerum Mitt.

Leucoloma* Subsection *Serrata La Farge-England ***subsect. nov.***

Type: *Leucoloma fuscifolium* Besch.

Caules densis foliis, filum centrale praesentia vel abscentia; folia distalia *serrata ab brevibus cellulis lamellatis, non ab hyalinis, linearibus, marginalis cellulis. Cellulae juxtacostales laevi vel cum pagina adaxiali et abaxiali papillosa.*

Stems densely foliate; central strand present or absent. Leaves with upper margins entire or serrate from short laminal cells, serrations not from a hyaline margin; hyaline margin restricted to the proximal 2/3 of the leaf. Juxtacostal cells smooth or with papillae equally developed on the adaxial and abaxial surfaces.

Leucoloma* Series *Teretia* La Farge-England *ser. nov.

Type: *Leucoloma perviride* Broth.

Folia elliptica-lanceolata cum crassae, teretibus acumenibus, cellulae juxtacostales distales cum paginibus adaxialibus et abaxialibus papillosis vel laevibus.

Stems without central strand. Leaves elliptic lanceolate with stout, terete acumen. Juxtacostal cells smooth or papillose on abaxial surface.

Series *Teretia*: 3 species

L. amoene-virens Mitt.
  L. amoene-virens var. *humilis* Thér. & P. Varde
L. annamense Thér.
L. perviride Broth.

Leucoloma* Series *Serrata

Type: *Leucoloma fuscifolium* Besch.

Leaves basally elliptic with long slender, setaceous acumen. Juxtacostal cells densely papillose distally on abaxial and adaxial surfaces.

Series *Serrata*: 5 species

L. capillifolium Ren.

L. chlorophyllum Broth.
L. fuscifolium Besch.
  L. fuscifolium var. *crispatulum* Ren.
L. serraticuspis P. Varde
L. subsecundifolium Broth.

Leucoloma **Subsection** ***Holomitrioidea*** Ren., Prodr. Fl. Bryol. Madag. 74. 1898.
Type: *Leucoloma cuneifolium* (Hampe ex C. Muell. et Geh.) Wright

Stems densely foiliate, central strand present or absent. Leaves contorted, apiculate, truncate, obtuse, or rounded, upper margins entire or entire crenulate; hyaline margin restricted to lower 1/2 to 1/3 of leaf. Upper cells with lumen irregular or slightly sinuose. Juxtacostal cells with papillae equally developed on abaxial and adaxial surface or with adaxial surface smooth in lower 1/2 of leaf.

Leucoloma **Series** ***Holomitrioidea*** (Ren.) La Farge-England ***comb. nov.***
Basionym: Subsection *Holomitrioidea* Ren., Prodr. Fl. Bryol. Madag. 74. 1898.
Type: *Leucoloma cuneifolium* (Hampe ex C. Muell. et Geh.) Wright

Stem withot central strand. Leaves obovate or elliptic lanceolate, contorted, apiculate, upper margin entire; upper-basal cell transition sharply differentiated; upper cells pluripapillose, chlorophyllose, short, isodiametric, with papillae biseriate along the margins of the cell; in transverse section papillae coalesce over adjacent cell walls, leaving a distinctive "groove" over the lumen of each cell, sharply differentiated from basal cells. Basal cells smooth, hyaline, elongate to linear, porose. Alar cells bulging, longitudinally thickened walls, dark red-brown, or hyaline.

Series *Holomitrioidea*: 4 species

L. circinale La Farge-England

L. cuneifolium (Hampe ex C. Muell. & Geh.) Wright
L. grimmioides P. Varde
L. marojeziense La Farge-England

Leucoloma circinale La Farge-England ***sp. nov.*** Figures II.10-12

Type: Tanzania: Nguru Mts., Morogoro District. Elfin rainforest at west end of the Dikurura Valley, dominated by *Garcinia volkensii*, W. of Mohonda Mission. 6°06'S, 37°32'E, 1900 m, *La Farge-England 5614*. **Holotype:** ALTA, **isotypes:** MO, TAN

Paratypes: Tanzania: Uluguru Mts., *Pócs & van Zanten 86113/E, Pócs & Lungwecha 6876/B, Pócs & Nchimbi 6285/BB*; *Pócs, Mwanjabe, Sharma 6548/L* (EGR); Nguru Mts.: *La Farge-England 5575A, 5585, 5588, 5610, 5618* (ALTA, MO, TAN).

Plantae parvae, ad 2.5 cm altae, pallide virides vel virides, fuscae ad basim. Rami remoti, laterales fragiles. Folia sicca crispata, contorta, basi obovata ad raptim breviter subulata, 0.3-0.6 mm late, 1.4-2.3 mm longa, acumen circinatus vel falcata, apice apiculato. Cellulae supra medium isodiametrae, oblongae vel elongatae, sinuosae, papillosae, densissimiae, obscurae, reticulatae in superficiebus ambabus foliis, formans duo series per cellula, ad marginem oblata. Cellulae ad basim linearibus, incrassatis, formans basi scariosa vaginans. Cellulae alares protruberans, croceo-fuscis, scalariformes. Flores dioici. Species haec ab Leucoloma grimmioides P. Varde differt ab plus valde curvatibus acumenibus et plus longiores et latiores foliae.

Plants small, light green to green distally, dark brown proximally, in loose tufts, with erect to spreading stems. Stems to 2.5 cm long, red, densely to somewhat distantly foliate; stem with leaves 1.5-2.5 mm wide when moist, simple or branched: branching sympodial by 1-3 subapical innovations or monopodial by fragile lateral branches.

Leaves 0.3-0.5 mm wide, 1.4-2.3 mm long, concave, elliptic to obovate, base clasping, membranous, abruptly narrowed to a caniculate, long acumen, tapered to an acute apex with a pellucid point, a few acumina with lamina torn to costa; habit patent to squarrose with strongly contorted, crisped, or spirally curled acumens when dry, apices falcate to circinate when moist. Margins plane, entire distally to subentire proximally; bordered in the basal region. Costa 24-36 µm wide above the base, excurrent as short apiculus; transverse section plano-convex to elliptic, abaxial and adaxial stereid bands of 1-2 layers, guides 3-4 cells. Upper cells 7.0-9.5 µm wide, (2.5) 6.0-12.0 µm long, oblate to oblong or shortly elongate, longer basally, irregularly sinuose, opaque, papillose, extending from apex to mid-basal region. Basal cells 5-7 µm wide, 22-72 µm long, elongate to linear, smooth, tinged, extending as a marginal wedge between chlorophyllose cells and hyaline border. Basal marginal cells 2.5 µm wide, 40-120 µm long, linear, hyaline, smooth, thick-walled, forming a differentiated border 12-19 µm wide (3-5 cells) in lower 1/3 of leaf, ending at base of acumen. Alar cells 12-19 µm wide, 12-70 µm long, quadrate to rectangular; alar region 5-6 cells wide by 3-4 cells long, sharply differentiated, not reaching the costa.

Dioicous. Perichaetia terminal; perichaetial leaves 0.5-0.6 mm wide, (1.5) 2.0-2.4 mm long, broadly obovate, abruptly narrowed to a long, gradually tapered acumen, clasping, with convolute leaf bases. Perigonia not seen, although sex presumed dioicous. Sporophyte not seen.

Diagnostic Characters: *Leucoloma circinale* has leaves with intact apices that are falcate to circinate when moist, and opaque laminal cells that reach the upper to mid-basal region and are oblong to shortly elongate basally. The Tanzanian material has previously been named either *L. cuneifolium* or *L. grimmioides*, indicating the problem of existing species concepts within the section. All of the continental African material examined to date belongs to *L. circinale*. *Leucoloma cuneifolium*, an endemic species of Madagascar, differs from *L. circinale* by having isodiametric cells in the lower part of the opaque region of the leaf and fragile apices. *Leucoloma circinale* is closely related to *L. grimmioides*, although the diminuitive size of *L. grimmioides*, with shorter, more slender leaves and a wet habit with erect to falcate leaf apices, easily separate it from *L. circinale*. The former has distinctly narrower foliate stems upon wetting: 0.5-1.0 mm wide, opposed to 1.5-2.5 mm wide of the latter. *Leucoloma circinale* is distinguished from *L. marojeziense* by its smaller size, strongly contorted leaf habit, and circinate wet leaves.

Variation: The leaf apices vary from falcate to circinate in the wet habit, although the dominant curvature is circinate. In some leaves the lamina is torn to the costa, suggestive of *L. cuneifolium*, yet the number is minimal within single specimens. In general, *L. circinale* has a smaller habit than *L. cuneifolium*. In some specimens the leaf bases are visible, as in *L. grimmioides*, and in others the bases are obscured by the leaf below it.

Habitat: *Leucoloma circinale* is corticolous on saplings, trunks of trees, or branches within 2 m of the forest floor. It occurs in montane to elfin rainforests, in ombrophilous, moist, high humidity forests with a high coverage of epiphytic mosses, between 1390-1950 m.

Distribution: *Leucoloma circinale* is endemic to eastern Tanzania, known only from the Uluguru and Nguru Mts. Its apparent absence from Mt. Kilimanjaro, one of the best bryologically collected sites in East Africa, suggests an affinity for the rainforests of the Precambrain massifs, opposed to rainforests on orogenies of volcanic origin.

Etymology: The specific epithet refers to the curved, circinate acumen of the wet leaves.

Leucoloma cuneifolium (Hampe ex C. Muell. et Geh.) Wright Figures II.13-15 J. Bot. 26: 263. 1888. **Basionym:** *Dicranum cuneifolium* Hampe ex C. Muell. et Geh., Abh. Naturw. Ver. Bremen 7: 206.1881. **Type:** "Wald von Ambatondrazaka, 6 Decbr. 1877." Leg. Rutenberg, Hb. Geheeb. **Lectotype:** PC! (Hb. Cardot - Hb. Geheeb); **isotypes:** PC! (2 specimens - Hb. Cardot and Hb. Renauld).

Nomenclatural notes: *Leucoloma cuneifolium* is lectotypified from three Rutenberg specimens found in PC, for no type material was found in B, BM, JE, M, or NY. The specimen indicating Geheeb's herbarium is chosen as the lectotype, based on the shared authority of Mueller and Geheeb. No type material was found in Rutenberg's herbarium in Bremen.

Plants medium, green to yellow-green distally, with proximal stems brown, in loose tufts. Stems 0.1-3.5 cm long, red, densely foliate, mostly obscuring stem, simple or branched: branching sympodial by 1-3 subapical innovations or monopodial by fragile, lateral branches; stems with leaves 1.5-2.0 mm wide when moist.

Leaves 0.40-0.65 mm wide, 1.5-2.5 mm long, obovate to elliptic, sheathing at base, auriculate or not, abruptly contracted to a long, caniculate acumen, tapered to an acute apex with a pellucid point, apices fragile and lamina commonly torn in acumen , wide-spreading to squarrose with strongly contorted acumen, crisped when dry, patent with intact apices gently curved when moist. Margins plane, entire distally to subentire or serrulate proximally, bordered in the basal 1/3 to 1/2 of leaf. Costa 30-48 μm wide at base, shortly excurrent; guide cells in a single row of 4 cells, commonly with 1-2 bistratose rows in transition to the laminal cells. Upper cells 7.2-12.0 μm wide, 4.8-12.0 (24.4) μm long, oblate to shortly elongate, isodiametric in lower opaque region, irregularly sinuose, opaque with dense papillae, extending from apex to the upper basal region, tapering from the margins at the base of the acumen to the costa as a V-shaped region. Basal cells 5-7 μm wide, 22-84 μm long, elongate to linear, shorter in the upper marginal region, smooth, non-porose, thick-walled. Marginal cells 2.5 μm wide, 36-132 µm long, narrowly linear, hyaline, smooth, thick-walled; differentiated border 12-19 µm wide (3-6 cells) in basal region. Alar cells 10-17 µm wide, 10-60 µm long, quadrate to elongate; alar region 6-8 cells wide, 2-4 cells long, not reaching the costa.

Dioicous. Perichaetia terminal, cryptic within stem leaves or perichaetial leaves protruding as a convolute "tube"; perichaetial leaves 0.4-0.6 mm wide, 1.7-3.0 mm long, leaf bases obovate, convolute, 1-2 mm long, abruptly contracted to a long, fragile acumen, progressively shorter on inner leaves. Perigonia terminal; perigonial leaves 0.8-1.5 mm long, orbicular, elliptic to elliptic-ovate, strongly concave, sharply contracted to fragile, short acumen or acute apex.

Sporophyte monosetous. Seta 3.5-7.0 mm long, slender, smooth, translucent, red, slightly twisted to the right below capsule. Capsules 1.5-1.8 mm long, exserted, short cylindric, erect, brown. Operculum 1.0 mm long, rostrate (immature state). Peristome 16 teeth, inserted below mouth of capsule (single mature capsule seen with broken teeth). Calyptra cucullate, reddish-brown, slightly roughened above. Spores not seen.

Diagnostic Characters: The densely foliose stems obscured by the squarrose leaves, fragile apices, and irregularly sinuose and isodiametric cells in the lower opaque region distinguish this species within *Leucoloma* ser. *Holomitrioidea*. As well, the costa is broader and the upper cells are more densely papillose than in the other species of the series. *Leucoloma cuneifolium* is typically yellow-green and is the only species that has been found with sporophytes. For contrast with its two most similar species, *L. circinale* and *L. grimmioides*, see "Diagnostic Characters" under each species, respectively.

Variation: *Leucoloma cuneifolium* is the most common species of the series. The most striking variation observed in the specimens is the size of the perichaetial leaf bases. Specimens with strongly protruding perichaetial leaves (*Frizzard* (L, S) and *Tixier*

11707 (PC)) have leaf bases twice the length of the other specimens. These plants also have intact, spiralled leaves at the terminus of the stems, and appear slightly more "robust" than the other specimens.

One specimen of *L. cuneifolium* had an aberrant leaf with two costae developed and two apices. This is interpreted as a mechanical damage to the apical cell in the early stages of leaf development.

Habitat: *Leucoloma cuneifolium* is corticolous on base of tree or sapling trunks within a meter of the forest floor, on fine twigs on forest floor, on lianas, horizontal branches, or on rotting bark. Its known elevation range is 920-1700 m, in primary or degraded, montane rainforests.

Distribution: *Leucoloma cuneifolium* is restricted to east-central rainforests of Madagascar, reaching its western limit on the central plateau northwest of Antananarivo. The present distribution is based on 50 specimens.

Specimens examined: MADAGASCAR: Prov. Fianarantsoa: Ambohimahsoa: *Onraedt 70.M.528* (BR), *70.M.0528, 70.M.0559* (Hb. Onraedt); Ambatofitorahana: *Onraedt 70.M.0416, 71.M.05390* (Hb. Onraedt); Ranomafana: *Crosby & Crosby 8618* (FH, L, S); *Tixier 11707* (PC); Ambatofitorahna: *Tixier 12176* (PC); Ambositra: *Frizzard*, 21.viii.1905 ex hb. E.G. Paris (L, S-2 specimens); **Prov. Tamatave:** Analamazoatra: *Camboué 272* (BR); Andasibe: *La Farge-England 5796, 5808, 5811, 5815, 5838, 5846, 5853, 5857, 5870, 5913, 5942, 5958, 5964, 5967, 5981, 5990, 6038, 6054, 6061, 6062* (ALTA, MO, TAN); *Dorr 3142* (MO); Lakato: *Tixier 12451, 12639, 12881, "Lakato 7"* (PC); Ambotofito: *Tixier 11926* (PC); **Prov. Tananarive:** lac de Mantasoa: *Onraedt 74.M.2229* (Hb. Onraedt), *74.M.2230* (EGR); Ambohitantely: *Cremers 1800* (Hb. Onraedt), S.O. de Tananarive: *Carrougeau 1922* (Hb. P. Varde ex Hb. Thériot) (BR, FH); Mandraka: *Dorr & Rakotozafy 2797* (MO); *Tixier 11276* (PC).

Etymology: The specific epithet refers to the wedge-shaped opaque region of the lamina.

Leucoloma grimmioides P. Varde Figures II.16-18

Rev. Bryol. Lichénol. 19: 150. 3. 1950. **Type:** Madagascar: "Hab. Vallée de la Lokoho, Mont Beondroka, roches de la crête, en très petit quantité parmi Lichens et Fougères naines. Alt 1400-1450 m. Leg. Humbert; 17-22.mars.1949. det. P.V. 10944.D". **Holotype:** PC! (Hb. P. de la Varde)

Leucoloma guehoi Tixier, Proc. Roy. Soc. Arts Sci. Mauritius 5: 41. 1993, *synon. nov.***Type:** "Holotype: Mauritius valley above "500 foot falls" on Rivière des Galets, growing on wet rock of rivulet at top of the valley, J. *Guého* 424 (MAU 21 729)". **Holotype:** not seen; **isotype:** PC!; **paratypes:** *Guého 347*, PC!; *Gueho 352*, PC!

Nomenclatural notes: *Leucoloma grimmioides* was originally described in a monotypic section, Section *Rhacomitrioidea* P. Varde. Section *Rhacomitrioidea* is a synonym of Section *Holomitrioidea* (Ren.) Ren. The original concept of the taxon is here treated at the rank of series. Three specimens of *L. guehoi* Tixier were found in PC, and indicated as duplicates of material in MAU. The original material was not seen in the loan from MAU.

Plants minute, slender, light-green to green distally, proximally brown, in loose tufts. Stems to 2.3 cm, red, densely foliate to more distantly arranged, stem with leaves 0.5-1.0 mm wide when moist, simple or branched: branching sympodial by 1-3 subapical innovations or monopodial by fragile, lateral branches.

Leaves 0.2-0.3 mm wide, 0.6-1.4 mm long, concave, elliptic to obovate, clasping, membranous at base with abruptly contracted, long, caniculate acumen, ending as an acute apex with a pellucid point; habit erect to patent with strongly contorted, crisped, spirally twisted acumen when dry, apices erect to falcate when moist. Margins plane, entire to subentire, bordered in the basal region. Costa 24-29 µm wide at base, subpercurrent, transverse section with a single row of 3-4 guide cells. Upper cells 7.0-9.5 µm wide, (5) 7-24 µm long, oblate, irregularly isodiametric, oblong to shortly elongate, irregularly sinuose, opaque, papillose, extending from apex to the mid-basal region. Basal cells 5-7 µm wide, 19-72 µm long, elongate to linear, smooth, non-chlorophyllose, non-porose, thick-walled. Basal marginal cells 2.5 µm wide, 48.0-96.0 µm long, linear, hyaline, smooth, forming border 5-7 µm wide (2-3 cells). Alar cells 7.0-19.0 µm wide, 12.0-36.0 µm long, quadrate to elongate, orange-brown (hyaline), longitudinally thick-walled, slightly bulging; alar region 3-6 (8) cells wide by 2-3 (5) cells long, sharply defined, not reaching the costa.

Dioicous. Perichaetia terminal; perichaetial leaves 0.30-0.35 mm wide, 0.4-1.5 mm long, obovate with abruptly contracted to an acumen. Sex presumed dioicous, although perigonia not seen. Sporophyte not seen.

Diagnostic Characters: Within series *Holomitrioidea*, *Leucoloma grimmioides* is distinguished by its extremely slender, foliate stems, with narrow, short leaves. When moist, it has erect-spreading leaves with erect, slightly curved, or falcate apices. The continental African endemic, *L. circinale* of Tanzania, has wider and longer leaves, with falcate to circinate apices in the wet habit, and broader and more densely foliate stems. In *L. cuneifolium*, the yellow-green color, fragile leaf apices, and predominantly isodiametric cholorophyllose cells in the lower opaque region distinguish it from *L. grimmioides*. The robust habit of *L. marojeziense* clearly separates it from L. *grimmioides*.

Variation: The specimens from Mauritius form slightly more compact turfs. The phyllotaxy varies from densely foliate to leaves somewhat distantly arranged, making the leaf bases visible in some specimens. The curvature of the apex varies from erect to falcate, approaching the apices found in *L. circinale*.

Habitat: *Leucoloma grimmioides* is corticolous on fine twigs, branches, and trunks of saplings or trees, or saxicolous in "rivulet" bed or on ridge exposures. The specimens show a broad elevational range of 200-1450 m, primarily in exposed habitats of lowland and degraded montane rainforests, or ridges of elfin rainforests.

Distribution: *Leucoloma grimmioides* is known from Madagascar in the northeast from the Marojezy forest reserve, Tahiry Nanaharin'i Marojezy (14°28' S) and in the east-central zone from the Andasibe (Perinet) forest reserve (18°56' S). It is also known from 4 collections in Mauritius: 1) Mont. Pouce, 2) Mont. Deux Mamelles, 3) above La Grande Case Noyale (20°25' S), and 4) from the valley above 500 foot falls on Rivière des Galets. The present distribution is based on 17 specimens. Futher collecting is likely to produce specimens from localities between the two Madagascan forest reserves, and probably from Réunion. (Note that the most of the known specimens are from recent collections. The diminuitive size of the plant may be the primary reason for it being overlooked in the field.)

Specimens examined: MADAGASACAR: Prov. Diégo Suarez: Marojezy: *La Farge-England 6027, 6053, 6278, 6293, 6294, 6308, 6315, 6361, 6366A, 6366* (ALTA, MO, TAN). **MAURITIUS:** *Crosby & Crosby 5644* (ALTA, MO); *Pócs, Guého, Florens 9530/K, 9529/J* (ALTA); *Rodriguez*, 27.9.1922 (PC - Hb. Thériot).

Leucoloma marojeziense La Farge-England ***sp. nov.*** Figures II.19-21

Type: Madagascar: Prov. Diégo Suarez. Tahiry Nanaharin'i Marojezy, north of Manantenia and Loko River Valley, on the S.E. slopes of the massif de Marojezy above Mandena Village. 14°26'S, 49°44'E. **Holotype:** *La Farge-England 6298* (ALTA); **isotypes:** MO, TAN.

Paratypes: Madagascar: Prov. Diégo Suarez. Tahiry Nanaharin'i Marojezy: *LaFarge-England 6353, 6374* (ALTA, MO, TAN).

Plantae robustae ad 3.5 cm altae, caespitosae, pallide flavo virens vel pallide virides, fuscae ad basim. Caules folibus densibus, rami romoti 1-5 fasciculatae. Folia sicca, patentes vel squarrosa, 0.7-8.8-1.1 mm late, 1.5 2.5-3.5 mm longa. Cellulae ad basim 6-8 µm late, 50-130 µm longae, lineares, incrassatae, porosae, formans basim scariosam. Cellulae alares protuberantes, croceo-fuscae, scalariformes. Flores dioicous. Perichaetia terminales, occulta vel non. Perigonia non vidit! Species haec differt ab alteris species sectionis habit robustior, foliae flexuosae, cellulae chlorophyllosae valde sinuosae.

Plants robust, pale, yellow-green to light green distally, brown proximally, forming tufts or cushions. Stems 1.0-3.5 cm, red, densely foliose; foliate stem with leaves 2-3 mm wide when moist, simple to distally ramulose, branching sympodial by 1-5 fasciculate, subapical innovations or with monopodial lateral branches.

Leaves (0.7) 0.8-1.1 mm wide, (1.5) 2.5-3.5 mm long, elliptic to ovate-elliptic, concave, non-sheathing, tapering to a long, caniculate acumen, with a rounded, obtuse apex, auriculate at base; habit patent to squarrose with flexuose to incurled apices when dry, patent to wide-spreading when moist. Margins plane, entire to subentire distally, bordered from the base to 2/3 of leaf or just below the apex. Costa 24-36 µm wide at base, subpercurrent; guide cells in a single row of 4-6 cells. Upper cells 10-12 µm wide, (14) 22-53 µm long, rounded to oblong apically to elongate below, chlorophyllose, thick-walled, strongly sinuose, opaque with dense papillae, extending from apex to the upper basal region and from the costa to the marginal cells. Basal cells 6-8 µm wide, 53-132 µm long, linear, smooth, porose or not, thick-walled, extending as a narrow, marginal wedge between chlorophyllose cells and hyaline border. Marginal cells 2.5 µm wide, 60-168 µm long, linear, hyaline, smooth, thick-walled, forming a distinct, narrow, hyaline border, 7-17 µm wide (2-5 cells), widest in medial region. Alar cells 12-26 µm wide, 12-72 µm long, quadrate to elongate; alar region 6-8 cells wide, 2-4 cells long, sharply defined, not reaching the costa.

Dioicous. Perichaetia terminal; perichaetial leaves 0.4-0.6 mm wide, 1.2-2.3

mm long, leaf bases obovate with abruptly contracted acumen, inner leaves orbicular, lacking an acumen. Perigonia not seen.

Sporophyte not seen.

Diagnostic Characters: *Leucoloma marojeziense* shares the following characters with other species in series *Holomitrioidea*: 1) the distinct papillae formation, 2) bordered leaves, and 3) bulging red-brown alar cells. It is distinguished within series *Holomitrioidea* by 1) the robust, densely foliate stems, 2) leaves with non-sheathing, membranous bases, 3) a long leaf acumen tapered to a rounded, blunt apex, 4) flexuose, incurved leaf apices when dry, and 5) strongly sinuose, elongate, chlorophyllose leaf cells. The three other species of series *Holomitrioidea* have contorted leaf habits, more or less sheathing leaf bases, pellucid apiculi or fragile acumina, chlorophyllous cells that are not as distinctly sinuose, and non-robust plants.

Variation: The growth form of *Leucoloma marojeziense* varies from a loose cushion to turf, with the branching simple to fasciculate. The range of variation of leaf habit is squarrose to wide-spreading or patent when dry. The perichaetia are cryptic or conspicuous as a terminal "tube" on the shorter, less branched stems. The length of the hyaline border varies from 2/3 of the leaf to below the apex. The rhizoids, which are typically confined to the stem or branch base, have also been observed scattered along the stem. It lacks the tomentum development found in *Dicranum* or *Dicranoloma*.

Habitat: *Leucoloma marojeziense* is corticolous on tree trunks or branches, or lignicolous. It is found on exposed ridges of the humid, elfin forest within the canopy, where frequent misting by clouds occurs. The height of the elfin forests range from 2-5 m at an elevation of 1050-1450 m. This elevation range lies within the zone of the highest precipitation (Humbert 1955).

Distribution. - *Leucoloma marojeziense* has been collected only in the Marojezy forest reserve, Tahiry Nanaharin'i Marojezy (14°26'S), north eastern Madagascar. The region is part of the Precambrian, metamorphic massifs. The northern locality of the massif is within the wet tropical zone of the eastern forests. The species is endemic to Madagascar and may prove to be restricted to Marojezy. *Leucoloma humbertii* P. Varde is also endemic to Marojezy, which emphasizes the isolation of the this massif in northeastern Madagasacar.

Etymology: The specific epithet refers to the geographical location where it was collected, Tahiry Nanaharin'i Marojezy, Madagascar.

Series ***Contorta*** La Farge-England ***ser. nov.***

Type: *Leucoloma tortellum* (Mitt.) Jaeg.

Habitus contortus, folia apiculata, elliptica-lanceolata ad basim, acumen distale uni-, bi- vel tristratosa, marginatus distale crenulatus e papillosis projectis. Cellulae juxtacostales papillosae densissimiae utrinque super lumena in sectione tranversale. Cellulae alaris proparte auricularis, cum parietibus tenuibus, hyalinis, protuberantes.

Stem with or without central strand. Leaves elliptic-lanceolate to lanceolate, tapering to a narrow lingulate acumen, distally flattened, uni- to tristratose, contorted, apiculate; upper margin entire except crenulate by the projecting papillae. Upper cells pluripapillose or unipapillose, equally developed papillae on abaxial and adaxial surfaces distally, chlorophyllose, short, isodiametric, upper-basal cell transition gradual. Basal cells smooth, short elongate. Alar cells inflated thin-walled; alar region reduced auriculate.

Series *Contorta*: 12 species

L. circinatulum Bartr.

L. dussianum Besch. ex Ren. et Card.

L. guineense Broth. et Par.
L. herzogii Broth.
L. mittenii Fleisch.
L. normandii Par. & Broth. ex Ren. in Par.
  L. normandii var. alpinum Par. et Broth.
L. pobeguinii Par. & Broth.
L. pygmaeum Par.
L. sericeum P. Varde
L. tanganyikae P. Varde
L. taylorii (Schwaegr.) Mitt.
L. tortellum (Mitt.) Jaeg.

Leucoloma Subgenus *Leucoloma*

Type: *Leucoloma bifidum* (Brid.) Brid.

Subgenus *Euleucoloma* Ren., Prodr. Fl. Bryol. Madag. 61. 1898, *nom. illeg.*
Subgenus *Taeniodictyon* Ren., Rev. Bryol. 28: 86 1901, *nom. illeg.*

Plants ascending, downwardly outspreading, pendent, pale green, tan to brown below. Stems elliptic in transverse section, without central strand, outer cortical cells mostly 2-4, rarely 6, red brown, thick-walled, inner cortical cells larger lumened yellow to hyaline; branching sympodial, branches 1-3 from subapical innovations, monopodial branches fragile or not, common, oblique or perpendicular to main axis. Leaves ovate, ovate-lanceolate to elliptic-lanceolate, with differentiated juxtacostal bands of cells and hyaline border, laminal tissue membranous or not. Costa smooth, subpercurrent to excurrent; in transverse section guides 4-6, rarely with lateral doubling, abaxial and adaxial stereid bands in 1-5 layers, number of bistratose rows to laminal cells variable. Alar cells longitudinally thick-walled, alar region small to large, 6-31 (43) cells wide, 3-17 (21) cells long. Dioicous with single autoicous exception.

Sporophyte mono- or polysetous. Seta short, stout, tan, smooth; in transverse section with single layer of thickened outer cortical cells, with central strand. Capsules immersed, emergent, to shortly exserted, globose, ovoid, to short cylindric, tan, brown, to black-brown. Operculum conic to rostrate, erect or oblique. Calyptra mitrate, lobate.

Leucoloma* Section *Subvitatta (Ren.) Ren.

Essai Leucoloma 26. 1909. **Basionym:** *Leucoloma* Subsection *Subvittata* Ren., Prodr. Fl. Bryol. Madagascar 68. 1898. **Type:** *Leucoloma comorae* Ren.

Plants medium, stems erect, ascending,to downwardly out-spreading. Leaves caducous, narrowly lanceolate to ovate-lanceolate, flexuose, erect- to wide-spreading, with long gradually tapered acumen; papillae of juxtacostal bands restricted to the abaxial surface or with a few on the adaxial surface distally, differentiated bands reaching the base or not. Basal and interior cells commonly porose, 1-4 rows of isodiametric cells between basal and alar cells. Alar cells predominantly quadrate, evenly to slightly longitudinally thick-walled, vertically oriented toward basal cells. Rhizoids often developed on alar cells.

Nomenclatural notes: The taxon *Subvittata* was originally described as a monotypic subsection, with *Leucoloma comorae* as the only species. Renauld (1898) stated that some species (i.e., *L. chrysobasilare*) might be considered intermediate between subsections *Euvittata* and *Subvittata*. The character he used to distinguish the two subsections was the how far the differentiated juxtacostal cells extended to the leaf base. He described the juxtacostal cells in subsection *Subvittata* as longer, wider, and smoother (submembranaceous) toward the base. In fact *L chrysobasilare*, originally placed in subsection *Euvittata*, is an earlier name for *L. comorae*.

Section *Subvittata*: 11 species

L. bauerae (C. Muell.) Par.

L. caldense C. Muell. ex Aongstr.
L. chrysobasilare (C. Muell.) Jaeg.
  L. chrysobasilare ssp. *africana* La Farge-England
L. ecaudatum (C. Muell.) Kindb.
L. hawaiiense Broth.
L. insigne (C. Muell.) Jaeg.
L. kanakense Broth. & Par.
L. limbatulum Besch.
L. molle (C. Muell.) Mitt.
L. serrulatum Brid.
L. subintegrum Broth.
L. tenuifolium Mitt.

Leucoloma chrysobasilare (C. Muell.) Jaeg. Figures II.22-24

Ber. S. Gall. Naturw.Ges. 1877-78: 379. 1880. **Basionym:** *Dicranum chrysobasilare* C. Muell., Linnaea 40: 238. 1876. **Type:** "Comoro-insula Johanna. 400-1000 m supra mare, ad ramos arborum sylvae umbrosae madidae. *J.M. Hildebrandt 1840, 1842, 1846*; dat. 1875." **Lectotype:** *Hildebrandt 1840* (comm. Rensch.) BM! (sheet #9) (lectotype chosen here!); **syntype:** *Hildebrandt 1842* BM! (sheet #7); **isosyntypes:** *Hildebrandt* BM! (sheet #9 - Hb. Bescherelle, sheet #10, sheet #84 - *Hildebrandt 1842 & 1846* (as 1 specimen!) - *ex herbario* O. Rensch.

Leucoloma comorae Ren., Prod. Fl. Bryol. Madag. 69. 1898, *synon. nov.* **Type:** "Grande Comorae: Humblot, 1890." **Holotype:** PC! (Hb. Renauld); **isotype:** PC! (Hb. Thériot).

Nomenclatural Notes: The type material in BM is mixed for *Hildebrandt 1842*; therefore *Hildebrandt 1840*, comm. Rensch., is chosen as the lectotype. *Hildebrandt*

1842 in parte remains a syntype; one specimen in BM is indicated as *Hildebrandt 1846* and *1842*. The specimen appears as a single collection, thus it would be impossible to typify *Hildebrandt 1846* as a distinct syntype. A number of specimens are labelled *Hildebrandt* 1875, but lack a collecting number. These specimens cannot be differentiated into isolectotypes versus isosyntypes, thus I have designated them as isosyntypes, in light of the uncertainty. In BM (sheet #7), there is a specimen which was originally named *L. hildebrandtii* C. Muell. *sp. nov*. The name was crossed out and replaced with *L. chrysobasilare* C. Muell. This material was collected by Hildebrandt and communicated to Mueller by Al. Braun, with "*ex* Hb. Geheeb" indicated on the specimen. In S, a specimen with the same label data is named *L. hildebrandtii*. A third specimen with *comm*. Al Braun, *ex* Hb. Geheeb, named *L. chrysobasilare* is in S (!). These 3 specimens are not considered type material, although they are Hildebrandt specimens, for they lack the collecting number data and were originally named *L. hildebrandtii* or share the same label data. Another specimen in BM was named *L. chrysobasilare* var. *gracilicaulon*, but later was corrected to *L. chrysobasilare* C. Muell. It was referred to as No. 8, *comm*. Al. Braun, *leg*. Hildebrandt, *ex* Hb. Geheeb. This material is the same as the 3 specimens in S.

Dixon criticised Renauld's tendency to make numerous species based on costa width and juxtacostal band cells. It is clear that Dixon did not scrutinize the variation within the exotic material to the same extent as he had his homeland material. Renauld was perceptive to distinguish the often overlooked species. Sim (1926) adopted a broad concept of *Leucoloma chrysobasilare* and synonymised both *L. woodii* Rehmann & MacOw. and *L. zuluense* Broth. with it. A specimen from "Woodbush. Dec. 1911- Wager", *Wager 189*, named *L. woodii*, (PRE! - Hb T.R. Sim Herb. Prop. with *7728* indicated on it) is cited as the voucher for Sim's *L. chrysobasilare* description. This specimen represents the distinct species, *L. zuluense*. Another voucher used for the description was - *Wager #188* (Sim 7728-PRE! in T.R. Sim Herb. Prop.). This specimen is *L. scabricuspis* Broth. (*L. rehmannii* (C. Mueller) Rehm. *ex* Par. *synon. nov*.). Two specimens cited for *L. c.* var. *gracilicaulon* Ren., *Henkel* (Eyles 2624 PRE) and *Henkel* (Sim 10,143 PRE), do not compare with the type of the variety, but represent specimens of *L. schelpei* P. Varde and *L. zuluense*. *Leucoloma procerum* and *L. zuluense* lack rhizoid development on the alar cells, which is found in *L. chrysobasilare* and they lack the development of several rows of isodiametric cells between the basal and alar cells. Magill (1981) did not consider taxa below the species level, therefore *L. c.* var. *gracilicaulon* was not assessed in his floristic treatment. Magill considered *L. zuluense* a synonym of *L. chrysobasilare*, which I consider a distinct species, and did not mention *L. woodii* Rehmann and MacOw. *ex* Wager. *Leucoloma zuluense* is similar to *L. chrysobasilare*, but differs by the following characters: 1) juxtacostal cells mostly oblong to elongate with more or less thick walls, 2) lack of distinct rows of isodiametric cells between alar and basal cells, 3) lack of rhizoid development on alars, and 4) leaves shorter, 3-5 mm, crisped, "bowed", or flexuose.

Plants medium sized, 1-6 cm tall, in loose tufts of gregarious stems, green, light green, pale yellow-green, or tan. Stems red, blackened below, non-tomentous, densely foliate; central strand lacking, outer cortical cells of 2-4 layers, red-brown, thick-walled, inner cortical cells pale orange, yellow, or hyaline, larger lumened; sympodial branching from 1-3 subapical innovations, with monopodial branching sparse, solitary, lateral. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.40-0.73 mm wide, 3.5-8.2 mm long, narrowly lanceolate to ovate-lanceolate, gradually tapering to a slender or long filiform, flexuose acumen; habit patent, wide-spreading, to squarrose, similar wet or dry, apices more or less erect spreading when wet. Margins plane, entire to distally entire, serrulate or serrate, with a distinct hyaline border 12-50 µm wide. Costa 36-72 µm at base, subpercurrent, translucent; transverse section elliptic to plano-convex, abaxial and adaxial stereids in 2-4 layers, guides 4, obliquely oriented, with 1-3 bistratose rows of cells in transition to the laminal cells. Juxtacostal cells 5-7 µm wide, 5-24 (29)µm long, quadrate to rectangular, rounded or angular, porose above base or not, chlorophyllose, pluripapillose on abaxial surface, with papillae multifid, low and dense, forming parallel, narrow to broad bands tapering toward costa just above base, sharply defined laterally and basally, adaxial surface smooth. Interior and basal cells 5-7 µm wide, 17-72 µm long, smooth, elongate to linear, tinged, slightly porose or not, inner basal cells often rhomboidal and strongly porose. Marginal cells 2.5-3.6 µm wide, 60-132 µm long, narrowly linear, smooth, hyaline, incrassate. Alar cells 12-24 µm wide, 10-72 µm long, quadrate to rectangular, or elongate marginally, orange to red-brown or hyaline marginally, longitudinally thick-walled; alar region 12-16 cells wide, 5-9 cells long, reaching the costa or not, with a vertical or slightly angled orientation to basal cells, 1-4 rows of isodiametric cells between alar and basal cells,

Dioicous. Perichaetia terminal; perichaetial leaves 0.48-0.81 mm wide, 2.5-6.5 mm long, broadly obovate to elliptic, leaf base clasping to convolute, abruptly contracted to a long, gradually tapering, setaceous, erect or sinuose acumen; basal cells enlarged, thin-walled, hyaline, pale orange to orange-brown, papillae extending to the base of the acumen, alar cells not differentiated. Archegonia 0.80-0.95 mm long, red-brown, +/- 15 per perichaetium, with paraphyses. Perigonia not seen.

Sporophyte monosetous. Capsules immersed (only immature seen). Calyptra mitrate on immature sporophyte (*La Farge-England 5448*, ALTA).

Variation: *Leucoloma chrysobasilare sensu lato* is considerably variable over its East African and Comoran distribution. The leaf length ranges from 3.5 to 8.2 mm long. The longer leaves are more flexuose. The leaf width is also variable, with the Comoran material tending to have a narrower W:L ratio. The hyaline margin width is narrower in the Comoran material and broadest in the specimens from East Usambara Mts. of the African material. The degree of porosity of interior and basal cells varies within a specimen, as well as those specimens having non-porose or porose basal cells. The acumen shows a considerable amount of variation in the serrulation of the margin. The Comoran material typically has small serrulations regularly along the upper margin extending downward from the apex about 1/5 of the leaf length. The African material has a restricted serrulate upper margin not extending as far from the apex or it can be entire. The width of the juxtacostal bands varies from narrow, about 1/3 of the lamina, to more broad, about 2/3. The specimens can vary within the region, although there is a tendency for the African material to have broader juxtacostal bands. The African material is more ramose than the comoran material. The development of rows of more or less isodiametric cells between the basal and alar cells can be variable within a specimen or between specimens from the same locality. There is a trend for the Comoran material to have more rows of isodiametric cells than the African material.

KEY TO THE INFRASPECIFIC TAXA OF *L. CHRYSOBASILARE*

1. Hyaline margin 12-24 µm wide; leaves 5.0-8.2 mm long, acumen long filiform, with 2-4 rows of isodiametric cells between alars and basal cells; endemic to the Comoros . . . . ***L. chrysobasilare* ssp. *chrysobasilare***

1. Hyaline margin 24-50 µm wide; leaves 3.5-5.0 mm long, acumen slender, with 1-2 (3) isodiametric cells between alars and basal cells; distributed in East and South Africa . . . . ***L. chrysobasilare* ssp. *africana***

Leucoloma chrysobasilare* ssp. *chrysobasilare

Plants green, light green, yellow-green or tan. Stems unbranched to branched; sympodial branching from 1-2 subapical innovations, with monopodial branching sparse, solitary, lateral. Leaves 0.4-0.6 mm wide, 5.0-8.2 mm long, narrowly lanceolate to lanceolate, gradually tapering to a long filiform, flexuose acumen. Margins with a distinct, narrow, hyaline border 12-24 µm wide. Costa 38-60 µm at base, subpercurrent; costa transverse section with abaxial and adaxial stereids in 2-3 layers, guides 4, obliquely oriented, with 1-2 bistratose rows of cells in transition to the laminal cells. Alar region with 1-4 rows of isodiametric cells between alar and basal cells.

Sporophyte not seen.

Diagnostic Characters: *Leucoloma chrysobasilare* ssp. *chrysobasilare* is distinguished by 1) its long filiform, chlorophyllose acumen that is distally serrulate to minutely serrate, with a few larger serations at the apex; 2) a subpercurrent costa; 3) juxtacostal bands that are sharply defined by small quadrate to short elongate juxtacostal cells extending from the upper to basal region; 4) lanceolate leaves that have narrow bases (W:L is 1:12.5-13.6); 5) hyaline margins 12-24 µm wide; and 6) alar cells that occasionally produce rhizoids and typically have a vertical orientation to the basal cells, not forming a strongly decurrent region.

Leucoloma procerum Ren., which has previously been treated as conspecific with *L. chrysobasilare* ssp. *chrysobasilare*, is differentiated by its secund, crisped leaf habit, much broader leaf bases (0.7-1.1 mm wide), narrower hyaline margins (5-19 µm), excurrent costa, and an entire or serrulate distal margin. The scalariform alar region is much larger (to 33 cells wide) and lacks any rhizoid development on the alar cells.

The Comoran material of *Leucoloma chrysobasilare* ssp. *chrysobasilare* could be confused with Pacific Ocean material of *L. tenuifolium*. Both have a long, filiform acumen, but *L. c.* ssp. *chrysobasilare* differs by its subpercurrent costa, with dull and green, flexuose apices that are regularly serrulate to serrate distally, opposed to the subpercurrent to long excurrent costa, with glistening, more stiffly spreading apices, that are entire to weakly serrulate distally in *L. tenuifolium*. The basal costa width of *L. tenuifolium* is wider than *L. chrysobasilare* ssp. *chrysobasilare*. Both species have narrow juxtacostal bands of densely papillose cells to the base, and a porose inner basal region. *Leucoloma chrysobasilare* ssp. *chrysobasilare* is distinguished from the Indian - southeast Asian species, *Leucoloma insigne*, by its more slender, caducous leaves, with narrower hyaline margins. Both have long, serrulate to serrate distal acumen.

Variation: There is little variation between populations of the comoran material of *Leucoloma chrysobasilare* ssp. *chrysobasilare*, other than what has been stated above for *L. chrysobasilare sensu lato.*

Habitat: Specimens of *Leucoloma chrysobasilare* ssp. *chrysobasilare* are corticolous on trunk, root, buttress, stump, or sapling substrates, and occur as well as on tree ferns or rock. The species has been recorded from cloud forests, primary or secondary rainforests, some partly cultivated forests or plantations (*Eucalyptus* spp.), on slopes or in canyon habitats. The specimens examined indicate an elevational range of 510-1300 m.

Distribution: *Leucoloma chrysobasilare* ssp. *chrysobasilare* is endemic to the Comoros.

Specimens examined: **COMOROS:** *Magill and Pócs* **[Mayotte]** *11636, 11640, [Anjouan] 11170, 11175, 11206, 11263, 11295, 11321, [***Moheli]** *11685, 11702, 11723, 11743,* **[Grande Comore]** *10985, 11010, 11014, 11024, 11032, 11034, 11039, 11042, 11046, 11049,* (ALTA, MO) *Macé*, 1900 (BR, FH-2 specimens, H-Br, S-3 specimens), *Hildebrandt*, 1875 (S, H-Br).

Leucoloma chrysobasilare **ssp.** ***africana*** La Farge-England ***ssp. nov.***

Type: Tanzania: "East Usambara Mts.: ... submontane rainforests at the border of Kwamkoro and Kwamsambia forest reserves, at 1030 m, 15 Feb. 1987". *K. & T. Pócs 87033/CL.* **Holotype:** ALTA; **isotype:** not seen (? presumably, EGR).

Paratypes: **TANZANIA:** *Iversen, Farkas, Pócs, & Steiner 86244/U, 86244/S* (ALTA); *Pócs, Faden Harris & Csontos 6264/L* (G-2 specimens); *Pócs & Mabberley 6398/X* (G); *La Farge-England 5448* (ALTA, MO, TAN). **SOUTH**

AFRICA: *Bachmann*, 1888 (H-Br), *Reyrich* (H-Br), *Rehmann* (BM-sht. 93).

Dioicous. Plantae ad 6 cm altae. Folia 3.5-5.0 mm longa, ovato-lanceolata, acumen flexuosa, patent ad late patent, margo hyalino 24-50 µm lato. Subspecies haec ab Leucoloma chrysobasilare ssp. chrysobasilare differt folia acumen breviores, lamina ad basim latior, margo hyalino latior, caulis ramosior.

Plants yellow-green or pale tan-green. Stems unbranched to distally ramose; sympodial branching from 1-3 subapical innovations, with monopodial branching sparse, solitary, lateral. Leaves 0.48-0.73 mm wide, 3.5-5.0 mm long, lanceolate to ovate-lanceolate, gradually tapering to a slender, flexuose acumen. Margins with a distinct, hyaline border 24-50 µm wide. Costa 36-72 µm at base, subpercurrent; costa transverse section with abaxial and adaxial stereids in 2-4 layers, guides 4, obliquely oriented, with 1-3 bistratose rows of cells in transition to the laminal cells. Alar region with 1-2 (3) rows of isodiametric cells between alar and basal cells.

Sporophyte monosetous, only immature seen! Calyptra mitrate on immature sporophyte (*La Farge-England 5448*, ALTA).

Diagnostic characters: *Leucoloma chrysobasilare* ssp. *africana* is distinguished by its porose inner basal cells, 1-3 rows of isodiametric cells between the alar and basal cells, and comparatively short, broad leaves (W:L is 1:6.8-7.3) and broader hyaline margins with respect to the type subspecies. Both *L. chrysobasilare* ssp. *africana* and *L. insigne* (Asian species) have broad hyaline margins (36-50 and 60 µm, respectively). *Leucoloma insigne* differs by 1) non-caducous leaves that are slightly wider (0.58-0.85 mm) and longer (4.5-7.0 mm); 2) broader and more densely papillose juxtacostal bands that are not typically tapered at base; and 3) plants that are generally more robust.

Variation: The range of variation among the African specimens shows that 1) the hyaline leaf margin varies 24-50 µm, with the broadest measurements from the East Usambara Mts. material of Tanzania; 2) the length and width of the leaf also varies; again the broadest and shortest material is from the East Usambara Mts.

Habitat: *Leucoloma chrysobasilare* ssp. *africana* is corticolous and is found in lowland, submontane, and montane rainforests. It has also been found in more marginal habitats such as near the border of a forest reserve, in forest fragments within cardamon plantations, and in stands of mixed cultivation. The elevational range of the specimens is from 900-1190 m.

Distribution: *Leucoloma chrysobasilare* ssp. *africana* is distributed along the East African mountain archipelago in Tanzania including the East Usambara Mts., Nguru Mts, N. Uluguru Mts., and South Africa in Pondoland. The specimens cited by Sim (1926) and Magill (1981) from Rhodesia are not *L. chrysobasilare* (see nomenclatural notes above).

Leucoloma* Section *Leucoloma

Type: *Leucoloma bifidum* (Brid.) Brid.

Section *Vittata* Ren., Prod. Fl. Bryol. Madag. 63. 1898, *nom. illeg. incl. typ. sect.*

Subsection *Euvittata* Ren., Prod. Fl. Bryol. Madag. 63. 1898, *nom. illeg. incl. typ. subsect.*

Series *Distincta* Ren., Prod. Fl. Bryol. Madag. 63. 1898, *nom. illeg. incl. typ. ser.*

Section *Euvittata* (Ren.) Ren., Essai Leucoloma 26. 1909. *nom. illeg. incl. typ. sect.*

Nomenclatural notes: Bescherelle (1878) described the first subgeneric taxa of

Leucoloma. *Leucoloma bifidum* was included in Section *Dichelymoidea*. Bescherelle did not designate a type species at the time. In 1898, Renauld published a new infrageneric classification of *Leucoloma* that restricted the concept of section *Dichelymoidea* to a single species, *Leucoloma dichelymoides*. *Leucoloma bifidum* was transferred to a new section, section *Vittata* (= section *Leucoloma*). As type species of the genus, *Leucoloma bifidum*, is the type for section *Leucoloma* .

Plants small to large, with stem erect to downwardly outspreading or pendent. Leaves ovate to lanceolate, erect-spreading to squarrose, with long gradually tapered acumen, flexuose to spirally twisted, or crispate, erect-spreading to squarrose. Juxtacostal bands parallel, extending to the base or just above the base, well defined laterally. Juxtacostal cells pluripapillose with abaxial papillae low, dense, compactly arranged, to papillae distinct and separated, rarely in transverse rows toward the base; adaxial surface smooth or with a few papillae along the distal costa. Basal and interior cells porose or not, with one row of isodiametric cells between alar region and basal cells, or lacking. Alar cells predominantly elongate or rectangular; alar region with a slightly angled orientation toward basal cells. Rhizoids rarely developed on alar cells. Capsules immersed.

Section *Leucoloma*: 13 species

L. bifidum (Brid.) Brid.
L. cinclidiotioides Besch.
L. gracilescens Broth.
L. holstii Broth.
L. lepervancheri Besch.
L. madagascariense La Farge-England
L. nitens (Thwait. & Mitt.) Jaeg.
L. procerum Ren.
L. schelpei P. Varde
L. subbiplicatum Ren. et Card.

L. subchrysobasilare C. Muell. ex Ren.
L. triforme (Mitt.) Jaeg.
L. zuluense Broth. et Bryhn
  L. zuluense var. *ovatum* La Farge-England

Leucoloma bifidum **(Brid.) Brid.** Figures II.25-27

Bryol. Univ. 2: 218, 752. 1827. **Basionym:** *Hypnum bifidum Brid.*, Musc. Rec. 2(2): 51,tab. I, f. 4. 1801. **Type:** "Ex insula Bourbonis, a Commersono allatum mihique a Cel. de lussieu communicatum possideo. Tempus florescentiae et duratio ignota. In omnibus specimenibus quae videre contigit, fructificatio deerat". **Lectotype:** Commerson (L!)(lectotype chosen here!).

Trichostomum bifidum (Brid.) Brid., Musc. Rec. Suppl. 4. 84. 1819.
Leucoloma angustifolium Brid., Bryol. Univ. 2: Suppl. 752. 1827, *nom. illeg. incl. spec. prior.*
Macrodon aubertii Arnott, Mém. Soc. Linn Paris 5: 290. 1827, *nom. illeg. incl. spec. prior.*
Dicranum commersonianum C. Muell., Syn. I: 353. 1849, *nom. illeg. incl. spec. prior.*

Nomenclatural notes: Material in L (!) consists of several delicate stems. *Leucoloma bifidum* is the type species for the genus and thus for the type section *Leucoloma.* It has previously been ascribed to *Leucoloma* subgenus *Taeniodictyon* section *Euvittata.* These subgeneric names are illegitimate since they represent the type subgenus and type section of the genus, and thus are replaced with *L.* subg. *Leucoloma* sect. *Leucoloma.*

Plants small, delicate, to 7 cm tall, in loose tufts of gregarious stems, light green, green or tan, brown below. Stems red, blackened below, non-tomentous, leaves laxly foliate; central strand lacking, outer cortical cells of 2-5 layers, red-brown, thick-walled, inner cortical cells yellowed, larger lumened; sympodial branching from 1-3 subapical innovations, with sparse lateral monopodial branching, solitary. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.33-0.70 mm wide, 2.5-4.5 mm long, lanceolate to ovate-lanceolate, gradually tapering to a long acumen; habit with leaf bases erect-spreading, patent, or wide-spreading, distally flexuose, slightly spirally twisted, or slightly curled when dry, patent to wide-spreading, apices stiffly spreading when wet. Margins plane, entire to distally serrulate, with a distinct narrow hyaline border, 7-24 µm wide. Costa 26-48 µm at base, subpercurrent to excurrent, translucent; transverse section elliptic to plano-convex, abaxial and adaxial stereids in 2-4 layers, guides 4-5, obliquely oriented, with 1 bistratose row of cells in transition to the laminal cells. Juxtacostal cells 5-7 (10) µm wide, 6-24 µm long, subquadrate, oblong to short elongate, chlorophyllose, pluripapillose on abaxial surface, papillae multifid, low and dense or forming distinct transverse rows in the basal region, ending above alar region, sharply defined laterally, diffuse basally, adaxial surface smooth or with scattered papillae along the costa. Interior and basal cells 5-6 µm wide, 17-72 µm long, elongate to linear, smooth, non-porose, tinged. Marginal cells 2.5 µm wide, 132-168 µm long, narrowly linear, smooth, hyaline, thick-walled. Alar cells 7-19 µm wide, 12-48 µm long, quadrate to rectangular, red-brown to hyaline marginally, longitudinally thick-walled; alar region 8-26 cells wide, 4-11 cells long, reaching the costa or not, slightly angled orientation to basal cells, with 1 row of isodiametric cells between alar and basal cells, or lacking.

Dioicous. Perichaetia terminal; perichaetial leaves 0.36-0.48 mm wide, 2.7-4.1 mm long, broad leaf base gradually tapered to a long, setaceous, erect acumen. Archegonia 0.6 0.63 mm long, red-brown, +/- 15 per perichaetium intermixed with paraphyses. Perigonia terminal; perigonial leaves ovate-elliptic bases sharply contracted to a long or short acumen, gradually tapered or rounded at apex, basal portion of leaf orange, basal cells thick-walled and porose; perigonia flask shaped, 0.45-0.5 mm, intermixed with hyaline paraphyses.

Sporophyte monosetous. Seta 0.5 mm long, stout, tan to brown, slightly twisted to right, smooth; vaginula 0.5 mm long. Capsules 0.7 mm long, immersed, oval, brown. Operculum not seen. Peristome 16 asymmetric teeth, long slender, filiform distally, bifid nearly 1/2-3/4 of tooth, 84 -96 µm wide at base, red-brown, PPL external surface smooth at base, papillose distally; IPL internal surface smooth at base, papillose distally. Calyptra not seen. Spores not seen.

Diagnostic Characters: *Leucoloma bifidum* is distinguished by 1) its long, slender, flexuose leaves that are arranged radially; 2) juxtacostal cells that are densely papillose in the upper region and with dense or spaced papillae in the basal region; 3) the differentiated juxtacostal bands extend to the basal region; and 4) the costal transverse section shows a single bistratose row of cells in transition to the laminal cells. *Leucoloma bifidum* is differentiated from *L. mafatense*, a sympatric species, by narrower lanceolate leaves that are less crisped or contorted, a narrower hyaline margin, and narrower juxtacostal cells (5-7 µm wide). Another species that could be confused with *L. bifidum* is *L. zuluense*. The latter is distinguished by having 1) elongate juxtacostal cells throughout the lamina, 2) leaves more densely arranged along the stem, 3) plants more robust and less flexuose, and 4) basal and interior cells porose and longer in length. *Leucoloma madagascariense*, an allopatric species, has smaller, differentiated juxtacostal cells that extend to the alar region as broad bands. Additionally, in transverse section there several rows of bistratose cells between the costa and unistratose lamina.

Variation: The most apparent variation is the papillae ornamentation, which has been a basic source of confusion in identification. The type material, *Commerson* (L!), does not exhibit spaced papillae in irregular transverse rows, as most of the remaining specimens. The SEM micrographs illustrate the variation well (Fig.II.26). The distal leaves of well developed specimens exhibit papillae density from dense, coalescing papillae in the basal portion of the leaf to distinctly spaced papillae in irregular transverse rows. This arrangement of papillae in distinct, transverse rows is characteristic of section *Dichelymoidea* and atypical of the species in section *Leucoloma*. The more elongate cells at the base of the leaf in well developed specimens have papillae that do not cover the entire lumen, but are restricted to the center. *Leucoloma bifidum* is transitional between section *Leucoloma* and section *Dichelymoidea*, with regard to papillae formation. The lack of an enlarged alar region separates it from the species of section *Dichelymoidea*.

Habitat: *Leucoloma bifidum* occurs on roots of *Hymenophyllum* and is corticolous on branches. It has been found along a streamlet habitat and label data indicate an elevation range of 630-750 m.

Distribution: *Leucoloma bifidum* is endemic to the islands of Réunion and Mauritius.

Specimens examined: Réunion: *Chauvet*, iv.9.1895 (JENA, FH); *Crosby & Crosby 8276* (MO), *8916* (L); *De Sloover 17.679*; *Lépervanche* (G); *Piette*, 1886 (NY); *G. de l'Isle 284* (NY); *Lépervanche* (*ex* Hb. Thuret) (NY); *Lépervanche*, iv.9.37 (*ex* Hb. Bescherelle) (M); *Lépervanche*, 1903 (G); *Pócs 9504/BH* (ALTA). **Mauritius:** *Voeltzkow* (H-Br); *Robillard* (G, H-Br).

Leucoloma cinclidiotioides Besch. Figures II.28-29

Ann. Sci. Nat. Bot. sér. 9: 310. 1878. **Type:** "La Réunion: Lépervanche 1876". **Lectotype:** BM! (lectotype chosen here!); **isotypes:** BM!, PC! (Hb. Thériot, Hb. Bescherelle).

Nomenclatural notes: The type specimen in BM is chosen as the lectotype, since the one in Bescherelle's herbarium book in PC is a single stem. Bescherelle's herbarium was obtained by BM, with the exception of stems from the types that were glued into a book at PC for Bescherelle's personal reference.

Plants small sized, to 3 cm tall, in loose tufts, olive-green, to blackish green below. Stems red, blackened below, non-tomentous, leaves radially, densely foliate; central strand lacking, outer cortical cells of 3-4 layers, red-brown, thick-walled, inner cortical cells yellowed, larger lumened; sympodial branching from 1-4 subapical innovations, with lateral monopodial branching, solitary. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.42-0.74 mm wide, 2.0-3.5 mm long, elliptic-lanceolate to lanceolate, tapered to a stout, terete acumen, distally flexuose; habit patent when dry, patent to wide-spreading when wet. Margins plane, entire proximally, roughened by papillose cells distally, serrulate at apex, with a narrow hyaline border ending at base of acumen, 2.5-7.0 µm wide, or lacking. Costa 48-84 µm at base, subpercurrent, translucent below; transverse section elliptic to plano-convex, abaxial and adaxial stereids in 2-3 layers, guides 4, obliquely oriented, with 1-2 (3) bistratose rows of cells in transition to the laminal cells. Juxtacostal cells 5-10 µm wide, 5-19 (29) µm long, subquadrate to subrectangular, irregularly angled, chlorophyllose, pluripapillose on abaxial surface with papillae multifid, low, dense, obscuring cells and forming sharply defined juxtacostal bands to the alar region, adaxial surface smooth. Interior and basal cells 5-7 µm wide, 24-72 µm long, elongate to linear, smooth, non-porose, tinged. Marginal cells 2.5 µm wide, 144-240 µm long, narrowly linear, smooth, hyaline, thick-walled. Alar cells 12-22 µm wide, 12-48 µm long, quadrate to rectangular, red-brown to hyaline at margin, longitudinally thick-walled; alar region 11-16 cells wide, 4-9 cells long, not reaching the costa, slightly angled orientation to basal cells. Perichaetia not seen. Perigonia not seen.

Sporophyte not seen.

Diagnostic Characters: *Leucoloma cinclidiotioides* is characterised by gregarious stems that are naked at the base, elliptic-lanceolate to lanceolate leaves with terete apices that lack a hyaline border distally, dense abaxial papillae that extend to the leaf apex with juxtacostal bands reaching the leaf base, and a very narrow margin 1-3 cells wide. It was originally placed in section *Dichelymoidea* by Bescherelle, and in Section *Obscura* by Renauld (1909). It is transferred to section *Leucoloma*, since it lacks symmetric development of papillae on the abaxial and adaxial surface of the juxtacostal cells. This species is similar to an undescribed species collected from Andringitra in southeastern Madagascar (*La Farge-England 7351* ALTA, MO, TAN). This material differs from *L. cinclidiotioides* in having weakly papillose juxtacostal cells on the abaxial and adaxial surfaces, entire apices that are not papillose to the apex, and a costal transverse section more strongly developed with lateral doubling of the medial guide cells. As well, the leaf shape is typically broader and the acumen is shorter. The rheophytic taxon *L. garnieri* f. *aquaticum*, also from Andringitra, southeastern Madagascar, is distinct from the above two species by having more slender, elliptic leaf bases; smooth laminal cells; and lateral doubling of the guide cells with a reduction of the stereid bands to a single row.

Variation: The development of the bi- to tristratose rows transitional to the laminal cells varies from 2-5 rows. Based on the single collection other variation is difficult to determine.

Habitat: "Rivière au Marsouins" is indicated on the lectotype specimen. This river valley is a "very rich mossy forest, and is called Forêt de Bebour" (Tamas Pócs (EGR) 1996, personal comm.). At the base of the stems there is a mass of rhizoids, lacking any soil or bark, thus the microhabitat is difficult to determine from the available material.

Distribution: *Leucoloma cinclidiotioides* is known only from the type specimen from Réunion, "Rivière au Marsouins".

Specimens examined: *Leucoloma cinclidiotioides* is known only from type material.

Leucoloma gracilescens Broth. Figures II.30-31

Bol. Soc. Brot. 8: 174. 1890. **Type:** "Patria. Ins. S. Thomé, ubi corticem arborum specimina perfecte sterilia legit Fr. Quintas". **Holotype:** H-Br!; **isotypes:** BR!, PC! (2 specimens), S! (2 specimens).

Plants small sized, to 6 cm tall, in loose tufts of gregarious stems, glossy, light green, green or tan, brown below. Stems red, blackened below, non-tomentous, radially, densely foliate; central strand lacking, outer cortical cells of 1-3 layers, red-brown, thick-walled, inner cortical cells yellowed, larger lumened; sympodial branching from 1-4 subapical innovations, monopodial branching scattered, solitary, lateral. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.40-0.75 mm wide, 2.5-4.0 mm long, ovate-lanceolate to lanceolate, gradually tapering to a fine, slender acumen; habit crisped when dry, patent when wet. Margins plane, entire proximally to distally entire or serrulate, with a narrow hyaline border, 2.5-12 (17) µm wide, or lacking. Costa 24-48 µm at base, subpercurrent, translucent; in transverse section elliptic, abaxial and adaxial stereids in 1-3 layers, guides 3-6, obliquely oriented, with 1 bistratose row of cells in transition to the laminal cells, or lacking. Juxtacostal cells 5-10 µm wide, 5-24 µm long, subquadrate, oblong to short elongate, chlorophyllose, pluripapillose on abaxial surface, with papillae multifid, low, forming well differentiated juxtacostal bands that end above the alar region, defined laterally and more gradually at the leaf base, adaxial surface smooth. Interior and basal cells 5-7 µm wide, (24) 48-96 (108) µm long, elongate to linear, smooth, non-porose, tinged. Marginal cells 2.5 µm wide, 132-168 µm long, narrowly linear, smooth, hyaline, thick-walled. Alar cells 12-19 µm wide, 12-38 µm long, quadrate to rectangular, red-brown to hyaline marginally, longitudinally thick-walled; alar region 12-16 cells wide, 6-8 cells long, not reaching the costa, lacking isodiametric cells between alar and basal cells, slightly angled orientation to basal cells.

Dioicous. Perichaetia terminal; perichaetial leaves 0.57-0.70 mm wide, 2.5-3.5

mm long, broadly ovate to elliptic leaf base, gradually or abruptly contracted to a long acumen, bases yellow-orange to orange-brown. Archegonia 0.7-0.75 mm long, red-brown, +/- 20 per perichaetium intermixed with paraphyses. Perigonia not seen.

Sporophyte not seen.

Diagnostic Characters: The distinguishing characters are an extremely narrow margin and broad ovate to ovate-lanceolate, fine, slenderly acuminate, crisped leaves. *Leucoloma gracilescens* is gametophytically similar to *L. lepervancheri*, from which it can be separated by its more robust stature and longer leaves.

Material of *Leucoloma holstii* has been confused with *L. gracilescens*. The former has juxtacostal cells that are smaller, typically quadrate or isodiametric with a dense cell areolation to the base of the leaf. Also the hyaline margins are typically broader, yet material collected by De Sloover from Rwanda and Frahm and Pócs from Zaire have very narrow margins, as in the slender material of *L. gracilescens*. Typically the *L. holstii* material is smaller and has been found with sporophytes. None of the *L. gracilescens* material has been found with sporophytes to date.

Leucoloma zuluense var. *zuluense* has a bowed leaf habit, not tightly crisped as typical *L. gracilescens*, broader hyaline margins varying from 12-24 µm wide, longer leaves 3-5 mm long, with excurrent costa and longer juxtacostal cells, as well the basal cells are porose and reach a length of 120 µm. *Leucoloma zuluense* var. *zuluense* has subpercurrent leaf apices and more variable and broader hyaline margins 12-48 (60)µm. The leaf apices of *L. z.* var. *ovatum* are more stout than in *L. gracilescens* and the leaves are broadly ovate to ovate-lanceolate, with broader hyaline margins. *Leucoloma procerum* as well has a narrow margin and crisped leaves that are longer (4.5-6.0 mm) and broader (0.7-1.1 mm) at the base. The stems are longer as well, to 12 cm. The juxtacostal cells are quadrate and extend to the leaf base as quadrate, small cells. *Leucoloma subbiplicatum* is similar in habit but is much smaller than *L. gracilescens*, with narrower leaves (0.35-0.55 mm), short leaves to 2.5 mm, more stout opaque apices, and very dense, small juxtacostal cells (5-7 µm wide).

Variation: The type material of *L. gracilescens* has leaves that range from ovate to ovate lanceolate. Material from Rwanda and Zaire can have more slender leaves. The hyaline margin can be lacking in some leaves within a specimen or be 12 µm wide.

Habitat: *Leucoloma gracilescens* is a corticolous epiphyte that occurs on branches, trunk of *Syzygium*, stem of *Canthium*, in montane or elfin rainforests between 1950-2500 m.

Distribution: *Leucoloma gracilescens* occurs in equatorial west Africa and east central Africa in western Zaire, Rwanda, and the northern Pare mountains of Tanzania.

Specimens examined: GUINEA EQUATORIAL: (mainland) *Müller B5, B9* (ALTA); **RWANDA:** *De Sloover 12486, 12497, 13745, 18.980* (BR, Hb. De Sloover),*19.038* (Hb. De Sloover), *Frahm 6336, 7982* (Hb. Frahm), *Pócs 6111* (EGR); **TANZANIA: N. Pare Mts.:** *Pócs 90073/K*; **ZAIRE: Mt. Kahuzi:** *De Sloover 12599* (Hb. De Sloover), *Pócs 7838* (EGR).

Leucoloma holstii Broth. Figures II.32-33

Bot. Jahrb. Syst. 20: 178. 1894. **Type:** Tanzania: " Usambara: Lutindi, Hochwald (*Holst n. 3478*), Hochwald bei Tewe Bangorro anderen Moosen eingemischt (*Holst n. 3286* p.p., *3291* p.p.) An Baumrinde." **Lectotype:** *Holst 3478* (H-Br!) (lectotype chosen here!); **isotype:** *Holst 3478* (S!); **syntypes:** *Holst 3286* (BM!); *Holst 3291* (H-Br!) **isosyntypes:** *Holst 3286* (PC!, S!, W!).

Plants small sized, to 3.5 cm tall, in loose tufts, green to pale green or tan distally, brown proximally. Stems red, non-tomentous, densely foliate; central strand lacking, outer cortical cells of 2-4 layers, red-brown, thick-walled, inner cortical cells yellow to hyaline, larger lumened; unbranched to distally ramose, branches fragile, sympodial branching from 1-3 subapical innovations, with monopodial branching as lateral shorter branches. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.34-0.55 mm wide, 1.8-3.0 mm long, ovate-lanceolate to lanceolate, gradually tapering to a stout, short acumen; habit wide-spreading bases with distal portion flexuose to slightly spirally curled , when dry, erect to patent spreading when wet, with apices more or less erect-spreading. Margins plane, entire to distally serrulate, with a distinct, hyaline border 17-36 µm wide. Costa 26-43 µm at base, subpercurrent, translucent, smooth; transverse section elliptic, abaxial and adaxial stereids in 1-2 layers, guides 4-6 obliquely oriented, with 1-3 bistratose rows of cells in transition to the laminal cells or lacking. Juxtacostal cells 5-7 µm wide, 7-14 µm long, quadrate, to rectangular, chlorophyllose, pluripapillose on abaxial surface, with multifid papillae restricted to cell lumen, adaxial surface smooth, forming broad, parallel bands ending just above base, sharply defined laterally. Interior and basal cells 5-7 µm wide, 14-72 µm long, smooth, elongate to linear, tinged, non-porose. Marginal cells 2.5 µm wide, 84-144 µm long, narrowly linear, smooth, hyaline, thick-walled. Alar cells 10-17 µm wide, 12-60 µm long, quadrate to rectangular, paled red-brown to hyaline marginally, longitudinally thick-walled; alar region 13-19 cells wide, 5-8 cells long, not reaching the costa, slightly angled orientation to basal cells.

Dioicous. Perichaetia terminal; perichaetial leaves 0.55-0.65 mm wide, 2.9-3.4 mm long, broadly obovate, clasping leaf base abruptly contracted to a gradually tapering, setaceous, erect acumen, basal cells porose, thick-walled , orange-brown, papillae extending to the base of the acumen. Archegonia 0.6 mm long, red-brown, +/- 15 per perichaetium, with paraphyses. Perigonia terminal; perigonial leaves 0.6-0.7 mm wide, 1.2-3.5 mm long, ovate to ovate lanceolate, abruptly to more gradually tapered to a short or long acumen, with strongly concave bases, erect acumen, basal cells thin-walled hyaline or orange brown, papillae extending to the basal region and progressively less extensive in the shorter perigonial leaves. Antheridia flask shaped, yellow tan, +/- 12 per perigonium, with paraphyses.

Sporophyte monosetous. Seta 0.7-0.8 mm, stout, tan to red-brown, smooth.

Capsules 0.8-1.2 mm long, 0.7 mm wide, immersed, short cylindric, tan to red-brown. Operculum 0.8 mm long, rostrate, erect, red-brown. Peristome 16, asymmetric teeth, bifid to 3/4 of the tooth length, lanceolate, distally slender, basal width 72-77 µm, red-brown. PPL: external surface pitted striate at base, transversely striate mid tooth, distally papillose; IPL: smooth at base, transversely striate mid tooth, to distally papillose. Calyptra mitrate, lobate, whitish yellow to tan below, orange-brown above, smooth to slightly roughened above. Spores 22-26 µm wide, finely granulose.

Diagnostic Characters: *Leucoloma holstii* is a small plant with leaves densely arranged along the stem that are strongly to slightly crisped with blunt, opaque, serrulate apices. The juxtacostal cells are dense, narrow and short (5-7 µm wide, mostly < 14 µm long). The basal cells are predominantly short (< 60 µm long), non-porose, and narrow (5-7 µm wide). The juxtacostal bands are generally broad, 2/3-3/4 of the basal leaf width, with distinct hyaline margins typically 24-36 µm wide.

The closely related species, *Leucoloma schelpei*, which was previously known only from the type specimen in PC, is distinct and has been commonly confused with *L. holstii*. It is a larger taxon with broader hyaline margins, longer leaves, and peristome teeth with a smooth PPL (Table.II.10). The *L. holstii-schelpei* complex may represent a "recent" speciation event, representing minimal divergence. Further research is needed to clarify the relationship, yet I choose at this time to keep the taxa separate based primarily on peristomial differences. *Leucoloma holstii* shares the small dense juxtacostal cell type of *L. madagascariense*, as well as the bistratose transitional cells to the lamina, although the latter character is variable in *L. holstii*.

Variation: *Leucoloma holstii* varies in its degree of crisped leaves. The type material has leaves that are only slightly crisped, whereas most of the material examined has strongly crisped leaves. As well, the bluntness of the apex can vary from almost truncate with serrulations to a more tapered serrulate apex. The width of the leaves is generally lanceolate to slightly ovate-lanceolate, with the tendency to be narrow, opposed to broad as in *L. schelpei*. The juxtacostal cells at the base of the leaf shows some variation in the length, with these cells in some leaves reaching 21 µm.

Habitat: *Leucoloma holstii* is an epiphyte that is corticolous on branches, sapling stems, tree trunks, or on decaying wood in montane and upper montane rainforests, between 860-2200 m elevation.

Distribution: *Leucoloma holstii* is known from the eastern mountains of central Africa in Malawi, Tanzania, and Rwanda.

Specimens examined: TANZANIA: N-Pare Mts.: *Pócs & Mioga 90071/T, 90071/O* (ALTA); **S-Pare Mts.:** *Pócs 89248/M* (ALTA); **Usambara:** *Soul* (H-Br, *ex* PC-Hb. P.Varde, BR), *Pócs et al. 86202/B* (ALTA), *Jones & Pócs 6370/AH* (EGR); **Mt. Kilimanjaro:** *Soul* (PC-Hb. P. Varde), *Pócs 90015/Z* (ALTA); **Nguru Mts.:** *La Farge-England 5481, 5506, 5525* (ALTA, MO, TAN); **Uluguru Mts.:** *Pócs & Lungwecha 6881/V* (EGR); **MALAWI: Mulanje Mts.** *O'Shea M7465a* (E), *Ryvarden 11743* (EGR); **RWANDA:** *De Sloover 12487* (BR).

Leucoloma lepervancheri Besch. Figures II.34-35

Ann. Sci. Nat. Bot. ser. 6, 9: 311. 1878. **Type:** "La Réunion: sommet de la Rivière de Roches, Lépervanche, 1877". **Holotype:** BM! (Hb. Bescherelle).

Leucoloma leptocladum Ren., Rev. Bryol. 28: 90. 1901, *synon. nov.* **Type:** "Hab. Madagascar, in silva Fito Tamatave Jul. 1897 Leg. Perrot". **Lectotype:** PC! (Hb. Renauld)(lectotype chosen here!); **isotypes:** PC!, M!, BR!

Nomenclatural notes: The type material of *Leucoloma lepervancheri* in BM (Hb. Bescherelle) has a label with Bescherelle's handwriting, therefore it is the holotype. No type material was found in PC.

The type specimen of *Leucoloma leptocladum* in PC (Hb. Cardot) agrees with the protologue information having the correct number 25, has *sp. nova* indicated on the label , and shows that it was determined by Renauld, thus is chosen here as the lectotype. The material in PC (Hb. Renauld) differs only by the number 26, which refers to *Leucoloma levieri* in the original publication. This could have been a misnumbering problem, which also is found on the isotype material in M and BR. Thus from the type the material in PC, the specimen in Hb. Cardot is chosen as the lectotype.

Plants delicate, slender, long flexuose to 10 cm tall, in loose tufts of gregarious stems, light green, brown, to dark brown. Stems red, blackened below, non-tomentous, radially laxly foliate; central strand lacking, outer cortical cells of 1-3 layers, red-brown, thick-walled, inner cortical cells yellowed, larger lumened; unbranched or sympodial branching by 1-5 subapical innovations, commonly with sparse, lateral monopodial branching that is solitary, formed by fragile branches. Rhizoids few, restricted to the base of stem or branch, or occasionally on rhizoids, red-brown, smooth.

Leaves 0.35-0.73 mm wide, 2-3 mm long, ovate to ovate-lanceolate, distally tapered to a short, slender acumen; habit slightly crisped, erect-spreading to patent, apices flexuose when dry, erect-spreading or patent, with apices stiffly spreading when wet. Margins plane, entire to distally serrulate, with a narrow hyaline border 2.5-7.0 µm wide, or lacking. Costa 24-48 µm at base, subpercurrent to slightly excurrent; transverse section elliptic, abaxial and adaxial stereids in 1-2 layers, guides 4-6 obliquely oriented, one bistratose row of cells in transition to the laminal cells, or lacking. Juxtacostal cells 5-10 µm wide, 7-36 µm long, subquadrate distally, oblong to elongate proximally, chlorophyllose, bulging, pluripapillose on abaxial surface, with multifid papillae, extending to basal region ending above the alar region, sharply defined laterally, more gradual toward base, adaxial surface smooth. Interior cells 5-7 µm wide, 24-62 µm long, smooth, elongate to linear, non-porose, tinged. Basal cells 5-

7 µm wide, 24-108 µm long, smooth, elongate to linear, non-porose, thick-walled, tinged. Marginal cells 2.5 µm wide, 120-240 µm long, narrowly linear, smooth, hyaline, thick-walled. Alar cells 12-22 µm wide, 12-53 µm long, quadrate to rectangular, red-brown to hyaline marginally, longitudinally thick-walled; alar region 7-13 cells wide, 5-7 cells long, not reaching the costa, lacking isodiametric cells between alar and basal cells, slightly angled orientation to basal cells.

Dioicous. Perichaetia terminal, most often sterile; perichaetial leaves 0.30-0.56 mm wide, 2.7-3.5 mm long, base orange-red brown, broad, clasping to convolute, gradually tapered to a setaceous, erect acumen, distally papillose. Archegonia 0.7 mm, +/- 10 per perichaetium, red brown, paraphyses intermixed. Perigonia not seen.

Sporophyte not seen.

Diagnostic Characters: *Leucoloma lepervancheri* Besch. is distinguished by 1) the long flexuose stems, with secondary branches commonly produced; 2) slightly crisped leaves with the alar region often visible; 3) elongate, bulging, broad juxtacostal cells; 4) a reduced differentiated margin (1-3 cells wide, or lacking); 5) fine, slender, entire to weakly serrulate, flexuose leaf apices; and 6) typically ovate to ovate-lanceolate leaves with the juxtacostal bands ending above the alar region.

It is similar in size and stature to *Leucoloma subbiplicatum*, which is distinguished by 1) its narrower leaf bases; 2) longer, more stout, serrulate, opaque, and distinctly green apices; 3) the juxtacostal bands that extend to the alar region as dense mostly quadrate, papillose cells; and 4) the juxtacostal cells that are quadrate to oblong, not distinctly elongate. The leaf habit is variable in both species from slightly crisped to erect. Another taxon that could be confused with *L. lepervancheri* is *L. zuluense* var. *zuluense*. The latter has a larger stature, a more gradually tapered acumen, a more lanceolate leaf shape, and a broader hyaline margin.

Variation: The material from Rwanda and Zaire has more stout apices than the Mascaren or Madagascan material. The Madagascan material was less branched than either the African or Mascaren material. The leaf shape varied considerably from ovate with a short acumen to ovate-lanceolate with longer acumen. The elongate bulging juxtacostal cells were not apparent in every leaf of each specimen. It is important to examine the mature leaves on the primary axes, since the branch leaves are much reduced in size.

Habitat: *Leucoloma lepervancheri* is corticolous on tree trunks, on *Pandanus* roots, saxicolous on cliffs, and possibly terricolous (*Barclay 620*). Specimens have been found in the heath forests of Rwanda, the dry cental plateau forests of Madagascar, the wet elfin forest of ridges in northeastern Madagascar, and the submontane rainforests of Zaire, within a range of 800-2000 m elevation. It is worth noting that one specimen (*La Farge-England 6359*) had an orchid embedded in it.

Distribution: *Leucoloma lepervancheri* has an African - western Indian Ocean distribution, and was previously considered restricted to Réunion.

Specimens examined: RWANDA: *Pócs 6244* (EGR); **ZAIRE:** *Frahm 7558* (Hb. Frahm); **MADAGASCAR: Prov. Diégo Suarez:** Marojezy: *La Farge-England 6359* (ALTA, MO, TAN); **Prov. Tamatave:** Andasibe: *La Farge-England 5970, 5989, 5996* (ALTA, MO, TAN); **Prov. Tananarive:** *Onraedt 74.M.2228* (Hb. Onraedt); **Prov. Fianarantsoa:** *Onraedt 71.M.5347* (Hb. Onraedt); **RÉUNION:** *Crosby & Crosby 7422* (L), *De Sloover 17.333, 17.673, 17.801* (Hb. De Sloover); **MAURITIUS:** *Barclay 620* (MAUR).

Leucoloma madagascariense La Farge-England ***sp. nov.*** Figures II.36-37

Type: Madagascar: Prov. Tamatave: Andasibe (Perinet), Reserve Forestière, E of Station de "Pisciculture", montane rainforest with shady, wet habitats along stream leading to "lac vert". Canopy reaching 25m, mostly closed, with tall palms and bamboo. 18°54'00"S, 48°25'30"E. elev. 920-980 m. 16.III.90.

Holotype: *La Farge-England 5788*, ALTA; **isotypes:** MO, TAN.

Paratypes: MADAGASCAR: Prov. Tamatave: Andasibe: *La Farge-England 5717, 5720, 5724, 5753, 5757, 5822, 5879, 5895, 5897, 5908, 5979, 5988, 6057* (ALTA, MO, TAN); *Crosby & Crosby 5408* (ALTA, MO); **Prov. Diégo Suarez:** Marojezy: *La Farge-England* 6235, 6264, 6265, 6283, 6295 (ALTA, MO, TAN); **Prov. Fianarantsoa:** Betsitra: *d'Alleisette 97* (H-Br); Ranomafana: *Zavada 583* (ALTA); Reserve Naturelle Integrale d'Andringitra: *Nicoll 282* (MO); Ambohimahasoa: *Onraedt 79.M.0526* (Hb. Onraedt).

Subspecies haec ab L. bifidum differt habitus folii complanatae plerumque, folii squarrosae ad basim, transverse sectione costarum cum 2-4 seriebus bistratosibus cellulibus. Cellulae juxtacostales formans latiories vittas, dense papillosas, opaquas. Apices opaquae, serrulatae, cum costis subpercurrentibus.

Plants small, to 4 cm tall, in loose tufts of gregarious, pendent stems, light green or tan. Stems red, blackened below, non-tomentous; central strand lacking, outer cortical cells of 2-5 layers, red-brown, thick-walled, inner cortical cells yellowed, larger lumened; sympodial branching from 1-4 subapical innovations, with scattered, solitary, lateral monopodial branching. Rhizoids few, restricted to the base of stem or branch or scattered in leaf axils, red-brown, smooth.

Leaves 0.24-0.64 mm wide, 2.0-3.5 mm long, lanceolate to ovate-lanceolate, gradually tapering to a long, slender, subulate acumen; habit with leaf bases squarrose, wide-spreading to patent, distally flexuose, slightly curled to stiffly spreading when dry, patent to wide-spreading, apices stiffly spreading when wet. Margins plane, entire to distally serrulate, with a distinct narrow hyaline border, 7-17 µm wide. Costa 36-48 µm at base, subpercurrent, translucent; transverse section elliptic, abaxial and adaxial stereids in 1-2 layers, guides 4, obliquely oriented, with 1-4 bistratose rows of cells in transition to the laminal cells. Juxtacostal cells 5-6 µm wide, 5-14 µm long, subquadrate to short elongate, chlorophyllose, pluripapillose on abaxial surface, papillae multifid, low and dense, extending to alar region, sharply defined laterally and basally, adaxial surface smooth. Interior and basal cells 5-6 µm wide, 12-53 µm long, elongate, smooth, non-porose, tinged. Marginal cells 2.5 µm wide, 132-168 µm long, narrowly linear, smooth, hyaline, thick-walled. Alar cells 2-14 µm wide, 12-48µm long, quadrate to rectangular, red-brown to hyaline marginally, longitudinally thick-walled; alar region 13-21 cells wide, 5-13 cells long, reaching the costa or not, lacking or with 1 row of isodiametric cells between alar and basal cells, slightly angled orientation to basal cells.

Dioicous. Perichaetia terminal; perichaetial leaves 0.4-0.5 mm wide, 3.0-3.5 mm long, leaf base obovate, abruptly contracted to a long, setaceous, erect acumen. Archegonia 0.6-0.7 mm long, red-brown, +/- 12 per perichaetium, intermixed with paraphyses. Perigonia terminal; perigonial leaves 2.3-7.0 mm long, strongly concave, ovate to ovate lanceolate, basal portion orange brown with thick-walled cells, papillae to the base of the acumen. Antheridia terminal tan, +/- 10 per perigonium, with paraphyses.

Sporophyte monosetous or polysetous. Seta 1 mm long, stout, brown, slightly twisted to right. Capsules 0.5 mm wide, 0.9-1.3 mm long, immersed, short cylindric, brown. Operculum not seen. Peristome 16 teeth, asymmetric, bifid to the base, lanceolate distally slender, 48 µm wide at base, red. PPL: external surface pitted striate at base, distally papillose; IPL: internal surface smooth at base, distally papillose. Calyptra mitrate, red-brown distally, slightly roughened, pale to straw colored below. Spores 24 µm wide, granulose.

Diagnostic characters: *Leucoloma madagascariense* is distinguished by its long slender leaves that are more or less complanate. The leaves have squarrose bases with the acumen mostly stiffly spreading in the dry state. The transverse section of the costa typically has 2-4 bistratose transitional cells to the laminal cells. The juxtacostal bands are broad (>3/4 leaf width) and reach the alar region. The juxtacostal cells are small and densely papillose throughout. Previously *L. madagascariense* has been considered conspecific with *L. bifidum*. For distinguishing characters see the latter species above. *Leucoloma subbiplicatum*, a sympatric species, can be separated by its smaller leaves with shorter apices that are densely and radially arranged along the stem. *Leucoloma zuluense* has broader, elongate juxtacostal cells and more densely arranged, radial leaves.

Variation: There is variation in the leaf length that effects the general habit of the plants. The longer the leaf the more spreading the acumina tend to be, which emphasizes the complanate habit of the leaves.

Habitat: *Leucoloma madagascariense* is corticolous and occurs on exposed or aerial roots, logs, tree or sapling trunks, within 2 meters of the forest floor, in primary and degraded montane rainforests, as well as elfin forests. The elevational range is from 800-1975m.

Distribution: *Leucoloma madagascariense* has a broad distribution in Madagascar, extending from the most northerly point at Diégo Suarez (12°30'S), along the eastern rainforests of Tahiry Nanaharin'i Marojezy (14°28'S), in the Province of Tamatav at Andasibe (Perinet Reserve) forest reserve (18°56'S), and south to the Province of Fianarantsoa at the Ranomafana National Parc and the Reserve Naturelle Intégrale de L'Andringitra (22°10'S). It occurs on the central plateau, which has slighlty drier forests at Ambohimahasoa, just north of Fianarantsoa. The distribution of *L. madagascariense* should be expected throughout the eastern rainforests and mesic-wet forests of the central plateau.

Etymology: The specific epithet refers to the restricted distribution of the species to Madagascar.

Leucoloma procerum **Ren.** Figures II.38-39

Prodr. Fl. Bryol. Madag. 65. 1898. **Type:** "Grand Comorae: *Humblot* 1890". **Lectotype:** PC! (Hb. Cardot, reçu 1891) (lectotype chosen here!); **isotypes:** BM! (sheet 5), E!, FH! (3 specimens), H-Br!, NY! (2 specimens), PC! (Hb. Cardot - 2 specimens, Hb. Thériot), S! (2 specimens).

Dicranum chrysobasilare var. *gracilicaulon* C. Muell., Linnaea. 40: 238. 1876. **Type:** "Patria. Comoro-insula Johanna. 1300 m supra mare, ad truncos arborum, leg. J.M. Hildebrandt # 1838". **Lectotype:** BM! (lectotype chosen here); **isotype:** E!

Leucoloma chrysobasilare var. *gracilicaulon* (C. Muell.) Jaeg., Ber. St. Gall. Naturw. Ges. 1877-1878: 379. 1880.

Leucoloma chrysobasilare spp. *procerum* (Ren.) Broth., Nat. Pfl. 1(3): 324. 1901.

Nomenclatural notes: The lectotype in PC has two numbers: leg. Humblot "1890" and reçu "1891". Most of the duplicates have a single number, without indicating whether it is a collecting number or a date. My interpretation is that "1890" refers to the date that Humblot collected the specimen and "1891" refers to the date that Renauld received the specimen for determination. Therefore, I include all the Humblot specimens with 1890 or 1891 as type material. The specimen, *J.M. Hildebrandt 1842* (NY!), was one of the syntypes originally cited for *L. chrysobasilare* (C. Mueller) Jaeg., and is put in synonymy here.

Plants medium sized, to 12 cm tall, in loose tufts, gregarious stems, light green to green, tan, brown below. Stems red, blackened below, non-tomentous; central strand lacking, outer cortical cells of 3-6 layers, red-brown, thick-walled, inner cortical cells yellow, larger lumened; branching sparse or distally ramose, sympodial branching from 1-3 subapical innovations, monopodial branching, solitary, lateral. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.7-1.1 mm wide, 4.5-6.0 mm long, shiny, membraneous, plane, ovate-lanceolate to broadly ovate-lanceolate, strongly decurrent, gradually tapering to a long, slender to filiform, glistening, flexuous acumen; habit wide-spreading to erect-spreading, secund, crisped to spirally twisted when dry, apices erect-spreading, when wet. Margins plane, entire to distally serrulate, with a distinct narrow hyaline border 5-19 µm wide. Costa 48-60 µm at base, percurrent to excurrent, translucent; transverse section plano-convex, abaxial and adaxial stereids in 2-3 layers, guides 4-5, obliquely oriented, with 1-2 bistratose rows of cells in transition to laminal cells. Juxtacostal cells 5-7 µm wide, 5-17 (29) µm long, subquadrate, oblong, to shortly elongate, rounded or angular, chlorophyllose, opaque, adaxial surface smooth, pluripapillose on abaxial surface, with multifid papillae low and dense, extending to leaf base, thick-walled or not at base, forming parallel bands sharply defined from basal and interior cells. Interior and basal cells 5-7 µm wide, 24-72 µm long, smooth, elongate, tinged, non-porose. Marginal cells 2.5 µm wide, 72-156 µm long, extremely, narrowly linear, smooth, hyaline. Alar cells 12-24 µm wide, 12-60 (84) µm long, quadrate to rectangular, bright red-brown to hyaline, longitudinally thick-walled; alar region 26-33 cells wide, 8-12 cells long, reaching the costa or not, lacking isodiametric cells between alar and basal cells, sharply angled orientation to basal cells.

Dioicous. Perichaetia terminal; perichaetial leaves 0.55-0.96 mm wide, 3.0-6.0 mm long, broadly obovate to orbicular leaf base, clasping to convolute, abruptly contracted to a long, setaceous, erect or sinuous acumen, distally serrulate, porose, basal cells thick-walled, hyaline to orange-brown, papillae extending to the base of the acumen, alar cells undifferentiated. Archegonia 0.87-1.00 mm long, red-brown, -/+ 15 per perichaetium, with paraphyses. Perigonia terminal; perigonial leaves 0.7-0.8 mm wide, 1.5-4.2 mm long, broadly ovate to orbicular bases, concave, abruptly contracted to a long to short setaceous acumen, distally serrate, basal laminal cells longitudinally thick-walled, porose, orange-brown, papillae extending to the base or the acumen, alar cells undifferentiated; Antheridia 0.7-0.8 mm long, tan, on short stalk, +/- 15 per perigonium, with paraphyses.

Sporophyte not seen.

Diagnostic characters: *Leucoloma procerum* is distinguished by 1) the broad, glossy lamina with the enlarged alar region up to 33 cells wide by 12 cells long; 2) the strongly crisped to spirally twisted, secund leaves, distantly arranged on the stem with the strongly decurrent alar region visible; 3) the very fine filiform apices, which have predominantly excurrent costae; and 4) upper margins entire or with a few serrulations. A phenotypically similar species from Madagascar, *L. subchrysobasilare*, shares a very narrow hyaline margin and ovate-lanceolate leaves. In the latter species the leaves are not as wide and are not crisped, but are "bowed", based on the less developed alar region, and the stems are more densely foliate. The transverse section of the costa shows that *L. subchrysobasilare* has laterally doubled guides typically with substereid cells. Distally the leaves are terete, serrulate, and chlorophyllose.

Leucoloma procerum is placed is a different section than *Leucoloma chrysobasilare*, based primarily on the basal and alar cell types. The latter species is more slenderly foliate, with the alar region vertically oriented to the basal cells and with several rows of isodiametric cells between the basal and alar region. For differentiation from *L. gracilescens*, see the latter.

Variation: The width of the leaves varies from 0.7-1.1 mm. The alar region varies from 26-33 cells wide, and is typifically deep red-brown. The long fine apices can be excurrent versus subpercurrent.

Habitat: *Leucoloma procerum* is corticolous and occurs on trunks, logs, or vines in primary montane rainforests or cloud forests, with an elevation range 600-1860 m.

Distribution: *Leucoloma procerum* is endemic to the islands of Grande Comore and Anjouan in the Comoros, 11°50'-12°12'52" S.

Specimens examined: COMOROS: *Humblot s. loc.* (JENA, PC, W - 2 specimens); **Anjouan:** *Hildebrandt 1842* (NY as *L. chrysobasilare* C. Muell.), *Hildebrandt* (BR-Hb. Boissier), *Magill & Pócs 11059a, 11222, 11146* (ALTA, MO); **Grande Comore:** *Humblot* (BM, FH, G, H, S - 4 specimens).

Leucoloma schelpei P. Varde Figures II.40-41

Rev. Bryol. Lichénol. 26: 4. 1957. **Type:** Mozambique: "Hab.: Gorongosa Mtn. 5.600 ft. on streamside boulders in deep forest shade"; *Schelpe 5574*, 6.7.1957. **Holotype:** PC! (Hb. P. Varde).

Plants medium sized, to 4 cm tall, flexuose, in loose tufts, green to light or pale yellow green distally, brown proximally. Stems red, blackened below, non-tomentous, densely foliate; central strand lacking, outer cortical cells of 3-5 layers, red-brown, thick-walled, inner cortical cells yellow to hyaline, larger lumened; unbranched to distally ramose, branches fragile, sympodial branching from 1-3 subapical innovations, with monopodial branching lateral. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.35-0.65 mm wide, 3.0-4.0 mm long, ovate-lanceolate, gradually tapering to a slender acumen with a stout apex; habit patent to wide-spreading to somewhat bowed at bases, with distal portion flexuose to slightly spirally curled or when dry, erect to patent spreading when wet with apices more or less erect-spreading. Margins plane, entire to distally serrulate, with a distinct, hyaline border abruptly tapered at base, 17-64 µm wide. Costa 29-60 µm at base, subpercurrent, translucent, smooth; transverse section elliptic, abaxial and adaxial stereids in 1-3 layers, guides 4-6, obliquely oriented, some lateral doubling, with 1-4 bi- or rarely multistratose rows of cells in transition to the laminal cells or lacking. Juxtacostal cells 5-7 µm wide, 5-17 µm long, subquadrate, oblong to short elongate, chlorophyllose, pluripapillose on abaxial surface, with multifid papillae restricted to cell lumen, adaxial surface smooth, forming parallel bands ending at the alar region, sharply defined laterally. Interior and basal cells 5-6 µm wide, 17-74 µm long, smooth, elongate to linear, tinged, non-porose to slightly porose, lengthening toward margins at base. Marginal cells 2.5 µm wide, 84-132 µm long, narrowly linear, smooth, hyaline, thick-walled. Alar cells 12-22 µm wide, 12-72 µm long, quadrate to rectangular, red-brown to hyaline marginally, longitudinally thick-walled; alar region 11-20 cells wide, 5-7 cells long, not reaching the costa, slightly angled orientation to basal cells.

Dioicous. Perichaetia terminal; perichaetial leaves 0.5-0.6 mm wide, 3.0-3.5 mm long, broadly obovate leaf base, clasping, abruptly contracted to a gradually tapering, setaceous, erect acumen, basal cells enlarged, thin-walled, pale orange-brown, papillae extending to the base of the acumen. Archegonia 0.8-0.9 mm long, red-brown, +/-10 per perichaetium, with paraphyses. Perigonia not seen.

Sporophyte mono- or polysetous. Seta 0.5-1.0 mm long, stout, smooth, opaque tan; transverse section with cell wall thickenings restricted to the single, outermost cells. Capsules 0.9-1.1 mm, immersed, globose, ovoid, or short cylindric, light to dark brown. Operculum rostrate, erect. Peristome 16, asymmetric teeth, 72-96 µm wide at base, 0.4-0.6 mm long, bifid, and distally filiform. PPL: smooth at base, obliquely striate mid portion, and distally scattered papillae; IPL smooth below, distally papillose. Calyptra 1.0-1.5 mm long, mitrate, lobed, hyaline to straw colored below, orange-brown above. Spores 19-29 µm, granulose.

Diagnostic Characters: *Leucoloma schelpei* has ovate-lanceolate, crisped leaves, with small juxtacostal cells (5-7 µm wide) that reach the alar region; often stout apices that are serrulate; broad hyaline margins; and a peristome with a smooth basal PPL. *Leucoloma zuluense* differs by wider (to 10 µm) and longer (to 36 µm) juxtacostal cells and the peristome basal PPL surface faintly to distinctly pitted striate. As well, the leaves tend to be broader and longer. *Leucoloma holstii* is similar to *Leucoloma schelpei* with a crisped habit, but is smaller with shorter leaves and the PPL ornamentation is pitted striate at the base (see Table II.10).

Variation: There is variation in the width of the hyaline margin ranging from 24-60 µm. The leaf apex can vary from serrulate to entire.

Habitat: *Leucoloma schelpei* occurs on tree trunks, in mixed evergreen forests, and wet montane rainforests, between 1500-2050 m.

Distribution: *Leucoloma schelpei* is restricted to Mozambique and Zimbabwe in mainland Africa.

Specimens examined: ZIMBABWE - Inyanga: *Eyles 2635a* - J.S. Henkle Aug. 1920, *Eyles 2624* - J.S. Henkle Aug. 1920 (PRE), *Eyles 2624/A* (SRGH), *Müller 2628, 2640,* (L, PRE), *2612* (PRE), *2638, 2640* (L); **Umtali:** *Müller 2528, 2586, 2602* (L, PRE) *2578* (PRE).

Leucoloma subbiplicatum Ren.et Card. Figures II.42-43

Bull. Soc. Roy. Bot. Belgique 33(2): 109. 1895. **Type:** "Hab. Madagascar: Diégo Suarez: (*Chenagon*). Bourbon, *sine loco* (*G. de l'Isle*, 1875, in herb. Mus. Par.)". **Lectotype:** *Chenagon* PC! (Hb. J. Cardot) (lectotype chosen here!); **isotypes:** PC! BR!; **syntype:** *G. de l'Isle* (not seen).

Leucoloma subbifidum Ren., Prodr. Fl. Bryol. Madag. 64. 1898. **Type:** "Madagascar: Dans e trajet de Fianarantsoa à Mananjary, Dr. Besson, 1891". **Holotype:** PC!

Leucoloma squarrosulum ssp. *subbiplicatum* (Ren.et Card.) Broth., Nat. Pflanzenfam. 1(3): 34. 1901.

Leucoloma forsythii Thér., Bull. Mus. Hist. Nat. (Paris) 29: 457. 1923. **Type:** "Madagascar: Ambohimitombo, Tanala, alt. 1350-1440 m. (leg. Dr. Forsyth Major, ex hb Levier)", section *Euvittata*. **Holotype:** PC! (Hb. Thériot); **isotype:** PC!

Nomenclatural notes: Type material of a purportedly closely related species *Leucoloma squarrosulum* has not been seen. An illustration has been found in PC, but is not determined as the type at this time. Thus the relationship of *L. squarrosulum* and *L. subbiplicatum* is not resolved. *Leucoloma squarrosulum* is the earlier name than *L. subbiplicatum*, if they are conspecific.

Plants small, delicate, to 3 cm tall, in loose tufts of gregarious stems, pendent, light green to green distally, light or brown below. Stems red, blackened below, non-tomentous, radially and densely foliate, unbranched or distally ramulose, innovations common; central strand lacking, outer cortical cells of 2-3 layers, red-brown, thick-walled, inner cortical cells yellowed, larger lumened; sympodial branching by 1-6 subapical innovations, with monopodial branching sparse, solitary, lateral, branches slender and fragile. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.35-0.55 mm wide, 1.5-2.5 mm long, ovate-lanceolate to lanceolate, gradually tapering to a stout, opaque acumen; habit erect-spreading to patent, distally flexuose when dry, erect-spreading or patent, with apices stiffly spreading when wet. Margins plane, entire to distally serrulate, with a narrow hyaline border 2.5-7 µm wide, or lacking. Costa 29-36 µm at base, subpercurrent; transverse section elliptic, abaxial and adaxial stereids in 1-2 layers, guides 4-6 obliquely oriented, one bistratose row of cells in transition to the laminal cells, or lacking. Juxtacostal cells 5-7 µm wide, 6-26 µm long, subquadrate to oblong, elongate, chlorophyllose, pluripapillose on abaxial surface, with multifid papillae prominent, dense, extending to leaf base, sharply defined laterally and basally, adaxial surface smooth. Interior cells 5-7 µm wide, 24-72 µm long, smooth, elongate to linear, slightly porose, tinged. Basal cells 5-7 µm wide, 24-89 µm long, smooth elongate to linear, slightly porose or not, thick-walled, tinged. Marginal cells 2.5 µm wide, 132-168 µm long, narrowly linear, smooth, hyaline, thick-walled. Alar cells 12-22 µm wide, 12-48 µm long, quadrate to rectangular, red-brown to hyaline marginally, longitudinally thick-walled; alar region

7-13 cells wide, 3-6 cells long, not reaching the costa, lacking isodiametric cells between alar and basal cells, slightly angled orientation to basal cells.

Dioicous. Perichaetia terminal on primary and secondary axes; perichaetial leaves 3.2-5.2 mm wide, 1.6-3.3 mm long, base broad, clasping to convolute, gradually tapered to a setaceous, erect acumen. Archegonia +/- 13 per perichaetium, red-brown, paraphyses intermixed. Perigonia not seen.

Sporophyte mono- or polysetous. Seta 0.6-1.2 mm long, short and stout, slightly twisted toward the right, red-brown, smooth. Operculum not seen. Capsules immersed (only immature seen). Calyptra mitrate (only immature state seen).

Diagnostic Characters: *Leucoloma subbiplicatum* is distinguished by 1) its small stature, 2) densely foliate stems, 3) the short (< 2.5 mm), non- to slightly crisped leaves that are radially arranged, 4) reduced hyaline margin (1-3 cells, or lacking), and 5) a relatively stout, serrulate, opaque acumen. It is closely related to *L. madagascariense*, which differs by longer, complanate leaves with broader hyaline margins; in transverse section of the costa there are one to several bistratose rows in transition to the laminal cells. *Leucoloma lepervancheri* is similar in size to *L. subbiplicatum*, but is distinguished by the broader, less dense, more elongate juxtacostal cells; the more broadly ovate to ovate-lanceolate leaves with slender, glistening apices; and longer stems. Within *L. lepervancheri* there is a distinct lack of fertile material, whereas perichaetia are easily found within specimens of *L. subbiplicatum*. The cell areolation distinguishes *L. subbiplicatum* from *L. bifidum* of Réunion, which has more distally arranged leaves along the stem, and papillae in the basal portion of the leaf that are often arranged in irregular transverse rows.

Variation: The size of the plants are consistently small to minute. The secondary branches have smaller leaves than the main axes. The degree of branching varies within and between specimens.

Habitat: *Leucoloma subbiplicatum* is corticolous on branch, sapling or tree trunk substrates within 2 m of the forest floor. It has also been found on bark of rotting logs. It occurs in primary or logged montane rainforests, ranging from 920-1010 m in elevation.

Distribution: *Leucoloma subbiplicatum* is known from the central eastern primary and logged montane rainforests of Madagascar. A broader distribution is expected with further collections.

Specimens examined: MADAGASCAR: Prov. Tamatave: Andasibe: *La Farge-England 5727, 5732, 5767, 5782, 5810, 5812, 5868, 5890, 5907, 5919, 5920, 5969, 5993, 6024, 6031, 6056, 6055, 6065* (ALTA, MO, TAN); **Prov. Diégo Suarez:** Marojezy: *La Farge-England 6366A* (ALTA, MO, TAN)

Leucoloma subchrysobasilare C. Muell. ex Ren. Figures II.44-45

Prodr. Fl. Bryol. Madag. 65. 1898. **Type:** "Madagascar: Monts Ankaratra, *Borgen* (hb. Kiaer); région supérieure des fôret à Ambondromba, *Rev. Talazac* 1894" (= *L. subtuberculosum* Ren.). **Lectotype:** *Borgen*, PC! (Hb. Cardot) (lectotype chosen here!); **isotypes:** BM! (2 specimens), H-Br!, L!, PC! (Hb. Cardot, Hb. Thériot), S!

Nomenclatural notes: In the original protologue two specimens were cited. In the notes following the description Renauld (1898) designated the Borgen specimen as the basis for the description. By 1915, Renauld and Cardot no longer cite Rev. Talazac 1894 as a specimen typifying *L. subchrysobasilare*, but transfer it to the specimen citations for *L. ochrobasilare*. The isotypes of *L. ochrobasilare* (*Rev. Talazac* 1894, S! and PC! - Hb Cardot, with Renauld's handwriting) are intermixed with stems of *L. subchrysobasilare*. *Leucoloma subchrysobasilare* is the dominant material in both packets, thus perpetuating the confusion with the concept of *L. ochrobasilare*. Of the three Borgen specimens found in PC (Hb. Cardot - 2, Hb. Thériot), the one with Renauld's handwriting was selected here as the lectotype. In Renauld and Cardot (1915), *Leucoloma subchrysobasilare* is described "*pro parte*" (Borgen), and *Leucoloma subchrysobasilare* "*pro parte*" (Talazac) was synonymised with *L. ochrobasilare*. This has caused confusion for identifying specimens.

Plants small to medium sized, to 7 cm tall, in loose tufts, pale green to yellow-green, tan, or brown, dull, not glossy. Stems erect or curved at apex, densely foliate; outer cortical cells of 3-5 layers, red-brown, thick-walled, inner cortical cells yellow, larger lumened; sparsely to distally branched, sympodial branches from 1-3 subapical innovations, monopodial branches solitary, lateral.

Leaves 0.35-0.68 mm wide, 2.5-4.0 mm long, concave proximally, subtubulose, narrowly ovate-lanceolate to lanceolate, gradually tapering to a terete acumen, apex multistratose; habit erect-spreading to squarrose basally, apices flexuous, falcate-secund when dry, erect to patent with erect-spreading apices when wet. Margins plane, entire or serrulate distally, with an indistinct, narrow, hyaline border 2.5-12.0 µm wide. Costa 36-48 µm at base, subpercurrent to short excurrent; transverse section elliptic, abaxial and adaxial stereids in 1-2 layers, substereids or lateral doubling of guides, guides 4-5, obliquely oriented, with 1-2 rows of bistratose transitional cells to laminal cells. Juxtacostal cells 5-7 µm wide, 5-17 (26) µm long, subquadrate, oblong, to shortly elongate, rounded or angular, chlorophyllose, pluripapillose on abaxial surface, multifid papillae, centered over lumen, extending to leaf base, sharply defined from basal and interior cells, adaxial surface smooth. Interior cells 5-7 µm wide, 15-55 µm long, smooth, elongate, tinged, porose or not. Basal cells 5-7 µm wide, 17-72 µm long, smooth, elongate, tinged, porose, narrowing toward margin. Marginal cells 2.5 µm wide, 108-168 µm long, narrowly linear, smooth, hyaline. Alar region 14-18 cells wide, 6-8 cells long, not reaching the costa, slightly angled orientation to basal cells, not strongly decurrent.

Dioicous. Perichaetia terminal; perichaetial leaves 0.6-0.7 mm wide, 3.0-3.5

mm long, decreasing in length toward antheridia, obovate to elliptic leaf base, convolute, abruptly contracted to a stiff, setaceous, erect acumen, basal cells enlarged, thin-walled, orange-brown, papillae extending to the base of the acumen, alar cells not differentiated. Perigonia terminal; perigonial leaves 0.46-0.65 mm wide, 1.0-2.3 mm long, ovate or obovate to ovate lanceolate, bases abruptly contracted to a short or long acumen, strongly concave, basal cells enlarged, thin-walled, orange to red brown.

Sporophyte mono- or polysetous. Seta 0.5-1.2 mm long. Capsules 1.0-1.2 mm long, immersed, oval to shortly cylindric, light to reddish-brown. Operculum rostrate, erect, red-brown to blackish red-brown. Peristome 16 teeth, 0.5 mm long, basal width 52-72 µm, asymmetric, bifid, split nearly to base, distally filiform, red-brown, commonly curved into urn; PPL surface pitted striate basally, gradually becoming obliquely striolate medially to papillose distally; IPL surface smooth basally, papillose distally. Calyptra mitrate, lobate, hyaline to pale yellow, or tan below, dark brown above, smooth to slightly roughened above, on mature capsule covering operculum and uppermost portion of urn. Spores 20-24 µm, finely granulose.

Diagnostic Characters: *Leucoloma subchrysobasilare* is easily recognised by 1) its "dull" appearance, 2) extremely narrow or absent hyaline margin, 3) the "bowed", non-crisped, somewhat secund leaves, 4) densely foliate stems obscuring the alar cells, 5) short leaves, 3-4 mm long, 6) acumen terete distally, and 7) costal transverse section typically with lateral substereids. From *L. zuluense*, it lacks the broader hyaline margin, has the substereid cells in transverse section of the costa, a more slender costa, and the leaf length range of *L. zuluense* is greater, 3-5 mm. *Leucoloma gracilescens* is strongly crisped and has finer, more slender apices. *Leucoloma procerum* has much broader leaf bases, which have distinctly decurrent, bright red-brown, large alar regions that are visible on the stem because of distantly arranged leaves. *Leucoloma ochrobasilare* is distinguished from *L. subchrysobasilare* by 1) papillae developed on both surfaces, 2) the substereid development in the costa transverse section lacking, 3) strongly spirally twisted leaves, 4) a larger developed alar region, and 5) elliptic to broadly ovate-lanceolate leaves. From *L. gracilescens*, *L. subchrysobasilare* is distinguished by its terete distal acumen, more slender leaves, and falcate-secund leaf habit.

Variation: There is variation in the robustness of the plants. The branching pattern varies from appearing unbranched with single subapical innovations to ramose, with multiple distal branches from 2-3 subapical innovations. The ramose stems have the branches at close intervals.

Habitat: *Leucoloma subchrysobasilare* is corticolous and occurs on branches or tree trunks in degraded or primary montane, humid, sclerophyllous forests or humid rainforests. The habitats include somewhat exposed sites, including closed forests (e.g., on scrubby south facing hill, on moist south facing valley, on trees at roadside). The elevation range is 1300-2060 m.

Distribution: *Leucoloma subchrysobasilare* occurs on the central plateau from the forest reserve at Ankaratra, to Reserve Naturelle Integrale in central Madagascar, and to Andringitra in the south, in humid sclerophyllous forests. As well, it occurs in the humid rainforests of the eastern domain from Maroantsetra (15°26'S) to Ranamafana (21° 14'S) of Madagascar.

Specimens examined: MADAGASCAR: Prov. Tananarive: Ankaratra: *Crosby & Crosby 5239* (ALTA, L, MO), *5249A* (MO), *5267* (MO), *6666* (ALTA, L, MO), *6674* (ALTA, L, MO); *Cremers 1748* (Hb. Onraedt); *Tixier 9425, 9532, 9534, 10074, 10075, 11435* (ALTA, PC); **Prov. Fianarantsoa:** Ranomafana: *Crosby & Crosby 6973* (MO); Ambatofitorahana: *Onraedt 70.M.0413, 71.M.5313* (*in parte*), *70.M.5314*, (Hb. Onraedt). Ambondromoba: *Rev. Talazac 1894* (H-Br *in parte*, male plants!); Andringitra: *Nicoll 280* (MO).

Leucoloma zuluense Broth. et Bryhn. Figures II.46-49

Forh. Vidensk.- Selsk. Christiania 1911 (4): 6 (1911). **Type:**: South Africa: "Ekombe. In sylva Ntingwe ad truncum infinum arboris mense; Titlestad s. n.; Julio anni 1907". **Holotype:** *Titlestad* (H-Br!); **isotype:** PC! (Hb. Thériot).

Leucoloma woodii Rehm. et MacOw. *ex* Wag., ***synon. nov.***, Trans. Roy. Soc. South Africa : 2. ic. 1914. **Type:** type not designated. **Lectotype:** *Wager 189* PRE! (lectotype chosen here!).
Leucoloma bifidum var. *tanganikae* P. Varde & Thér., ***synon. nov.***, Bull. Soc. Bot. France 87: 354. 1940. **Type:** Tanzania: "Hab.: Tanganika Territory, Ululu Gebirge,alt. 2100m. 12.xi.1932, leg. Schlieben". **Holotype:** PC! (Hb. Potier de la Varde, #7675); **isotype:** PC! (Hb. Thériot).

Nomenclatural Notes: Dr. A. Rehmann published Exsicc. Musci Austro-Africani, 1875-1877, which included the first reference to *L. woodii sp. nov.* as a *nomen nudum*. Wager's original description was based only on the sporophyte (Wager 1914) . He made reference to Rehmann and Mac Owan's naming and placement of the species in a new genus that was based only on foliage. No reference was made to an original description, and one has not been seen. Wager (1914) made no reference to the original type material or type locality in his sporophyte description, nor did he cite a specimen for his sporophyte material, although he did illustrate it. From Wager's description my interpretation is that he had seen new material that provided previously undescribed sporophytic characters. It is deduced that the material was not the Rehmann exsiccate material #444.

Dixon and Gepp (1923), in "Rehmann's South African mosses", explained that no list of the exsiccate was ever published and that the exsiccate was issued in two sets. The second set, including #444, was issued in or before 1886. Therefore, Dixon and Gepp (1923) published the list that included: "444 *Leucoloma woodii* Rehm. et Mac Owan *n. sp.* c. fr.! Transvaalia: ad truncos arborum vetustorum in mont.

Lechlaba. R.". Although Dixon and Gepp cite a particular specimen for *Leucoloma woodii*, as part of Rehmann's herbarium collection and part of the exsiccate, Rehmann and Mac Owan's name has no validity. Therefore the name *L. woodii* is typified here as a Wager's name, *L. woodii* Rehm. & Mac Ow. ex Wager and *Wager 189* (PRE) specimen is chosen as the lectotype.

Plants small to medium, to 7 cm tall, flexuose in loose tufts or as gregarious stems, light to yellow-green, or tan. Stems red, blackened below, non-tomentous, somewhat laxly foliate; central strand lacking, outer cortical cells of 2-5 layers, red-brown, thick-walled, inner cortical cells yellow to hyaline, larger lumened; unbranched to distally ramose, branches fragile, sympodial branching from 1-7 subapical innovations, with monopodial branching lateral, fragile. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.4-0.95 mm wide, 2.3-5 mm long, ovate-lanceolate to lanceolate, gradually tapered to a long slender acumen; habit patent to wide-spreading, "bowed" with flexuose to slightly crisped acumen often spirally twisted when dry; habit leaves stiffly patent to wide-spreading when wet. Margins plane, entire below, entire or serrulate distally, with a distinct hyaline border, 12-48 (60) µm wide. Costa 36-50 µm wide at base, subpercurrent to excurrent, smooth, translucent; transverse section with 4-6 guide cells, typically obliquely oriented, with 1-2 bistratose rows of cells in transition to the laminal cells or lacking, abaxial and adaxial stereid layers 1-3. Juxtacostal cells 5-10 µm wide, 7-36 µm long, isodiametric, oblong to elongate, chlorophyllose, pluripapillose with abaxial, papillae multifid confined to the cell lumen, forming parallel bands ending above the alar region, sharply defined laterally. Interior and basal cells 5-10 µm wide, 14-120 µm long, elongate, smooth, tinged, thick-walled, porose to non-porose. Marginal cells 2.5 µm wide, 72-180 µm long, linear, hyaline, thick-walled. Alar cells 7-24 µm wide, 12-84 µm long, quadrate to rectangular, orange-red brown, scalariform, oriented obliquely toward basal laminal cells; alar region 13-22 cells wide, 5-9 cells long, strongly decurrent, not reaching the costa, isodiametric transitional cells between basal and alar cells lacking.

Dioicous, or rarely autoicous. Perichaetia terminal; perichaetial leaves 0.44-0.75 mm wide, 1.5-4.2 mm long, bases convolute, obovate, abruptly tapering to a long stout acumen. Archegonia 0.70-0.95 mm, red brown, 10-15 per perichaetium, intermixed with numerous paraphyses, hyaline, unicellular. Perigonia terminal; perigonial leaves 1-3 mm long, 0.8-0.85 mm wide, ovate-lanceolate to ovate with abruptly narrowing, short or long acuminate apices, strongly concave, orange to red-brown basally. Antheridia not seen.

Sporophyte mono-or polysetous. Seta 0.7-1.0 mm long, stout, smooth, opaque, tan; transverse section with cell wall thickenings restricted to the outer wall of the epidermal layer. Capsules 0.6-1.0 mm long, immersed, ovoid to short cylindric, light to dark brown. Operculum rostrate, erect. Peristome 16 teeth, 48-96 µm wide at base, 0.55 mm long, asymmetric, bifid, distally filiform; PPL pitted striate below, obliquely striate mid portion, and distally scattered papillae; IPL smooth below, distally papillose. Calyptra 1.5 mm long, mitrate, lobed, hyaline to straw colored below, orange-brown above. Spores 21-24 µm, minutely granulose.

Diagnostic Characters: Few specimens have been named *Leucoloma zuluense* since it was put into synonymy with *Leucoloma chrysobasilare* var. *gracilicaulon* (Sim 1926, Magill 1981). *Leucoloma woodii* was the most common name used for the *L. zuluense* material. It is easily distinguished from *Leucoloma chrysobasilare* by its strongly developed alar region in which the cells are at a distinct angle to the basal cells, and the several (up to 4) rows of isodiametric cells between the elongate basal cells and the alar cells are lacking. As well, the acumen is shorter and less flexuose than in *Leucoloma chrysobasilare*. *Leucoloma procerum* (synonym = *L. chrysobasilare* var. *gracilicaulon*) is a more robust plant with an excurrent costa, broader leaf bases (to 1.1 mm wide), narrower (5-7 µm wide) juxtacostal cells, and a larger alar region (to 33 cells wide).

Leucoloma zuluense is a highly variable species which is characterised by having oblong to elongate juxtacostal cells that are predominantly 7-10 µm wide, with a length to 24 or rarely 36 µm long. The hyaline margin is variable in width, mostly between 24-36 µm, yet having a range of 12 to 48 µm. The juxtacostal bands weaken at the base of the leaf just above the alar region, with the cells becoming smooth and more elongate. The gametophytic characters overlap with *L. schelpei* at one end of the variation and *L. gracilescens* at the other end (Table II.10). The diagnostic characters differentiating *L. zuluense* from *L. schelpei* are the pitted-striate PPL surface of the peristome, the juxtacostal bands grading into the basal cells above the alar region, the thicker walled juxtacostal cells that are mostly 7-10 µm wide, and the bowed to slighlty crisped leaf habit. *Leucoloma zuluense* is differentiated from *L. gracilescens* by broader hyaline margins (12-48 µm wide) and more slender apices.

The type specimens of *L. bifidum* var. *tanganikae*, included here within the concept of *L. zuluense*, have slightly more elongate juxtacostal cells (36 µm); an excurrent costa; a more slender acumen that is entire or with a few serrulations; narrower hyaline margins (12 µm), and linear and porose basal cells.

Variation: The hyaline margin width is highly variable from 12-48 µm wide, the acumen is either entire or serrulate at the apex, and the costa is either excurrent or subpercurrent. The variation can be present within a specimen or between specimens. This variation may reflect the highly variable climatic conditions that exist within the range of the species (Pócs 1976). Further studies using molecular techniques may reveal whether there is any genetic basis for the morphological variation. A single exception to the dioicous condition of *L. zuluense* was found in the autoicous specimen, *Crosby & Crosby 13,184* (MO).

Distribution: *Leucoloma zuluense* is distributed throughout the East African mountain archipelago of Kenya, Tanzania, Zimbabwe to the Transvaal, Venda, and Natal regions of South African.

KEY TO THE INFRASPECIFIC TAXA OF L. ZULUENSE BROTH.

1. Leaves ovate-lanceolate to lanceolate, 2.8-5.0 mm long, 0.38-0.84 mm wide; acumen long, slender, entire or serrulate; costa excurrent or subpercurrent; hyaline margin 12-48 µm wide .... *L. zuluense* var. *zuluense*

1. Leaves ovate to broadly ovate-lanceolate, 2.3-3.5 mm long, 0.53-0.95 mm wide; acumen short, stout, mostly entire to finely serrulate; costa subpercurrent; hyaline margin 12-24 µm wide .... *L. zuluense* var. *ovatum*

L. zuluense* var. *zuluense

Leaves 0.38-0.84 mm wide, 2.8-5.0 mm long, ovate-lanceolate to lanceolate, gradually tapered to a long, slender acumen; habit patent to wide-spreading bases, distally flexuose, "bowed" non to slightly crisped, or spirally twisted when dry, erect to patent spreading when wet. Margins plane, entire to distally serrulate, with a distinct, hyaline border 12-36 (48) µm wide. Costa in transverse section with 1(2) bistratose rows of cells in transition to the laminal cells, or lacking. Juxtacostal cells 7-10 µm wide, 10-36 µm long, oblong to elongate, rounded, chlorophyllose, abaxial surface pluripapillose, with multifid papillae, low and dense, adaxial surface smooth, that extend to the basal region.

Habitat: *Leucoloma zuluense* var. *zuluense* is corticolous on twigs of shrubs, branches, saplings, or tree trunk bases less than 1-2 m above forest floor, or it occurs on decaying logs or rocks. It is found in montane or elfin rainforests between 1580-2450 m.

Specimens examined: SOUTH AFRICA: Natal: *van Rooy 105* (PRE); **Transvaal:** *Crosby & Crosby 13,410, 7722* (PRE), *von Breitenbach 217a* (PRE), *Sim 236* (PRE), *Wager 54* (PRE); **Venda:** *van Rooy 766* (PRE); **Zululand:** *Dr. F. Wilms.* (H-Br).

TANZANIA: Kilimanjaro: *La Farge-England 5321, 5355, 5357, 5380, 5385, 5387* (ALTA, MO, TAN), *Jones & Pócs 6351/U* (EGR), *6352/AQ* (EGR), *6359/Z* (PRE); **Meru:** *A.J.& E. Sharp 7766/A* (EGR); **S. Pare Mts.:** *Pócs 89248/AD* (ALTA); **N. Pare Mts.:** *Pócs 86206/B, 90071/S, 90072/M, 90073/R* (ALTA), *Pócs &Mioga 90073/T* (EGR); **Nguru Mts.:** *La Farge-England 5557, 5603, 5609, 5638, 5641*; **Uluguru Mts.:** *Crosby & Crosby 13,410* (MO), *Crosby & Crosby 7276* (L), *7229* (MO, L), *13,184* (MO), *Pócs 6914/K, 6578/AM, 86142/AQ, Pócs 6232* (EGR); *Pócs & Csontos 6072/BA* (EGR); *Pócs & Nichimbi 6285/CM, 6285/V* (EGR); *Pócs & Gibbon 6052/AG* (EGR); *Schliechen* (PC); **S. Uluguru Mts.:** *Pócs 6418/AR, 6824/I (EGR), 88110/J* (ALTA dupl); **Ukaguru Mts.:** *Pócs 6742/L* (EGR); *Pócs, Chamshama, Sylvander 86100/AH* (ALTA); *Pócs, Puff, Krisai, & van Zanten 86142/H* (ALTA); **W. Usambara Mts.:** *Brenan M.1600* (ALTA), *Pócs & Farkas 86206/B* (ALTA); **KENYA: Mt. Kenya:** *Pócs & Faden 6603/* ? (EGR). **ZIMBABWE: Inyanga:** *Henkel* Aug.1920 (PRE - Sim 10143), *Müller 2648* (PRE, L).

Leucoloma zuluense* var. *ovatum La Farge-England ***var. nov.***

Type: Tanzania: "Ukaguru Mts. N. of Kilosa. Narrow strip of mossy forest on SSW slope of Mamiwa range range below Mnyera peak 1950-2050 m, Pócs and Mabberley 6742/L, 30.July.1972". **Holotype:** EGR!

Paratype: TANZANIA: Kilimanjaro: *La Farge-England 5371* (ALTA); **Nguru Mts.:** *La Farge-England 5540* (ALTA, MO, TAN); **S. Pare Mts.:** *Pócs 89249/*N (ALTA); **Uluguru Mts.:** *Pócs 6426/C, Pócs and Harris 6172/J* (EGR), *Pócs et al. 6076/BB* (L), *6123/E* (G); **COMOROS:** *Magill & Pócs 11284* (ALTA, MO).

Varietas haec differt ab typo varietate ab folii robustioribus sed brevioribus et latioribus, acumen brevior, marginem hyalinam angustior.

Leaves 0.53-0.95 mm wide, 2.3-3.5 mm long, ovate to ovate-lanceolate, gradually tapering to a short, stout acumen; habit patent to wide-spreading bases, distally flexuose, crisped, or slightly spirally twisted when dry, erect to patent spreading when wet, with apices more or less erect-spreading. Margins plane, entire to distally serrulate, with a distinct, hyaline border 12-26 µm wide. Costa in transverse section elliptic, with 1 bistratose row of cells in transition to the laminal cells, or lacking. Juxtacostal cells 7-10 µm wide, 7-36 µm long, subquadrate, oblong to elongate, rounded, chlorophyllose, pluripapillose on abaxial surface with multifid papillae that end in the basal region, adaxial surface smooth. Dioicous.

Sporophyte not seen.

Diagnostic Characters: *Leucoloma zuluense* var. *ovatum* is distinguished by its broad, ovate to ovate-lanceolate leaves (to 0.95 mm wide); shorter leaves (to 3.5 mm long); and more stout acumen. The Tanzanian material of *Leucoloma holstii* also has short leaves, yet differs by the following characters: 1) the juxtacostal cells are smaller (5-7 µm width) and mostly quadrate; 2) the papillose juxtacostal cells form parallel bands that reach the alar region; and 3) the apices are opaque, somewhat truncate, and serrulate.

Variation: There is some variation in the leaf length and width, and hyaline margin width.

Habitat: *Leucoloma zuluense* var. *ovatum* is epiphytic and corticolous on lianas, fallen logs, roots, and tree buttress with an elevation range of 950-2200 m.

Distribution: Specimens of *Leucoloma zuluense* var. *ovatum* have been found in montane rainforests of the eastern mountain archipelago in Tanzania and on Anjouan in the Comoros.

Etymology: The varietal epithet refers to the ovate leaf shape.

Leucoloma* Section *Obscura (Ren.) Ren., Essai Leucoloma 27. 1909.

Basionym: *Leucoloma* series *Obscura* Ren., Prod. Fl. Bryol. Madag. 63. 1898.

Lectotype: *L. sanctae-mariae* Besch. (lectotype chosen here!)

Leaves ovate-lanceolate to elliptic-lanceolate, with acumen gradually or abruptly tapered, slender or stout. Juxtacostal bands opaque, parallel. Juxtacostal cells narrow, 5-7 µm wide, pluripapillose, with low, dense, papillae equally developed on the adaxial and abaxial surface. Interior and basal cells forming narrow membranous lamina. Alar cells predominantly elongate or rectangular, with a slightly angled orientation toward basal cells. Capsules immersed, emergent or shortly exserted. Rhizoids not developed on alar cells.

Section *Obscura*: 3 spp

L. sanctae-mariae Besch.
L. thraustum Besch.
L. thuretii Besch.

Leucoloma sanctae-mariae Besch. Figures II.50-51

Ann. Sci. Nat. Bot. sér. 6, 9: 311-312. 1878. **Type:** "Madagascar: Du Petit-Thouars (hb. Mus. Par.); Bernier (hb. Thuret); Sainte-Mariae de Madagascar: sur le tronc des arbes, dans les parties les plus sombres et les plus humides de la forêt de Lafondrou, décembre 1849, Boivin, no. 1580 (hb. Mus. Par.)". **Lectotype:** *Boivin*, BM! (Hb. Bescherelle, sheet # 30) (lectotype chosen here!); **isotypes:** BM! (sheet #29), BR!, H-Br!, M!, S!; **syntypes:** *Bernier, Du Petit-Thouars*, BM! (Hb. Bescherelle (sheet #30).

Trichostomum leucoloma Schwaegr., Spec. Musc. Suppl. 2(1):76. 122. 1827, *synon. nov*. **Type:**"Lectum in Madagascar a cl. Aubert du Petit

Thouars.4". **Holotype:** G! (Hb. Hedwig-Schwaegr.).

Nomenclatural notes: Based on the original syntypes, *Leucoloma sanctae-mariae* is lectotypified here. In 1827, Schwaegrichen described *Trichostomum leucoloma* and put *Hypnum bifidum* Brid. in synonymy with it. Since then, *Trichostomum leucoloma* has been treated as a synonym of *Leucoloma bifidum* in the literature. The type specimen of *T. leucoloma* in G (!) is *Leucoloma sanctae-mariae*, not *L. bifidum* (Brid.) Brid. Therefore, even though "*leucoloma*" is the earliest specific epithet for the taxon, it would be an invalid tautonym within *Leucoloma.*

Plants medium sized, to 12 cm, in loose tufts or as gregarious stems, horizontally to downwardly out-spreading, glaucous to pale green, tan to light brown. Stems red to blackened, densely foliate, caducous below; central strand lacking, outer cortical cells 2-5 layers, red-brown, thick-walled, inner cortical cells, yellow to tan, larger lumened; sympodial branching from 1-2 subapical innovations. Rhizoids smooth, red-brown, restricted to the base of stem or branch; tomentum rare, scattered, papillose or smooth.

Leaves 0.4-0.8 mm wide, 2.5-4.5 mm long, concave, ovate-lanceolate, gradually tapering to a slender, subulate, flexuose apex; habit of leaf bases squarrose, distally erect or incurved. Margins entire to subentire below, serrulate at apex, with a broad hyaline border 48-77 µm wide, widest at mid-leaf; Costa translucent, subpercurrent to percurrent, 29-60 µm above the base; transverse section plano-convex, abaxial and adaxial stereid bands of 2-3 layers, guide cells 4, oblique, with 1-3 rows of bistratose cells between the costal and laminal cells. Juxtacostal cells 5-6 µm wide, 5-10 µm long, isodiametric to short elongate, thicker walled in basal region, obscure, pluripapillose, with low, multifid, abaxial and adaxial papillae, forming broad, opaque, parallel bands extending to just above the base. Interior cells 5-7 µm wide, 12-50 (58) µm long, rectangular to elongate, smooth, tinged, slightly porose, restricted to a narrow band between the juxtacostal cells and the marginal cells. Marginal cells

2.5-3.5 µm wide, 168-288 µm long, linear, hyaline, smooth. Alar cells 12-19 µm wide, 12-72 µm long, quadrate to rectangular, red-brown, marginal cells often hyaline, flat, longitudinally thick-walled; alar region 12-14 cells wide by 4-6 cells long, not reaching the costa.

Dioicous. Perichaetia terminal; perichaetial leaves 0.6-0.8 mm wide, 2.0-4.0 mm long, broadly ovate to cordate lanceolate, abruptly narrowed to long, acuminate, setaceous apex, erect, leaf bases broad, clasping, convolute, distally papillose, to base of acumen. Archegonia 0.7-0.9 mm long, red-brown, 20-40 per perichaetium, intermixed with hyaline paraphyses. Perigonia terminal; perigonial leaves 2.5-3.5 mm long, broadly rounded, concave, cordate-ovate base with abruptly narrowing, short, acuminate, setaceous apices, erect. Antheridia 0.6-0.7 mm long, yellow-brown, intermixed with hyaline paraphyses.

Sporophyte mono- or polysetous. Seta 2.5-3.0 mm long, stout, slightly twisted toward the right, opaque, orange-tan, smooth. Capsules 1.5-2.0 mm long, emergent to exserted, ovoid to shortly cylindric, light to dark brown. Operculum conic to shortly rostrate, roughened above, yellow-tan below, orange-brown above. Peristome 16 teeth, red-brown, asymmetric, bifid nearly to base, distally filiform; PPL surface smooth to roughened below, gradually becoming striate mid-tooth to papillose-striate distally; IPL surface smooth at base, irregularly striate becoming striate-papillose distally. Calyptra mitrate, broadly lobate (2-4 lobes), hyaline or pale yellow to tan below, orange-brown above, smooth to slightly roughened above. Spores 24-31 µm, finely granulose.

Diagnostic Characters: *Leucoloma sanctae-mariae* is easily distinguished by its broad, opaque, juxtacostal bands which occupy most of the lamina and reach the leaf base. These chlorophyllose bands form a sharp contrast with the broad, hyaline, marginal bands at mid-leaf. The tinged interior cells are restricted to the basal portion of the leaf. The squarrose leaf habit with distally erect apices, combined with the above characteristics, distinguish this taxon.

Leucoloma thuretii, a closely related species that shares the squarrose leaf habit and opaque juxtacostal bands, can be easily separated from *L. sanctae-mariae* by its stout, terete apex and narrow hyaline margins. A mono- versus polysetous condition, initially used to separate the taxa, is not valid.

Variation: Based on the specimens examined, there is some variation in the fineness of the apices. Fruiting specimens show both monosetous and polysetous perichaetia. The occurrence of tomentum on a single specimen indicates the rarity of the feature (*La Farge-England 6284*, ALTA). The clustered tomentum develops from the smooth, red-brown rhizoids.

Habitat: *Leucoloma sanctae-mariae* is corticolous on branches, saplings, and tree trunk bases, and has been collected on the stem of *Tabernaemontanum longituba* Pichon. It also occurs on fallen logs. It is found less than 1 meter above the forest floor in lowland to montane rainforests. The elevation range of the specimens is from sea level to 1050 m.

Distribution: *Leucoloma sanctae-mariae* is restricted to the eastern rainforests of Madagascar, with localities ranging from 14°28' S at Tahiry Nanaharini'i Marojezy, to 17°16'S at Forest Reserve at Tampolo, Nosy Sainte Marie, to Sakana, 19°28' S.

Specimens examined: MADAGASCAR: *Arbogast 103* (BM, FH, H-Br, S, W), *Perrot 39* (M, S), *Schatz, Lowry II, & Floret 2365* (MO), *Voeltzkow* (H-Br), *Crosby & Crosby 5435* (MO), *Du Petit-Thouars* (G), *LaFarge-England 6015, 6157, 6166, 6171, 6188, 6201, 6229, 6233, 6275, 6284*, 7183 (ALTA, MO, TAN) ,*Tixier 7087, 7810, 10454, 10455, 10303* (ALTA, PC).

Leucoloma thraustum Hampe ex Besch. Figures II.52-53

Ann. Sci. Nat. Bot. sér. 6, 9: 317. 1878. **Type** "Linn., XXXVIII p.209, sub

Dicrano. Madagascar: "Alamazantraskoven, Borchgrevink". **Lectotype:** BM! (Hb. Hampe)(lectotype chosen here!); **isotypes:** BR!, PC! (Hb. Renauld, Hb. Thériot).

Dicranum (Leucoloma) thraustum Hampe, Linnaea 38: 209-210. 1874. *hom. illeg.*

Leucoloma silvaticum Ren., Prodr. Fl. Bryol. Madag. 66. 1898. *synon. nov.* **Type:** "Madagascar: zone des forêts: forêt d'Analamazaotra, Cambouė et Campenon." **Lectotype:** PC! (Hb. Cardot)(lectotype chosen here!); **isotypes:** BR! PC! (Hb. Thériot), S!

Leucoloma sanctae-mariae var. *leptolimbatum* Ren., Suppl. Prodr. Fl. Bryol. Madagascar 16. 1909 *synon. nov.* **Type:** "Madagascar: Forêt de Ambohimitombo: Dr. Forsyth Major. (Hb. Levier)". No type seen.

Nomenclatural notes: *Leucoloma thraustum* had been placed in subgenus *Taeniodictyon* section *Euvittata* (Renauld & Cardot 1915, Brotherus 1924). Based on opaque, parallel, juxtacostal bands that are composed of cells with equally developed abaxial and adaxial papillae, it is transferred here to section *Obscura.*

From the available isotypes from Bescherelle's herbarium material in BM, the specimen that includes the original handwritten description and has Hampe's herbarium indicated on the label is chosen here as the lectotype (sheet #18). The type locality, Alamazantraskoven [sic] is Analamazoatra, Prov. Tananarive. No type material of *Leucoloma sanctae-mariae* var. *leptolimbatum* was seen in PC. From the description I tentatively placed it in synonymy with the concept of *L. thraustum.*

Plants small to medium sized, to 6 cm long, in loose tufts, stems horizontal to pendulous, out-spreading, glaucous to light green (tan to light brown below). Stems blackened distally red, densely foliate; central strand lacking, outer cortical cells 3-4 layers red-brown, thick-walled, inner cortical cells larger lumened, yellow to tan;

sympodial branching from 1-4 subapical innovations below gametangia. Rhizoids smooth, red-brown, restricted to the base of stem or branch.

Leaves 0.4-0.8 mm wide, 2.0-3.5 mm long, concave, ovate lanceolate, distally incurved, tapering gradually to a stout, acuminate, entire serrulate apex; habit crisped to falcate-secund with acumen erect to flexuose, slightly spirally twisted, bases squarrose to wide-spreading when dry, patent to wide-spreading when dry. Margins entire below, distally subentire to serrulate at apex, with a narrow hyaline border 10-29 µm wide. Costa translucent, subpercurrent to shortly excurrent, 36-48 (60) µm at base; transverse section plano-convex, abaxial and adaxial stereid bands of 2-3 layers, guides 4, obliquely oriented, with 1-3 rows of bistratose (or multistratose) cells in transition to the laminal cells. Juxtacostal cells 5-7 µm wide, 5-12 µm long, isodiametric, quadrate to elongate, rounded to irregularly angular, progressively thicker-walled in basal region, chlorophyllose, obscure, pluripapillose by low, multifid, abaxial and adaxial papillae, forming broad, opaque, parallel bands extending to just above the base, sharply differentiated from the smooth interior and basal cells proximally and from the hyaline marginal cells distally. Interior and basal cells 5-7 µm wide, 12-50 µm long, thick-walled, smooth, elongate, slightly porose or not, tinged (chlorophyllose in fresh specimens). Marginal cells 2.5-3.5 µm wide, 72-168 µm long, linear, hyaline, smooth, shiny. Alar cells 12-17 µm wide, 12-60 µm long, quadrate to rectangular, becoming elongate marginally, scalariform, flat, red-brown, marginally hyaline, lumen granulose; alar region 10-22 cells wide, 5-10 cells long, not reaching costa or rarely reaching the costa on one side.

Dioicous. Perichaetia terminal; perichaetial leaves 0.7-0.8 mm wide, 3.0-4.0 mm long, broadly obovate to elliptic lanceolate base with tapered acumen, stiffly erect-spreading, bases strongly concave and clasping, with enlarged, yellow-brown to orange-brown cells, upper cells isodiametric, with abaxial and adaxial papillae, chlorophyllose, forming differentiated juxtacostal extending from the apex to the base of the acumen, alar cells not differentiated. Margins entire to subentire, plane. Costa 36-48 µm wide at base, excurrent. Archegonia 0.7 mm long, red brown, numerous, +/-

30, intermixed with numerous hyaline uniseriate paraphyses. Perigonia terminal; perigonial leaves 0.65-0.7 mm wide, 1-2 mm long, broadly ovate to obovate with short acumen or with a longer abruptly contracted acumen.

Sporophyte monosetous. Seta 0.8 mm long, stout, smooth, opaque tan. Capsules 1.2 mm long, immersed, short cylindric, brown. Peristome not seen intact. Operculum not seen. Calyptra not seen. Spores not seen.

Diagnostic Characters: *Leucoloma thraustum* is recognised by 1) its small stature, 2) crisped leaves that have opaque, parallel, juxtacostal bands extending to the basal region, 3) juxtacostal cells with abaxial and adaxial papillae, 4) a narrow hyaline border, and 5) immersed capsules. It is closely related to *L. sanctae-mariae*, but the latter is more robust, has a broader hyaline margin (48-77 µm wide), and an exserted capsule. *Leucoloma thuretii* shares a similar combination of characters as *L. thraustum*, but differs by having a more stout, shorter acumen with a subpercurrent to percurrent costa, and an exserted capsule.

Variation: Among the specimens examined there is considerable variation in the extent of the juxtacostal bands in the basal region. Some leaves have the bands reaching the alar region, while others have them ending well above the alar region. This character in particular may have been the rationale for Renauld assigning it to section *Euvittata* (= section *Leucoloma*).

Habitat: *Leucoloma thraustum* is corticolous on sapling trunks (to 7 cm in diameter), within 1.5 m from the forest floor. It occurs in montane rainforests between 800-980 m.

Distribution: *Leucoloma thraustum* is endemic to the eastern, montane rainforests of Madagascar.

Specimens Examined: MADAGASCAR: *Cremers 3154, 3152* (Hb. Onraedt), *Crosby and Crosby 6784* (ALTA, L, MO), *La Farge-England 5785* (ALTA, MO, TAN), *Tixier 10553* (ALTA, PC).

Leucoloma thuretii Besch. Figures II.54-55

Ann. Sci. Nat. Bot. sér. 6, 9: 312. 1878. **Type:** "Madagascar: Bernier, no. 30 (Hb. Thuret)". **Lectotype:** BM! (Hb. Bescherelle - Hb. Thuret, sheet #17)(lectotype chosen here!); **isotypes:** BM! (Hb. Bescherelle - no. 6! (sheet #17), s.n. (sheet #16)), BR! (*ex* Hb. Thuret), PC! (Hb. Cardot).

Nomenclatural notes: From the available type specimens with capsules in Bescherelle's herbarium, the specimen with "hb. Thuret" and without a number indicated is chosen as the lectotype, since the other specimen has the wrong number (#6). No specimen was found with #30 indicated.

Plants medium sized, 2-4 cm tall, in loose tufts, pale yellow green to tan above, brown below. Stems red to blackened, densely foliate; central strand lacking, with 2-4 layers of thick-walled, red-brown, outer cortical cells; unbranched or distally ramose, sympodial branching from 2-3 subapical innovations. Rhizoids few, restricted to the base of stem or branch, red-brown, smooth.

Leaves 0.5-0.9 mm wide, 2.2-3.5 mm long, broadly elliptic-lanceolate to slightly ovate-lanceolate, abruptly narrowed to a stout broad acumen with an obtuse to rounded apex; habit with leaf bases squarrose, distally erect to incurved apices when dry, erect-spreading to patent when wet. Margins entire to serrulate or weakly serrate distally, with a narrow hyaline border, 7-22 µm wide. Costa 48-60 µm wide at base, subpercurrent, translucent; transverse section plano-convex, abaxial stereids in 2-4 layers, adaxial stereids in 2-3 layers, guides 4, oblique, with some lateral doubling, with 2-5 bi- or multistratose rows in transition to laminal cells. Juxtacostal cells 6-7 µm wide, 5-12 µm long, rounded quadrate to rectangular, or irregularly angular, progressively longer and thick-walled toward base, chlorophyllose, pluripapillose, obscured by low multifid papillae on abaxial and adaxial surfaces, forming opaque, parallel bands extending to the leaf base. Interior and basal cells 5-7 µm wide, (17) 28-60 (96) µm long, elongate, smooth, non- to slightly porose, tinged, restricted to a narrow band between juxtacostal cells and marginal cells. Marginal cells linear, hyaline, smooth. Alar cells 10-24 µm wide, 26-72 µm long, quadrate to rectangular, flat, equally or longitudinally thick-walled, red-brown, marginally hyaline; alar region 9-16 cells wide, 5-6 cells long, not extending to costa.

Dioicous. Perichaetia terminal, sessile; perichaetial leaves 0.7-1.0 mm wide, 3.0-3.7 mm long, base broad, obovate, clasping to convolute with an abruptly narrowed acumen, stiffly erect, stout, basal region yellow to orange-brown. Archegonia 0.75-0.8 mm long, red-brown, +/- 15 per perichaetium intermixed with paraphyses. Perigonia not seen.

Sporophyte monosetous or polysetous. Seta short, stout, 1.5-2.0 mm, light brown, smooth; transverse section with a single outer cortical layer slightly thickened. Capsules 0.9-1.5 mm long, emergent to slightly exserted, globose, oblong to short cylindric, dark brown. Operculum not seen. Peristome 16, asymmetric teeth, bifid, split to 1/2 to 2/3, distally filiform, strongly incurved distally in dry state; PPL smooth at base, distally striate-papillose mid tooth, distally papillose, IPL smooth at base, striate-papillose mid tooth, to papillose distally. Calyptra dark brown above, reddish brown below, enveloping immature sporophyte (single example seen, still immersed in perichaetial leaves). Spores 22-31 µm wide, granulose.

Diagnostic Characters: *Leucoloma thuretii* is differentiated by 1) the opaque juxtacostal bands occupying most of the lamina; 2) papillae restricted to cell lumen; 3) stout, serrulate to weakly serrate apex, with the papillose cells ending just below the apex; 4) emergent to exserted capsules; and 5) narrow hyaline marginal bands. It is closely related to *L. thraustum*, which is differentiated by its smaller habit, finer apices, and mostly narrower leaves. The acumen of *L. thraustum* is more gradually tapered to the apex, in which the costa is often shortly excurrent. In the original description, Bescherelle distinguished *L. sanctae-mariae* from *L. thuretii* by the polysetous condition and "globuleuses tronquees". The isotype of *L. thuretii* in BM (Hb. Bescherelle, # 6, sheet #17) has the polysetous condition and the capsules are oblong to short cylindric, and thus are not distinguishing characters.

Variation: Between the type specimen, available type duplicates, and the specimens of Fr. M. Onraedt, the width of the hyaline margin can vary from 7 to 12 µm in one specimen to 12-22 µm in another. The apices vary from entire to weakly serrulate, and the degree of stoutness varies.

Habitat: *Leucoloma thuretii* occurs on granitic rocks or is corticolous on shrubs. The limited specimens available indicate an elevation range of 1450-1700 m.

Distribution: *Leucoloma thuretii* is endemic to the east-central rainforests of Madagascar.

Specimens examined: **MADAGASCAR:** *Onraedt 71.M.5218, 70.M.0569* (Hb. Onraedt).

Leucoloma **Section** ***Attenuata*** Ren., Prod. Fl. Bryol. Madag. 69. 1898.

Lectotype: *Leucoloma seychellense* Besch. (lectotype chosen here!)

Subgenus *Sphenodictyon* Ren., Rev. Bryol. 28: 86. 1901. **Lectotype:** *Leucoloma seychellense* Besch. (lectotype chosen here!)

Leaves lanceolate to elliptic-lanceolate, with acumen gradually or abruptly tapered, slender or stout, fragile or not. Juxtacostal bands opaque, often rugose, tapered toward the costa. Juxtacostal cells narrow, 5-7 µm wide, pluripapillose, papillae low, dense, multifid, equally developed on the adaxial and abaxial surface. Interior and basal cells forming broad membraneous lamina. Alar cells predominantly elongate or rectangular, with a obliquely angled orientation toward basal cells; alar region enlarged. Capsules immersed. Rhizoids not developed on alar cells.

Section *Attenuata*: 5 species

L. crosbyi La Farge-England
L. grandidieri Ren. & Card.
L. membranaceum La Farge-England
L. seychellense Besch.
L. talazaccii Ren. & Card.

Leucoloma crosbyi La Farge-England Figures II.56-57

Novon 2: 119-122. 1992.**Type:**"Madagascar, Diégo Suarez: Montagne d'Ambre, Parc National, 10 km along trail between Petit Lac and Grand Lac, 12° 34' S, 49°12'E, 13.xi.1972, 1200m, Crosby and Crosby 7167". **Holotype:** MO!; **isotype:** ALTA!

Paratypes: MADAGASCAR: Diégo Suarez: Montagne d'Ambre, Parc National, 10 km along trail between Petit Lac and Grand Lac, 12° 34' S, 49°12'E, 13.xi.1972, 1200m, *Crosby and Crosby 7170* (MO); Montagne d'Ambre, Parc National, 0-5 km along trail between Petit Lac and Grand Lac, 12° 34' S, 49°12'E, 12.xi.1972, 900-1100m, *Crosby and Crosby 7304* (L).

Plants robust, to 5 cm tall, erect to spreading, pale to glaucous green or tan to light-brown, in loose tufts. Stems red, non-tomentose, densely foliate; central strand lacking, outer cortical cells of 3-5 layers, red-brown, thick-walled, inner cortical cells, yellow to tan, with larger lumen; unbranched or branched, distally ramose, sympodial branching 1-3 subapical innovation. Rhizoids smooth, red-brown, restricted to the base of stem or branch.

Leaves 0.7-1.2 mm wide, 4.0-6.5 mm long, narrowly ovate-lanceolate to lanceolate, plane to slightly concave below, slightly transversely rugose or not in medial region, gradually tapered to a long, subtubulose, non-rugose acumen; habit distally flexuose to slightly incurved when dry, below erect-spreading to wide-spreading wet or dry, erect-spreading above when wet. Margins plane, entire to serrulate distally, with distinct, narrow, hyaline border 10-17 µm wide ending below apex. Costa 53-106 µm wide at base, subpercurrent, translucent; in transverse section plano-convex to elliptic, abaxial and adaxial stereids in 3-5 layers, guides 4-6 cells, occasionally doubling, with 2-6 (9) bi- to multistratose rows of cells in transition to laminal cells. Juxtacostal cells 5-7 µm wide, 5-12 µm long, irregularly quadrate, rounded to oblong, opaque, pluripapillose, with low multifid papillae on abaxial and adaxial surfaces, extending to the basal region, tapered as a narrow v-shaped wedge, sharply delimited from smooth interior cells. Interior and basal cells 6-11 µm wide, 24-132 µm long, elongate to linear, non- to strongly porose, smooth, tinged, forming a broad scarious laminal region. Marginal cells 2.5 µm wide, 168-204 µm, narrowly linear, hyaline, smooth. Alar cells 12-34 µm wide, 12-72 µm long, quadrate to rectangular, flat, scalariform, longitudinally thick-walled, red brown; alar region 11-17 cells wide, 6-8 cells long, not reaching the costa.

Dioicous. Perichaetia terminal; perichaetial leaves 0.75-1.10 mm wide, 2-6 mm long, leaf bases clasping convolute, broadly ovate-lanceolate, sharply contracted to long, narrow, acuminate to aristate, flexuose apex; alar cells not differentiated; basal cells strongly porose, yellow-brown to orange-brown. Archegonia 0.8-1.4 mm long, red-brown, numerous, 20-28 per perichaetium, with paraphyses intermixed; Perigonia terminal, or terminal on short subapical branches, 1-4; perigonial leaves 0.9-1.6 mm long, convolute, ovate with abruptly narrowing, short, acumen, basal region yellow to yellow-orange. Antheridia 0.8 mm long, red-brown to yellow-brown, intermixed with numerous hyaline paraphyses.

Sporophyte mono- or polysetous (1-4). Seta 1.0-2.0 mm long, stout, smooth, opaque, orange-tan. Capsules 0.9-1.5 mm long, immersed, ovoid to oblong, light brown to tan. Operculum conic with flanged base. Peristome 16 teeth, asymmetric, bifid, red-brown, bases commonly reflexed, distally erect or incurved, filiform distally, inserted well below rim, trabeculae strongly developed on inner surface; PPL surface smooth at base, to striolate-papillose or papillose distally; IPL surface smooth at base, papillose-striolate to papillose distally. Calyptra mitrate, broadly fringed to lobate (7-20 lobes), hyaline or pale yellow to tan below, orange-brown above, smooth to slightly roughened above. Spores 24-31 µm, finely granulose.

Diagnostic Characters: *Leucoloma crosbyi* is distinguished by its 1) robust habit; 2) erect- to wide-spreading leaves; 3) a membraneous lamina, sharply differentiated from the narrow juxtacostal band; 4) a juxtacostal band not to slightly rugose, formed by opaque, densely papillose cells, that tapers toward the costa in the basal region; and 5) the transverse section of the costa with 2-6 (9) bi- to multistratose rows of cells in transition to the unistratose lamina. The closely related species, *Leucoloma grandidieri*, is differentiated by its 1) more "bowed" or incurved leaves; 2) strongly rugose juxtacostal bands; 3) 1-3 bistratose rows of cells between the costa; and 4) a unistratose lamina. *Leucoloma crosbyi* is endemic to Mt. Ambré at the northern tip of Madagascar. *Leucoloma grandidieri* is more widespread in the eastern forests from Mt. Ambré to Andringitra in the southeast. *Leucoloma talazaccii* is differentiated from *L. crosbyi* by 1) a less robust habit, 2) more slender leaves, 3) short inner basal cells, and 4) fragile alar cells that result in caducous leaves on the lower stems.

Variation: The leaves have juxtacostal bands that vary from smooth to slightly rugose in the medial region. The leaf apices are flexuose to slightly incurved and acute to rounded with teeth. The lamina varies in the number of rows of bi- to multistratose cells between the costa and the unistratose lamina (2-9). Rarely, isolated rows of bistratose cells have been observed within the opaque juxtacostal bands, as well as the more common multistratose to bistratose transition region between the costa and unistratose lamina.

Habitat: *Leucoloma crosbyi* is corticolous on branches and has an elevation range of 900-1200 m.

Distribution: *Leucoloma crosbyi* is known only from Montagne d'Ambre, Province de Diégo Suarez, Madagascar. The distribution is based on 4 specimens that constitute the type material for the species.

Leucoloma grandidieri Ren. et Card. Figures II.58-59

Bull. Soc. Roy. Bot. Belgique 31(2): 101 1892. **Type:**"Hab. Madagascar: in silva Analamazoatra (Rev. Camboué et Campenon); in silvis e Fianarantsoa ad Mananjary (Dr. Besson)". **Lectotype:** *Camboué & Campenon*, PC! (lectotype chosen here!); **syntype:** *Besson*, PC!; **isosyntype:** Z!

Nomenclatural notes: From the syntype material, the specimen collected by Rev. Camboué and Campenon in PC is chosen here as the lectotype. The remaining type material for *L. grandidieri* was collected by Besson from "entre Fianarantsoa et Mananjary" and is cited here as syntype or isosyntype material in PC or Z, respectively.

There are numerous specimens collected by Besson with a variety of locality data on the packets. The label information on the specimens is often in Renauld's or Cardot's handwriting with some indicated as "*n. sp.*". The specimens that indicated "*sp. nova*" on the label included the following locality data: "entre Fianarantsoa et Masindrano", "entre Vinanitelo et Ikongo", "Ikongo", "Masindrano", or just Madagascar. Only the *Besson* specimens with label data congruent with the protologue were considered as type material for the species, despite the indication of "species nova " on several specimens. One Besson specimen from S, has "specim. originale" in Brotherus' handwriting, but with no label data that would identify it as an isosyntype. The 3 specimens seen from H-Br do not include any type material as defined by the protologue, therefore the duplicate material from Brotherus in S is not considered type material.

Plants robust, to 11 cm tall, in loose tufts, pale to glaucous green or tan to light-brown. Stems red, blackened below, non-tomentose, densely foliate; elliptic in transverse section, central strand lacking, outer cortical cells of 2-3 layers, red-brown, thick-walled, inner cortical cells yellow to tan, larger lumened; rarely unbranched to distally ramose, sympodial branching from 1 to 3 subapical innovations, these branches potentially deciduous. Rhizoids smooth, red-brown, restricted to the base of stem or branch.

Leaves 0.9-1.3 mm wide, 2.5-5.0 mm long, broadly to narrowly elliptic-lanceolate to lanceolate, strongly concave, incurved from an erect clasping base, transversely rugose in medial section, tapered abruptly to a long, flexuose, strongly incurved, or slightly twisted, subtubulose, non-rugose acumen, erect to patent when dry, erect to patent when wet. Margins plane, entire to serrulate distally, with a distinct, narrow, hyaline border, 7-19 µm wide. Costa 38-62 µm wide at base, percurrent to excurrent, smooth, translucent; transverse section elliptic, abaxial and adaxial stereids in 2-3 layers; guides 4-5 cells, obliquely oriented with 1-2 (3) bistratose rows of cells in transition to the laminal cells. Juxtacostal cells 4.8-12.0 µm long, 4.8-7.2 µm wide, irregularly quadrate, rounded, or oblong, chlorophyllose, opaque, pluripapillose with low, multifid papillae on abaxial and adaxial surfaces, extending to medial or upper basal region; juxtacostal bands tapered as irregular, broad, v-shaped wedge, sharply delimited from smooth interior cells. Interior and basal cells, 5-7 µm wide, 19-132 µm long, elongate to linear, slightly to strongly porose, smooth, lightly tinged, forming a broad scarious region of the lamina. Marginal cells 2.4 µm wide, 124-132 µm long, narrowly linear, hyaline, smooth. Alar cells 12-34 µm wide, 12-72 µm long, quadrate to rectangular, flat, sclariform, longitudinally thick-walled, red-brown, often hyaline at margins; alar region 10-16 cells wide, 6-8 cells long, not reaching the costa.

Dioicous. Perichaetia terminal; perichaetial leaves 0.7-0.8 mm wide, 2-5 mm long, broadly ovate-lanceolate, bases clasping, sharply contracted to a long, narrow, stiffly erect setaceous acumen, basal portion yellow-brown to orange-brown. Archegonia 0.9-1.5 mm long, red-brown, +/- 20-28 per perichaetium; intermixed with paraphyses. Perigonia terminal or terminal on short, subapical lateral branches (1-4); perigonial leaves 0.5-1.0 mm wide, 0.9-1.6 mm long, ovate with abruptly narrowing, short acumen. Antheridia 0.08-0.11 mm wide, 0.8 mm long, red-brown to yellow-brown, with numerous paraphyses.

Sporophyte mono- or polysetous (to 3). Seta 1.5-2.0 mm long, stout, smooth, opaque tan to red-brown; in transverse section cell wall thickenings restricted to a single layer of outermost cells. Capsules 0.9-1.5 mm long, immersed, ovoid to oblong, light brown to tan. Operculum not seen. Peristome 16 teeth, 60-84 µm wide at base, 0.5-0.6 mm long, asymmetric, bifid, distally filiform, red-brown; PPL pitted-striate at base, distally papillose; IPL irregularly papillose from base to mid-tooth, distally striate to strongly papillose-striate. Calyptra mitrate, lobate (10-12 lobes), whitish yellow to tan below, red-brown above, slightly roughened distally. Spores 24-31 µm, finely granulose.

Diagnostic Characters: *Leucoloma grandidieri* Ren. & Card. is distinguished by its robust habit and typically rugose, incurved "hunchbacked" leaves from erect bases that have flexuose to non-rugose apices. The juxtacostal bands are sharply defined in the upper 2/3 of the leaf by opaque, densely papillose cells that taper as a broad to narrow V-shaped wedge to the costa. The interior cells form a broad, non-chlorophyllose region of the lamina in the base that extends to the shoulders of the leaf. The leaves have a narrow hyaline margin and sharply defined, plane alar cells that are thick-walled, red-brown, and form a broad region 10-16 cells wide. The transverse section of the costa is used to distinguish *L. grandidieri* from *L. crosbyi* by the number of multistratose rows of cells between the costal guide cells and the unistratose laminal cells. *Leucoloma grandidieri* has 1-3 rows, whereas *L. crosbyi* has 2-6. The juxtacostal bands of *L. crosbyi* are less rugose than those of *L. grandidieri*. The reduced number of the multistratose rows between the guide and laminal cells results in the strong rugosity of the juxtacostal bands. *Leucoloma grandidieri* has vertically pitted PPL peristome bases, whereas those of *L. crosbyi* are smooth. In fertile specimens, the pitting can be difficult to observe because of the closely arranged trabeculae at the base of the teeth.

Variation: Variation within the species is expressed by the degree of rugosity in the medial portion of the leaf - slightly to strongly rugose. The leaf shape varies in the abruptness of the narrowing acumen from sharply to more gradually. The width of the terminus of the opaque juxtacostal region varies from broad to narrow.

Habitat: *Leucoloma grandidieri* is corticolous on tree trunks, lianas, and horizontal branches up to 3 m above the forest floor, in primary or secondary montane forests. It has also been collected on a scrubby south-facing hillside, indicating a more exposed habitat. The range of elevation is between 800-1650 m.

Distribution: *Leucoloma grandidieri* is restricted to Madagascar, and known from Diégo Suarez at the northern tip, Marojezy in the northeast, Andasibe (east central), to Andringitra (south east) along the eastern escarpment. Previously this species was reported as restricted to east central Madagascar (La Farge-England 1992). Additional specimens from PC and collections of the author has extended the range of this species to the Province of Diégo Suarez and to Andringitra.

Specimens examined: MADAGASCAR: Prov. Diégo Suarez: Diégo Suarez: *Drouhard* (sp?) (PC - Hb. Thériot); Marojezy: *La Farge-England 9292, 6397, 6471* (ALTA, MO, TAN). **Prov. Fianarantsoa:** *Berthier* 1892 (BR, FH); *Besson*, 1892 (BM - 3 specimens, H-Br); *Besson* (S - 4 specimens); *Crosby & Crosby 9286* (MO), *6863* (H); *La Farge-England 7589* (ALTA, MO, TAN); *Onraedt 71.M5363, 74.M2119* (Hb Onraedt). **Prov. Tamatave:** *Cremers 3108* (Hb. Onraedt); *Crosby & Crosby 6782* (H, M, MICH); *La Farge-England 5741, 5777, 5867A, 5957, 5965, 5984, 5916, 6011, 7156* (ALTA, MO, TAN). **Prov. Tananarive:** lac de Mantasoa - *Onraedt 74.M.2119.*

Leucoloma membranaceum La Farge-England ***sp. nov.*** Figures II.60-61

Type: Île de la Réunion. Art du Vent: Recently cutover woods along road CD-57. 40 km SE of St. Denis. 21°09'S, 55°48'E. Elevation 460 m. 24.xi.1972, *Crosby & Crosby 8368.* **Holotype:** MO; **isotypes:** ALTA, L.

Paratypes: MADAGASCAR: Prov. Tamatave: à 7 km de Perinet route Tananarive-Tamatave -30/03/1974, alt. 900 m., *G. Cremers 3099* (Hb. Onraedt); **Prov. Fianarantsoa:** Ivohibe - *P. Tixier 10553* (PC); **RÉUNION:** Plaine des Cafres - 12.10.1962, alt. 1800 m., *Een 494* (Hb. Een).

Plantae epiphyticae, pallide vel luteo-virides ad 6.5 cm altae. Folia late ovata ad ovata-lanceolata et flexuosa ad apicem. Cellulae juxtacostales papillosae densissimiae obscurae in vittis utrinque costae latere dispositae, contractae ad basim. Latibasis scariosa sensim angustata versus marginem hyalinam. Cellulae alares planae, rufo-fuscis, scalariformes. Species haec ab Leucoloma crosbyi differt cellulae juxtacostales papillosae in vittis plus contractiores, breviores foliae, et plantae plus parvae.

Plants medium size, to 6.5 cm tall, in loose tufts, pale to yellowish green, tan below. Stems distally red, black proximally, non-tomentous; central strand lacking, outer cortical cells of 4-5 layers, red-brown, thick-walled, inner cortical cells larger lumened, yellowish to hyaline; distally ramulose, sympodial branching by 1-3 subapical innovations. Rhizoids few, smooth red-brown, restricted to the base of stem or branch or scattered along the stem.

Leaves 0.65-0.95 mm wide, 2.5-4.0 mm long, broadly ovate to ovate, gradually tapering to a short or long, slender acumen; habit patent, wide-spreading, to squarrose at leaf bases with flexuose slightly crisped or falcate secund apices when dry, patent to wide-spreading when wet. Margins plane, entire or serrulate distally, with a distinct, hyaline border 12-24 µm wide. Costa 36-48 µm wide at base, subpercurrent to shortly excurrent, translucent; in transverse section guides 4, with 1-2 bistratose rows in transition to the laminal cells. Juxtacostal cells 5-7 µm wide, 5-17 µm long, isodiametric, oblong, short elongate, rounded or irregularly angled, chlorophyllose, opaque, pluripapillose, with low multifid papillae on abaxial and adaxial surfaces from just below apex to the basal region, tapered as a V-shaped wedge toward the costa. Interior and basal cells 5-7 µm wide, 19-96 µm long, elongate to linear, thick-walled, non-chlorophyllose, tinged, smooth, not or slightly porose. Marginal cells 2.5-3.5 µm wide, 96-120 µm long, narrowly linear, thick-walled, hyaline, smooth. Alar cells 7-24 µm wide, 7-84 µm long, quadrate to rectangular, orange to red-brown, longitudinally thick-walled; alar region 17-23 cells wide, 6-7 cells long, not reaching the costa, with an angled orientation to the basal cells.

Dioicous. Perichaetia terminal; perichaetial leaves 0.8-1.1 mm wide, 3.5-4.0 mm long, leaf base broadly ovate to obovate, convolute, abruptly contracted to a tapered, erect acumen, basal portion of leaf yellowish brown, cells strongly porose. Archegonia red-brown, 0.50-0.55 mm long, 20-25 per perichaetium, with numerous hyaline paraphyses. Perigonia not seen.

Sporophyte not seen.

Diagnostic Characters: *Leucoloma membranaceum* is distinguished by 1) broadly ovate leaves; 2) strongly tapered, juxtacostal bands that lack rugosity, extend 1/2-2/3 the width of the lamina, and end in the basal region; and 3) the short to long, slender, entire acumen with an excurrent to subpercurrent costa. The leaf habit is slightly crisped to falcate-secund and the stems are distally ramulose. A closely related species is *Leucoloma seychellense*, which is differentiated by more slender lanceolate leaves with narrower, less abruptly tapered juxtacostal bands that are typically dorsally rugose, and a patent to erect-spreading leaf habit. *Leucoloma crosbyi*, from Mt. Ambré in northern Madagascar, differs by its more robust habit, more erect-spreading leaves, the narrower juxtacostal cells, and the more numerous bi- to multistratose rows in transition between the costa and the lamina.

Habitat: *Leucoloma membranaceum* is corticolous on trees. It has been found in a secondary lowland rainforest and montane rainforests from 460-1800 m in elevation.

Distribution: *Leucoloma membranaceum* is known from 4 collections: 2 from the eastern rainforests of Madagascar - Perinet, Prov. of Tamatave and Ivohibe, Prov. of Fianarantsoa between 18° 54' S and 22° 29' S; and 2 from the rainforests of Réunion 21° 09' S.

Etymology: The specific epithet refers to the broad membranaceous lamina which has a shiny, translucent appearance.

Leucoloma seychellense Besch. Figures II.62-63

Ann. Sci. Nat. Bot. ser. 6, 9: 310. 1878. **Type:** "Seychelles: sur les arbres (G. De L'Isle)". **Lectotype:** PC! (lectotype chosen here!); **isotypes:** BM! (2 specimens - sht 26, 1 specimen - sht 25), BR! (2 specimens), G!, S!

Leucoloma bifidum var. *orthothecioides* Besch., Ann. Sci. Nat. Bot. ser. 6, 9: 310. 1878. **Type:** "Maurice: sur la terre, montagne du Pouce, Darnty, juin. 1874, no. 25 (hb. Schimper)". **Lectotype:** BM! (Hb. Bescherelle, sht 77)(lectotype chosen here!); **isotype:** BM! (sht. 26).

Leucoloma crepinii Ren. & Card., Bull. Soc. Roy. Bot. Belgique 31(2): 102. 1892., *syn. nov.* **Type:** "Maurice (Duisabo, in Herb. hort. bot. bruxell., sub nomine *L. bifidum* Brid. var.; Rev. Rodriguez 1889!); sur la terre, montagne du Pouce (Danty, hb. Schimper in Besch. Fl. Réunion)". **Lectotype:** *Rodriguez*, 1899, PC! (Hb. Cardot)(lectotype chosen here!); **isotypes:** BM! BR!

PC!; **syntype:** *Duisabo*, BR!; **isosyntypes:** BM! (sht 77), PC!.

Leucoloma crepinii var. orthothecioides (Besch.) Ren., Prodr Fl. Bryol. Madag. 70. 188.

Leucoloma acutum Mitt. *ex* C. Muell., Gen. Musc. Fr. 281.1900. **Type:** "Sowie aber in *L. acutum* Mitt. (sub Poecilophyllo) von der Insel Mauritius die über einander liegenden Blatter und vollkommen aufrechte Astspitzen wiederkebren, so stellt sich auch der ausserordentlich breite Rand des Blattes ein".*(see nomenclatural notes below).

Leucoloma trachynotus C. Muell., Gen. Musc. Fr. 281. 1900. **Type:**"von Madagascar mit Öllirauhem Blattrücken". Madagascar: Andrangolonka, inter *Orthostichellum rostrifolium*. 1892. Leg. F. Likora. (ex herb. C.M.). **Lectotype:** PC! (lectotype chosen here!).

Nomenclatural notes: The possible type material for *Leucoloma acutum* C. Muell. is in BM, FH, PC. All are Mauritius specimens, with the name *Poecilophyllum acutum* indicated. Further information about the type specimen is not given in the "protologue" by Mueller, and there is no indication that these specimens were from Mueller's herbarium. Lectotypification is needed.

Plants small to medium, 3-12 cm, in loose tufts, downwardly outspreading, light green to yellow-green distally, dark brown below, tan to brown in older specimens. Stems red to blackened below; central strand lacking, outer cortical cells 3-4 layers thick-walled, red-brown, with inner cortical cells larger lumened, yellow-brown, thinner walled; sympodial branching from 1-3 subapical innovations below gametangia, monopodial branching lateral along the stem. Rhizoids smooth, red-brown, restricted to the base of stem or branch.

Leaves 0.5-1.0 mm wide, 2-4 mm long, ovate, ovate-lanceolate, to elliptic-lanceolate, tapered at leaf base and somewhat clasping, stiffly erect-spreading, patent to wide-spreading, or squarrose, distally stiffly erect to flexuose, slightly crisped, falcate secund, or spirally twisted, incurved at base of acumen, plane below, transversely rugose along juxtacostal bands, tapering as a short or long, subtubulose, slender finely pointed acumen. Margins plane, entire below, distally subentire or serrulate with a narrow, hyaline border from the leaf base to the apex, with a maximum width 7-21 µm. Costa 29-48 µm at base, percurrent to long excurrent, smooth, translucent; in transverse section abaxial and adaxial stereids in 2-3 layers, guide cells 4-5, with one row of bistratose cells in transition to the laminal cells. Juxtacostal cells 5-7 µm wide, 7-12 (17) µm long, rounded, oblong to short elongate, chlorophyllose, densely pluripapillose on abaxial and adaxial surface, papillae multifid; juxtacostal bands opaque, extremely narrow to medium width, extending to basal region, tapering gradually toward the costa. Interior and basal cells 5-7 µm wide, 12-72 µm long, elongate to linear, smooth, non-porose to strongly porose, tinged, forming a broad membraneous tissue. Marginal cells 2.5 µm wide, 96-240 µm long, linear (extremely narrow), hyaline, smooth. Alar cells 12-22 µm wide, 12-60 (72) µm long, quadrate to rectangular, red-brown (commonly hyaline at margins), scalariform; alar region 16-21 cells wide, 5-7 cells long, not reaching the costa, with an angled orientation to the basal cells, isodiametric basal-alar transitional cells lacking.

Dioicous. Perichaetia terminal; perichaetial leaves 0.8 mm wide, 2.5-3.8 mm long, broadly ovate to obovate leaf bases, clasping, orange-brown, abruptly narrowing to an aristate acumen, papillose from apex to base of acumen. Archegonia 0.70-0.85 mm long, numerous, -/+ 20 per perichaetium, red-brown, necks long (0.65 mm), with paraphyses hyaline, uniseriate. Perigonia terminal on primary axis or subapical, short lateral branches, 1-3; perigonial leaves 0.25-0.3 mm wide, 1-3 mm long, ovate to ovate-lanceolate, abruptly tapered to a long or short acumen, leaf bases strongly concave, orange-brown. Antheridia orange brown to tan, +/- 10 per perigonium, with hyaline paraphyses intermixed.

Sporophyte not seen.

Diagnostic Characters: *Leucoloma seychellense* is easily distinguished from other species by 1) broadly ovate to elliptic-lanceolate leaves that taper to a very fine point, typically ending in a long excurrent or rarely percurrent costa; 2) the distinctive, narrow, juxtacostal bands which end in the basal region and are typically rugose dorsally when wet; the rugosity is restricted to the base of the acumen or extends along most of the juxtacostal band length; 3) chlorophyllose cells densely papillose on both surfaces; and 4) the very narrow hyaline marginal band 3-5 cells wide. *Leucoloma talazaccii* can appear similar to *L. seychellense* by sharing the narrow juxtacostal bands, but differs in having 1) caducous leaves, 2) fragile leaf apicies that are more stout, 3) a reduced alar region that lacks an angled orientation of the basal-alar cells, 4) basal cells that are typically broader and somewhat rhomboidal, and 5) non-rugose juxtacostal bands. The medium to small size, fine apices, and narrower juxtacostal bands will distinguish *L. seychellense* from *L. grandidieri*.

Variation: *Leucoloma seychellense* shows a considerable amount of variation in the dry habit. The specimens from Mauritius have typically shorter stems with erect to patent leaf habits, whereas the few specimens from Réunion have longer, more flexuose stems and a more lax, wide-spreading to squarrose leaf habit; the plants are small in comparison to the type material. The variation in the porosity of the basal and interior cells has been the rationale used to separate *L. crepinii* from *L. seychellense*. By carefully examining the range of specimens, it is evident that within a single specimen there are leaves with both types of basal cells. On well developed specimens, smaller subsidiary stems can have less porose leaf cells as well as broader juxtacostal cells. The type material of *L. crepinii* (*Rodriguez* 1889, PC!: LT, IT) represents a poorly developed specimen of *L. seychellense*. With optimal growing conditions, plants of *L. seychellense* develop into medium to small sized plants with stems to 12 cm long. The type material for *L. bifidum* var. *orthothecioides* has leaves that are more densely arranged on the stem. The leaf shape variation within the type overlaps with that of *L. crepinii* and *L. seychellense*. There is a complete continuum in the leaf size and excurrent costa length between the two types, thus one cannot justify the recognition of separate varieties.

Habitat: *Leucoloma seychellense* is typically epiphytic on tree trunks or exposed roots up to 3 m above the forest floor, but as well has been found on soil, rock, decaying wood, and one specimen was epiphyllous (*Jegffrey et al. 1219*, KEW - Hb. Townsend). It has an elevation range of 4 - 980 m, in coastal lowland dune forests, montane rainforests, elfin forests and in exposed, open heathlands of Mauritius.

Distribution: *Leucoloma seychellense* is widespread, although confined to the eastern rainforests in Madagascar from Marojezy in the northeast, south to the Province of Fianarantsoa with no specific locality designated. It also occurs in the lowland to elfin forests of Mauritius, Réunion, and the Seychelles. It is endemic to the western Indian Ocean islands, with a latitudinal range from 4°30'-22°00' S.

Specimens examined: Over 100 specimens from the following herbaria were examined ALTA, BM, BR, FH, G, H-Br, JENA, KEW (Townsend), L, LUND, MAUR, M, MICH, MO, NY, PC, S, and from the private Herbaria of G. Een, J.- P. Frahm, Fr. M. Onraedt. Selected specimens used for mapping include: **MADAGASCAR: Prov. Diégo Suarez:** *La Farge-England 6203* (ALTA, MO, TAN); **Prov. Tamatave:** *La Farge-England 5776, 5683* (ALTA, MO, TAN), *Decary* (FH, JENA), *Perrot* (M, S); **Prov. Fianarantsoa:** without locality specified ex Hb Paris (FH, G). **MAURITIUS:***Crosby & Crosby 5679b* (MAUR), *Lorence 859* (MO), *Lecoultre* (BM), *Vaughan M/97* (MAUR). **RÉUNION:** *Barclay 654* (KEW), *Crosby & Crosby 8961* (ALTA, MO), *Een 513* (Hb. Een). **SEYCHELLES:** *Rev. Quirin 183* (BM, BR, FH, G, LUND), *Schlieben 11809* (BM).

Leucoloma talazaccii Ren. et Card. Figures II.64-65

Bull. Soc. Roy. Bot. Belgique 34 (2): 58-59. 1896. **Type:** "Hab. Madagascar: Ambondromba, specimina perpauca (rev. Talazac)". **Holotype:** PC! (Hb.

Renauld); **isotypes:** BR!, PC! (Hb. Renauld, Hb. Cardot), S!

Leucoloma talazaccii var. *fragilifolium* Thér. et P. Varde, Recueil Publ. Soc. Havraise, Étud. Div. 1924 (1): 84, *syn. nov.* **Type:** "S.O. de Tananarive, Forêt (C.)"; legit Carrougeau. **Holotype:** PC! (Hb. P. Varde *ex* Hb. Charrier).

Nomenclatural notes: The specimen designated "*L. talazacii* var." in Thériot's herbarium does not include a varietal name, yet "ex herb Charrier 1922 P.V." matches with the material in Potier de la Varde's herbarium for the type of the variety. Thus it is likely that the material in Thériot's herbarium represents an isotype for variety *fragilifolium*.

Plants small to medium, light green to green or tan, in loose tufts. Stems 1-4 cm tall, black, distally reddish, non-tomentose, distally comose; in transverse section central strand lacking, outer cortex of 3-4 layers of thick-walled cells, red-brown, inner cortex of thinner walled cells, yellow to hyaline; sympodial branching from 1-2 (3) subapical innovations. Rhizoids smooth, red-brown, few to densely clustered at the base of stem and branches.

Leaves 0.5-0.8 mm wide, 3.5-5.0 mm long, caducous, elliptic-lanceolate to narrowly ovate-lanceolate, concave, non-rugose, tapering gradually to a long, slender, subulate, bistratose acumen; habit erect-spreading distally to squarrose proximally with erect to slightly flexuose apices, wet or dry. Margins plane, entire below, serrulate at apex, with a hyaline border (10) 19-26 (43) µm wide. Costa 36-48 µm wide at base, smooth, translucent or partially covered with papillose cells, percurrent to excurrent; transverse section elliptic to plano-convex, adaxial and abaxial stereid bands of 1-3 layers, guide cells 4-6, with 1-3 bistratose rows in transition to the laminal cells, also occasional lateral doubling of the guides. Juxtacostal cells 5-7 µm wide, 5-17 µm long, rounded quadrate or irregularly angled, to oblong, chlorophyllose, opaque, pluripapillose with low, dense, simple to multifid papillae, dense on both adaxial and abaxial surfaces, unistratose below, bistratose in upper region, forming narrow juxtacostal bands from the apex to the upper basal region, gradually tapered. Interior and basal cells 5-12 µm wide, (12) 24-84 (96) µm long, rhomboidal rectangular, elongate, linear, nonporose to porose, tinged, smooth, lengthening toward margin. Marginal cells 2.5 µm wide, 72-216 µm long, narrowly linear, thick-walled, hyaline, smooth. Alar cells 12-29 µm wide, 12-36 µm long, oblate to isodiametric, quadrate or rectangular, lumen lightly granulose or not, fragile, hyaline or red-brown, slightly auriculate, non-decurrent, cell walls slightly thickened longitudinally; alar region 9-11 cells wide, 5-10 cells long, not reaching costa.

Dioicous. Perichaetia terminal; perichaetial leaves) 0.5-0.7 mm wide, 2.5-3.5 mm long, broadly ovate-lanceolate, abruptly narrowing to a long acuminate, setaceous apex, leaf bases clasping to convolute; basal cells slightly inflated, tinged red-orange; alar cells not differentiated. Archegonia red-brown, numerous (+/- 15), 0.7-10.0 mm long; paraphyses hyaline, unicellular, 0.4-0.6 mm long. Perigonia not seen.

Sporophyte terminal, mono-or polysetous. Seta 1-2 mm long, stout, opaque, tan. Capsules 1 mm long, immersed, oval, oblong to short cylindric, brown. Operculum not seen. Peristome 16 asymetric teeth, split to 3/4 of length or to base of tooth, 48 µm wide at base, 0.3 mm long, red-brown; PPL and IPL with striate ridges, distally papillose. Calyptra mitrate. Spores not seen.

Diagnostic Characters: *Leucoloma talazaccii* is easily distinguished by its 1) caducous leaves, which typically leave a denuded black stem with only a distal tuft of leaves; 2) long, stiffly erect-spreading leaves with narrow, opaque, non-rugose juxtacostal bands; 3) broad rhomboidal inner basal cells (to 12 µm wide); and 4) fragile, non-decurrent, typically rounded-quadrate alar cells that are often hyaline. This species might be confused with the larger *L. crosbyi*, which shares the gradually tapering, narrow juxtacostal bands, but that species is differentiated by its persistent, decurrent, red-brown, large alar region and broader (0.8-1.2 mm), slighlty longer leaves (4-6 mm). *Lecuoloma seychellense* is another species which can have the narrow juxtacostal bands. It is typically rugose at the narrowing of the acumen; lacks the caducous leaves stems; has more broadly ovate-lanceolate leaves; narrower and longer basal cells; and decurrent, persistent alar cells.

Variation: *Leucoloma talazaccii* shows some variation in the basal cells. They can be porose or not, and the extent of the inner basal cell region of shorter, broader cells can vary. The apices can be either percurrent or excurrent, which had been used as one of the main characters defining *L. talazaccii* var. *fragilifolium*. This character in addition to the tufted stem leaves character is typical of the type variety, thus precluding the justification for a distinct variety.

Habitat: *Leucoloma talazacci* is corticolous on the bases of tree trunks, on branches and fine twigs in primary or secondary montane rainforests of Madagascar, with an elevation range of 900-1300 m. A single specimen, *Tixier 12425*, from Maroantsetra (northeastern Madagascar) is presumably from a lower elevation, but elevation data were lacking on the packet.

Distribution: *Leucoloma talazaccii* is restricted to the eastern montane forests of Madagascar, between 15°26'S and 21°15'S, in the provinces of Fianarantsoa and Tamatave. The precise locality of the type specimen is not known; "Andrombromba" was thought to be from the "pays des Bestileo, qui est sud des monts Ankaratra, entre 20 et 22 degres de latitude, et qui comprend la plus grande partie des bassins superieurs du Mania et du Mangoka..." (Renauld 1915, p.34). There are 4 localities with the same place name Amboondrombe in the gazetteer, all between 21°25' S-24°43' S and 44°58'-45° 39' E.

Specimens examined: MADAGASCAR: *Dr. Meller* (BM); *La Farge-England 5802, 5804, 5834* (ALTA, MO, TAN); *Crosby & Crosby 6998* (MO), *6805* (MO, ALTA); *Tixier 9168, 9857, 9870, 10185, 10726, 10754, 11525, 11527, 12199, 12281, 12283,* *12425* (ALTA, PC).

Leucoloma* Section *Dichelymoidea Besch., Ann. Sci. Nat. Bot. sér. 6, 9: 315. 1878.
Lectotype: *Leucoloma dichelymoides* (C. Muell.) Jaeg., cf. Ren., Prodr. Fl. Bryol. Madag. 86. 1898.

Subsection *Dichelymoidea* (Besch.) Ren., Prodr. Fl. Bryol. Madag. 86. 1898.

Plants with branching sympodial by subapical innovations or monopodial by lateral innovations; the branches are perpendicularly or obliquely oriented. Leaves lanceolate to elliptic-lanceolate, with a gradual or abruptly tapered acumen. Juxtacostal bands translucent, non-opaque, abaxial surface corrugated or smooth, parallel to the costa and differentiated. Juxtacostal cells 5-12 µm wide, often broad, irregularly angled and shaped, uni- to pluripapillose, abaxial surface smooth or with prominent multifid papillae developed in irregular transverse rows, adaxial surface with scattered low papillae, papillose cells often restricted to the distal lamina. Interior and basal cells forming a broad scarious region of the lamina. Alar cells predominantly elongate or rectangular, with a obliquely angled orientation toward basal cells; alar region enlarged, to 43 cells wide, and 21 long cells, often convolute or clasping at base. Rhizoids not developed on alar cells. Capsules immersed.

Nomenclatural notes: Bescherelle (1878) originally described a heterogeneous Section *Dichelymoidea* with 7 species. Subsequently, Renauld (1898) removed six species from the taxon to establish the monotypic subsection, *Dichelymoidea* (Besch.) Ren. within *Leucoloma* sect. *Transmutantia* (= *L.* subg. *Syncratodictyon*). Renauld established the subsection based on the unique, thin, slender stems; distantly arranged leaves; and flat alar region composed of numerous quadrate to rectangular cells of *L. dichelymoides* (C. Muell.) Jaeg. He noted the alar region was similar to species in his section *Vittata* (equivalent to the concept of subg. *Leucoloma*, here), yet the juxtacostal cells were similar to those in *L.* sect. *Transmutantia*. With the expansion and reclassification of the genus in 1909, Renauld reinstated the taxon at the sectional rank, but with a restricted concept of Bescherelle's original section. The systematic position of this section has remained uncontested until now, with *Leucoloma dichelymoides* the only species included in the section.

Examination of available specimens with the light and scanning electron microscope has shown that the papillae in the upper lamina on the abaxial surface are similar in structure to a group of species scattered in Renauld's subgenera *Taeniodictyon* and *Sphenodictyon* (=subg. *Leucoloma*). The justification for transferring section *Dichelymoidea* from subgenus *Syncratodictyon* to subgenus *Leucoloma* is based on following combined characters: 1) an enlarged, clasping alar region of longitudinally thickened cells; 2) the prominent dorsal papillae of the upper lamina; 3) the broad, irregularly angled juxtacostal cells; and 4) lateral, monopodial branches commonly with a perpendicular orientation to the main axis.

Section *Dichelymoidea*: 5 species

L. dichelymoides (C. Muell.) Jaeg.
L. fontinalis Dix.
L. mafatense Ren.
L. ochrobasilare Ren.
L. tuberculosum Ren.

Leucoloma dichelymoides (C.Muell.) Jaeg. Figures II.66-67

Ber. St. Gall. Naturw. Ges. 1877-78: 380. 1880 (Ad.2:644). **Basionym:** *Dicranum dichelymoides* C. Muell., Linnaea 40: 240. 1876. **Type:** "Comoro insula Johanna 1300m supra mare, in silva umbrosa. J.M. Hildebrandt 1875, coll. no. 1841". **Lectotype:** *Hildebrandt 1841* (NY! - Hb. Jaeger)(lectotype chosen here!); **isotypes:** BM! (Hb. Geheeb), BM! (Hb. Bescherelle), BM!, BR! (2 specimens), E!

Leucoloma holomitrioides C. Muell., Gen. Musc. Frond. 281. 1900, synon. nov. **Type:** "Alamaz(g)antra-Kover auf Madagascar". **Lectotype:** PC! (Hb. Renauld; Borchgrevinck 1871 Hampe misit C. Mueller, Hb. C. Mueller) (lectotype chosen here!); **isotype:** PC!

Nomenclatural notes: *Leucoloma dichelymoides* has been classified within *L.* subgenus *Syncratodictyon* section *Dichelymoidea* Besch., based on the gradual transition of the juxtacostal cells into the interior or basal cells. Even though it has not been found fruiting, the distinctive, enlarged, scalariform alar region is characteristic of subgenus *Leucoloma*. The lack of the opaque, dense papillae on both surfaces excludes it from *L.* section *Attenuata*, which shares the enlarged alar region.

Plants delicate to medium sized, in loose, erect tufts 1-3 cm tall with slender, flexuose, pendulous stems to 20 cm long, pale to yellow-green, dark-brown below, or tan to light-brown. Stems red, blackened below, non-tomentous; in transverse section central strand lacking, outer cortical cells of 2-4 layers, red-brown, thick-walled, inner cortical cells yellow to hyaline, larger lumened; sympodial branching from 1-3 subapical innovations, monopodial branching, lateral, solitary, typically at right angles to the supporting axis. Rhizoids few to numerous, restricted to the base of stem or solitary to several in leaf axils, red-brown, smooth.

Leaves 0.4-1.0 mm wide, 3.0-5.5 mm long, concave below, subtubulose distally, ovate-lanceolate with long, gradually tapered, slender, filiform acumen, erect to slightly flexuose, or occasionally sinuose; habit erect-spreading to patent, densely arranged on erect stems, typically patent to squarrose, distantly arranged on pendulous stems, with the convolute leaf bases exposed, similar wet or dry. Margins plane, entire, serrulate or serrate distally, with a distinct, narrow, hyaline border, 7-12 (14) µm wide. Costa 29-48 µm wide at base, subpercurrent to excurrent, translucent; transverse section plano-convex, abaxial stereids in 1-2 layers, adaxial stereids in 1-3 layers, guide cells 4-5, obliquely oriented, with 1 row of bistratose transitional cells to laminal cells, or lacking. Juxtacostal cells 5-10 µm wide, 5-31 µm long, rounded to elongate or quadrate to irregularly angular, smooth or uni- or pluripapillose, with low to projecting abaxial, simple to weakly multifid papillae, restricted to the upper leaf or extending to the basal region, cells lengthened toward margins and base, thick-walled or not, porose or not, sinuose or not. Basal and interior cells 7-10 µm wide, 26-60 µm long, lengthened toward the margins, thick-walled, porose, or slightly sinuose, smooth, tinged. Marginal cells 2.5 µm wide, 125-132 µm long, narrowly linear, smooth, hyaline, forming a border 3-6 cells wide. Alar cells 17-26 µm long, 14-24 µm wide, quadrate to rectangular, red-brown to black, scalariform; alar region 11-14 cells wide, 7-10 cells long, convolute, distinctly decurrent.

Dioicous. Perichaetia terminal; perichaetial leaves 0.4-0.5 mm wide, 2.5-4.5 mm long, ovate-lanceolate, sharply contracted to acuminate to filiform, serrate acumen. Archegonia 0.7-0.8 mm long, red-brown. Perigonia not seen. Sporophyte not seen.

Diagnostic Characters: *Leucoloma dichelymoides* is one of the most distinctive species of the genus and is characterized by the following attributes: 1) delicate, slender, pendent branches with leaves distantly arranged along the stem; 2) wide-spreading to squarrose leaves, with an enlarged, convolute, strongly decurrent alar region; 3) strongly scalariform alar cells; and 4) basal cells obliquely angled to the alar cells. A strong example of convergent evolution is *Dicranoloma blumei,* which has also evolved the pendent growth form, but differs by 1) the lack of a strongly scalariform alar region, 2) stem tomentum, 3) a central strand in the stem, and 4) strongly serrate upper leaf margins with teeth on the back of the costa. *Dicranoloma blumei* is a much more robust species found from India to the South Pacific islands (Norris & Koponen 1990). The median laminal cell width of *Dicranoloma blumei,* (10-18 µm) is distinctly wider than that in *Leucoloma dichelymoides* (5-10 µm). *Leucoloma dichelymoides* is clearly related to *L. fontinaloides*, *L. tuberculosum*, and *L. ochrobasilare*, sharing the pendent growth form, sparsely papillose abaxial surface arranged in irregular transverse rows, monopodial branching at right angles to the supporting axis, and strongly decurrent, clasping alar region.

Variation: The specimen named *Leucoloma dichelymaceum* C. Muell. (*nom. nudum*, JENA!), represents one extreme in variation of developed, papillose juxtacostal bands. Compared to the type specimen, the juxtacostal bands extend to the base of the lamina, opposed to being confined to the upper portion of the leaf. Intermediate specimens have been observed, as well as specimens with both "smooth" versus "papillose" type leaves. In addition, papillae vary from slightly roughened to distinctly prominent. The degree of cell size, shape, porosity, and sinuosity varies as well. There is a strong correlation between the quadrate to shortly rectangular cells with papillae versus oblong, porose, smooth cells. The apical margins vary from entire to serrate. The other variation within a population is the ability to produce short erect stems that are densely foliate, as well as very long, delicate, slender, pendent stems with distantly arranged leaves. Lateral branches can have a perpendicular or oblique orientation to the supporting axis.

The type of *Leucoloma holomitrioides* represents a small form of *L. dichelymoides* with the very long slender apices typical of the species. The specimen represents the material with the juxtacostal bands less sharply defined with low abaxial papillae, broad juxtacostal cells that show a gradual transition to the interior and basal cells, and narrow hyaline margins.

Habitat: *Leucoloma dichelymoides* is corticolous on tree trunks or on fine branches of saplings, 1-2 m above the forest floor. It occurs in exposed habitats in the mist forest belt, and forms small, sparse to large, dense, pendulous populations in montane to elfin rainforests. It is rarely terricolous. The elevational range of the specimens examined is 800-1650 m in Madagascar, 660-670 m in Mauritius, and a single collection from 1380 m in the Comoros.

Distribution: *Leucoloma dichelymoides* is locally widespread within the East African islands - the Comoros, Mauritius, and Madagascar. The lack of specimens from Réunion emphasizes the endemic trend of the *Leucoloma* flora within the islands.

Specimens examined: COMOROS: *Hildebrandt* (BM, BR); *Macé* 1900 (E); *Magill & Pócs 11211, 11216* (ALTA, MO). **MADAGASCAR:** *Pool sine loc.* (NY); **Prov. Tamatave:** *Crosby & Crosby 5569A* (L), *La Farge-England 5839, 6029* (ALTA, MO, TAN); **Prov. Diégo Suarez:** *Crosby & Crosby 7297* (L), *Guillaumet 4193, La Farge-England 6206, 6207, 6331,* (ALTA, MO, TAN), *P. de la Bathie* (FH, S), *P. de la Bathie 197* (JENA, MO); **Prov. Fianarantsoa:** *Besson 102* (Z), *Forsyth-Major 491* (G), *Hildebrandt 1881* (S), *Hildebrandt,* 1880 (JENA), *Talazac,* 1894 (FH, M, S, Z), *Talazac* (BM); *Thompson 1814* (BM); **Prov. Tananarive:** *Borgen 6* (L, BM), *Cremers 1888*; *Onraedt 74.M.2140* (Hb. Onraedt). **MAURITIUS:** *Coode 3979A, 4000, 4498A, 4489, 4755; Barclay 403, 1697, 1703, 2848b, 2858* (KEW - Hb. Townsend); *Een 481, 40* (Hb. Een); *Guého 42* (MAUR); *Vaughan 1935* (BM, E), *M/94* (E, MAUR, Hb. Een); *Crosby & Crosby 5593* (FH, L, MAUR), *9065* (L).

Leucoloma fontinaloides Dixon Figures II.68-69

J. Bot. 80: 43, f.2. 1942. **Type:** Madagascar: "Ambohimitomba forest, Tanala, 5 Jan. 1895, coll. C. Forsyth-Major 473b". **Holotype:** BM! (Hb. Dixon).

Leucoloma meteorioides P. Varde, Rev. Bryol. Lichénol. 19: 148. 3. 1950, *synon. nov.* **Type:** Madgasacar: "Hab. Vallèe du Mandrére, affluent de la Manamapanihy (S.E.) montagne au sud de Tanandava. Forêt ombrophile sur argiles latèritiques. Alt. 800-850 m summet de la montagne. 11-16 mars 1947 (6e voyage)". Leg. Humbert. **Holotype:** PC! (Hb. P. de la Varde).

Nomenclatural Notes: Dixon originally classified *L. fontinaloides* in subgenus *Sphenodictyon* Ren. (= section *Attenuata*), based on the strikingly large size of the plant with "subcomplanate", divergent leaves that mimic *L. grandidieri.* Potier de la

Varde ascribed *L. meteorioides* to subgenus *Taeniodictyon* section *Subvittata* (= *Leucoloma* section *Subvittata*) and compared the material to *L. comorae*. He pointed out the robust habit of the plant, as in *L. fontinaloides*, and noted the branching inserted at right angles, the large leaves, and described the alar cells as "thin" walled, not at all thickened! This description is misleading, since the alar region is clearly composed of scalariform cells, with strongly thickened, longitudinal walls. The placement of *L. meteorioides* in section *Subvittata* was based on the somewhat gradual transition of the papillose chlorophyllose, juxtacostal cells into the interior and basal cells. The only other species in section *Subvittata* at the time was *L. comorae* Ren. (= *L. chrysobasilare*). The cell architecture of *L. fontinaloides* differs from *L. chrysobasilare* by 1) having wider juxtacostal cells, 2) less densely papillose cells, 3) a more strongly developed alar region, 4) papillae arranged in irregular transverse rows (note placement on cell, see above), and 5) scattered adaxial papillae. It is interesting to note that the original specimens of *L. fontinaloides* and *L. meteorioides* were classified into 2 different subgenera, as well as 2 different sections within the genus! With careful examination of the available specimens, it is apparent that the two species should be synonymised. The pendulous growth form must contribute to the high degree of phenotypic expression, as is found in pendent species of the Meteoriaceae.

Plants robust, 10-25 cm long, as pendent, gregarious stems, pale yellow-green above to light tan or brown below. Stems red, non-tomentous, laxly foliate; central strand lacking, outer cortical cells 4-6 layers, red-brown, thick-walled, inner cortical cells yellow to hyaline, larger lumened, thinner walled; sympodial branches from 1-2 subapical innovations, monopodial branches solitary, mostly perpendicular to supporting axis.

Leaves 0.9-1.8 mm wide, 3.5-5.5 mm long, broadly ovate, elliptic-ovate lanceolate, to ovate-lanceolate, membraneous, concave, abruptly or more gradually narrowed to a short or long, slender, acuminate apex, leaf bases strongly clasping, caducous below; habit patent to wide-spreading, or sometimes squarrose, slightly corrugated at neck of acumen on abaxial surface, apices slightly flexuose, curled or spirally twisted when dry, patent to wide-spreading leaves with apices erect when wet. Margins plane, entire below, serrulate to slighlty serrate at apex, with a distinct hyaline border 12-29 µm wide, ending just below apex. Costa 36-48 µm at base, subpercurrent to excurrent; transverse section elliptic to plano-convex, abaxial and adaxial stereid bands of 1-2 layers, guide cells 4-5, occasionally laterally doubled, with a single row of bistratose cells in transition to laminal cells, or lacking. Juxtacostal cells 5-10 µm wide, 5-14 (24) µm long, rounded to oblong or slightly elongate, or irregularly triangular to quadrate, thick-walled basally, with abaxial papillae, simple, acute or bifid, most prominent in distal lamina that extend to the medial region, forming parallel bands from the upper lamina to the basal region, with a gradual gradation into the basal and interior cells in lower portion. Interior and basal cells 5-10 µm wide, 12-72 µm long, smooth, elongate to linear, slightly porose, thick-walled, tinged, lengthening toward base. Marginal cells 2.5 µm wide, 79-180 µm long, narrowly linear, hyaline smooth, border 3-10 cells wide. Alar cells (7) 12-24 µm wide, 17-72 (132) µm long, quadrate to rectangular (linear), longitudinally thick-walled, cell lumen typically granulose with anti-sinuose walls, red-brown; alar region 26-31 (43) cells wide, 9-17 (21) long, not reaching costa, obliquely oriented to the basal cells, decurrent.

Dioicous. Perichaetia terminal; perichaetial leaves 0.7-0.9 mm wide, 3-5 mm long, lanceolate with broad clasping base and a sharply contracted, long, erect, setaceous acumen, yellowed basal region with strongly porose basal cells. Archegonia 0.80-0.96 mm long, red-brown, intermixed with paraphyses. Perigonia not seen. Sporophyte not seen.

Diagnostic Characters: *Leucoloma fontinaloides* is easily distinguished by its 1) robust, pendulous, growth form with perpendicular monopodial branches; 2) strongly decurrent, clasping, extremely large alar regions of longitudinally thick-walled cells; 3) sparsely developed papillae in irregular transverse rows of the medial region that form a low corrugated abaxial surface, 4) hollow papillae restricted to the abaxial surface of the distal lamina or extending to the medial region, 5) broadly ovate to elliptic-lanceolate leaf bases, and 6) short, abruptly to gradually acuminate apex. The broad dimension of the leaves is similar to that of *L. grandidieri*, but the lack of opaque juxtacostal bands formed by dense, equally developed papillae on the abaxial and adaxial surfaces will easily separate the two species. In *L. grandidieri* the juxtacostal bands are distinctly transversely rugose and appear as a velvety, undulating surface. The abaxial surface of *L. fontinaloides* is rough and corrugated, due to the irregularly developed papillae. This is a diagnostic character of the taxa in section *Dichelymoidea.*

Variation: There is variation in leaf shape from broadly ovate, elliptic-ovate, elliptic-lanceolate, to ovate-lanceolate. The length of the acumen varies from short with a subpercurrent costa, to longer and more attenuate with an excurrent costa. The leaves of the lateral branches are slightly narrower and more attenuate than those of the main axis. The holotype of *L. meteorioides* has leaves with longer acumen when compared to the variation within the specimens of *L. fontinaloides.*

The extent of the papillose region varies within and between specimens. In some specimens the papillose region is restricted to the extreme upper region of the leaf, whereas in other leaves the papillose cells extend to the medial portion of the leaf. The differentiated juxtacostal cells extend to the upper basal region, where there is a gradual transition into the longer basal cells. The width of the alar region varies from 22-43 cells wide. The larger the alar region, the more strongly clasping it is. The leaf habit varies from patent to squarrose.

Habitat: *Leucoloma fontinaloides* is corticolous on thin branches of trees in eastern montane rainforests. The known elevation range is 800-1700 m. Frère M. Onraedt's specimens indicate that the trees were from degraded primary montane forests. Detailed habitat data is lacking on remaining specimens.

Distribution: *Leucoloma fontinaloides* is endemic to Madagascar and occurs in the eastern montane rainforests from the wet northeast at Marojezy, to the slighlty drier southeastern forests in the vicinity of Manampanihy. It also occurs in the montane forest patches of the central plateau in the vicinity of Ambositra and Antananarivo.

Specimens examined: MADAGASCAR: Prov. Diégo Suarez: *La Farge-England 6328* (ALTA, MO, TAN); **Prov. Fianarantsoa:** *Forsyth-Major 473* (BM - sheet # 53); *Onraedt 71.M.0529, 71.M.5315* (Hb. Onraedt); *Onraedt 71.M.529* (F, is dupl. of 0529); **Prov. Tananarive:** *Pool s.n.* (BM - sheet # 99 *ex* Hb. Dixon, MICH, NY - Hb. Mitten).

Leucoloma mafatense Ren. Figures II.70-71

Prodr. Fl. Bryol. Madag. 66. 1898. **Type:** "La Réunion: Mafaté, Fre. Rodriguez 1889". **Holotype:** PC! (Hb. F. Renauld); **isotypes:** BM!, BR!, L!, PC! (Hb. Cardot - 6 specimens; Hb. Thériot).

Nomenclatural notes: Numerous duplicates of the holotype were found in PC in Hb. Thériot and Hb. Cardot. One specimen in BM under the name of *Leucoloma bifidum* may be type material as well, but is mislabelled.

Plants small to medium sized, to 9cm long, in loose tufts, spreading, light yellow-green above, tan below. Stems with outer cortical cells 3-4 layers, red-brown, thick-walled, inner cortical cells larger lumened, yellowish; sympodial branching from 1-3 subapical innovations, with monopodial branching not associated with the gametangia. Rhizoids smooth, red-brown, very sparse, restricted to the base of stem or branch or 1-2 at the very base of the alar cells on the stem.

Leaves 0.5-0.9 mm wide, 3-4 mm long,ovate-lanceolate, leaf bases clasping, concave, distally subtubulose, acumen gradually tapered, slender, flexuose to slighlty falcate or slighlty crisped, distally spirally twisted when dry; habit erect-spreading, patent to wide-spreading to somewhat squarrose at leaf base when dry, patent to wide-spreading when wet. Margins plane, entire to serrulate distally, with a differentiated hyaline border, 17-48 µm wide. Costa percurrent to excurrent, 36-48 (60) µm wide at the base; transverse section plano-convex, abaxial and adaxial stereid bands of 2-3 layers, guide cells 4-6, with single row of bistratose cells in transition to laminal cells, or not. Juxtacostal cells 7-12 µm wide, 7-24 µm long, isodiametric subquadrate to elongate, thick-walled, chlorophyllose, abaxial surface uni- to pluripapillose, papillae multifid, prominent, arranged in irregular transverse rows, adaxial surface mostly smooth with a few scattered, low, simple to bifid papillae, along costa, forming parallel bands to the leaf base. Interior and basal cells 5-7 µm wide, 24-60 (72) µm, smooth, tinged, non-porose, restricted to a band of cells between juxtacostal and marginal cells. Marginal cells hyaline, linear, smooth, thick-walled. Alar cells 12-19 mm wide, 12-60 µm long, quadrate to rectangular, thick-walled, red-brown; alar region 17-23 cells wide, 6-11 cells long, with an angled orientation to the basal cells, decurrent.

Dioicous. Perichaetia terminal; perichaetial leaves 0.4-0.7 mm wide, 3.0-3.7 mm long, ovate-lanceolate with abruptly tapered, setaceous, stiffly erect acumen, leaf bases orange-brown. Archegonia 0.55-0.70 mm, red-brown, 7-23 per perichaetium, intermixed with numerous hyaline paraphyses. Perigonia not seen.

Sporophyte mono- or polysetous (to 3). Seta 1 mm long, stout, short, tan, smooth. Capsules 1.0-1.4 mm long, 0.50-0.85 mm wide, immersed, short, cylindric, brown. Operculum 0.5-0.8 mm long, rostrate, light brown or red-brown. Peristome 16 asymmetric teeth, 0.5-0.6 mm long, slender, filiform distally, bifid nearly 1/2-3/4 of tooth, 60-84 µm wide at bases, red-brown; PPL external surface smooth at base, papillose distally; IPL internal surface smooth at base, papillose distally. Calyptra mitrate, lobate, hyaline to pale yellow to tan below, red-brown above, roughened distally. Spores 19-24 µm, finely granulose.

Diagnostic Characters: *Leucoloma mafatense* is smallest species of the section and distinguished by its medium to broad hyaline margin and less prominent papillae on the abaxial surface, with transverse rows not sharply delineated as in *L. tuberculosum*. The papillae have a "salt and pepper" appearance as in *L. ochrobasilare* and the basal portion of *L. bifidum*. The closely related, allopatric species, *L. ochrobasilare*, is differentiated by having 1) a narrower hyaline border, 2) larger, more robust habit, 3) smaller more irregular shaped juxtacostal cells, and 4) more squarrose leaves. *Leucoloma mafatense* has been confused with *L. bifidum*, a sympatric species. The latter has a more slender, flexuose, delicate habit; narrower hyaline margins; narrower leaf bases; and papillae in irregular transverse rows restricted to the basal portion of the leaf.

Variation: The color of the plants varies from light green, tan, to a dark brown. There is little variation in the available material.

Habitat: *Leucoloma mafatense* is corticolous on trees or branches in montane rainforests. It has an elevation range between 1100-1800 m.

Distribution: *Leucoloma mafatense* is an endemic species known from Réunion.

Specimens examined: RÉUNION: *Crosby and Crosby 8329* (ALTA), *8984* (ALTA, L, MO), *De Sloover 17.709* (Hb. De Sloover), *Een 190, 490, 495* (Hb. Een); *Richard 682* (BM - sheet # 6 as *bifidum*), *Rodriguez s. n.* (BM - sheet # 6 *ex* Hb. Renauld).

Leucoloma ochrobasilare Ren. Figures II.72-74

Rev. Bryol. 28: 91. 1901. **Type:** "Madagascar: Ambondrombomba (Betsileo), 1893 leg. Rev. Talazac, (1894 on all specimens!); Ambohimitombo (Tanala), alt. 1350-1440 m, 1895 leg. Forsyth-Major". **Lectotype:** *Rev. Talazac*, 1894 (PC! - Hb. Renauld) (lectotype chosen here!); **isotypes:** H-Br! (in part), PC! (Hb. Cardot in part), S! (in part); **syntype:** *Dr. Major Forsyth* (*ex* Hb. Levier), PC!

Leucoloma subtuberculosum Ren., Suppl. Prodr. Fl. Bryol. Madag. 16. 1909. *synon. nov.* **Type:** Madagascar: "Ambositra (Bestileo), Rev. Villaume, 1906 (Hb. Lacoutre)". **Lectotype:** PC! (Hb. Renauld) (lectotype chosen here!); **isotypes:** BR! (*ex* Hb. Cardot), PC! (Hb. Cardot, Hb. Thériot).

Plants small to medium sized, to 10 cm, in loose tufts, downwardly spreading, light green to pale yellow green, brown below. Stems red, blackened below, non-tomentous; in transverse section central strand lacking, outer cortical cells of 3-4 layers, red-brown, thick-walled, inner cortical cells yellow-orange, yellow to hyaline, larger lumened; branching sympodial from 1-2 (4) subapical innovations, commonly at right angles to supporting axis. Rhizoids few, smooth red-brown, restricted to the base of stem or branch.

Leaves 0.65-1.30 mm wide, 3-5 mm long, narrowly to broadly ovate-lanceolate or elliptic-lanceolate, gradually tapering to a short to long, subtubulose to terete acumen; habit squarrose, wide-spreading to patent, some specimens more or less secund, distally flexuose, crisped, or spirally twisted when dry; habit wide-spreading to patent, +/- secund when wet. Margins entire below, distally serrulate, with a narrow hyaline border 2.5-12.0 µm wide. Costa 24-72 µm wide at base, subpercurrent to shortly excurrent; transverse section plano-convex, abaxial and adaxial stereid bands in 1-3 layers, guides 4-5, obliquely oriented, with 1-3 bistratose or multistratose rows in transition to the laminal cells. Juxtacostal cells 5-10 µm wide, 7-24 (36) µm long, isodiametric or irregularly angled, oblong to short elongate, walls irregularly thickened, angular to irregularly sinuose (porose) toward the basal region, increasingly thick-walled and longer basally, abaxial surface somewhat densely papillose above, less densely papillose basally, typically unipapillose basally to bi- or pluripapillose above, papillae simple to multifid, adaxial surface with scattered, sparse papillae, more densely papillose distally; juxtacostal bands extending to the basal region, sharply defined at base or grading into basal and interior cells. Interior and basal cells 5.0-9.6 µm wide, 19-72 µm long, elongate, smooth, tinged, slightly porose or not, or slightly sinuose, inner basal cells slightly thicker walled. Marginal cells 2.5-3.6 µm wide, 168-240 µm long, linear, hyaline, smooth. Alar cells 12-19 µm wide, 12-72 µm long, quadrate to rectangular, red-brown (hyaline marginally), scalariform; alar region 16-27 cells wide, 7-15 cells long, sometimes reaching the costa.

Dioicous. Perichaetia terminal; perichaetial leaves 0.4-0.8 mm wide, 2.0-4.5 mm long, ovate-lanceolate to lanceolate tapering gradually to an acuminate, setaceous, stiffly erect acumen, bases clasping, basal portion of leaf red to orange brown, more or less with porose cells. Perigonia not seen.

Sporophytes mono- or polysetous. Seta 0.3-0.9 mm long, stout, slightly twisted to the right, opaque, brown to tan. Capsules 0.6-0.8 mm wide, 1.0-1.2 mm long, immersed, ovoid to short cylindric, brown. Operculum 0.5-0.6 mm long, conic to shortly rostrate, erect, brown. Peristome 16 asymmetric teeth, 0.5 mm long, 48-84 µm at base bifid, split nearly to base, distally filiform, red- to orange-brown; PPL surface smooth or vertically pitted striate at base, becoming strongly papillose distally; IPL basal surface smooth distally strongly papillose. Calyptra 1 mm long, mitrate, lobed at base, yellowish or hyaline below, dark red-brown and scabrous above, covering operculum on mature capsule. Spores 19-24 µm, finely granulose.

KEY TO INFRASPECIFIC TAXA OF *L. OCHROBASILARE* REN.

1. The basal PPL surface of peristome smooth; papillose juxtacostal cells ending in mid leaf to lower basal region, 7-36 µm long, rounded, oblong to shortly elongate, thick-walled, irregularly sinuose; stem leaves flexuose to spirally twisted with acumen short; costa mostly 24-48 µm wide at base; hyaline margin ending as a single cell just below the apex .... subsp. *ochrobasilare*

1. The basal PPL surface of peristome vertically pitted striate; papillose juxtacostal

cells reaching the lower basal region, 5-14 µm long, triangular, quadrate, oblong, not distinctly thick-walled, irregularly thick-walled, angular; stem leaves often tightly spirally twisted with acumen long and gradually tapered; costa stout, 48-72 µm wide at base; hyaline margin ending at the base of acumen .... subsp. *longifolium*

Leucoloma ochrobasilare ssp. *ochrobasilare*

Nomenclatural notes: The type material of *Leucoloma ochrobasilare* ssp. *ochrobasilare* is a mixture with *L. subchrysobasilare*. This has been a source of confusion for the concept of *L. ochrobasilare*, which caused Renauld and Cardot (1915) to place *L. subchrysobasilare* in synonymy with it. Since then, the erroneous concept of *L. ochrobasilare* has been that of *L subchrysobasilare*. In Renauld's discussion of *L. ochrobasilare*, he placed it within section *Euvittata* Ren. (= section *Leucoloma*), but explained that it has papillae on both surfaces, atypical of the subgenus (Renauld 1901). The placement of *L. ochrobasilare* within section *Dichelymoidea*, here, conforms to the key characters of the section.

Plants small to medium sized, to 10 cm, in loose tufts, downwardly spreading, light green to pale yellow green, brown below. Stems with sympodial branches of 1-2 (4) subapical innovations, commonly perpendicular to supporting axis. Rhizoids few, restricted to the base of stem or branch.

Leaves 0.7-1.3 mm wide, 3.0-4.5 mm long, ovate-lanceolate to broadly ovate-lanceolate or elliptic-lanceolate, gradually tapering to a short, subtubulose acumen, distally secund, flexuose, crisped, or spirally twisted. Margins plane, entire below, serrulate distally, with hyaline border ending just below apex. Costa 24-48 (60) µm wide at base, subpercurrent to shortly excurrent, with 1-2 bistratose rows in transition to the laminal cells, or lacking. Juxtacostal cells 5-10 µm wide, 7-24 (36) µm long, isodiametric, oblong to short elongate, irregularly thickened, angular or not, thicker walled and longer basally; differentiated juxtacostal bands extending to upper basal region and grading into basal cells laterally and basally.

Sporophytes mono- or polysetous. Seta 0.3-0.9 mm long, stout, slightly twisted to the right, opaque, brown to tan. Capsules 0.6-0.8 mm wide, 1.0-1.2 mm long, immersed, oval, oblong to short cylindric, brown. Operculum 0.5-0.6 mm long, conic to shortly rostrate, erect, brown. Peristome 16 asymmetric teeth, 0.5 mm long, 48-84 µm wide at base, bifid, split nearly to base, distally filiform, red- to orange-brown. PPL surface smooth basally, distally strongly papillose; IPL basal surface smooth distally strongly papillose. Calyptra 1 mm long, mitrate, lobed at base, yellowish hyaline below, dark, reddish brown and scabrous above, covering operculum on mature capsule. Spores 19-24 µm, finely granulose.

Diagnostic Characters: *Leucoloma ochrobasilare* ssp. *ochrobasilare* can be distinguished by the following characters: 1) stems typically with 2 subapical innovations, at right angles to the supporting axis (appearing dichotomous); 2) leaves with spaced papillae arranged in irregular transverse rows; and 3) abaxial papillae not as prominent as in *L. tuberculosum* (thus the dorsal corrugated profile is less pronounced). Renauld compared *L. subtuberculosum* (= *L. ochrobasilare ssp. ochrobasilare*) to *L. tuberculosum* and stated that the former had leaves "non ridées en travers, et par les papilles denses simplement bifides et beaucoup moins saillantes sur la face dorsale". The less prominent papillae still show the pattern of transverse rows. The narrow, hyaline margin distinguishes this species from *L. mafatense*, as well the abaxial papillae are less prominent. The leaves are broad at the base and taper distally to a more or less short acumen, which can be twisted or curled, but mostly lacking the tightly spirally twisted leaves of *L. ochrobasilare* ssp. *longifolium*. The differentiated juxtacostal cells are oblong to irregularly shaped, thick-walled, more less porose/sinuose toward the base, and end well above the leaf base. Fruiting material shows the basal PPL surface of the peristome is smooth, unlike *L. ochrobasilare* spp. *longifolium*, which is clearly vertically pitted-striate. As well the hyaline margin ends just below the apex, whereas in *L. o.* spp. *longifolium* the hyaline margin ends at the base of the acumen. *Leucoloma ochrobasilare* was originally placed in *L.* subg. *Taeniodictyon* sect. *Obscura* based on the parallel juxtacostal bands that end just above the base. The lack of opaque papillae equally developed on the ab- and adaxial surfaces of the juxtacostal cells distinguishes this species from those in section *Attenuata* or section *Obscura*. From the species in sections *Subvittata* and *Leucoloma*, it has scattered, prominent, adaxial papillae in the mid leaf region. The former 2 sections have species with smooth adaxial surfaces at mid-leaf. The distinct, unipapillose juxtacostal cells also occur in section *Albescentia*, yet the longitudinally thick-walled alar cells, immersed capsules, seta transverse section with single outer layer of thick-walled cells, and mitrate calyptrae, clearly exclude it from that taxon.

Variation: The typical branching pattern shows 2 subapical innovations at right angles to the supporting axis. The range of variation within the specimens observed shows that the branching pattern can have up to 4 subapical innovations, which are not always at right angles to the supporting axis. The distal portion of the leaves are either spirally twisted (though never tightly so) or flexuose to curled. The dry leaf habit varies from squarrose to patent. The extent of papillose juxtacostal cells varies from the midleaf to the lower basal region.

Habitat: *Leucoloma ochrobasilare* ssp. *ochrobasilare* is corticolous, and ramicolous on trees in primary or degraded montane rainforests with an elevation range of 1300-1650 m. It has been found growing with 3 other species of *Leucoloma*: L. *grandidieri*, *L. talazaccii*, and *L. tuberculosum*.

Distribution: *Leucoloma ochrobasilare* ssp. *ochrobasilare* is endemic to the eastern rainforests of central Madagascar and has been found between 20° 49' S and 21°15' S.

Specimens examined: MADAGASCAR: Prov. Tananarive: *Benoist 580* (ALTA, PC); *Cremers 1685* (Hb. Onraedt); *Tixier 10752, 11836, 11839* (ALTA, PC); **Prov.**

Fianarantsoa: *Crosby & Crosby 6827, 6960* (ALTA, MO), *6998* (ALTA, L, MO); *Onraedt 70.M.030, 71.M.5309, 71.M.5311, 71.M.5312* (Hb. Onraedt); *Onraedt 71.M.5310* (F); *Tixier 9192, 10115* (ALTA, PC); **Prov. Tamatave:** *Tixier 10660, 12756, 12319* (ALTA, PC).

Leucoloma ochrobasilare* ssp. *longifolium (Thér.) La Farge-England ***comb. nov.***

Basionym: *Leucoloma subtuberculosum* var. *longifolium* Thér., Recueil Publ. Soc. Havraise Études Diverses 1925: 133, ic. 1926. **Type:** "Madagascar: Mt. Tsaratanana, 1200-2400 m, M. Perrier de la Bathie, avril 1924, "dans la forêt à sous-bois herbacé". **Lectotype:** PC! (Hb. Thériot, # 189)(lectotype chosen here!); **isotypes:** FH!, G!, H-Br!, JENA!, PC! (Hb. P. Varde), S! (2 specimens).

Nomenclatural notes: Thériot described the variety from a single collection by M. Perrier de la Bathie. Subsequently the material was divided into 8 duplicates and distributed to a number of herbaria. The variety is transferred here to the subspecific rank of *Leucoloma ochrobasilare*, emphasizing its restricted distribution and distinguishing characters of the sporophyte and gametophyte. In addition, the lack of sympatric populations of two subspecies supports their divergence. I refrain from elevating the taxon to specific rank based on a single collection.

Plants medium sized, to 10 cm, in loose tufts, downwardly spreading, light green to pale yellow-green above, brown below. Stems with sympodial branches of 1-2 subapical innovations, commonly perpendicular to supporting axis. Rhizoids few, restricted to the base of stem or branch.

Leaves 0.65-0.95 mm wide, 3.5-5.0 mm long, ovate lanceolate, tightly spirally twisted leaves with a terete acumen. Margins entire below, serrulate distally, with hyaline border that ends at the base of the acumen. Costa 48-72 µm wide at base, subpercurrent to percurrent, with 1-4 rows of bi- or multistratose transitional cells between the guides and laminal cells,. Juxtacostal cells irregularly angled, isodiametric; juxtacostal bands extending to lower the basal region, remaining sharply defined from interior and basal cells.

Sporophytes mono- or polysetous. Seta 0.7-0.9 mm long, stout, slightly twisted to the right, opaque, brown to tan. Capsules 0.6 mm wide, 1.0-1.2 mm long, immersed, oval, oblong to short cylindric, brown. Operculum 0.5-0.6 mm long, conic to shortly rostrate, erect, brown. Peristome teeth: PPL vertically pitted striations at base, distally papillose; IPL: smooth at base, distally papillose.

Diagnostic characters: *Leucoloma ochrobasilare* spp. *longifolium* is distinguished by 1) leaves with low abaxial papillae that are developed in more or less transverse rows across the lamina, 2) scattered adaxial papillae, 3) differentiated juxtacostal bands extending to the alar region, 4) narrow hyaline margins that end at the base of the acumen, 5) terete acumina that are tightly spirally twisted, and 6) vertically pitted base of the peristome PPL surface. See *Leucoloma ochrobasilare* spp. *ochrobasilare* for differentiating characters and comparison to other species.

Habitat: *Leucoloma ochrobasilare* ssp. *longifolium* is an epiphyte on trees in montane rainforests with an elevation range of 1200-2400 m.

Distribution: *Leucoloma ochrobasilare* ssp. *longifolium* is known from a single collection in an isolated locality in the northern part of Madagascar on the highest massif, Mt. Tsaratanana.

Leucoloma tuberculosum Ren. Figures II.75-76

Prodr. Fl. Bryol. Madag. 71. 1898. **Type:** Madagascar: "Forêt de Analamazaotra Camboué et Campenon, 1891". **Holotype:** PC! (Hb. Renauld); **isotype:** PC! (Hb. Cardot).

Leucoloma levieri Ren., Rev. Bryol. Lichénol. 28: 91. 1901, *synon. nov.* **Type:**

"Hab. Madagascar, in silva Fito (dit. Tamatave) July 1897, leg. Perrot". **Holotype:** PC! (Hb. Renauld); **isotypes:** BR!, H-Br!, PC! (Hb. Cardot - 2 specimens), S! (2 specimens).

Nomenclatural notes: The type specimens designated as "Hb. F. Renauld" in PC are typified as the respective holotypes of *Leucoloma tuberculosum* and *L. levieri*.

Plants medium sized, to 11 cm, in loose tufts or gregarious stems, downwardly outspreading, green to pale yellow-green or tan above, tan to brown below. Stems red, blackened below; central strand lacking, outer cortical cells 3-4 layers red-brown, thick-walled, inner cortical cells hyaline-yellow, larger lumened; sympodial branching from 1-4 subapical innovations, monopodial branching lateral. Rhizoids smooth, red-brown, few, restricted to the base of stem or branch, or 1-2 robust (42 µm wide) in leaf axils.

Leaves 0.6-1.0 mm wide, 3.0-5.0 mm long, narrowly or broadly ovate-lanceolate to elliptic or elliptic-lanceolate, concave, gradually tapering to a short or long, subtubulose, fine point; habit squarrose to patent leaf bases with flexuose, curled or incurved acumen when dry, wide-spreading to patent, stiff distally, when wet. Margins entire, or distally serrulate or with small serrations, with a narrow hyaline border, 5-22 µm wide. Costa 36-60 µm wide at base, subpercurrent to long excurrent, translucent; transverse section plano-convex, abaxial and adaxial stereid bands in 1-3 layers, guides 4, obliquely oriented, with 1 row of bistratose cells in transition to laminal cells. Juxtacostal cells 5-10 µm wide, 6-14 (17) µm long, isodiametric oblong to shortly elongate, rounded to angled, lengthening near base, abaxial surface strongly corrugated, uni- to bipapillose, papillae simple to multifid, acute or stalked, strongly prominent on abaxial surface in irregular, transverse rows, less prominent and scattered on adaxial surface, papillae reaching the base of the leaf, juxtacostal broad bands to the basal region. Interior and basal cells 5-7 µm wide, (17) 24-60 (84) µm long, smooth, elongate to linear, tinged, slightly porose or non-porose. Marginal cells 2.5

µm wide, 168-204 µm long, linear, smooth, hyaline. Alar cells 10-18 µm wide, 12-55 (72) µm long, quadrate to rectangular, red-brown to hyaline at margin, scalariform; alar region 16-28 cells wide, 6-13 cells long, reaching the costa in some leaves, strong, angled orientation to basal cells.

Dioicous. Perichaetia terminal; perichaetial leaves 0.5-0.6 mm wide, 3.5-4.5 mm long, ovate-lanceolate abruptly to gradually tapering to a long, fine point, stiffly erect, bases clasping, orange-brown, with porose cells. Perigonia terminal or terminal on short, lateral branches; perigonial leaves 0.6 mm wide, 1.3-3.5 mm long, orbicular to ovate leaf bases, abruptly contracted to a short or long, fine acumen, bases strongly concave.

Sporophyte mono- or polysetous. Seta 2 mm long, stout, red-brown, opaque, slighlty twisted to the right; transverse section with a single outer layer of thick-walled cells. Capsules 1.3-1.5 cm long, emergent to shortly exserted, ovoid to short cylindric, brown. Operculum 0.5 mm long, rostrate, erect, brown. Peristome 16 asymmetric teeth, 72 µm wide at base, bifid, red-brown, split 1/2 to 3/4 of length, distally filiform; PPL vertically pitted striate at base, distally papillose; IPL: smooth at base, distally striate. Calyptra not seen. Spores not seen.

Diagnostic Characters: *Leucoloma tuberculosum* can be easily distinguished by its sparsely papillose juxtacostal cells with abaxial, prominent papillae arranged in irregular transverse rows, forming a pronounced, corrugated abaxial surface. None of the remaining species within section *Dichelymoidea* has as prominent papillae.

Variation: The most variable character of this species is the length of the excurrent costa. Within the type material the costa can be subpercurrent to distinctly excurrent. An extreme expression has been found in specimens from Marojezy which have slender leaves with long, excurrent costae. The upper margin also has a high degree of variation from apices that are entire and smooth to those that are sparsely serrulate or distinctly toothed with small serrations. This variation can be expressed within a single specimen. The leaf shape varies from broadly elliptic with a short acumen to narrowly ovate-lanceolate with a long, slender acumen. There are a few specimens which have hyaline margins reaching 24 µm wide, although most of the leaves have very narrow margins 5-12 µm wide. The dry habit varies with leaves squarrose to patent. Usually the lower leaves are more squarrose than the distal leaves, with some specimens more distinctly squarrose than others.

The type material of *Leucoloma levieri* falls within the variation of characters for *L. tuberculosum*, including the leaf shape, shape of the acumen, and prominence of the abaxial papillae. The Marojezy material has slender leaves opposed to the broadly elliptic expression found in most of the Andasibe material. There is a correlation between the excurrency of the costa and the slenderness of the leaf.

Leucoloma grandidieri and *L. tuberculosum* both have an undulate abaxial surface of the juxtacostal bands as a result of different characters. In *L. tuberculosum* the papillae are arranged in transverse rows and are distinctly spaced. They develop at the ends of the cells, at the proximal end of one and the distal end of the adjacent cell basal to it. The papillae are hollow, acute to multifid. These cells have a strong tendency to be unipapillose with the papillae forming over the cell lumina, but are not necessarily centered over them. The adaxial surface is smooth or has only scattered low papillae; this results in differentially papillose surfaces, that are strongly corrugated (Figs. II.75.c,i; 5f). This is differentiated from the rugose juxtacostal bands of *L. grandidieri* that has opaque, dense, low papillae equally developed on the abaxial and adaxial surfaces. These papillae are solid thickenings (Figs.II.58a; 5c).

Habitat: *Leucoloma tuberculosum* is corticolous on branches, small twigs, stilt roots, tree fern trunks, and tree trunks at the base less than 2 meters above the forest floor, as well as on rotting stumps, in lowland or montane rainforests with an elevation range of 200-1050 m.

Distribution: *Leucoloma tuberculosum* has been collected from the natural reserve, Tahiry Nanaharin'i Marojezy, in northeastern Madagascar, south along the east coast to the special reserve of Analamazaotra, and without locality in the Prov. of Fianarantsoa. Renauld and Cardot (1915) cited a specimen, *R.P. Villaume*, Ambositra, Prov. de Bestileo, although no specimen was seen in PC!

Specimens examined: MADAGASCAR: Prov. Diégo Suarez: *La Farge-England 6135, 6266* (ALTA, MO, TAN); **Prov. Tamatave**: *La Farge-England 5481, 5742, 5828* (ALTA, MO, TAN); *Crosby & Crosby 6688, 6998,* (MO); *Croat 32318A* (MO); *Tixier 11704, 11725, 11727* (PC); **Prov. Fianarantsoa:** *indigen. collect.* dat. 1900 com. Paris (NSW), #15 Madagascar Prov. de Fianarantsoa, *ex* Hb. Paris (PC - Hb. F. Renauld), Madagascar Prov. de Fianarantsoa, *ex* Hb. Paris (G, FH); Hb. F. Renauld, dat. 1899 (H-Br, S), Madagascar, Prov. de Fianarantsoa, com. Paris (H-Br, S).

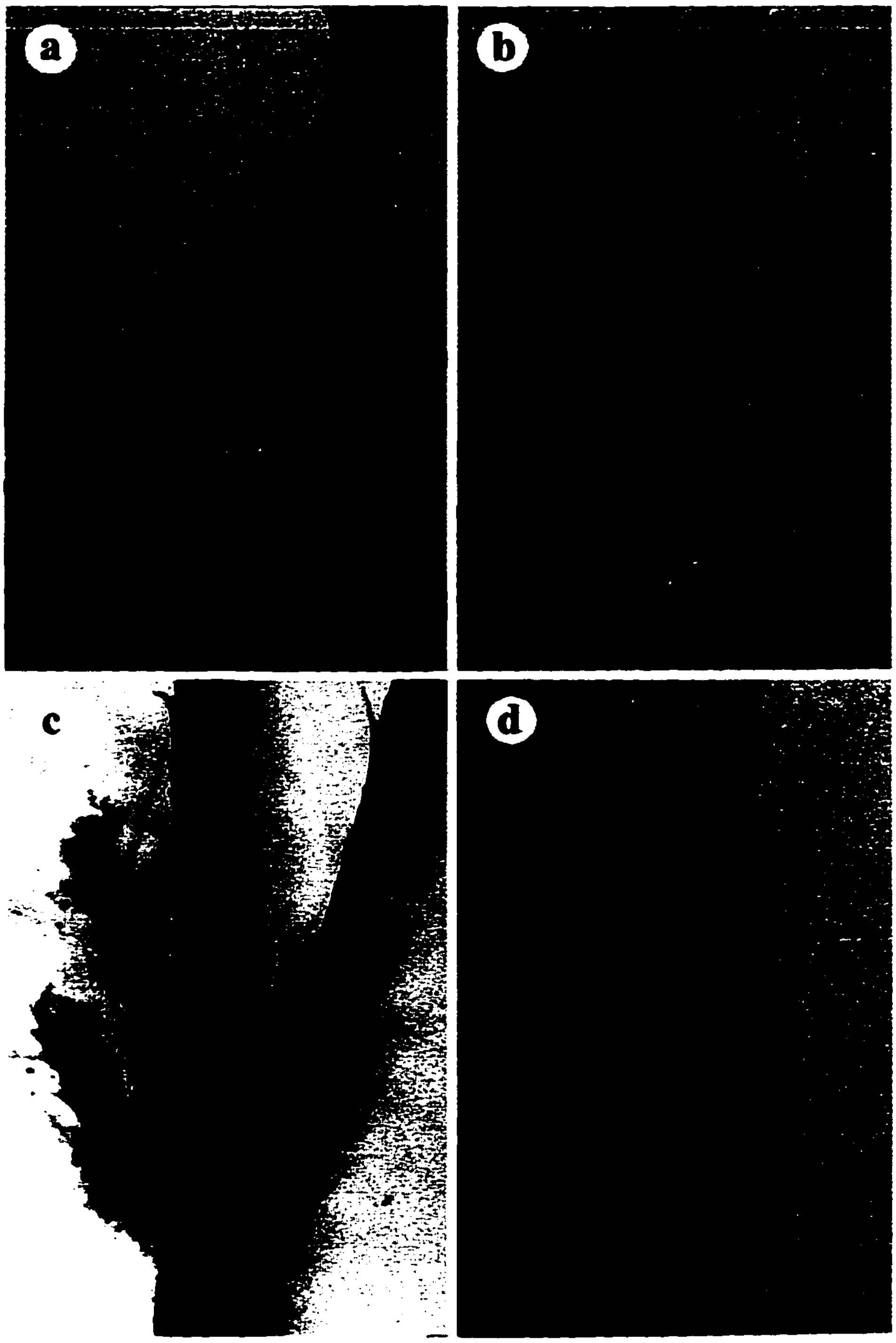


Figure II.1 a-d. Branching patterns in *Leucoloma*: a) *L. sanctae-mariae* with two subterminal innovations (*La Farge-England 6201* ALTA); b) *L. albo-cinctum* with a single subterminal innovation; c) *L. dichelymoides* with lateral monopodial branches; it also has single, sympodial branch below the terminal perichaetium (*La Farge-England 5960* ALTA); d) *L. humbertii* with monopodial branching along the main axis; this particular main axis lacked a terminal perichaetium at this stage of growth (*La Farge-England 6325* ALTA).

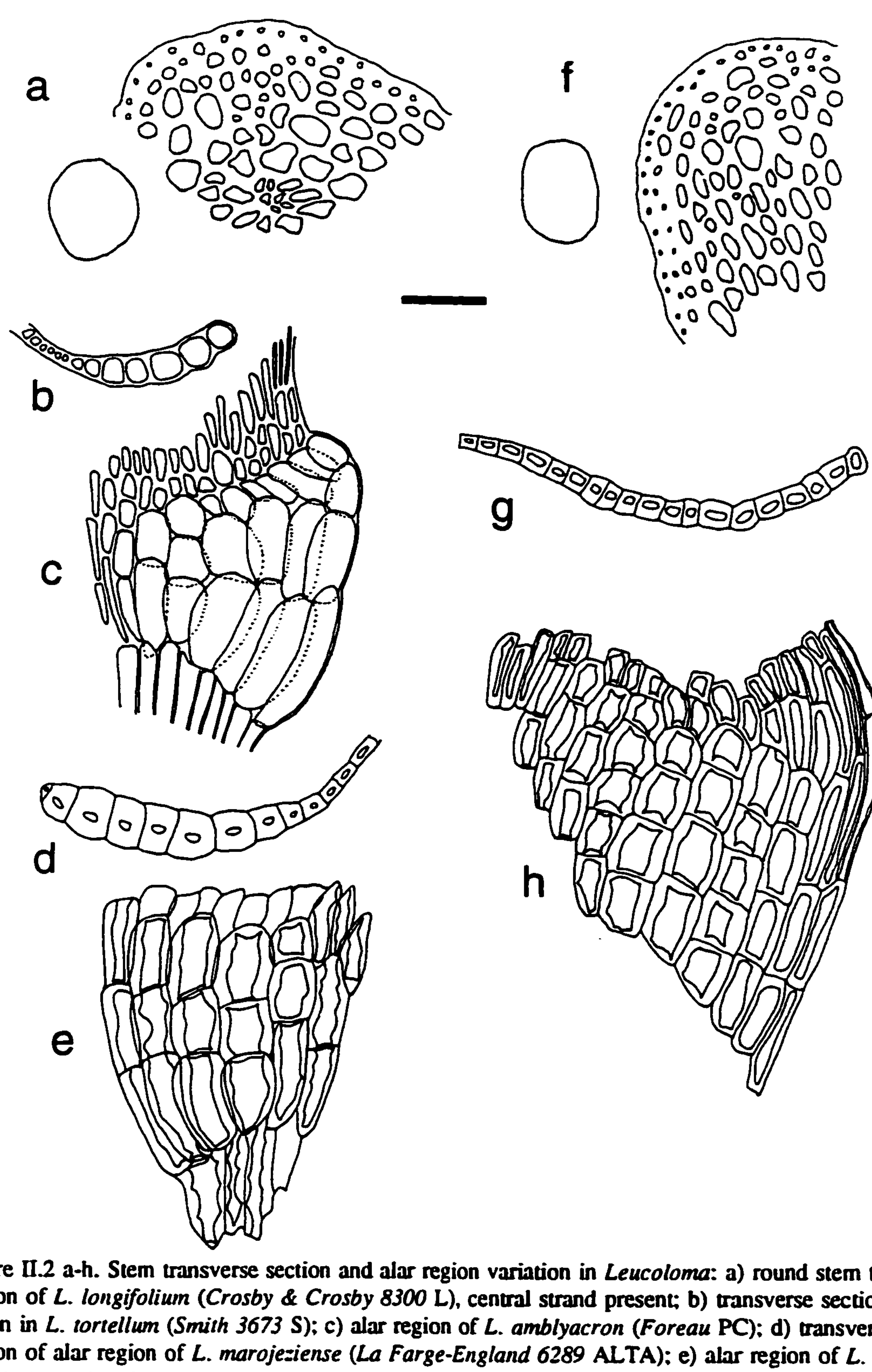


Figure II.2 a-h. Stem transverse section and alar region variation in *Leucoloma*: a) round stem transverse section of *L. longifolium* (*Crosby & Crosby 8300* L), central strand present; b) transverse section of alar region in *L. tortellum* (*Smith 3673* S); c) alar region of *L. amblyacron* (*Foreau* PC); d) transverse section of alar region of *L. marojeziense* (*La Farge-England 6289* ALTA); e) alar region of *L. marojeziense* (*La Farge-England 6289* ALTA); f) elliptic stem transverse section of *L. chrysobasilare* (*Magill & Pócs 11636* ALTA), central strand lacking; g) transverse section of *L. zuluense* (*La Farge-England 5385* ALTA); h) alar region of *L. grandidieri* (*Crosby & Crosby 6782* FH). Scale bar = 48µm.

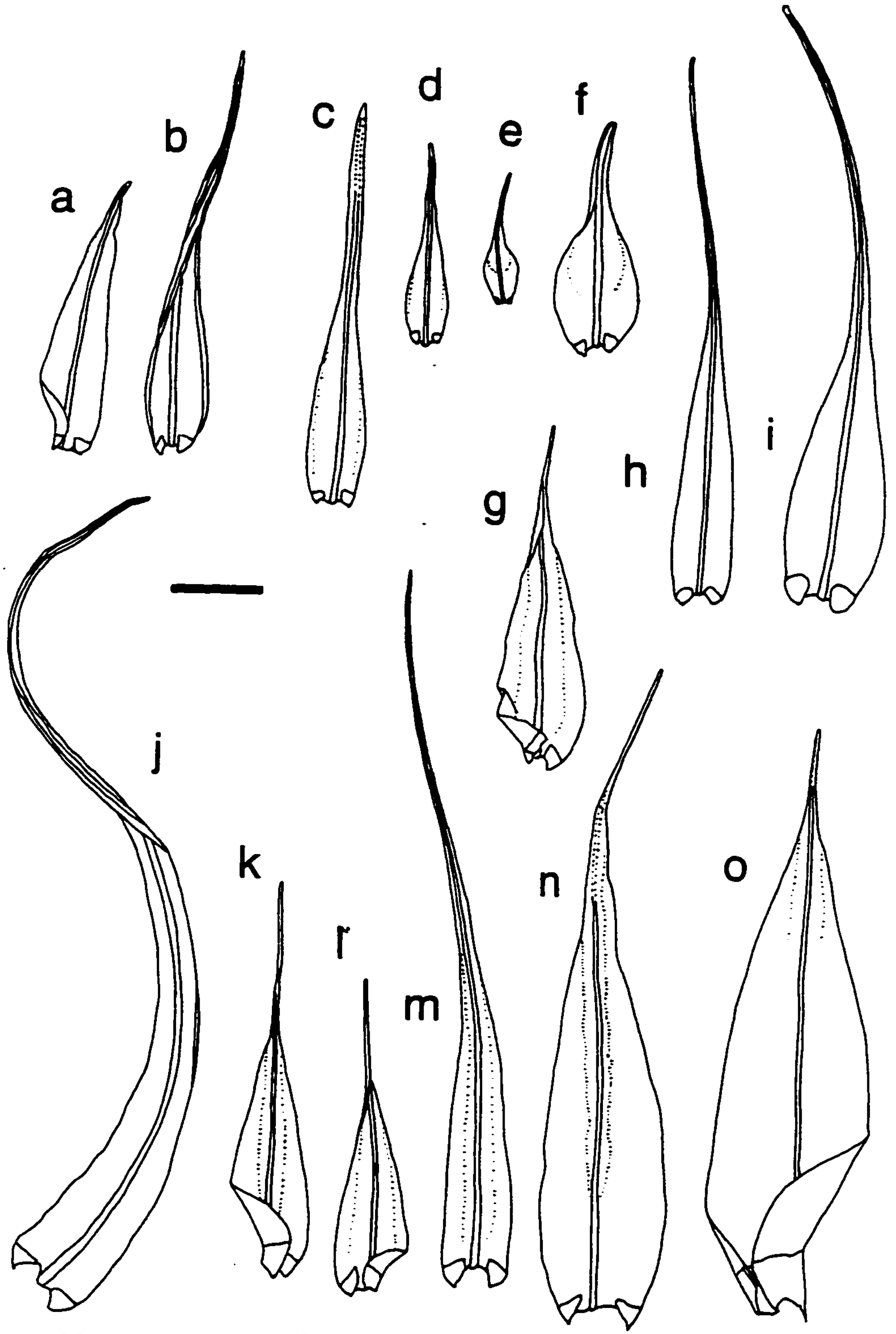


Figure II.3 a-o. Variation of leaf shape in *Leucoloma*: a) *L. amblyacron* (*Robillard* BM); b) *L. candidulum* (*Robillard* BM); c) *L. tortellum* (*Goffinet 2852* ALTA); d) *L. sericeum* (*Jaeger 698* PC); e) *L. grimmioides* (*Crosby &Crosby 5644* MO); f) *L. cuneifolium* (*La Farge-England 5913* ALTA); g) *L. tuberculosum* (*Perrot* H-Br); h) *L. tenerum* (*Rev. Parish* NY); i) *L. fuscifolium* (*Duby* BM); j) *L. rutenbergii* var. *perrotii* H-Br); k) *L. seychellense* (*Schliechen 11809* BM); l) *L. lepervancheri* (*Lépervanche* BM); m) *L. chrysobasilare* (*Magill & Pócs 11702* ALTA); n) *L. grandidieri* (*La Farge-England 6292* ALTA); o) *L. fontinaloides* (*Onraedt 71.M.5315* Hb. Onraedt).

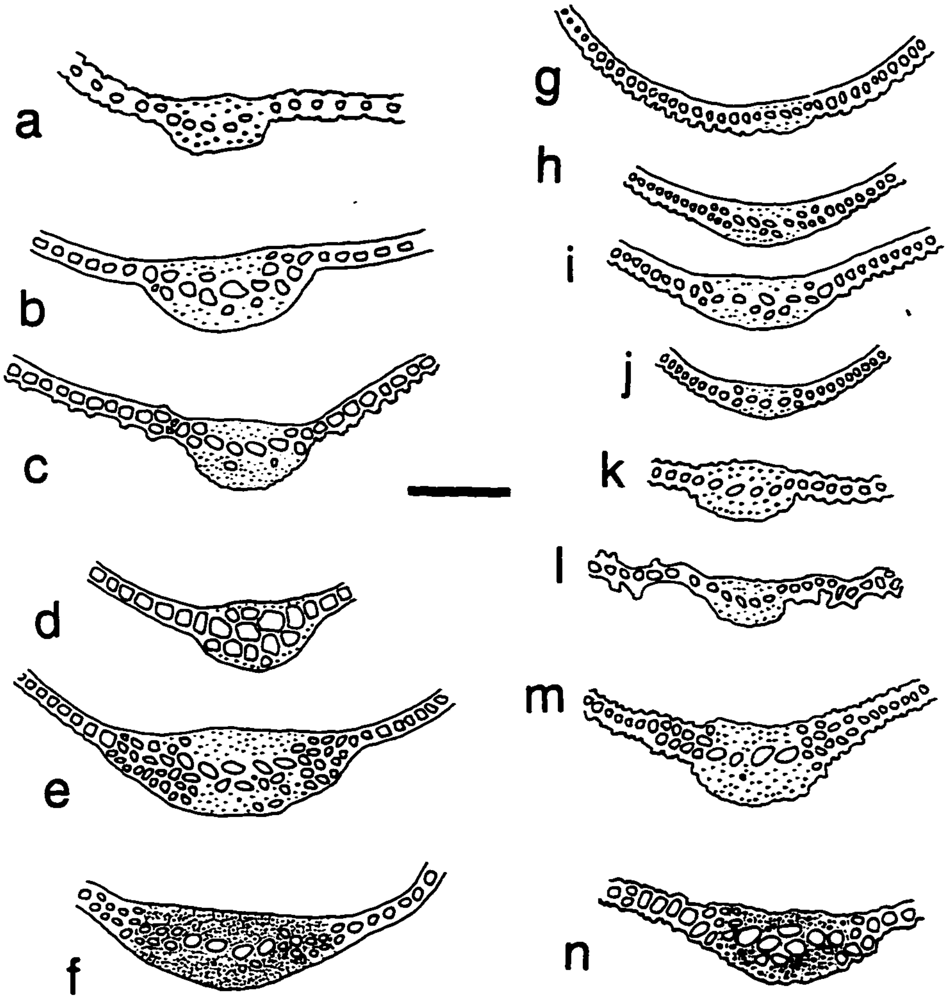


Figure II.4 a-n. Costal transverse section variation in *Leucoloma*: a) *L. marojeziense* (*La Farge-England 6374* ALTA); b) *L. taylorii* (*Touw 9457* MO); c) *L. amblyacron* (*Magill 11474* ALTA); d) *L. charrieri* (*Carrougeau* BM); e) *L. fuscifolium* (*Genet* FH); f) *L. longifolium* (*P. de la Bathie* FH); g) *L. lepervancheri* (*Perrot* PC); h) *L. madagascariense* (*La Farge-England 6235* ALTA); i) *L. subchrysobasilare* (*Borgen* L); j) *L. holstii* (*Pócs 90015/Z* EGR); k) *L. membranaceum* (*Een 494* Hb. Een); l) *L. tuberculosum* (*Crosby & Crosby 6688* ALTA); m) *L. crosbyi* (*Crosby & Crosby 7167* MO); n) *L. thuretii* (*Bernier* BM).

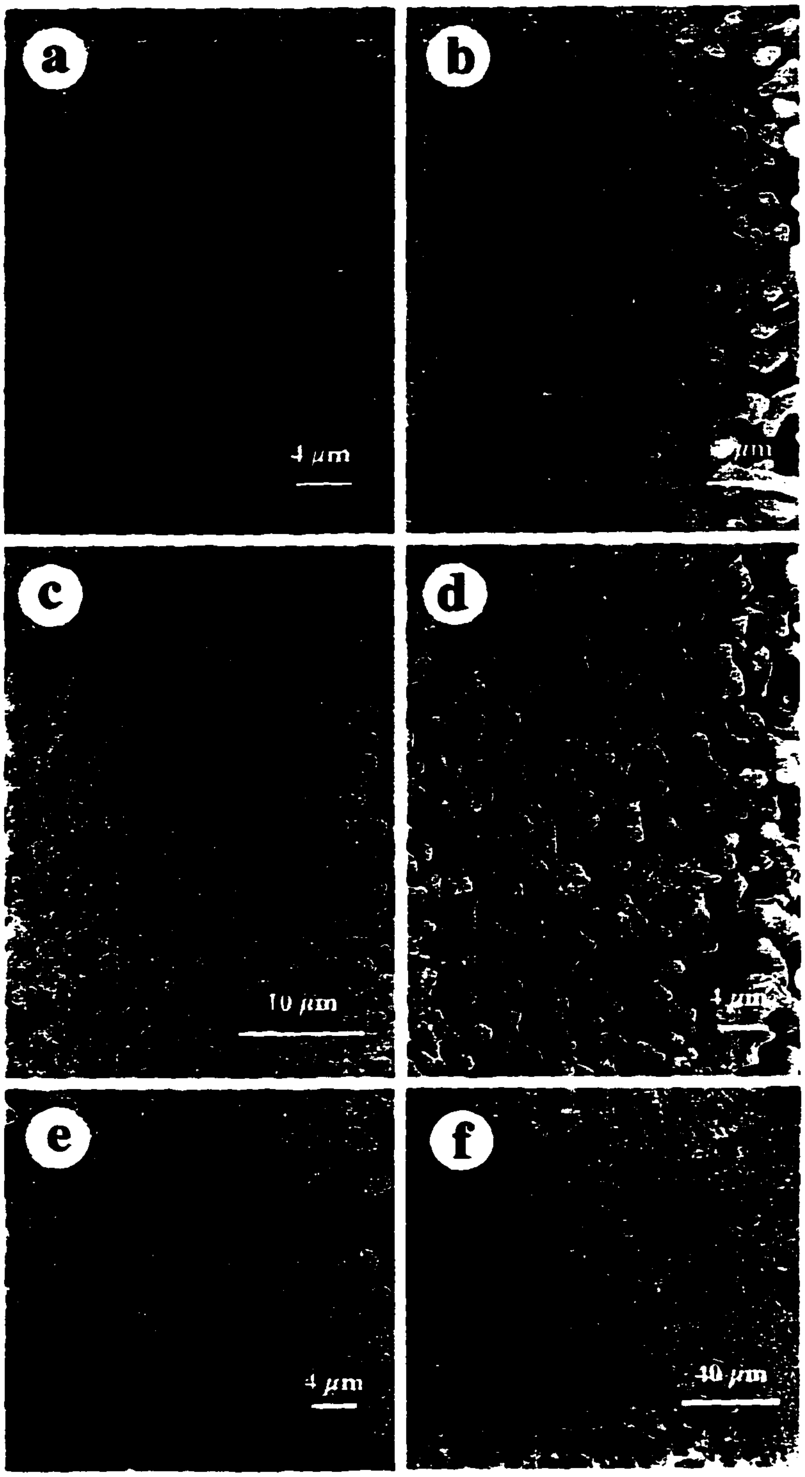


Figure II.5 a-f. Papillae variation in *Leucoloma*: a) stellate papillae of *L. scabricuspis* (*von Breitenbach 477* PRE); b) multifid papillae of *L. tortellum* (*Bermudez PA 00278* NY); c) low dense papillae of *Leucoloma grandidieri* (*Cremers 3108* Hb. Onraedt); d) low, dense, multifid papillae of *L. crosbyi* (*Crosby & Crosby 7167* ALTA); e) prominent abaxial papillae in distinct transverse rows of *L. mafatense* (*Crosby & Crosby 8329* MO); f) prominent abaxial papillae of *L. tuberculosum* (*Crosby & Crosby 6688* L).

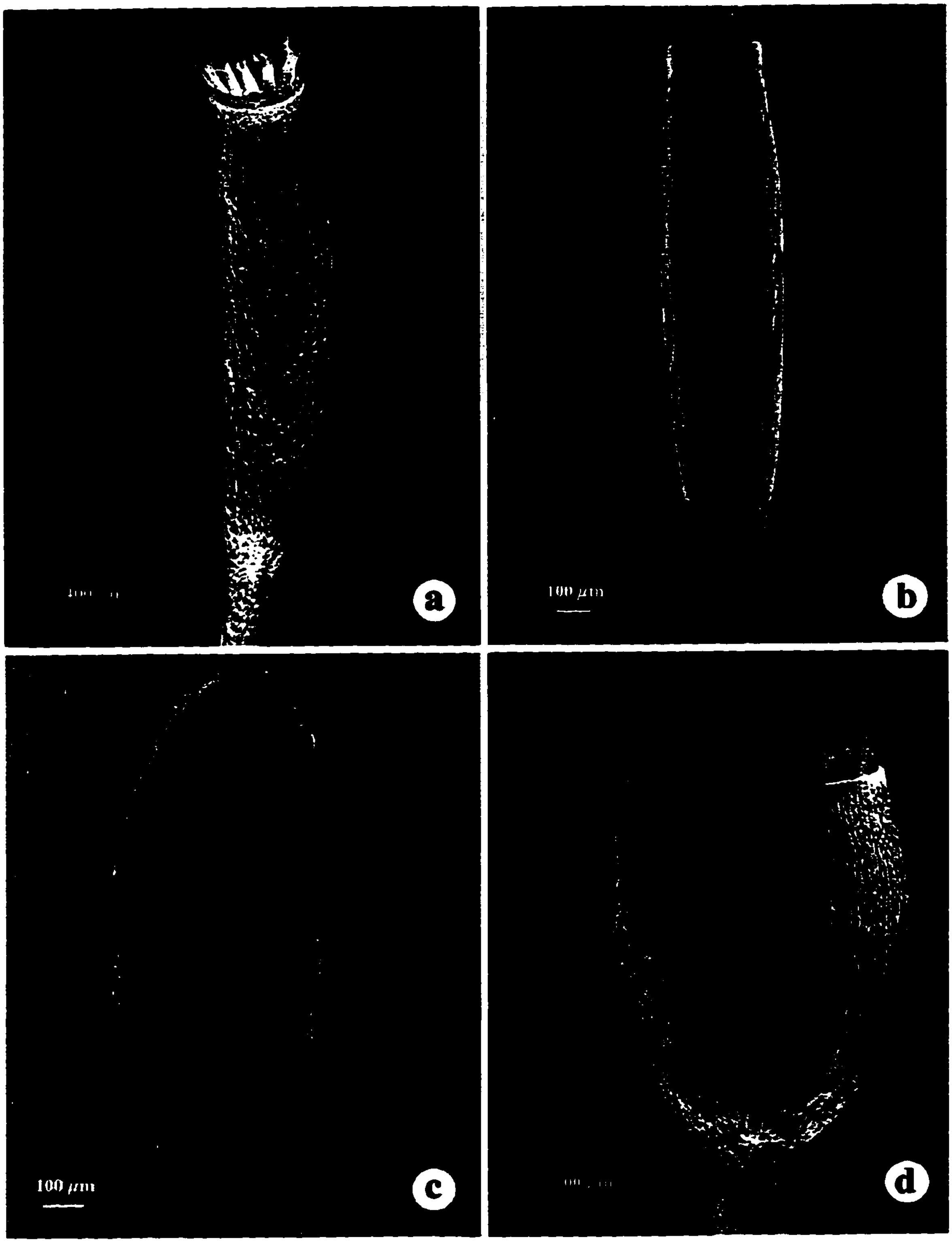


Figure II.6 a-d. Capsule shape variation in *Leucoloma*: a) *L. persecundum* (*Magill 11088* MO); b) *L. taylorii* (*Touw 10321* MO); c) *L. amoene-virens* (*Beckell* NSW); d) *L. grandidieri* (*Crosby & Crosby 6863* H).

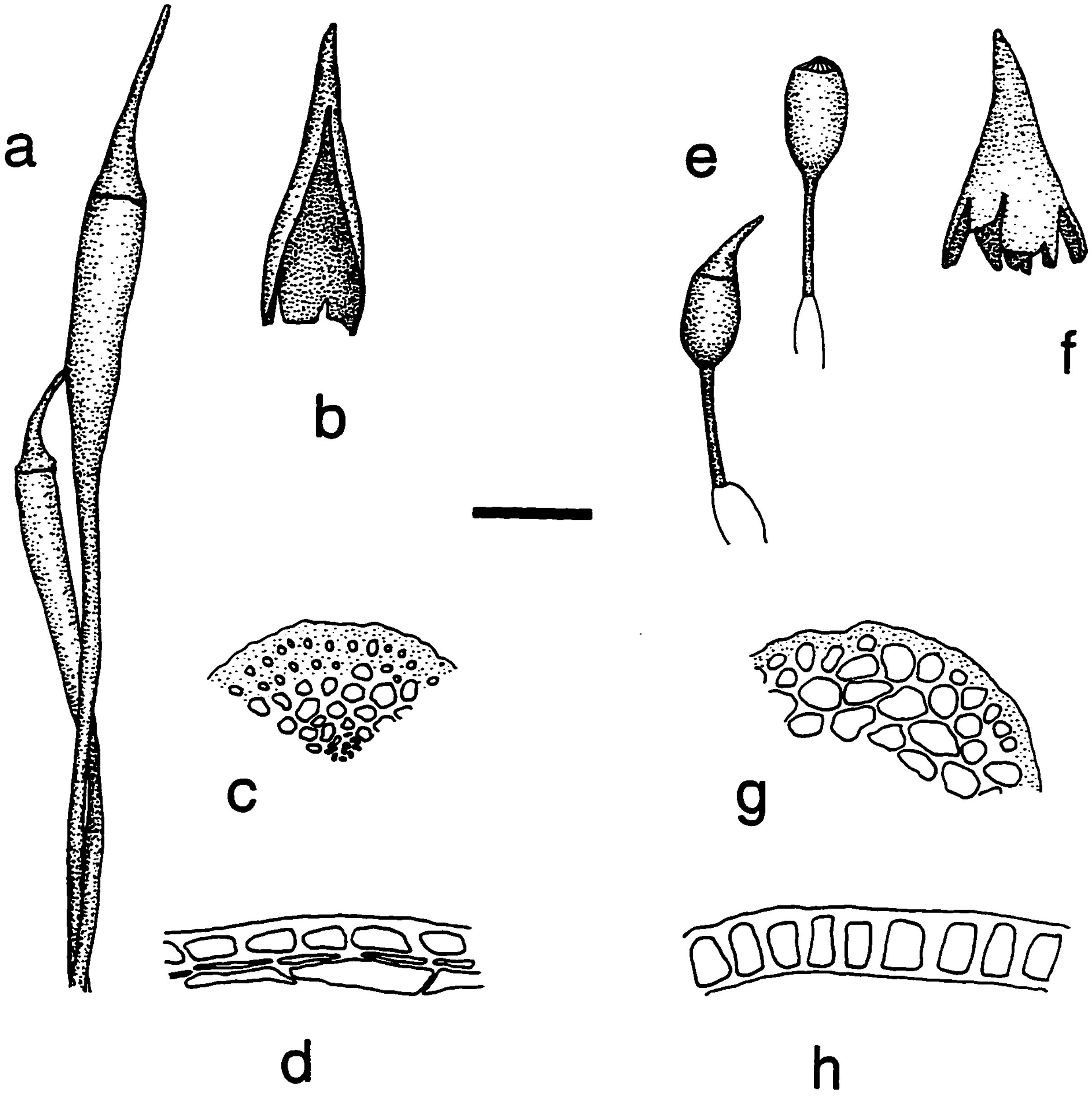


Figure II.7 a-h. Sporophyte characters of subgenus *Syncratodictyon* and subgenus *Leucoloma*: a) polysetous, cylindric capsules of *Leucoloma longifolium* (*Crosby & Crosby 8300* L); b) cucullate of *L. amoene-virens* (*Beinutt* NY); c) seta transverse section with several layers of eccentric outer cortical cells, thick-walled : *L. cunefolium* (*Tixier 11707* PC); d) transverse section with with longest dimension of outer cells parallel to capsule wall of *L. longifolium* (*Crosby & Crosby 8300* L); e) ovoid capsules of *L. holstii* (*O' Shea M7465a* E); f) mitrate calyptra of *L. schelpei* (*Müller 2578* PRE); g) seta transverse section of *L. tuberculosum* (*Camboué & Campenon* PC); h) transverse section with longest dimension of outer cells perpendicular to capsule wall of *L. subchrysobasilare* (*Tixier 9425* PC).

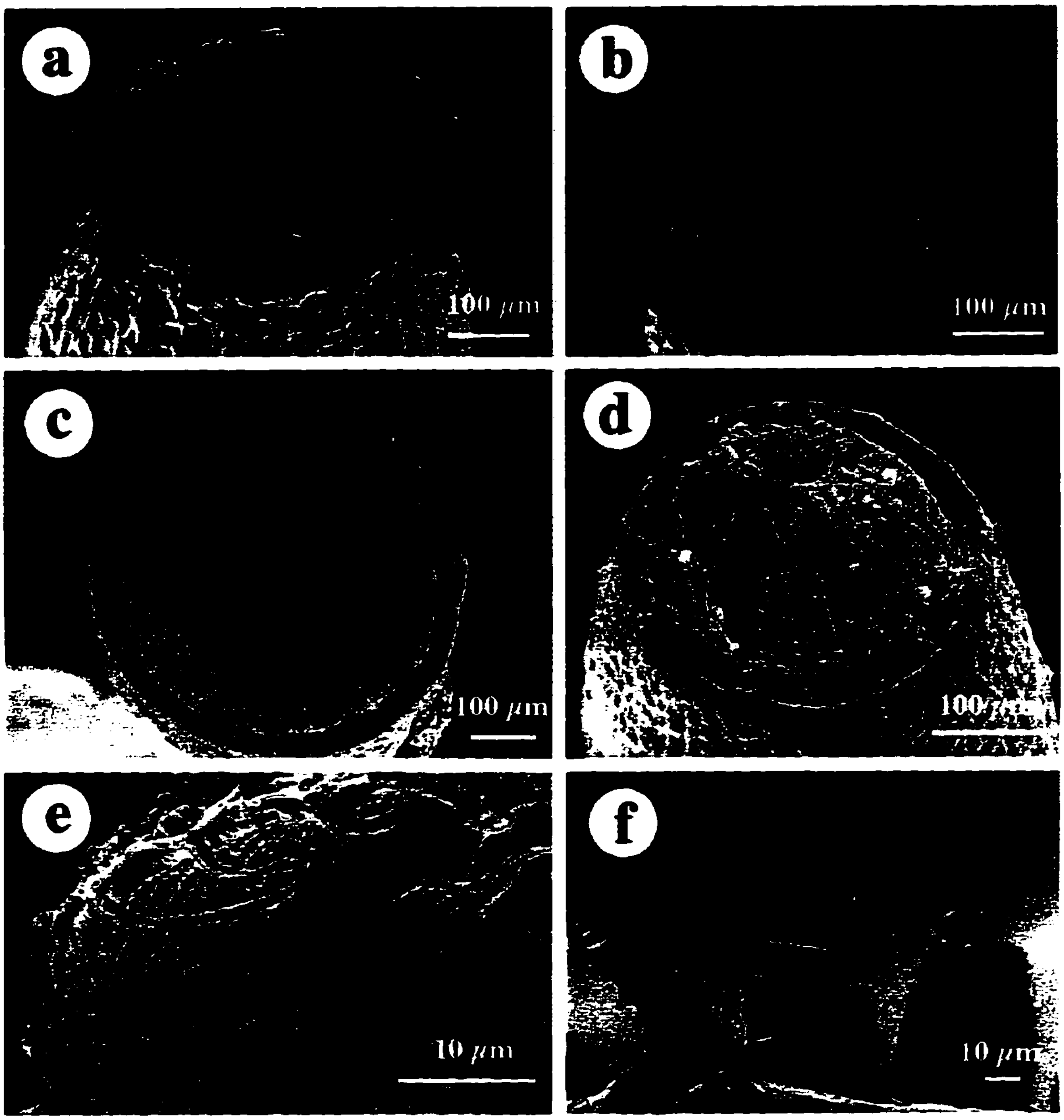


Figure.II.8a-f. Peristome variation in *Leucoloma*. a) Basally recurved teeth of *Leucoloma amoene-virens* (*Mueller 25* H-Br); b) reduced peristome of *Leucoloma chlorophyllum* (*Magill 11110* ALTA); c) the long, filiform peristome of *Leucoloma* cf. *secundifolium* (*La Farge-England 5605* ALTA); d) long filiform peristome of *Leucoloma zuluense* var. *zuluense* (*Crosby & Crosby 13410* MO); e) outer surface of peristome,PPL, pitted striate (*Leucoloma sprengelianum* (*Perold 1189* PRE); f) outer surface of peristome,PPL, smooth in *Leucoloma chlorophyllum* (*Magill 11110* ALTA).

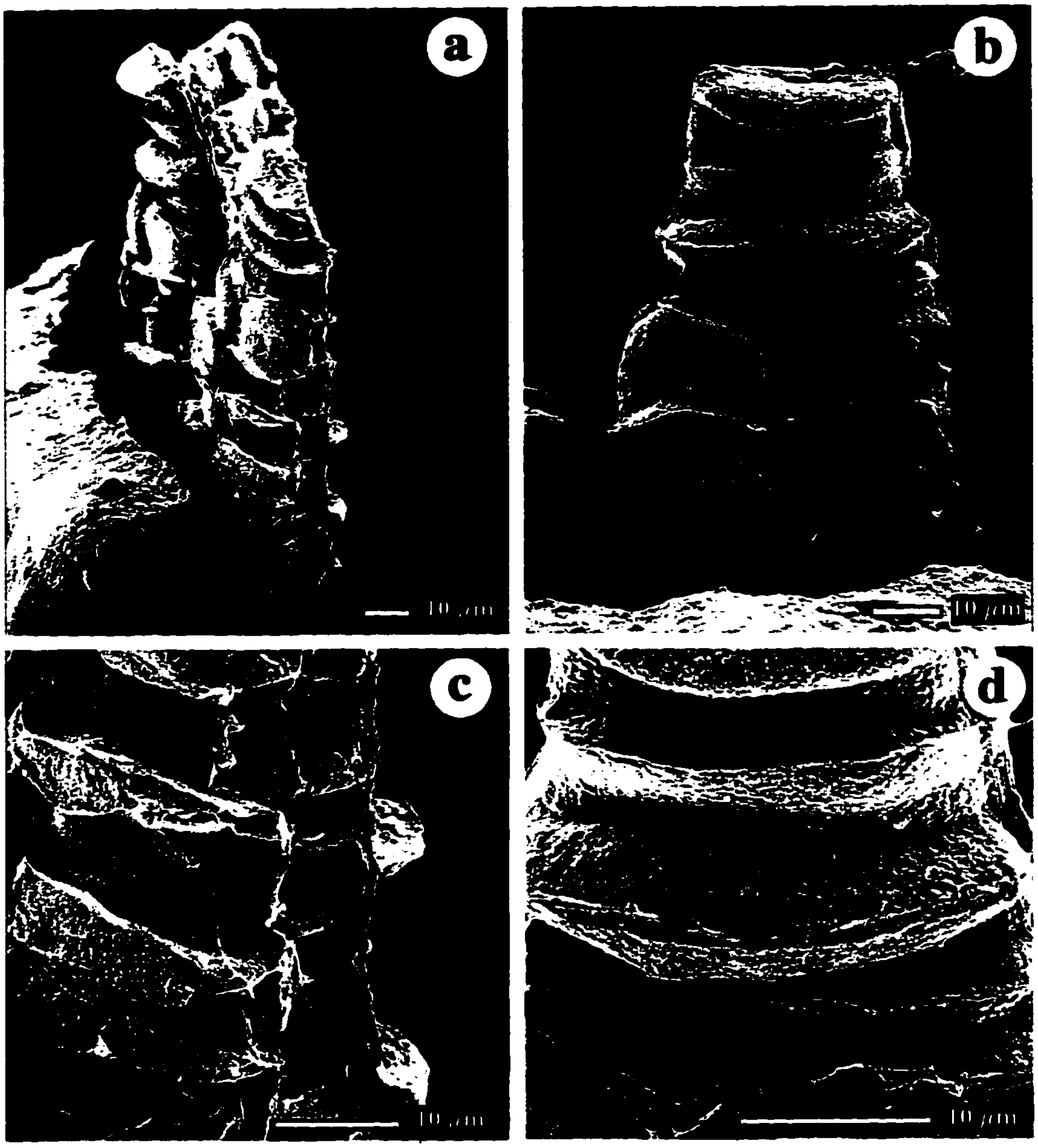


Figure.II. 9. a-d. Peristomial thickening in *Leucoloma amblyacron*. a) The basal portion of the peristome showing three fused layers: OPL,PPL,IPL. b) The outer surface of the peristome showing an incompletely developed OPL layer, although the 4:2 pattern is evident from the OPL and PPL layers. c) A detailed view of the fusion of the 3 layers - the OPL - PPL - IPL layers with preperistomial remants attached to the OPL layer. d) The detail of the cell wall thickening of the PPL surface. All from *Magill 11496*(MO).

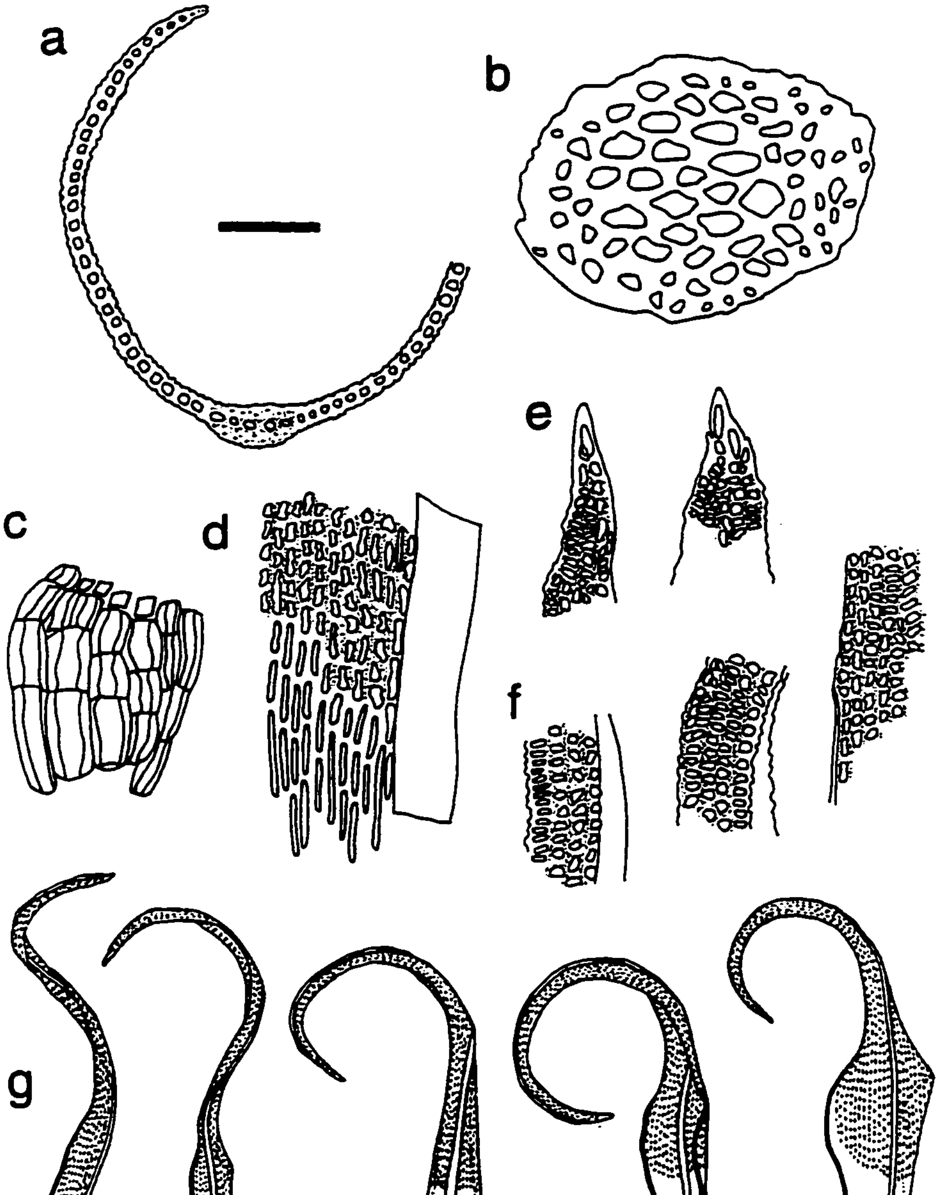


Figure II.10 a-g. *Leucoloma circinale*: a) costa transverse section (*La Farge-England 5610* ALTA); b) stem transverse section (*La Farge-England 5618* ALTA); c) alar cell region (*Pócs & Nchimbi 6285/BB* EGR); d) basal - medial cell transition (La Farge-England 5618 ALTA); e) leaf apices (*La Farge-England 5618* ALTA); f) upper marginal cells (*La Farge-England 5618* ALTA), medial margin with hyaline margin cells (*La Farge-England 5618* ALTA); g) stem leaves (*La Farge-England 5618* ALTA, *Pócs & Nchimbi 6285/BB* EGR). Scale bar = 48 µm for a-f, 0.32 mm for g.

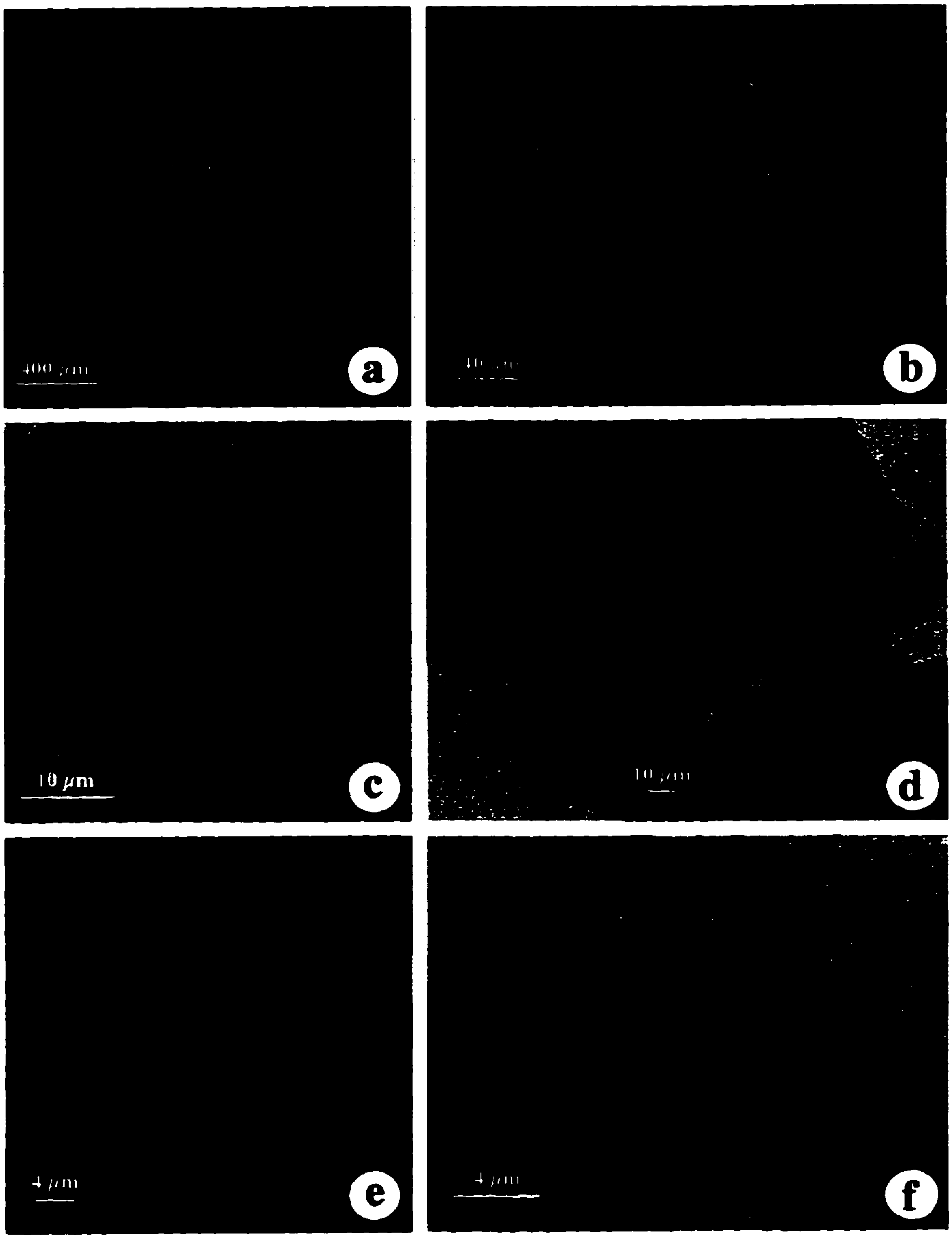


Figure II.11 a-g. *Leucoloma circinale*: a) habit; b) spirally twisted leaf apex; c) abaxial upper leaf lamina, multifid papillae; d) equally papillose abaxial and adaxial surface of upper lamina; e) transverse section of lamina with papillae development over cell wall; f) detail of biseraite papillae with 'groove' over cell lumen. All micrographs from *La Farge-England 5618* ALTA.

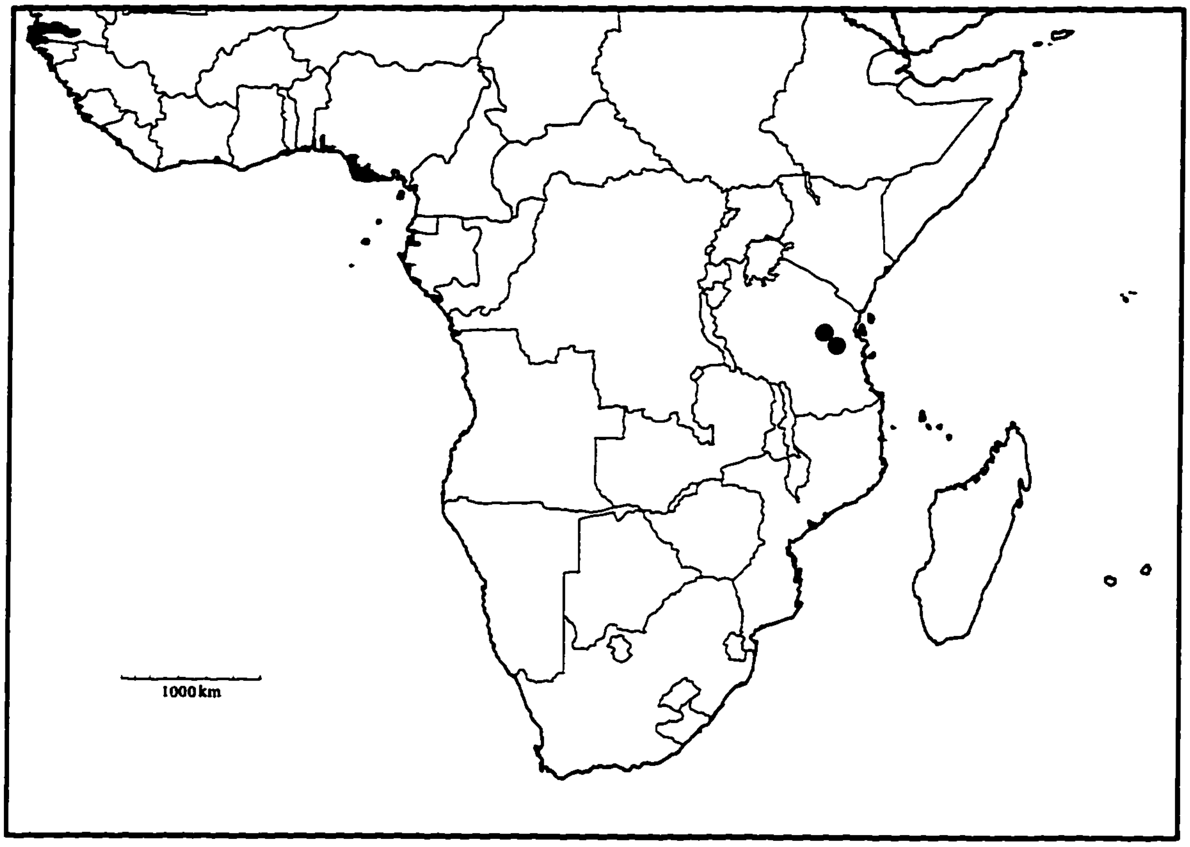


Figure II.12. Distribution of *Leucoloma circinale*

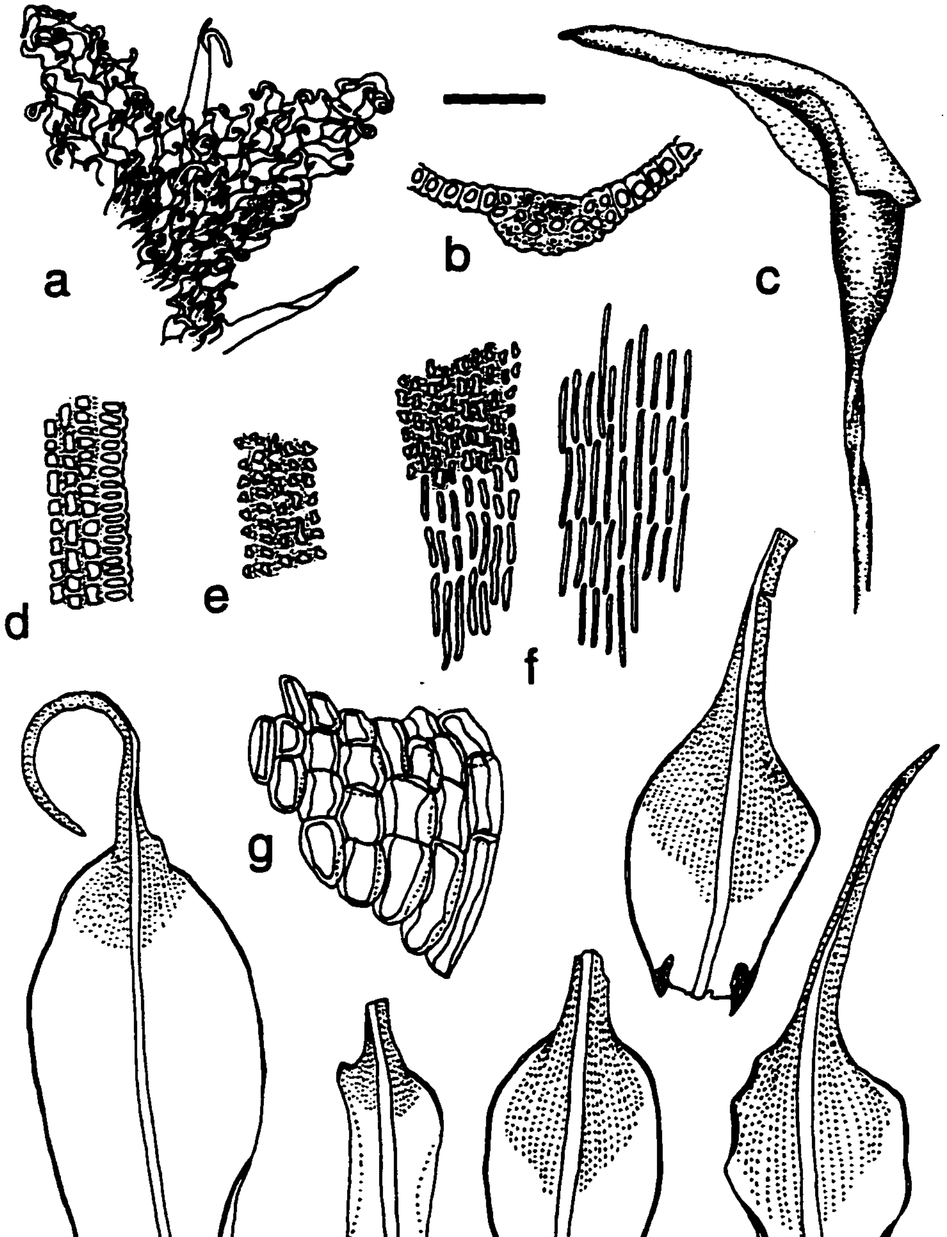


Figure II.13 a-i. *Leucoloma cuneifolium*: a) habit (*Frissard* L); b) costa transverse section (*Onraedt 71.M.05390* priv. Herb. M. Onraedt); c) capsule with calyptra (*Tixier 11707* ALTA); d) upper marginal cells (*Onraedt 71.M.05390* Hb. Onraedt); e) upper cells (*Crosby & Crosby 8618* S); f) upper-basal cells (*Crosby & Crosby 8618* S), basal cells (*Onraedt 71.M.05390* Hb. Onraedt); g) alar region (*Onraedt 71.M.05390* Hb. Onraedt); h) perichaetial leaf (*Frissard* L); i) stem leaves (*Crosby & Crosby 8618* S, *Onraedt 71.M.05390* Hb. Onraedt). Scale bar = 48 µm for b,d-g, 1 mm for a, 0.5 mm for c, 0.32 mm for h,i.

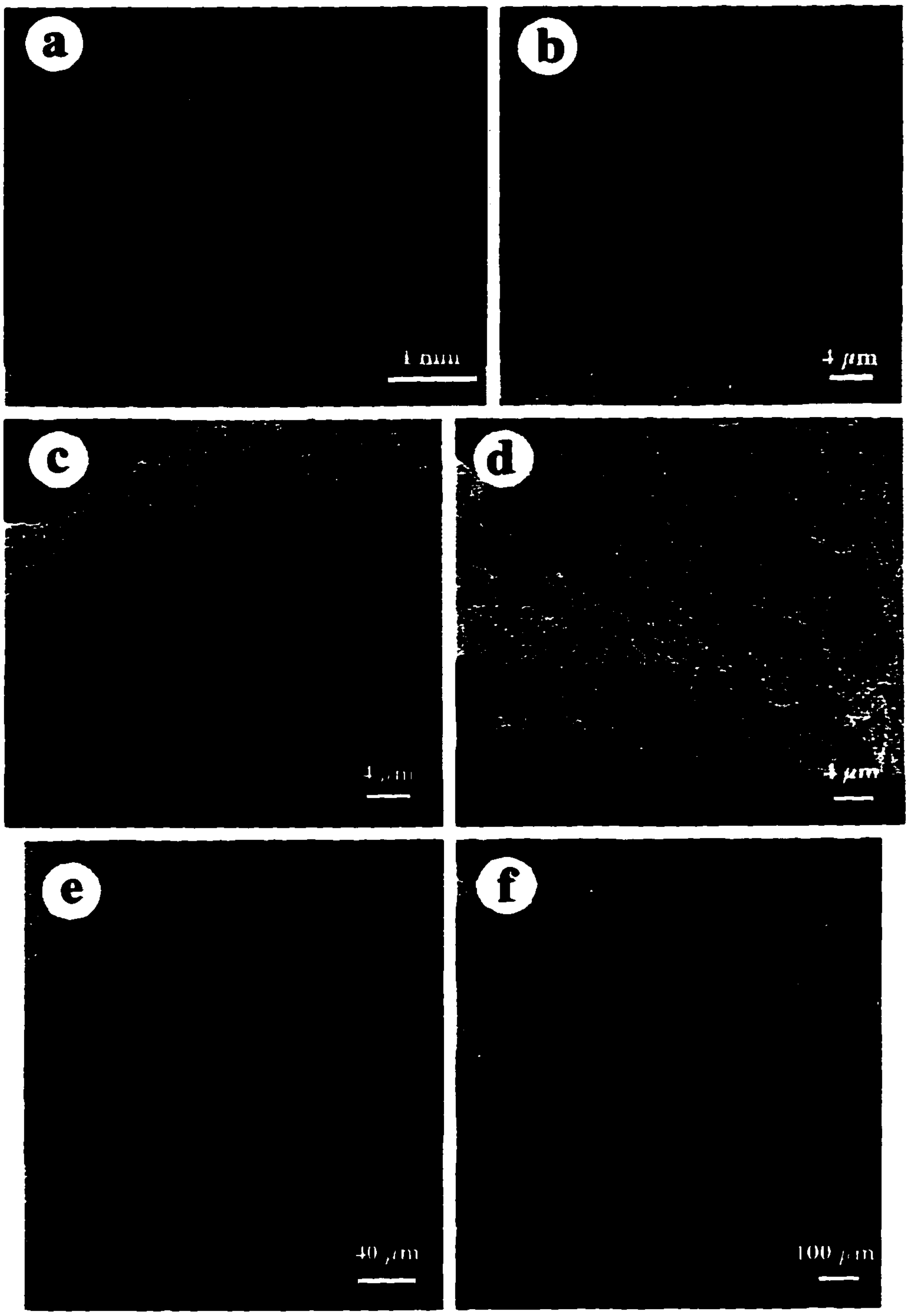


Figure II.14 a-f. *Leucoloma cuneifolium*: a) habit; b) abaxial surface of upper laminal cells, multifid papillae in rows; c) transverse section of upper laminal cells with groove over cell lumen; d) transition between papillose and smooth cells - cell thickening over wall; e) abaxial surface of obovate leaf with papillose upper cells, acumen with laminal tear; f) contorted leaf habit, fragile leaf apices. Micrographs from *Crosby & Crosby 8618* (a,e,f); *Dorr 3142* MO (b-d).

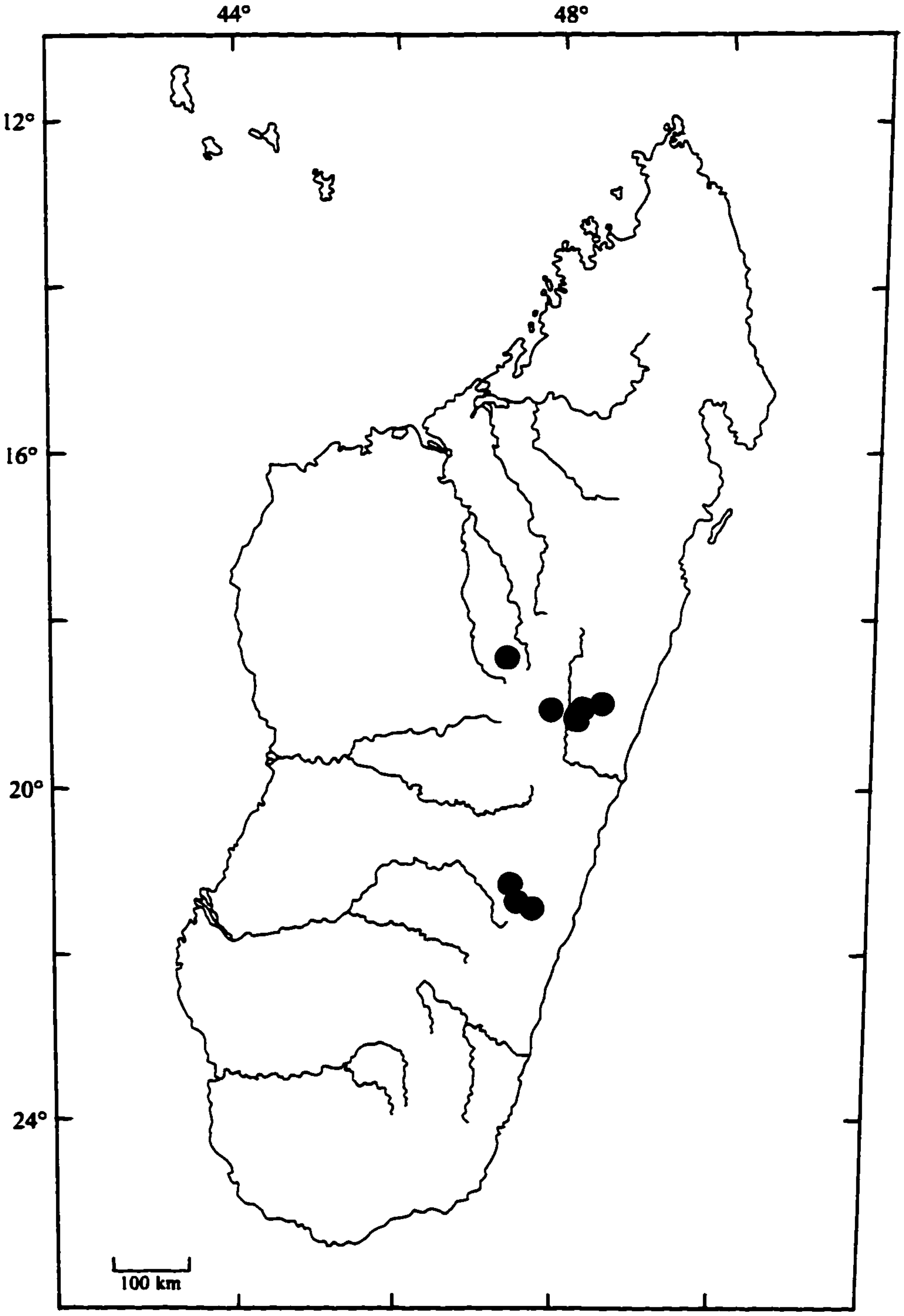


Figure II.15. Distribution of *Leucoloma cuneifolium*

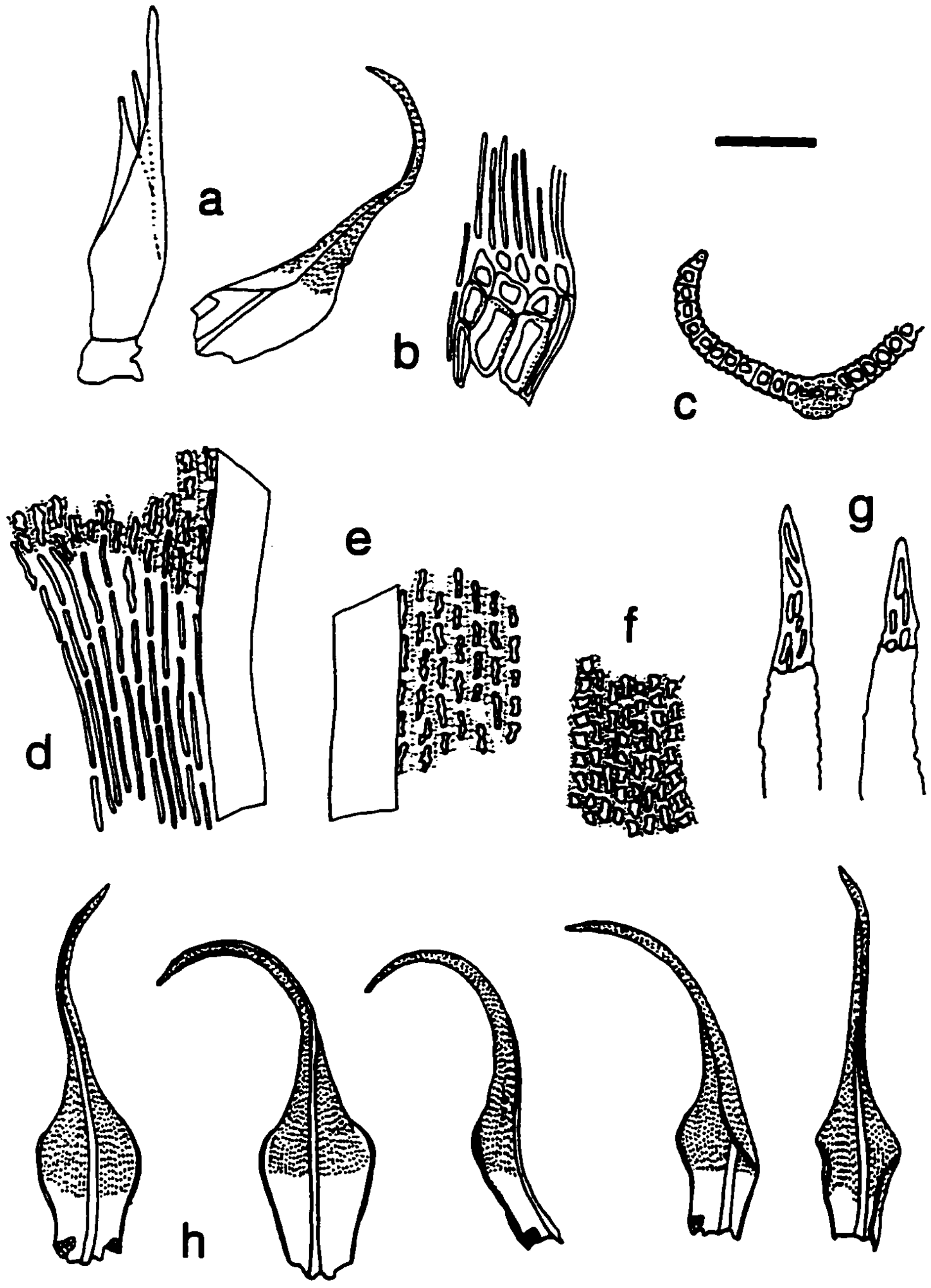


Figure II.16 a-h. *Leucoloma grimmioides*: a) perichaetial leaves (*La Farge-England 6294* ALTA); b) alar region (*Humbert* PC); c) transverse costa section (*La Farge-England 6294* ALTA); d) basal-upper cell transition (*La Farge-England 6294* ALTA); e) lower upper cells (*La Farge-England 6294* ALTA); f) upper cells (*La Farge-England 6294* ALTA); g) leaf apices with pellucid cells (*La Farge-England 6294* ALTA); h) stem leaves (*La Farge-England 6294, 6366* ALTA). Scale bar = 48 µm for b-g, 0.32 mm for a,h.

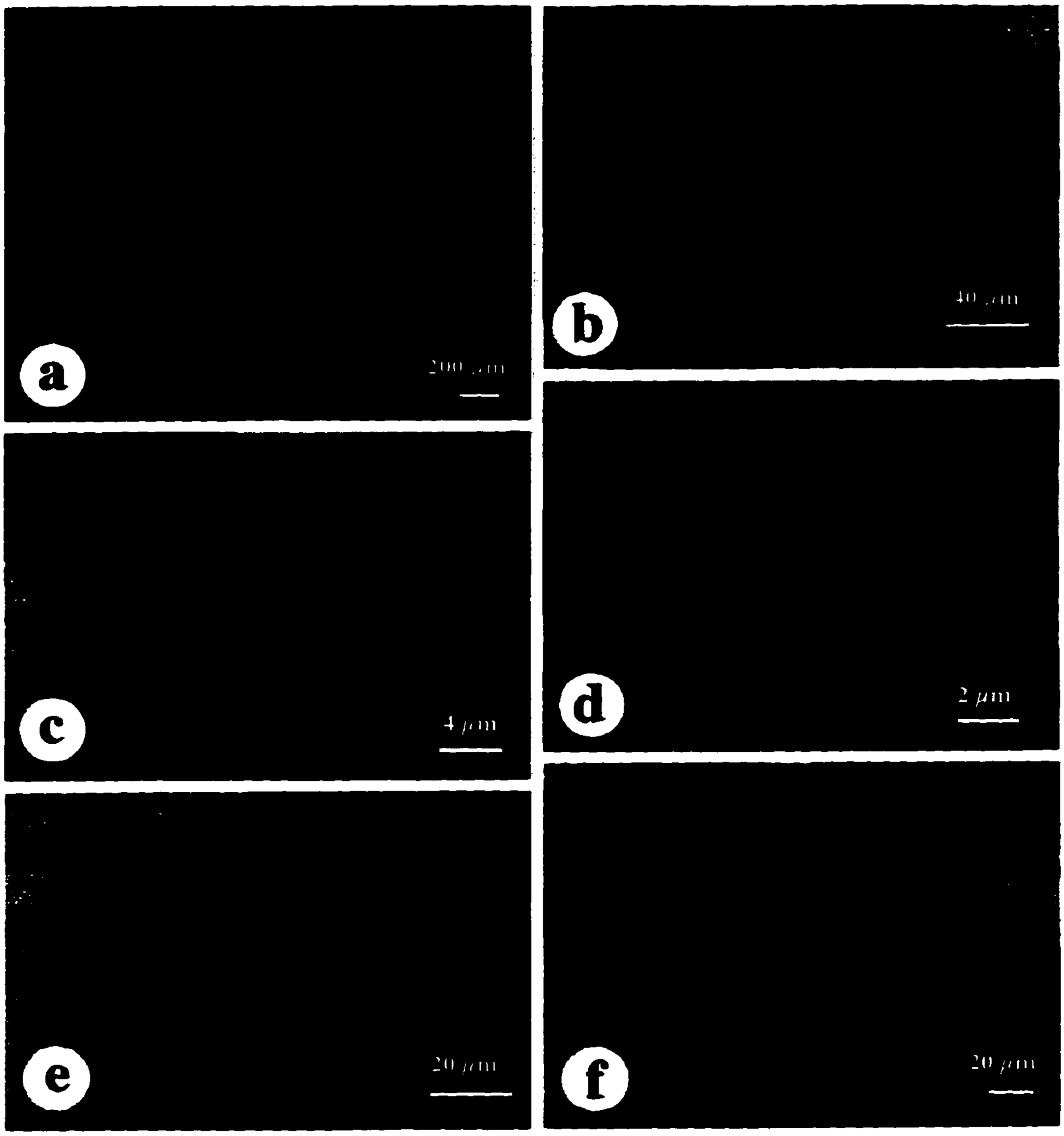


Figure II.17 a-f. *Leucoloma grimmioides*: a) habit; b) contorted leaf acumen; c) transverse section of lamina with papillae development over cell wall; d) transverse section detail, papillae thickening over anticlinal wall; e) transition of papillose cells to smooth basal cells; f) obovate leaf base. All micrographs from *La Farge-England 6294* ALTA.

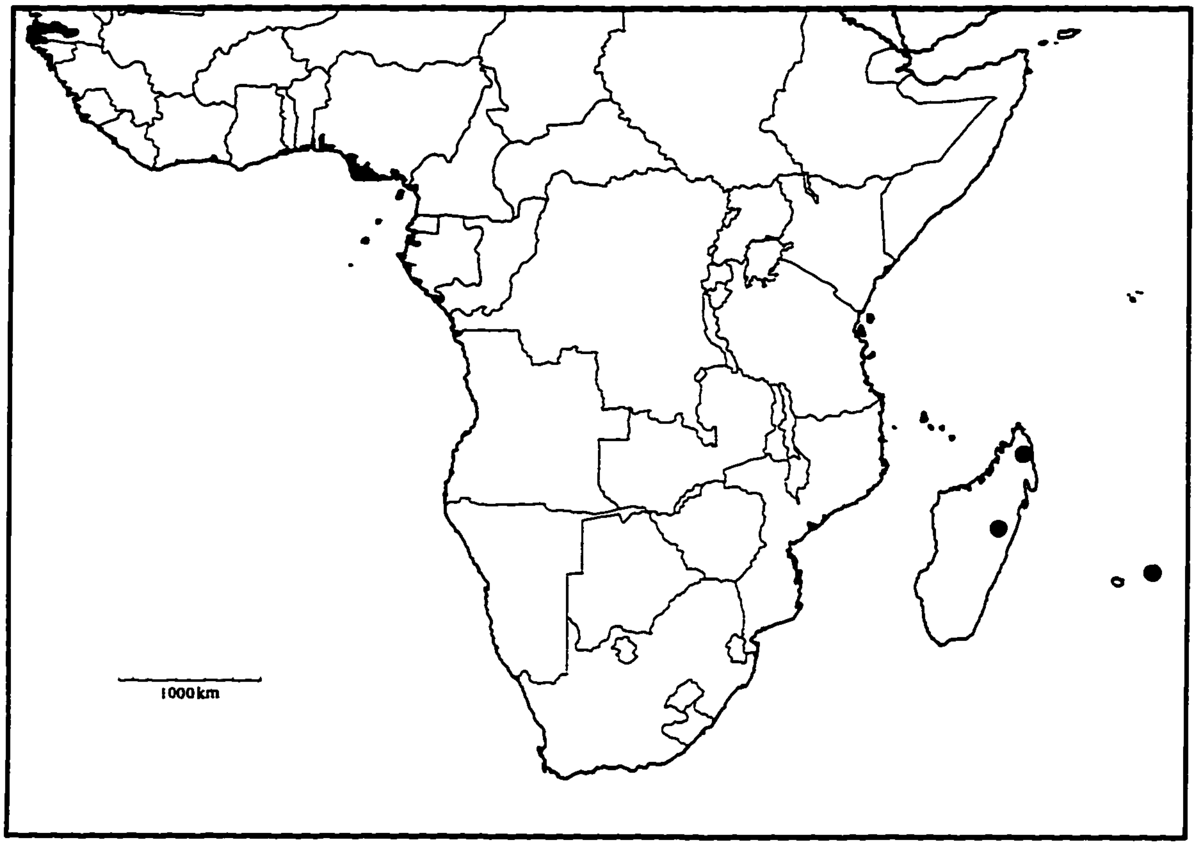


Figure II.18. Distribution of *Leucoloma grimmioides*

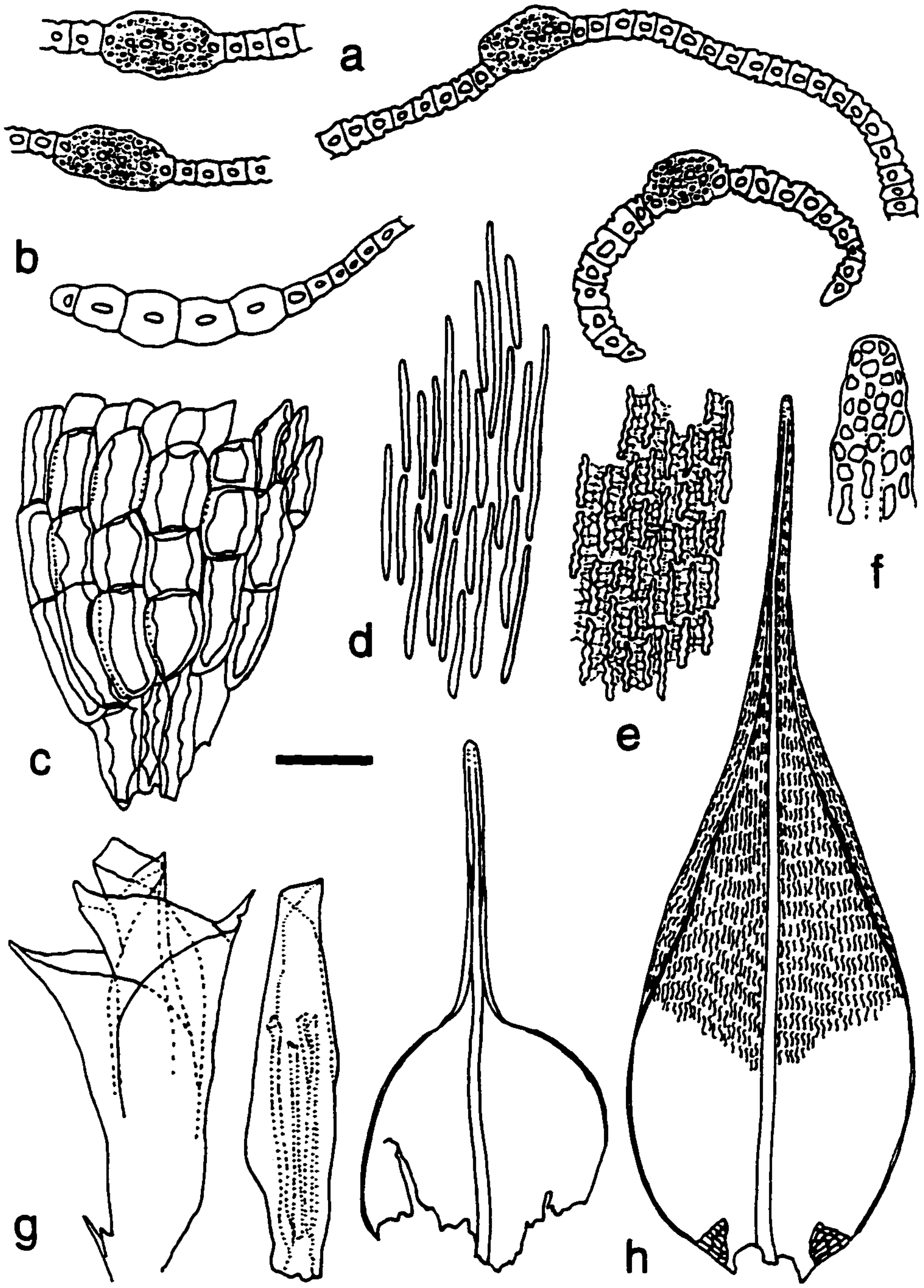


Figure II.19 a-h. *Leucoloma marojeziense*: a) transverse costa and lamina sections (*La Farge-England 6374* ALTA); b) alar transverse section (*La Farge-England 6298* ALTA);c) alar region (*La Farge-England 6374* ALTA); d) basal cells (*La Farge-England 6374* ALTA); e) upper cells (*La Farge-England 6374* ALTA); f) leaf apex (*La Farge-England 6374* ALTA); g) perichaetial leaves (*La Farge-England 6298* ALTA); h) stem leaf (*La Farge-England 6374* ALTA). Scale bar = 48 µm for a-f, 0.32 mm for g, h.

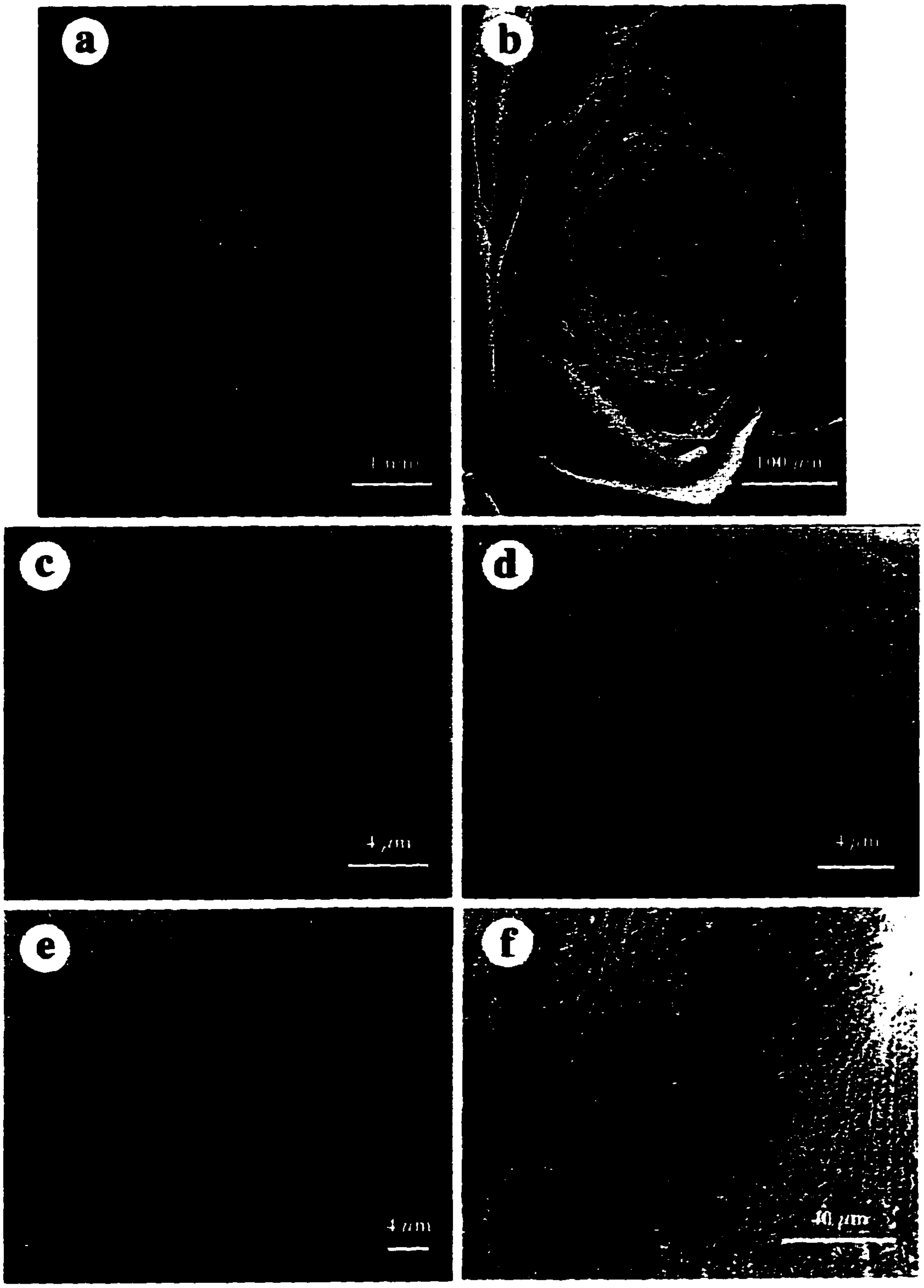


Figure II.20 a-f. *Leucoloma marojeziense*: a) habit; b) stem transverse section with leaves; c) abaxial biseriate papillae; d) transverse section of lamina with papillae over cell wall; e) detail of biseriate papillae development at transition to smooth basal cells; f) overview of transition between papillose upper cells and smooth basal cells. Micrographs from *La Farge-England 6374* (a,b,f), *6298* (c-e) ALTA.

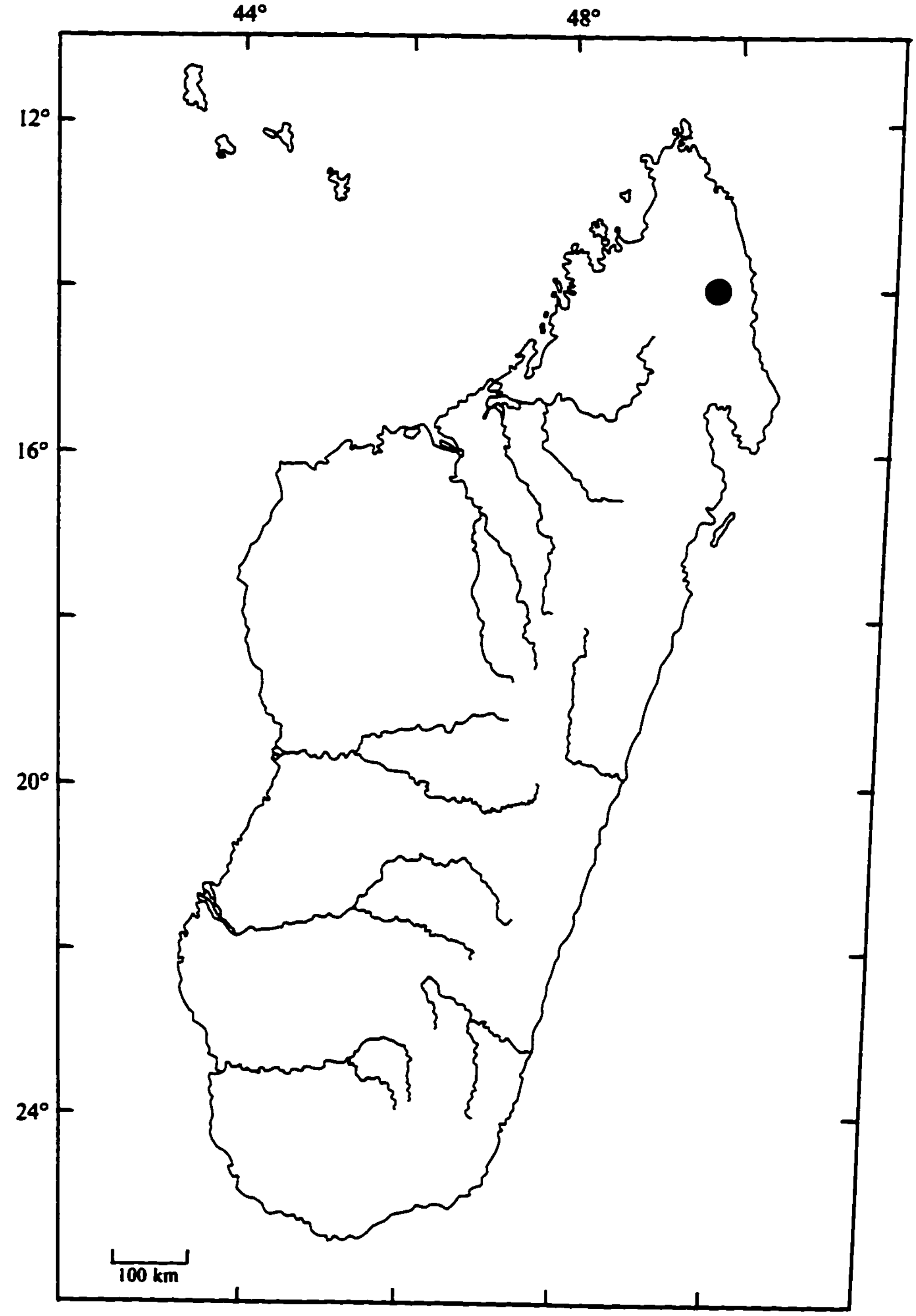


Figure II.21. Distribution of *Leucoloma marojeziense*

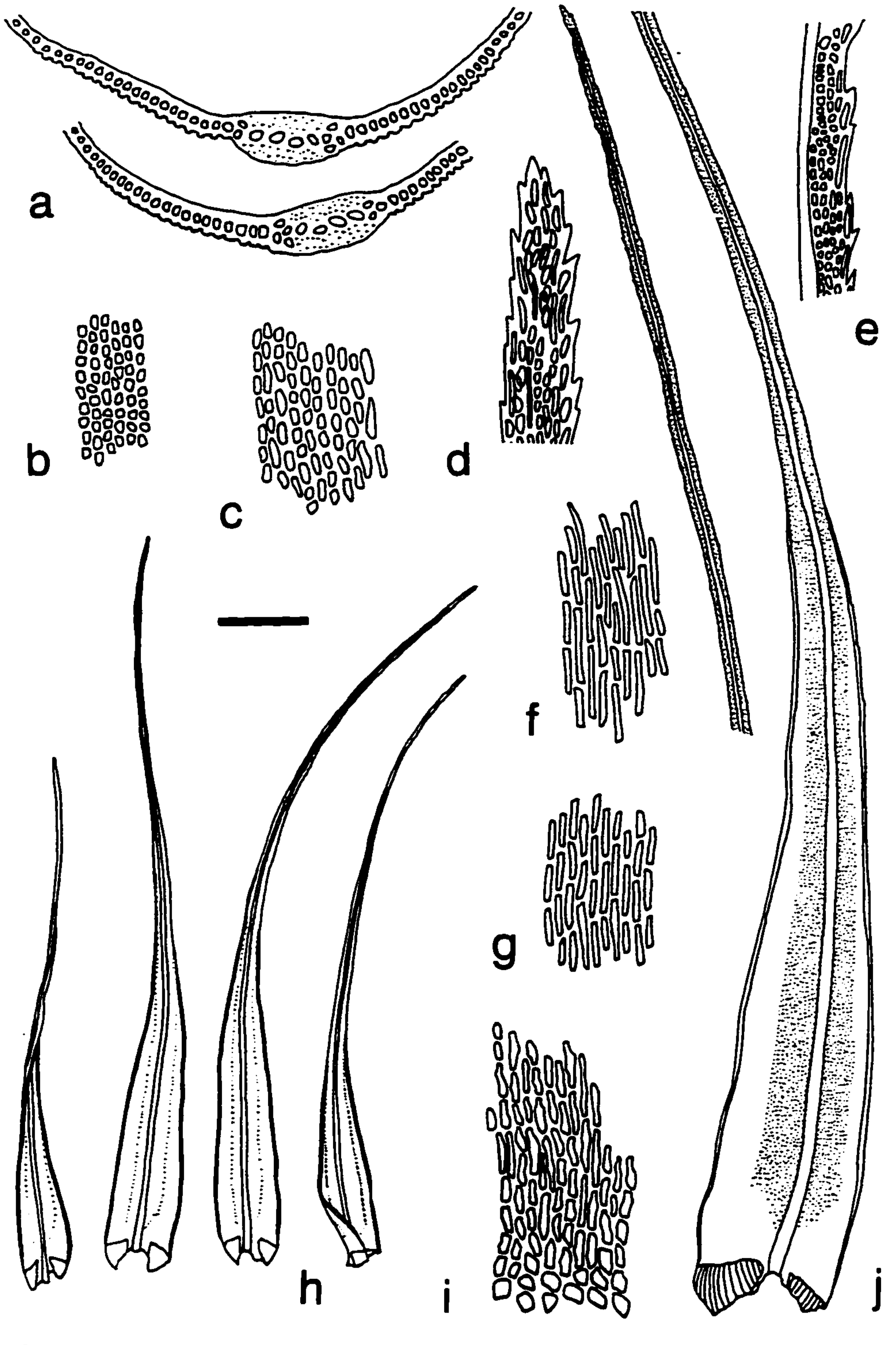


Figure II.22 a-j. *Leucoloma chrysobasilare* ssp. *chrysobasilare*: a) costa transverse sections (*Magill 11206* ALTA); b,c) basal juxtacostal cells (*Magill 11723, 11263* ALTA); d) leaf apex (*Hildebrandt* BM); e) upper margin (*Hildebrandt* BM); f) medial interior cells (*Magill 11206* ALTA); g) basal interior cells (*Magill 11206* ALTA); h, j) stem leaves (*Hildebrandt* BM, *Magill & Pócs 11702* ALTA, *Magill 11723* ALTA); i) basal-alar transitional cells (*Magill 11723* ALTA). Scale bar = 48 μm for a-g,i; 0.76 mm for h; and 0.32 mm for j.

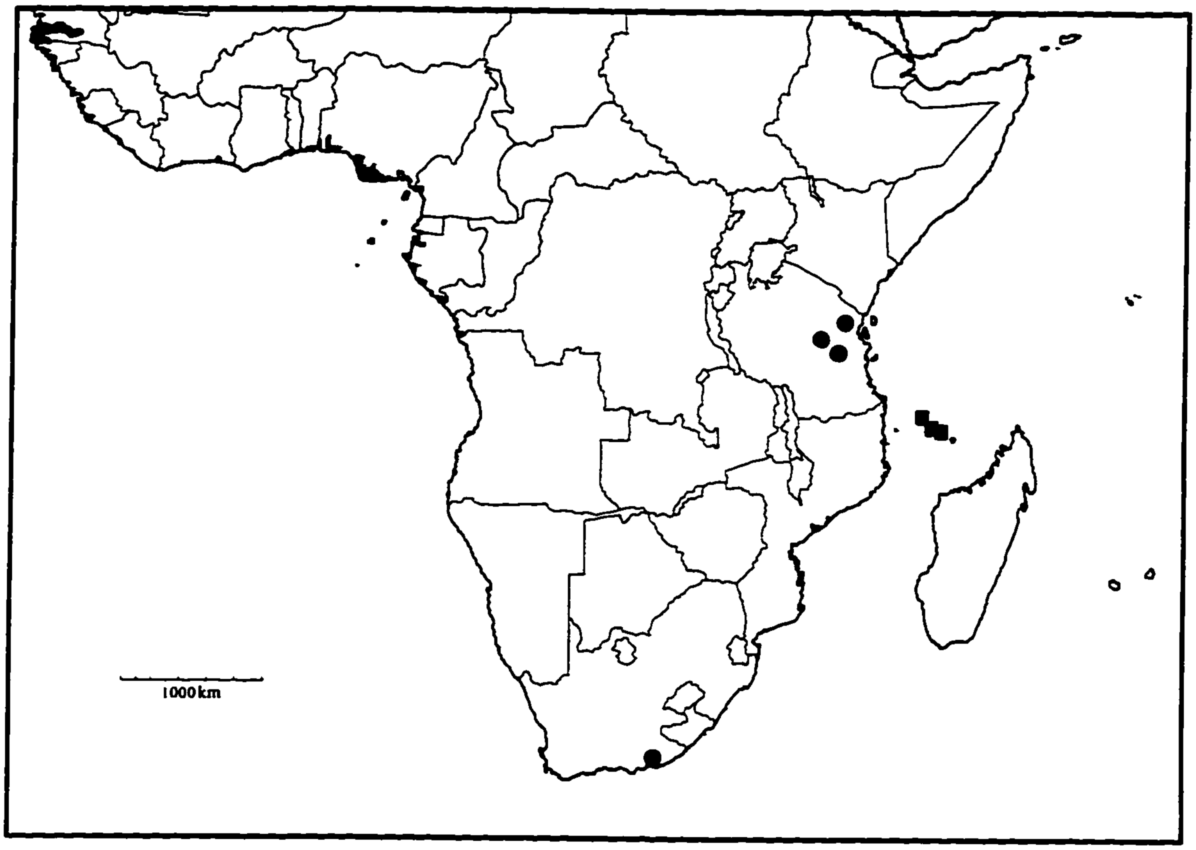


Figure II.23. Distribution of *Leucoloma chrysobasilare* ssp. *chrysobasilare* ●
and *Leucoloma chrysobasilare* ssp. *africana* ■

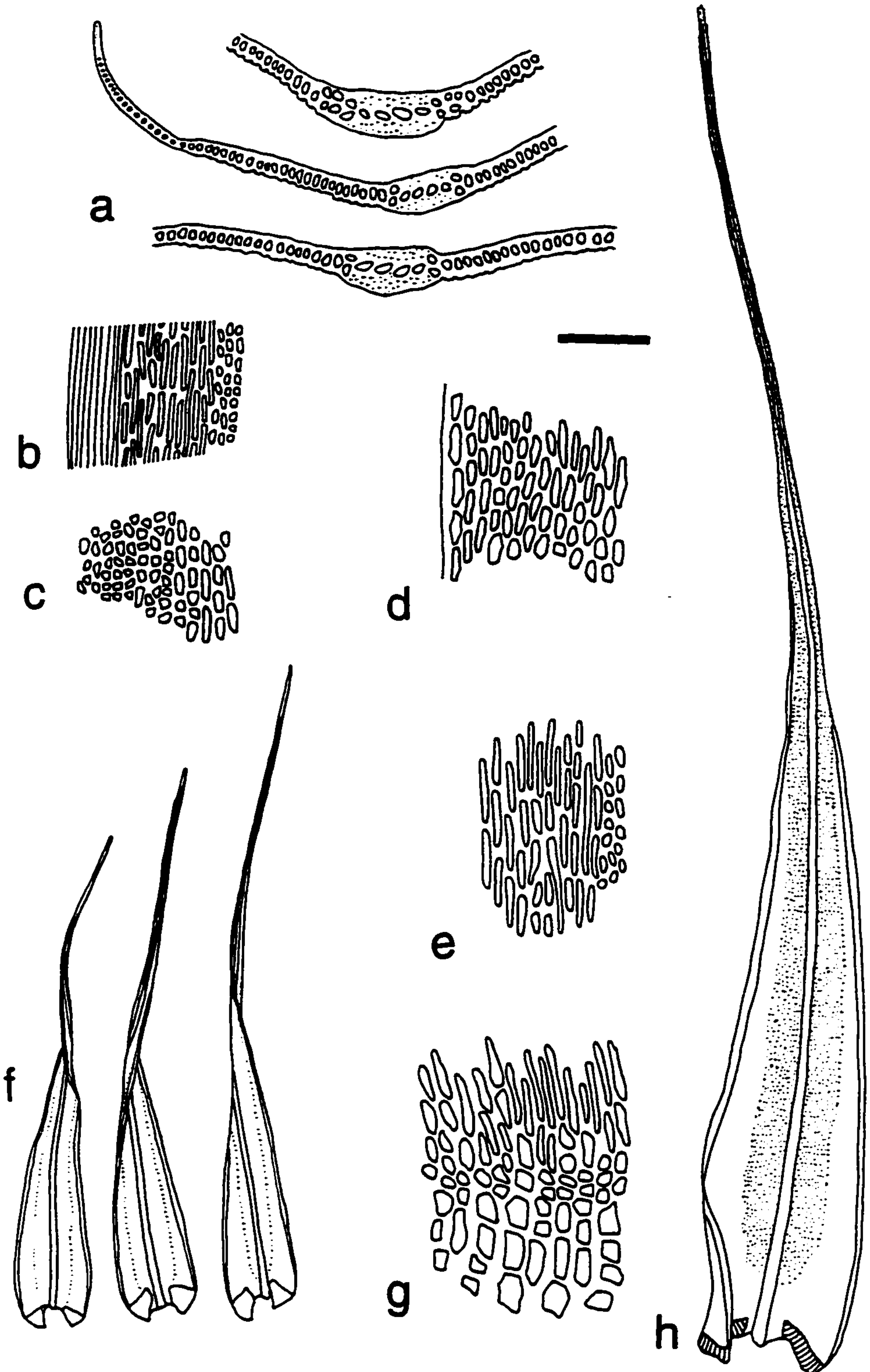


Figure II.24 a-h. *Leucoloma chrysobasilare* ssp. *africana*: a) costa transverse section (*Iversen, Farkas, Pócs, & Steiner 86244/S* ALTA, *Pócs 87033/CL* ALTA); b) medial marginal and interior cells (*Pócs & Mahberley 6398/X* G); c) basal juxtacostal and interior cells (*Pócs & Mahberley 6398/X* G); d) basal interior cells (*Pócs & Mahberley 6398/X* G); e) medial interior cells (*Pócs & Mahberley 6398/X* G); f, h) stem leaves (*La Farge-England 5448* ALTA, *Pócs 87033/CL* ALTA); g) basal alar transitional cells (*Iversen, Farkas, Pócs, & Steiner 86244/S* ALTA). Scale bar = 48 µm for a-e,g; 0.76 mm for f; and 0.32 mm for h.

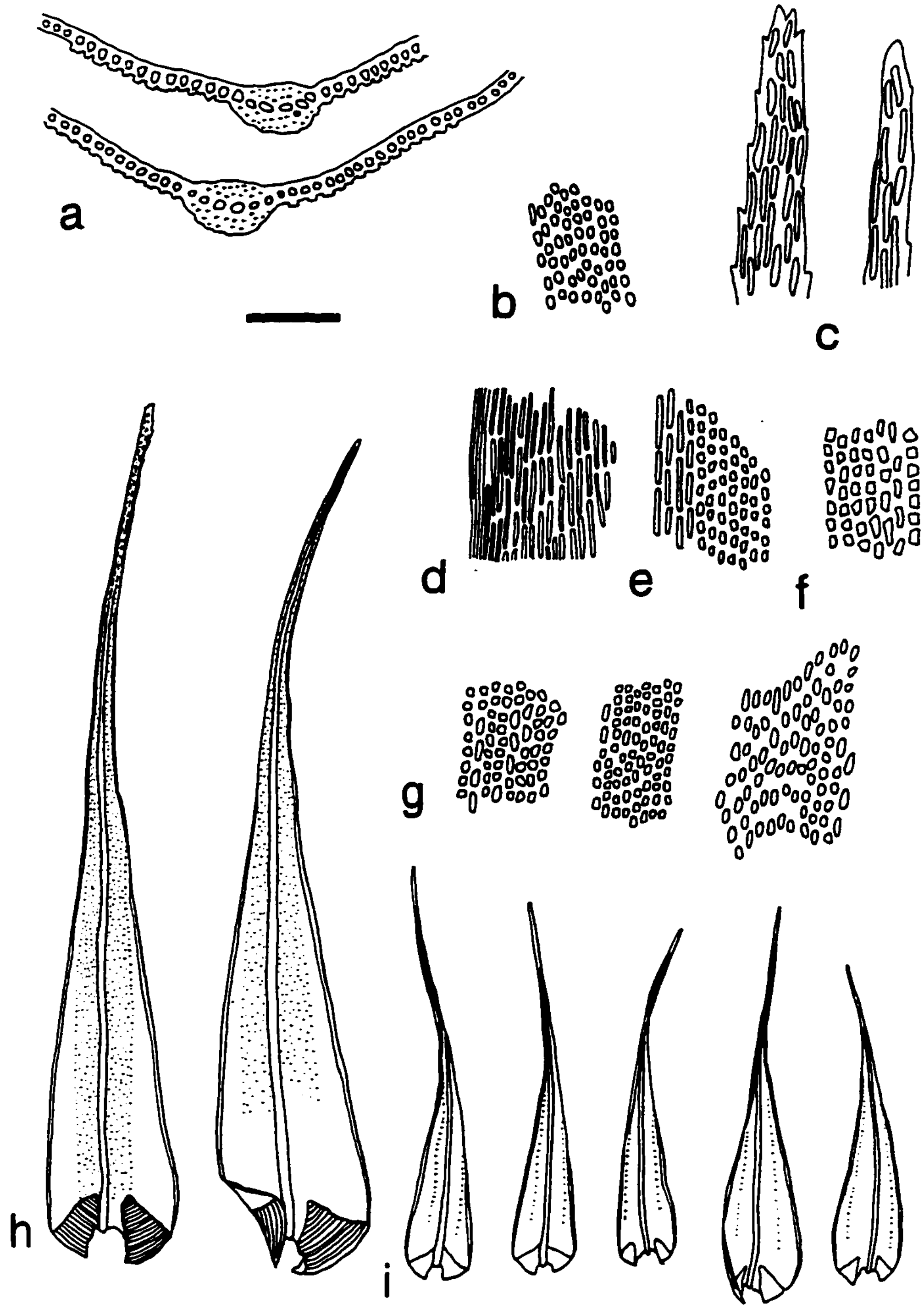


Figure II.25 a-i. *Leucoloma bifidum*: a) costa transverse section (*Pócs 9504/BH*, *Voeltzkow* H-Br); b) upper juxtacostal cells (*Crosby & Crosby 8276* L); c) leaf apices (*Commerson* L, *Crosby & Crosby 8276* L); d) marginal and basal interior cells (*Commerson* L); e) medial interior and juxtacostal cells (*Commerson* L); f) medial juxtacostal cells (*Pócs 9504/BH* ALTA); g) basal juxtacostal cells (*De Sloover 17.679* Hb. De Sloover, *Commerson* L, *Crosby & Crosby 8276* L); h, i) stem leaves (*Commerson* L, *Crosby & Crosby 8276* L). Scale bar = 48 µm for a-g; 0.32 mm for h; and 0.76 mm for i.

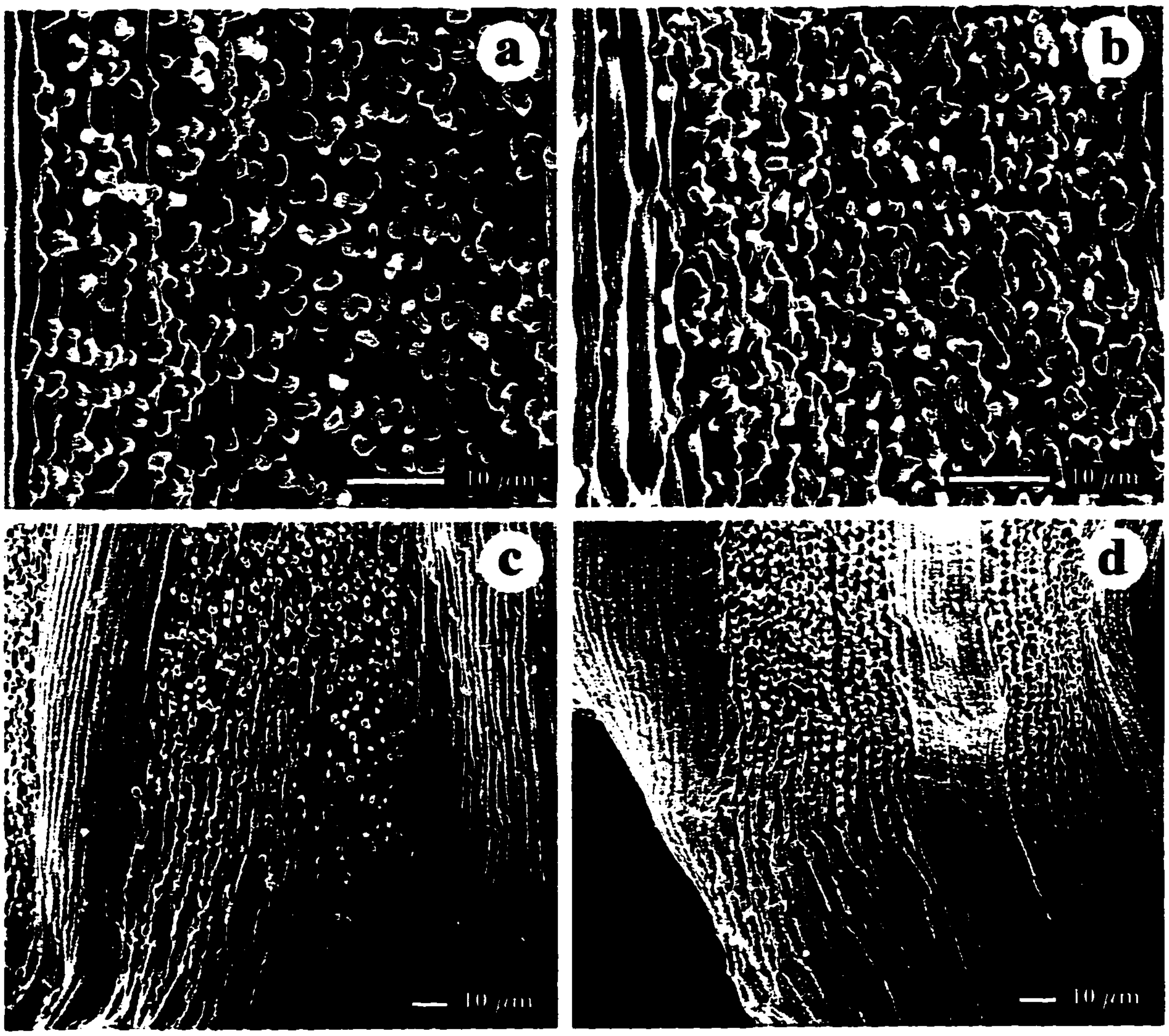


Figure II.26.a-d. Papillae density differences between *Leucoloma bifidum* and *Leucoloma madagascariense*. a) *L. bifidum* mid leaf papillae development less dense, with clear separation between them. b) *L. madagascariense* mid leaf papillae development densely compact. c) *L. bifidum* leaf base with less prominent and more spaced papillae. d) *L. madagascariense* leaf base with dense papillae development to the base. Specimen citations: *Leucoloma bifidum, Crosby & Crosby 8276* (L) ; *Leucoloma madagascariense, La Farge-England 6279* (ALTA).

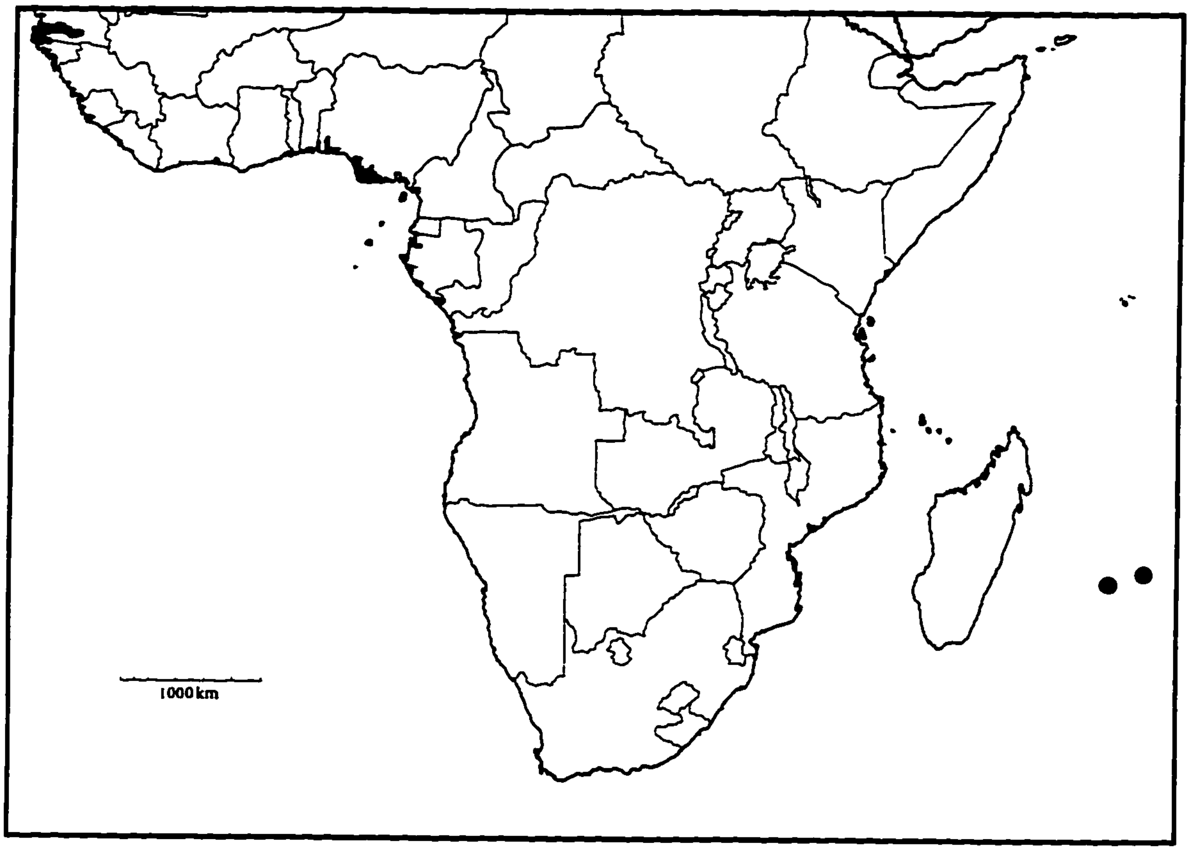


Figure II.27. Distribution of *Leucoloma bifidum*

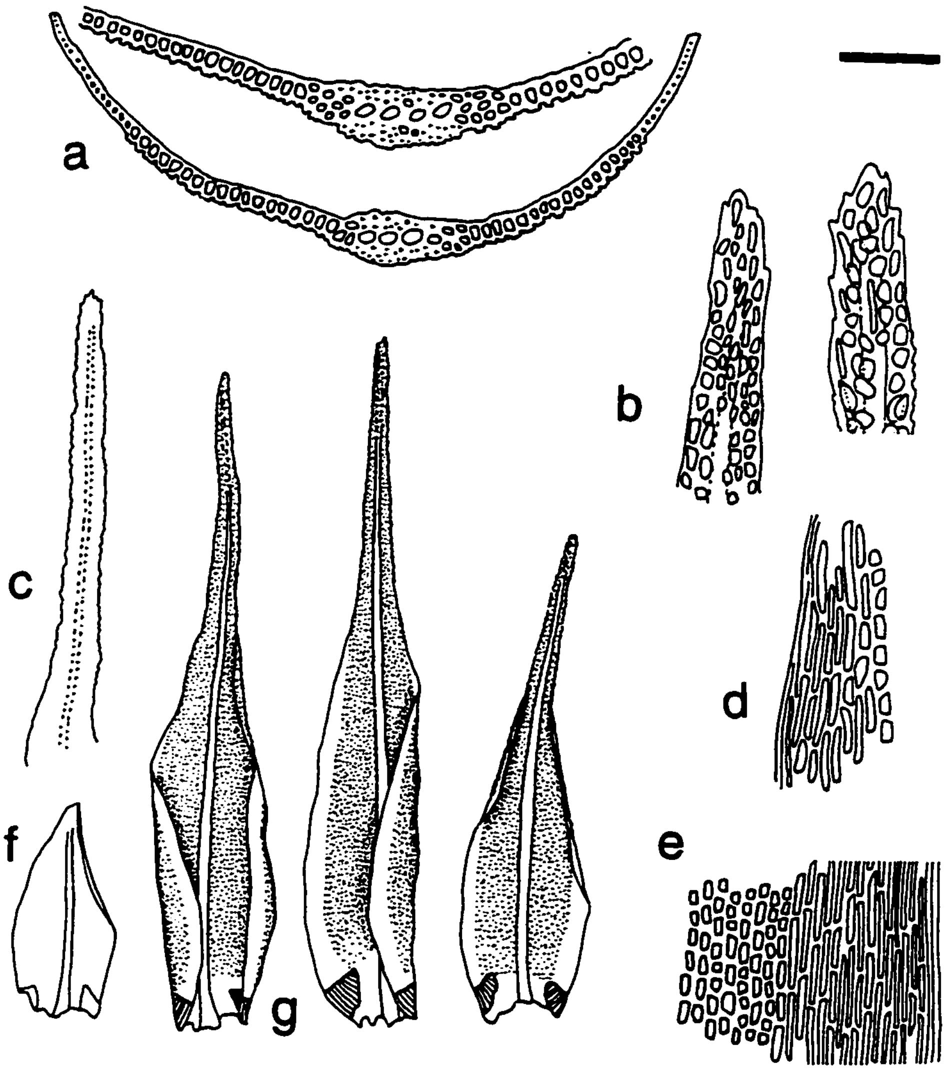


Figure II.28 a-g. *Leucoloma cinclidiotioides*: a) leaf transverse sections; b) leaf apices; c) leaf acumen; d) medial marginal, interior, and juxtacostal cells; e) basal juxtacostal, interior, and marginal cells; f) juvenile leaf; g) stem leaves. Scale bar = 48 µm for a,b,d,e; 0.2 mm for c; and 0.32 mm for f, g. All illustrations are from *Lépervanche* BM.

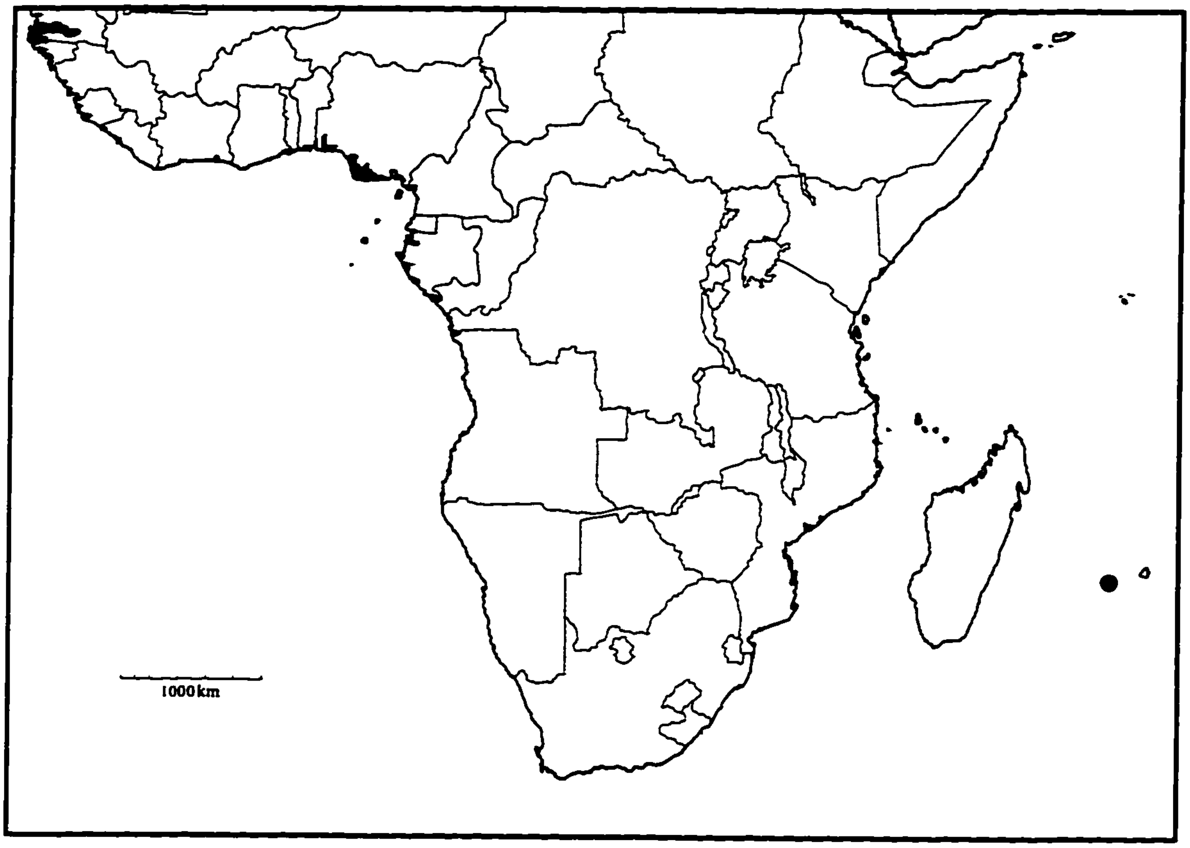


Figure II.29. Distribution of *Leucoloma cinclidiotioides*

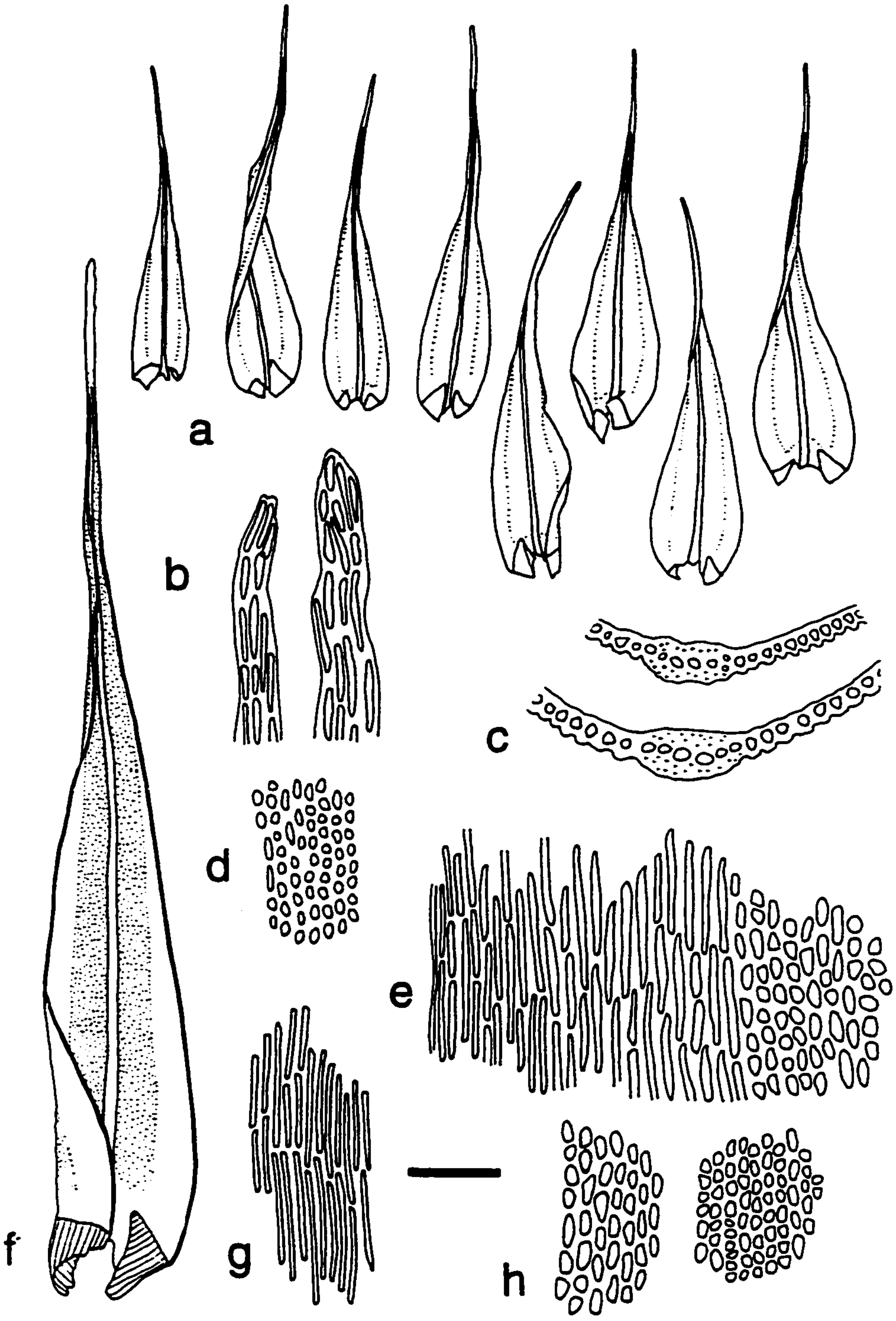


Figure II.30 a-h. *Leucoloma gracilescens*: a, f) stem leaves (*Muller B5, B9* ALTA, *Quintas* H-Br); b) leaf apices (*Muller B5* ALTA); c) costa transverse section *Quintas* H-Br, *Muller B9* ALTA); d) upper juxtacostal cells (*Quintas* H-Br); e) medial marginal, interior and juxtacostal cells (*Muller B9* ALTA); g) basal interior cells (*Quintas* H-Br); h) basal juxtacostal cells (*Quintas* H-Br). Scale bar = 48 µm for b-e, g, h; 0.76 mm for a; and 0.32 mm for f.

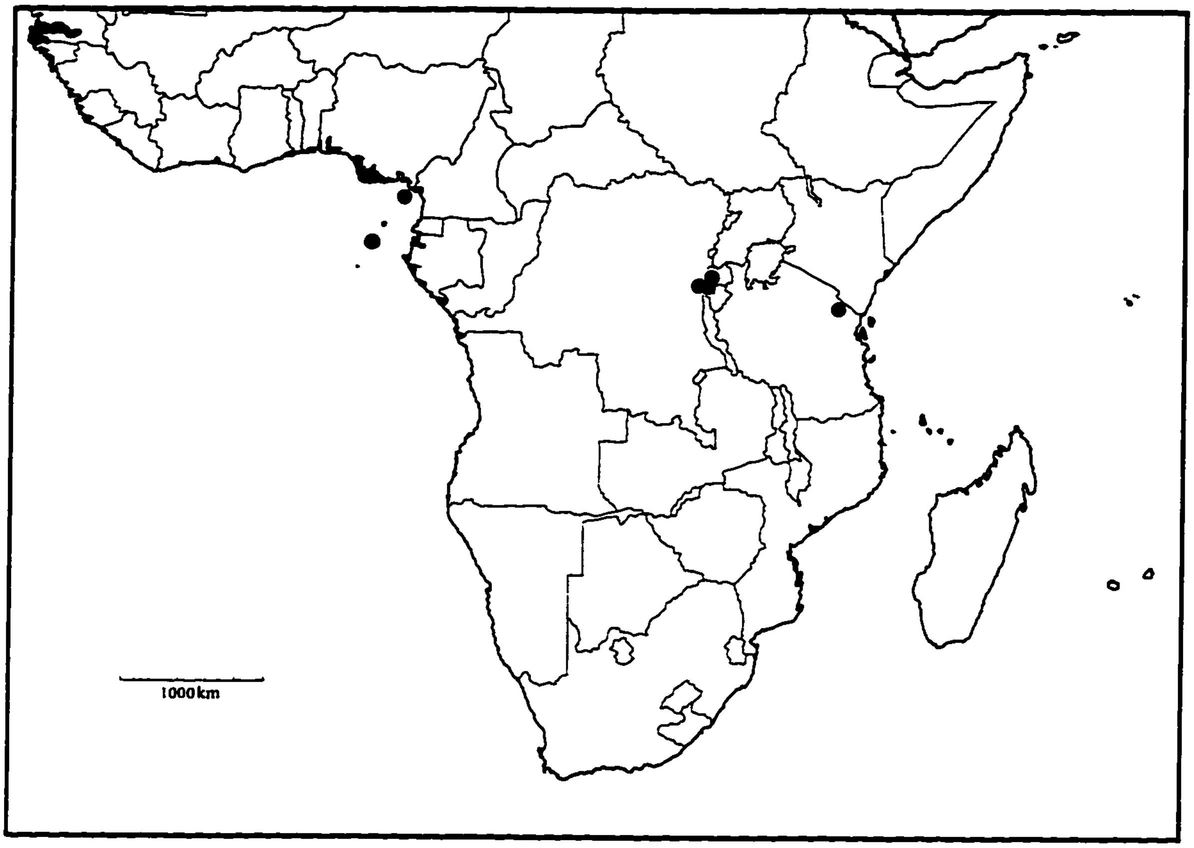


Figure II.31. Distribution of *Leucoloma gracilescens*

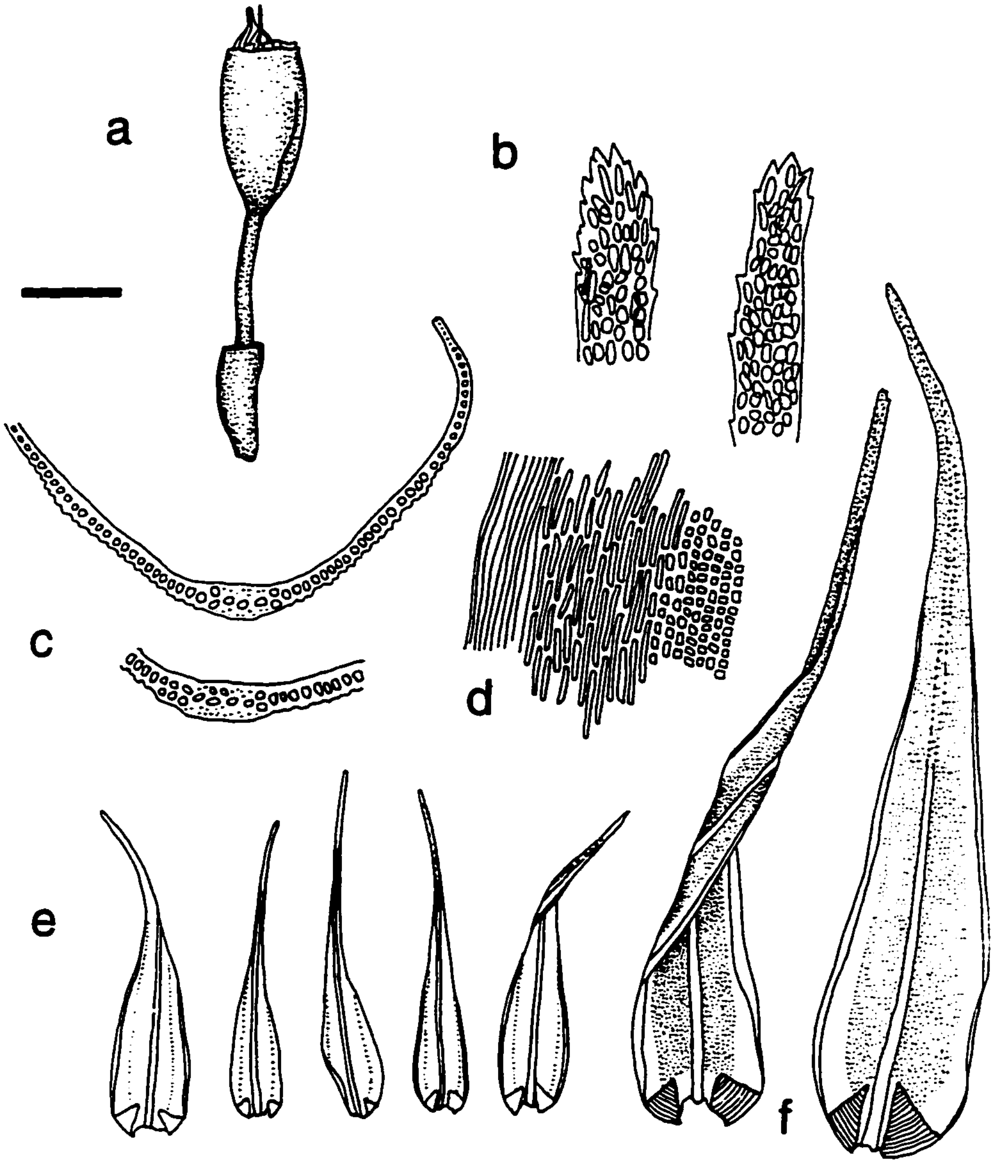


Figure II.32 a-f. *Leucoloma holstii*: a) capsule (*De Sloover 12487* BR); b) leaf apices (*Pócs 90015/Z* ALTA); c) costa transverse section (*Pócs 90015/Z* ALTA, *Holst 3291* H-Br); d) basal marginal, interior, and juxtacostal cells (*Holst 3291* H-Br); e,f) stem leaves (*Pócs 90015/Z* EGR, *Holst 3291* H-Br). Scale bar = 48µm for b-d; 0.5 mm for a; 0.76 mm for e; 0.32 mm for f.

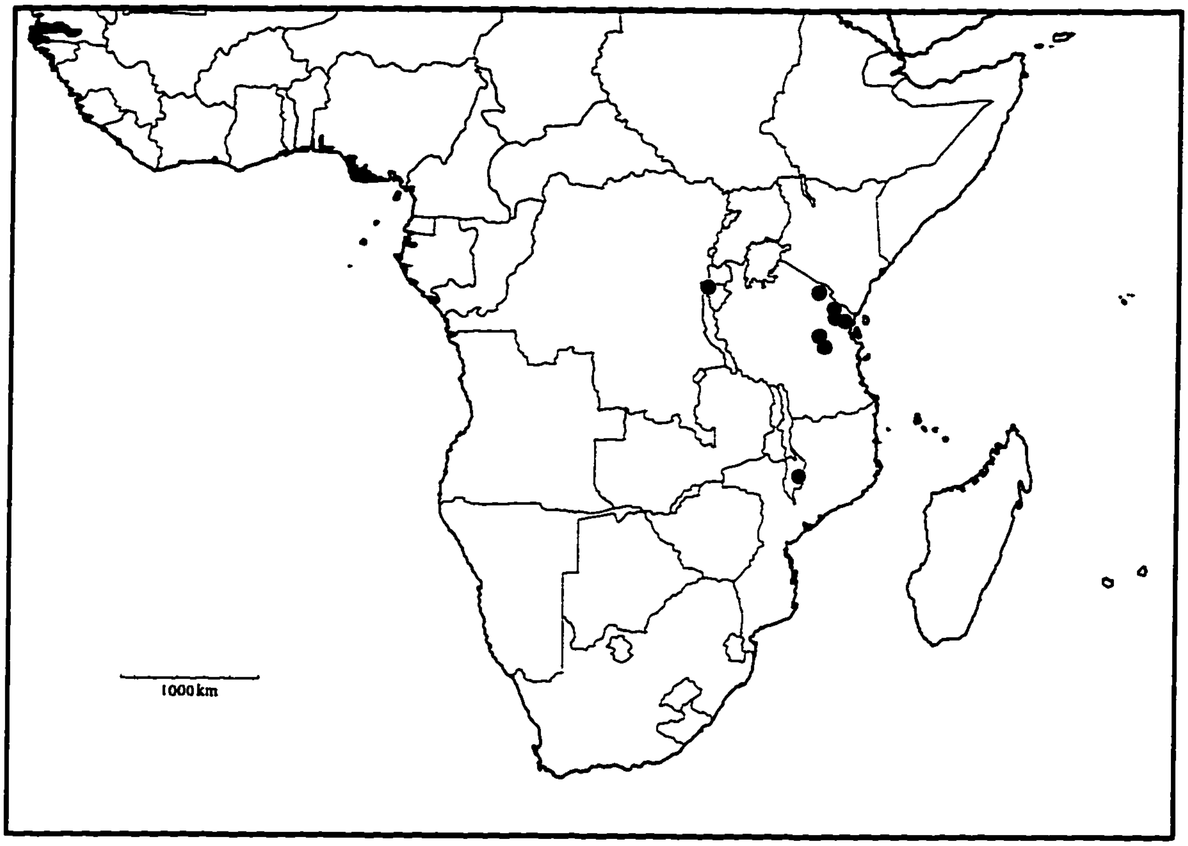


Figure II.33. Distribution of *Leucoloma holstii*

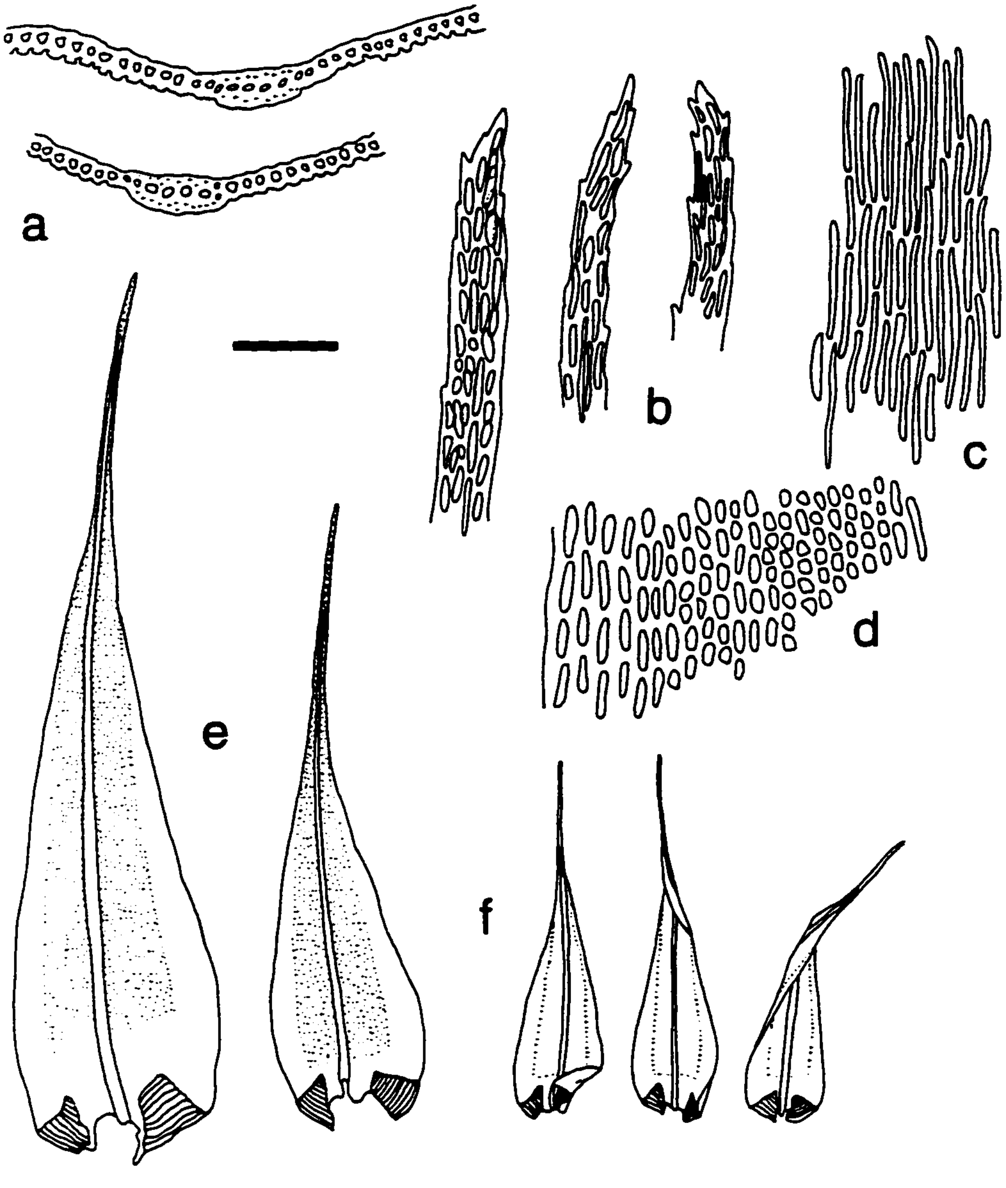


Figure II.34 a-f. *Leucoloma lepervancheri*: a) costa transverse section (*Lépervanche* BM); b) leaf apices (*Lépervanche* BM, *Perrot* BR); c) basal cells (*Lépervanche* BM) d) basal juxtacostal cells (*Lépervanche* BM); e-f) stem leaves (*Lépervanche* BM, *Perrot* BR). Scale bar = 48 µm for a-d; 0.32 mm for e; and 0.76 mm for f.

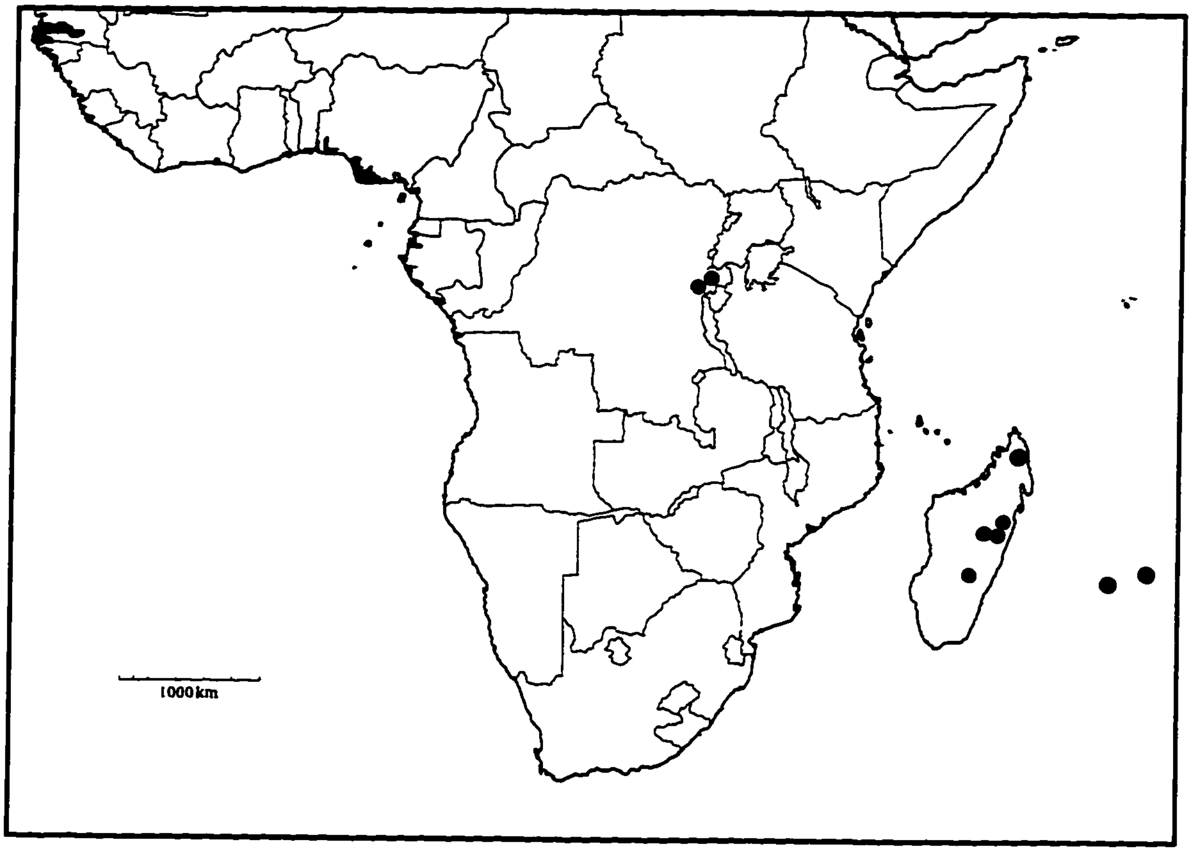


Figure II.35. Distribution of *Leucoloma lepervancheri*

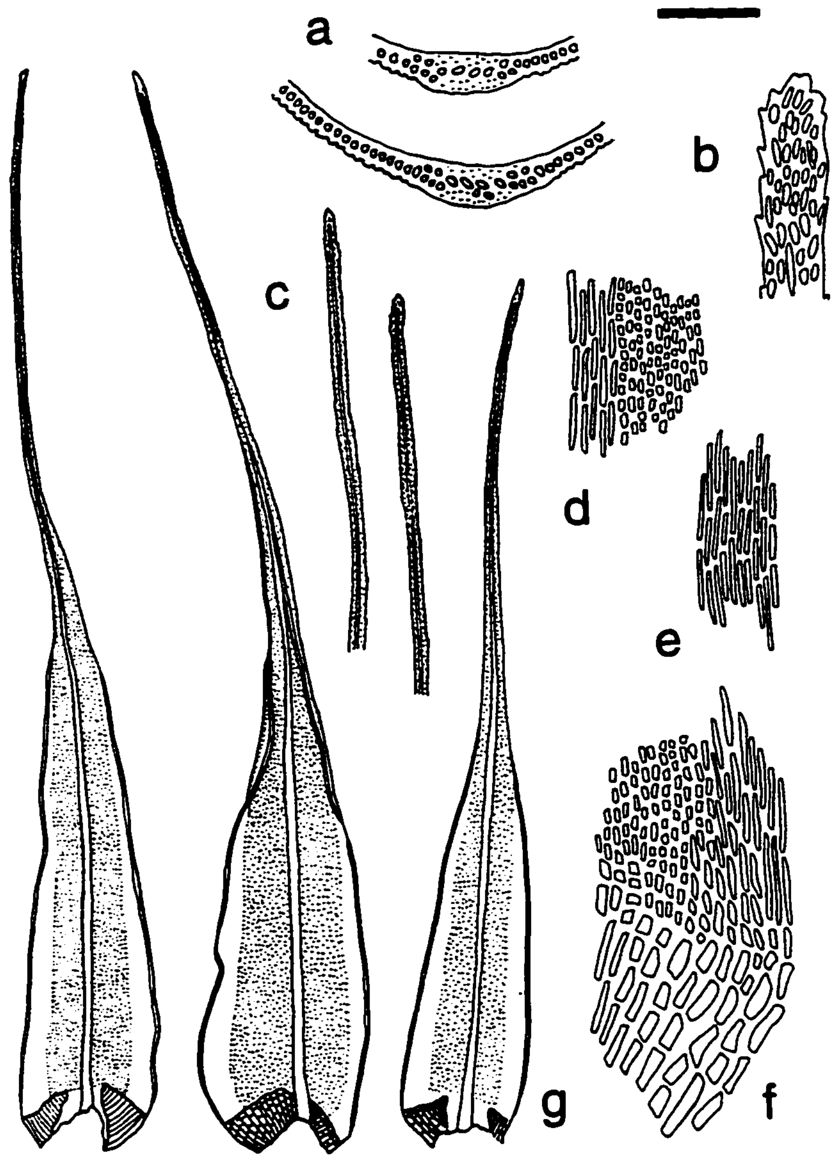


Figure II.36 a-f. *Leucoloma madagascariense*: a) costa transverse sections (*La Farge-England 6235* ALTA); b) leaf apex (*La Farge-England* 5753 ALTA); c) leaf apices (*La Farge-England 6235* ALTA); d) basal juxtacostal interior cells (*La Farge-England 6235* ALTA); e) basal cells (*La Farge-England* 5753 ALTA); f) alar, basal juxtacostal and basal interior cells (*La Farge-England 6235* ALTA); g stem leaves (*La Farge-England 5753,6235* ALTA, *Chenagon* PC). Scale bar = 48 µm for a,b,d-f; 0.2 mm for c; and 0.32 mm for g.

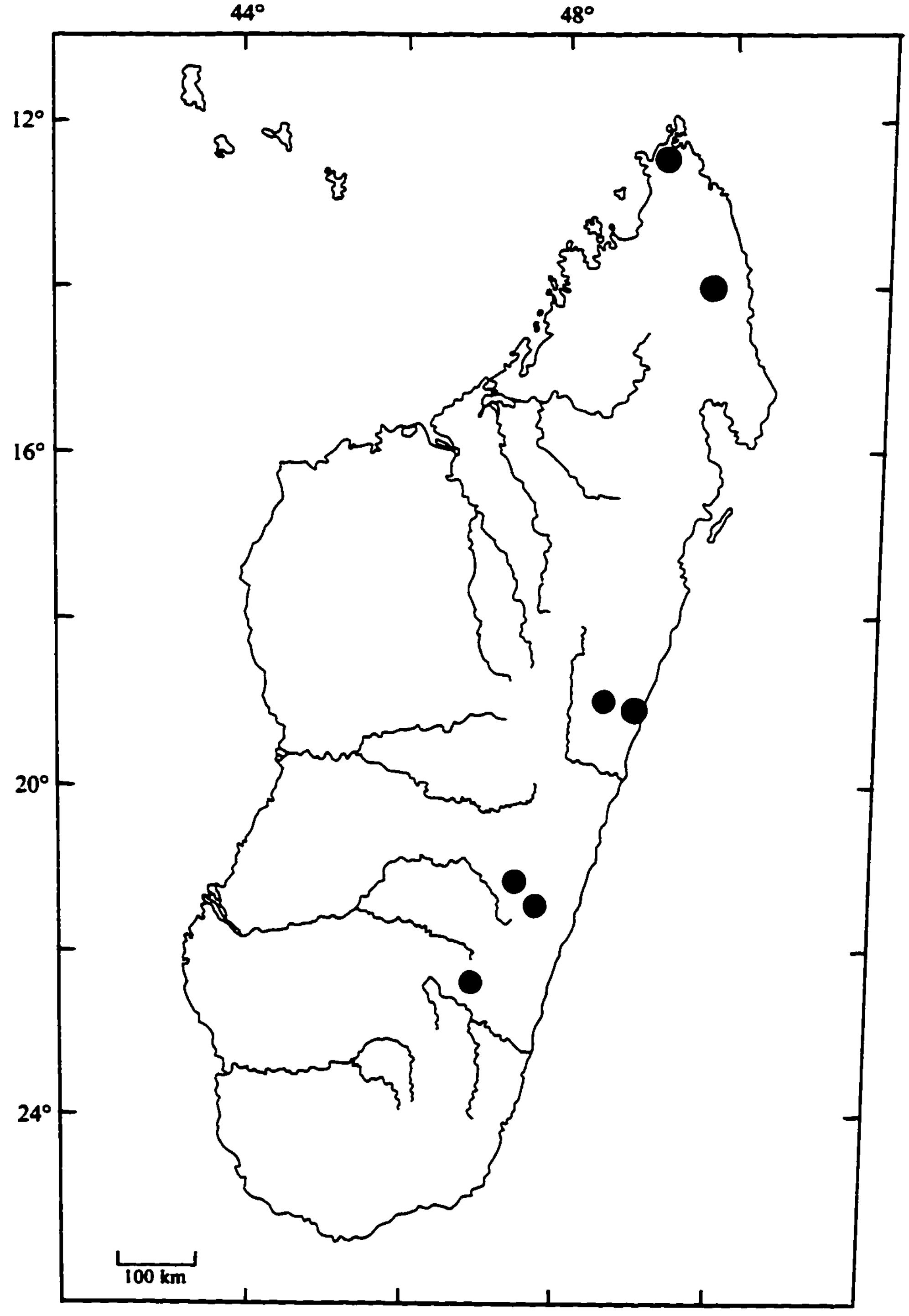


Figure II.37. Distribution of *Leucoloma madagascariense*

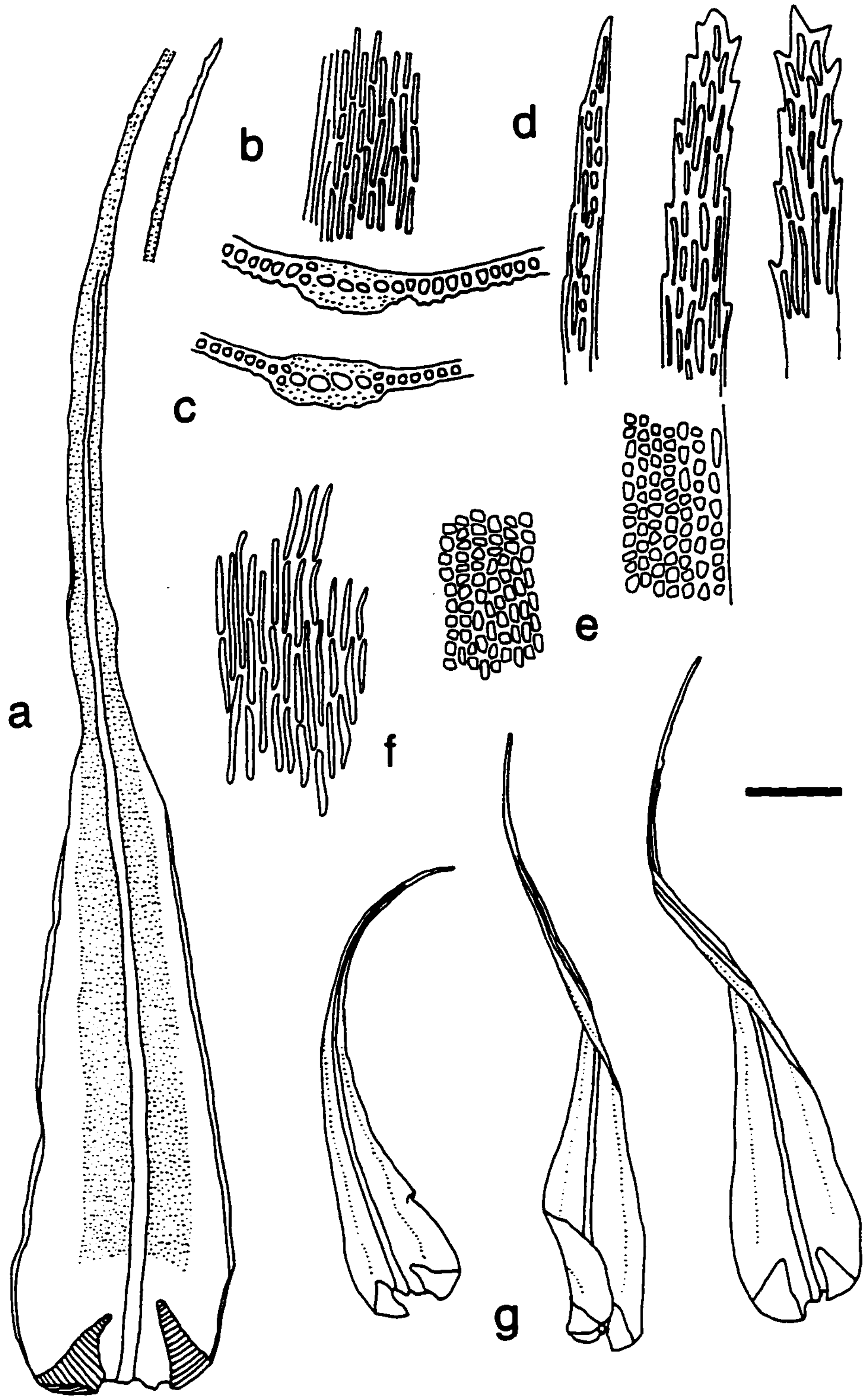


Figure II.38 a-g. *Leucoloma procerum*: a,g) stem leaves (*Magill 11105* ALTA, *Humblot* S); b) medial marginal and interior cells (*Hildebrandt 1842* BM); c) costa transverse sections (*Hildebrandt 1842* BM, *Humblot* S); d) leaf apices (*Magill 11107* ALTA, *Hildebrandt 1839* BM); e) medial and basal juxtacostal cells (*Humblot* S); f) basal cells (*Humblot* S). Scale bar = 48 µm for b-f; 0.32 mm for a; and 0.76 mm for g.

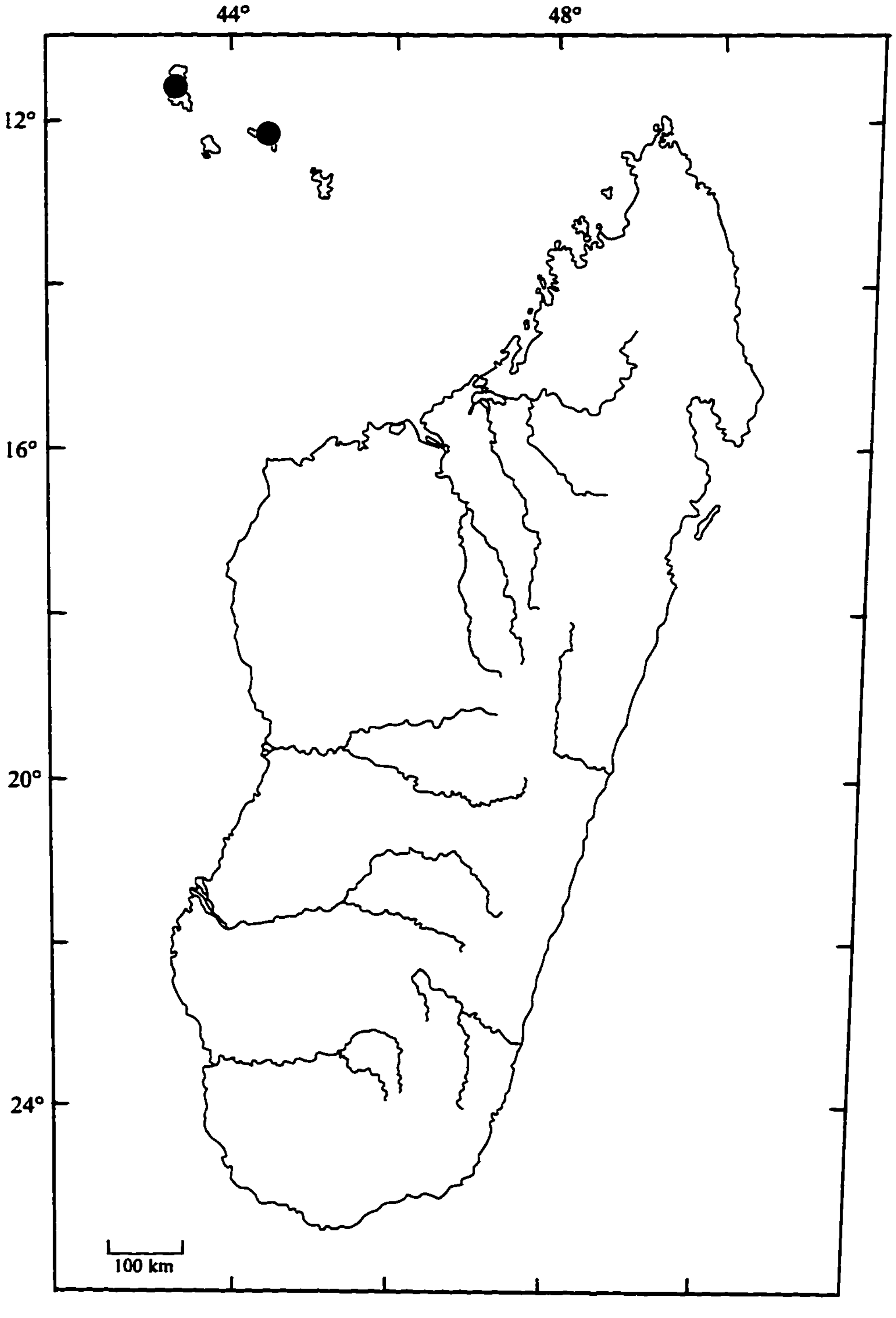


Figure II.39. Distribution of *Leucoloma procerum*

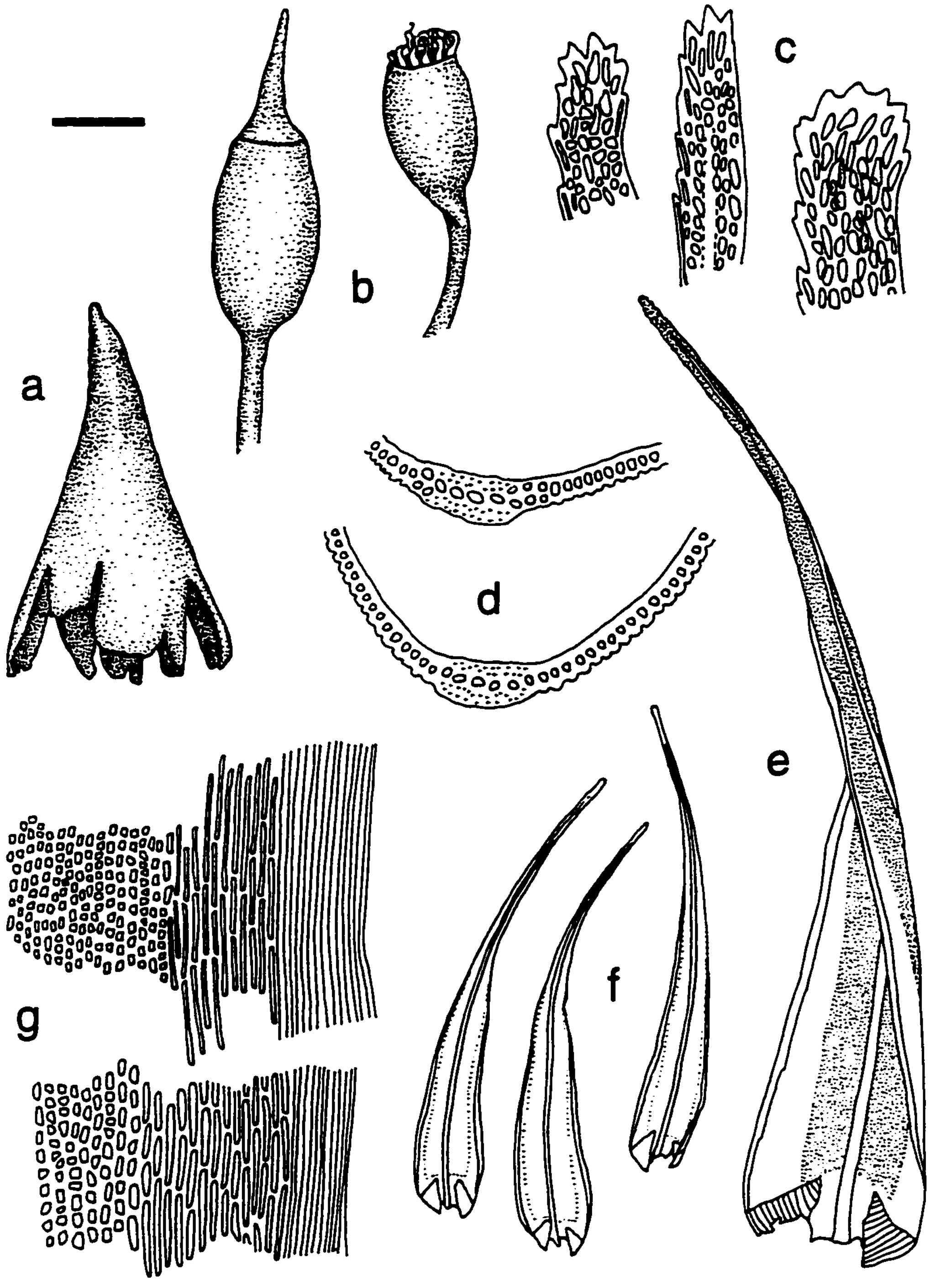


Figure II.40 a-f. *Leucoloma schelpei*: a) calyptra (*Müller 2578* PRE); b) capsules (*Müller 2576* L); c) leaf apices (*Müller 2578* PRE, *2528* L; *Schelpe* PC); d) costa transverse sections (*Müller 2578* L); e,f) stem leaves (*Müller 2528* L, *2638* L); g) medial juxtaxcostal, interior, and marginal cells (*Müller 2578* PRE, *Schelpe* PC). Scale bar = 48 µm for c,d,g; 0.32 mm for a,e; 0.5 mm for b; and 0.76 mm for f.

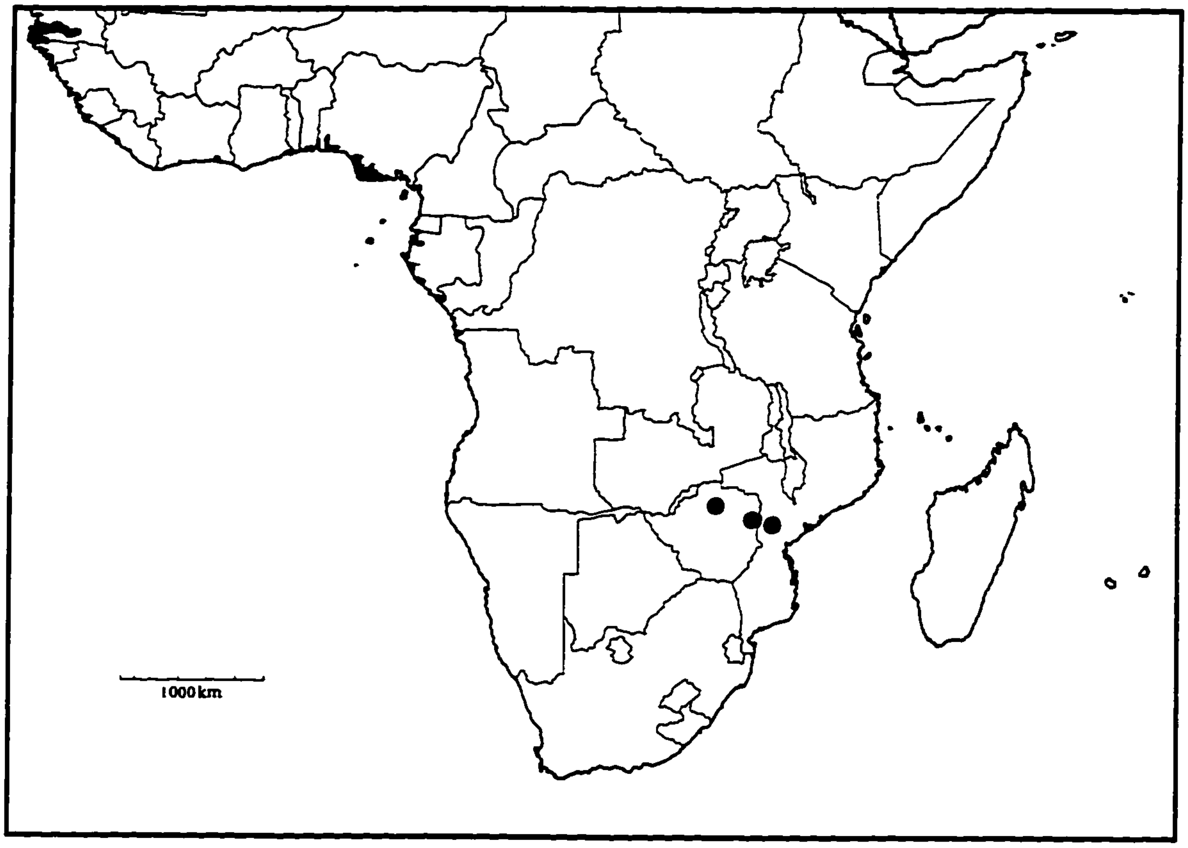


Figure II.41. Distribution of *Leucoloma schelpei*

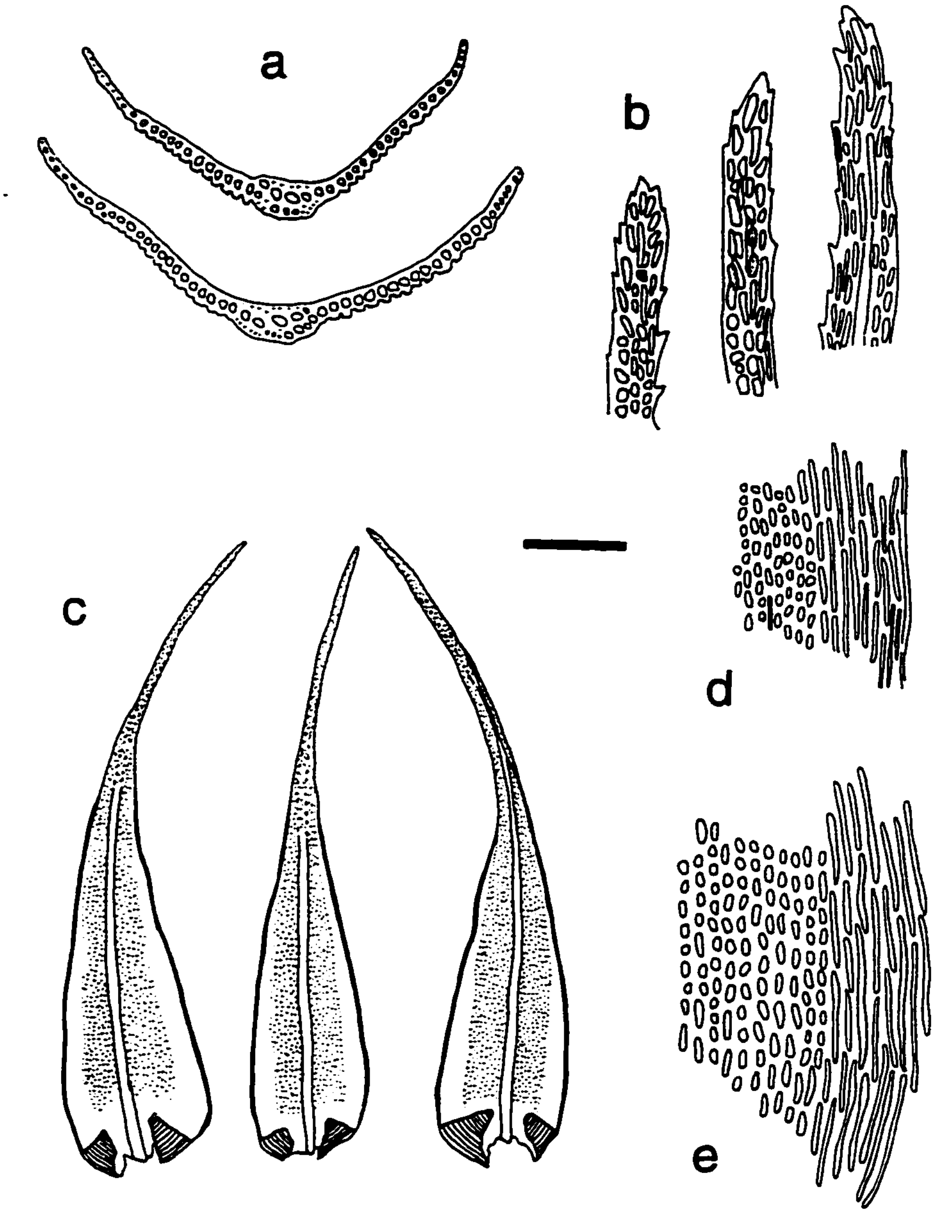


Figure II.42 a-e. *Leucoloma subbiplicatum*: a) lamina transverse sections (*Chenagon* PC); b) leaf apices (*Chenagon* PC, *Forsyth Major* PC); c) stem leaves (*Chenagon* PC, Chenagon BR); d) medial juxtacostal, interior, and marginal cells (*Chenagon* BR); e) basal juxtacostal and interior cells (*Chenagon* BR). Scale bar = 48 µm for a,b,d,e; 0.32 mm for c.

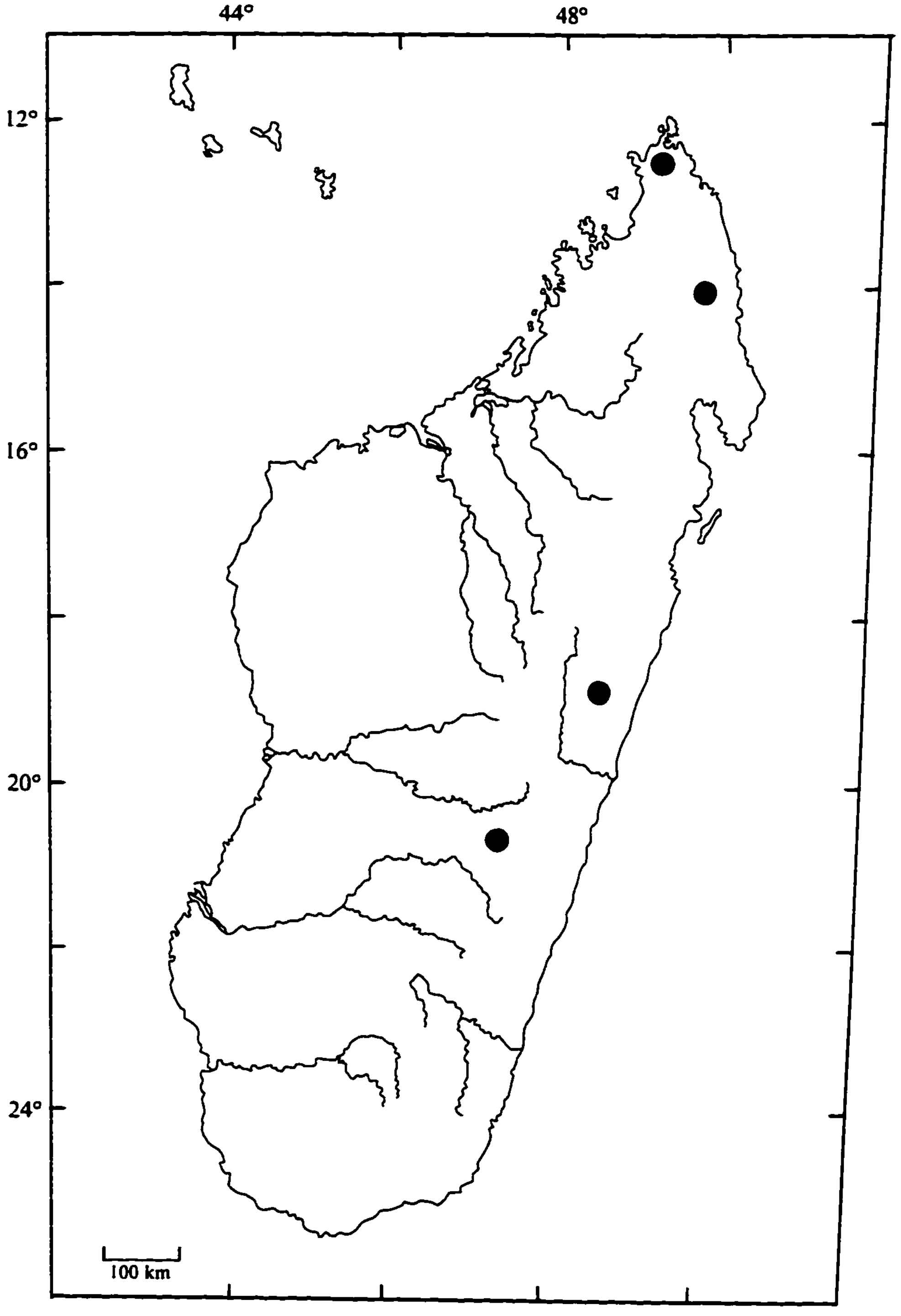


Figure II.43. Distribution of *Leucoloma subbiplicatum*

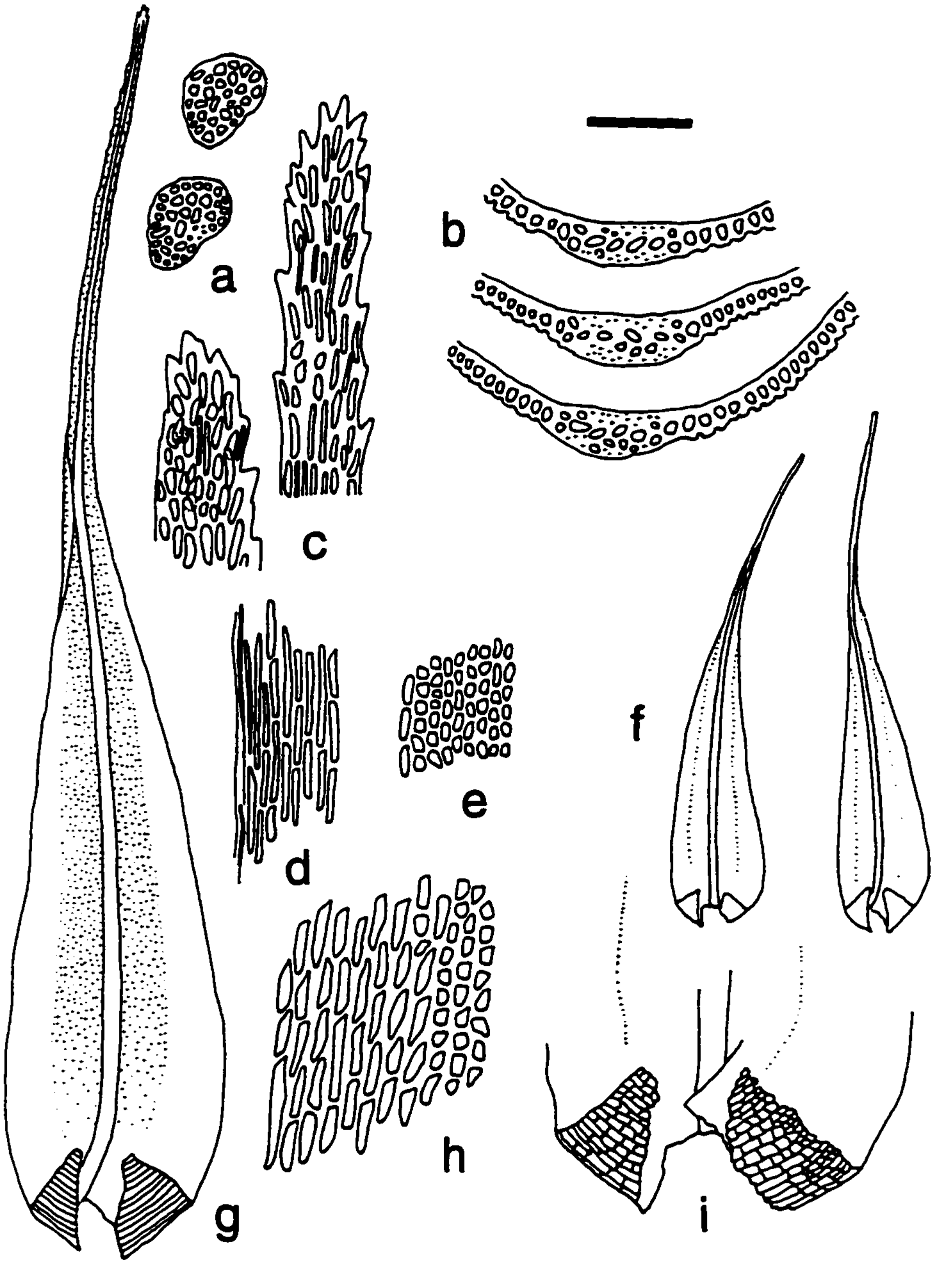


Figure II.44 a-i. *Leucoloma subchrysobasilare*: a) acumen transverse sections (*Tixier 11435* PC); b) costa transverse section (*Borgen* L); c) leaf apices (*Onraedt 70.M.0413*, Hb. Onraedt); d) medial marginal and interior cells (*Onraedt 70.M.0413*, Hb. Onraedt); e) medial juxtacostal cells (*Onraedt 70.M.0413*, Hb. Onraedt); f, g)stem leaves (*Tixier 11435* PC); h) basal interior and juxtacostal cells (*Onraedt 70.M.0413*, Hb. Onraedt); i) leaf base (*Tixier 11435* PC). Scale bar = 48 µm for a-e,h; 0.76 mm for f; 0.32 mm for g; 0.2 mm for i.

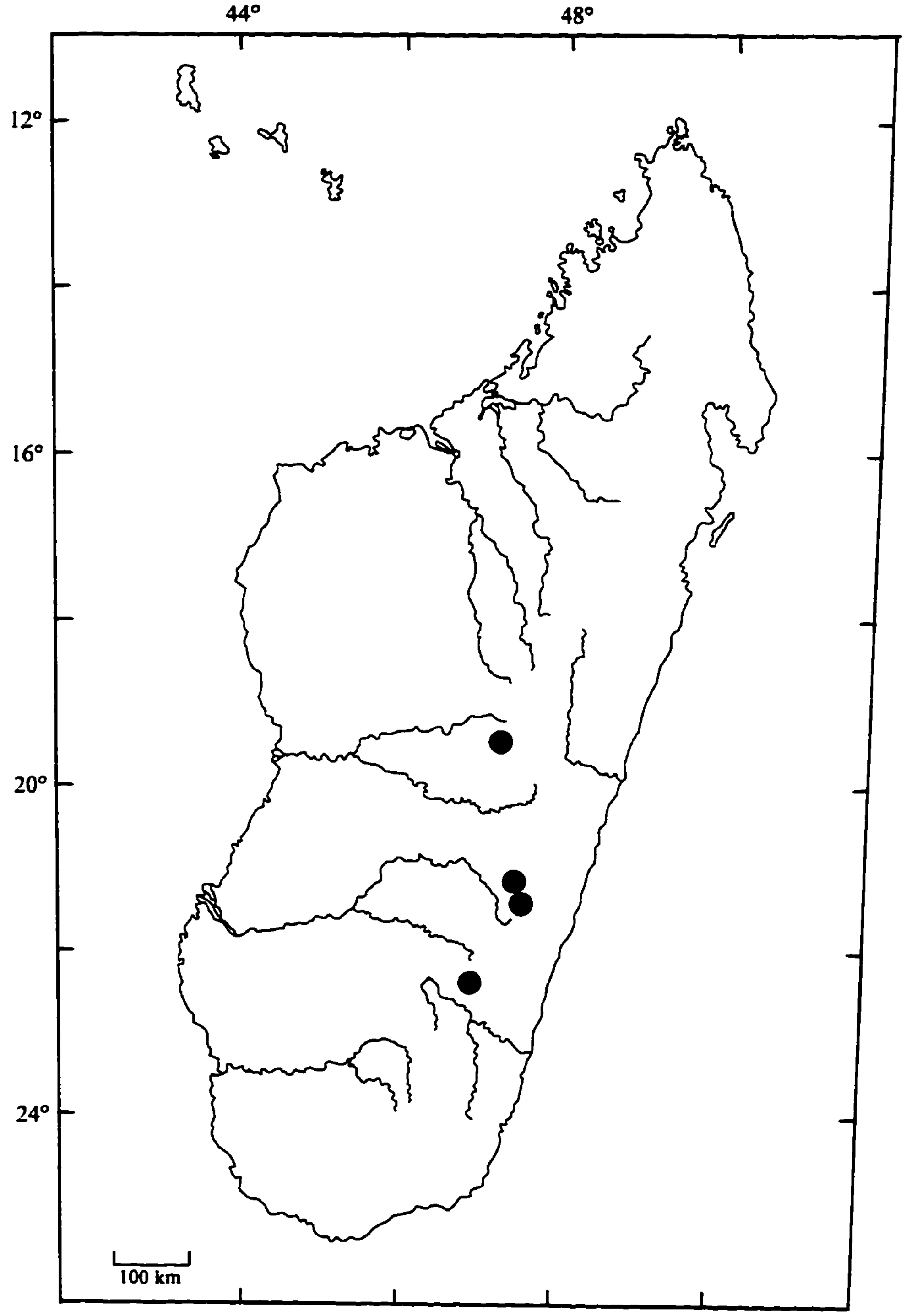


Figure II.45. Distribution of *Leucoloma subchrysobasilare*

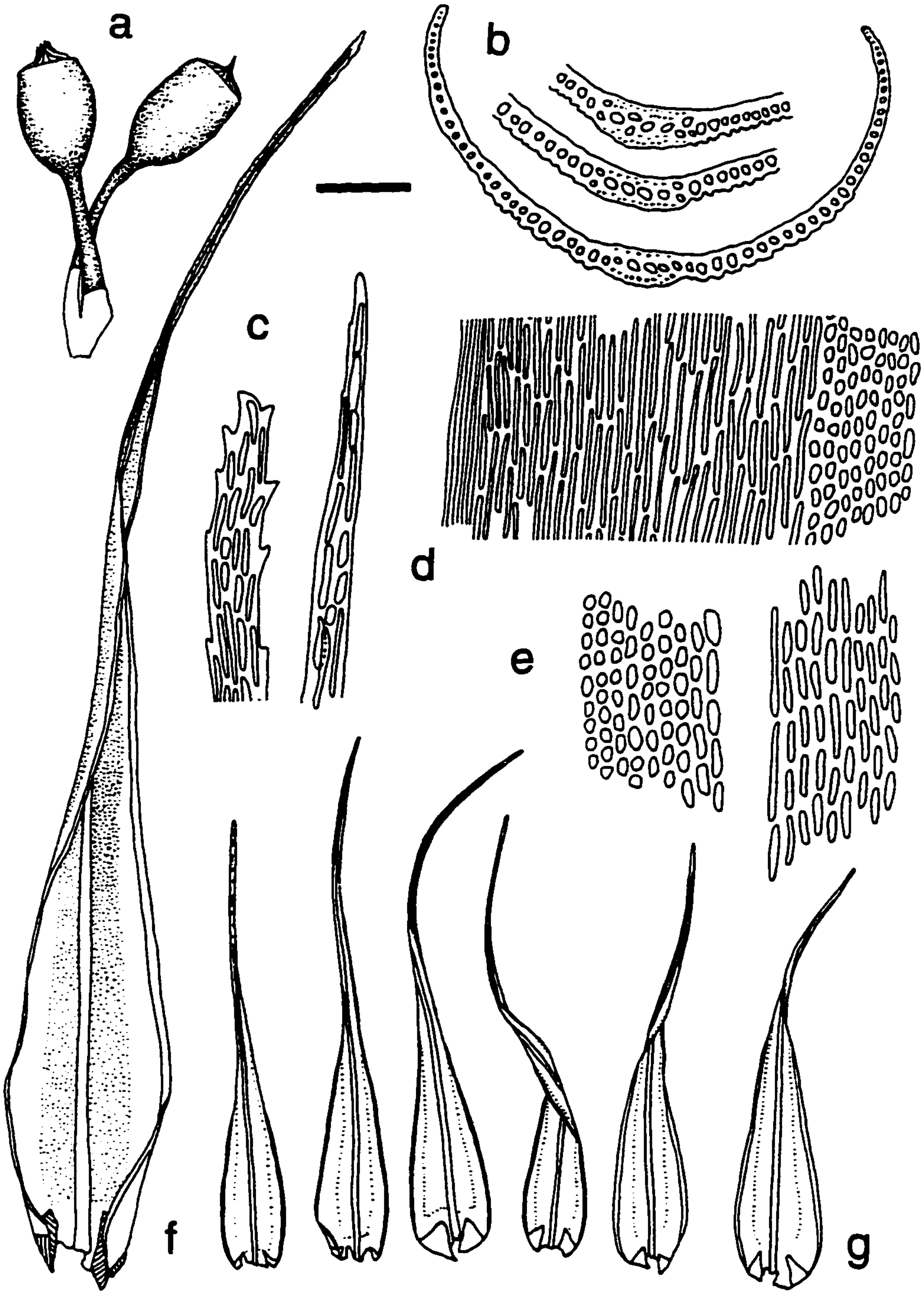


Figure II.46 a-g. *Leucoloma zuluense* var. *zuluense*: a) capsules (*Jones & Pócs 6352/AQ* EGR); b) costa and lamina transverse sections (*La Farge-England 5609* ALTA, *Schliechen* PC); c) leaf apices (*La Farge-England 5609* ALTA); d) medial marginal, interior, and juxtacostal cells (*Pócs & Kornas 86241/I* EGR); e) basal juxtacostal cells (*Pócs & Mioga 900/73/T* EGR, *Schliechen* PC); f,g) stem leaves (*La Farge-England 5603, 5355,* 5609 ALTA). Scale bar = 48 μm for b-e; 0.5 mm for a; 0.32 mm for f; 0.76 mm for g.

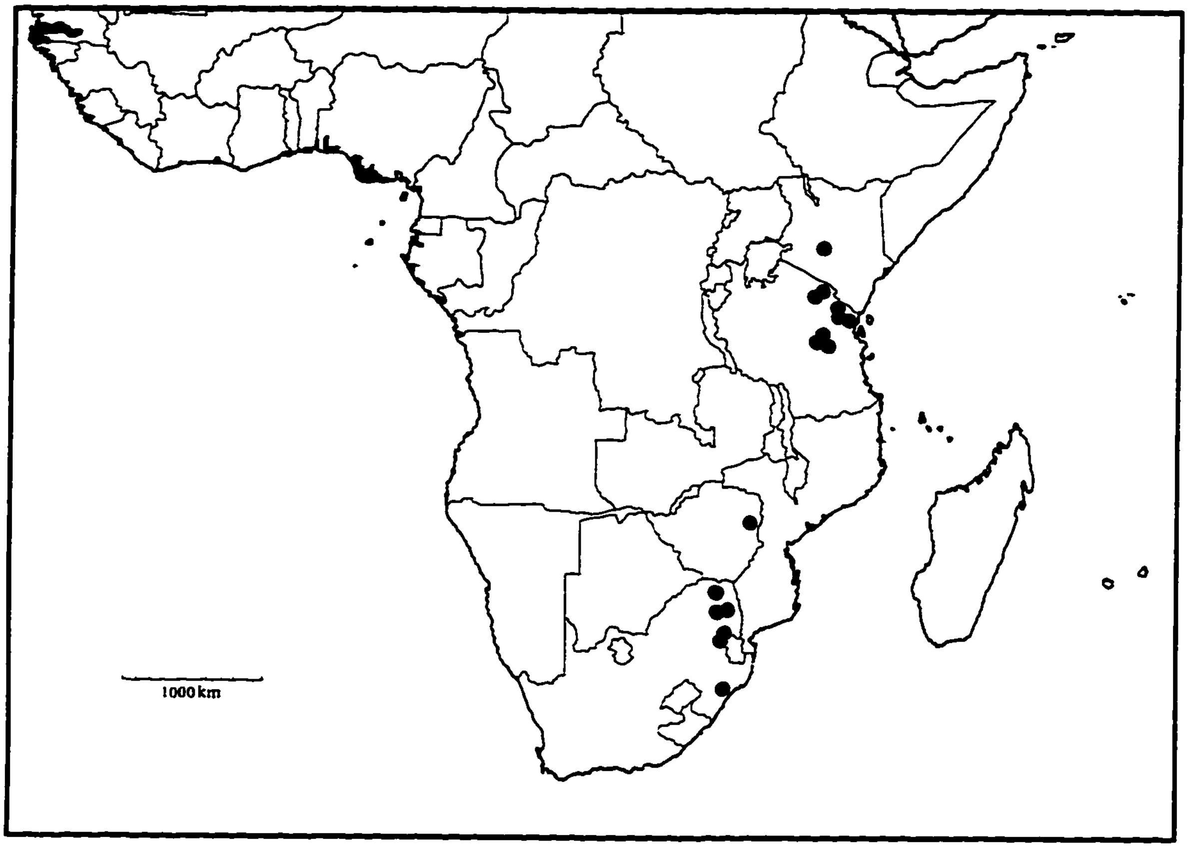


Figure II.47. Distribution of *Leucoloma zuluense* var. *zuluense*

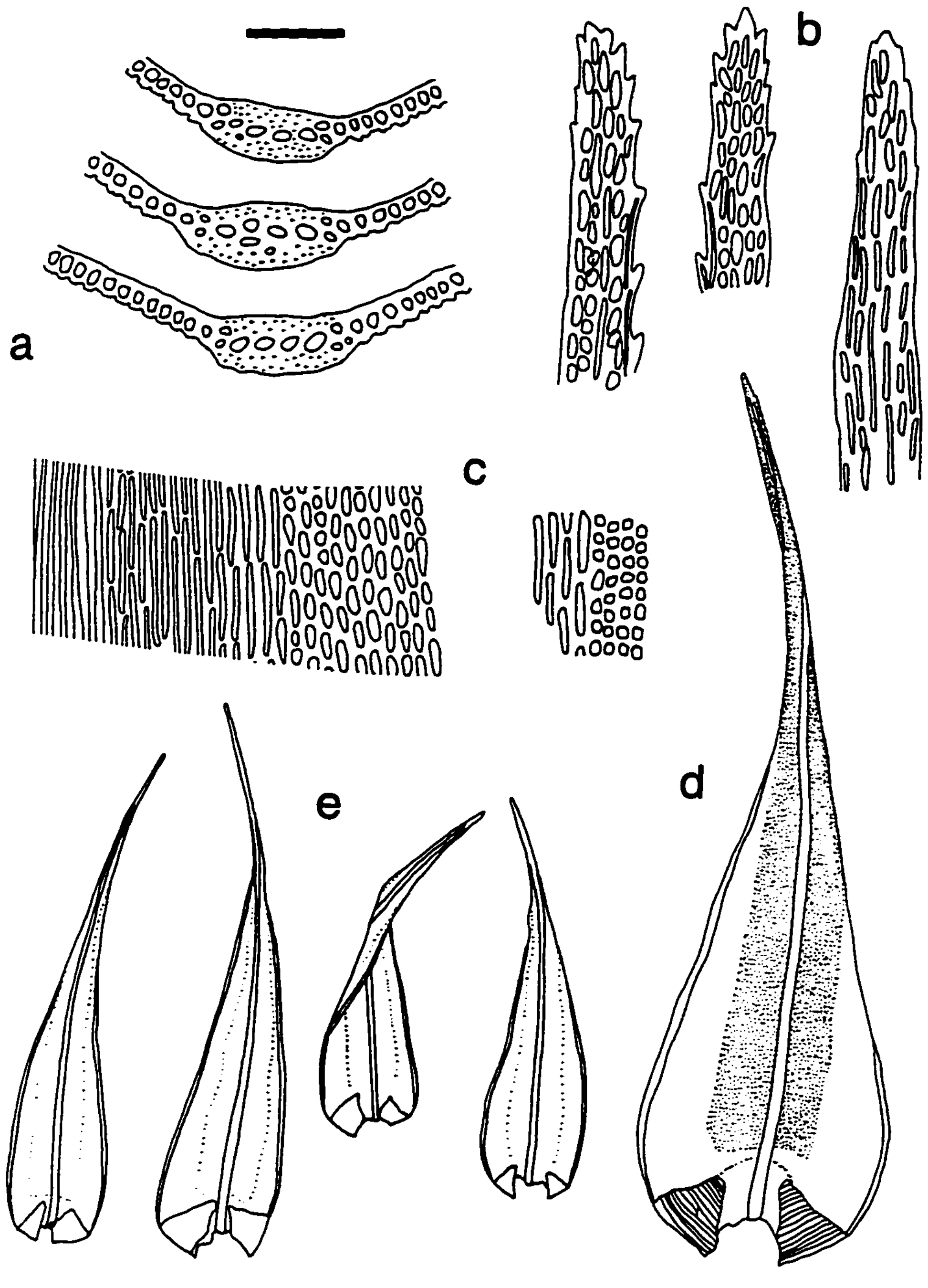


Figure II.48 a-e. *Leucoloma zuluense* var. *ovatum*: a) costa transverse sections (*Pócs & al. 6076/BB* L); b) leaf apices (*Pócs & Harris 6123/E* G); c) medial marginal, interior, and juxtacostal cells (*Pócs & Harris 6123/E* G); d,e) stem leaves (*Pócs & al. 6076/BB* L, *Pócs 8949/N* ALTA, *Pócs & Harris 6123/E* G). Scale bar = 48 µm for a-c; 0.32 mm for d; 0.76 mm for e.

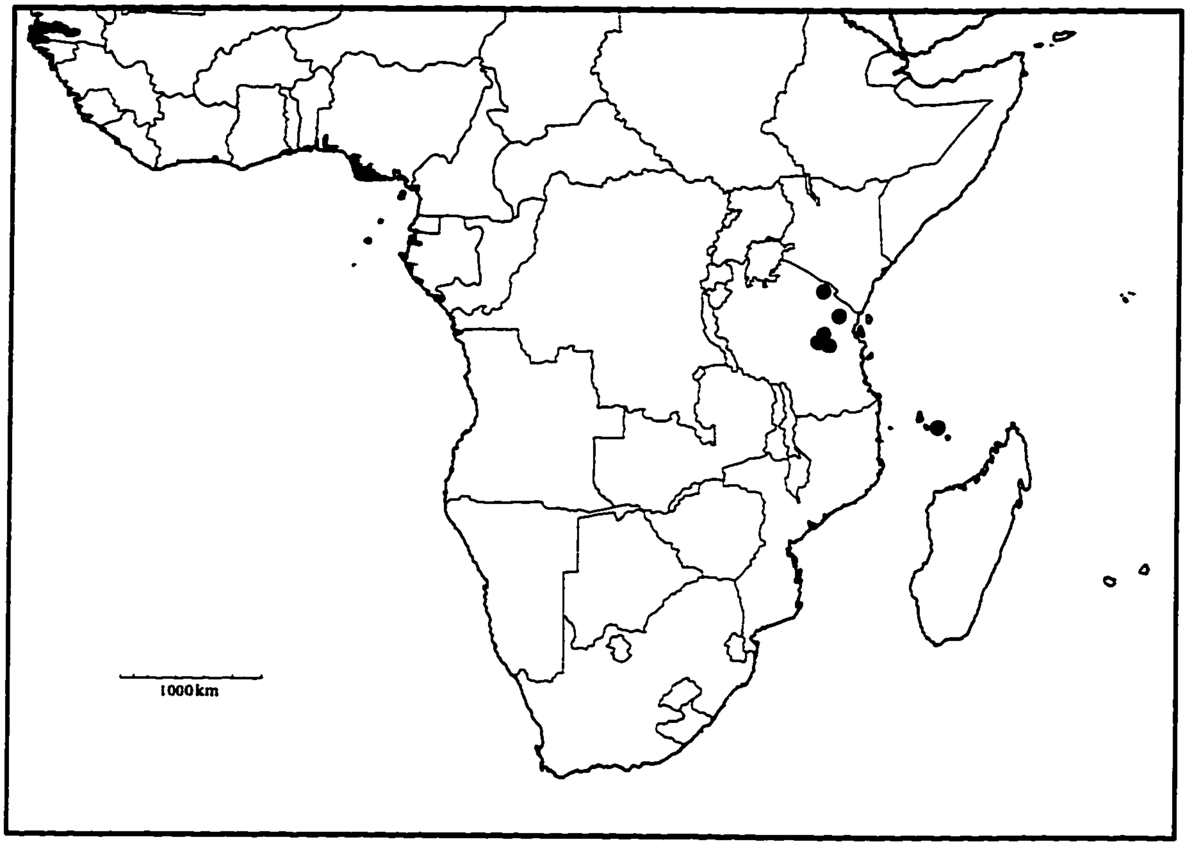


Figure II.49. Distribution of*Leucoloma zuluense* var. *ovatum*

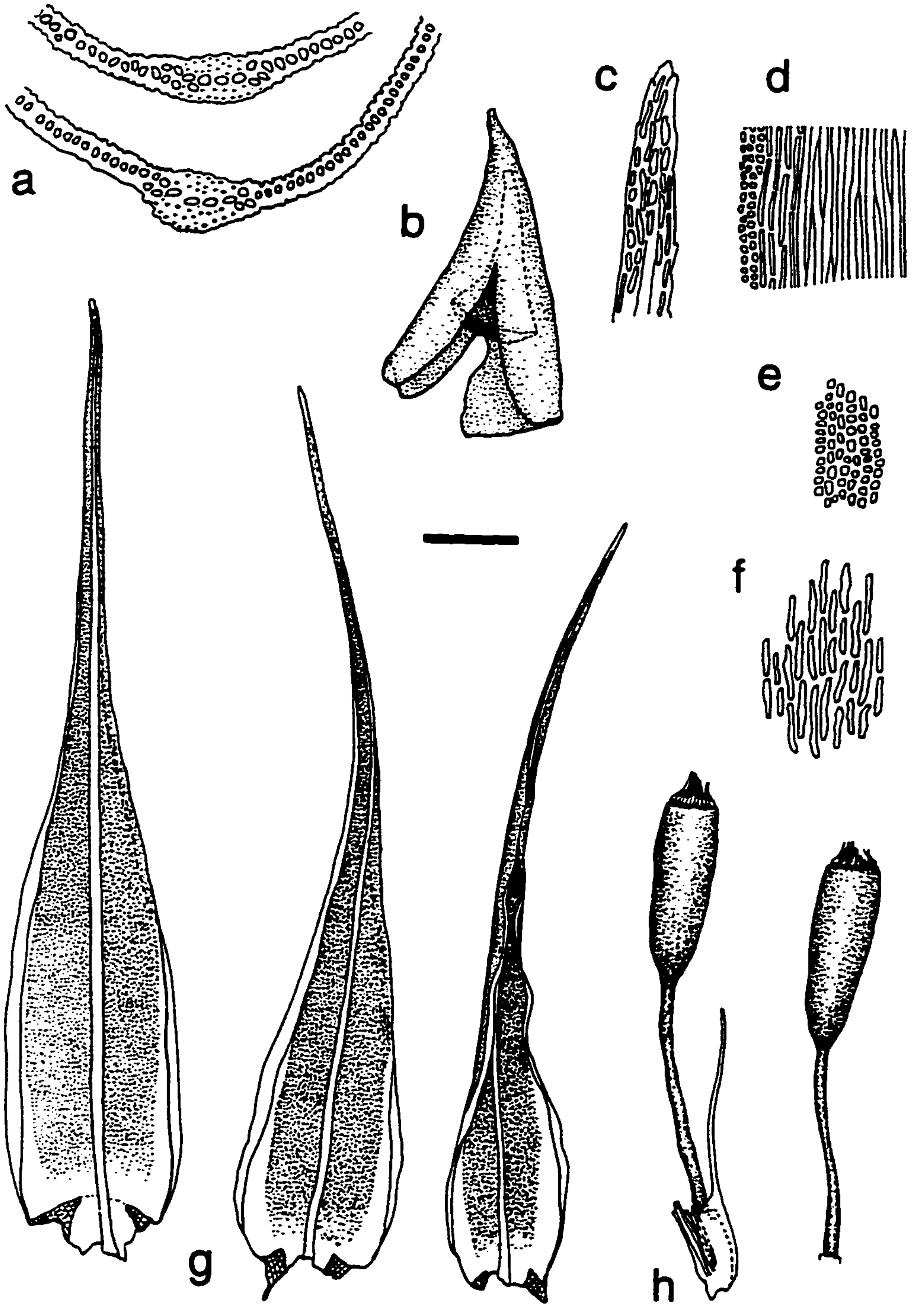


Figure II.50 a-h. *Leucoloma sanctae-mariae*: a) costa transverse sections (*Boivin* BM); b) calyptra with operculum (*Boivin* BM); c) leaf apex (*Crosby & Crosby 5435* MO); d) juxtacostal interior and marginal cells (*Crosby & Crosby 5435* MO); e) medial juxtacostal cells (*La Farge-England 6136* ALTA); f) basal interior cells (*Crosby & Crosby 5435* MO); g) stem leaves (*Boivin* BM, *Crosby & Crosby 5435* MO); h) capsules (*Boivin* BM). Scale bar = 48 µm for a,c-f; 0.5 mm for b; 0.32 mm for g; 1 mm for h.

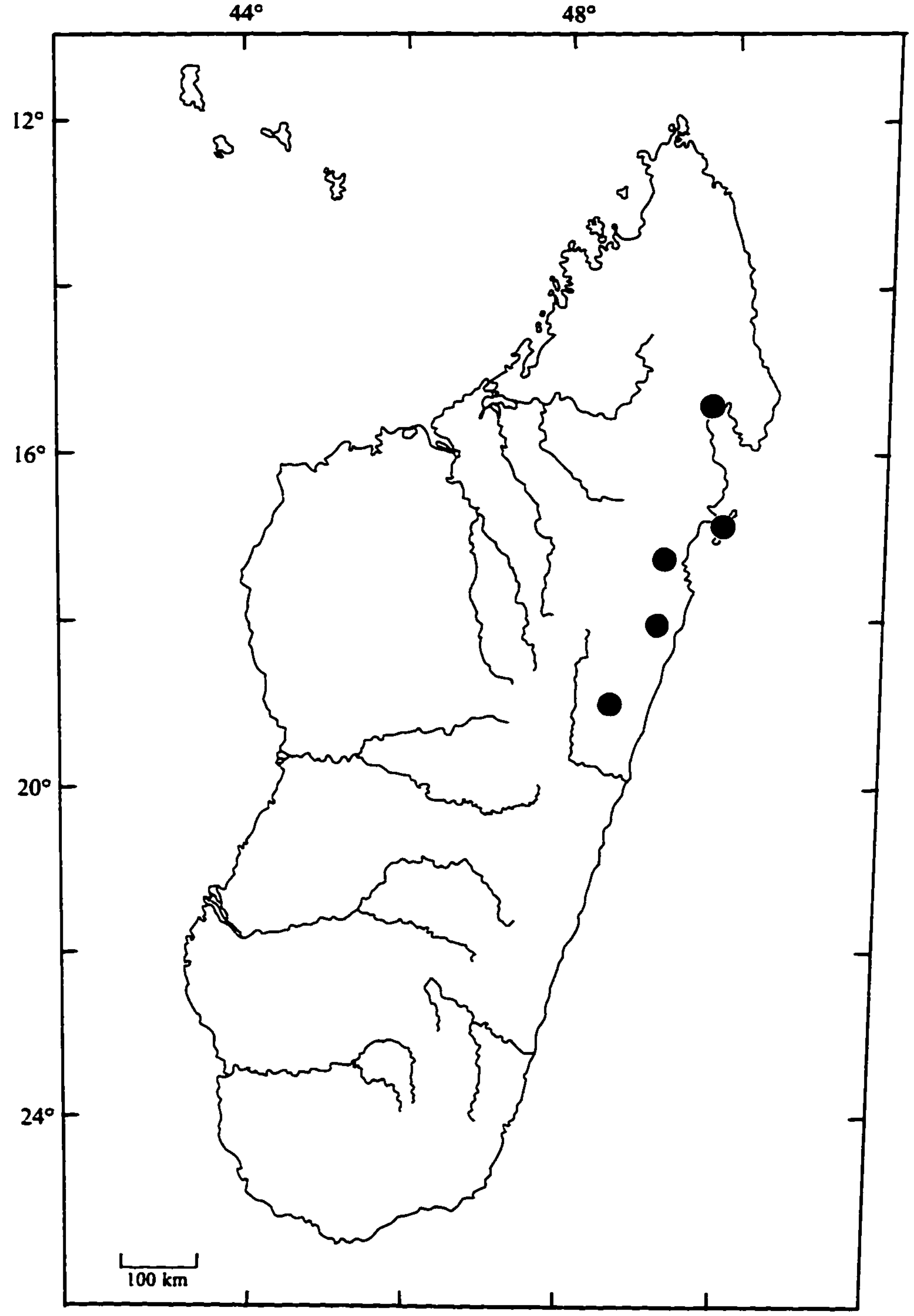


Figure II.51. Distribution of *Leucoloma sanctae-mariae*

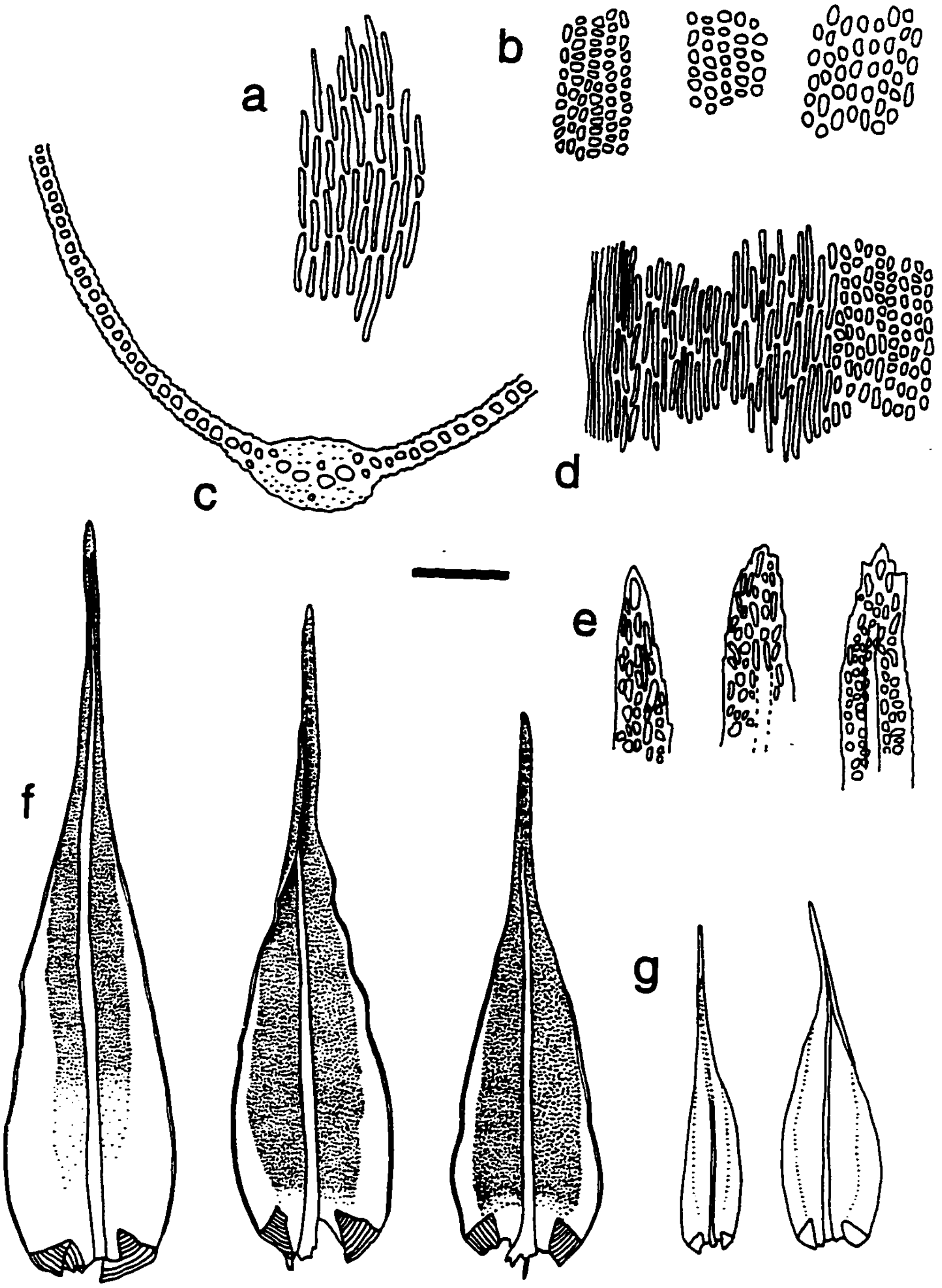


Figure II.52 a-g. *Leucoloma thraustum*: a) basal interior cells (*Borchgrevink* BR); b upper juxtacostal cells (*Borchgrevink* BM, *Crosby & Crosby 6784* ALTA); c) transverse section of costa (*Crosby & Crosby 6784* ALTA); d) medial marginal, interior, and juxtacostal cells (*Crosby & Crosby 6784* ALTA); e) leaf apices (*Cremer 3154* Hb. Onraedt); f,g) stem leaves (*Borchgrevink* BM, *Cremers 3154* Hb. Onraedt). Scale bar = 48 µm for a-e; 0.32 mm for f; 0.76 mm for g.

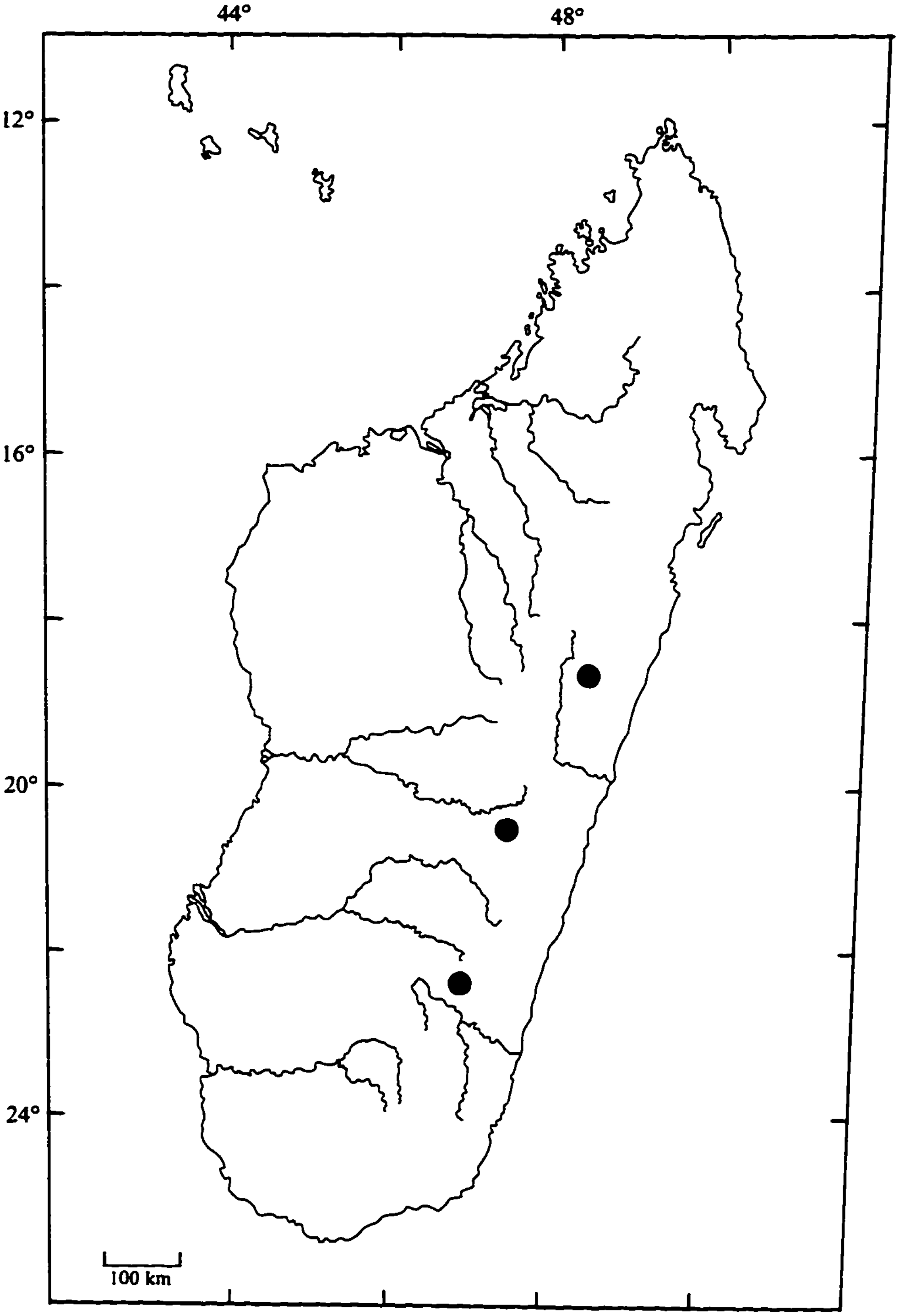


Figure II.53. Distribution of *Leucoloma thraustum*

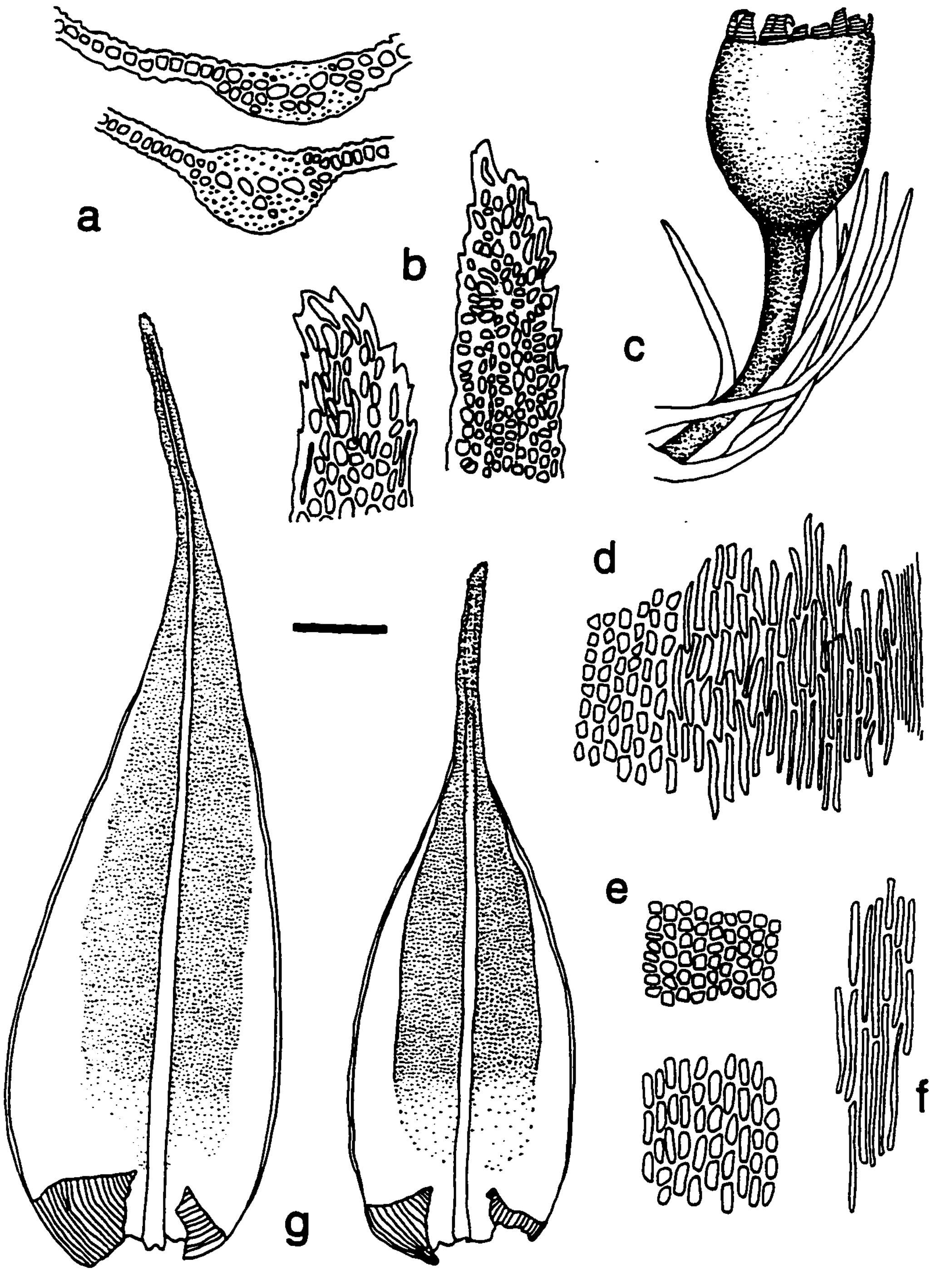


Figure II.54 a-g. *Leucoloma thuretii*: a) costa transverse section (*Bernier* BM); b) leaf apices (*Bernier* BM); c) capsule with apices of perichaetial leaves (*Bernier* PC); d) medial juxtacostal, interior, and marginal cells (*Bernier* BM); e) upper juxtacostal cells (*Bernier* BM), basal juxtacostal cells (*Bernier* BM); f) basal interior cells (*Bernier* BM); g) stem leaves (*Onraedt 0569* Hb. Onraedt). Scale bar = 48 µm for a-b,d-f; 0.5 mm for c; 0.32 mm for g.

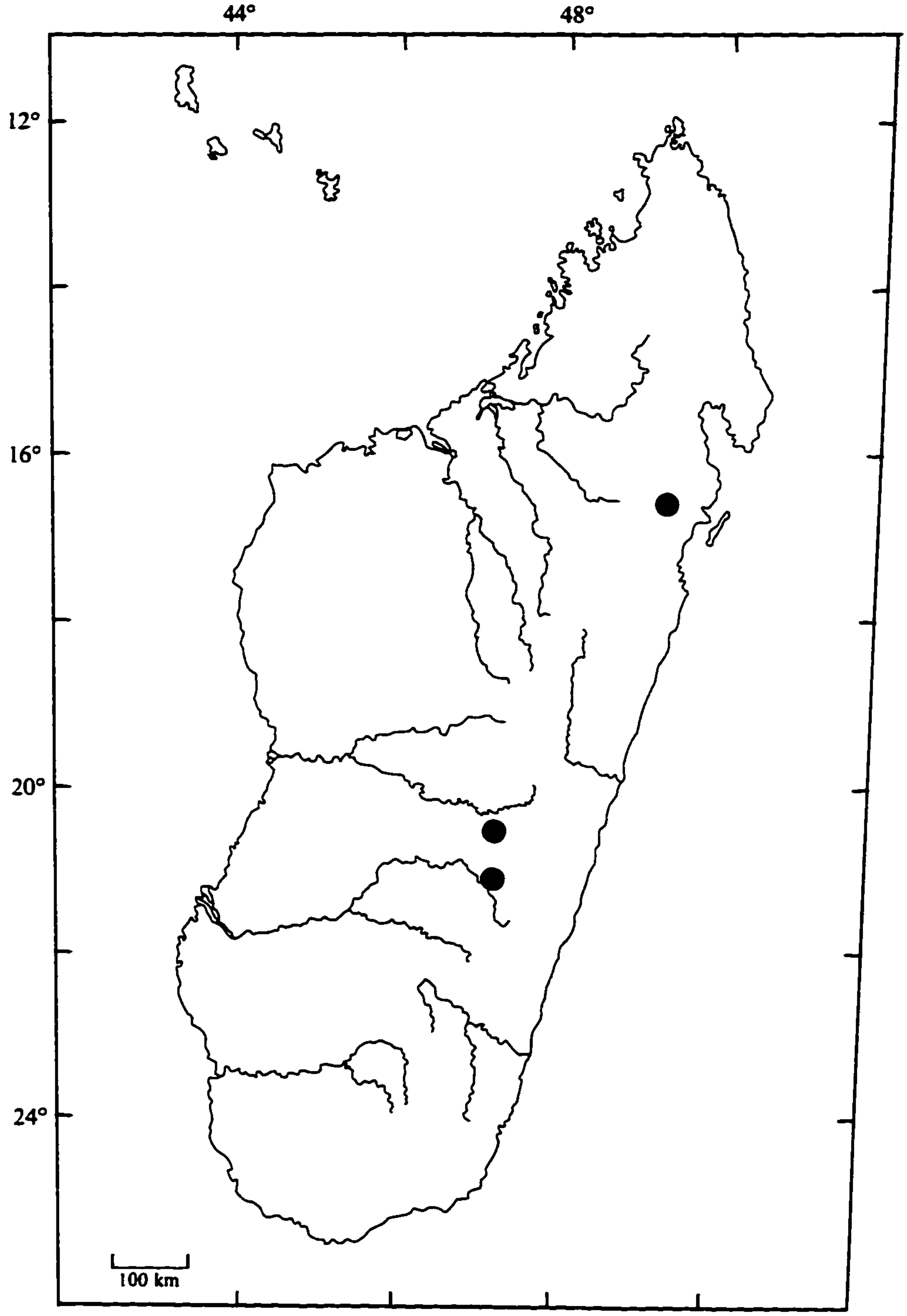


Figure II.55. Distribution of *Leucoloma thuretii*

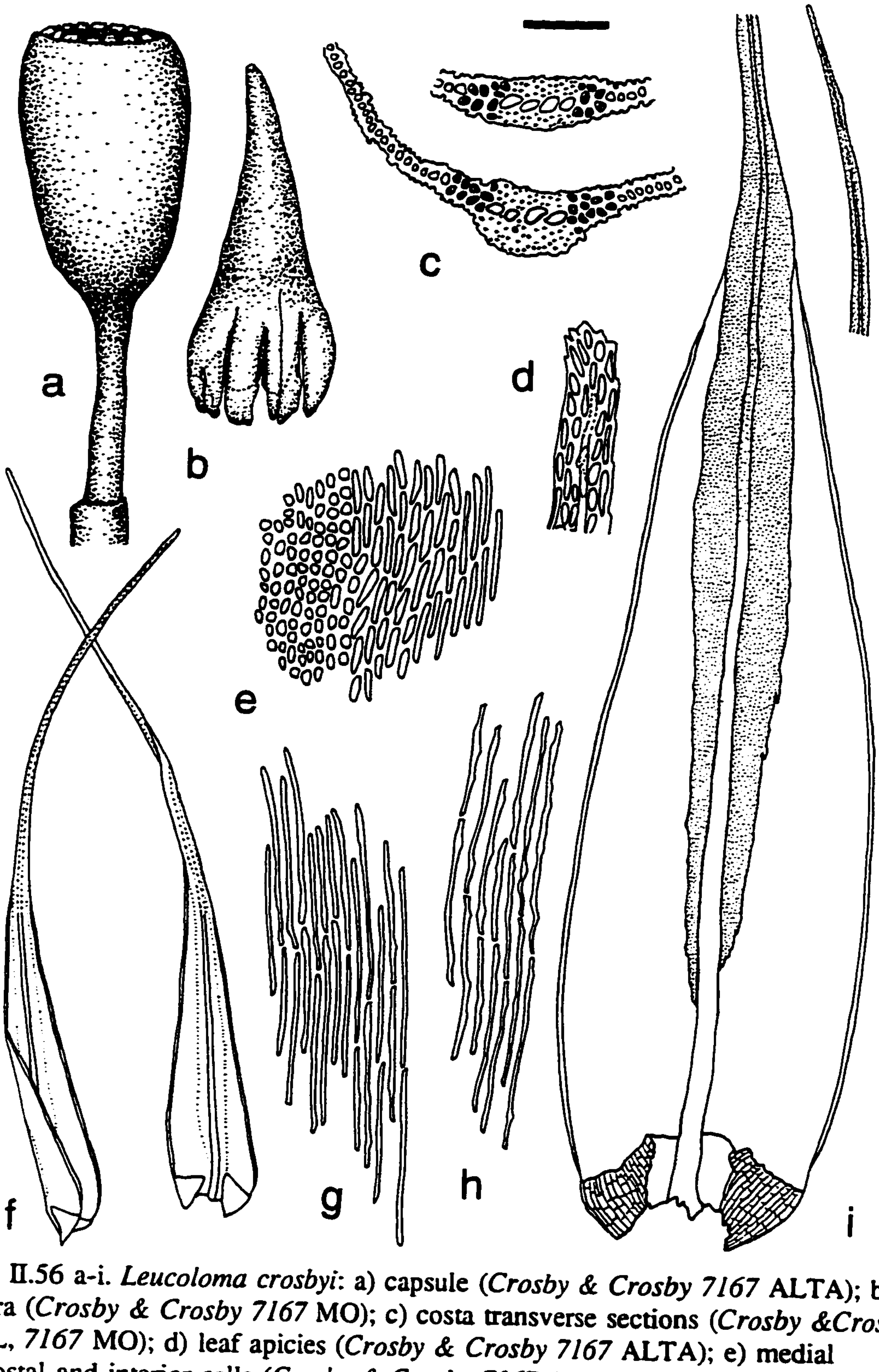


Figure II.56 a-i. *Leucoloma crosbyi*: a) capsule (*Crosby & Crosby 7167* ALTA); b) calyptra (*Crosby & Crosby 7167* MO); c) costa transverse sections (*Crosby &Crosby 7304* L, *7167* MO); d) leaf apicies (*Crosby & Crosby 7167* ALTA); e) medial juxtacostal and interior cells (*Crosby & Crosby 7167* ALTA); f,i) stem leaves (*Crosby & Crosby 7170* MO); g, h) basal interior cells (*Crosby & Crosby 7170* MO). Scale bar = 48 µm for c-e, g-h; 0.5 mm for a,b; 0.76 mm for f; 0.32 mm for i.

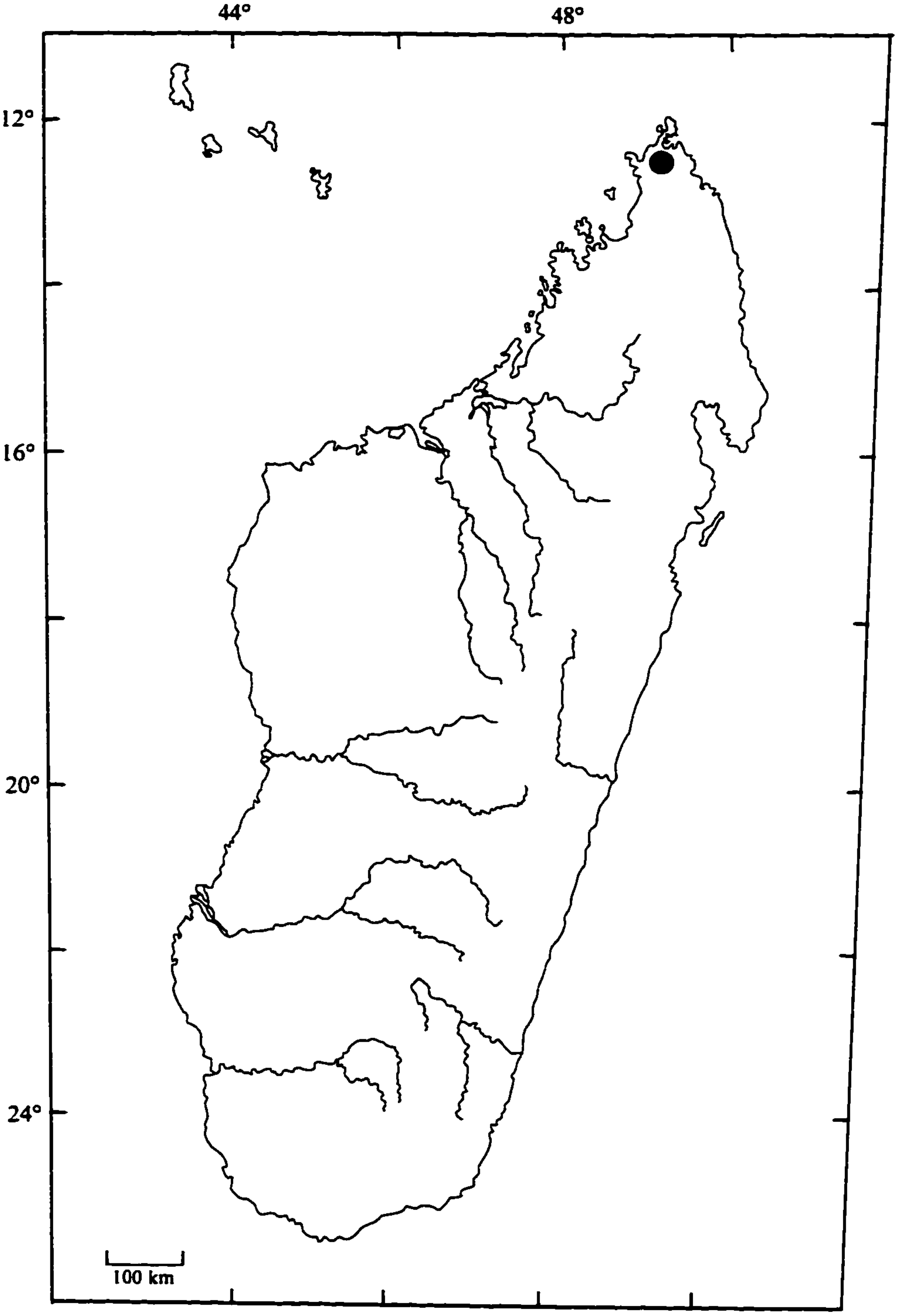


Figure II.57. Distribution of *Leucoloma crosbyi*

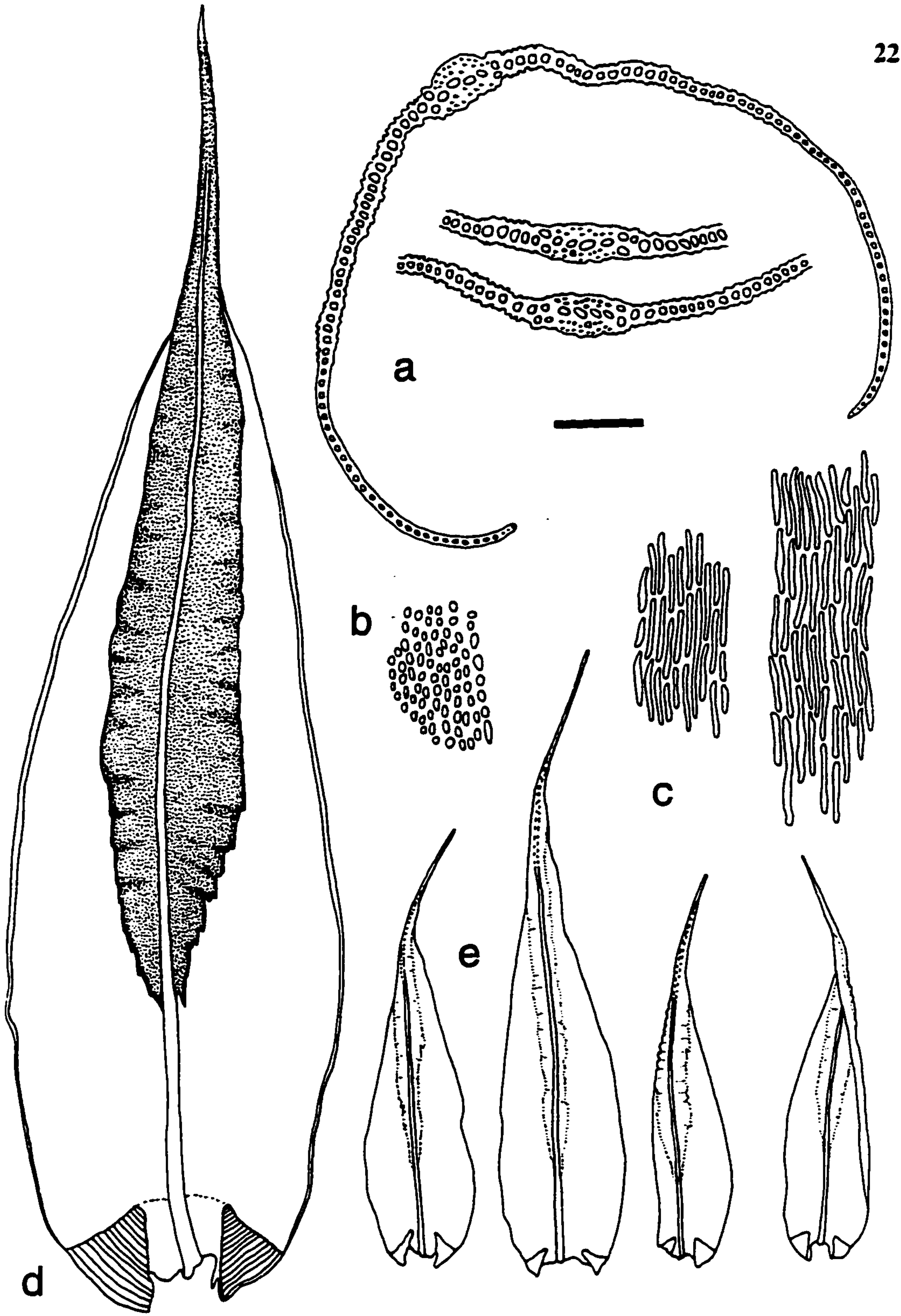


Figure II.58.a-e. *Leucoloma grandidieri*: a) costa and lamina transverse sections (*Crosby & Crosby 6782* F); b) medial juxtacostal cells (*La Farge-England 6292* ALTA); c) medial interior (*Besson* Z); d,e) stem leaves (*Crosby & Crosby 6863* H, *La Farge-England 6292* ALTA, *Drouhard* (sp?) PC). Scale bar = 48 µm for a-c; 0.32 mm for d; 0.76 mm for e.

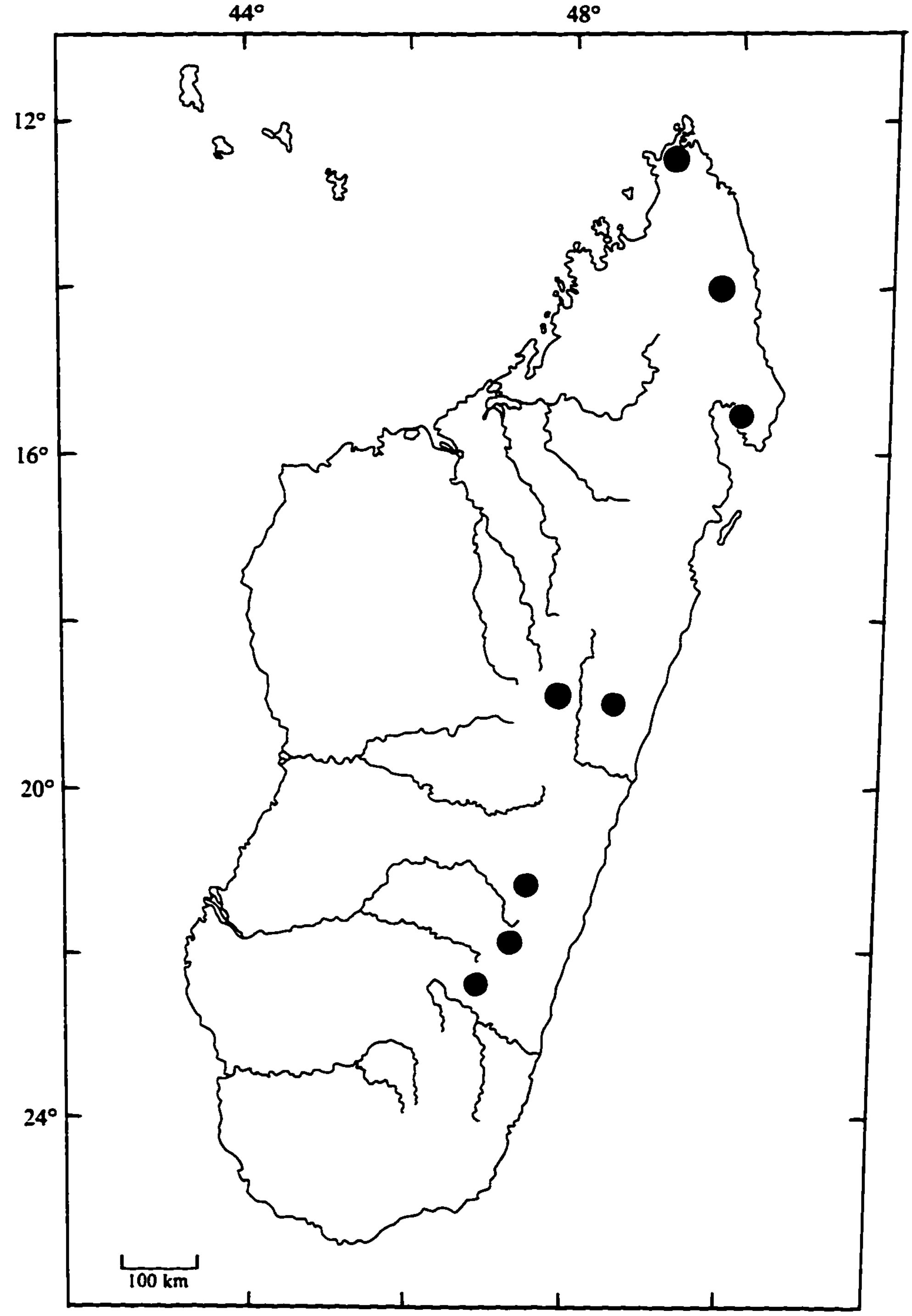


Figure II.59. Distribution of *Leucoloma grandidieri*

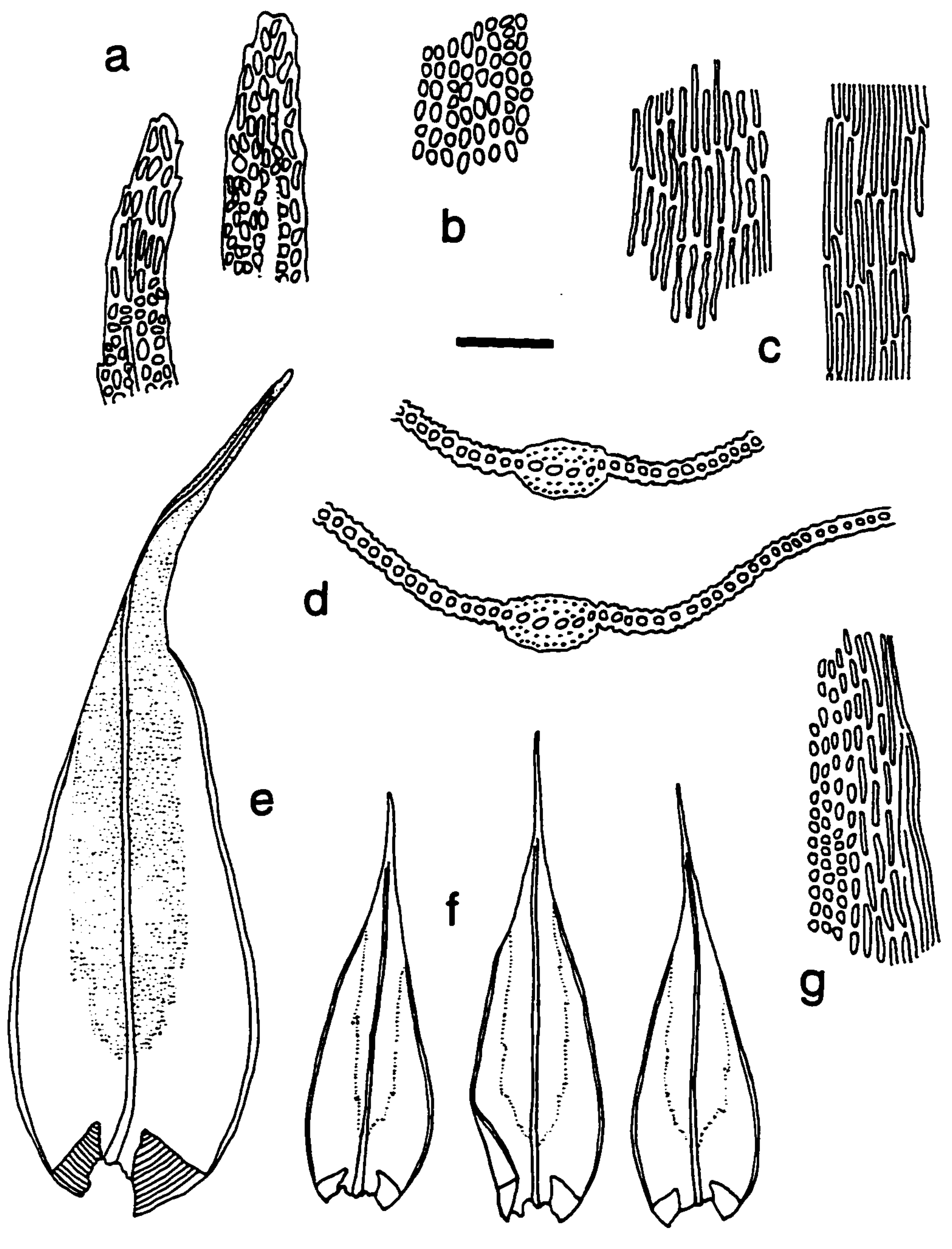


Figure II.60 a-g. *Leucoloma membranaceum*: a) leaf apices (*Een 494* Hb. Een; *Tixier 10553* PC); b) medial juxtacostal cells (*Een 494* Hb. Een); c) slightly porose upper medial interior cells (*Een 494* Hb. Een); non-porose basal interior cells (*Crosby & Crosby 8368* L); d) costa transverse sections (*Een 494* Hb. Een); e,f stem leaves (*Een 494* Hb. Een); g) upper juxtacostal, interior and marginal cells (*Een 494* Hb. Een). Scale bar = 48 μm for a-d,g; 0.32 mm for e; 0.76 mm for f.

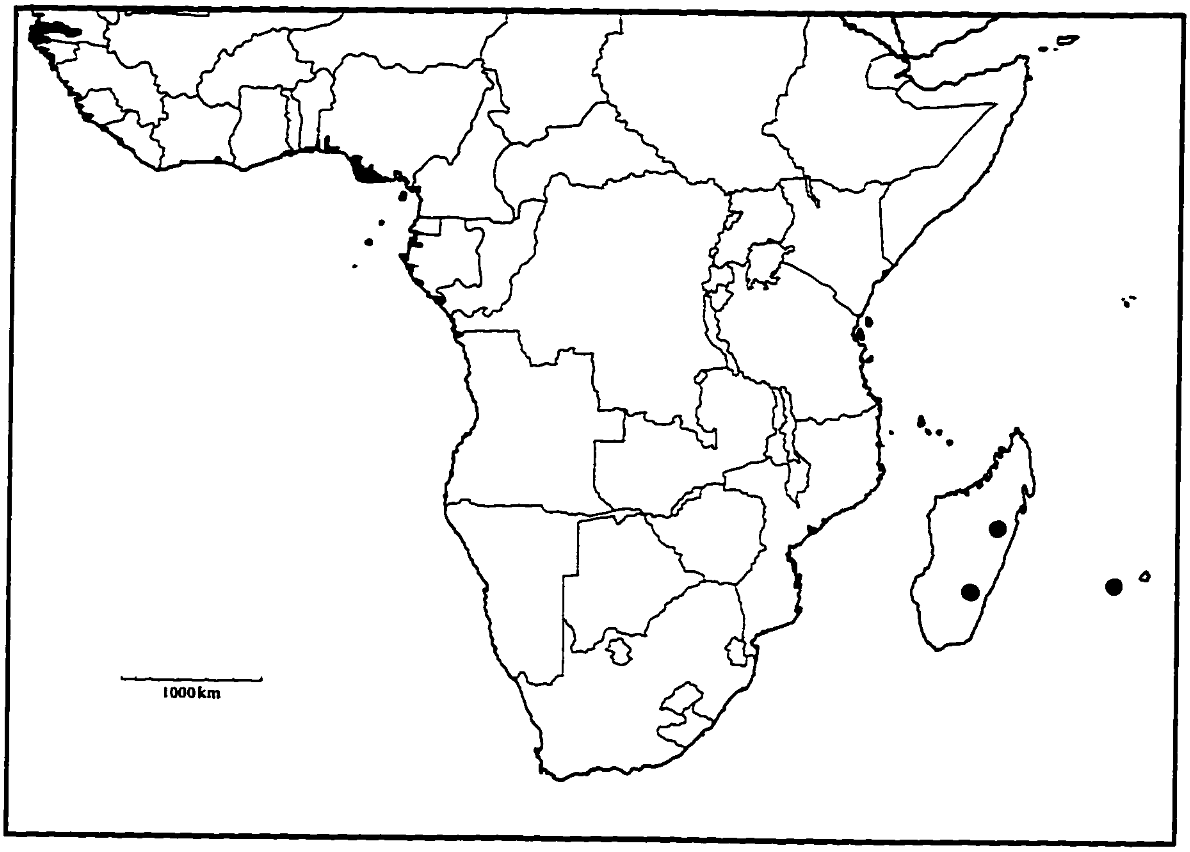


Figure II.61. Distribution of *Leucoloma membranaceum*

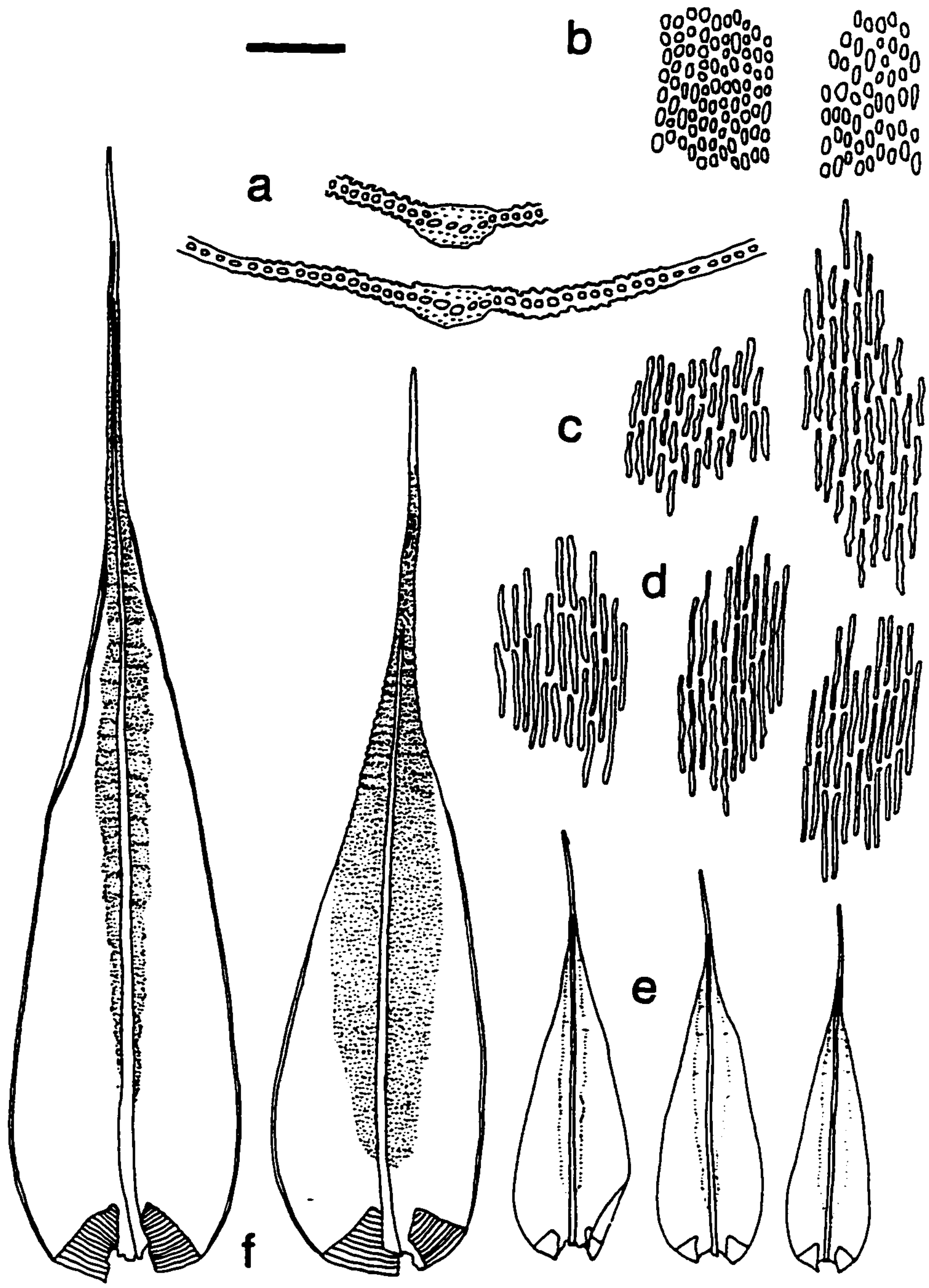


Figure II.62 a-e. *Leucoloma seychellense*: a) costa transverse sections (*Balfour* BM); medial juxtacostal cells (*G. de l'Isle* BM, *Rev. Quirin* BM); c) medial interior cells (*Rev. Quirin* BR, *G. de l'Isle* BM) d) basal interior cells (*Rev. Quirin* BR, *G. de l'Isle* BM); e,f) stem leaves (*Rev. Quirin* BR, *Crosby & Crosby 8916* MO, *Lorence* 676 MO). Scale bar = 48 µm for a-d; 0.76 mm for e; 0.32 mm for f.

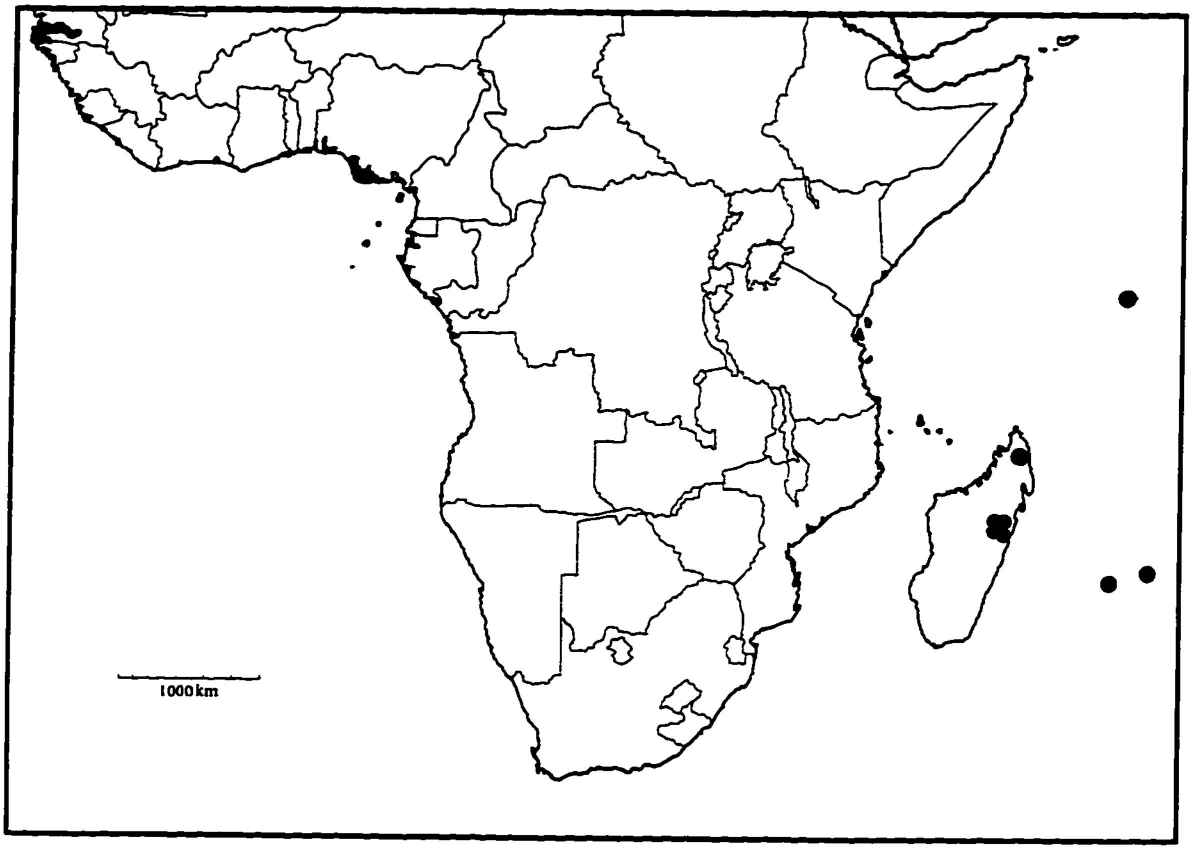


Figure II.63. Distribution of *Leucoloma seychellense*

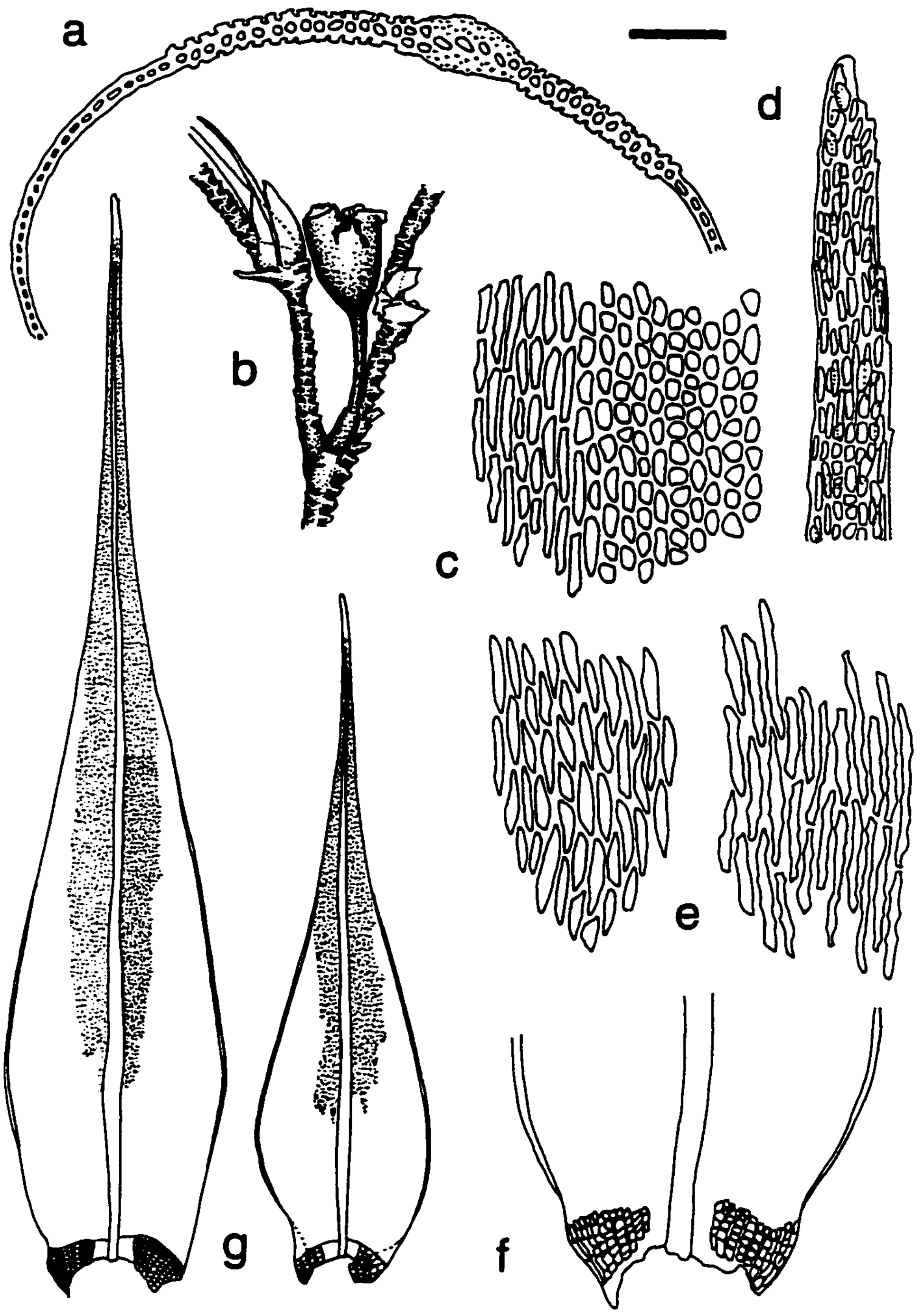


Figure II.64 a-f. *Leucoloma talazaccii*: a) costa transverse section (*Talazacc* S); b) capsule on denuded stem (*Dr. Meller* BM); c) medial interior juxtacostal cells (*La Farge-England 5804* ALTA); d) leaf apex (*La Farge-England 5802* ALTA); e) basal interior cells (*La Farge-England 5804* ALTA, *Crosby & Crosby 6888* ALTA); f) leaf base (*La Farge-England 5804* ALTA); g) stem leaves (*Dr. Meller* BM). Scale bar = 48 µm for a,c-e; 0.5 mm for b; 0.2 mm for f; 0.32 mm for g.

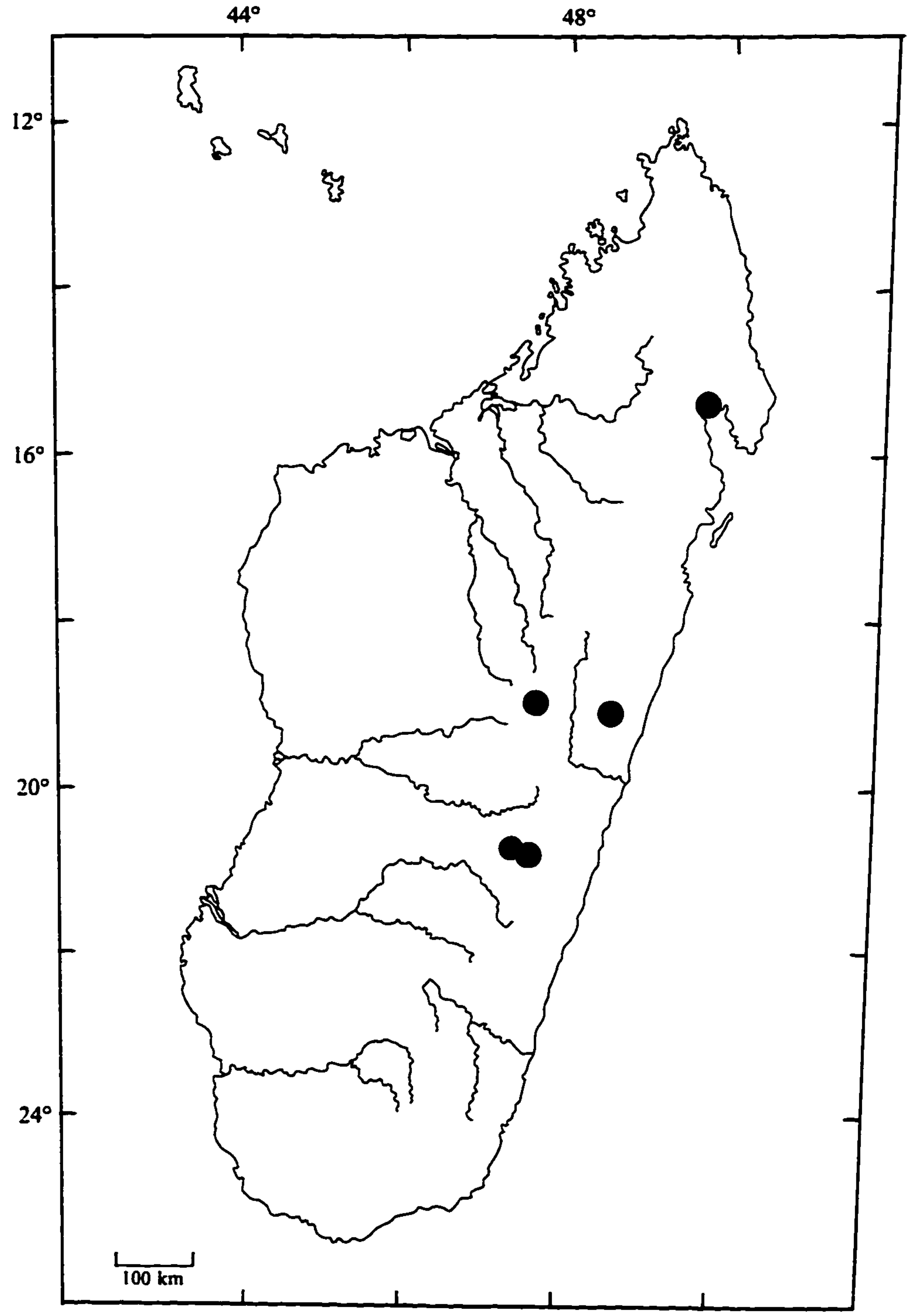


Figure II.65. Distribution of *Leucoloma talazaccii*

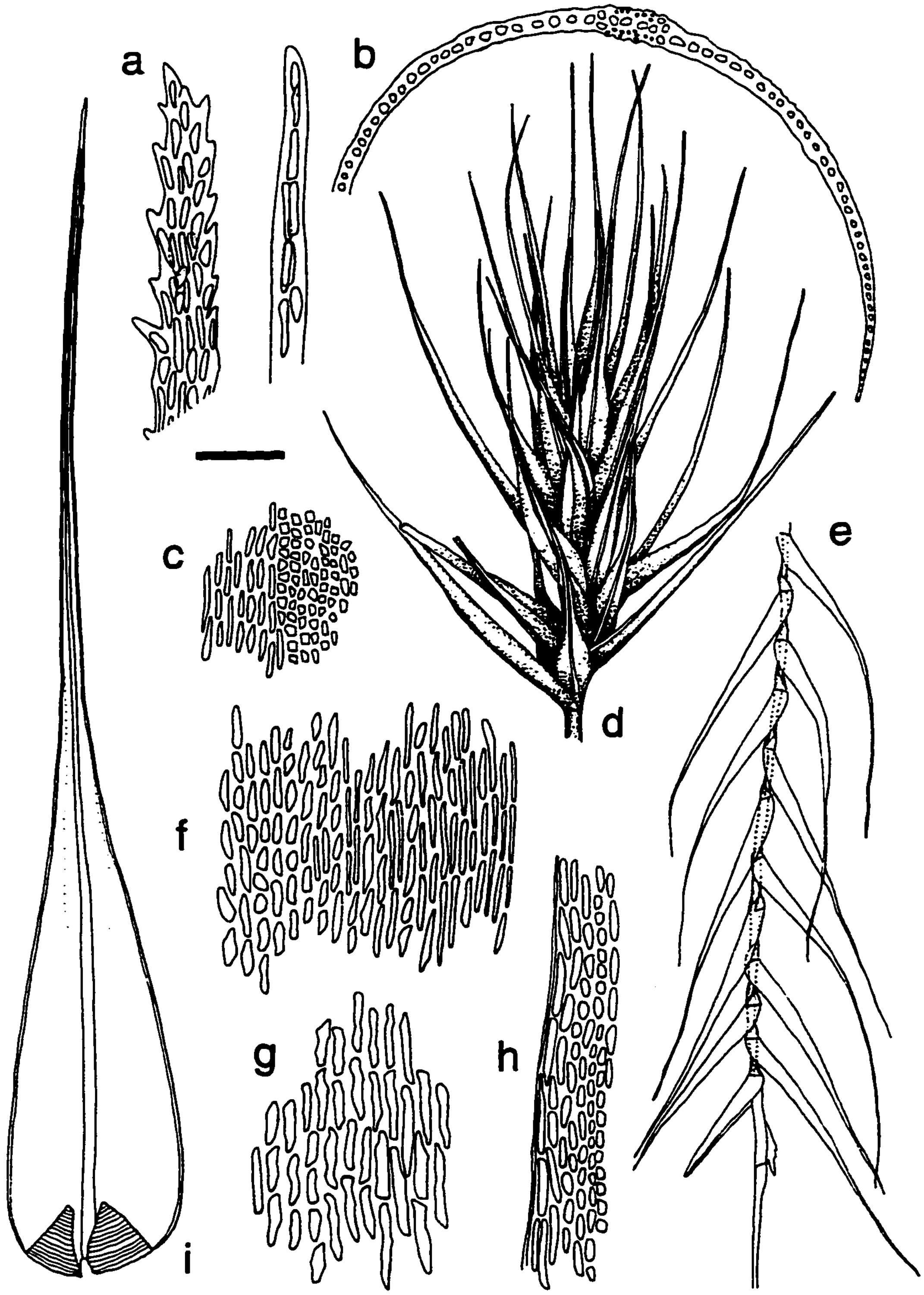


Figure II.66 a-i. *Leucoloma dichelymoides*: a) leaf apices (*Talazacc* BM, *Barclay 403* MAU; b) costa transverse section (*Hildebrandt 1841* NY); c) basal interior and juxtacostal cells (*P. de la Bathie 197* MO); d) erect stem (*Crosby & Crosby 5593* FH); e) pendulous stem (*Crosby & Crosby 5593* FH); f) basal juxtacostal and interior cells (*Hildebrandt* BM); g) basal interior cells (*Barclay 403* MAU); h) upper marginal, interior and juxtacostal cells (*Hildebrandt* BM); i) stem leaf (*Barclay 403* MAU). Scale bar = 48 μm for a-c,f-h; 1 mm for d,e; 0.32 mm for i.

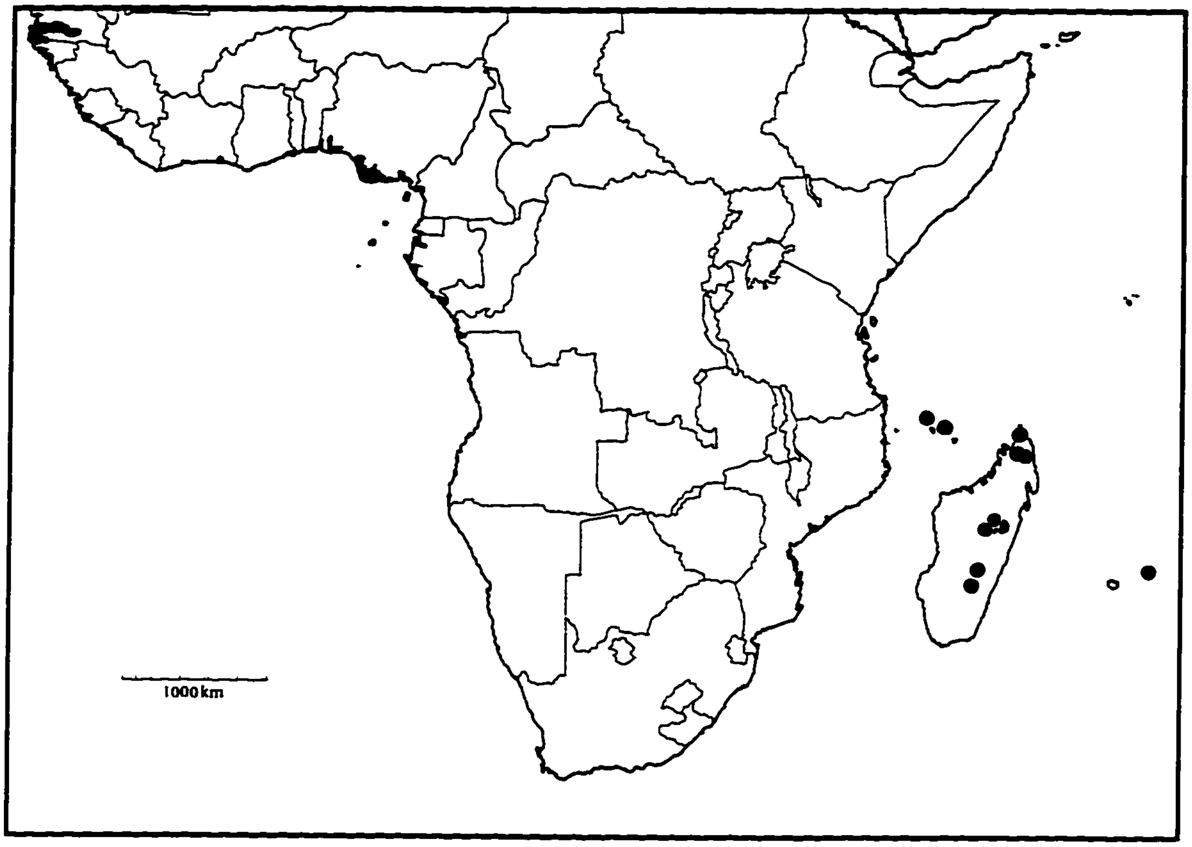


Figure II.67. Distribution of *Leucoloma dichelymoides*

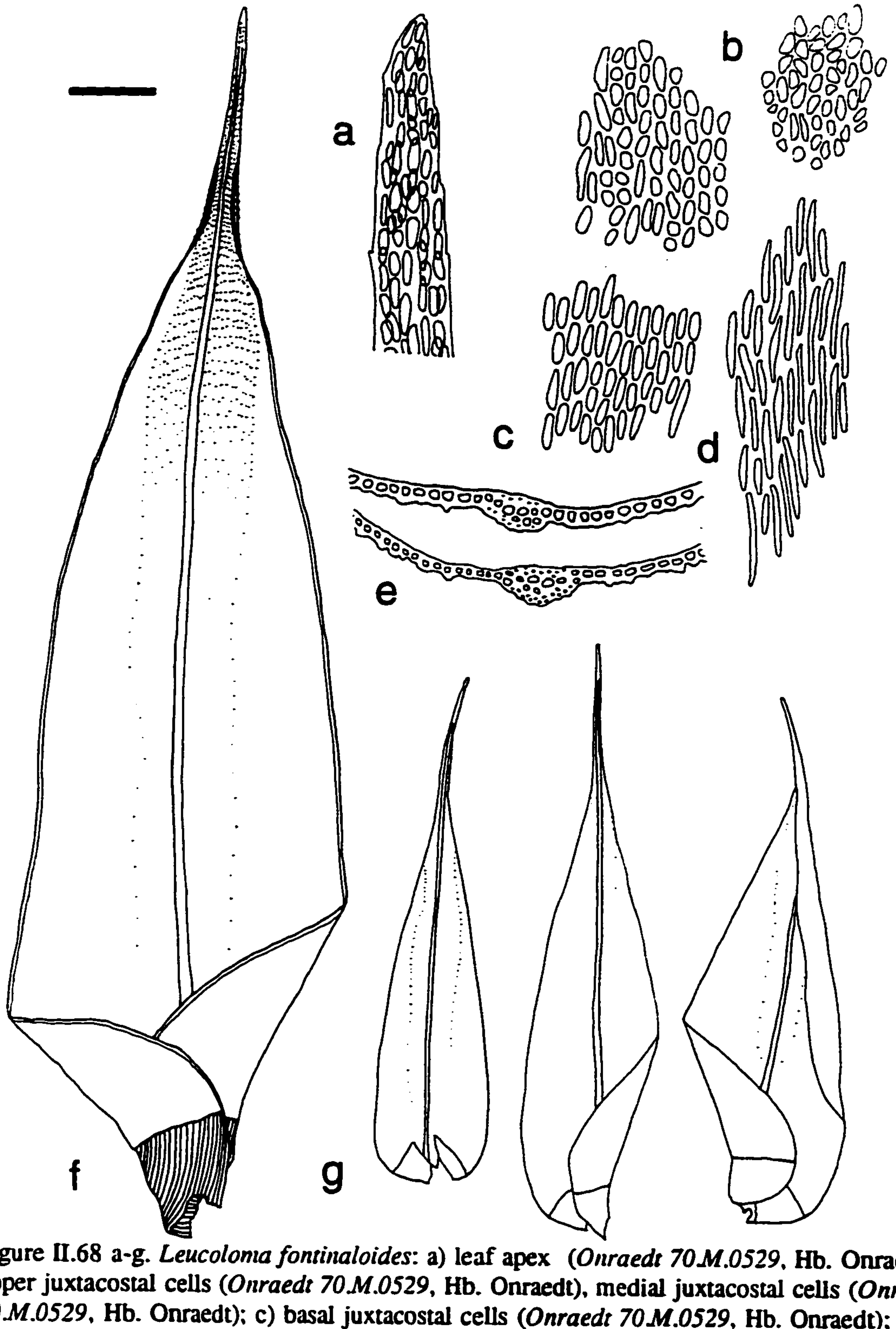


Figure II.68 a-g. *Leucoloma fontinaloides*: a) leaf apex (*Onraedt 70.M.0529*, Hb. Onraedt); b) upper juxtacostal cells (*Onraedt 70.M.0529*, Hb. Onraedt), medial juxtacostal cells (*Onraedt 70.M.0529*, Hb. Onraedt); c) basal juxtacostal cells (*Onraedt 70.M.0529*, Hb. Onraedt); d) basal cells (*Onraedt 70.M.0529*, Hb. Onraedt); e) costa transverse section (*Onraedt 70.M.0529*, Hb. Onraedt, *La Farge-England 6382* ALTA); f,g) stem leaves (*Onraedt 71.M.5315*, Hb. Onraedt, *Forsyth Major 473b* BM, *Humbert* PC). Scale bar = 48 µm for a-e; 0.32 mm for f; 0.76 mm for g.

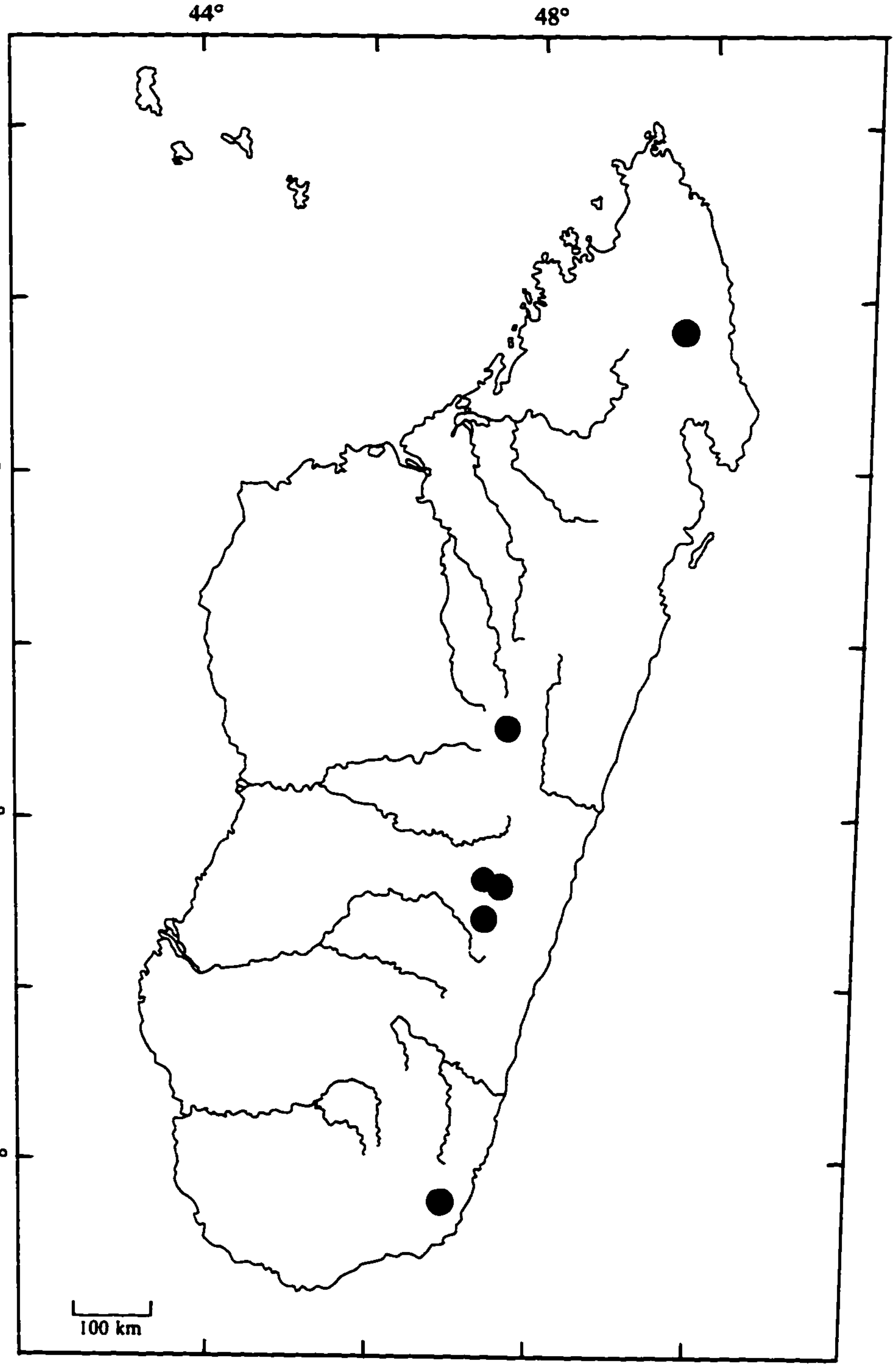


Figure II.69. Distribution of *Leucoloma fontinaloides*

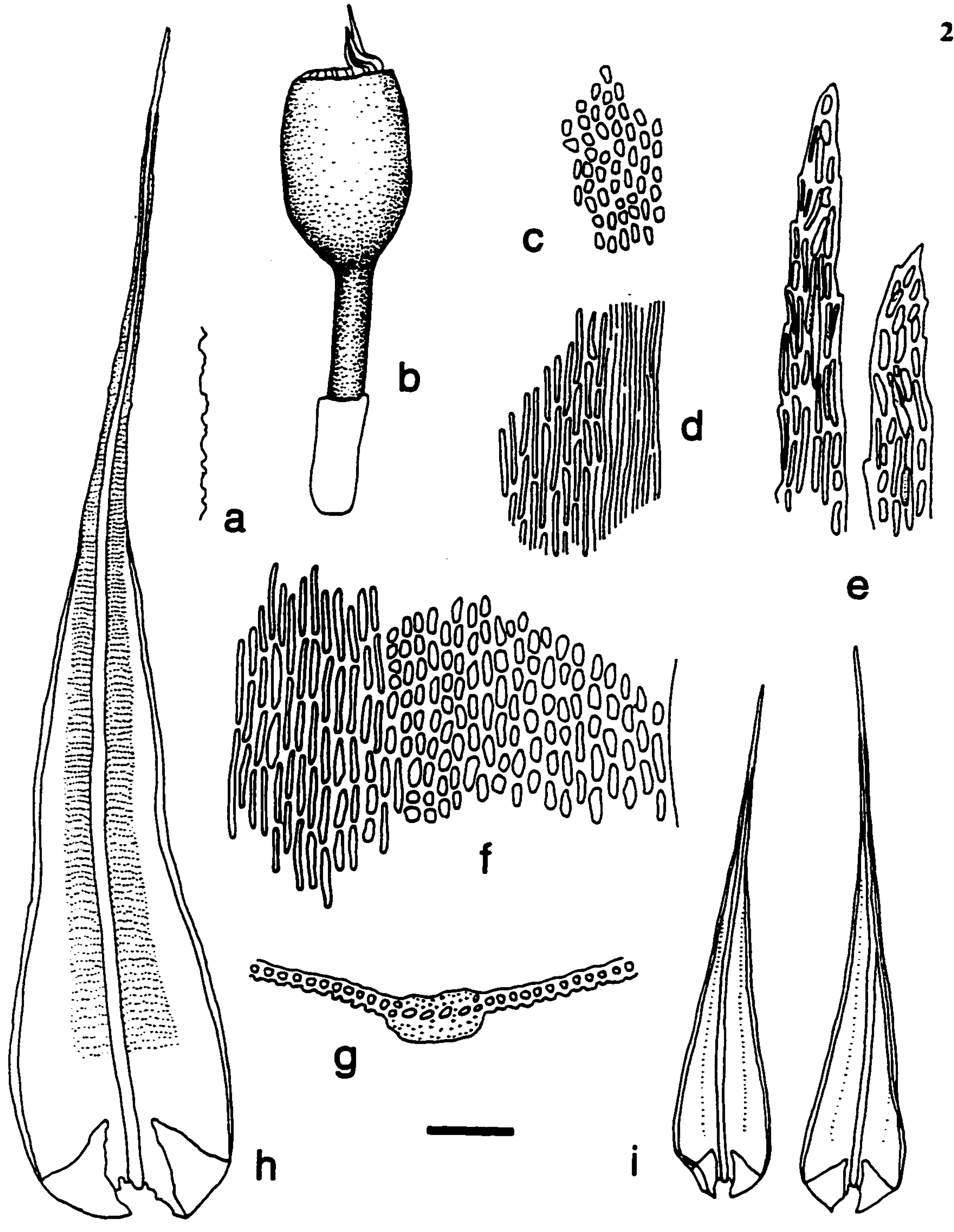


Figure II.70 a-i. *Leucoloma mafatense*: a) profile of abaxial leaf surface (*Rodriguez* L); b) capsule (*Crosby & Crosby 8984* L); c) medial juxtacostal cells (*Rodriguez* PC); d) medial interior and marginal cells (*Rodriguez* PC); e) apices (*Crosby & Crosby 8329* MO); f)basal interior and juxtacostal cells (*Crosby & Crosby 8329* MO); g) costa transverse section (*Rodriguez* PC); h,i) stem leaves (*Crosby & Crosby 8984* L). Scale bar = 48 µm for a,c-g; 0.5 mm for b; 0.32 mm for h, 0.76 mm for i.

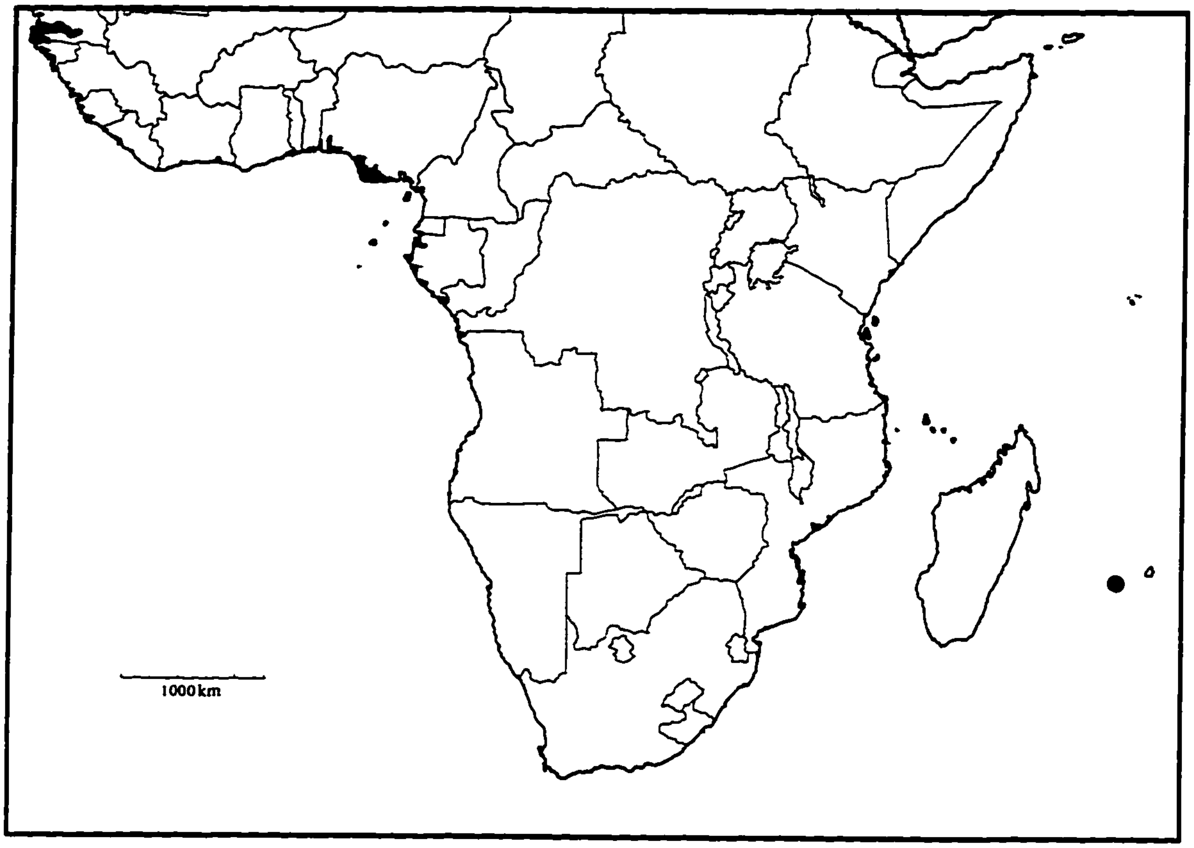


Figure II.71. Distribution of *Leucoloma mafatense*

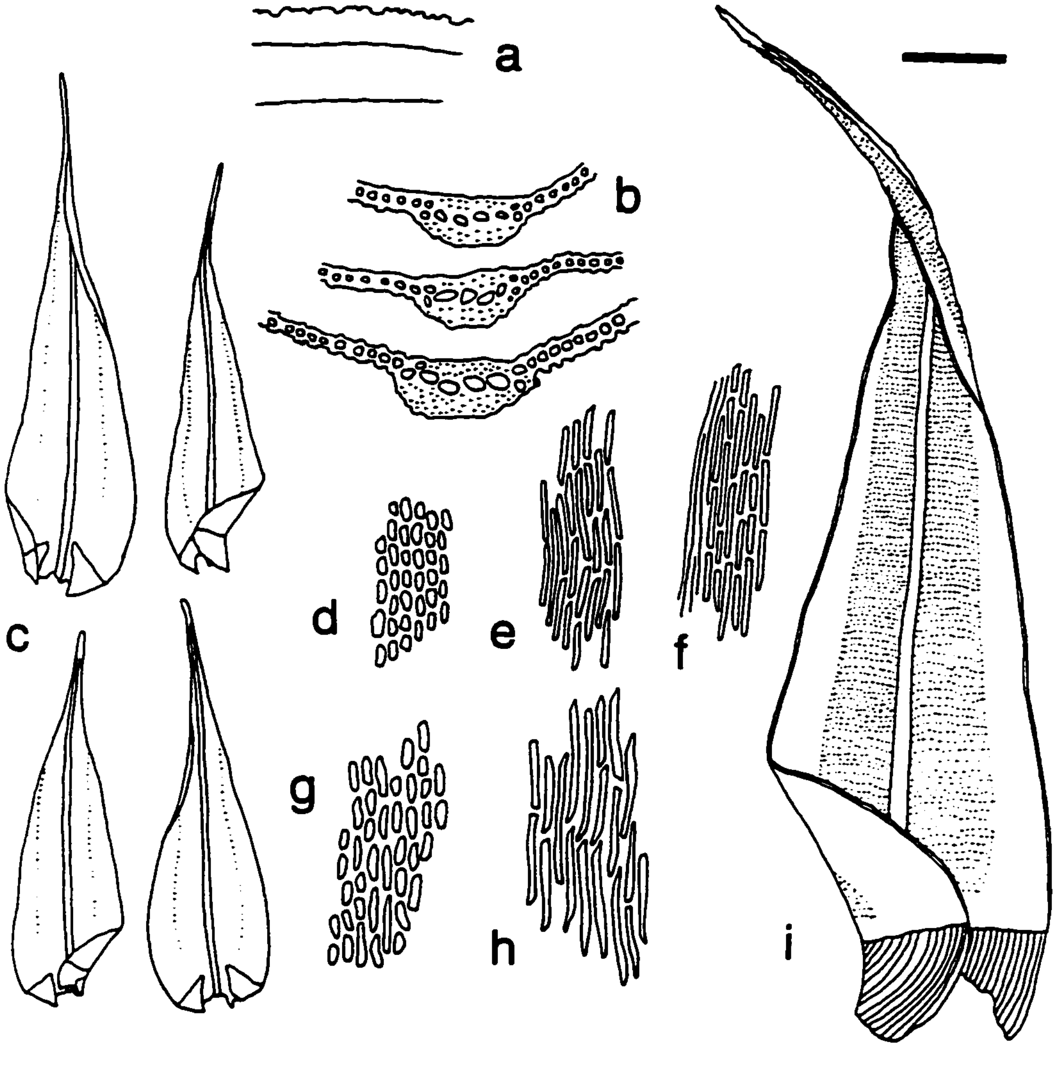


Figure II.72 a-i. *Leucoloma ochrobasilare* ssp. *ochrobasilare*: a) profile of abaxial leaf surface (*Crosby & Crosby 6960* ALTA); b) costa transverse sections (*Crosby & Crosby 6960* ALTA, *Onraedt 70.M.5310* F); c) stem leaves (*Onraedt 70.M.5310* F, *Crosby & Crosby 6998* ALTA); d) medial juxtacostal cells (*Onraedt 70.M.5310* F); e) medial interior cells (*Onraedt 70.M.5310* F); f) medial marginal and interior cells (*Crosby & Crosby 6998* ALTA); g) basal juxtacostal cells (*Onraedt 70.M.5310* F); h) basal interior cells (*Onraedt 70.M.5310* F); i) stem leaf (*Onraedt 70.M.5310* F). Scale bar = 48 µm for a-b,d-h; 0.76 mm for c; 0.32 mm for i.

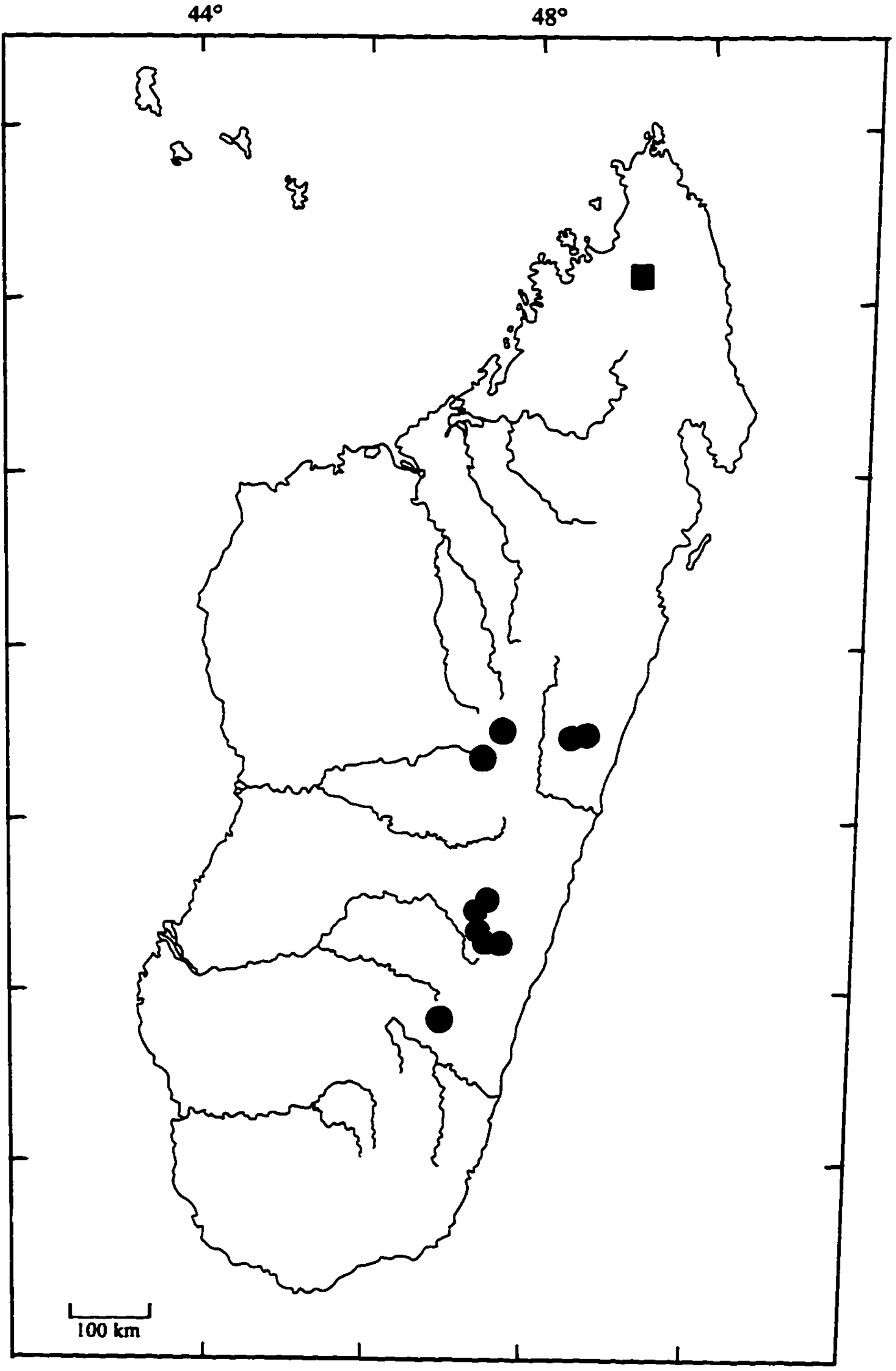


Figure II.73. Distribution of *Leucoloma ochrobasilare* ssp. *ochrobasilare* ●
and *Leucoloma ochrobasilare* ssp. *longifolium* ■

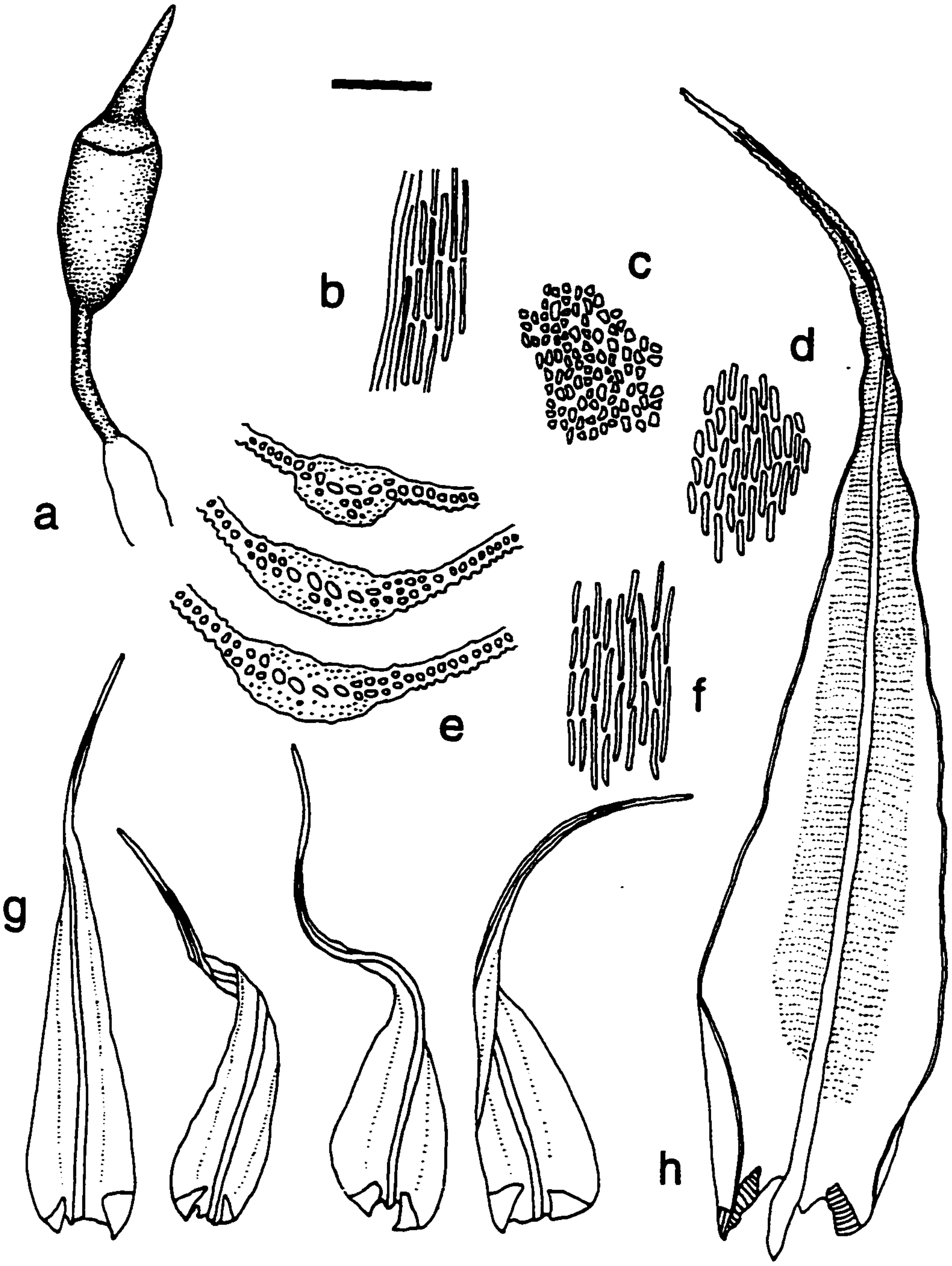


Figure II.74 a-h. *Leucoloma ochrobasilare* ssp. *longifolium*: a) capsule with operculum; b) medial marginal and interior cells; c) upper juxtacostal cells; d) medial interior cells; e) costa transverse section; f) basal interior cells; g, h) stem leaves. Scale bar = 48 µm for b-f; 0.5 mm for a; 0.76 mm for g; 0.32 mm for h. All illustrations from *P. de la Bathie* G (a-f, h), S (e,g).

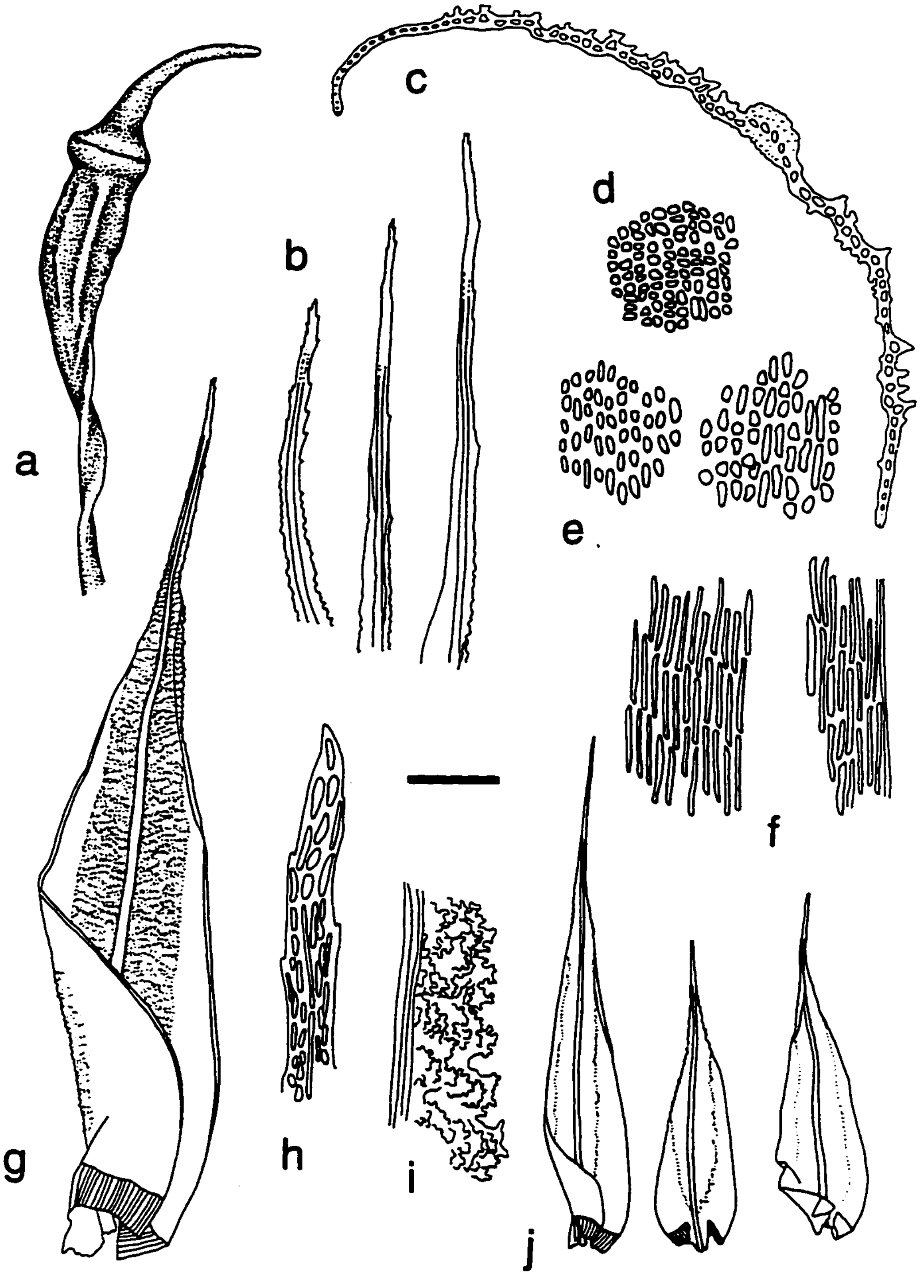


Figure II.75 a-j. *Leucoloma tuberculosum*: a) capsule ("Prov. de Fianarantsoa 1899" H-Br); b) leaf apices (*Perrot frères* H-Br, *La Farge-England 6266* ALTA); c) lamina transverse section (*Crosby & Crosby 6688* ALTA); d) medial juxtacostal cells (*Perrot frères* H-Br); e) basal juxtacostal cells (*Camboué & Campenon* PC, *Perrot frères* H-Br); f) basal interior cells (*Perrot frères* H-Br), medial interior and marginal cells (*Perrot frères* H-Br); g) stem leaf (*Camboué & Campenon* PC); h) leaf apex (*Perrot frères* H-Br); i) profile of abaxial leaf surface (*Perrot frères* H-Br); j) stem leaves (*Perrot frères* H-Br). Scale bar = 48 µm for c-f,h; 0.5 mm for a; 0.2 mm for b; 0.32 mm for g, 0.76 mm for j.

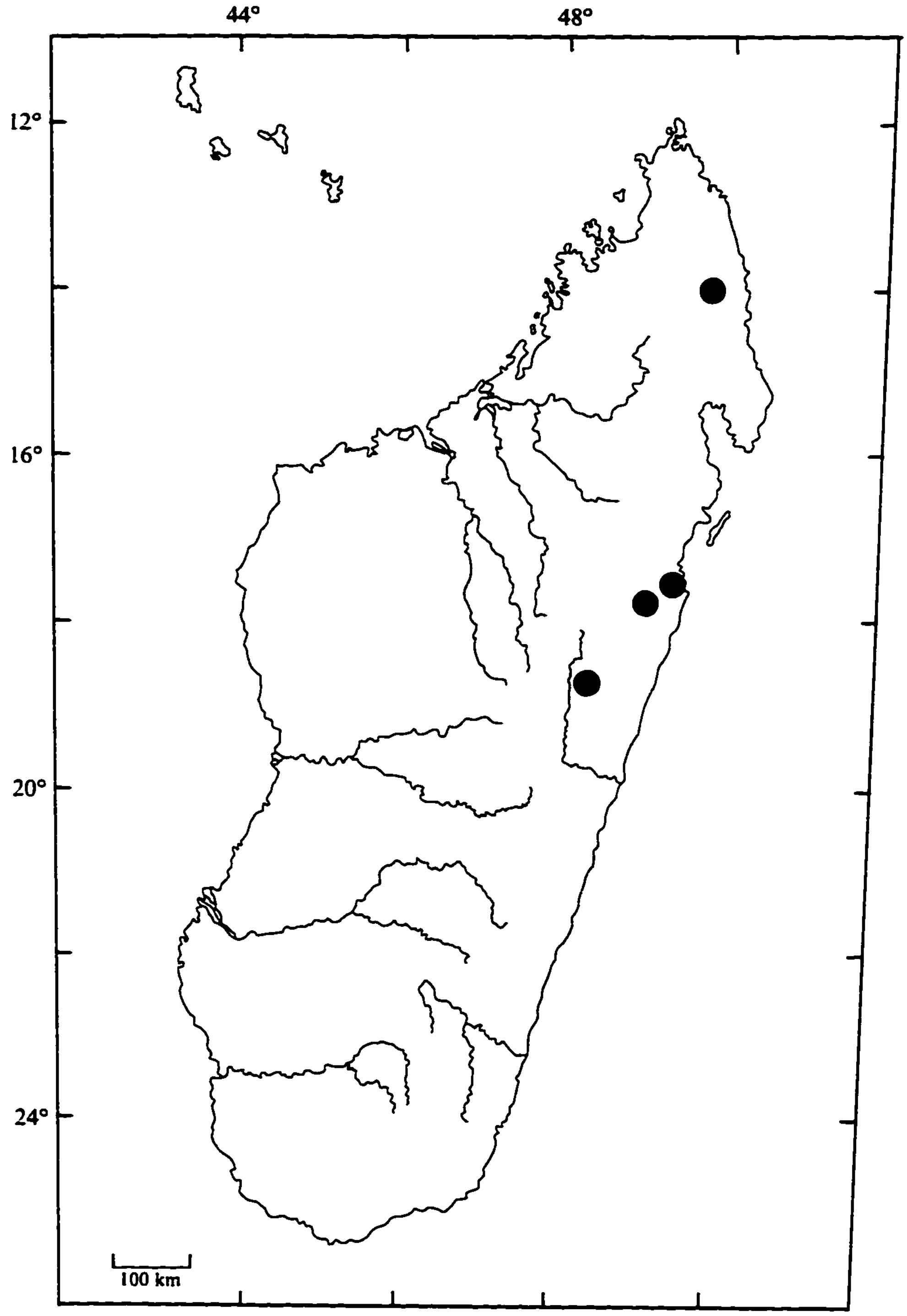


Figure II.76. Distribution of *Leucoloma tuberculosum*

Table II.1 Historical review of *Leucoloma* Brid., *nom. cons.* - a chronological list of infrageneric taxa.

1827 Bridel
Leucoloma Brid.
T: Hypnum bifidum Brid.

1827 Schwaegrichen
Leucoloma Brid.
L. bifidum
L. angustifolium
L. serrulatum

1848 C. Mueller
Dicranum Sect. Leucoloma
(Brid.) C. Muell.
D. siberianum
D. sprengelianum
D. zeyheri
D. commersonianum
D. bridelianum
D. molle
D. sinuosum

1869 Mitten
Leucoloma Brid.
L. mollissimum

Poecilophyllum Mitt.
P. cruegerianum
P. serrulatum
P. macrodon
P. albulum
P. vincentinum
P. tortellum
P. procumbens
P. triforme
P. submarginatum

1878 Bescherelle
Leucoloma Brid.
sect. Albescentia Besch.
sect. Caespitulosa Besch.
sect. Dichelymoidea Besch.
sect. Dicranoidea Besch.
sect. Prinodontoidea Besch.

1898 Renauld
Leucoloma Brid.
subg. Euleucoloma Ren.
sect. Vittata Ren.
subsect. Euvittata Ren.
ser. Distincta Ren.
ser. Obscura Ren.
sbsect. Subvittata Ren.
sect. Attenuata Ren.
sect. Transmutantia Ren.
subsect. Albescentia (Besch.) Ren.
subsect. Caespitulosa (Besch.) Ren.
subsect. Holomitrioidea Ren.
subsect. Pseudocaespitulosa Ren.
subsect. Dicranoidea (Besch.) Ren.
subsect. Dichelymoidea(Besch.)Ren.

subg. Dicranoloma Ren.
sect. Oncophoroidea Ren.
sect. Scoparioidea Ren.

subg. Dicnemoloma Ren.

1900 Paris
sect. Dicnemoloma (Ren.) Par.
sect. Dicranoloma (Ren.) Par.

1901 Renauld
Leucoloma Brid.
subg. Sphenodictyon Ren.
subg. Taeniodictyon Ren.
subg. Syncratodictyon Ren.

Dicranoloma (Ren.) Ren.

Dicnemoloma (Ren.) Ren.

1901 Brotherus
sect. Semivittata Broth.

1909 Renauld
Leucoloma Brid.
subg. Sphenodictyon Ren.
subg. Taeniodictyon Ren.
sect. Euvittata (Ren.) Ren.
sect. Obscura (Ren.) Ren.
sect. Subvittata (Ren.) Ren.
subg. Syncratodictyon Ren.
sect. Caespitulosa Besch.
sect. Holomitrioidea (Ren.) Ren.
sect. Albescentia Besch.
sect. Dicranoidea Besch.
sect. Dichelymoidea Besch.
sect. Pseudocaespitulosa(Ren.)Ren.
sect. Semivittata Broth.

1950 Potier de la Varde
sect. Rhacomitrioidea P. Vard.

Table II.2 The differentiation of *Leucoloma, Dicranoloma, Dicnemoloma* (Renauld 1901, 1909)

	Leucoloma	***Dicranoloma***	***Dicnemoloma***
1. hyaline margin	present	present	present
2. laminal cell differentiation	a) juxtacostal cells = "internes" b) interior = "intermediaire"	transversely uniform usually sinuose and porose	a) juxtacostal cells extending down along margins. b) inner basal, smooth, restricted
3. eurycysts = guide cells	4, rarely 5-6	variable (2-10)	4 rarely 5-6,
4. alar cells	flat or inflated ("excavée")	+/- subhexagonal not scalariform	flat, plane
5. calyptra	cucullate or mitrate to base of operculum, pluri-lobed or entire	cucullate extending well below base of operculum	cucullate
6. peristome	divided to middle or below	split to middle	divided to above middle or only at summit

Table II.3. Renauld's (1901,1909) subgeneric differentiation of *Leucoloma*.

	Taeniodictyon	***Sphenodictyon***	***Syncratodictyon***
juxtacostal cells	parallel to leaf base	tapered basally toward costa	+/- parallel
intermediate cells= interior	sharply defined	sharply defined	gradual transition
papillae	salient abaxial	low dense abaxial/adaxial	projecting, sparse abaxial
alar cells	scalariform	scalariform	inflated ("excavée")
seta	short	short	elongate
capsule	"renflée" oval-oblong, subglobose	"renflée" oval-oblong, subglobose	narrow, subcylindric

Table II.4. Species names described or transferred per interval of time to *Leucoloma*. The numbers in parentheses refer to names that are co-authored. Number of species per interval (# of sp); Species per year (sp/yr) refers to the average number of species described or transferred for a particular interval of time.

1827-1869		1870-1899		1900-1910		1911-1929		1930-present	
# of sp	11		122		165		32		26
Bridel	3	Bescherelle	24	Bescherelle	3	Thériot	9(3)	Thériot	5 (2)
Mitten	8	Renauld	21(7)	Renauld	11(3)	Renauld/Cardot	1(1)	Potier de la Varde	8
		Brotherus	15(1)	Brotherus	79(6)	Brotherus	3(6)		
		Mueller	9	Mueller	17	Mueller	1		
		Paris	2	Paris	23	Dixon	3(1)	Dixon	2(1)
		Jaeger	24	Dusen	16				
		others	21	others	23	others	2	others	7
sp/yr	0.26/yr		4.2/yr		16.5/yr		1.8/yr		0.4/yr

Table II.5. The number of species accepted for *Leucoloma* in periodic publications.

Bridel (1827)	Paris (1896)	Paris (1900)	Brotherus(1901-9)	Renauld (1909)	Brotherus (1924)	Wijk et al. (1964,1969)
3	85	122	176	114	102	134
			(Euleucoloma 95)			
			(Dicranoloma 74)			
			(Dicnemoloma 8)			

Table II.6. Novelties (*) and the nomenclatural status of species in *Leucoloma* Brid.

taxon		status
L. albo-cinctum **Ren. et Card. in Ren.**		
L. albulum (Sull.) Jaeg.	= *L. cruegerianum*	*in synon.*
L. allorgei **Thér.**		
L. amblyacron **C. Muell. ex Besch.**		
L. ambreanum **Ren. et Card. in Ren.**		
L. amoene-virens **Mitt.**		
L. amoene-virens **var.** ***humilis*** **Thér. et P. Varde**		
L. angustifolium Brid.	= *L. bifidum*	*nom. illeg. incl. sp. prior.*
L. annamense **Thér.**		
L. arbusculum C. Muell.	= *L. rutenbergii* var. *elatum*	*in synon.*
L. aspericuspis P. Varde	= *L. subsecundifolium*	*in synon.*
L. asperrimum **(C. Muell.) Kindb.**		
L. bauerae **(C. Muell.) Par.**		
L. beautei Besch. in Ren. et Card.	= *L. siamense*	*in synon.*
L. bifidum **(Brid.) Brid.**		
L. bifidum var. tanganikae P. Varde et Thér.	= *L. zuluense*	*in synon.*
L. bifidum var. orthothecioides Besch.	= *L. seychellense*	*in synon.*
L. biplicatum (Hampe) Jaeg.	= *L. triforme*	*in synon.*
L. boivinianum **Besch.**		
L. boivinianum var. angasizae (Ren.) Par.	= *L. subsecundifolium*	*in synon.*
L. boivinii Ren.	= *L. boivinianum*	*nom. illeg incl. sp. prior.*
L. boivinii var. angasizae (Ren.) Par.	= *L. subsecundifolium*	*in synon.*
L. brevifolium Dix. et P. Varde	= *L. amblyacron*	*in synon.*
L. brevioperculatum **Dix.**		
L. bridelianum (C. Muell.) C. Muell.	= *L. serrulatum*	*nom. illeg. incl. sp. prior.*
L. brotheri **Ren. in Levier**		
L. caespitulans **(C. Muell.) Jaeg.**		
L. caldense **C. Muell. ex Aongstr.**		
****L. cameruniae*** **Par. ex La Farge-England**		*ined.*
L. candidulum **C. Muell. ex Besch.**		

L. candidum Broth. in Voeltzk.		
L. capillifolium Broth. in Dus.		*hom. illeg.*
L. capillifolium Ren.		
L. charrieri Thér. et P. Varde	= *L. oncophorellum*	*in synon.*
L. cheesemanii Ren.	= *L. tenuifolium*	*in synon.*
L. chlorophyllum Broth. in Dryg.		
L. chrysobasilare (C. Muell.) Jaeg.		
****L. chrysobasilare* ssp. *africana*** La Farge-England		*subsp. nov.*
L. chrysobasilare var. gracilicaulon (C. Muell.) Jaeg.	= *L. procerum*	*in synon.*
L. chrysobasilare ssp. procerum (Ren.) Broth.	= *L. procerum*	*in synon.*
L. cinclidotioides Besch.		
****L. circinale*** La Farge-England		*spec. nov.*
L. circinatulum Bartr.		
L. cirrosulum Ren.		
L. comorae Ren.	= *L. chrysobasilare*	*in synon.*
L. convolutaceum Ren.	= *L. delicatulum*	*in synon.*
L. crepinii Ren. et Card.	= *L. seychellense*	*in synon.*
L. crepinii var. orthothecioides (Besch.) Ren.	= *L. seychellense*	*in synon.*
L. crosbyi La Farge-England		
L. cruegerianum (C. Muell.) Jaeg.		
L. cryptocarpum (C. Muell.) Jaeg.	= *L. serrulatum*	*in synon.*
L. cuneifolium (C. Muell. et Geh.) Wright		
L. decaryi Thér.		
L. decaryi var. comorense Thér.		
L. decolor Wright	= *L. rutenbergii* var. *elatum*	*in synon.*
L. delicatulum Ren.		
L. delicatulum var. laxobasis Ren. et Card. in Grand.	= *L. delicatulum*	*in synon.*
L. dichelymoides (C. Muell.) Jaeg.		
L. dubyanum Besch.	= *L. fuscifolium*	*in synon.*
L. dussianum Besch. ex Ren. et Card.		
L. ecaudatum (C. Muell.) Kindb.		
L. ecklonianum Lor. ex C. Muell.	= *L. zeyheri*	*nom. illeg. incl. sp. prior.*
L. ecklonii (Lor.) Jaeg.	= *L. zeyheri*	*in synon.*
****L. entabiense*** (Magill) La Farge-England		*comb. nov.*

L. fontinaloides Dix.		
L. forsythii Thér.	*= L. subbiplicatum*	*in synon.*
L. fuscifolium Besch.		
L. fuscifolium* var. *crispatulum Ren.		
L. garnieri Par. et Ren.		
L. garnieri* f. *aquaticum Thér.		
L. guehoi Tix.	*= L. grimmioides*	*in synon.*
L. gracilescens Broth.		
L. grandidieri Ren. et Card.		
L. grimmioides P. Varde		
L. guineense Broth. et Par.		
L. haakonii Broth. et Bryhn	*= L. syrrhopodontoides*	*in synon.*
L. hawaiiense Broth.		
L. herzogii Broth.		
L. holomitrioides C. Muell.	*= L. dichelymoides*	*in synon.*
L. holstii Broth.		
L. humbertii P. Varde		
L. incrassatum Thér.		
L. insigne (C. Muell.) Jaeg.		
L. isleanum Besch. in Par.		
L. isleanum* var. *subtortile Ren.		
L. itatiaiense Broth.		
L. kanakense Broth. et Par.		
L. krempfii Thér.	*= L. perviride*	*in synon.*
L. latifolium Broth. et P. Varde		
L. lepervancheri Besch.		
L. leptocladum Ren.	*= L. lepervancheri*	*in synon.*
L. levieri Ren.	*= L. tuberculosum*	*in synon.*
L. limbatulum Besch.		
L. longifolium (Brid.) Wijk et Marg.		
L. longicapillare (C. Muell.) Par.	*= L. serrulatum*	*in synon.*
****L. madagascariense*** La Farge-England		*sp. nov.*
L. mafatense Ren.		
L. malabarense Besch. ex Ren. et Card.		

L. mariei Besch.
****L. marojeziense*** LaFarge-England *sp. nov.*
****L. membranaceum*** LaFarge-England *sp. nov.*
L. meteorioides P. Varde = *L. fontinaloides* *in synon.*
L. mittenii Fleisch.
L. molle (C. Muell.) Mitt.
  L. molle var. longipilum Fleisch. = *L. insigne* *in synon.*
L. mollissimum Mitt. = *L. serrulatum* *in synon.*
L. mosenii Broth.
L. nitens (Thwait. et Mitt.) Jaeg.
L. normandii Par. et Broth. ex Ren. in Par.
  L. normandii* var. *alpinum Par. et Broth.
L. oceanicum (C. Muell.) Jaeg. = *L. tenuifolium* *nom. illeg. incl. sp. prior.*
L. ochrobasilare Ren.
  ****L. ochrobasilare* ssp. *longifolium*** (Thér.) La Farge-England *comb. nov.*
L. okamurae Broth.
L. oncophorellum C. Muell.
****L. onraedtii*** (Biz.) La Farge-England *comb. nov.*
L. pallidulum Thér.
L. perrieri Thér.
L. persecundum C. Muell. ex Besch.
  L. persecundum* var. *perrotii Ren.
L. perviride Broth.
L. pobeguinii Par. et Broth.
L. porto-ricense (C. Muell.) Par. = *L. cruegerianum* *in synon.*
L. procerum Ren.
L. procerum var. elatum (Ren.) Par. = *L. rutenbergii* var. *elatum* *in synon.*
L. procerum var. abbreviatum (Ren.) Par. = *L. rutenbergii* var. *abbreviatum* *in synon.*
L. procerum var. perrotii (Ren.) Par. = *L. rutenbergii* var. *perrotii* *in synon.*
L. procumbens (Mitt.) Jaeg. = *L. subimmarginatum* *in synon.*
L. pumilum Wright
L. pusillum Card. in Grand.
L. pygmaeum Par.
L. rehmannii (C. Muell.) Rehm. ex Par. = *L. scabricuspis* *in synon.*

L. renauldii Broth.	= *L. tenerum*	*in synon.*
L. riedlei Besch.	= *L. serrulatum*	*in synon.*
L. rutenbergii (Geh.) Wright		
L. rutenbergii* var. *abbreviatum Ren.		
L. rutenbergii arbusculum (C. Muell.) Ren.	= *L. rutenbergii* var. *elatum*	*in synon.*
L. rutenbergii* var. *elatum Ren.		*in synon.*
L. rutenbergii* var. *perrotii Ren.		
L. rutenbergii* var. *porosis Thér.		
L. sanctae-mariae Besch.		
L. sanctae-mariae var. leptolimbatum Ren.	= *L. thraustum*	*in synon.*
L. scaberulum Bartr.		
L. scabricuspis Broth.		
L. schelpei P. Varde		
L. schwaneckeanum (Hampe) Broth.		
L. secundifolium Besch.	= *L. isleaneum*	*hom. illeg.*
L. secundifolium Mitt.		
L. sericeum P. Varde		
L. serraticuspis P. Varde		
L. serrulatum Brid.		
L. serrulatum var. viride Besch. in Card.	= *L. serrulatum*	*in synon.*
L. seychellense Besch.		
L. siamense Broth.		
L. silvaticum Ren.	= *L. thraustum*	*in synon.*
L. sinuosulum C. Muell. ex Besch.		
L. sinuosum (Brid.) Jaeg.	= *L. longifolium*	*in synon. fid* Mueller 1948
L. sinuosum var. cirrhosum Thér.	= *L. rutenbergii var. elatum*	*in synon.*
L. sinuosum var. setifolium Besch.	= *L. longifolium*	*in synon.*
L. sprengelianum (C. Muell.) Jaeg.		
L. squarrosulum ssp. subbiplicatum (Ren. et Card.) Broth.	= *L. subbiplicatum*	*in synon.*
L. strictifolium Dix.	= *L. tenerum*	*in synon.*
L. subalbulum Ren.	= *L. cruegerianum*	*in synon.*
L. subbifidum Ren.	= *L. subbiplicatum*	*in synon.*
L. subbiplicatum Ren. et Card.		
L. subcespitulans Besch.		

L. subchrysobasilare C. Muell. ex Ren.
L. subimmarginatum (C. Muell.) Jaeg.
L. subintegrum Broth.
L. subsecundifolium Broth.
L. subtenuifolium Broth. et Watts = *L. limbatulum* *in synon.*
L. subtuberculosum Ren. = *L. ochrobasilare* *in synon.*
L. subtuberculosum var. longifolium Thér. = *L. ochrobasilare* ssp. *longifolium in synon.*
L. syrrhopodontoides Broth.
L. talazaccii Ren. et Card.
L. talazaccii var. fragilifolium Thér. et P. Varde = *L. talazaccii* *in synon.*
L. tanganyikae P. Varde
L. taylorii (Schwaegr.) Mitt.
L. tenerum Mitt.
L. tenuifolium Mitt.
L. terricola Broth. = *L. subsecundifolium* *in synon.*
L. theriotii Ren. et Card.
L. thraustum Besch.
L. thuretii Besch.
L. tonkinense Broth. et Par. = *L. insigne* *in synon.*
L. tonkinense var. elatum Broth. et Par. = *L. insigne* *in synon.*
L. tortellum (Mitt.) Jaeg.
L. tortuosulum C. Muell. = *L. isleanum* *in synon.*
L. trachynotus C. Muell. = *L. seychellense* *in synon.*
L. triforme (Mitt.) Jaeg.
L. tuberculosum Ren.
L. villaumei Thér.
L. vincentinum (Mitt.) Jaeg. = *L. serrulatum* *in synon.*
L. volkensii Broth. = *L. subsecundifolium* *in synon.*
L. walkeri Broth. = *L. taylorii* *in synon.*
L. woodii Rehmann et MacOwan ex Wag. = *L. zuluense* *in synon.*
L. zanzibarense Besch. = *L. sprengelianum* *in synon.*
L. zeyheri (C. Muell.) Kindb.
L. zuluense Broth. et Bryhn
L. zuluense* var. *ovatum La Farge-England *var. nov.*

INSUFFICIENTLY KNOWN SPECIES+

L. aduncum (Hampe) Par.	no type material seen!
L. squarrosulum (Geh.) Wright	no type material seen!*drawing in PC! Hb. Ren.
L. walkeri var. stenocarpum Card. et Dix.	no type material seen!

+An additional 13 taxa have not been described or their names synonymised at this time.

Table II.7. *Nomina Invalida, Nuda*, and *Herbariora* in *Leucoloma*

NOMINA INVALIDA

taxon	**status**
L. birmense C. Muell. ex Tixier	*nom. inval. typ. non cit.*
L. crispatum Tixier	*nom. inval. typ. non cit.*
L. phumiengsis Tixier	*nom. inval. herb. non cit.*
Leucoloma Bifida C. Muell., Gen. Musc. Frond. 279. 1900	*nom. inval.*
Leucoloma Cespitulantia C. Muell., Gen. Musc. Frond. 281. 1900	*nom. inval.*
Leucoloma Compacta C. Muell., Gen. Musc. Frond. 283. 1900	*nom. inval.*
Leucoloma Crispata C. Muell., Gen. Musc. Frond. 283. 1900	*nom. inval.*
Leucoloma Dichelymacea C. Muell., Gen. Musc. Frond. 280. 1900	*nom. inval.*
Leucoloma Orthophylla C. Muell., Gen. Musc. Frond. 280. 1900	*nom. inval.*
Leucoloma Platybasea C. Muell., Gen. Musc. Frond. 282. 1900	*nom. inval.*

***NOMINA NUDA, HERBARIORA*, AND ORTHOGRAPHIC VARIATIONS**

taxon	**status**	**notes**[1]
L. acutum C. Muell.	*nom. nud.*	1900
L. albidum C. Muell.	*nom. herb.*	W!
L. albulum f. robusta Thér.	*nom. herb.*	PC! Hb. Thér.
L. albulum f. minor Thér.	*nom. herb.*	PC! Hb. Thér.
L. ambreanum var. tapes	*nom. herb.*	PC! Hb. Ren.
L. amoene-virens var. novae-hollandia Thér.	*nom. herb.*	PC! Hb. Thér.
L. annamense var. malayanum Dix.	*nom. herb.*	BR! G! GRO!
L. angustatum Brid.	*nom. nud.*	pc tropicos
L. arbuscula C. Muell.	*ortho. pro*	*=L. arbusculum*
L. baldwinii Broth.	*nom. nud.*	1904
L. bifidum var. brevifolium ?	*nom. herb.*	L!
L. bifidum var. gracile Ren.	*nom. herb.*	PC!

---

[1] Herbaria where specimen seen, date of published name, current synonymy, or other notation in reference to the name.

L. birmense C. Muell.	*nom. herb.*	E!,PC!
L. boivinianum (?) brevifolium Ren.	*nom. herb.*	FH! = *L. serraticuspis*
L. boivinianum f. crispofalcaltum Besch.	*nom. herb.*	Hb. M. Onr.!
L. borchgrevinki C. Muell.	*nom. nud.*	1900, PC! - Hb. Thér.
L. brachypelmatum C. Muell. in Watts et Whitel.	*nom. nud.*	1902, NSW! S!
L. brevifolium C. Muell.	*nom. nud.*	1900
L. bridelii Hampe	*nom. herb.*	
L. bridelii Kindb.	*nom. nud.*	1888
L. bridelii C. Muell. in Kindb.	*nom. herb.*	E! FH! H-Br!LD! M! PC! RO!
L. bridelii var. major Kindb.	*nom. herb.*	PC!
L. cameruniae Par.	*nom. nud.*	= *L. cameruniae* Par. *ex* LaFarge-England
L. catharinae C. Muell. in Par.	*nom. nud.*	1897
L. cespitulans (C. Muell.) Jaeg.	*ortho. pro.*	= *L. caespitulans*
L. chlorophyllosum Broth.	*nom. herb.*	H-Br! = *L herzogii*
L. chrysobasilare var. gracilescens ?	*nom. herb.*	S!
L. chrysobasilarioides Broth.	*nom. herb.*	H-Br! = *L. zuluense*
L. costaricense Ren.	*nom. herb.*	PC!
L. crispatum var. Ren.	*nom. herb.*	PC! Hb. Thér. , Hb. Ren.
L. crispofalcaltum Broth.	*nom. herb.*	H-BR!, PC! = *L. taylorii*
L. cruegeri C. Muell. in Kindb.	*nom. nud.*	1888
L. cruegeri Kindb.	*nom. nud.*	=*L. cruegerianum*
L. dichelymaceum C. Muell.	*nom. nud.*	= *L. dichelymoides* (C. Muell.) Jaeg.
L. dubyi Besch. in Kindb.	*nom. nud.*	1889
L. dubyi Kindb.	*nom. nud.*	1889 = *L. fuscifolium*
L. dubium ?	*nom. herb.*	S!
L. duisabonianum Besch.	*nom. herb.*	BM! Dicranoidea
L. dussii ?	*nom. herb.*	H-Br!
L. eggersii C. Muell. in Kindb.	*nom. nud.*	1888
L. euryphyllum ?	*nom. herb.*	GRO!
L. erosum Mitt. in Dix.	*nom. nud.*	= *L. taylori*
L. fuscifolium f. abbreviata ?	*nom. herb.*	PC!
L. gerberianum ?	*nom. herb.*	UPS!
L. gracilicaule Ren. in Grand.	*nom. nud.*	1915 = *L. procerum*
L. gracilicaulon Ren.	*nom. herb.*	PC ! *err. ortho. pro* L. gracilicaule

L. hildebrandtii C. Muell. in Kindb.	*nom. nud.*	1889 = *L. chrysobasilare*
L. holstii (?) decoloree P. Varde	*nom. herb.*	PC! Hb. P. Varde
L. hyaloma ?	*nom. herb.*	H!
L. insigne var. minor Hampe	*nom. herb.*	BM! = *L. chrysobasilare*
L. isleanum var. molle Card. in Thér.	*nom. nud.*	1926
L. japonicum Dix. et Thér. in Sak.	*nom. nud.*	= *L. okamurae*
L. kanakense f./var. brevifolium Thér.	*nom. herb.*	PC! Hb. Thér.
L. kurzii ?	*nom. herb.*	H-Br!
L. latelimbatum Froelich.	*nom. herb.*	S!
L. lavardii Bizot et Demaret	*nom. herb.*	BR!
L. liabuschii Broth.	*nom. herb.*	H-Br!
L. longifolium (?) setifolium Besch.	*nom. herb.*	PC! Hb. Besch.
L. longifolium Besch. in C. Muell.	*nom. nud.*	1900
L. lucinense Mitt.	*nom. herb.*	PC! *err. ortho. pro* L.lucinerve?
L. lucinerve Mitt. in Besch.	*nom. nud.*	1890 = *L. insigne*
L. malaccense Broth.	*nom. herb.*	H-Br!
L. malayanum Dix.	*nom. nud.*	1926
L. montanum Ren.	*nom. herb.*	PC!
L. mosenii var. pallida Broth.	*nom. herb.*	H-Br! PC!
L. nilghirense Card.	*nom. herb.*	PC! Hb. Card.
L. noumeanum C. Muell.	*nom. nud.*	1900
L. novae-guineae Par.	*nom. nud.*	1900
L. ochrobasilare var. limbatum Biz.	*nom. herb.*	G! L! = *L. zuluense* var. *ovatum*
L. pallescens Wils. in Jaeg.	*nom. nud.*	H! 1872
L. pallidicaule Par.	*nom. nud.*	1900
L. pallidum Dix.	*nom. nud.*	1926
L. patentifolium ?	*nom. herb.*	G!
L. pennequinii Par.	*nom. nud.*	1900
L. peralbidum Broth.	*nom. herb.*	H-Br!
L. peralbidum f. (?) Thér.	*nom. herb.*	PC! Hb. Thér.
L. pertriforme Broth.	*nom. herb.*	H-Br!
L. petriforme Card.	*nom. herb.*	PC! Hb. Thér.
L. ricolei Besch. ex Par.	*ortho. pro*	=*L. riedlei*
L. rugescens C. Muell. in Geh.	*nom. nud.*	1878

L. rutenbergii (?) arbusculum	*nom. herb.*	PC!
L. sanctae-mariae (?) madagassum Ren.	*nom. herb.*	PC!
L. sanctae-mariae var. subelimbatum Ren.	*nom. nud.*	1901, PC!
L. sandvicense Aongstr. in Kindb.	*nom. nud.*	1888
L. sandwicense Aongstr. in Kindb.	*nom. nud.*	1888
L. sarcotrichum C. Muell. in Ren.	*nom. nud.*	= *L. taylorii* 1898
L. selaginoides C. Muell. in Kindb.	*nom. nud.*	1888
L. semibrunneum C. Muell.	*nom. nud.*	1900, PC! Hb. Thér.
L. setaceum Schimp. in C. Muell.	*nom. nud.*	1900
L. sigmatelloides C. Muell.	*nom. nud.*	1900, PC!
L. sinuosulum f. minor Thér.	*nom. herb.*	PC! Hb Thér.
L. sinuosulum var. sublaense Ren. et Card.	*nom. herb.*	PC!
L. sprengelii C. Muell. in Kindb.	*nom. nud.*	1888
L. sprengelii Kindb.	*nom. nud.*	1888 = *L. sprengelianum*
L. suberianum ?	*nom. herb.*	NY!
L. subnigricaule Dusen in Par.	*nom. nud.*	1905, NY!
L. subpiligerum Ren.	*nom. herb.*	H-Br!
L. subsericeum Biz. et P. Varde	*nom. herb.*	PC! Hb. P. Varde
L. subserrulatum Broth.	*nom. herb.*	H-Br!
L. traustum Wright	*ortho. pro*	=*L. thraustum*
L. viride ?	*nom. herb.*	H!
L. viridissimum Par.	*nom. nud.*	1900, H-Br!
L. wolkensii Broth. ex. Par.	*ortho. pro*	L. volkensii
L. zeyheri var. compactum C. Muell. in Dix. et Gepp	*nom. nud.*	1923
L. zeyherianum Jaeg.	*nom. nud.*	= *L. zeyheri*

Table II.8. Excluded names from *Leucoloma*. The following have been considered species or infraspecific taxa of other genera according to the citations in *Index Muscorum*. *The first date refers to the date published in *Leucoloma*; the second date is the date published within designated genus. Herbaria where a specimen has been seen are indicated with (!).

EXCLUDED TAXA

taxon	**status**	**date***
Braunfelsia **Par.**		
L. involutum Broth.		1901; fid. Par. 1894
Dicranoloma **(Ren.) Ren.**		
L. aciphyllum	*nom. herb.*	L!
L. albersii Broth.	*nom. herb.*	DUKE!,M!
L. alboalare Dus. in Card.	*nom. nud.*	1908; fid. Card. 1908
L. angustinerve (Mitt.) Broth.		1901; fid. Dix. 1913
L. arctoaecoides (C. Muell.) Broth.		1901; fid. Roiv. 1937
L. arfakianum (Geh.) Broth.		1901; fid. Ren. 1909
L. argutum (Hampe) Broth.		1901; fid. Par. 1904
L. armitii (C. Muell.) Broth.		1901; fid. Bartr. 1838 = *Cryptodicranum armitii*
L. assimile (Hampe) Broth.		1901; fid. Par. 1904
L. australe (C. Muell.) Broth.		1901; fid. Par. 1904
L. austro-congestum (C. Muell.) Broth.		1901; fid. Dix. 1913 = *Dicranoloma billardieri*
L. austro-scoparium C. Muell. ex Broth.		1895; fid. Ren. 1909
L. baileyanum (C. Muell.) Broth.		1901; fid. Dix. 1913 = *Dicranoloma billardieri*
L. bartramioides (Broth.) Broth.		1901; fid. Par. 1904
L. billardieri (Brid.) Broth.		1901; fid. Par. 1904
L. blumii (Nees) Broth.		1901; fid. Par. 1904
L. brachypelma Broth.		1901; fid. Par. 1904
L. brachysteleum (C. Muell.) Broth.		1901; fid. Par. 1904
L. braunii (C. Muell.) Broth.		1901; fid. Par. 1904
L. breviflagellare (C. Muell.) Broth.		1901; fid. Par. 1904
L. calymperaceum (C. Muell.) Broth.		1901; fid. Par. 1904
L. capillare Dus.		1905; fid. Broth. 1909

L. calymperoideum (C. Muell.) Par.		1900; fid. Dix. 1923 = *Dicranoloma menzesii*
L. chlorocladum (C. Muell.) Broth.		1901; fid. Par. 1904
L. commutatum Broth.		1901; fid. Broth. 1913
L. confine (C. Muell. et Hampe) Broth.		1901; fid. Par. 1904
L. deplanchei (Duby) Broth.		1901; fid. Par. 1904
L. diaphanoneurum (Hampe et C. Muell.) Hampe et C. Muell.		1901; fid. Par. 1904
L. dicarpum (Nees) Broth.		1901; fid. Par. 1904
L. dichotomum Brid.	*nom. nud.*	Z!
L. dichotomum (P. Beauv.) Ren.		1898; fid. Ren. 1901
L. dicranoides Broth.		1901; fid. Par. 1904
L. dives (Bosch et Lac.) Broth.		1901; fid. Par. 1904
L. donaldi Broth. in Par.		1904; fid. Par. 1904? = *Dicarnoloma laevifolium*
L. drepanocladium (C. Muell.) Kindb.		1891; fid. Ren. in Par. 1904
L. dusenii Broth. in Dus.		1905; fid. Broth. 1909
L. eucamptodontoides (Broth. et Geh.) Broth.		1901; fid. Par. 1904
L. fasciatum (Hedw.) Broth.		1901; fid. Par. 1904
L. formosum Ren. in Broth.	*nom. nud.*	1901; fid. Broth. 1928
L. fuegianum Dus.		1905; fid. Broth. 1909
L. fuegianum var. laxum Dus.		1905; fid. Roiv. 1938
L. fulvum Broth.		1901; fid. Par. 1904
L. graeffeanum (C. Muell.) Broth.		1901; fid. Par. 1904
L. grandialare Dus.		1905; fid. Card. 1908
L. hariotii (C. Muell.) Broth.		1901; fid. Par. 1904
L. harrisii Geh. in Watts et Whitel.	*nom. nud*	1902; fid. Dix 1941 as *D. serratum*
L. imponens (Mont.) Dus.		1905; fid. Ren. 1909
L. integerrimum (Broth. et Geh.) Broth.		1901; fid. Dix. 1929
L. kerguelense (C. Muell.) Broth.		1901; fid. Par. 1904
L. kroneanum (C. Muell.) Broth.		1901; fid. Par. 1904
L. laevifolium (Broth. et Geh.) Broth.		1901; fid. Par. 1904
L. leichhardtii (Hampe) Jaeg.		1872; fid. La Farge-E.
L. leucophyllum (Lac.) Broth.		1901; fid. Par. 1904
L. macrodon (Hook.) Jaeg.		1872; fid. La Farge-E., PC! type seen
L. menziesii (Hook. f. et Wils.) Broth.		1901; fid. Par. 1904
L. menziesii var. rigidum (Wils.) Dix.		1912; fid. Par. 1904

L. muelleri Dus.		1905; fid. Roiv. 1937
L. muelleri var. strictifolium Dus.		1905; fid. Wijk et al. 1964
L. nelsoni (C. Muell.) Broth.		1901; fid. Par. 1904
L. nematosum (Broth. et Geh.) Broth.		1901; fid. Par. 1904
L. nigricaule (Aongstr.) Broth.		1901; fid. Par. 1904
L. nigricaule var. flexuosulum Dus.		1905; fid. Bartr. in Roiv. 1937
L. nigricaule var. gracile Dus.		1905 ; fid. Card. 1908 as *D. capillare*
L. nitidulum (C. Muell.) Par.		1900; fid. Par. 1904
L. novo-guineense (Broth. et Geh.) Broth.		1901; fid. Par. 1904
L. obsoletinerve (Hampe et C. Muell.) Broth.		1901; fid. Par. 1904
L. oedithecium (C. Muell.) Broth.		1901; fid. Par. 1904
L. pancheri (C. Muell.) Broth.		1901; fid. Par. 1904
L. perremotifolium Dusen		1905; fid. Broth. 1924
L. perremotifolium var. fragile Dus.		1905; fid. Thér. 1935
L. peruncinatum Dus.		1905; fid. Broth. 1909
L. peruncinatum var. gracile Dus. in Roiv.	*nom. nud.*	1937; = *D. capillare* fid. Roiv.
L. platyloma (Besch.) C. Muell. in Broth.		1901; fid. Par. 1904
L. polysetum Broth.		1901; fid. Par. 1904
L. punctulatum (Hampe) Broth.		1901; fid. Par. 1904
L. pungens (Hook. f. et Wils.) Broth.		1901; fid. Par. 1904
L. pungentella (C. Muell.) Broth.		1901; fid. Par. 1904
L. pycnoloma Par.	*nom. nud.*	1900; fid Ren. 1909
L. reflexifolium (C. Muell.) Broth.		1901; fid. Par. 1904
L. rigens Broth.		1901; fid. Par. 1904
L. robustum (Hook f. et Wils.) Broth.		1901; fid. Par. 1904
?L. robustum var. flexuosum Dus.		1905; fid. La Farge-E.
L. robustum var. lagunicola Dus.		1905; fid. Roiv. 1937
L. rodriguezii C. Muell. in Ren.	*nom. nud.*	1891; = fid. Sim 1926 *D. billardieri*
L. rufifolium (Besch.) Broth.		1901; fid. Par. 1904
L. scopareolum (C. Muell.) Ren.		1898; fid. Par. 1904
L. scopelloides (Par.) Broth.		1901; fid. Par. 1904
L. serratum Broth.		1891; fid. Par. 1904
L. setosum (Hook. f. et Wils.) Broth.		1901; fid. Par. 1904
L. speightii (R. Brown ter.) Broth.		1901; fid. Par. 1904

L. subconfine (Besch.) Broth.	1901; fid. Par. 1904
L. suberectum (Hampe) Broth.	1901; fid. Par. 1904
L. subpungens (Hampe) Broth.	1901; fid. Par. 1904
L. subreflexifolium (C. Muell.) Broth.	1901; fid. Par. 1904
L. subsetosum (C. Muell.) Broth.	1901; fid. Par. 1904
L. sullivanii (C. Muell.) Par.	1900; fid. Par. 1904
L. sumatranum (Broth.) Broth.	1901; fid. Ren. 1909
L. syrrhodictyon C.Muell. in Broth.	1901; fid. Ren. 1909
L. trichophyllum (Hampe) Broth.	1901; fid. Par. 1904
L. weymouthii (C. Muell.) Broth.	1901; fid. Par. 1904
L. wheeleri (C. Muell.) Broth.	1901; fid. Par. 1904
L. whiteleggei (Broth.) Par.	1900; fid. Par. 1904

Dicranum Hedw.

L. sandwicense (Sull.) Broth.		1901; fid. Bartr. 1933
L. syrrhodictyon C. Muell. in Broth.	*=D. syrrhopodontoides*?	1901; fid. Wijk et al. 1964

Leucophanes Besch.

L. horridum Broth. ex Par.	*nom. inval. err. pro Leucophanes horridulum*	1900; fid. Broth. 1898

Megalostelium Dozy et Molk.

L. brevisetum (Dozy et Molk.) Broth.	1901; 1854

Rutenbergia Geh. et Hampe in Besch.

L. prionodon Besch.	1880; fid Ren. 1898

Sclerodontium Schwaegr. fid. Crum 1986

L. brachypelmatum C. Muell. in Watts et Whitel.	*nom. nud.*	1902;	*= S. pallidum*
L. celebesiae Broth. in Warb.		1899	= *S. pallidum* ssp. *celebesiae*
L. clavinerve C. Muell. ex Broth.		1893;	*= S. clavinerve*
L. imbricatum Broth. et Geh. ex Broth.		1898;	*= S. pallidum*
L. incanum (Mitt.) Mitt. in Jaeg.		1872;	*= S. pallidum*
L. kunertii C. Muell.	*nom. nud.*	1900;	*= S. clavinerve*

L. piliferum Broth. et Par. ex Broth.		1911;	= *S. pallidum*
L. sieberi (Hornsch.) in Kindb.	*nom. nud.*		
L. sieberi Mitt.	*nom. illeg.*	1856;	= *S. pallidum*
L. sieberi f. longifolium Broth.	*nom. nud.*		= *S. pallidum*
L. sieberianum (Hornsch.) Jaeg.		1872;	= *S. pallidum*
L. sieberianum var. rigida Broth. in Watts et Whitel.	*ortho. pro*	L.s. var. rigidum	*S. pallidum*
L. sieberianum var. rigidum Broth. ex Watts et Whitel.	*nom. nud.*	1902	= *S. pallidum*
L. strictipilum (C. Muell.) Par.		1900;	= *S. pallidum*
L. fraseri (Mitt.) Kindb.	*nom. nud.*	1889;	=*S. pallidum*
L. uncinatum Fleisch.		1904	= *S. pallidum ssp. celebesiae*

Poecilophyllum Mitt. = *Leucoloma* Brid. *1869

P. acutum Mitt. in Wright		*nom. nud.*	1888
P. albulum (Sull.) Mitt.	= *L. cruegerianum*		1869; 1872
P. amoene-virens (Mitt.) Mitt.	= *L. amoene-virens*		1873; 1859
P. cruegerianum (C. Muell.) Mitt.	= *L. cruegerianum*		1869; 1872
P. flexifolium Mitt.		*nom. herb.*	BM!
P. leichhardtii (Hampe) Mitt.	= *Dicranoloma leichhardtii*		1883; 1872
P. macrodon (Hook.) Mitt.	= *Dicranoloma macrodon*		1869; 1872.
P. nitens Thwait. et Mitt.	= *L. nitens*		1873; 1880
P. procumbens Mitt.	= *L. subimmarginatum*		1869; 1872
P. serrulatum (Brid.)	= *L. serrulatum*		1869; 1827
P. subimmarginatum (C. Muell.) Mitt.	= *L. subimmarginatum*		1869; 1872
P. taylorii Mitt.		*nom nud.*	1904
P. tortellum Mitt.	= *L. tortellum*		1869; 1872
P. triforme Mitt.	= *L. triforme*		1869; 1872
P. vincentinum Mitt.	= *L. serrulatum*		1869; 1872

---

* The first date refers to when described in *Poecilophyllum*, the second refers to when transferred to *Leucoloma*.

Table. II.9. Current Synonymy in *Leucoloma* not included in species revision. * Refers to new taxa or combinations.

Leucoloma amblyacron C. Muell. ex Besch., Ann. Sci. Nat. Bot. ser. 6,9: 313. 1878. **T:** Ile Maurice, leg. Robillard (Hb. Geheeb). **Lectotype:** PC!; **isotype:** PC!

Leucoloma brevifolium Dix. & P. Varde, Ann. Cryptog. Exot. 3: 170. 1930. **T:** Hab. India: Kuttalam Tinnevelly, ad corticem arboris, leg. Foreau, # 1013b. **Holotype:** PC! (Hb. P. Varde)

Leucoloma cameruniae Par. ex La Farge-England ***ined.***

This species was originally presented as a *nomen nudum* and subsequently it has been treated as a "synonym" of *L. chrysobasilare*. It is distinct and should be recognised at the species level. It is included in the subsection *Acuminata*, based on its reduced alar region of bulging slightly longitudinally thickened alar cells. The distal juxtacostal cells have papillae equally developed on both surfaces in transverse section with the thickening over the cell wall opposed to lumen. The juxtacostal bands grade imperceptibly into the basal and interior cells. It is closely related to *L. tenerum* of India, and is restricted to the Congo region of Africa. A formal description and typification of this species will be treated in a separate paper.

Leucoloma cruegerianum (C. Muell.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 412. 1872. **Basionym:** *Dicranum cruegerianum* C. Muell. Syn. 2: 588. 1851. **T:** "Insula Antillarum Trinidad, monte Tocuche, 28 Mart. 1847: (leg.) Crüger." **Lectotype:** PC! Hb. Renauld.

Note: The type material is mixed and according to the description the hyaline margin is undulate, although narrow. Because the type description includes a description of the sporophyte, it is presumed that Mueller based his description on the material with sporophytes. The sporophytic material within the type specimen is conspecific with *L. albulum* (Sull.) Jaeg., a later described species. The PC specimen is the only type material that I have seen. The type specimen is mixed with material of *L. subimmarginatum* which was described in the same article by Mueller, and is differentiated from *L. cruegerianum* by a less glossy appearance and smaller plants that lack a central strand in stem section. The leaf habit of *L. subimmarginatum* is contorted to curled, with the hyaline margin, described as scarcely present, is only 1-3 cells wide. This lectotypification alters the present day usage of *L. albulum*, *L. cruegerianum* and *L. subimmarginatum* as presented in recent floras of the neotropics (e.g., Sharp et al. 1994, Allen 1994, Crum & Steere 1957).

Dicranum albulum Sull., Proc. Amer. Acad. Arts 5:278. 1861. **T:** "on decayed logs". Musci Cubensis. in Eastern part of the island of Cuba during years 1856, 1857, 1858; leg. Charles Wright #35. **Isotypes:** G! S!

Poecilophyllum cruegerianum (C. Muell.) Mitt., J. Linn. Soc., Bot. 12: 92.1869.

Poecilophyllum albulum (Sull.) Mitt., J. Linn. Soc., Bot. 12: 93. 1869.

Leucoloma albulum (Sull.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 412. 1872. (Ad. 1: 116).

Dicranum porto-ricense C. Muell., Hedwigia 37:226. 1898. **T:** "Habitatio. Portorico, Sierra de Luquillo, regione media montis Hymene, Junio 1885: P. Sintenis in Hb. Krug et Urban; Sierra de Naguabo, in monte Piedra pelata, leg. Majo, 1885; idem." **Lectotype:** Sintenis, Sierra de Naguabo PC! - Hb. Cardot; **isotypes:** S!, H-Br!; **syntype:** not seen.

Leucoloma subalbulum Ren. in Grand., Hist. Madag. Atlas Mouss. 15A. 1898. **T:** Guadeloupe, leg. Husnot, # 120. **Holotype:** PC! Hb. Renauld; **isotypes:** PC! Hb. Thériot, H-Br!

Note: This is reference is to an illustration only, which according to ICBN 4.2 is sufficient to serve as a description. Renauld's Essai sur les Leucoloma 44. 1909, has a description and a comparison to *L. albulum.*

Leucoloma porto-ricense (C. Muell.) Par., Index Bryol. Suppl. 233. 1900.

Leucoloma delicatulum Ren., Prodr. Fl. Bryol. Madag. 76. 1898. **T:** "Madagascar: Montagne d'Ambre près Diégo Suarez, sur les écorces où il forme de petits groupes mêlés à *Taxathelium argyrophyllum* R.C.; Chenagon, 1890". **Holotype:** PC!

Leucoloma delicatulum var. *laxobasis* Ren. & Card. in Grand., Hist. Phys. Madagascar, Mousses 39: 89. 1915. **T:** "Zone inférieure des forêts: Diégo-Suarez, sur écorces, avec *L. convolutaceum* et *pusillum* (Chenagon)." **Holotype:** PC!; **isotype:** PC! (Hb. Thériot).

Leucoloma convolutaceum Ren., Prodr. Fl. Bryol. Madag. 76. 1898. **T:** "Madagascar: Montagne d'Ambre près Diégo Suarez, Chenagon, 1890." **T: Lectotype:** PC! (Hb Renauld); **isotypes:** PC! (Hb. Cardot - 10 specimens).

Leucoloma entabiense (Magill) La Farge-England ***comb. nov.***

Dicranoloma entabiense Magill, Mem. Bot. Surv. S. Afr. 43:3 1979. **T:** South Africa: Transvaal, Soutpansberg, Entabeni Forest, Bottomley PRE-CH3381. **Holotype:** PRE!

Leucoloma fuscifolium Besch., Ann. Sci. Nat. Bot. ser. 6, 9: 315. 1878. **T:** "La Réunion, Bory (Hb. Cosson sub Campylopodo setacea Sch. et Dicrano sinuoso Brid.); Frappier (Hb. Mus. Par.)".

Lectotype: *Frappier* PC! **isotypes:** BM! (2 specimens), E!, H-Br!; **syntype:** not seen.

Leucoloma dubyanum Besch., Ann. Sci. Nat. Bot. ser. 6, 9: 316. 1878. **T:** "Maurice: Mme. Lecoultre (Hb. Duby)". **Lectotype:** PC! (Hb. Besch.); **isotypes:** PC! (3 specimens), BM! (2 specimens).

Note: Two specimens are in PC with Hb. Bescherelle indicated, therefore one of the two specimens in the general herbarium was chosen as a lectotype. Two other specimens can be found in the separated herbaria of Thériot and P. de la Varde.

Leucoloma insigne (C. Muell.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 412. 1872. (Ad. 1: 116). **Basionym:** *Dicranum insigne* C. Muell., Linnaea 36: 33 1869. **T:** Ceylon: Nietner. **Lectotype:** PC! (ex Museum botanicum Berolinense, Type!); **isotypes:** NY! PC!(2 specimens) W!

Leucoloma molle var. *longipilum* Fleisch., Musci Fl. Buitenzorg 1: 124. 1904, *in parte*. **T:**"(Java: Tjiburrum, 1600 m! (F) = *L. molle* var. *molle* (C. Muell.) Mitt. - LT: L!); Krawang, Mt. Parang, 700 m., Ceylon, Britt. NeuGuinea, District Moresby, Berg Woroka, 1300 m. (Lamberto Loria). (Exsiccata: M. Fleischer, Musc. Archip. Ind., No. 255)". **Lectotype:** Z! Ceylon: no. 255. febr. 1898. legit M. Fleischer; **isotypes:** NY! JENA!; **syntype:** Britt. Neu Guinea, Lamberto Loria not seen.

Note: This taxon has been the source of confusion around *L. molle*, since it was based on 3 specimens from remote localities. The syntypes are heterogeneous. The Ceylon material is distinct from the Java material and synonymised with *L. insigne*. Until recently *L. insigne* has been considered a synonym of *L. molle* var. *longipilum* (fid. Par., Ind. Bryol. ed 2, 2: 48. 1908), if considered at the subspecific rank. The lectotype material has narrow leaves and the hyaline margins at the widest measurement are 36 µm, the juxtacostal bands form sharply defined bands that appear opaque under the dissecting scope. *L. insigne* is distinguished by its more robust nature with broad shiny hyaline margins in the mid portion of the leaf. The juxtacostal cells are oval to elongate and the juxtacostal bands are narrow.

Leucoloma tonkinense Broth. et Par., Rev. Bryol. 35: 43. 1908. **T:**"dans les environs immediats de la cascade d'Argent, dans la chaîne du Tam Dao, province de Vinh Yen, S.E. Tonkin, entre 950 - 1100 m alt". Dr. Eberhardt, 13 au 27 juillet 1907. **Holotype:** H-Br!, #934; **isotype:** PC! ex Hb. Paris.

Leucoloma tonkinense var. *elatum* Broth. et Par., Rev. Bryol. 35: 43. 1908. **T:**" dans les environs immediats dela cascade d'Argent, dans la chaîne du Tam Dao, province de Vinh Yen, S.E. Tonkin, entre 950 - 1100 m alt". Dr. Eberhardt, 13 au 27 juillet 1907. **Holotype:** H-Br! # 935; **isotype:** PC! (Hb. Thériot # 377, comm. E.G. Paris).

Leucoloma isleanum Besch. ex Ren., Prodr. Fl. Bryol. Madag. 76. 1898. **T:** "Seychelles: Mahé, G. de L'Isle". **Lectotype:** BM! (sht. 45); **isotypes:** BM! (sht. 44),H-Br!, PC!

Leucoloma secundifolium Besch. Ann. Sci. Nat. Bot. sér. 6, 9: 313. 1878, *hom. illeg.* **T:** "Iles Seychelles: Mahé, leg. G. de L'Isle, 1874".

Leucoloma tortuosulum C. Muell. Gen. Musc. Frond. 280. 1900. *nom. illeg. includ. spec. prior.*

Leucoloma limbatulum Besch., Bull. Soc. Bot. France 45: 54. 1898. **T:** Tahiti: "Sur les arbres de l'intérieur de l'(i)le vers 1000 m d'altitude.(2e herbor., #205)...montagnes des environs de Marciati au fond de la vallée de Papenoo, et au fond de la grande vallée de Punarua, au pied de l'Orohena 1896, sans date." leg. Nadeaud. **Lectotype:** W!; **isotypes:** S! PC!

Leucoloma subtenuifolium Broth. et Watts ***syn. nov.***, Proc. Linn. Soc. N. S. Wales Suppl. 40: 128. 1915. **T:** New Hebrides: "Futuna: Gunn, March April 1910 (Hb. Lillie); Aneityum: Gunn, 1911 (Hb. Lillie 544, 694), Aug. 1912 (Hb. Watts 271, Hb. Lillie 728), Feb. 1913 (Hb. Watts 344); May- June, 1913 (Hb. Watts 407, 421)". **Lectotype:** *Gunn 271* (H-Br!); **syntypes:** misit *Gunn 344, 407, 421, 523, 544, 601, 694, 728, 832* (H-Br!); **isosyntype:** *Gunn 544* (FH!).

Leucoloma longifolium (Brid.) Wijk & Marg., Taxon 9: 190. 1960. **Basionym:** *Trichostomum longifolium* Brid., Spec. Musc. 2: 23. 1806. **T:** "In arboribus putrescentibus sylvarum in gentium Insulae Bourbonis habitat. Bory St. Vincent invenit et communicavit. Fl...4." **Lectotype:** JE! (ex Hb. Bridel).

Dicranum sinuosum Brid., Mant. Musc. 59. 1819. **T:** "In Insula Madagascar habitat unde Aubert du Petit Thouars". *synon. fid.* C. Muell., Syn. 1: 355. 1848 (no type material seen!).

Leucoloma sinuosum (Brid.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 413. (Ad. 1: 117). 1872.

Leucoloma sinuosum var. *setifolium* Besch. Ann. Sci. Nat. Bot. ser. 6, 9: 315. 1878. **T:** "La Réunion: sommet de la Rivière de Roches, P. Lépervanche". **Holotype:** BM!; **isotypes:** BM! PC!

Leucoloma molle (C. Muell.) Mitt., J. Linn. Soc. Bot. Suppl. 1: 13. 1859. **Basionym:** *Dicranum molle* C. Muell. Syn. 1: 354. 1849. **T:** "Patria. Java inter muscos alios a Cl. Junghuhn lectos." In silvis umbrosis montis Pangerango 5000'. Martio. **Lectotype:** L!; **isotypes:** NY! S!

Note: Fleischer described *Leucoloma molle* var. *longipilum* based on 3 specimens: Java, Ceylon, and New Guinea. The type specimen from Java is synonymous with *L. molle* var. *molle*. The Ceylon material is conspecific with *L. insigne* (C. Muell.) Jaeg. and *L. tonkinense*. *L. insigne* was synonymised with *L. molle* var. *longipilum* by Paris (1904), and has been traditionally treated as a synonym since then. *Leucoloma molle* is distinguished from *L. insigne* by its narrower hyaline margin (5-24 µm versus 36-60 µm wide), the juxtacostal bands are less opaque looking through the dissecting scope and the leaves are often concave opposed to flat. In general the plants of *L. insigne* are more robust than *L. molle*.

Leucoloma oncophorellum C. Muell., Gen. Musc. Frond. 283. 1900. **T:** "Auf Madagascar stellt sich ihnen..., nur etwas lockerere Rasen bildend, an die Seite." label: **Lectotype:** PC!

Note: Mueller's name is considered the earliest validly published name for this species, for there was a description along with the name, although not recognised in *Index Muscorum*. The label data included "Central Madagascar: Ost Imerina Andrangoloaka xi. 1880 leg. Hildebrandt".

Leucoloma charrieri Thér. & P. Varde, Recueil Publ. Soc. Havraise Études Diverses 1924(1): 85-86. 1924. **T:** Madagascar: "S.O. de Tananarive, forêt (leg. Carrougeau, comm. Charrier)". **Holotype:** PC! (Hb. P. Varde); **isotypes:** PC! (Hb. Thér.) BM!

****L. onraedtii*** (Biz.) La Farge-England, ***comb. nov.***

Dicranoloma onraedtii Biz., Rev. Bryol. Lichénol. 42: 852. 1976: **T:** "Réunion Pas de Bellecomb, Piton de la Fournaise, Onraedt 309. Holotype Hb. Bizot; isotype Hb. Onraedt". **Isotype:** Hb. Onraedt!

Leucoloma perviride Broth., Philipp. J. Sci. 5: 139. 1910. T: Philippines: "Luzon, Province of Bataan, Mount Mariveles, Merrill, 6281". **Holotype:** H-Br!

Leucoloma krempfii Thér., Recueil Publ. Soc. Havraise Études Diverses 1919: 34. 1919. **T:** Vietnam: Annam - "Hab.Vallée du Fong Man, alt. 1200 m , (n. 1624 pp.)". **Holotype:** PC! Hb. Thériot.

Leucoloma rutenbergii* var. *elatum Ren., Prodr. Fl. Bryol. Madag. 85. 1898. **T:** "Madagascar - entre Savondronina et Ranomafana, Dr. Besson." **Lectotype:** PC!; **isotypes:** H-Br! PC! (2 specimens)

Leucoloma decolor Wright, J. Bot. 30: 263. 1892. **T:** Tanzania: "Hab. Zanzibar. Legit J.T. Last". **Holotype:** BM!

Leucoloma arbusculum* C. Muell., Gen. Musc. Frond. 283. 1900. **T: Madagascar (without collector designated). **Lectotype:** BM! (sterile e Madagascar 1874, ex Hb. Kiaer misit Borgen).

Note: The original description does not cite a type specimen, but indicates that the material is from Madagascar. The earliest reference to the *L. arbusculum* names cites the

Borgen specimen, 1874, from Madagascar. Mueller identified the Chenagon specimens from Diégo Suarez found in Renauld's herbarium at PC. The annotations on the specimens of *L. arbusculum* C. Muell., "in litt. et in Musc. Borgenianis", indicates that Mueller already had a concept of the species before returning the specimens. Thus the Borgen specimen is chosen as the lectotype.

Leucoloma procerum var. *elatum* (Ren.) Par., Index Bryol. Suppl. 233. 1900.

Leucoloma sinuosum var. *cirrhosum* Thér., Recueil Publ. Soc. Havraise Études Diverses 1929: 104. 1930. **T:** Montagne d'Ambre, Andasibe; alt. 1000 a 1400 m, Septembre 1926, leg. M. R. Perrier de la Bathie. **Holotype:** PC! (Hb. Thériot).

Leucoloma rutenbergii* var. *perrotii Ren., Prodr. Fl. Bryol. Madag. 85. 1898. **T:** Madagascar - environs d'Andevorante, leg. Perrot frères; dat. 1895. **Lectotype:** H-Br!

Leucoloma procerum var. *perrotii* (Ren.) Par., Index Bryol. Suppl. 233. 1900.

Leucoloma scabricuspis Broth. Bot. Jahrb. Syst. 24: 236. 1897. **T:** "Deutsch-Ostafrika: Uluguru, Berwald 1500 - 1700 m, an Baumwurzein (Stuhlmann n. 8725). **Holotype:** H-Br!

Note: This is slightly more robust than *L. rehmannii*. Both have broad margins, stellate prominent dorsal papillae, somewhat truncate apices, serrulations at the back of the costa.

Dicranum rehmannii C. Muell., Hedwigia 38: 87. 1899. **T:** "Habitatio. Prom. bonae spei, Knysna District., in silvis prope Esternek, Nov. 1875, in faucibus umbrosis prope Claremont, Oct. 1876 (= *L. sprengelianum* (C. Mueller) Jaeg. - LT: BM!); Dr. A. Rehmann Coll. Musc. A.A. No. 29 in silvis prope Blanco, Oct. 1875: idem, ubique c. fr. vetustis." **Lectotype:** Knysna 29b NY!; **isotype:** BM! E!

Leucoloma rehmannii (C. Mueller) Rehm. ex Par., Index Bryol. Suppl. 233. 1900.

Leucoloma schwaneckeanum (Hampe) Broth., Nat. Pflanzenfam. 1(3): 324. 1901.

Dicranum schwaneckeanum Hampe, Linnaea 25: 361. 1853. **T:** Portorico: "Ad arbor trunc", leg. Schwanecke. **Lectotype:** NY!

Leucoloma serrulatum Brid., Bryol. Univ. 2: 752. 1827. **T:** In Hispaniola habitat, leg. Clar. Desvaux. **Lectotype:** B!; **isotypes:** G! JE!

Leucoloma mollissimum Mitt., J. Linn. Soc., Bot. 12: 91. 1869. **T:** "Hab. Andes Quitenses, in silva Canelos (3000 ped.), Spruce n. 68. Venezuela absque fructu, Funck et Schlim". **Lectotype:** *Spruce* S!; **syntype:** not seen.

Poecilophyllum serrulatum (Brid.) Mitt., J. Linn. Soc., Bot. 12: 93. 1869.

Poecilophyllum vincentinum Mitt., J. Linn. Soc., Bot. 12: 93. 1869. **T:**"Hab. Ins. St. Vincent, Guilding in Herb. Hooker; Trinidad, Crüger." **Lectotype:** *Guilding* S!; **syntype:** *Crüger* not seen!

Note: The specimen seen has strongly porose basal cells, margin, distal acumen with small serrations and elongate cells, not looking opaque and chlorophyllous as in "subserrulatum", with juxtacostal cells oblong to shortly elongate.

Leucoloma vincentinum (Mitt.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 412. 1872. (Ad. 1: 116).

Dicranum cryptocarpum C. Muell., Linnaea 38: 626. 1874. **T:** "Mexico: Mirador, 4300 pedes altum: Sartorius in Hb. C. Mohr". **Lectotype:** S!; **isotype:** PC! - Hb. Renauld.

Note: Although different elevation data is different on the lectotype than in the protologue, the rest of the information is correct and the material is fruiting as the original description indicates. The label on the PC material is agrees with the protologue, but the specimen is restricted to a few leaves.

Leucoloma cryptocarpum (C. Muell.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1877-78: 379. 1888. (Ad. 2: 643).

Leucoloma riedlei Besch., J. Bot. (Morot) 5: 146. 1891. **T:** Antilles, île Saint-Thomas, leg. Riedle Hb. Mus. Par. **Lectotype:** PC!

Dicranum longicapillare C. Muell., Bull. Boiss. 5:553. 1897. **T:** Habitatio. Jamaica, Morces Pass, 4900 ped. alt., W. Harris; 24 IV 1896. **Isotypes:** PC! Hb. Renauld, NY! Hb Mitten.

Leucoloma longicapillare (C. Muell.) Par., Index Bryol. Suppl. 233. 1900.

Leucoloma serrulatum var. *viride* Besch. in Card., Rev. Bryol. Lichènol. 37: 119. 1910. **T:** Mexico: État de Vera-Cruz: Jalapa, troncos d'arbres; Zacuapan; Guatemala: Alta Vera Paz, Coban, leg. Barnes and Land, # 578 in parte - 1908; Purpus, # 4309 - 1908; H. von Turckheim - 1908: Hb. Levier Mexico, Guatemala. **Lectotype:** *Purpus 4309* PC!; **isotypes:** PC! (Hb. Thériot, Hb. Cardot) JE! S!; **syntypes:** *Türkheim 7755* PC! (Hb Cardot); *Barnes & Land 578 in parte* PC! (Hb. Cardot).

Note: This material fits within the concept of *L. serrulatum*: broad leaf bases porose basal cells serrulate distal acumnen. The variety that should be distinguished is *L. s.* var. *pendulum* for material that has longer stems and that is pendulous off branches: the apices tend to be less serrate and less opaque, all in all a more robust form that may not be easily separated.

Leucoloma siamense Broth., Bot. Tidsskr. 24: 115. 1901. **T:** Siam: Koh Chang, "Klong Munse, common in the jungle on rocks exposed to the sun", Schimdt. **Lectotype:** H-Br! (#3); **isotypes:** H-Br! (#6, #17).

Note: There are three specimens in HBR that are Schimdt collections with identical label information indicated in Brotherus' handwriting. A single specimen has "n.sp." indicated and thus is chosen as the lectotype!

Leucoloma beautei Besch. in Ren. & Card., Bull. Soc. Roy. Bot. Belgique 41(1): 15. 1905. **T:** "Hab. Siam (sine loco)..., communiquée en 1889 par R.P. Beauté". **Holotype:** PC!; **isotype:** PC! (Hb. Thériot).

Leucoloma sprengelianum (C. Muell.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 411. 1872. (Ad. 1: 115). **Basionym:** *Dicranum sprengelianum* C. Muell., Syn. 1: 353. 1849. **T:** "Patria Prom. bonae spei. Hb. Sprengel. Ex habitu D. congesti formis minoribus simillimum". **Lectotype:** BM!

Note: "*D. fasicatum* Spr. in litt., mit Sprengel" is included on the label of the specimen.

Leucoloma sprengelii Kindb., Enum. Bryin. Exot. 64. 1888. *nom. illeg. incl. spec. prior., nom nud.*

Leucoloma zanzibarense Besch., J. Bot. (Morot) 5: 143. 1891. **T:** "Zanzibar (in Hb. Mus. Par., colleg.?)". **Holotype:** PC! (Hb. Bescherelle); **isotype:** PC! (Hb. Thériot), BM!.

Leucoloma subimmarginatum (C. Muell.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 412. 1872. (Ad. 1: 116). **Basionym:** *Dicranum subimmarginatum* C. Muell., Syn. 2:589. 1851. **T:** Patria: America centralis, Costa Rica, inter elev. 5000 - 8000 pedum; inter Campylopodem specimen unicum sterile invenimus, leg. A.S. Oersted. **Lectotype:** PC!

Note: The type material consists of only 3 stems.

Poecilophyllum subimmarginatum (C. Muell.) Mitt., J. Linn. Soc., Bot. 12: 94. 1869.

Poecilophyllum procumbens Mitt., J. Linn. Soc., Bot. 12: 94. 1869. **T:** "Hab. Andes Peruvianae, in monte Campana at Pingullu ad truncos vetustos (3000 - 4000 ped.), Spruce n. 69. Andes Bogotenses, in sylvis prope Pacho (6000 ped.), ad arborum truncos, Weir, n. 263.; Venezuela, Funck et Schlim s.n.". **Lectotype:** *Spruce n. 69* PC! **isotype:s** E! G!; **isosyntypes:** *Weir 263*, G! FH! S! PC! (Hb. Thériot) H-Br! E!

Leucoloma procumbens (Mitt.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 413. 1872. (Ad. 1: 117).

Leucoloma subsecundifolium Broth., Bot. Jahrb. Syst. 20: 177. 1894. **T:** "Usambara: one nähere

Standorte (Holst n. 1088). **Isotype:** S!

Leucoloma terricola Broth., Bot. Jahrb. Syst. 20: 178. 1894. **T:** "Usambara: Waldungen, auf Erde (Holst n. 115)". **Holotype:** H-Br!; **isotypes:** BM! (shts 19, 20).

Leucoloma volkensii Broth., Bot. Jahrb. Syst. 24: 236. 1897. **T:** "Kilimandscharo: Landschaft Marangu, häufiges Moos an Bäumen 2000 m (Volkens n. 2262). **Holotype:** H-Br!

Leucoloma wolkensii Broth. ex. Par., Index Bryol. (ed. 2) 3: 188. 1905, *err. pro. L. volkensii* Broth.

Leucoloma boivinii var. *angasizae* Ren., Prodr. Fl. Bryol. Madag. 83. 1898. **T:** "Grande Comorae: Humblot, 1890." **Holotype:** PC! Hb. Renauld.

Leucoloma boivinianum var. *angasizae* (Ren.) Par., Index Bryol. Suppl. 1900.

Leucoloma aspericuspis P. Varde, Svensk Bot. Tidskr. 41: 5. 2. 1947. **T:** "Afr. or.: Mt. Kenia, 1911; leg. E. Lönnberg s.n.". **Holotype:** S!

Leucoloma syrrhopodontoides Broth., Bot. Jahrb. Syst. 24: 236. 1897. **T:** "Pondoland: one nähere Standorte an Baumrinde (Bachmann n. 10). **Holotype:** H-Br!

Leucoloma haakonii Broth. & Bryhn, Forh. Vidensk.- Selsk. Christiania 1911 (4): 6. 1911. **T:**"Eschowe. Adtruncum arboris mense Januario anni 1909, legit Haakon Bryhn." Zululand. **Holotype:** H-Br!

Leucoloma taylorii (Schwaegr.) Mitt., Kew J. Bot. 8: 353. 1856. **Basionym:** *Syrrhopodon taylorii* Schwaegr., Spec. Musc. Suppl. 2 (1): 115.132. 1824. **T:** In cortice arborum putrido in Nepal Indiae, leg.Taylor. **Holotype:** G! Hb. Schwaegr.

Leucoloma walkeri Broth., Rec. Bot. Surv. India 1: 313. 1899. **T:** India: "South Coorg: decayed wood in shady jungle (n. 294)", leg. T. L. Walker. **Holotype:** H-Br!

Leucoloma tenerum Mitt., Kew J. Bot. 8: 353. 1856. **T:** Burma: "Hab. Moulmein. (No. 0.)", leg. Rev. Charles Parish. **Holotype:** NY!

Leucoloma renauldii Broth., Rec. Bot. Surv. India 1: 313. 1899. **T:** India: "Coorg: on trees in very dense jungle, 7 miles S.W. of Verajpet (n. 293)", leg. T.L. Walker. **Holotype:** H-Br!; **isotype:** FH!

Leucoloma strictifolium Dix., J. Indian Bot. 2: 176. 1921. **T:** India: "Hab. On *Calophyllum*, Sampkhand (6444)", leg. L.J. Sedgewick, F.L.S., N. Kanara, India. **Lectotype:** H-Br!; **isotype:** G!

Leucoloma tenuifolium Mitt., J. Linn. Soc. Bot. 10: 192 1868. **T:** Samoa: "Tutuila and Upolu, on trees.

No. 98." leg. Rev. Thomas Powell. **Holotype:** NY!

Dicranum oceanicum C. Muell., J. Mus. Godeffroy 3 (6): 62.1874. *nom. illegl. incl. sp. prior.*

Leucoloma cheesmanii Ren. *syn. nov.* Bull. Soc. Roy. Bot. Belgique 41(1): 13. 1905.

T: "Hab. Pacifique: archipel de Cook, ile Raratong (F. Cheeseman; herb. E Levier). **Lectotype:** PC! (Hb. Renauld) Cheeseman, dat. 1899; **isotype:** NY!

Leucoloma oceanicum (C. Muell.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1877-78: 379. 1880. (Ad. 2: 643), *nom. illegl. incl. sp. prior.*

Leucoloma triforme (Mitt.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 413. 1872. (Ad. 1: 117). **Basionym:** *Poecilophyllum triforme* Mitt., J. Linn. Soc., Bot. 12: 94. 1869. **T:** "Hab. Brasilia; Rio de Janeiro, Heward s.n." **Holotype:** NY!

Dicranum biplicatum Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn ser. 3, 9-10: 253. 1878. **T:** Brasil: In vicinia urbis Rio de Janeiro, leg. Dr. A. Glaziou, # 7898, # 9087. **Lectotype:** *Glaziou 9087* BR!; **isotype:** H-Br! **isosyntypes:** *Glaziou 7898* NY! S!(2 specimens)

Leucoloma biplicatum (Hampe) Jaeg. Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1877-78: 496. 1880. (Ad. 2: 760).

Leucoloma zeyheri (C. Muell.) Kindb., Enum. Bryin. Exot. 64. 1888. **Basionym:** *Dicranum zeyheri* C. Muell. Syn. 1: 353. 1849. **T:** "Weissia n. sp. Zeyher: Coll. Pl. Cap. 496. Patria. Prom. bon. spei.". **Lectotype:** H-Br!; **isotype:** H-Br!

Dicranum ecklonii Lor., Moosstud. 158. 1864. **T:** "Hab. In monte Tabulari Capitis Bonae Spei leg. Eklon.". **Lectotype:** H-Br!

Leucoloma ecklonii (Lor.) Jaeg., Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1870-71: 411. 1872. (Ad. 1: 115).

Leucoloma ecklonianum Lor. ex C. Muell., Gen. Musc. Frond. 283. 1900. *nom. illeg incl. spec. prior.*

Note: The type material for *L. sprengelianum* and *L zeyheri* are both from C.B.Sp. This has led to the confusion of the two species. The species are distinguished by a number of characters: 1) the arrangement of papillae in the basal cells. In *L. sprengelianum* the reduced papillae are uniseriate, distinctly similar to peas in a pod. In *L zeyheri* the reduced basal papillae are bi- or multiseriate, scattered over the basal surface, not in sharply defined rows. 2) The distal papillae differ between the two species: In *L. zeyheri* the papillae are low in profile and less distinctly stellate, whereas in *L sprengelianum* the upper papillae are prominent and stellate in shape. The hyaline margin reaches the apex in *L. sprengelianum*, whereas in *L. zeyheri* the hyaline margin ends below the apex. The material seen for the South African Flora for *L. sprengelianum* is actually *L. zeyheri*, rather than *L. sprengelianum* as cited and noted on the label in BM!

Table II.10. Character comparison of selected species of Section *Leucoloma*

	holstii	***schelpei***	***zuluense* var. *ovatum***	***zuluense* var. *zuluense***	***gracilescens***	***subchryso-basilare***	***subbiplicatum.***	***lepervancheri***
habit	crisped	crisped	flexuose to crisped	bowed to slightly crisped	crisped	flexuose to falcate secund	flexuose	cripsed or flexuose
ovate-lanceolate	ovate-lanceolate to lanceolate	ovate-lanceolate	ovate to ovate-lanceolate	ovate-lanceolate to lanceolate	ovate-lanceolate to lanceolate	ovate-lanceolate to lanceolate	ovate-lanceolate to lanceolate	ovate to ovate-lanceolate
margin width (μm)	17-36	17-64	12-26	12-36 (48)	0-12	2.5-12.0	2.5-7.0	0-7.2
costa	subpercurrent	subpercurrent	subpercurrent	subpercurrent to excurrent	subpercurrent	subpercurrent to excurrent	subpercurrent	subpercurrent to excurrent
juxtacostal cells: shape	quadrate to rectangular	quadrate to short elongate	oblong to short elongate	oblong to short elongate	subquadrate to short elongate	subquadrate to short elongate	subquadrate to short elongate	quadrate to short elongate
width (μm)	5-7	5-7	7-10	7-10	5-10	5-7	5-7	5-10
leaf base width (mm)	0.34-.0.55	0.35-0.65	0.53-0.95	0.38-0.84	0.4-0.75	0.35-0.68	0.35-0.55	0.35-0.73
leaf length (mm)	1.8-3.0	3-4	2.3-3.5	3-5	2.5-4.0	2.5-4.0	1.5-2.5	2-3
acumen	stout	stout	stout	slender	slender	stout	slender	slender
peristome PPL base	pitted striate	smooth	pitted striate	pitted striate	--	pitted striate	--	--

Bibliography

Allen, B. H. 1987. A revision of the genus *Mesotus* (Musci: Dicranaceae). Journal of Bryology 14: 441-452.

Arnott, G. A. W. 1827. Nouvelle disposition méthodique des espèces de mousses exactement connues. Mémoires de la Société linnéenne de Paris 5(3): 214-323.

Bescherelle, E. 1878. Florule bryologique de la Réunion et des autres îles austro-africaines de l'océan indien. Annales Sciences Naturelles Botanique sér. 6, 9: 291-380.

Bridel, S.E. 1801. Muscologia recentiorum seu analysis, historia et descriptio methodica. Tom.2 pars 2. Gothae, Parisiis.

______. 1827. Bryologia universa seu Systematica ad Novam Methodum Dispositio, Historia et Descriptio omnium Muscorum Frondosorum Hucusque cognitorum cum Synonymia ex Auctoribus Probatissimis. Volumen Secundum et suppl., 848 pp. Joan. Ambros. Barth., Leipzig.

Briquet, J. 1930. Avis préable du Bureau Permanent et des Commissions de nomenclature sur les motions soumises aux débats de la sous-section de nomenclature du Vme Congrès International de Botanique, Cambridge (Angleterre) 1930. Berlin.

Brotherus, V. F. 1901-1909. Musci (Laubmoose) III. Unterklasse Bryales: II. Spezieller Teil., pp. 322-325. In Engler, A., K. Prantl (eds.). Die Natürlichen Pflanzenfamilien. W. Engelmann, Leipzig.

______. 1924. Musci (Laubmoose). In Ergebnisse der botanischen Expedition der Kaiserlichen Akademie der Wissenschaften nach Sübrasilien 1901, herausgegeben von Prof. Dr. V. Schiffner. Denschriften der Kaiserlichen Akademie der Wissenschaften. 83: 251-358.

______. 1924. Musci (Laubmoose) III. Unterklasse Bryales: Spezieller Teil. 10 Band, 1 Hälfte, pp. 209-211. In Engler, A. and K. Prantl (eds). Die Natürlichen Pflanzenfamilien. W. Engelmann, Leipzig.

Bruch, P., W. P. Schimper, T. Gümbel 1836-55. Bryologia Europaea seu Genera

Muscorum Europaeorum Monographice Illustrata. In Schimper, W. P. (ed). Schweizerbart, Stuttgartiae.

Burger, W.C. 1975 The species concept in *Quercus*. Taxon 24: 45-50.

Cardot, J. 1910. Musci. In: J. Briquet (ed.), Recueil des documents destinés a servir de base aux débats de la section de nomenclature systématique du Congrès International de Botanique de Bruxelles 1910. Berlin.

Clausen, J., D.D. Keck, & W.M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Publ. Carnegie Inst. (Washington) 520: 1-452.

Clymo, R. S. & J. G. Duckett. 1986. Regeneration of *Sphagnum*. New Phytologist 102: 589-614.

Crosby, M. R. & R.E. Magill. 1981. A dictionary of mosses. Monographs in Systematic Botany from the Missouri Botanical Garden 3: 1-43.

______ & ______. 1994. Index of mosses. Monographs in Systematic Botany from the Missouri Botanical Garden 50: 1-87.

______, ______, C. R. Bauer. 1992. Index of mosses. Monographs in Systematic Botany from the Missouri Botanical Garden. 42: 1-646.

Crum, H. A. & L. E. Anderson. 1981. Mosses of Eastern North America. Vol.1: 1-663. Columbia University Press, NY.

Crundwell, A. C. 1979. Rhizoids and moss taxonomy, pp. 347-367. In Clarke, G. C. S., J. G. (eds). Duckett. Bryophyte Systematics. Academic Press, London.

Darwin, C. 1859. The Origin of Species by means of natural selection or the preservation of favoured races in the struggle of life. John Murray.

de Vries, A., B.O. van Zanten, & H. van Dijk. 1983. Genetic variability within and between populations of two species of *Racopilum* (Racopilaceae, Bryopsida) Lindbergia 9: 73-80.

Dixon, H. N. 1932. The Classification of Mosses, pp. 396-431. In Verdoorn, F. (ed.). Manual of Bryology. Martius Nijhoff, The Hague.

______ & A. Gepp. 1923. Rehmann's South African mosses. Kew Bulletin 6: 193-238.

Donoghue, M. J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. The Bryologist 88: 172-181.

During, H.J. & B. ter Horst. 1983. The diaspore bank of bryophytes and ferns in chalk grassland. Lindbergia 9:57-64.

Edwards, S. R. 1979. Taxonomic implications of cell patterns in haplolepideous moss peristomes, pp. 317-356. In Clarke, G. C. S., J. G. (eds). Duckett. Bryophyte Systematics. Academic Press, London.

______. 1984. Homologies and inter-relationships of moss peristomes, pp. 658-695. In Schuster, R. M. (ed). New Manual of Bryology. Hattori Botanical Laboratory, Nichinan, Japan.

Fleischer, M. 1902-1923. Die Musci der Flora von Buitenzorg (Zugleich Laubmoosflora von Java). E.J. Brill, Leiden.

Frahm, J. -P. 1991. A phenetic and cladistic study of the Campylopodioideae. Journal of the Hattori Botanical Laboratory 69: 65-78.

______. 1983. A new infrageneric classification in the genus *Campylopus* Brid. Journal of the Hattori Botanical Laboratory 54: 207-225.

Gangulee, H. C. 1971. Mosses of eastern India and adjacent regions. A monograph. Fascicle 2. Archidiales, Dicranales & Fissidentales. Systematic Biology. Calcutta.

Gradstein, S. R. & J.- P. Frahm. 1987. Die floristische Höhengliederung der Moose entlang des BRYOTROP-Transektes in no- Peru. Beiheft zur Nova Hedwigia 88: 105-113.

______ & T. Pócs. 1989. The biogeography of tropical rainforest bryophytes. In H. Lieth and M.J.A. Weger (eds.) Tropical rain forest Ecosystems, 311-325 Ecosystems of the world. Vol 14A. Elsevier, Amsterdam.

Hedwig, J. 1782 Fundamentum Historiae Naturalis Muscorum Frondosorum concernens Eorum Flores,Fructuus, seminalem propagationem adiecta generum dispositione methodica iconibus illustratis. Pars I, 112 pp.; Pars II, 107 pp. Lebrecht Crusius, Lipsiae.

______. 1801. Species muscorum frondosorum descriptae et tabulis aeneis LXXVII coloratis illustratae. Joannis Ambrosii Barthii, Lipsiae.

Horikawa, Y. & H. Ando. 1952. A short study on growth-forms of bryophytes and its ecological significance. Hikobia 1: 119-129.

Hornschuch, C. F. 1825. "Review of " Species muscorum frondosorum Supplementum 2 vol. 1(1). Flora 8: 1-23.

Humbert, H. 1955. Une merveille de la nature à Madagascar. Première exploration botanique du Massif de Marojezy et ses satellites. Mémoires de l' institut scientifique de Madagascar. Série B. 6: 271.

Jaeger, A. & F. Sauerbeck. 1872. Genera et species muscorum systemaice disposita seu adumbratio florae muscorum totis orbis terrarum. Bericht über die Tätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft 1870-1871: 357-451.

Kawai, I. 1979. Systematic studies on the conducting tissue of the gametophyte in Musci. (9) On regularity among anatomical characteristics os stems in some species of Dicranaceae. Science reports of the Kanazawa University 24: 13-43.

Koponen, T. 1982. Rhizoid topography and branching patterns in moss taxonomy. Nova Hedwigia 71: 95-99.

La Farge-England, C. 1992. *Leucoloma crosbyi* (Dicranaceae), a new species endemic to northern Madagascar. Novon 2: 119-122.

______. 1996. Growth form, branching pattern, and perichaetial position in mosses: cladocarpy and pleurocarpy redefined. The Bryologist 99: 170-186.

______ & ______1985. A taxonomic study of *Tayloria hornschuii* and *T. froelichiana* in North America. Bryologist 88: 82-93.

______, ______, & J. England. 1991. Holocene soligenous fens on a high arctic fault block, northern Ellesmere Island (82), N.W.T. Arctic and Alpine Research 23(1): 80-98.

Linnaeus, C. 1753. Species plantarum, exhibentes plantas rite cognitas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas II, pp.561-1200. Holmiae.

Longton, R.E. 1990. Sexual reproduction in bryophytes in relation to physical factors of the environment. In R.N. Chopra and S.C. Bhatla (eds.) Bryophyte

Development: Physiology and Biochemistry 139-166. CRC Press, Boca Raton, Florida.

Magill, R.E. 1981. Flora of southern Africa. Bryophyta. Part 1. mosses Fascicle 1. Sphagnaceae-Grimmiaceae. Botanical Res. Inst. Dept. Agri. and Fisheries, 1-291.

______. 1982. Exotic Bryophytes. Beihefte zur Nova Hedwigia 71: 317-322.

______. 1993. Conserved names for mosses: a brief history. Taxon 42: 5-15.

McDade, L. A. 1995. Species concepts and problems in practice: insight from botanical monographs. Systematic Botany 20: 606-622.

Miles, C.J. & R.E. Longton. 1990. The role of spores in reproduction in mosses. Botanical Journal of the Linnean Society 104: 149-173.

Mishler, B.D. & R.N. Brandon. 1987. Individuality, pluralism, and the phylogenetic species concept. Biology and Philosophy 2: 397-414.

______ & A.F. Budd. 1990. Species and evolution in clonal oragnisms -Introduction. Systematic Botany 15: 79-85.

__________. & M.J. Donoghue. 1982. Species concepts a case for pluralism. Systematic Zoology 31: 491-503.

Mitten, W. 1859. Musci Indiae Orientalis. An enumeration of the mosses of the East Indies. Journal of the Proceedings of the Linnean. Society. Botany. London Suppl. 1: 1-171.

______. 1869. Musci Austro-americani. Journal of the Proceedings of the Linnean. Society. Botany. London 12: 1-659.

Mueller, C. 1948. Synopsis muscorum frondosorum omnium hucusque cognitorum pars prima. Musci vegetationis acrocarpicae. 812 pp. Alb. Foerstner, Berolini.

Newton, A.E. & B.D. Mishler. 1994. The evolutionary significance of asexual reproduction in mosses. Journal of the Hattori Botanical Laboratory 76: 127-145.

______ & H. Robinson. 1994. The structure of the leaf and peristome of *Holomitriopsis laevifolia* (Broth.) H. Robins. illustrated with scanning electron microscopy. Tropical Bryology 9: 111-1116.

Nixon, K.C. & Q.D. Wheeler 1990. An amplification of the phylogenetic species concept. Cladistics 6: 211-223.

Norris, D. H. & T. Koponen. 1990. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXXV. Dicranaceae and Dicneonaceae (Musci). Acta Botanica Fennica 1:1-64.

Nyholm, E. 1954. Illustrated flora of Fennoscandia. II. Musci. Fasc. I. The Botanical Society of Lund (ed.). CWK Gleerup, Lund.

Odu, E.A. 1981. Reproductive phenology of some tropical african mosses. Cryptogamie, Bryologie- Lichénologie 2: 91-99.

Olmstead, R.G. 1995. Species concepts and plesiomorphic species. Systematic Botany 20: 623-630.

Paris, E.G. 1900. Index Bryologicus sive enumeratio muscorum hucusque cognitorum adjunctis synonymia distributioneque geographica locupletissimis. Supplem. Primum. Paris.

Parihar, N.S. 1961. An introduction to Embryophyta. Vol. 1. Bryophyta. Central Book Depot, Allahabad. 338 pp.

Peterson, W. 1979. A revision of the genera *Dicranum* and *Orthodicranum* (Musci) in North America north of Mexico. Ph.D. Thesis. University of Alberta, Edmonton, Alberta.

Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru mountains (Tanzania, East Africa). Acta Botanica Academiae Scientiarum Hungaricae 26: 143-167.

Potier de la Varde, R. 1950. Espèces et variétés nouvelles récoltées à Madagascar par M. le Professeur H. Humbert, au cours de son 6^e et de son 7^e voyage. Revue Bryologique et Lichénologique 19: 145-154.

Reese, W.D. 1987. World ranges, implications for patterns of historical dispersal and speciation, and comments on phylogeny of *Syrrhopodon* (Calymperacaeae). Memoirs of the New York Botanical Garden 45: 426-445.

Renauld, F. 1898. Prodrome de la flore bryologique de Madagascar des Mascareignes et des Comores publié par ordre de S.A.S. Le Prince Albert 1er. Imprimerie

Monaco.

______. 1901. Nouvelle classification des *Leucoloma*. Revue Bryologique et Lichénologique 28: 66-70.

______. 1909. Essai sur les *Leucoloma* et supplément au prodrome de la flore bryologique de Madagascar des Mascareignes et des Comores. Imprimerie Monaco.

______ & J. Cardot 1915. Les mousses de Madagascar. In Grandidier, A. & G. Grandidier (eds.). Histoire Physique, Naturelle et Politique de Madagascar (Mousses) 39: 1-560.

Salazar Allen. 1985. The life-form and presence of epigametophytic plants in the genus *Leucophanes*. The Bryologist 88: 94-97.

Schofield, W. 1985. An introduction to bryology. MacMmillan Publishing Co. New York.

Schwaegrichen, C. F. 1823-1827. Species muscorum frondosorum descriptae et tabulis-aeneis coloratis illustratae. Opus posthumum. Supplementum 2. Lipsiae. Johannis Ambrosii Barth.

Sillet, S.C., S.R. Gardstein, & D. Griffin,III. 1995. Bryophyte diversity of Ficus tree crowns from cloud forest and pasture in Costa Rica. The Bryologist. 98: 251-260.

Sim , T.R. 1926. The Bryophyta of South Africa. Tranactions of the Royal Society of South Africa 15: 1-475.

Stearn, W.T. 1983. Botanical Latin. Fitzhenry & Whiteside, Toronto.

Taylor, E.C. 1962. The Philibert peristome articles. An abridged translation. The Bryologist 65: 175-212.

Touw, A. 1974. Some notes on taxonomic and floristic research on exotic mosses. The Journal of the Hattori Botanical Laboratory 38: 123-128.

Wyatt, R. 1985, Species concepts in bryophytes: input from population biology. The Bryologist 88: 182-189.

______, I.J. Odrzykoski, & A. Stoneburner. 1992. Isozyme evidence of reticulate evolution in mosses: *Plagiomnium medium* is an allopolyploid of *P. ellipticum* x *P. insigne*. Systematic Botany 17: 532-550.

Vitt, D. H. 1984. Classification of Bryopsida. In Schuster, R. M. (ed.). New Manual of Bryology Hattori Botanical Laboratory, Nichinan, Japan.

______, S.R. Gradstein, & Z. Iwatsuki. 1985. Compendium of bryology: a world listing of herbaria, collectors, bryologists, and current research. Bryophytorum Bibliotheca 30: 1-355.

Wijk, R. van der, W.D. Margadant, & P.A. Florschutz. 1964. *Leucoloma*. Index Muscorum. 3: 287-299. Bureau for Plant Taxonomy and Nomenclature, Utrecht.

______, ______, & ______. 1969. *Leucoloma*. Index Muscorum 5: 759-761. Bureau for Plant Taxonomy and Nomenclature, Utrecht.

Zander, R. 1993. Genera of the Pottiaceae: mosses of harsh environments. Bulletin of the Buffalo Society of Natural Sciences 32: 1-378.

Chapter III

THE INFRAGENERIC PHYLOGENY, CLASSIFICATION AND PHYTOGEOGRAPHY OF *LEUCOLOMA*

Phylogenetic Analysis

Introduction

A fundamental task of the systematist is to establish the "natural order" or evolutionary relationships between organisms. In 1966, Willi Hennig published *Phylogenetic Systematics* which has become the cornerstone for cladistics. The theory of descent is the basis for phylogenetic systematics (Wenzel 1938 in Hennig 1966). Hennig emphasized the difference between homology (common descent) versus homoplasy (similarity-parallelism or convergence) for characters used in phylogenetic analyses. He described two types of homologous characters, apomorphic and plesiomorphic and emphasized that systematics should recognize monophyletic taxa defined by synapomorphies, not symplesiomorphies or homoplasies.

Evolution is descent with modification. The evolutionary novelties within a common ancestor are critical for establishing genealogical relationships of taxa. In a phylogenetic analysis, the definition of attributes is primary for the taxa under study (Felsenstein 1985, Stevens 1984). From the list of attributes, the characters used are selected on the basis of informative criteria: 1) discrete states; 2) invariance within an OTU (operational taxonomic unit); and 3) potential homology (Mishler 1994). Although discrete characters represent the ideal, it is not always possible to find distinct gaps in quantative characters, especially in morphologically reduced plants, such as bryophytes (Hedenäs 1994). Although the use of continuous characters has been controversial in phylogenetic analyses, they are used in the following analysis for they have been found to have some phylogenetic information (e.g., Hedenäs 1994, Stevens 1991). Mishler concluded that the potentially informative characters are not a random selection of potential homologues, but are carefully chosen. Mishler and De

Luna (1991) outlined the criteria required for a character to be considered a homologue: 1) describable, 2) variable within the OTUs, 3) heritable and independent, and 4) congruent with the cladogram based on all available characters. Mishler (1994) emphasized that all "good" characters should be used in a cladistic analysis and that autapomorphies should be included in the overall CI (consistency index) calculation. He argued that the evaluation of a particular data matrix should be based on the total data set. Depending on the level of analysis (taxon rank) a particular character may lose its informativeness (e.g., dependent sporophytes for an analysis of moss genera).

The potential homologues are assigned a character state [0,1]. For multistate characters, more than two states are assigned; these characters are coded either as ordered or unordered. (For binomial characters it is equivocal whether they are coded as ordered or unordered.) The ordered character states can be interpreted as a linear transformation 0>1>2>3>4, a bifurcation 3<2<0>1>4, or other specified order. Unordered character states require a single step from any state to another. The characters are polarized into plesiomorphic and apomorphic states by the determination of the outgroup (Watrous and Wheeler 1981, Maddison et al. 1984). Preferably more than one taxon is chosen for the outgroup (Donoghue and Cantino 1984). The main objective is to establish global parsimony over the ingroup and outgroup considered together (Maddison et al. 1984).

The types of data that have been used for phylogenetic reconstruction are varied: morphological, anatomical, ontogenetic, biochemical, and molecular. Each data set contributes information on a different aspect of the organism, and may suggest conflicting hypotheses of phylogenetic relationships. All available data should be considered when testing evolutionary hypotheses. With the rapid escalation of the use of molecular data in systematic studies and its potential for providing phylogenies, some reserved enthusiasm has been noted (Donoghue 1994, Huelsenbeck and Bull 1996, Mishler 1994). Different opinions on how to compare data sets have not been resolved (e.g., to run data sets separately or to combine them: e.g., morphology and molecular). The lack of congruence between data sets prevents the acceptance of a single true phylogeny (e.g., between two molecular phylogenies, two morphological phylogenies, or molecular versus morphological phylogeny). Mishler (1994) stressed that the comparison of different sets of data is preferable to a larger data set from a single type of data. The comparison of trees from each data set will identify the congruent clades and clades that remain unresolved or have diverse solutions for the natural relationships. Depending on the base of knowledge of a particular group of organisms, morphology remains the fundamental discipline for forming preliminary hypotheses of genealogical relationships.

Morphological characters have been used traditionally in bryology to form evolutionary hypotheses of taxa at diverse ranks (e.g., species: Hyvönen 1989, Koponen 1968, Vitt and Ramsay 1985, Vitt 1995, Zomlefer 1993; family: De Luna 1995; subfamily: Frahm 1991, Zander 1993; "pleurocarps" Hedenäs 1994, 1995; the major clades within Musci: Mishler et al. 1994; the Antherocerotae: Hasegawa 1994, Hyvönen and Piippo 1993; and an analysis of bryophytes in relation to algae and tracheophytes: Mishler and Churchill 1985, Graham et al. 1991). "Bryophytes" are structurally simple organisms that frequently result in analyses with high homoplasy indices, especially in studies of increasingly higher taxonomic levels (Frahm 1991, Mishler 1994, Zander 1993). Yet without the morphological data to formulate phylogenetic hypotheses, the choice of taxa for molecular and biochemical analyses would be random. The need for rigorous reconstructed phylogenies based on morphological features is emphasized by Donoghue and Sanderson (1992). The evaluation of characters used in phylogenies based on morphology is critical for a robust cladogram (Buck 1986, Hyvönen 1989, Mishler and Deluna 1991).

The present phylogenetic analysis evaluates the hypothesis of *Leucoloma* as a monophyletic taxon, based on morphological and anatomical data. *Dicranum*, *Dicranoloma*, and *Sclerodontium* were chosen as the outgroup taxa. The two latter genera have been treated as subgenera within *Leucoloma* (Renauld 1898), and all have been included in an antiquated concept of *Dicranum* (Mueller 1848). The distinction of the genus *Dicranoloma* from *Dicranum* has been debated since its conception (Eddy 1988, Norris and Koponen 1989, 1990, Renauld 1909, Sainsbury 1955, Takaki 1966, Tan and Koponen 1983). The delineation of *Dicranoloma, sensu* Renauld (1901), has been based on the presence of a hyaline margin, uniform laminal cells in transverse section, and a Southern Hemisphere distribution. Norris and Koponen (1989) have recently typified and restricted the concept of *Dicranoloma* to 6 species from Australia and New Caledonia. Whether the concept of *Dicranoloma* is *sensu* Renauld (1901) or *sensu* Norris and Koponen (1989) the coding of the morphological characters for *Dicranoloma* would not differ in the analyses below.

Based on the heterogeneous morphological and anatomical data there was reason to re-examine the infrageneric taxa of *Leucoloma* (Brotherus 1924a, Renauld 1909). The phylogenetic relationship of these taxa and new taxonomic groupings were analysed. The questions addressed include: 1) what is the relationship of the phenotypically similar *Sclerodontium* to *Leucoloma*; 2) should subgenus *Leucoloma* be a distinct genus; 3) Should section *Holomitrioidea* be considered a distinct genus; 4) is subgenus *Sphenodictyon* a separate lineage from subgenus *Leucoloma*; and 5) what is the proper placement of section *Dichelymoidea*, and 6) what is the phylogenetic relationship of the taxonomically discrete species groups within subgenus *Syncratodictyon*.

Methods

Two methods have been used to select taxa for the following analyses. The exemplar approach is the selection of one to several representatives of the OTU (operational taxonomic unit), with postulated basal taxa being chosen where possible (Mishler 1994). The second approach is compartmentalization in which the scored character states for each OTU are based on all the taxa of that group (Mishler 1994). The characters assigned to the OTU represent a hypothetical ancestor, that may differ from any extant taxon of the clade. Although compartmentalisation will inevitably produce more polymorphic taxa, it does not constrain the analysis by a selection of preconceived primitive species to represent a terminal taxon. This allows one to determine the robust clades of large data set. Subsequently, analyses of weaker clades can be performed using a refined data set with less potential for high homoplasy.

The cladistic analyses were executed by the software program Phylogenetic Analysis Using Parsimony (PAUP) version 3.1.1 (Swofford 1993) to find the optimal tree(s). Heuristic and Branch and Bound searches were performed on the data matrix below. The approximate heuristic method was used to establish an upper boundary for tree length. A subsequent analysis, using an exact method - branch and bound, was performed to find the most parsimonious tree(s). MacClade version 3.0 has been used to edit the data matrix, examine trees resulting from the PAUP searches, and trace the characters and state changes (Maddison and Maddison 1992). Unambiguous characters only are plotted by Mac Clade. Consistency indices produced by PAUP and Mac Clade were the same.

The robustness of the clades was evaluated by a decay analysis (combinable component consensus - Bremer 1990), using the constraint option in PAUP. An index of 2 was assigned to a clade, if it collapsed 2 steps longer than the most parsimonious tree(s). A heuristic bootstrap analysis was also run to determine relative support for the clades. One hundred bootstrap replicates were run, using the random addition sequence, with tree-bisection-reconnection and the steepest descent options in effect. Only those branches supported by more than 50% frequency were enumerated.

All characters were run unweighted and unordered. Thus the multistate characters have been treated as "maximally connected" *sensu* Slowinski (1993). This prevents a bias toward the characters in an a priori weighting scheme. The analyses were run with the outgroup not designated and subsequently with it designated, to see if the results differed. If a character was not applicable to a taxon (e.g., papillae type), it was scored a character state "0" (Maddison 1993). Multistate characters and polymorphic taxa occurred within the data matrix. The taxa with more than one character state were designated as polymorphic, opposed to uncertainty in PAUP.

Operational Taxonomic Units

An infrageneric analysis of *Leucoloma* was made using 3 closely related genera as the outgroup taxa: *Dicranum*, *Dicranoloma*, and *Sclerodontium*. The analysis consisted of 17 taxa and 60 characters. The morphological and anatomical data were compiled from specimens of 112 available *Leucoloma* species. Subgenus

Syncratodictyon includes a number of heterogeneous, previously described taxa. In order to decrease the number of polymorphic terminal taxa, a more refined grouping was used, based on the character discontinuities. The infrageneric taxa used for the OTUs in the analysis are presented in Table III.1, with a comparison to the taxa of the most recent classification (Renauld 1909).

The *tortellum* species group has been distinguished from section *Caespitulosa*; section *Pseudocaespitulosa* has been synonymized with section *Caespitulosa*; the *sprengelianum* species group is distinguished within section *Albescentia*; the *fuscifolium*, *perviride*, and *tenerum* species groups are differentiated from section *Dicranoidea*; and section *Semivittata* is synonymized with section *Dicranoidea*. The informal species groups were analysed for their infrageneric affinities and robustness.

A selected subspecies, *Dicranum bonjeanii* ssp. *angustum*, was chosen to represent the outgroup genus *Dicranum*, based on a cladistic analysis of the data matrix coded by Peterson (1979), using PAUP 3.1.1. (not presented). The results supported *Dicranum bonjeanii* ssp. *angustum*, along with other species of *Dicranum* subgenus *Dicranum*, to represent the basal taxon within *Dicranum*. The exemplar approach for OTU representation was followed in this analysis, due to the the existing phylogenetic hypothesis for species relationship and the impracticality of examining the entire genus (Mishler 1994).

For *Dicranoloma*, the six species designated by Norris and Koponen (1989) were examined for the character analysis. Material of the two species of *Sclerodontium*, recognised by Crum (1986), was examined for the analysis. The compartmentalization approach was used for these two genera, for no phylogenetic hypotheses of the species have been proposed.

Characters

The morphological characters used for the analysis are described in detail below. Based on outgroup comparison, an asterisck (*) designates the plesiomorphic state. The numbers refer to the characters in the data matrix with their distribution shown on the trees. The data matrix used for the analysis is presented in Table III.2.

GAMETOPHYTIC CHARACTERS

1. **growth form**: **0*** erect; **1** downwardly outspreading/pendulous; **2** creeping. The species of *Leucoloma* are predominantly epiphytic which facilitates a downwardly outspreading or pendent growth form. Those taxa that are terricolous, saxicolous, growing on humus or logs have erect growth. *Sclerodontium* was the only taxon to have a creeping habit, with the prostrate stems attached to the substrate by rhizoids.
2. **stem transverse section**: **0*** round; **1** elliptic, flattened. Subgenus *Leucoloma* has stems that are distinctly elliptic in transverse section. Other taxa may have stems that appear flattened in the dry, unsectioned state, yet upon wetting and cutting the sections are round.
3. **stem central strand**: **0*** present; **1** absent. *Dicranum*, *Dicranoloma*, and the more a number of taxa within *Leucoloma* have central strands in the stem. The loss of a central strand is interpreted as a reductionary trend.
4. **stem tomentum**: **0*** present; **1** absent. *Dicranum* and *Dicranoloma* have stem tomentum and are the plesiomorphic taxa, thus the lack of stem tomentum is considered apomorphic. *Leucoloma* lacks stem tomentum with the exception of a few specimens of *Leucoloma humbertii* and *L. sanctae-mariae*, yet the tomentum in these taxa is restricted to a few patches along the stem.
5. **rhizoid organography**: (excluded) **0*** scattered along stem or restricted to stem or branch base; **1** developed from alar cells. Often species of section *Subvittata* have alar cells that produce rhizoids. Scattered specimens with alar rhizoids have been seen in subgenus *Syncratodictyon* and section *Leucoloma*. The distribution of this character is not fully understood and thus has been excluded from the analysis. Its inclusion did not affect the topology of the most parsimonious tree, although the consistency index was affected.

    Specialized rhizoid production is known from other genera in the Dicranales. The Dicnemonaceae and *Mesotus* have nematogenous laminal cells that produce rhizoids (Allen 1987). Within the Dicranaceae, subfamilies

Paraleucobryoideae and Campylopoideae, species produce rhizoids on the abaxial surface at the base of the costa (Frahm 1991).

6. **laminal cell differentiation, 3 types**: **0*** absent; **1** present. The basal taxa of *Dicranum* (cf. Peterson 1979) lack a hyaline margin, and as a result have uniform cells in a transverse section across the lamina. Renauld (1901) described *Dicranoloma* as having uniform cells across the lamina, with the exception of a hyaline margin. Both *Sclerodontium* and *Leucoloma* have 3 differentiated cell types: linear, hyaline marginal cells; chlorophyllose, quadrate to short elongate juxtacostal or upper cells; and tinged more elongated interior/basal cells.
7. **laminal cell bands**: **0*** undifferentiated; **1** lateral juxtacostal bands; **2** basal hyaline windows with chlorophyllous cells descending along the margin. Taxa with defined juxtacostal bands or specialized hyaline windows are considered apomorphic. The degree of cell differentiation is variable within *Leucoloma*, and is considered a separate character. In *Sclerodontium* the descent of shorter cells along the margin is somewhat similar to *Mesotus* and some species of *Holomitrium* and reminiscent of *Tortula*: Pottiaceae.
8. **cells sharply defined**: **0** N/A; **1*** gradual transition; **2** sharp definition. The juxtacostal cells or upper cells are either sharply differentiated from the interior and basal cells or have a gradual transition. A more gradual transition is considered plesiomorphic.
9. **juxtacostal bands smooth or not**: **0*** smooth; **1** rugose; **2** corrugate. Two taxa have non-smooth juxtacostal bands, subgenus *Sphenodictyon* and section *Dichelymoidea*. The former taxon has species with rugose juxtacostal bands that are undulate or "buckled" in appearance, with a "velvet" smooth profile. The latter taxa have corrugated juxtacostal bands with papillae that form transverse rows across the lamina. The "corrugation" is the result of differential papillae formation on the abaxial and adaxial surface and prominently projecting papillae.

10. **juxtacostal cells with irregular or sinuose lumina: 0*** absent; **1** irregular or sinuose lumina. Four taxa have species that develop irregular or sinuose eshaped lumen: *Sclerodontium*, section *Holomitrioidea*, and the *sprengelianum* and *tortellum* species groups. The other taxa examined have more round or squared lumina.

11. **juxtacostal cells oblate: 0*** absent; **1** present. Within the chlorophyllose cells there is a tendency to develop an oblate-shaped lumina, especially along the upper margins. This is most pronounced in section *Holomitrioidea*. The oblate lumen is rounded or angular.

12. **abaxial papillae: 0*** absent; **1** present. Typically, the abaxial surface of the distal lamina is scabrous or with elaborate papillae. A number of species in the section *Dicranoidea* and a few scattered taxa in other sections lack papillae development on the abaxial surface. Predominantly *Leucoloma* is typified by papillose distal cells. Within *Dicranum* there are taxa that develop abaxial papillae, yet they are restricted to the more derived groups (Peterson 1979, Gao and Cao 1992). The type and degree of papillae formation within *Leucoloma* is diverse; therefore, a number of papillae characters have been defined to examine the variation (see 13, 14, 15, 16, 17, 18). A similar diversity of papillae formation occurs in *Racomitrium*.

13. **adaxial papillae: 0*** absent; **1** present. The coding for this character is based on a transverse section of the mid-leaf. Most taxa of *Leucoloma* develop at least some adaxial papillae near the apex, thus the character is defined on a mid-leaf transverse section.

14. **adaxial papillae development: 0*** N/A; **1** adaxial and abaxial equally developed; **2** adaxial less prominent than abaxial papillae; **3** adaxial papillae scattered. The development of papillae on the adaxial surface is either consistent with the abaxial surface or not.

15. **papillae distribution in transverse section: 0*** N/A; **1** lumen; **2** inter-luminal; **3** indistinctly over lumen or interlumina. In transverse section the development of

papillae is either over the cell lumen or over the inter-luminal cell wall. Each cell of section *Holomitrioidea* develops 2 rows of cells at the margins of the cell. Adjacent cells have coalescent papillae over the adjoining cell walls. In transverse section of the lamina there is a distinctive "groove" over the lumen of each cell, with the papillae thickenings over the inter-luminal walls. This atypical papillae formation also occurs in the species group *tenerum*, the genus *Mesotus*, Dicranaceae subfamily Mesotoideae (Allen 1987), and a distantly related genus *Racomitrium*, Grimmiaceae. Proctor (1979) referred to this type of cell wall thickening as an adaptation to facilitate water movement over the lamina. The most common papillae formation in *Leucoloma*, *Dicranum*, and *Sclerodontium* is restricted to the cell lumen.

16. **papillae single or uniseriate: 0*** absent; **1** present. Taxa with juxtacostal cells that are unipapillose or uniseriately papillose include the following: section *Dichelymoidea*, section *Albescentia*, section *Caespitulosa*, *sprengelianum* species group, and *Sclerodontium*. The upper cells are unipapillose in the *sprengelianum* species group, with distinct uniseriate papillae basally. Depending on the length of the cells the papillae are single or uniseriately bi-, or multi- papillose.

17. **papillae stellate: 0*** absent; **1** present. The development of pronounced stellate papillae is restricted to two taxa, *Sclerodontium* and section *Albescentia*. This is considered a specialised apomorphic state.

18. **pluripapillose cells: 0*** absent; **1** present. The formation of pluripapillose cells is differentiated from character 16, for both unipapillose and pluripapillose cells occur on different surfaces in *Sclerodontium*.

19. **papillae hooked apically: 0*** absent; **1** present. Abaxial, prominent papillae that are apically hooked develop in three taxa, *Sclerodontium* and section *Albescentia*, and section *Caespitulosa*.

20. **abaxial papillae prominence: 0*** low; **1** prominent. Abaxial, prominent papillae occur in 3 taxa and are typically stalked: *Sclerodontium* and section *Albescentia*

and section *Dichelymoidea*.

21. **paired papillae**: **0*** absent; **1** present. Papillae are distributed in pairs in the section *Caespitulosa* across the lamina. They occur at the bottom of one cell and the top of the cell below it.

22. **basal cell width**: **0*** ≥14 (rarely 12) µm; **1** ≤ 14 (mostly 5-12) µm. Although this is a continuous character there is a perceptible, reductionary trend in basal cell size from the outgroup taxa *Dicranum* and *Dicranoloma* to *Sclerodontium* and *Leucoloma*.

23. **smooth basal cells short: 0*** elongate, linear; **1** short, short elongate. Cells with a < 3:1 length-width ratio are considered short to short elongate. The decrease in basal cell length is considered an apomorphic state restricted to 4 taxa: section *Caespitulosa*, and the *tortellum*, *perviride*, and *fuscifolium* species groups.

24. **abaxial/adaxial laminal section thick-walled: 0*** present; **1** absent. From outgroup comparison, the thickened abaxial-adaxial wall of the basal cells in transverse section is plesiomorphic. The lumen is rectangular in section and is narrower or the same thickness as the abaxial and adaxial cell walls. In the more derived taxa the ab-adaxial walls are thinner than the lumen.

25. **transitional basal-alar cells**: **0*** absent; **1** present. One to several rows of isodiametric cells form between the elongate basal cells and the sharply differentiated alar cells.

26. **alar cells**: **0*** inflated, thin-walled, equally thickened, or inflated with slightly longitudinally thickened walls, all red-brown or hyaline; **1** bulging, longitudinally thick-walled, dark red-brown (marginally hyaline); **2** plane, evenly to slightly longitudinally thickened, red-brown to hyaline marginally; **3** plane, firm, with pronounced longitudinally thick-walled (scalariform), orange red brown to hyaline marginally. All of the examined taxa have sharply differentiated alar cells, that vary in wall development. Within a single specimen, the younger leaves can have slightly longitudinally thickened alar cells with the older leaves having inflated thin-walled alar cells. This variation

is coded as a single character state (0). *Sclerodontium* and section *Holomitrioidea* have distinct, bulging, longitudinally thickened alar cells. In *Dicranum* and *Dicranoloma* the inner cells have a tendency to be hyaline and thinner walled, whereas in *Leucoloma* and *Sclerodontium*, the marginal cells have a tendency to become thin-walled, more elongate, and hyaline.

27. **alar region**: **0*** intermediate (10-19); **1** reduced (3-9); **2** enlarged (>20). The size of the alar region is based on the number of cells in width. The plesiomorphic state is considered the intermediate size. Within *Leucoloma* there are two evolutionary trends: reduction and enlargement.

28. **alar cells**: **0*** unistratose; **1** bistratose. Bistratose alar cells are restricted to *Dicranum*. Peterson (1979) designated the bistratose character state as plesiomorphic within *Dicranum*. It is considered here an autapomorphy for *Dicranum*.

29. **orientation of alar cells**: **0*** vertical; **1** obliquely angled; **2** extreme obliquely angled. The alar cells are either vertically or obliquely oriented to the basal cells. The plesiomorphic state is the vertical orientation. The strongly angled alar cells of section *Dichelymoidea* and subgenus *Sphenodictyon* correspond to the decurrent alar regions and squarrose leaf sets.

30. **alar cell shape**: **0*** elongate or rectangular; **1** quadrate, isodiametric, oblong. *Dicranoloma*, *Sclerodontium*, and sections *Dicranoidea* and *Subvittata* have more or less shortened alar cells. The remaining taxa have rectangular or elongate cells.

31. **hyaline margin**: **0** N/A; **1*** extending from the base to apical region; **2** restricted to basal 1/2-2/3 leaf; **3** not reaching the alar region. The development of the hyaline margin is restricted in 5 of the taxa. *Sclerodontium* has a unique development, by lacking the differentiated marginal cells at the base of the leaf. Taxa with differentiated marginal cells that extend to the apex or just below are considered plesiomorphic.

32. **upper margin**: **0*** serrate; **1** serrulate; **2** entire. The plesiomorphic state is serrate

from outgroup comparison. Three taxa have entire upper leaf margins: section *Holomitrioidea* and the *perviride* and *tortellum* species groups. *Sclerodontium* has a serrulate or entire upper margin. There are 5 polymorphic taxa for this character.

33. **upper margin crenulate**: **0*** absent; **1** present. The *tortellum* species group has an "crenulate" upper margin formed by the projecting papillae. It is an autapomorphy for the group.

34. **marginal serrations from short laminal cells: 0*** present; **1** absent. The serrations are formed from short laminal cells opposed to differentiated, linear, hyaline marginal cells. The *perviride* and *fuscifolium* spp. groups have this specialized upper margin.

35. **margin undulate**: **0*** absent; **1** present. Undulate hyaline margins are conspicuous in species of section *Albescentia.*

36. **hyaline margin cell width: 0*** N/A **1** broad, 5.0 µm; **2** narrow, 2.5 µm. The marginal cells of the *Dicranoloma* species are double the width of the marginal cells in *Leucoloma* and *Sclerodontium.*

37. **apiculus**: **0*** absent; **1** present. Leaves with one to several pellucid cells at the apex is considered an apomorphic state. It occurs in section *Holomitrioidea* and the *tortellum* species group.

38. **apex with hair point**: **0*** absent; **1** present. The development of a hair point is restricted to *Sclerodontium* and is an extension of the costa, therefore differentiated from apiculate leaves.

39. **abaxial costa**: **0*** toothed; **1** smooth; **2** serrulate. The plesiomorphic state is the presence of teeth on the dorsal surface of the costa. There is a reduction trend from distinct teeth to serrulations, to an entire, smooth surface.

40. **costa width**: **0*** >72 µm; **1** <72 µm. There is a reduction trend in costa width from *Dicranum* and *Dicranoloma* to *Leucoloma* and *Sclerodontium.* Sections *Dicranoidea* and *Albescentia* are polymorphic.

41. **distal costal with substereids**: **0*** distal costa with stereid bands; **1** distal costa

with substereids. Two species groups are characterised by having substereid development in the distal costa, the *fuscifolium* and *pervirde* species groups.

42. **distal acumen**: **0*** subtubulose; **1** flat or terete. The plesiomorphic state is leaves with the distal acumen subtubulose. The apomorphic state, flattened or terete acumen, is associated with the thickening of the distal laminal layers.

43. **apex shape: 0*** long, gradually acuminate; **1** obtuse, rounded, or truncate. Based on outgroup comparison the long, acuminate state is considered plesiomorphic.

44. **leaf strongly contorted: 0*** absent; **1** present. Stems with strongly contorted leaves are considered apomorphic. This character does not consider those taxa with spirally twisted apices, but is limited to contorted leaves.

45. **leaves caducous**: **0*** absent; **1** present. Section *Subvittata* is characterised by species with caducous leaves. This condition is due to fragile alar cells.

46. **male plants**: **0*** monomorphic; **1** heteromorphic. The hormonal reduction of size in male plants is considered apomorphic. Both *Dicranum* and *Dicranoloma* have taxa that produce dwarfed males on the stem tomentum or female leaves (Nyholm 1954, Norris and Koponen 1989). Size reduction of males within the Dicranaceae has been attributed to chemical inhibition by the female plants (Loveland 1956).

SPOROPHYTIC CHARACTERS

47. **seta transverse section**: **0*** outer layers (3-4) thick-walled, tinged; **1** single outer layer thick-walled, colored; **2** outer layers, 2 thick-walled, tinged. In subgenus *Leucoloma*, the seta section shows a differentially thickened outer wall of the epidermal cells. This wall thickening is distinct from the remaining taxa that have 2-4 layers with thickened colored walls. *Sclerodontium* is unique within the taxa examined by having the 2 outer layers thickened.

48. **seta color**: **0*** red, translucent; **1** tan, opaque. The color of the seta is a character that is informative at the subgeneric level of analysis. The opaque, tan (or orange-tan) seta of subgenus *Leucoloma* is distinct from the "cranberry" red

setae that appear translucent of the remaining taxa.

49. **seta**: **0*** long, > 4 mm; **1** short, < 3 mm. A short seta is a synapomorphy for the sections of subgenus *Leucoloma*. Within *Dicranum* (*sensu* Norris and Koponen 1990) there are scattered species with reduced setae, yet they are not < 3 mm long. Along with the other distinctive seta characters, subgenus *Leucoloma* suggests a separate line of reduction evolution.

50. **capsule shape**: **0*** N/A; **1** long cylindric; **2** short cylindric, ovoid to globose. Within the erect capsules, two states are recognised: the long cylindric capsule (5-8:1), versus short (1.5-5.0:1). The capsules of *Leucoloma* range from 1-4 mm long and 0.5 - 1.0 mm wide. The ovoid capsules are the broadest with the long cylindric capsules the most slender.

51. **capsule orientation**: **0*** arcuate; **1** erect. All of the outgroup taxa, *Dicranum*, *Dicranoloma*, and *Sclerodontium*, have arcuate capsules. Erect capsules are considered a synapomorphy for the ingroup.

52. **asymmetric capsule base**: **0*** absent; **1** present. Within section *Dicranoidea*, section *Albescentia*, and the *fuscifolium* species group, there are species with slightly asymmetric capsules bases. This character is considered distinct from the arcuate capsules of the outgroup taxa. Most species of *Leucoloma* have symmetric capsules.

53. **stomates**: **0*** present; **1** absent. *Leucoloma* and *Sclerodontium* lack the development of stomates. The loss of stomates is a reductionary trend in mosses, that occurs in separate lineages within the Dicranaceae (e.g., Campylopoideae, Frahm 1991). *Orthodicranum* has stomates that are reduced to a single row at the base of the capsule (Peterson 1979).

54. **exothecial cells in transverse section**: **0*** cells with longest axis perpendicular to the capsule wall, epidermal layer thick; **1**cells with longest axis parallel to the capsule wall, epidermal layer reduced; **2** cells more or less "isodiametric", lacking a pronounced orientation to the capsule wall. In transverse section the longest axis of the cells is either perpendicular to the capsule wall

(plesiomorphic) or parallel to the capsule wall (apomorphic). In addition, the apomorphic condition exhibits a reduced capsule wall thickness. Capsules with the exothecial cells perpendicular to the capsule wall are found in a few species within section *Dicranoidea* of subgenus *Syncratodictyon* and all of the capsules examined of subg. *Leucoloma*, *Dicranoloma* and *Dicranum*. *Sclerodontium* and species of the *sprengelianum* species group have large, more or less quadrate exothecial cells.

55. **peristome teeth split: 0*** to 1/2 or just distally; **1** to 1/2-3/4 of tooth or more. The peristome teeth of *Leucoloma* are divided below the mid tooth. Occasionally the teeth are trifid. The outgroup taxa have peristome teeth divided in the distal portion.

56. **peristome teeth basal width: 0*** broad, 96-120 µm; **1** narrow, 35-96 µm. *Leucoloma* is characterised by peristome with a reduced width in comparison to the outgroup taxa.

57. **peristome: PPL surface: 0*** pitted striations lacking just below apex; **1** vertically pitted striate to just below apex. The peristome ornamentation of the outer surface (PPL) is dicranoid in most of the taxa: basal portion pitted striate, the mid region with obliquely or vertically striate, and with the distal portion papillose. In *Dicranum*, *Dicranoloma*, and a few species of *Leucoloma* the pitted striolate portion extends to the mid tooth. Otherwise in *Leucoloma* the vertically pitted striations are restricted to the lower portion of the tooth and are less strongly developed, or smooth or papillose. In *Sclerodontium* the pitted striolate surface extends well above mid-tooth with nonpapillose, weakly striate or smooth apices.

58. **calyptra: 0*** cucullate, entire; **1** mitrate, lobate. (Although a gametophytic character, it is placed with the sporophyte characters because of its association with the capsule.) A long cucullate calyptra that covers most of the capsule is plesiomorphic for the examined taxa. Subgenus *Leucoloma* has mitrate calyptrae that are lobate. These calyptrae are reduced in size and cover the

operculum and upper portion of the capsule. Mitrate calyptrae are rare in subfamily Dicranoideae, and has been used as a diagnostic character for subfamily Mesotoideae (Allen 1987).

59. **annulus: 0*** present; **1** absent. The lack of an annulus is considered the apomorphic state, found in *Leucoloma* and *Sclerodontium*.

60. **peristome: 0*** well developed; **1** reduced. The plesiomorphic peristome is well developed with a length of 0.5-0.6 mm long. There is an reductionary trend within subgenus *Syncratodictyon* to produce peristomes 1.5-0.4 mm long.

Results

A single most parsimonious tree with a length of 146 steps resulted from the performed searches, heuristic and branch and bound (Fig.III.1). The consistency of the data matrix to the tree topology is shown in the following indices: CI=0.74; RI=0.74; RC=0.55. The character state distribution includes synapomorphies without homoplasy (CI=1), and those with homoplasy or reversals (CI<1). The characters presented on the most parsimonious tree are restricted to those that change unambiguously on the tree, with the exception of character 54 (see discussion below). Decay indices (DI) show the relative robustness of the individual clades (Fig.III.2).

The global parsimony of the ingroup - outgroup indicates that *Leucoloma* and *Sclerodontium* form a clade based on the following homologous synapomorphies (CI=1): lack of stem tomentum (4), laminal cells of 3 distinct types (6), abaxial surface of laminal cells papillose (12), basal cell width reduced (22), basal cells abaxial-adaxial cell wall reduced (24), costa width < 72 µm (40), stomates absent (53), and annulus absent (59). Additional homoplasious synapomorphies, excluding reversals, are papillae development over lumen (15) and pluripapillose cells (18). Synapomorphies with subsequent reversals include stem central strand absent (3), leaves with sharply differentiated laminal cells (8), abaxial costa smooth (39), and upper margin serrate (32). This clade is well supported, having a decay index of greater than 8, and a bootstrap value of 100%. Based on these shared synapomorphies, *Sclerodontium* and *Leucoloma* form a strong clade, with *Dicranum* and *Dicranoloma* as more distant outgroup taxa.

The topology of the tree supports *Leucoloma* as a monophyletic taxon. The ingroup is defined by 4 homologous synapomorphies: short or long cylindric capsules (50), erect capsules (51), peristome that are split 1/2 or 3/4 of the tooth (55), and narrow peristome bases (56). The decay index for this clade is 2, with less than 50% bootstrap support.

Sclerodontium is defined by 5 autapomorphies with a CI=1: creeping growth form (1), hair point (38), seta transverse section (47), transverse section of exothecial cells (54), distal peristome ornamentation (57). Ten homoplasious synapomorphies occur in *Sclerodontium* that also develop within *Leucoloma*. These include irregular or sinuose lumina (10), oblate cells (11), adaxial papillae (14), unipapillose cells (16), stellate papillae (17), apically hooked papillae (19), prominent abaxial papillae (20), bulging longitudinally thickened alar cells (26), hyaline margin not reaching the alar region (31), and obtuse apices (43). The complexity of the cell architecture and ornamentation prompted the detailed analysis to evaluate these characters as potential homologues for *Leucoloma* and *Sclerodontium*. The results indicate that *Sclerodontium* is a distinct monophyletic taxon, despite the high number of homoplasies that also occur in *Leucoloma*.

The topology of the cladogram indicates two primary clades within *Leucoloma*. The first clade includes five taxa: section *Subvittata*, section *Leucoloma*, section *Obscura*, subgenus *Sphenodictyon*, and section *Dichelymoidea* (Fig. III.1). This robust clade has a decay index of 5 and a bootstrap value of 94%. Six synapomorphies define this clade: downwardly spreading or pendent growth form (1), stem elliptic in transverse section (2), transverse section of the seta with a single epidermal wall thickened (47), seta tan and opaque (48), seta short (49), and mitrate calyptra (58).

The second clade is defined by a single character: differentiated juxtacostal bands have a gradual transition into basal and interior cells (8). Although the CI<1 for this multistate character, the character state (1) is unique within the tree. A change of this character state (1 to 2) occurs within a distal taxon of the lineage (Fig.III.1). The decay index is 1, indicating a less robust clade. The heterogeneity of the taxa in this clade is reflected in the lack of synapomorphies to define it. The character 54: 1 - epidermal cells of capsule wall with a parallel orientation is polymorphic for section *Dicranoidea* and monomorphic for the remainder of the taxa in the clade. It is considered as an ambiguous character by MacClade, yet plotted by PAUP at this node. The reduction of the capsule wall and orientation of the epidermal cells is considered here as an important character. Thus although the basal taxon is polymorphic for the character, the ancestral state indicates the origin of the novel character state. The CI value for the synapomorphy is 1.

This latter clade consists of three major lineages that include 9 taxa: 1) section *Dicranoidea*; 2) section *Albescentia* with two related taxa *sprengelianum* and section *Caespitulosa*, and 3) section *Holomitrioidea* and species groups *tenerum*, *fuscifolium*, *perviride*, and *tortellum* (Fig.III.1). The basal lineage of this clade is Section *Dicranoidea* with the latter two groups forming a separate lineage. This latter clade has a decay index of 2 and a bootstrap of 65%. It is supported by 4 characters: a reduced alar region (27), alar cells predominantly elongate (30), transverse section of exothecial cells with cells parallel to capsule wall (54), and peristome teeth length reduced (60). The second lineage, including sections *Albescentia* and *Caespitulosa*, has a decay index of 1 and is defined by 3 synapomorphies: unipapillose cells (16), pluripapillose cells absent (reversal: 18), and the abaxial costa serrulate (39). The third lineage is more heterogeneous consisting of 5 taxa, and is defined by flat or terete acumina (42). This clade consists of 3 lineages: 1) section *Holomitrioidea* and the *tortellum* species group that share a unique synapomorphy - an apiculate apex (37), plus two homoplasious characters - contorted leaf habit (44) and lumen shape sinuose or irregular (10); 2) a clade including the *perviride* and *fuscifolium* species groups based on the synapomorphy - serrations from short laminal cells (34); 3) and the *tenerum* species group defined by - papillae development over inter-lumen wall (15). The topology of the most parsimonious tree indicates the heterogeneity of *Leucoloma* with one robust, monophyletic internal clade (DI=5, bootstrap 94%) and another less robust, clade (DI=1).

Implications of the Phylogenetic analysis

The systematic implications of the analysis are: 1) *Leucoloma* is a monophyletic taxon; 2) *Sclerodontium* is the sister group to *Leucoloma* based on the defined outgroup, and a distinct monophyletic taxon; 3) The results of the infrageneric analysis do not support the division of*Leucoloma* into 3 subgenera circumscribed by Renauld (1909): *Syncratodictyon*, *Taeniodictyon* (= subgenus *Leucoloma*), and *Sphenodictyon*. Rather the analysis indicates that subgenus *Sphenodictyon* forms a lineage within the subgenus *Leucoloma*; 4) Section *Dichelymoidea* is transferred from subgenus *Syncratodictyon* to subgenus *Leucoloma*, and forms a sister clade to "subgenus" *Sphenodictyon*. 5) Subgenus *Syncratodictyon* is circumscribed as a heterogeneous taxon with 3 distinct clades. The topology of the most parsimonious tree indicates that the former concept of section *Dicranoidea* (including *tenerum*, *fuscifolium* and *perviride* species groups) is paraphyletic. As well, section *Caespitulosa* (including the *tortellum* species group) is polyphyletic (Fig.III.1); 6) The retention of section *Holomitrioidea* within *Leucoloma* is confirmed by the topology of the tree, and supported by a progression of synapomorphies through the related taxa in subgenus *Syncratodictyon*.

Constraint analyses were applied to the data matrix to test the previous hypotheses of phylogenetic relationship. The results showed the following: 1) To maintain subgenus *Sphenodictyon* as a separate lineage from sections *Subvittata*, *Leucoloma*, *Obscura*, and *Dichelymoidea* within *Leucoloma*, the shortest tree length was 5 steps longer with 4 MP (most parsimonious) trees found. It remained sister to the sections of subgenus *Leucoloma*. 2) To maintain section *Dichelymoidea* within subgenus *Syncratodictyon* the shortest tree was 9 steps longer than the MP tree, with 4 MP trees found. 3) If Renauld's concept of section *Caespitulosa* is tested, the *tortellum* species group constrained with section *Caespitulosa*, the results produced 8 MP trees 3 steps longer than the MP tree. 4) If section *Holomitrioidea* is considered as a distinct genus from *Leucoloma* the cost would be a tree length 8 steps longer than the MP tree, and two equally parsimonious trees. The results of the constraint analyses show that the current most parsimonious tree does support the monophyly of *Leucoloma* and a sister group relationship of *Sclerodontium*. The infrageneric relationships of taxa examined suggest a new classification. These results form the basis for a reclassification of *Leucoloma* (see Classification below).

Character evolution

The evolutionary trends within *Leucoloma* include reduction and amplification. The two major clades of *Leucoloma* exhibit independent trends in the gametophyte and sporophyte. The diversity of character expression within *Leucoloma* provides a useful data set to examine adaptive modes to increased epiphytism in mosses.

From the topology of the most parsimonious tree, *Dicranum* and *Dicranoloma* are designated as the more distant outgroup taxa. A number of reduction trends are evident from these plesiomorphic genera to the more apomorphic genera, *Leucoloma* and *Sclerodontium*. These include the losses of stomata, annuli, and stem tomentum, and the general decrease of robustness that is expressed in cell width of the basal, juxtacostal and marginal cells, the reduction of thickness of the abaxial and adaxial cell wall, and costa width. Amplification trends include leaf cell differentiation into 3 cell types and elaboration of papillae development.

SPOROPHYTIC TRENDS

Vitt (1981) reviewed sporophytic adaptations by mosses that are correlated with increased xerophytism and epiphytism. These adaptations in *Leucoloma* are as follows: 1) Within the epiphytic subgenus *Leucoloma* the seta is shortened to produce immersed or emergent capsules. Unlike the reduction trend in *Orthotrichum* (Vitt 1981), these capsules have well developed peristomes. Under dry conditions the peristome bases are often recurved along the mouth of capsule with the apices curved back into the capsule, presumably to aid in spore dispersal (Fig.II.6.d). The peristome of subgenus *Leucoloma* is typically dicranoid with the adaxial trabeculae more pronounced than the abaxial trabeculae.

The capsule shape is from short cylindric to ovoid or globose. Within subgenus *Syncratodictyon* there is a reduction trend in capsule length from long to short cylindric, that is paralleled by reduction of peristome length (Fig.II.8 c,b,f). The reduced peristome differs in that the abaxial trabeculae are more pronounced than or equally pronounced as the adaxial trabeculae. A single example of a fused basal layers of OPL-PPL-IPL thickening (4:2:3-4), representing a *Seligeria*-type peristome (Edwards 1979), was found among the derived taxa of section *Caespitulosa* (Fig.II.9). Rarely the OPL layer is thickened within the haplolepideous lineage (Edwards 1979), although it may prove to be more common as species revisions are completed.

Reduction of the peristome coincides with the evolution of species from forest floor habitats (lowland and montane saxicolous, terrestrial, exposed roots, tree buttresses, tree trunk bases) to more exposed saxicolous or epiphytic habitats with higher light intensity and greater variability of temperature and humidity (e.g., tree trunks, branches, or decaying wood habitats in elfin forests).

In *Leucoloma* reduction of the peristome does not correspond to the reduction of the rostrum. Species with long rostrate opercula do not necessarily have the long peristome teeth, as observed for *Dicranum* and *Dicranoloma* (Norris and Koponen 1989). For example within subgenus *Syncratodictyon*, *L. chlorophyllum* has a long rostrate operculum, yet reduced peristome teeth (0.15 mm long), while within subgenus *Leucoloma*, *L. sanctae-mariae* has a conic operculum, yet has long peristome teeth (0.60 mm long). Generally *Leucoloma* has a long rostrate operculum that is erect or oblique. The reduction to a conic operculum is the exception within the genus (e.g., *L. brevioperculatum*). Therefore reduction of the peristome versus operculum is considered independent.

The transverse section of the capsule wall also indicates a reduction trend within *Leucoloma* (Fig.II.7.d,h). The orientation of the long axis of the exothecial cells in transverse section is either perpendicular or parallel to the capsule wall (character 54). Capsules with cells perpendicular to the capsule wall form a layer up to twice the width of those with parallel cells. Both the exserted capsules of *Dicranum*, *Dicranoloma*, and section *Dicranoidea* and immersed capsules of subgenus *Leucoloma* have epidermal cells with a perpendicular orientation. Thus this character state is not correlated with immersed versus exserted capsules. The perpendicular orientation is correlated with the ovoid capsule shape within *Leucoloma*. The more slender, cylindric capsules have parallel exothecial cells with a thickened outer wall to protect the spores within the capsule from periodic drying (e.g., section *Albescentia*, section *Caespitulosa*, section *Holomitrioidea*). Section *Dicranoidea* is polymorphic for this character. The reduction of the capsule wall, with respect to exothecial cell orientation, is restricted to subgenus *Syncratodiction*. There is some reduction of cell width in capsules of subgenus *Leucoloma*, but the perpendicular cell orientation is retained.

There is a reduction of the thickened outer cortical layers in the seta in subgenus *Leucoloma*. The seta transverse section shows the outermost cortical layer with only the outer wall slightly thickened, whereas there are one to several layers of thickened cells with reduced lumen in *Sclerodontium*, *Dicranum*, *Dicranoloma*, and subgenus *Syncratodictyon*. The outermost layer has a strong asymmetric thickening of the secondary wall that results in a reduced, eccentric lumen (Fig.II.7c,g). This secondary thickened layer(s) provides strength to the elongate setae, which is not necessary for the immersed capsules (e.g., subgenus *Leucoloma*). Chemical stains for pectin and cellulose on the walls of *Campylopus flexuosus* differentiated primary, secondary, and "tertiary" layers (Frahm and Frey 1987). Frahm and Frey (1987) used the eccentric thickening of the secondary wall to explain the twisting of the setae of *Campylopus*, *Cynodontium*, *Campylostelium*, *Dicranella*, and *Dicranum*. Examination of additional genera in the subfamily Dicranoideae that also have a similar outer cortical layer consisting of cells with reduced lumina and secondary thickening include *Holomitrium*, and *Orthodicranum*. The reduced seta of *Dicranum braunii* (*sensu* Norris and Koponen 1989, 1990) lacks the strong secondary thickening and has a seta transverse section similar to subgenus *Leucoloma*. It is interesting to note that the setae with multilayered thickening are translucent, whereas the setae with only the outer wall thickened is opaque. Trends of sporophyte reduction have been noted within the subfamily Dicranoideae, as well. Within a broad concept of *Dicranum*, there is a trend for the sporophyte to be modified from an arcuate to erect capsule (e.g., *D.* subgenus *Pseudochorisodontium* - Gao and Cao 1992 and *Orthodicranum* - Peterson 1979). Eddy (1988) distinguished two groups within a broad concept of *Dicranoloma*: one group has short erect setae with erect ovoid-cylindric capsules, and stems with the lack of a central strand. The reduction to short setae and erect capsules occurs within the *Dicranum-Dicranoloma* complex (*D. blumei, D. braunii, D. brevisetum, D. geluense, D. leucophyllum*, and *D. rugifolium*). The reduction of seta length; erect, long cylindric to short cylindric or ovoid capsules; and the lack of a central strand in the more apomorphic taxa, are convergent trends within the *Dicranum - Dicranoloma* complex and *Leucoloma*. Another example of reduction within the *Dicranum* complex is the monotypic genus *Cryptodicranum* from the Solomon Islands, based on the reduced sporophyte and smooth peristome teeth (Bartram 1938). Aikyama (1989), Eddy (1988), and Walther (1983) recognized this taxon at the generic rank, while Norris and Koponen (1989) retained it within the concept of *Dicranum*; whereas Tan and Koponen (1983) considered it closely related to *Dicranoloma brevisetum*, and thus classified it as a *Dicranoloma*. The gametophyte of *Cryptodicranum armittii* superficially resembles the *fuscifolium* species group of *Leucoloma*, having a broad elliptic leaf base and a long setaceous apex. It has an immersed capsule, as in subgenus *Leucoloma*. The robust size of the plant, the homogeneous smooth, laminal cells, tomentose stem, dwarf males on the tomentum, and a broad costae with abaxial teeth are characters that exclude it from *Leucoloma*.

GAMETOPHYTIC TRENDS

The calyptra is a gametophytic structure closely associated with the sporophyte. The mitrate, lobate calyptrae of subgenus *Leucoloma* are restricted to the distal portion of the capsule, and are reduced in size compared with the cucullate calyptrae of subgenus *Syncratodictyon*. Allen (1987) proposed a monotypic subfamily, Mesotoideae, based on characters he considered unique within the Dicranaceae. These included: "immersed capsules, mitriform calyptrae, conic opercula, rhizoids associated with leaf cells, massive endosporic protonemata, and reduced peristome teeth in which the dorsal trabeculae are more heavily thickened than the ventral trabeculae". With the exception of massive endosporic protonemata, all of these character states occur within *Leucoloma*. However, rhizoids develop from alar cells in *Leucoloma*, rather than from laminal cells. The development of rhizoids from the base of the costa is not uncommon within the Dicranaceae (Frahm 1991). Therefore, the justification for a new subfamily may not be warranted. Preliminary, phylogenetic analyses suggest that *Mesotus* is more closely related to *Holomitrium* than to *Sclerodontium* or *Leucoloma*.

The growth form of subgenus *Leucoloma* exhibits an evolutionary trend from erect to pendent stems. This character is linked to an increasingly epiphytic habitat (i.e., from tree or sapling trunks and buttresses to lianas and fine branches). Stems may initially grow erect or perpendicular to their substrate, but with increased growth the stems typically grow in a downward, outspreading or pendent direction. In addition to the pendent stems, species of section *Dichelymoidea* have monopodial branches commonly perpendicular to the supporting axis. These branches are similar to the monopodial branches of pleurocarpous taxa (e.g., *Meteorium*). Branching patterns in mosses are discussed in detail in Chapter IV (La Farge-England 1996).

The diversity of papillae formation in *Leucoloma* is extensive: unipapillose, pluripapillose, uniseriate, biseriate, or with a scattered distribution. The papillae also have a wide range of variation in developmental patterns (i.e., equal on both surfaces, differentially developed on both surfaces, or lacking on one surface). Without ordering the papillae characters, the most derived taxa have pluripapillose cells, well developed on both surfaces. The elaborate and diverse papillae in *Leucoloma* are interpreted here as adaptations to a more variable epiphytic habitat. The taxa of section *Dicranoidea*, section *Albescentia*, and section *Subvittata* commonly occur on rocks, fallen logs, exposed roots, the base of tree trunks and on buttresses within the montane rainforests. The more derived taxa section *Dichelymoidea*, section *Holomitrioidea*, and subgenus *Sphenodictyon* occur in elfin forests and exposed upper montane ridge forests where periodic drying by the tropical sun is common. The papillae may provide a natural protection to the living protoplast, as well as an irregular surface for rapid water uptake or a densely papillose surface that may trap air for gas exchange during photosynthesis (Proctor 1979). This series of characters reflects an evolutionary trend within *Leucoloma* to move off the forest floor, rocks, or logs to the epiphytic habitat, where periodic drying occurs. Within section *Holomitrioidea* and the *tenerum* species group, an atypical papillae thickening has developed. A progression of papillae development can be seen through the species of the *perviride* and *tortellum* groups, in which the papillae form indistinctly over the cell wall in a few taxa, to the well developed pattern in most of the species of section *Holomitrioidea* and the *tenerum* group. The homoplasious nature of this type of papillae development is confirmed by its occurrence in *Mesotus celatus* (Dicranaceae) and *Racomitrium aquaticum*, *R. lanuginosum*, and *Grimmia anomala* (Grimmiaceae). The development of papillae is a common homoplasy in mosses, yet for any given level of analysis, the papillae type may provide a synapomorphy, as is so for section *Holomitrioidea*.

Leucoloma subgenus *Leucoloma* has elaborate papillae development. The basal sections, *Subvittata* and *Leucoloma*, have pluripapillose cells restricted to the abaxial surface. Section *Dichelymoidea* has unipapillae on both surfaces, but uneven development. Section *Obscura* and subgenus *Sphenodictyon* develop dense, obscure papillae evenly on both surfaces. The evolution of specialised papillae is also apparent in subgenus *Syncratodictyon*, as well as *Sclerodontium*.

The trend of an enlarged alar region occurs within subgenus *Leucoloma*. Change is progressive in the orientation of the alar cells with respect to the basal cells, from vertical to a sharply oblique orientation. In its extreme, the alar region is convolute around the stem (e.g.,. *L. dichelymoides* and *L. fontinaloides*). In addition, the alar region is scalariform or with strongly, longitudinally thickened cells.

The evolutionary trends expressed in *Leucoloma* subgenus *Leucoloma* can be summarized as: 1) seta reduction; 2) papillae elaboration; 3) alar region enlargement; and 4) calyptra reduction. These are adaptations to the epiphytic habitat, where the diurnal climatic regimes can oscillate between high humidity near saturation in elfin forests to periodic drying in intense tropical sun. The evolutionary trends within subgenus *Syncratodictyon* can be summarised by: 1) two distinct lineages for papillae development: a) unipapillose or uniseriate papillae that are prominent, hooked apically, or stellate and develop over the cell lumen; and b) pluripapillose to pluripapillose biseriate that, in specialised cases, develop over the cell wall; 2) adaxial and abaxial papillae equally developed; 3) restriction of the hyaline margin; 4) reduction in the capsule wall thickness, with the long axis of the epidermal cells parallel to capsule wall; 5) peristome reduction; 6) a flattening or thickening of the distal acumen; 7) the upper margin with teeth from laminal cells or entire; and 8) the contorted leaf habit opposed to the flexuose or falcate-secund habit.

In the present analysis, the arcuate capsule of *Sclerodontium* is a plesiomorphic character, shared with *Dicranum* and *Dicranoloma*. The sporophytic apomorphies that distinguish *Sclerodontium* are: the seta transverse section, the broad peristome teeth with the PPL ornamentation pitted striolate from the base to just below apex; and the peristome bifid only in the distal portion (Fig.III.3). The gametophytic characters show a strong convergence with section *Albescentia*, yet the cell architecture remains distinct. An examination of juvenile leaves from *Sclerodontium* shows that the "hyaline window" basal cell formation is present, with the shorter laminal cells near the margins. Within *Leucoloma* the cell development in the juvenile leaves shows an early lateral arrangement, with the outermost cells longer than the inner. These data support two distinct lineages.

Distance Matrix

A patristic distance matrix provides a comparison of pairwise relationship between the taxa, based on branch length differences. The distances calculated by PAUP do not include multistate characters. By using *Dicranum* as the basal plesiomorphic taxon of the analysis, one can estimate a relative, evolutionary relationship of advancement for the remaining taxa (Fig.III.4). *Dicranoloma* has the shortest branch length with a patristic distance of 4, indicating its close patristic relationship to *Dicranum*. *Sclerodontium* has a long branch with a patristic distance of

21, that shows the relatively derived status of the taxon.

Leucoloma subgenus *Syncratodictyon* has the broadest range of patristic values, 16 - 30. Section *Dicranoidea* is the patristically closest taxon to *Dicranum*, with the exception of *Dicranoloma*. Section *Dicranoidea* also shows the highest number of polymorphic characters, suggesting its transitory position between the basal outgroup taxa and the more derived taxa within subgenus *Syncratodictyon*. Section *Holomitrioidea* and the *tortellum* species group are the most patristically advanced taxa of the subgenus. Subgenus *Leucoloma* has taxa with patristic distances between 20 - 24, with section *Dichelymoidea* the most derived taxon. A similar amount of evolution has occurred in the 2 major lineages of *Leucoloma* in different directions, as well as in *Sclerodontium*. The long branch of *Sclerodontium*, with the high number of homoplasious characters, is an example of the morphological limitations of mosses to evolve unique characters or charcaters states in distinct lineages.

The phylogenetic analysis of *Leucoloma* with three outgroup taxa supports *Sclerodontium* as the hypothetical sister group to *Leucoloma*. The independent lineage of *Sclerodontium* shares a high number of homoplasies with *Leucoloma* that suggests an equivalent amount of evolution has occurred based on patristic distances from the basal taxon *Dicranum*. The evolution of *Sclerodontium* may have suffered a number of extinctions that has resulted in the relatively derived clade reduced to two species. The lack of fossil evidence prevents a better interpretation based on the available data. *Dicranum* and *Dicranoloma* remain more distantly related to *Leucoloma* and show a close relationship. The distinction or lack of distinction at the generic level is the subject of a continuing study by Hans Kruijer at the Rijksherbarium, Leiden. The infrageneric relationships of *Leucoloma* have been reinterpreted and indicate two distinct clades that have diverged with similar amounts of evolution.

The Infrageneric Classification of *Leucoloma*

Based on the phylogenetic analysis of *Leucoloma*, a revised infrageneric classification of *Leucoloma* is proposed (Fig.III.5). The salient differences from

Renauld's 1909 classification include: 1) *Leucoloma* consists of two major clades: subgenus *Leucoloma* and subgenus *Syncratodictyon*. The former subgenus *Sphenodictyon* is ranked as a section within subgenus *Leucoloma*, as Renauld (1898) had originally ranked the taxon, section *Attenuata*; 2) Section *Dichelymoidea* is transferred from subgenus *Syncratodictyon* to subgenus *Leucoloma*; 3) Section *Caespitulosa* includes 3 subsections: *Albescentia*, *Caespitulosa* and a new subsection *Seriata*. The former two subsections have previously been treated at this rank (Renauld 1898); 4) Section *Holomitrioidea* is greatly expanded to include five new taxa at the subsection and series ranks, with the original concept of *Holomitrioidea* reduced to a series rank; and 5) *Sclerodontium* is retained at the generic rank based primarily on its distinctive sporophytic characters. The results of the phylogenetic analysis is a new classification (Fig.III.5).

A review of the major infrageneric classifications is in Table III.3. For a more detailed discussion of the historical development of the genus see Chapter II. The new infrageneric classification is presented in Table III.4. The morphological heterogeneity of subgenus *Syncratodictyon* is reflected by the number of taxa included. The homogeneity of each terminal taxon is high, with the exception of section *Dicranoidea*. Section *Dicranoidea* has a high number (11) of polymorphic characters that are shared with the outgroup (symplesiomorphies). As stated above this section is defined by the synapomorphies of the genus, subgenus, and two reversals and a homoplasious synapomorphy. Therefore the taxon remains a weakly defined group that needs further clarification. It is expected that a species level phylogeny of the genus will clarify this polymorphic section. Other types of data may provide new insights to infrageneric relationships (e.g., molecular), especially of subgenus *Syncratodictyon*. Two clades within the analysis that are strongly supported and unlikely to be modified are: 1) the *Sclerodontium* - *Leucoloma* clade, which is removed from *Dicranum* and *Dicranoloma*; and 2) Subgenus *Leucoloma*, that forms a robust clade distinguished from subgenus *Syncratodictyon*.

A synoptic key is presented below as a summary of the salient characters defining the infrageneric taxa of *Leucoloma*. The synapomorphies, defined by the phylogenetic analysis of the infrageneric taxa, are designated in italics. For typification and a Latin diagnosis of new taxa see Taxonomic Treatment, Chapter II. The classification and enumeration of the currently accepted species of *Leucoloma* is presented in Table III.5.

A SYNOPSIS OF THE INFRAGENERIC TAXA OF *LEUCOLOMA* BRID.

1. Leaves with differentiated alar cells *flat*, longitudinally thick-walled; juxtacostal cells with a sharp transition to the basal and interior cells; *seta shoridt, stout, tan to red-brown, opaque, < 3 mm*; *capsules immersed to emergent or shortly exserted*; transverse section of the capsule with long axis of the epidermal cells perpendicular to the capsule wall; transverse section of seta *with single layer of thick-walled, outer cortical cells*; *calyptra mitrate*; stem transverse section *elliptic* (or flattened); stems in loose tufts or gregarious, erect to *downwardly outspreading or pendent*, without central strand 2

1. Leaves with differentiated alar cells inflated and thin-walled or bulging with equally thickened or longitudinally thick-walled; juxtacostal bands with a *gradual transition* to the basal and interior cells; seta long, slender, red, translucent, > 4 mm long; capsules long exserted; transverse section of capsule with long axis of the epidermal cells perpendicular or *parallel* to the capsule wall; transverse section of seta with several layers of outer cortical cells thick-walled; calyptra cucullate; stem transverse section round; stems in dense to loose, mostly erect tufts, with or without central strand . . . 6

SUBGENUS *LEUCOLOMA*

2. Proximal stem lacking leaves; *leaves caducous, with 1-4 rows of isodiametric cells* between the alar region and basal cell; alar cells vertically oriented toward basal cells; alar cells predominantly quadrate . . . . **Section *Subvittata***

2. Proximal stem with leaves; leaves not distinctly caducous, with 1 row of or lacking

isodiametric cells between the alar region and basal cells; alar cells obliquely oriented toward basal cells; alar cells predominantly rectangular to elongate 3

3. Papillae not developed equally on adaxial and abaxial surface of differentiated juxtacostal cells, adaxial surface smooth with a few papillae restricted to the distal lamina along the costa . . . . **Section *Leucoloma***

3. Papillae developed equally on adaxial and abaxial surface of differentiated juxtacostal cells, or with scattered, less prominent, adaxial papillae and prominent abaxial papillae 4

4. Surface of differentiated juxtacostal cells unipapillose, with *scattered adaxial papillae and prominent abaxial papillae*; juxtacostal bands not opaque, *corrugated* . . . . **Section *Dichelymoidea***

4. Surface of differentiated juxtacostal cells pluripapillose, with papillae dense, *equally developed* on adaxial and abaxial surface of differentiated juxtacostal cells; juxtacostal bands *opaque, rugose* or smooth 5

5. Juxtacostal bands *parallel* to costa, smooth; alar region small to intermediate; alar cells obliquely orientation to the basal cells . . . . **Section *Obscura***

5. Juxtacostal bands *tapered* toward the costa, smooth or rugose; alar region intermediate to *enlarged*; alar cells with a *strongly oblique* orientation to the basal cells . . . . **Section *Attenuata***

SUBGENUS *SYNCRATODICTYON*

6. Leaves with upper margin with serrations from the marginal cells; costa with abaxial teeth; laminal cells with *one to several isodiametric transitional cells* between the elongate basal cells and differentiated alar cells; costa with abaxial teeth; alar region intermediate (10-19 cells wide); peristome teeth 0.5-0.6 mm long; transverse section of capsule with long axis of the exothecial cells perpendicular or parallel to

capsule wall . . . . **Section *Dicranoidea***

6. Leaves with upper margin serrulate or entire, or *serrate from short laminal cells*; costa with abaxial surface toothed, serrulate or smooth; laminal cells lacking isodiametric transitional cells between the elongate basal cells and differentiated alar cells; *alar region reduced* (3-9 cells wide); *peristome teeth reduced 0.2-0.4 mm*; transverse section of capsule with long axis of the *exothecial cells parallel* or to capsule wall 7

7. Distal acumen subtubulose; distal cells *unipapillose or uniseriate*ly *pluripapillose* on abaxial surface or smooth over lumen; distal *papillae commonly hooked* toward apex, adaxial papillae scattered long upper costa, few if any 8

7. Distal acumen *flattened or terete*; distal cells rarely unipapillose or, biseriately pluripapillose with equally papillose on both surfaces, scattered or over lumen; distal papillae low, dense, not hooked toward apex 10

8. Abaxial laminal cells pluripapillose, *distinctly uniseriate*; juxtacostal cells with *irregular or sinuose* walls; distal papillae not hooked toward apex

. . . . **subsection *Seriata***

8. Abaxial distal laminal cells unipapillose; juxtacostal cells more or less quadrate or rectangular; distal *papillae hooked* toward apex 9

9. Leaves *contorted*; *papillae formed in pairs*, the distal end of one cell and the proximal end of the cell above it in surface view; hyaline margin not undulate, *restricted to the lower 1/2 - 2/3 of leaf*; abaxial papillae multifid and low; *basal cells short (<3:1)* . . . . **subsection *Caespitulosa***

9. Leaves falcate secund or flexuose; papillae centered over lumen in surface view, not forming distinct pairs between cells; *hyaline margin undulate*, extending to apex; abaxial papillae stellate and prominent; basal cells long (>3:1) **subsection *Albescentia***

10. Dense abaxial and adaxial *papillae biseriate* at cell margins, in transverse section with a distinctive "depression" or lack of thickening over cell lumen
. . . . 11
10. Abaxial and adaxial papillae not biseriate, either scattered or over cell lumen in transverse section 12

11. Leaves flexuose to crispate, gradually tapered to a long acumen, not apiculate; lateral juxtacostal cells grading into basal and interior cells; hyaline margin extending to apex or ending just below . . . . subsection *Acuminata*
11. Leaves *slightly crispate or strongly contorted*, abruptly tapered or to a long acumen with *apiculate apices*; lateral *juxtacostal cells sharply defined* from smooth, linear basal and interior cells; hyaline margin restricted to the lower 1/2 - 2/3 of leaf
. . . . series ***Holomitrioidea***

12. Upper margins *crenulate*, formed by projecting papillae; alar cells thin walled inflated; apices often *apiculate* . . . . series ***Contorta***
12. Upper margins entire or serrate, formed from short laminal cells; apices serrate, not apiculate 13

13. Distal acumen, *terete*, stout, long or short; papillae evenly developed on abaxial and adaxial surfaces or laminal cells smooth; stem lacking central strand ***series Teretia***
13. Distal acumen somewhat flattened, long slender; papillae evenly developed on abaxial and adaxial surfaces; stem with central strand . . . . series ***Serrata***

The new classification provides a more refined assessment of subgenus *Syncratodictyon* and subgenus *Leucoloma*. Although the phylogenetic hypothesis of these infrageneric taxa does not have robust support as indicated by the bootstrap and decay indices, this does not preclude their recognition as formal taxa. The new classification provides a basis for examining the evolution of the genus at the sectional level in terms of its global distribution.

Leucoloma Brid., Bryol. Univer. 2: 218. 1827, ***nom. cons.***

Plants minute to robust, in tufts or gregarious stems. Stems non-tomentous, erect to pendent, with or without central strand; branching sympodial or monopodial, fragile or not. Rhizoids restricted to the base of branch or stem, rarely solitary at the base of leaf or on alar cells. Leaves ovate to lanceolate, elliptic-lanceolate or obovate, with 3 types of laminal cells: juxtacostal or upper cells, smooth tinged basal and interior cells, and extremely narrow hyaline marginal cells, the latter rarely lacking; leaf habit variable. Costa smooth or abaxially serrulate; in transverse section with abaxial and adaxial stereid bands in 1-5 layers, with a central layer of 4-6 (8) guide cells, often with bistratose rows of cells in transition to the laminal cells. Juxtacostal cells narrow, 5-12 µm wide, oblate, quadrate to elongate, sinuose, angular or rounded, often thick-walled, with abaxial papillae, simple to multifid, low to prominent, coalescent or distinct, uni- to pluripapillose, in distinct rows or not, rarely smooth, adaxial surface smooth, with scattered papillae or a few along the costa, or papillose as the abaxial surface. Basal and interior cells 5-12 µm wide, elongate to linear, porose or not, thick-walled, tinged, smooth. Alar cells longitudinally thick-walled to thin-walled, inflated, bulging or flat, decurrent or not, auriculate or not, red-brown to hyaline. Dioicous, rarely autoicous.

Sporophyte mono- or polysetous, immersed to exserted, acrocarpous. Seta short to long, tan and opaque or red and translucent, smooth, with central strand. Capsules *ovoid, short to long cylindric, erect,* symmetric to slightly asymmetric, stomata lacking, annulus undifferentiated. Operculum conic to rostrate, erect or oblique. Peristome teeth 0.2 - 0.6 mm long, *35-84 µm wide at base,* haplolepideous, 16, red brown, asymmetrical bifid teeth (rarely trifid), *split 1/2 to 3/4 to the base* or perforate, lanceolate, filiform or truncated distally; OPL:PPL:IPL - (4):2:3(4) basal cell pattern; *PPL pitted striate, papillose or smooth at base, mid portion distally papillose, transversely striate, or smooth*; IPL smooth or papillose. Calyptra mitrate or cucullate.

Spores small ,18-24 µm, unicellular, finely granulose.

Subgenus ***Syncratodictyon*** **Ren., Rev. Bryol. Lichénol. 28: 86. 1901.**

Plants erect to ascending, glaucous-green, green, black-green, or yellow-green. Stems mostly round in transverse section, with or without differentiated central strand. Leaves 0.6-20 mm long, minute to robust, obovate, elliptic lanceolate, ovate lanceolate, or lanceolate, flexuose, falcate secund, crispate or contorted. Juxtacostal bands with *a gradual transition into the basal cells* or with sharply defined upper-basal cells. Costa smooth or with low abaxial teeth, subpercurrent to excurrent; in transverse section guides 4-8, lateral doubling or not, abaxial and adaxial stereid bands in 1-5 layers. Alar cells inflated, thin-walled, hyaline, or evenly thickened walls red-brown, or bulging with slightly longitudinally thickened walls; alar region small to intermediate, 4-20 cells wide, 2-8 cells long. Dioicous.

Sporophyte mono - or polysetous, exserted, acrocarpus. Seta > 4 mm, long, slender, red, smooth, translucent; in transverse section with 2 or more thick-walled outer cortical cells. Capsules ovoid or short to long cylindric, symmetric or slightly asymmetric at base, tan, brown, to black-brown, long axis of the epidermal cells *in transverse section parallel* or perpendicular to capsule wall. Peristome teeth reduced or not, 0.15 - 0.6 mm long. Operculum rostrate, oblique. Calyptra cucullate, entire.

Section ***Dicranoidea*** Besch., Ann. Sci. Nat. Bot. sér. 6, 9: 315. 1878.

Leaves ovate-lanceolate, flexuose, upper margins *serrate*. Costa *abaxial surface toothed*. Juxtacostal cells papillose distally on adaxial and abaxial surface or smooth. Leaf base with *one to several isodiametric transitional cells* between the elongate basal cells and differentiated alar cells. Alar cells thin-walled, inflated or quadrate with cell walls evenly thickened; alar region intermediate, 10 - 19 cells wide. Capsules in transverse section with long axis of the exothecial cells perpendicular or parallel to capsule wall. Peristome well developed, 0.5 - 0.6 mm long.

Section *Caespitulosa* Besch., Ann. Sci. Nat. Bot. sér. 6, 9: 312. 1878.

Plants erect tufts. Leaves commonly falcate secund, contorted or spirally twisted distally, acumen caniculate or subtubulose. Costa abaxial surface *serrulate* or smooth. Juxtacostal cells with *abaxial surface unipapillose, or papillae uniseriate*, gradual transition into smooth basal cells or interior cells laterally. Alar cells thin-walled, inflated; alar region reduced, 3-9 cells wide. Sporophyte long exserted. Capsules cylindric to long cylindric, symmetric or slightly asymmetric at base. Peristome teeth reduced, 0.15 - 0.4 mm long.

Subsection *Seriata* La Farge-England ***subsect. nov.***

Stems without central strand. Leaves flexuose, falcate secund, unistratose, subtubulose. Juxtacostal cells with abaxial surface of *upper cells unipapillose or papillae uniseriate, papillae uniseriate basally*, abaxial papillae low, multifid, lumen shape *irregular or sinuose*. Costa abaxial surface *serrulate*. Alar cells thin-walled, inflated or with slightly longitudinally thickened walls. Capsules cylindric, erect, symmetric or slightly asymmetric at base.

Subsection *Caespitulosa* (Besch.) Ren., Prodr. Fl. Bryol. Madag. 72. 1898.

Stem with central strand. Leaves *contorted*, unistratose distally, caniculate, *hyaline margin restricted to lower 1/2-2/3* of leaf, not undulate. Juxtacostal cells with abaxial papillae, *unipapillose, paired papillae between the base of one cell and the top of the adjacent cell*, distally *hooked toward apex*. Basal cells *short to short elongate*, < *3:1*. Alar cells thin-walled, inflated.

Subsection *Albescentia* (Besch.) Ren., Prodr. Fl. Bryol. Madag. 77. 1898.

Stem with or without central strand. Leaves habit often falcate secund, with distally spirally twisted or contorted leaves, unistratose distally, caniculate, hyaline margin extending to the apex, commonly *undulate*. Juxtacostal cells not oblate, with unipapillose *abaxial, prominent, stellate papillae*, distal papillae *hooked toward apex*, papillae centered over cell lumen. Alar cells thin-walled, inflated. Capsules cylindric, erect, symmetric or slightly asymmetric at base.

Section *Holomitrioidea* (Ren.) Ren., Essai Leucoloma 28. 1909.

Leaves obovate, elliptic lanceolate, or lanceolate, flexose or crispate, or spirally twisted *distally, acumen flattened or terete*, upper margins entire or serrate. Costa abaxial surface smooth. Juxtacostal cells *commonly oblate*, papillose distally on adaxial and abaxial surface or smooth. Leaf base lacking rows of isodiametric cells between basal and alar cells. Alar cells thin-walled, inflated or bulging with longitudinally thickened walls; alar region *reduced, 3-9 cells wide*. Capsules in transverse section with long axis of the exothecial cells parallel to capsule wall. Peristome teeth *reduced*, < 0.4 mm long.

Subsection *Acuminata* LaFarge-Engalnd ***subsect. nov.***

Stems densely foliate; leaves long acuminate, flexuose to crispate distally. Juxtacostal cells with *papillae evenly developed on adaxial and abaxial surface, dense, developed over the interluminal cell wall in transverse section*. Transition from juxtacostal to basal interior or basal cells gradually thickened. Alar cells hyaline and thin-walled or red-brown, bulging, and with walls slightly thickened longitudinally.

Subsection *Serrata* La Farge-England ***subsect. nov.***

Stems densely leaved, central strand present or absent. Leaves distally *serrate from short laminal cells*, not hyaline, linear marginal cells. Juxtacostal cells with adaxial surface papillose or smooth.

Series *Teretia* La Farge-England ***ser. nov.***

Stems without central strand. Leaves elliptic lanceolate with stout, terete acumen; juxtacostal cells smooth, or papillose on abaxial and adaxial surface.

Series *Serrata*

Stems with *central strand.* Leaves basally elliptic with long slender, flattened, setaceous acumen. Juxtacostal cells distally, densely papillose on abaxial and adaxial surfaces.

Subsection *Holomitrioidea* Ren., Prodr. Fl. Bryol. Madag. 74. 1898.

Stems densely foliate, central strand present or absent. Leaves *contorted, apiculate*, truncate, obtuse, or rounded; upper margins entire or entire-crenulate; hyaline margin restricted, reaching 1/2 to 2/3 of the leaf length. Upper cells with *lumen irregular or slightly sinuose.* Juxtacostal cells with adaxial surface papillose or smooth.

Series *Holomitrioidea* (Ren.) La Farge-England ***comb. nov.***

Stem with central strand lacking. Leaves obovate or elliptic lanceolate, contorted, apiculate; upper margin entire; *upper-basal cell transition sharply differentiated.* Upper cells pluripapillose, chlorophyllose, short, isodiametric, with *papillae biseriate along the margins of the cell; in transverse section papillae coalesce over the adjoining cell walls, resulting in a distinctive "groove" over the lumen of each cell.* Basal cells smooth, hyaline, elongate to linear, porose. Alar cells *bulging, with longitudinally thickened walls, dark red-brown*, or hyaline.

Series *Contorta* La Farge-England ***ser. nov.***

Stem with central strand, or lacking. Leaves elliptic lanceolate to lanceolate, tapering to a narrow lingulate acumen, contorted, apiculate; upper margin entire except *crenulate of projecting papillae*; distal acumen flattened, uni- to tristratose; upper-basal cell transition gradual. Upper cells pluripapillose or *unipapillose*, equally developed papillae on abaxial and adaxial surfaces distally, chlorophyllose, short, isodiametric, grading into smooth, short elongate basal cells. Alar cells inflated thin-walled; alar region reduced auriculate.

Subgenus *Leucoloma*

Plants ascending, downwardly outspreading, *pendent*, pale green, tan to brown below. Stems *elliptic in transverse section*, without central strand. Leaves 2.5-10.0 mm long, small to robust, ovate, ovate-lanceolate to elliptic lanceolate. Juxtacostal bands sharply defined from the tinged, smooth interior cells and hyaline border cells; laminal tissue membranous or not. Costa smooth, subpercurrent to excurrent; in transverse section guides 4-6, rarely with lateral doubling, abaxial and adaxial stereid bands in 1-5 layers. Alar cells red-brown, flat, evenly thick-walled to strongly longitudinally thick-walled; alar region small to large, 6-31 (43) cells wide, 3-17 (21) cells long. Dioicous, or autoicous in a single exception.

Sporophyte mono- or polysetous, *immersed, emergent, to shortly exserted.* Seta *< 3 mm, short, stout, tan, opaque,* smooth; in *transverse section with single layer of thickened outer cortical cells.* Capsules globose, ovoid, to short cylindric, tan, brown, to black-brown. Peristome teeth 0.5-0.6 mm long, not reduced. Operculum conic to rostrate, erect or oblique. Calyptra *mitrate, lobate.*

Section *Subvittata* (Ren.) Ren., Essai Leucoloma 26. 1909.

Leaves ovate-lanceolate to narrowly lanceolate, with long gradually tapered acumen, *caducous*, flexuose, erect to wide-spreading. Juxtacostal bands reaching the base or not. Juxtacostal cells abaxially pluripapillose, papillae low, multifid, adaxial surface smooth or with a few distally. Basal and interior cells commonly porose; *1-4 rows of isodiametric cells between basal cells and alar cells.* Alar cells predominantly quadrate, evenly to slightly longitudinally thick-walled, vertically oriented toward basal cells. Rhizoids often developed on alar cells. Sporophytes immersed.

Section *Leucoloma*

Leaves ovate to lanceolate, with long gradually tapered acumen, flexuose to spirally twisted, or crispate, erect-spreading to squarrose. Juxtacostal bands extending to the base or just above the base. Juxtacostal cells abaxially pluripapillose, adaxial surface smooth or with a few papillae along the distal costa, papillae low, dense, indistinct and compactly arranged or distinct, separated, rarely in transverse rows toward the base. Basal and interior cells porose or not, with one row of isodiametric cells between alar region and basal cells, or lacking. Alar cells predominantly elongate or rectangular, with a slightly angled orientation toward basal cells. Rhizoids rarely developed on alar cells. Sporophytes immersed.

Section ***Obscura*** (Ren.) Ren., Essai Leucoloma 27. 1909.

Leaves ovate-lanceolate to elliptic-lanceolate, with a gradual or abruptly tapered acumen, slender or stout. Juxtacostal bands opaque, parallel. Juxtacostal cells narrow, 5-7 µm wide, pluripapillose, with low, dense *papillae equally developed on the adaxial and abaxial surface*. Interior and basal cells forming a narrow membranous lamina. Alar cells predominantly elongate or rectangular, with a slightly angled orientation toward basal cells. Rhizoids not developed on alar cells. Sporophytes immersed, emergent or shortly exserted.

Section ***Attenuata*** Ren., Prod. Fl. Bryol. Madag. 69. 1898.

Leaves lanceolate to elliptic-lanceolate, with a gradual or abruptly tapered acumen, slender or stout, fragile or not. Juxtacostal bands opaque, often *rugose, tapered toward the costa*. Juxtacostal cells narrow, 5-7 µm wide, pluripapillose, papillae low, dense, multifid, equally developed on the adaxial and abaxial surface. Interior and basal cells forming broad membraneous lamina. Alar cells predominantly elongate or rectangular, with a *obliquely angled orientation* toward basal cells; alar region *enlarged*. Sporophytes immersed. Rhizoids not developed on alar cells.

Section ***Dichelymoidea*** Besch., Ann. Sci. Nat. Bot. sér. 6, 9: 315 1878.

Plants with branching sympodial by subapical innovations or monopodial by perpendicular or obliquely oriented lateral innovations. Leaves lanceolate to elliptic-lanceolate, with a gradual or abruptly tapered acumen. Juxtacostal bands translucent, non-opaque, abaxial surface corrugated or smooth, parallel to the costa and differentiated. Juxtacostal cells *uni-* to pluripapillose, *abaxial* surface smooth or with *prominent multifid papillae* developed *in irregular transverse rows, adaxial surface with scattered low papillae*, papillose cells often restricted to the distal lamina. Interior and basal cells forming broad membraneous lamina. Juxtacostal cells broad, to 12 µm wide, irregularly angled and shaped. Alar cells predominantly elongate or rectangular, with a *obliquely angled* orientation toward basal cells; alar region *enlarged*, to 43 by 21 cells, often convolute or clasping at base. Rhizoids not developed on alar cells. Sporophyte immersed.

The Distribution and Diversity of the infrageneric taxa of *Leucoloma*

The phylogenetic analysis of the infrageneric taxa provides an evolutionary hypothesis to examine the distribution and diversity of *Leucoloma*. The following distributions of the infrageneric taxa represent a minimal estimate of their extent, based on a limited number of available collections for many of the species.

Leucoloma has a pantropical distribution with its northernmost locality in Honshu, Japan (34°N) and southernmost in the Cape Province, South Africa (34°S, Fig.III.6). In the New World, *Leucoloma* extends south to the state of Santa Catarina in southeastern Brazil (28°S), and north to Tamaulipas, northeastern Mexico (24-25°N). It is restricted to a subsarahan distribution in Africa. In central Asia it reaches Nepal and Bhutan in the north, through the Malay Peninsula to northeastern Australia. Although the genus extends into the temperate regions, it is primarily a tropical-subtropical genus, with a broad elevational range from sea level to 2800 m. Its distribution within Madagascar is especially ecologically. It occurs in the wettest region of Madagascar in humid lowland to elfin rainforests, where precipitation exceeds 4000 mm/yr (Nicoll & Langrand 1994), as well as in the drier western region in seasonal and dry forests of 1201 mm/yr (White 1983). Humbert (1955) distinguished two major phytogeographic regions of Madagasacar, based on high endemism at the family and generic level. Within these two regions he distinguished six domains. *Leucoloma* occurs in four of them, reflecting the varied adaptation of the genus.

The distribution of *Leucoloma* contrasts with those of the outgroup genera. *Sclerodontium* is a southern temperate genus extending from New Zealand and Australia to the Kerguélen Islands and Brazil (Crum 1986), whereas *Dicranum* is primarily a Northern Hemisphere genus, although cosmopolitan (Renauld 1901). *Dicranoloma* is either restricted to Australia and New Caledonia (sensu Norris and Koponen 1989) or is primarily a Southern Hemisphere genus (sensu Renauld 1901). The regions of high species richness for *Dicranum, Dicranoloma, Sclerodontium*, and *Leucoloma* differ for each genus, indicating unique evolutionary histories (Gangulee 1971, Crum 1986).

Infrageneric Distributions and Diversity

The present day distribution of the infrageneric taxa of *Leucoloma* is influenced by three groups of factors: 1) Life strategy - that includes attributes such as perennial life cycles, sexuality (i.e., dioicous with most of specimens lacking sporophytes), or modes of vegetative propagation versus spore dispersal within rainforests (e.g., fragile branches). Cyclonic disturbance within rainforests is an effective means for dispersing fragments or spores and creating new available niches. In addition to habitat availability and establishment in new ecosystems, stress and competition are constraints that affect the realised distribution of a species (During 1992). 2) Speciation events - (e.g., genetic mutations or recombinations, and hybridization) that result in the divergence of populations and ultimately species. New features incorporated into a species provide the potential to adapt or diversify within a mutable or organic environment. For example, the development of papillae and immersed capsules in mosses provide the ability to tolerate more exposed microhabitats (Proctor 1979, Vitt 1981). For a detailed review of factors that influence biotic diversification see Cracraft (1992). 3) Historical factors - vicariant events that effect the distribution patterns of species. For example, plate tectonic events that result in mountain and island arc formation; climatic change that causes fluctuations of latitudinal and altitudinal biome distributions (i.e. South America, Prance 1982; Tanzania, Lovett 1990), or intervals of eustatic sea level changes that either isolate or connect continental island floras.

The phylogeny of *Leucoloma* supports the evolution of 2 distinct lineages: subgenus *Leucoloma* and subgenus *Syncratodictyon*. The distribution patterns for their respective sections differ, suggesting divergent evolutionary histories within the genus. The more apomorphic sections of subgenus *Leucoloma* show a strong trend of increased endemism (Fig.III.7c). Section *Subvittata*, the basal taxon, is pantropical and has low diversity in the major regions of the world: Central and South America have three species; Africa one species; India, Melanesia, and southeastern China two species; and the Oceanic region two species in Australia and the highest species richness, five species, in the Pacific Ocean (Fig.III.7a). The distribution of the species in section *Subvittata* is compatible with recent theories of the breakup of Gondwana. The section shows affinities between Africa and South America, Africa and India, and Africa and Melanesia - southeastern China, Australia and Oceania. Geologic evidence has shown that the Malay Peninsula, southern Tibet, Burma and Sumatra were formerly continental fragments of northern Australia and New Guinea in the late Jurassic (Audley-Charles 1987). Diversification of the endemic species in this section is presumably "recent", because the Pacific Ocean islands are less than 45 million years old (see review in Vitt 1995). Section *Subvittata* is the only section of the genus that has its center of diversity in the Pacific Ocean region, and the only section that occurs in the Southern Pacific islands. Within the genus only two other sections have species in the Oceanic region: section *Caespitulosa* has a single representative in Hawaii and section *Holomitrioidea* has a single species that occurs in northern Australia (Fig. III.8b-c). The oceanic region represents the poorest region for species richness in the genus, yet the richest for section *Subvittata*.

Section *Leucoloma* has a single species in the neotropics (Brazil) and a single species in India and Ceylon. The remainder of the section is concentrated in Africa and Madagascar (Fig.III.7b). A single species, *L. gracilescens,* extends from West Africa to the East African moist forest montane archipelago. Three other species are restricted to east and South Africa. The remaining seven species are concentrated in Madagascar and the East African islands. One of these latter species, *L. lepervancheri,* also occurs in East Africa. The result is that nearly half of the species of the section are endemic to Madagascar and the surrounding islands (6/13 Table III.6). With the breakup of Gondwana, South America separated from Africa about 106-84 Ma (Goldblatt 1993). The distribution of section *Leucoloma* includes outlier species that support the floristic links between South America and West Africa. *Leucoloma triforme* in Brazil is the sole representative of the section in the New World. *Leucoloma nitens* of India and Ceylon supports the India-Madagascar connection, before the tectonic split around 88 Ma. An alternative interpretation of the distribution pattern in section *Leucoloma* is that more recent dispersal events have resulted in the establishment of single outlier species in South America and India. Definitive evidence for choosing one hypothesis over the other is lacking at present.

The most derived sections *Dichelymoidea*, *Attenuata*, and *Obscura* are endemic to Madagascar and the East African islands. Section *Obscura* is endemic to Madagascar, whereas sections *Attenuata* and *Dichelymoidea* also occur in the Seychelles, Mascarenes, and Comoros. Section *Dichelymoidea* has a single widespread species, *L. dichelymoides*, that occurs in the Comoros, Mascarenes, Madagascar, and is reported for the Seychelles (Tixier 1993). The remaining species are restricted to Madagascar or the Mascarenes. Section *Attenuata* has a similar pattern of distribution with a single widespread species, *L. seychellense,* and the remaining species restricted to Madagascar. These three lineages represent adaptive radiation to the epiphytic habitat in moist tropical rainforests. The most derived section, section *Dichelymoidea*, has species that form pendulous stems on fine branches in elfin forests or habitats of increased light availability. Their lack of occurrence in East Africa and India suggest that these sections postdate the separation of Madagascar from Africa (initiated 165 million years ago - ending 121 million years ago, Rabinowitz et al. 1983) and

Madagascar from India 88 million years ago (Storey et al. 1995).

Madagascar and the east african island region is the center of diversity for subgenus *Leucoloma* (Table III.6). The evolutionary trend of increased endemism in the East African island region is clear from the phylogeny of the sections. The distribution pattern has evolved from a pantropical, to an Indo/Afro/American distribution, to the East African island region (Fig.III.7). Twenty-one out of thirty-eight species of subgenus *Leucoloma* are endemic to the east african island region (Table III.6).

The distribution patterns, diversity, and endemism at the sectional level of subgenus *Syncratodictyon* also show a concentration of species richness in Madagascar and the East African islands (Fig.III.8, Table III.5). Two of the sections, *Holomitrioidea* and *Caespitulosa*, have broad distributions. *Caespitulosa* is centered in Madagascar, whereas *Holomitrioidea* has an equivalent representation in Madagascar, West Africa and India. The basal section *Dicranoidea* is strictly an African taxon with its concentration of species in Madagascar and surrounding islands. The distribution of the sections within subgenus *Syncratodictyon* also indicate that the center of diversification is in the Afro-Madgascaren-Indian region.

Generic Distribution and Diversity

Although *Leucoloma* is pantropical in distribution, its concentration in Madagascar of both plesiomorphic and apomorphic elements and species richness indicates the region as the center of origin for the genus. The 57 species in this region represent half of the diversity in the genus. Seventy-seven or two thirds of the species occur within and are restricted to the African region as a whole (Fig.III.11). A refined diversity map shows that high species richness is restricted to Tanzania, Madagascar, and the Mascarenes (Fig.III.14). The Guinea-Congolese region has a low diversity for any particular country (1-5 species), although taken as a whole there are 9 species known from west Africa (Table III.5). None of the neotropical species occurs in Africa, given the current species assessment. A single species has a broad distribution to India from Madagascar (see above). South Africa and the Comoros are regions of intermediate species richness (6-10 species). The species representation of the genus outside of the center of diversity is limited. Given the relative stability of the paleoclimate of Madagascar in comparison to Africa, the flora of Madagascar has had the opportunity to evolve without the same degree of devastation by aridity that took place in Africa during the Pleistocene (Livingston 1993, Raven and Axelrod 1974).

The phylogeny of *Leucoloma* indicates a pattern of adaptive radiation into a broad diversity of habitats in Madagascar (from the wettest rainforests to the dry spiny forests of the southwest, from sea level to the highest mountain regions (elfin forest habitats). This low number of species having distributions to Africa or India also be may a result of constraint by life strategy. For example, *Leucoloma* is primarily a dioicious genus, thus both male and female plants are necessary for sporophyte production and ultimately spore dispersal. The most of the specimens examined were restricted to non-fruiting female populations. The development of fragile branches as a means of asexual reproduction is prevalent in *Leucoloma*. The major constraint of this type of reproduction would be dispersal distance. Competition with existing species for available niches would be an added constraint for the establishment of new populations of *Leucoloma* within the rainforests. Thus, *Leucoloma* has undergone a major species explosion in Madagascar and has lacked a dominant pattern of widespread species between continents.

In an analysis of the *Campylopus* floras of Sri Lanka and Madagascar, Frahm (1994) reported a close affinity of the species of the two regions. Of the twelve species of Sri Lanka nine of them were "very closely related", including 4 that were identical. Therefore 74% of the Sri Lanka *Campylopus* flora has a close relationship with species in Madagascar. In comparison, *Leucoloma* has a similar number of species from the India-Sri Lanka region (10 spp.), yet the floristic affinities differ. A single species occurs in Madagascar and India, *L. amblyacron* (*L. brevifolium Dix.*). *Leucoloma nitens* is a related to *L. zuluense* of east Africa and a single specimen of an undetermined taxon from western Madagascar is closely related to *L. taylorii* of India and Sri Lanka. The remaining species of the Indian-Sri Lanka region are either endemic or have distributions that extend into southeast Asia and the Malensian region. Therefore only 10% of the India-Sri Lanka *Leucoloma* flora is conspecific with Madagascaren species.

Frahm (1994) found that 87% (14/16) of the *Campylopus* species from the East African region are common to Madagascar, with 2 species endemic to Madagascar. Based on a revision of the East African *Leucoloma* species (14 spp.) 4 species also occur in the East African island region (*L. chrysobasilare, L. lepervancheri, L. rutenbergii* var. *elatum*, and *L. subsecundifolium*). Pócs (1975) and Kis (1985) cited *L. bifidum* and *L. sinuosulum* as East African - Madagascan elements, although these species are restricted to the East African islands. The East African material is most commonly renamed as *L. zuluense* or *L. scabricuspes*, respectively. Therefore, four of the 14 species (or 28%) of *Leucoloma* that occur in east Africa, also occur in the East African islands. Six of the species (42%) are restricted to East Africa. The remaining five species have ranges that extend to southern Africa or West Africa. Thus the two dicranoid genera, *Leucoloma* and *Campylopus*, show different species distribution patterns, with the species of *Campylopus* having broader distribution patterns in general than *Leucoloma* species.

The distribution patterns of the most plesiomorphic section and the most apomorphic sections of subgenus *Leucoloma* overlap in Madagascar. As well, the greatest diversity or species richness of all sections is in Madagascar, with the exception of section *Subvittata*. Maisey (1993) cautioned the interpretation of present day distributions as Gondwanan elements. He stated that for most taxa there is little evidence to support from the fossil record that an ancestral taxon had a widespread Gondwana distribution before plate separation.

The earliest fossil moss dates back to the Carboniferous (about 320 million years ago). In comparison to the scant material from the Carboniferous, rich fossil beds from the Permian in Siberia were described by Neuberg (Smoot and Taylor 1986). Smoot and Taylor (1986) described a new genus and species of moss that represents the first Permian fossil with well preserved cell structure. They refrained from placing the species in any of the orders within the subclass Bryidae, but stated that it is comparable to taxa of the Bryales. Given this comparison, they concluded that "mosses were probably well established on the southern continents by late Palaeozoic time". Based on the description, features such as the costal width occupying up to 70% of the laminal width, the elongate laminal cells, uni- or bistratose juxtacostal region, and a multistratose costa, a possible relationship with the Dicranales cannot be discounted.

Therefore, some evidence may support an ancestral Gondwana taxon of *Leucoloma*. Nonetheless there are two possible interpretations of the evolution of *Leucoloma*: 1) The ancestral taxon to subgenus *Leucoloma* was a Gondwana element, as widespread and pantropical as the more plesiomorphic section *Subvittata*. Through vicariant events, evolutionary opportunities, and paleoclimatic change the remaining sections became more restricted in distribution and diversified in tropical forest habitats under various moisture regimes from moist lowland coastal forests to low canopied, elfin forests. The breakup of Gondwana, South America separating from Africa, and India rafting taxa north, can be seen in the species distribution of section *Leucoloma*. *Leucoloma triforme* and *L. nitens* represent geographically isolated species of the section. The vicariant interpretation of this distribution pattern would imply that the taxon ancestral to section *Leucoloma* had a broader distribution. 2) The alternative hypothesis would be that the ancestral taxon originated in Madagascar and through dispersal events *L. triforme* was established in southeastern Brazil, *L. nitens* in India, and *L. gracilescens* in West and East Africa.

Since Madagascar separated from Africa 121 million years ago (Rabinowitz et al. 1983), there has been a species explosion or marked diversification within Madagascar. As a result Madagascar represents a region of high biotic endemism, a "trove of endemics" (Campbell 1990). Examples from the flora include 7 endemic vascular plant families (e.g. Dideraceae). Baobabs have two species in Africa, with 7 species in Madagascar. Endemism is estimated at 81 % at the species level for vascular plants and 20% at the generic level (Campbell 1990). As well, Koechlin

(1972) has analysed the flora within Madagascar and concluded that the endemic pattern strongly applies. For example, an assessment of the flora showed that 48% of the genera were endemic to southern Madagascar with 95% specific endemism for the region.

Thus the global distribution of *Leucoloma* shows a marked concentration in Madagascar, with 51/112 species endemic to the East African island region for the genus. It should be emphasized that this endemic element is primarily restricted to the rapidly declining eastern forests of the island. The distribution in the western region of Madagascar is isolated to a few localities, and documented by a few specimens. The distribution patterns with respect to the phylogeny of the genus suggest: 1) major diversification post-dated the separation of Madagascar from Africa and India; 2) the genus is centered in Madagascar; 3) and the common ancestor of the genus had a Gondwanan origin.

The conclusions based on the analysis of the distribution patterns and diversity of the infrageneric taxa are as follows: 1) all sections occur in Madagascar and the surrounding islands, thus both plesiomorphic and apomorphic elements are represented; 2) seven of eight sections have their greatest diversity in Madagascar, or have an equal representation in that region; 3) 50% of the genus occurs in Madagascar, and 91% of those species are endemic to that region; and 4) the major geographical regions, the neotropics, Africa, India-Asia, and Oceania show few shared species. This suggests that speciation has taken place since the regions have separated, and that there has been little dispersal between regions since separation. Lacking fossil evidence it may be hypothesised that *Leucoloma* has diversified within the past 100 million years.

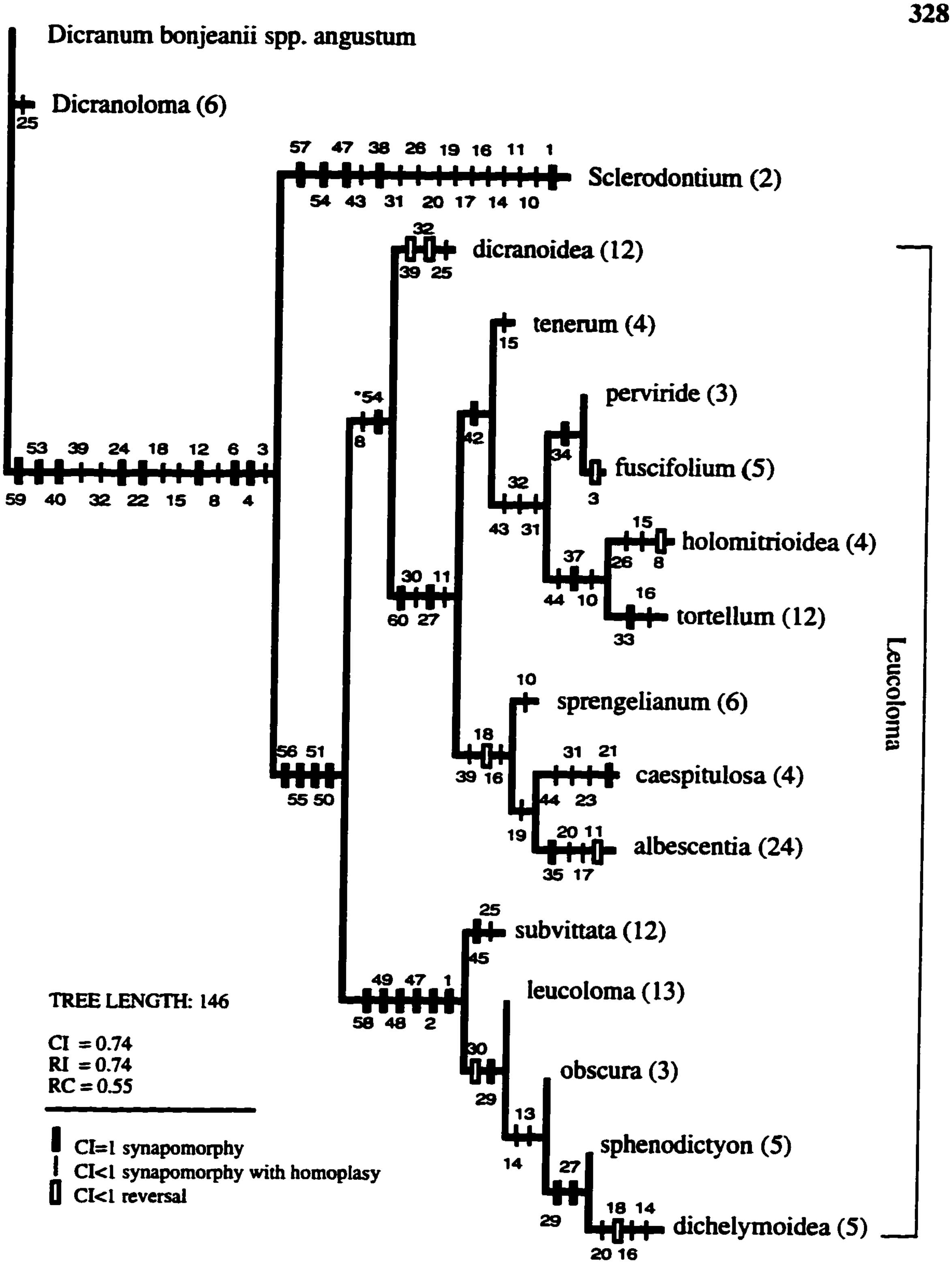


Figure III. 1. The phylogram of *Leucoloma* based on the single most parsimonious tree. Infrageneric taxa used for the analysis are explained in Table III.1. Three types of synapomorphies are indicated (see legend). The following statistical indices are given: CI - the consistency Index, RI - the retention Index, and RC - rescaled consistency index. Unambiguous characterstate changes only, with the exception of 54*. See text for explanation. Number of species per taxon is given in parentheses.

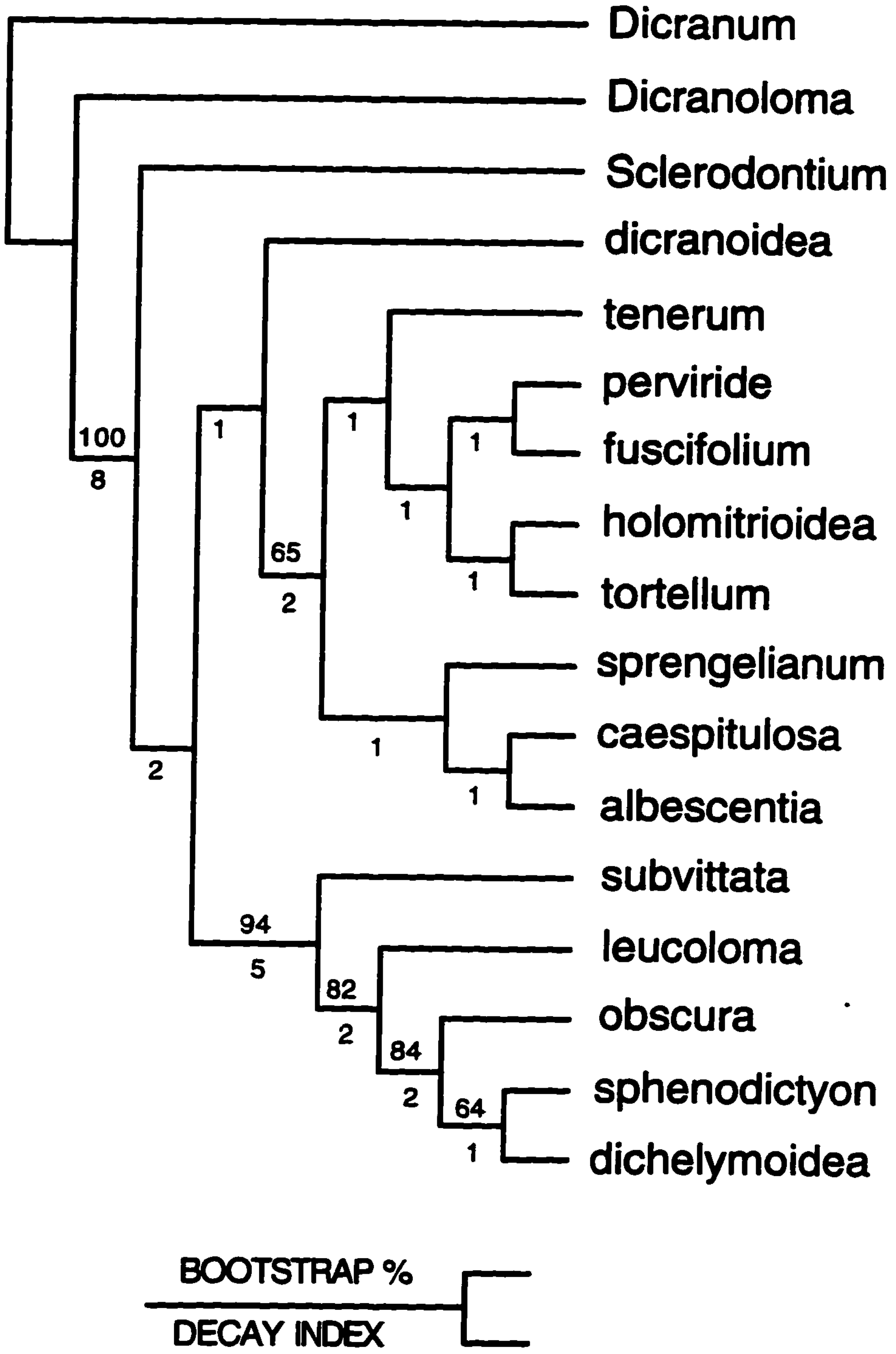


Figure III.2. The phylogeny of *Leucoloma* based on the most parsimonious tree. The species groups and infrageneric taxa used for the analysis are indicated. Statistical support using Bootstrap values > 50% are shown and Decay indices for the individual clades are given.

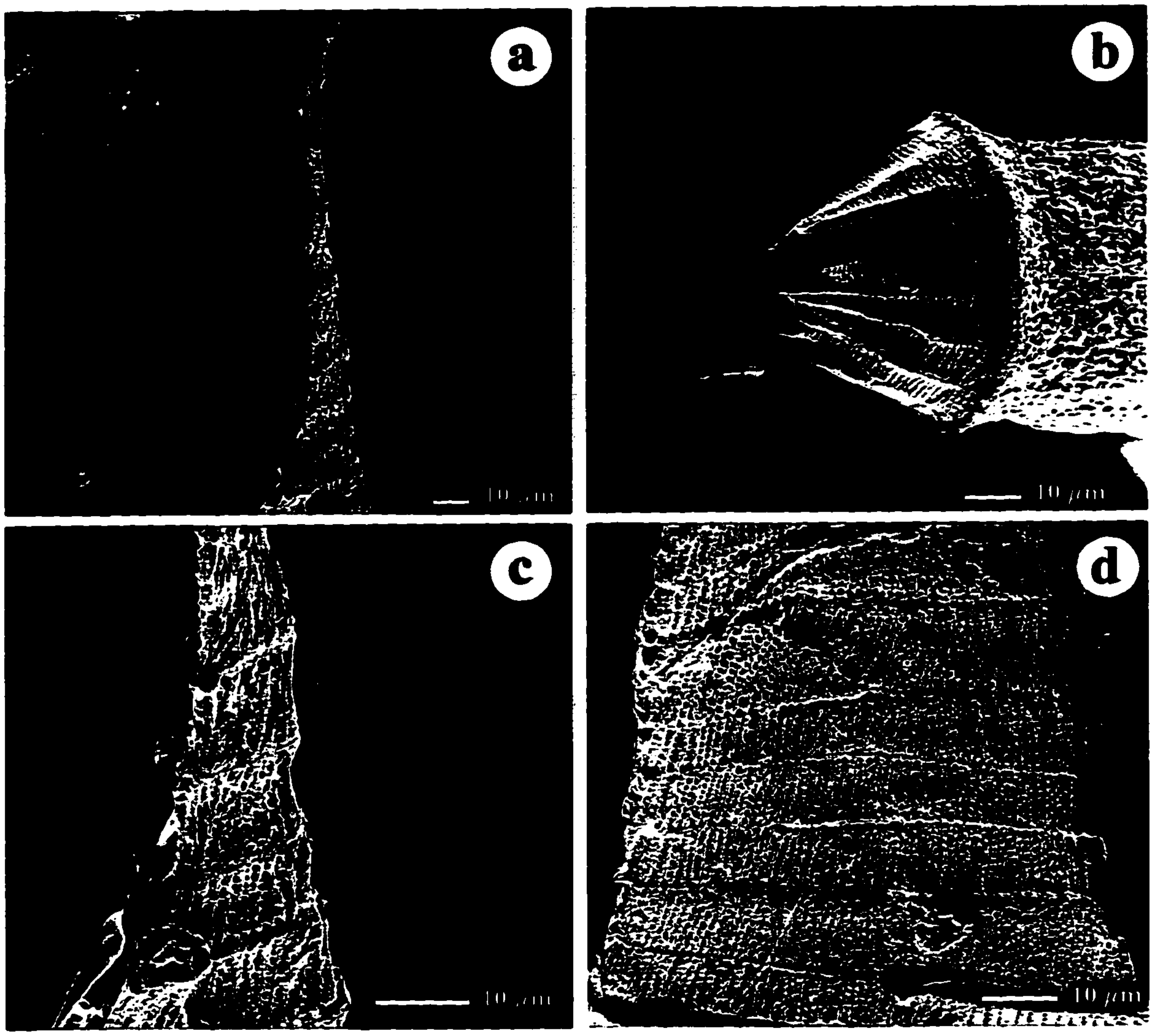


Figure III.3 a-d. The peristome of *Sclerodontium pallidum* (*Vitt 27162* ALTA). a) The vertically pitted striations extend to the distal portion of the peristome tooth. b) An overview of the peristome showing that the peristome teeth are bifid only in the upper portion of the tooth. c) A close up of the vertically pitted, distal portion of the peristome tooth. d) The peristome tooth with well developed pitted striations in the basal portion.

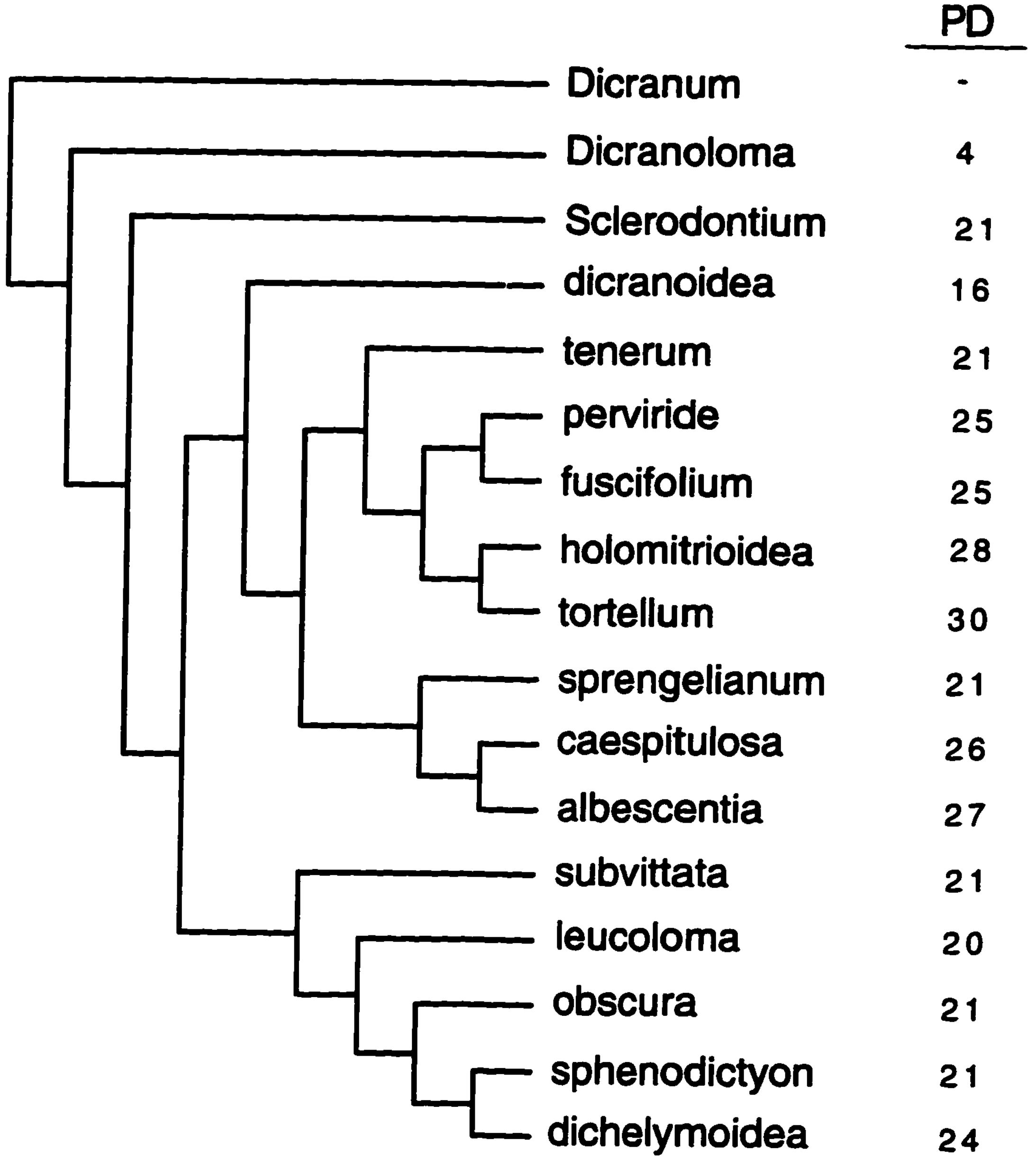
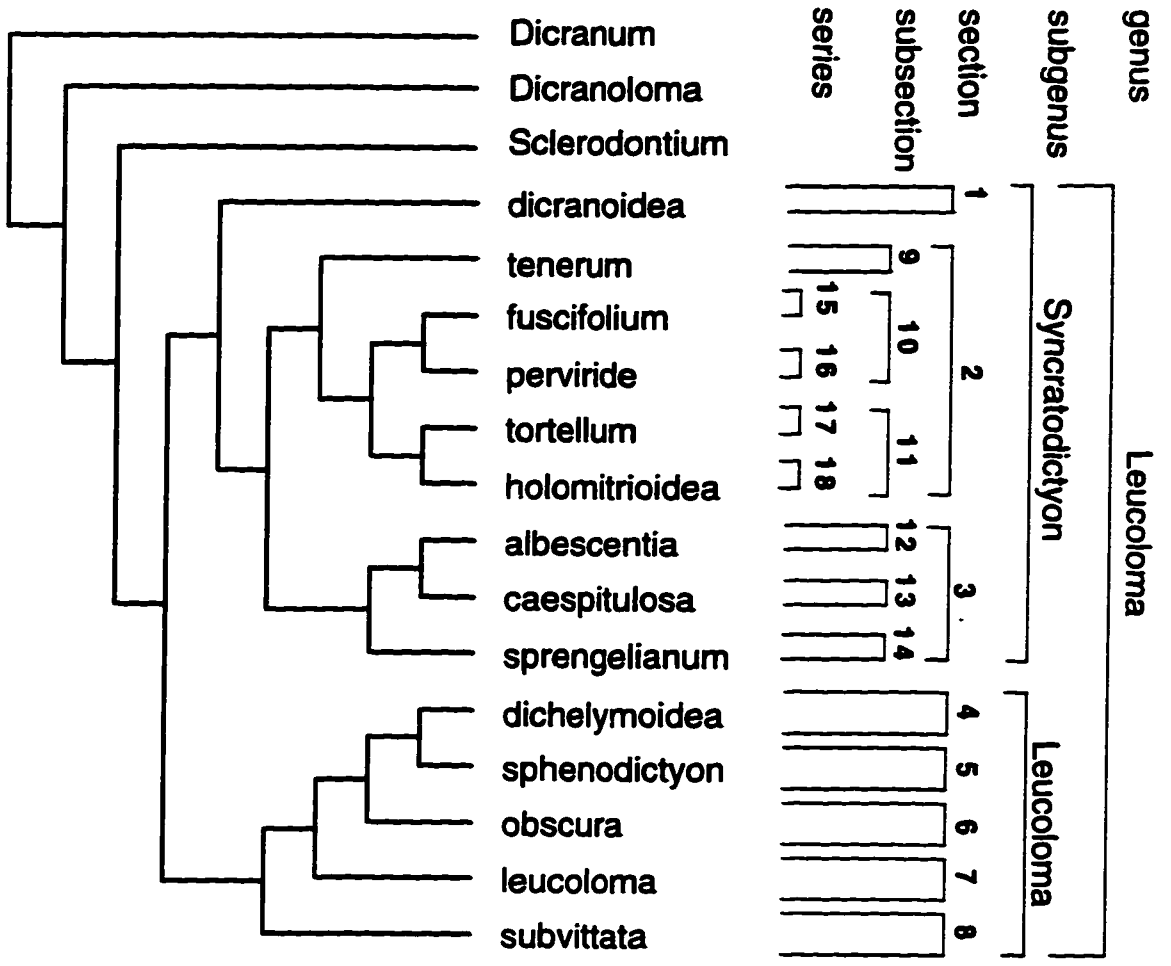


Figure III. 4. Partistric Distance values (PD) from the basal outgroup taxon *Dicranum*.



Classification Legend

section

1 Dicranoidea
2 Holomitrioidea
3 Caespitulosa
4 Dichelymoidea
5 Attenuata
6 Obscura
7 Leucoloma
8 Subvittata

subsection

9 Acuminata*
10 Serrata*
11 Holomitrioidea
12 Albescentia
13 Caespitulosa
14 Seriata*

series

15 Serrata*
16 Teretia*
17 Contorta*
18 Holomitrioidea*

Figure III.5. The infrageneric classification of *Leucoloma* based on the phylogenetic analysis. New taxa or new combinations are indicated with an asterisk (*).

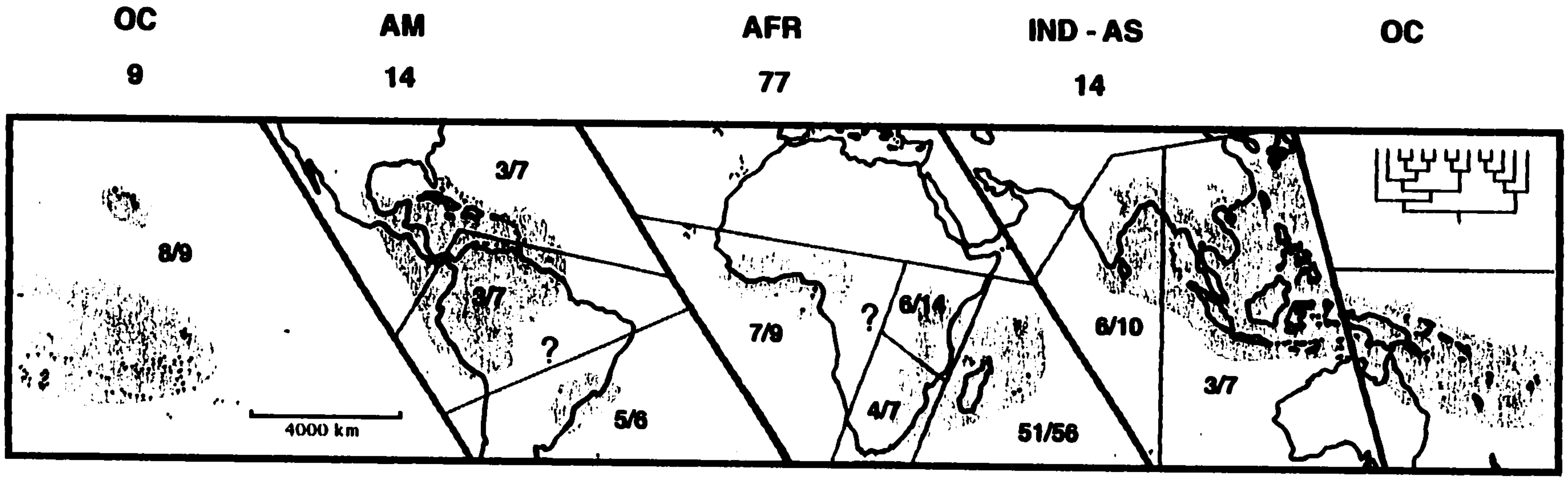


Figure III.6. The global distribution of *Leucoloma* with the endemics for each region (numerator) and the total number of species for a subregion (denominator) given. Total diversity is given for each major region is indicated above the map: OC, AM, AFR,IND-AS refer to Table III.6 for explanation of region abbreviations. The phylogeny of the genus is given in the upper right hand corner.

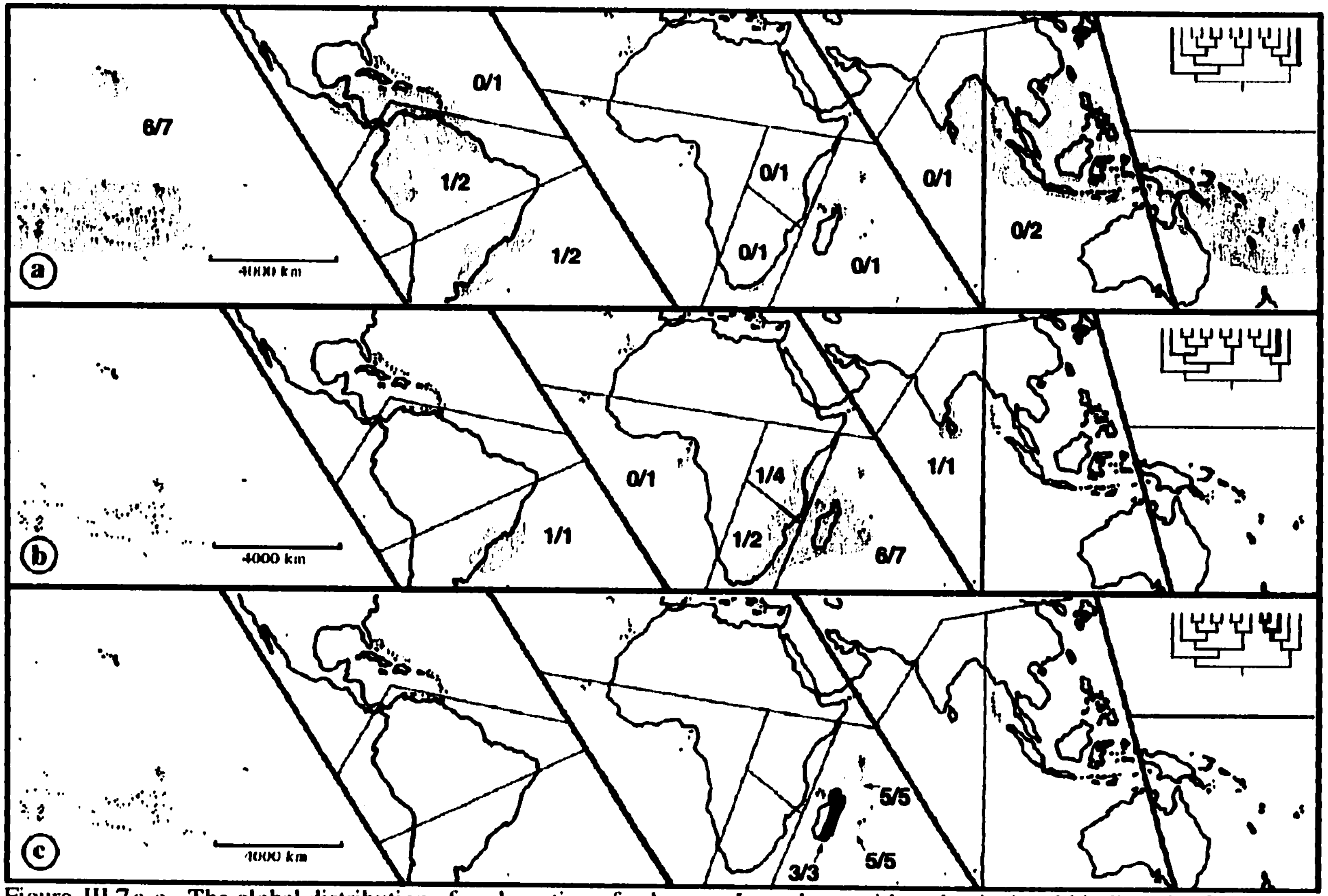


Figure. III.7 a-c. The global distribution of each section of subgenus *Leucoloma* with endemics/total biodiversity for a subregion given: a - *Subvittata* ; b - *Leucoloma* ; c - *Dichelymoidea* 5/5 and *Attenuata* 5/5 (lighter area), *Obscura* 3/3 (darker area). The cladogram in the upper right indicates the clade(s) represented in each map.

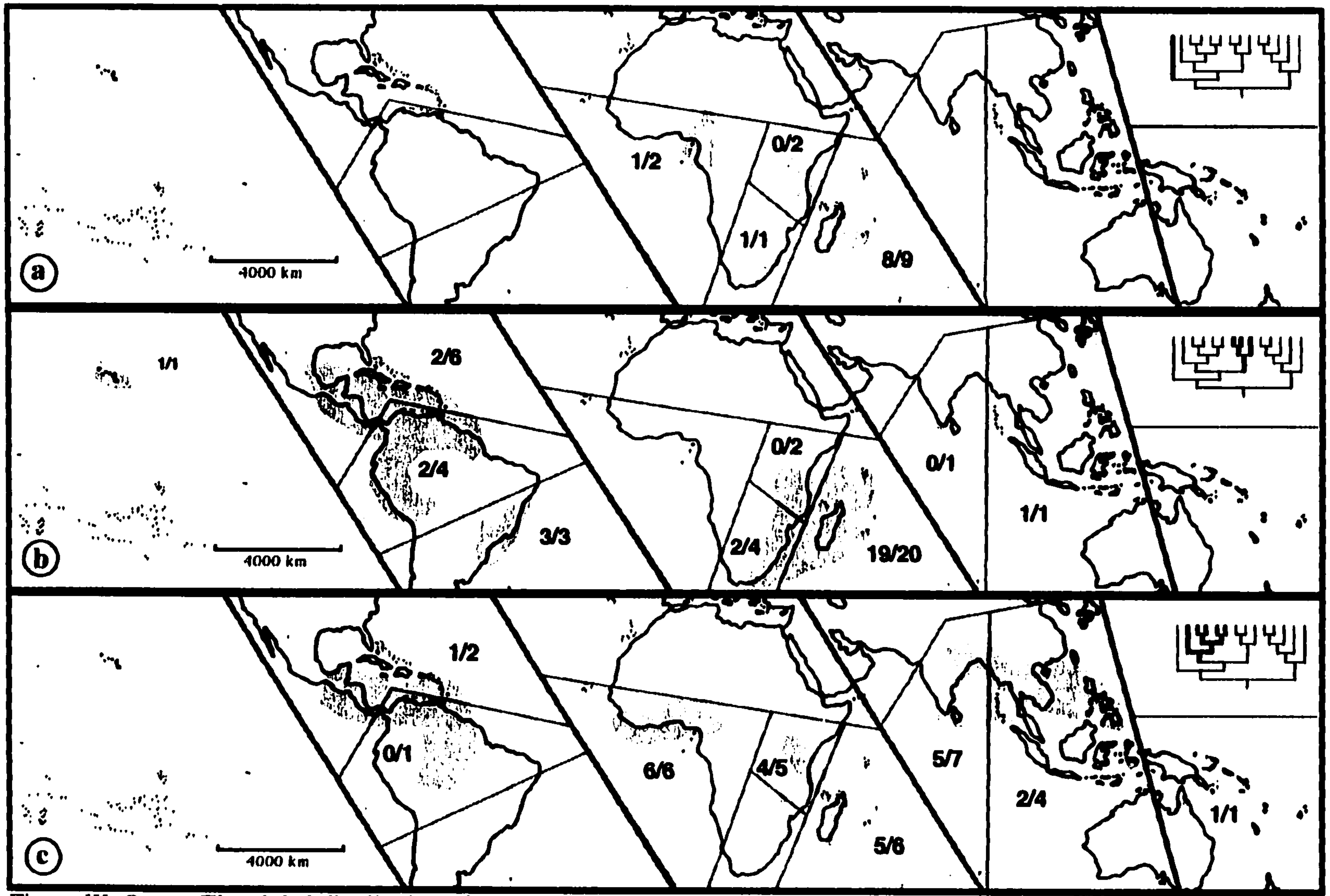


Figure.III. 8 a-c. The global distribution of each section of subgenus *Syncratodictyon* with endemics/total biodiversity for a subregion given:a -*Dicranoidea*; b -*Caespitulosa*; c -*Holomitrioidea*. The phylogram in the upper right indicates the clade represented in each map.

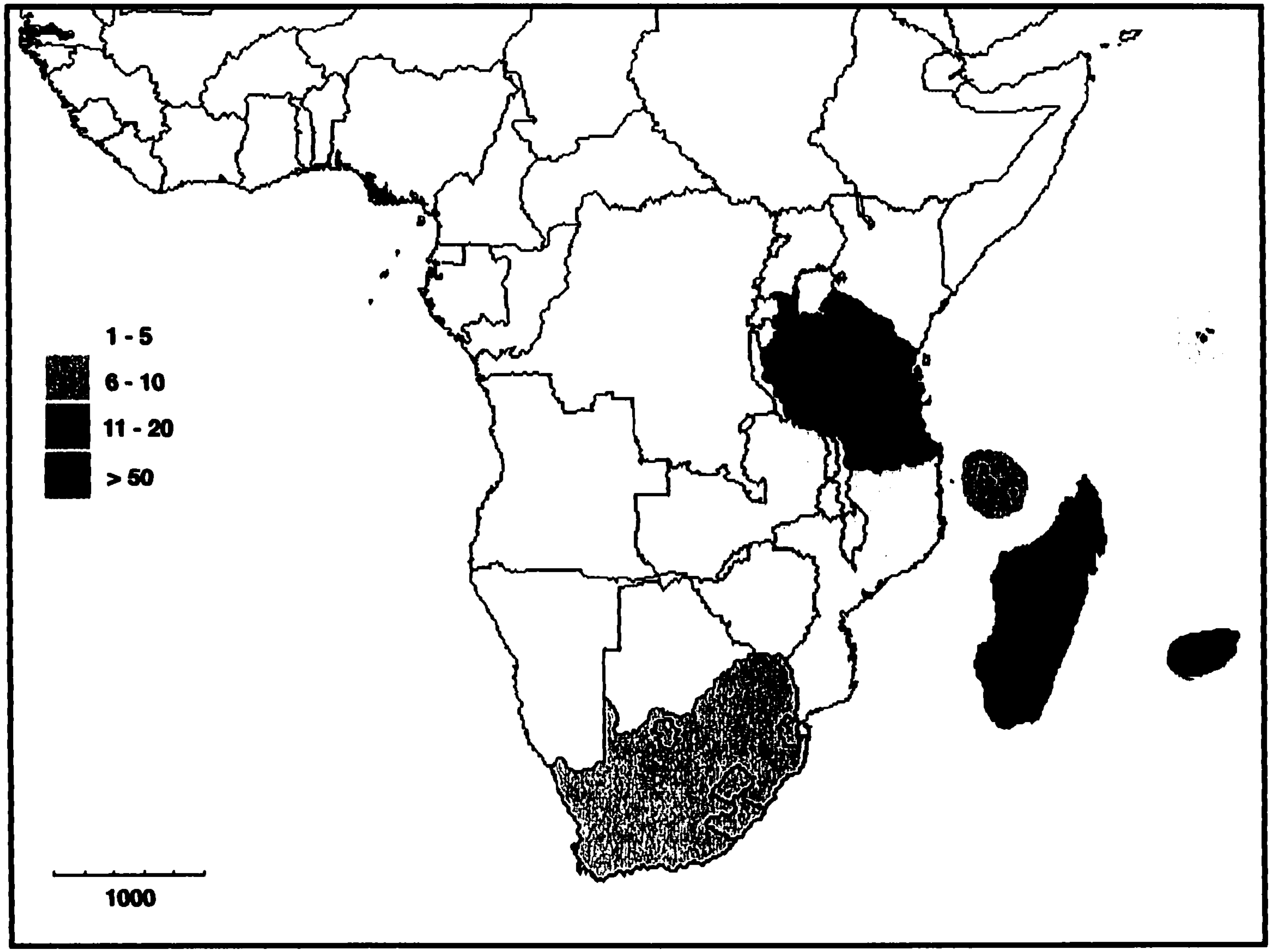


Figure III. 9. The diversity of *Leucoloma* in Africa. A shaded scale indicates the number of species for the political regions.

Table III.1. The infrageneric classification of Renauld (1909) including Potier de la Varde's section *Rhacomitrioidea* compared with taxa used for the phylogenetic analysis.

Renauld 1909	**Taxa For Phylogenetic Analysis**
Leucoloma Brid.	Leucoloma Brid.
subgenus Taeniodictyon	**subgenus** Leucoloma
section Euvittata	**section** Leucoloma
section Subvittata	**section** Subvittata
section Obscura	**section** Obscura
subgenus Sphenodictyon	**subgenus** Sphenodictyon
subgenus Syncratodictyon	**subgenus** Syncratodictyon
section Dicranoidea	**section** Dicranoidea
section Caespitulosa	tenerum spp. group
section Albescentia	fuscifolium spp. group
section Holomitrioidea	perviride spp. group
section Dichelymoidea	**section** Caespitulosa
section Pseudocaespitulosa*	tortellum spp. group
section Semivittata*	**section** Albescentia
section Rhacomitrioidea* (P. de la Varde 1950)	sprengelianum spp. group
	section Holomitrioidea
	section Dichelymoidea

*Taxa placed in synonymy for phylogenetic analysis.

Table III.2 Data matrix for the infrageneric cladistic analysis of *Leucoloma*

	Characters					
Taxon	10	20	30	40	50	60
dicranum	0000000000	0000000000	0000000100	0000000000	0000000000	0000000000
					1	
dicranoloma	0000000000	0000000000	0000100001	1000010000	0000010000	0000000000
sclerodontium	2011012201	1102111111	0101010001	3100020111	0010002000	0012001010
		1		2		
dicranoidea	0001011100	0000100100	0000100001	1000020000	0000000001	1010100010
	1	111	1 1	1	2	1 1 1
tenerum	0011011100	1111200100	0101001000	1000020011	1100000002	1011110011
				1		
albescentia	0001011100	0100111011	0100001000	1000120000	0000000001	1011110011
	1		1	1 21	1 2	1
sprengelianum	0011011101	1100110000	0101001000	1100020021	0000000002	1011110011
						2
fuscifolium	0001011100	1111100100	0111001000	2001020011	1110000001	1011110011
				2	2	1
perviride	0011011100	1000100100	0101001000	2001020011	1110000002	1011110011
		1	1	2		
caespitulosa	0001011100	1100110010	1111001000	2100020021	0011000002	1011110011
tortellum	0001011101	1100110100	0111001000	2210021011	0111000002	1011110011
	1					
holomitrioidea	0011011201	1111200100	0101011000	2200021011	0111000002	1011110011
dichelymoidea	1111011220	0113110001	0101032020	1100020011	0000001112	1010110110
subvittata	1111111200	0100100100	0101120001	1100020011	0000101112	1010110110
leucoloma	1111011200	0100100100	0101030010	1100020011	0000001112	1010110110
obscura	1111011200	0111300100	0101030010	1100020011	0000001112	1010110110
sphenodictyon	1111011210	0111300100	0101032020	1100020011	0000001112	1010110110

Table III.3. Historical outline of infrageneric classification of the genus *Leucoloma*. The taxa are presented in the order in which they were published by the respective authors.

Bescherelle 1878	**Renauld 1898**	**Renauld 1909**
Leucoloma Brid.	Leucoloma Brid.	Leucoloma Brid.
section	**subgenus** Euleucoloma	**subgenus** Taeniodictyon
Dichelymoidea	**section** Vittata	**section**
Caespitulosa	**subsection** Euvittata	Euvittata
Albescentia	**series** Distincta	Subvittata
Dicranoidea	Obscura	Obscura
Prinodontoidea	**subsection** Subvittata	
	section Attenuata	**subgenus** Sphenodictyon
	section Transmutantia	**subgenus** Syncratodictyon
	subsection	**section**
	Caespitulosa	Caespitulosa
	Holomitrioidea	Holomitrioidea
	Pseudocaespitulosa	Pseudocaespitulosa
	Albescentia	Albescentia
	Dicranoidea	Semivittata
	Dichelymoidea	Dicranoidea
		Dichelymoidea
		Rhacomitrioidea (P. de la Varde 1950)
	subgenus Dicnemoloma	Dicnemoloma
	subgenus Dicranoloma	Dicranoloma
	section	
	Oncophoroidea	
	Scoparioidea	

Table III.4. A New infrageneric classification of the genus *Leucoloma*.

- *Leucoloma* Brid.
    - Subgenus *Syncratodictyon* Ren.
        - Section *Dicranoidea* Besch.
        - Section *Caespitulosa* Besch.
            - Subsection *Seriata* La Farge-England
            - Subsection *Caespitulosa* Besch.
            - Subsection *Albescentia* (Besch.) Ren.
        - Section *Holomitrioidea* (Ren.) Ren.
            - Subsection *Acuminata* La Farge-England
            - Subsection *Serrata* La Farge-England
                - Series *Teretia* La Farge-England
                - Series *Serrata* La Farge-England
            - Subsection *Holomitrioidea* Ren.
                - Series *Holomitrioidea* (Ren.)
                - Series *Contorta* La Farge-England
    - Subgenus *Leucoloma*
        - Section *Subvittata* (Ren.) Ren.
        - Section *Leucoloma*
        - Section *Obscura* (Ren.) Ren.
        - Section *Attenuata* Ren.
        - Section *Dichelymoidea* Besch.

Table III. 5. Synopsis of *Leucoloma* - a classification of the infrageneric taxa with species listed alphabetically within their respective taxa. Asterisck (*) refers to new taxa or combinations.

Leucoloma **Brid.**	(112 spp)
Subgenus *Syncratodictyon* **Ren.**	(74 spp.)
Section *Dicranoidea* **Besch.**	(12 spp.)
L. allorgei Thér.	
L. boivinianum Besch.	
**L. entabiense* (Magill) La Farge-England	
L. garnieri Ren et Par.	
L. humbertii P. Varde	
L. incrassatum Thér.	
L. latifolium Broth. et P. Varde	
L. longifolium (Brid.) Wijk et Marg.	
L. oncophorellum C. Muell.	
**L. onraedtii* (Biz.) La Farge-England	
L. rutenbergii (Geh.) Wright	
L. rutenbergii var. *abbreviatum* Ren.	
L. rutenbergii var. *elatum* Ren.	
L. rutenbergii var. *porosis* Thér.	
L. rutenbergii var. *perrotii* Ren.	
L. secundifolium Mitt.	
status uncertain:	
L. garnieri f. *aquatica* Thér.	
Section *Caespitulosa* **Besch.**	(34 spp.)
Subsection *Seriata* La Farge-England	(6 spp.)
L. okamurae Broth.	
L. mariei Besch.	
L. mosenii Broth.	
L. scaberulum E. Bartr.	
L. sprengelianum (C. Muell.) Jaeg.	
L. zeyheri (C. Muell.) Kindb.	
Subsection *Caespitulosa* (Besch.) Ren.	(4 spp.)
L. amblyacron C. Muell. ex Besch.	
L. ambreanum Ren. et Card. in Ren.	
L. caespitulans (C. Muell.) Jaeg.	
L. subcespitulans Besch.	
Subsection *Albescentia* (Besch.) Ren.	(24 spp.)
L. albo-cinctum Ren. et Card. in Ren.	

- *L. albo-cinctum* var. *subelimbatum* Ren. in Levier
- *L. asperrimum* (C. Muell.) Kindb.
- *L. brevioperculatum* Dix.
- *L. brotheri* Ren.
- *L. candidulum* C. Muell. ex Besch.
- *L. candidum* Broth. in Voeltzk.
- *L. cirrosulum* Ren.
- *L. cruegerianum* (C. Muell.) Jaeg.
- *L. decaryi* Thér.
  - *L. decaryi* var. *comorense* Thér.
- *L. delicatulum* Ren.
- *L. isleanum* Besch. in Par.
  - *L. isleanum* var. *subtortile* Ren.
- *L. itatiaiense* Broth.
- *L. pallidulum* Thér.
- *L. perrieri* Thér.
- *L. persecundum* C. Muell. ex Besch.
  - *L. persecundum* var. *perrotii* Ren.
- *L. pumilum* Wright
- *L. pusillum* Card. in Grand.
- *L. scabricuspis* Broth.
- *L. schwaneckeanum* (Hampe) Broth.
- *L. sinuosulum* C. Muell. ex Besch.
- *L. subimmarginatum* (C. Muell.) Jaeg.
- *L. syrrhopodontoides* Broth.
- *L. theriotii* Ren. et Card.
- *L. villaumei* Thér.

Section ***Holomitrioidea*** (Ren.) Ren. (28 spp.)

Subsection ***Serrata*** La Farge-England (8 spp.)

Series ***Teretia*** La Farge-England (3 spp.)

- *L. amoene-virens* Mitt.
  - *L. amoene-virens* var. *humilis* Thér. et P. Varde
- *L. annamense* Thér.
- *L. perviride* Broth.

Series ***Serrata*** La Farge-England (5 spp.)

- *L. capillifolium* Ren.
- *L. chlorophyllum* Broth. in Dryg.
- *L. fuscifolium* Besch.
  - *L. fuscifolium* var. *crispatulum* Ren.
- *L. serraticuspis* P. Varde
- *L. subsecundifolium* Broth.

Subsection *Acuminata* La Farge-England (4 spp.)

- **L. cameruniae* Par. ex La Farge-England *ined.*
- L. *malabarense* Besch. ex Ren. et Card.
- *L. siamense* Broth.

L. tenerum Mitt.

Subsection *Holomitrioidea* Ren. (16 spp.)

Series ***Contorta*** La Farge-England (12 spp.)

L. circinatulum Bartr.
L. dussianum Besch. ex Ren. et Card.
L. guineense Broth. et Par.
L. herzogii Broth.
L. mittenii Fleisch.
L. normandii Par. et Broth. ex Ren. in Par.
  L. normandii var. *alpinum* Par. et Broth.
L. pobeguinii Par. et Broth.
L. pygmaeum Par.
L. sericeum P. Varde
L. tanganyikae P. Varde
L. taylorii (Schwaegr.) Mitt.
L. tortellum (Mitt.) Jaeg.

Series ***Holomitrioidea*** (Ren.) La Farge-England (4 spp.)

**L. circinale* La Farge-England
L. cuneifolium (C. Muell. et Geh.) C. H. Wright
L. grimmioides P. Varde
**L. marojeziense* La Farge-England

Subgenus ***Leucoloma*** (38 spp.)

Section ***Subvittata*** (Ren.) Ren. (12 spp.)

L. bauerae (C. Muell.) Par.
L. caldense C. Muell. ex Aongstr.
L. chrysobasilare (C. Muell.) Jaeg.
  * *L. chrysobasilare* ssp. *africana* La Farge-England
L. ecaudatum (C. Muell.) Kindb.
L. hawaiiense Broth.
L. insigne (C. Muell.) Jaeg.
L. kanakense Broth. et Par.
L. limbatulum Besch.
L. molle (C. Muell.) Mitt.
L. serrulatum Brid.
L. subintegrum Broth.
L. tenuifolium Mitt.

Section ***Leucoloma*** (13 spp.)

L. bifidum (Brid.) Brid.
L. cinclidiotioides Besch.
L. gracilescens Broth.
L. holstii Broth.
L. lepervancheri Besch.

L. madagascariense La Farge-England
L. nitens (Thwait. et Mitt.) Jaeg.
L. procerum Ren.
L. schelpei P. Varde
L. subbiplicatum Ren. et Card.
L. subchrysobasilare C. Muell. ex Ren.
L. triforme (Mitt.) Jaeg.
L. zuluense Broth. et Bryhn
L. zuluense var. *ovatum* La Farge-England

Section *Obscura* (Ren.) Ren. (3 spp.)

L. sanctae-mariae Besch.
L. thraustum Besch.
L. thuretii Besch.

Section *Attenuata* Ren. (5 spp.)

L. crosbyi La Farge-England
L. grandidieri Ren. et Card.
L. membranaceum LaFarge-England
L. seychellense Besch.
L. talazaccii Ren. et Card.

Section *Dichelymoidea* Besch. (5 spp.)

L. dichelymoides (C. Muell.) Jaeg.
L. fontinaloides Dix.
L. mafatense Ren.
L. ochrobasilare Ren.
* *L. ochrobasilare* Ren. ssp. *longifolium* (Thér.) LaFarge-England
L. tuberculosum Ren.

Table III.6. The diversity and endemism of *Leucoloma* at the sectional and generic rank. A total of 112 species for the world. The numerator represents number of endemic species per region. The denominator represents the total number of species per region. AFR = Africa, wAF = West Africa, sAF = South Africa, eAF = East Africa, eAFR Isl = East African Islands, AM = America, cAM = central America, nAM =northern South America, sAM= southern South America, IND = India, IND-AS= Indo-Malaysia-Southeast Asia, Mad/M/S/C = Madagascar/ Mascarenes/ Seychelles/ Comoros; OC= Pacific Ocean region.

	REGION										# of species	
	AM			AFR			eAFR Isl.					
	cAM	nAM	sAM	wAF	eAF	sAF	Mad/M/S/C	IND	IND-AS	OC		
SUBGENUS	**LEUCOLOMA**											
SECTION												
subvittata	0/1	1/2	1/2		0/1	0/1*	0/1	0/1	0/2	**6/7**	12	
%endemic	0	50	50		0	0	0	0	0	86		
leucoloma			1/1	0/1	1/4	1/2	**6/7**	1/1			13	
%endemic			100	0	25	50	86	100				
obscura							**3/3**				3	
%endemic							100					
attenuata							**5/5**				5	
%endemic							100					
dichelymoidea							**5/5**				5	
%endemic							100					38
SUBGENUS	**SYNCRATODICTYON**											
SECTION												
dicranoidea				1/2	0/2	1/1	**8/9**				12	
%endemic				50	0	100	89					
holomitrioidea	1/2	0/1		**6/6**	4/5		**5/6**	**5/7**	2/4	1/1	28	
%endemic	50	0		100	80		83	71	50	100		
caespitulosa	2/4	2/4	3/3		0/2	2/4	**19/20**	0/1	1/1*		34	
%endemic	50	50	100		0	50	95	0	100			74
GENUS												
Leucoloma	3/7	3/7	5/6	7/9	6/14	4/7	**51/56**	6/10	3/7	8/9	112	
% endemic	43	43	83	78	43	57	91	60	43	89		
#spp		14				77			14	9		
% endemism		100				99			83	89		

Bibliography

Akiyama, H. 1989. Taxonomic studies of mosses of Seram and Ambon (Moluccas, east Indonesia) collected by Indonesian-Japanese botanical expeditions. II. Acta Phytotaxonomica et Geobotanica 40: 147-162.

Allen, B.H. 1987. A revision of the Dicnemonaceae (Musci). Journal of the Hattori Botanical Laboratory 62: 1-100.

Audley-Charles, M.G. 1987. Dispersal of Gondwanaland: Relevance to evolution of the angiosperms, pp. 5-25. In: T.C. Whitmore (ed.), Biogeographical Evolution of the Malay Archipelago. Cambridge University Press, Cambridge.

Bartram, E.B. 1938. Mosses of the Solomon Islands. The Bryologist 41: 127-132.

Bremer, K. 1990. Combinable component concensus. Cladistics 6: 369-372.

Brenan, J.P.M. 1978. Some aspects of the phytogeography of tropical Africa. Annals of the Missouri Botanical Garden 65: 437-478.

Brotherus, V.F. 1924a. Musci (Laubmoose) III. Unterklasse Bryales: Spezieller Teil. 10 Band, 1 Hälfte, pp. 209-211. In: A. Engler & K. Prantl (eds.), Die Natürlichen Pflanzenfamilien, ed. 2. Leipzig: W. Engelmann.

______. 1924b. Musci (Laubmoose). In: Ergebnisse der botanischen Expedition der Kaiserlichen Akademie der Wissenschaften nach Südbrasilien 1901, herausgegeben von Prof. Dr. V. Schiffner. Denschriften der Kaiserlichen Akademie der Wissenschaften. 83: 251-358.

Buck, W.R. 1986. Traditional methods in taxonomy: a personal approbation. Taxon 35: 306-309.

Campbell, D.G. 1990. Rates of botanical exploration in Asia and Latin America; similarites and dissimilarities with Africa. Proceedings of the twelfth plenary meeting of AEFAT. Hamburg, September 4-10, 1988. Mitteilungen aus dem Institut für Allgemeine Botanik 23 a: 155-168.

Cracraft, J. 1992. Explaining patterns of biological diversity; integrating causation at different spatial and temporal scales. In: Eldredge, N. (ed.), Systematics, Ecology and the biodiversity crisis. Columbia University Press, New York.

Crum, H.A. 1986. A survey of the moss genus *Sclerodontium*. Hikobia 9: 289-295.

De Luna, E. 1995. The circumscription and phylogenetic relationships of the Hedwigiaceae (Musci). Systematic Botany 20: 347-373.

Donoghue, M.J. 1994. Progress and prospects in reconstructing plant phylogeny. Annals of the Missouri Botanical Garden 81: 405-418.

______ & P.D. Cantino. 1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. Systematic Botany 9: 192-202.

______ & M.J. Sanderson. 1992. The suitability of molecular and morphological evidence in reconstructing plant phylogeny, pp. 340-368. In: P.S. Soltis, D.E. Soltis & J. J. Doyle (eds.) Molecular Systematics of Plants. New York: Chapman & Hall.

During, H.J. 1992. Ecological classifications of bryophytes and lichens, pp. 1-31. In: J.W. Bates & A.M. Farmer (eds.), Bryophytes and Lichens in a Changing Environment. Clarendeon press, Oxford.

Eddy, A. 1988. A handbook of Malesian mosses. I. Sphagnales to Dicranales. London: British Museum of Natural History.

Edwards, S.R. 1979. Taxonomic implications of cell patterns in haplolepideous moss peristomes, pp. 317-356. In: G.C.S. Clarke & J.G. Duckett (eds). Bryophyte Systematics. Academic Press, London.

Felsentein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783-791.

Frahm, J.-P. 1991. A phenetic and cladistic study of the Campylopodioideae. Journal of the Hattori Botanical Laboratory 69: 65-78.

______. 1994. The affinities between the *Campylopus* floras of Sri Lanka and Madagascar - or: which species survived on Noah's Arc ? Hikobia 11: 371-376.

______ & Frey, W. 1987. The twist mechanism in cygneous setae of the moss genus *Campylopus*. Morphology, structure and function. Nova Hedwigia 44: 291-304.

Gangulee, H.C. 1971. Mosses of eastern India and adjacent regions. A monograph. Fascicle 2. Archidiales, Dicranales & Fissidentales. Systematic Biology.

Calcutta.

Gao, C. & T. Cao. 1992. A synopsis of Chinese *Dicranum* (Dicranaceae, Musci). Bryobrothera 1: 215-220.

Goldblatt, P. 1993. Fragmentation of Gondwana: the separation of Africa and South America, pp. 3-14. In: P. Goldblatt (ed.), Biological relationships between Africa and South America. Yale University Press, New Haven.

Graham, L.E., C.F. Delwiche & B.D. Mishler. 1991. Phylogenetic connections between the "green algae" and the "bryophytes". Advances in Bryology 4: 213-244.

Hasegawa, J. 1994. New classification of Anthocerotae. Journal of the Hattori Botanical Laboratory 76: 21-34.

Hedenäs, L. 1994. The basal pleurocarpous diplolepidous mosses - a cladistic approach. The Bryologist 97: 225-243.

______. 1995. Higher taxonomic level relationships among diplolepidous pleurocarpous mosses - cladistic overview. Journal of Bryology 18: 723-781.

Hennig, W. 1966. Phylogenetic Systematics. University of Illinois Press, Chicago.

Huelsenbeck, J.P. & J.J. Bull. 1996. A liklihood ratio test to detect conflicting phylogenetic signal. Systematic Botany 45: 92-98.

Humbert, H. 1955. Les territoires phytogéographiques de Madagascar. Leur cartographie. Ann. Biol. (Paris) 31: 439-448.

Hyvönen, J. 1989. A synopsis of the genus *Pogonatum* (Polytrichaceae). Acta Botanica Fennica 138: 1-87.

______ & S. Piippo. 1993. Cladistic analysis of the hornworts (Anthocerotophyta). Journal of the Hattori Botanical Laboratory 74: 105-119.

Kis, G. 1985. Mosses of southeast tropical Africa. An annotated list with distributional data. Vácrátót, Hungary, Instutute of Ecology and Botany of the Hungarian Academy of Sciences.

Koechlin, J. 1972. Flora and vegtation of Madagascar, pp. 145-199. In: R. Battistini & G. Richard-Vindard (eds.). Biogeography and ecology in Madagascar. W. Junk, The Hague.

Koponen, T. 1968. Generic revision of Mniaceae Mitt. (Bryophyta). Annales Botanici

Fennici 5: 117-151.

La Farge-England, C. 1996. Growth form, branching pattern, and perichaetial position in mosses: cladocarpy and pleurocarpy redefined. The Bryologist 99: 170-186.

Livingston, D.A. 1993. Evolution of African climate, pp. 455-472. In: P. Goldblatt (ed.), Biological relationships between Africa and South America. Yale University Press, New Haven.

Loveland, H.F. 1956. Sexual dimorphism in the moss genus *Dicranum* Hedw. Ph.D. Dissertation, University of Michigan, University Microfilms, Ann Arbor.

Lovett, J.C. 1988. Endemism and affinities of the Tanazanian montane rainforests flora. Monographs in Systematic Botany from the Missouri Botanical Garden 25: 591-598.

Maddison, W.P. 1993. Missing data versus missing characters in phylogenetic analysis. Systematic Biology 42: 576-581.

______ & D.R. Maddison. 1992. MacClade analysis of phylogeny and character evolution. Version 3. Sunderland, Mass.: Sinauer Associates, Inc.

______, M.J. Donoghue & D.R. Maddison. 1984. Outgroup analysis and parsimony. Systematic Zoology 33: 83-103.

Maisey, J.G. 1993. Tectonics, the Santana Lagerstätten, and the implcations for the late Gondwanan Biogeography, pp. 435-454. In: Goldblatt, P. (ed.). Biological relationships between Africa and South America. Yale University Press, New Haven.

Mishler, B.D. 1994. Cladistic analysis of molecular and morphological data. American Journal of Physical Anthropology 94: 143-156.

______ & S.P. Churchill. 1985. Transition to a land flora: phylogenetic relationships of the green algae and bryophytes. Cladistics 1: 305-328.

______ & E. De Luna. 1991. The use of ontogenetic data in phylogenetic analyses of mosses. Advances in Bryology 4: 121- 167.

______, L.A. Lewis, M.A. Buchheim, K.A. Renzaglia, D.J. Garbary, C.F. Delwiche, F.W. Zechman, T.S. Kantz & R.L. Chapman. 1994. Phylogenetic relationships of the "Green Algae" and "Bryophytes". Annals of the Missouri Botanical

Garden 81: 451-483.

Mueller, C. 1948-1951. Synopsis muscorum frondosorum omnium hucusque cognitorum pars prima. Musci vegetationis acrocarpicae. 812 pp. Pars secunda. Musci vegetationis pleurocarpicae. 772 pp. Berolini: Alb. Foerstner.

Nicoll, M.E. & O. Langrand. 1989. Madagascar: Revue de la conservation et des aires protégées. World Wide Fund for Nature, Gland, Suisse.

Norris, D.H. & T. Koponen. 1989. Typification of *Dicranoloma* Ren., a small genus of mosses from northern Australia and New Caledonia. Acta Bryolichenologica Asiatica 1: 1-4.

______ & ______. 1990. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXXV. Dicranaceae and Dicneonaceae (Musci). Acta Botanica Fennica 1: 1-64.

Nyholm, E. 1954. Musci. Vol. II, Fasc. I, pp. 1-87. In: The Botanical Society of Lund (ed.), Illustrated flora of Fennoscandia. CWK Gleerup, Lund.

Peterson, W. 1979. A revision of the genera *Dicranum* and *Orthodicranum* (Musci) in North America north of Mexico, 453 pp. Ph.D. Thesis, University of Alberta, Edmonton, Alberta.

Pócs, T. 1975. Affinities between the bryoflora of East Africa and Madagascar. Boissiera 24: 125-128.

Prance, G.T. 1982. Forest refuges: evidence from woody angiosperms, pp. 137-158. In: G.T. Prance (ed.). Biological diversification in the tropics. Columbia University Press, New York.

Procter, M.C.F. 1979. Structure and Eco-physiological adaptation in bryophytes, pp. 479-509. In: G.C.S. Clarke & J.G. Duckett (eds.), Bryophyte Systematics. Systematics Association Special Volume 14. Academic Press, London.

Rabinowitz, P.D., M.F. Coffin & D. Falvey. 1983. The separation of Madagascar and Africa. Science 220: 67-69.

Raven, P.H. & D.I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Annals of the Missouri Botanical Garden 61: 539-673.

Renauld, F. 1898. Prodrome de la flore bryologique de Madagascar des Mascareignes et des Comores publié par ordre de S.A.S. Le Prince Albert 1er. 296 pp. Imprimerie Monaco.

______. 1901. Nouvelle classification des *Leucoloma*. Revue Bryologique et Lichénologique 28: 66-70.

______. 1909. Essai sur les *Leucoloma* et supplément au prodrome de la flore bryologique de Madagascar des Mascareignes et des Comores. 139 pp. Imprimerie Monaco.

Sainsbury, G.O.K. 1955. A handbook of the New Zealand mosses. Royal Society of New Zealand, Bulletin 5: 1-490.

Slowinski, J.B. 1993. "Unordered" versus "ordered" characters. Systematic Biology 42: 155-165.

Smoot, E.L. & T.N. Taylor. 1986. Structurally preserved fossil plants from Antarctica: II. A Permian moss from the Transantarctic mountains. American Journal of Botany 73: 1683-1691.

Stevens, P.F. 1984. Homology and phylogeny: morphology and systematics. Systematic Botany 9: 395-409.

______. 1991. Character states, morphological variation, and phylogeneticanalysis: A review. Systematic Botany 16: 553-583.

Storey, M., J.J. Mahoney, A.D. Saunders, R.A. Duncan, S.P. Kelley & M.F. Coffin. 1995. Timing of hot spot-related volcanism and the breakup of Madagascar and India. Science 267: 852-855.

Swofford, D.L. 1993. Phylogenetic analysis using parsimony,ver.3.1.1. Computor program distributed by the Illinois Natural history Survey, Champaign, Illinois.

Takaki, N. 1966. A revision of Japanese *Dicranoloma*. Journal of the Hattori Botanical Laboratory 29: 214-222.

Tan, B.C. & T. Koponen. 1983. *Dicranoloma* (Musci, Dicranaceae) in Southeast Asia, with a special reference to the Philippine taxa. Annales Botanici Fennici 20: 317-334.

Tixier, P. 1993. Bryophyta exotica. Récoltes de F. Friedmann aux Seychelles (1987).

Proceedings of the Royal Society of Arts and Sciences of Mauritius 5 (3): 49-53.

Vitt, D.H. 1981. Adaptive modes of the sporophyte. The Bryologist 84: 166-186.

______. 1995. The genus *Calomnium* (Bryopsida): taxonomy, phylogeny, and biogeography. The Bryologist 98: 338-358.

______ & Ramsay, H.P. 1985 The *Macromitrium* complex in Australasia (Orthotrichaceae: Bryopsida). Part I. Taxonomy and phylogenetic relationships. Journal of the Hattori Botanical Laboratory 59: 325-451.

Walther, K. 1983. Bryophytina. Laubmoose, pp. In: J. Gerloff & J. Poelt (eds.), A. Engler's Syllabus der Pflanzenfamilien. Aufl. 13. V(2): 1-108. Berlin.

Watrous, L.E. & Q.D. Wheeler. 1981. The out-group comparison method of character analysis. Systematic Zoology 30: 1-11.

White, F. 1983. The Vegetation of Africa. Natural Resources Research 20. UNESCO, Paris.

Wiley, E.O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. New York: John Wiley & Sons.

Zander, R. 1993. Genera of the Pottiaceae: mosses of harsh environments. Bulletin of the Buffalo Society of Natural Sciences 32: 1-378.

Zomlefer, R. 1993. A revision of *Rigodium* (Musci: Rigodiaceae). The Bryologist 96: 1-72.

Chapter IV

GROWTH FORM, BRANCHING PATTERN, AND PERICHAETIAL POSITION IN MOSSES: CLADOCARPY AND PLEUROCARPY REDEFINED[1]

Introduction

Structural analyses of growth form, branching pattern, and perichaetial position form an integral component of systematic revisions. However in the recent publications, authors have used the same terms with different inferences (e.g., life form for growth form, pleurocarpy for prostrate growth form, pseudo-pleurocarpy for cladocarpy, pleurocarpy for cladocarpy), and this has resulted in confusion. Consistent use of terms in comparative and phylogenetic analyses is essential and will help determine the systematic value of these features as potential homologues. The objectives of this paper are to 1) review how terms have been applied to growth form, branching patterns, and perichaetial position, with a re-evaluation of cladocarpy and 2) provide a classification of terms with amended definitions.

The structural organization of the moss gametophyte is diverse, despite the comparatively simple organism. Most mosses have erect or prostrate leafy stems with respect to horizontal substrates, whereas some develop perpendicular or pendulous stems on vertical substrates (e.g., cliffs, tree trunks, branches, and lianas). Mosses form unbranched to multibranched axes with diverse patterns of length, frequency, and position of the branches (Meusel 1935). The development of a structural hierarchy of branches from the main axis is common, with some mosses having secondary or even tertiary branches.

Branches originate from lateral initials that occur in the outer cortical tissue (Berthier 1972). Along the developed branch, the first leaves are reduced in size and some are morphologically distinct from leaves produced later (Mishler & De Luna 1991). This heteroblastic sequence of leaves differentiates each connected branch.

---

[1] A version of this chapter was published in The Bryologist 99: 170-186, 1996

Most often, branches develop along the stem in two directions: from the apex downward and from the base upward. These developmental sequences ultimately affect the branching pattern.

Two basic branching patterns are found in mosses; one is a chain of connected branches of the same hierarchy; the other is a series of independent (or unconnected) branches developed along a supporting axis of a lower hierarchy. These two patterns can potentially be found at any given level of structural hierarchy.

In mosses, perichaetia are found in one of three basic positions 1) terminal on the primary axis; 2) terminal on lateral branches; or 3) terminal on lateral innovations that appear sessile and lateral along the primary or supporting axis. Individual species are characterized by a single position, indicating that the distribution of perichaetia is conservative.

Previous Definitions

Life and Growth Form

One of the earliest papers on bryophyte "growth forms" was based on tropical rainforest epiphytes (Geisenhagen 1910). A critical treatise on growth form ("Wuchsformen") of European mosses emphasized the general, structural organization of the plant (Meusel 1935). Subsequent literature on the classification of growth form has had an ecological emphasis (During 1979, 1990; Gimingham & Birse 1957; Horikawa & Ando 1952; Iwatsuki 1960; Mägdefrau 1982; Richards 1984, Proctor & Smith 1995). A comprehensive review of growth forms from an ontogenetic perspective was presented by Mishler and De Luna (1991). Other systematic studies have examined branch development in association with related structures - pseudoparaphyllia and scaly leaves, rhizoids, and phenology (Akiyama & Nishimura 1993, Ireland 1971, Koponen 1982, Stark 1985, respectively). However, there are few detailed systematic studies on growth form (Deguchi 1978; Nishimura 1985; Zomlefer 1993).

Mägdefrau (1982) restricted the germane use of the term growth form (Gimingham & Birse 1957) by the introduction of the term life form. He defined life form as "the habit of a plant in harmony with its life conditions,...the morphological structure of the colony of individuals, the growth form, and modification by external factors". Growth form was defined as the moss shoot or individual, which "has a genetically fixed method of ramification, depending on species, genus or family" (Mägdefrau 1982). His distinction between growth form and life form is clear: the former refers to an individual plant, whereas the latter refers to an aggregate or colony of individuals.

In Mägdefrau's (1982) classification of growth forms, direction of growth is primary: orthotropic versus plagiotropic. The misleading concept of his classification was that he equated orthotropic and plagiotropic with fruit terminal versus lateral, respectively. This feature of growth form - direction of growth - has often been included in the definition of pleurocarpy and acrocarpy (Flowers 1973; Magill 1990; Schofield & Hébant 1984; Smith 1978). As well, acrocarpy and pleurocarpy have been described as the two basic "growth forms" in mosses (Mishler & De Luna 1991). However, growth form is based on the structural development of the shoot and branches of an individual plant, including frequency, length, and orientation of the branches (branch system, *sensu* Mishler & De Luna 1991). Perichaetial position is independent of growth form and should be treated separately (Table.IV.1).

Recently, Buck and Vitt (1986) defined two types of branching in pleurocarpous mosses: cauline and axillary. Cauline branches develop on the stem between the leaves, whereas axillary branches develop in the axils of the stem leaves. They designated cauline lateral branching, and pseudoparaphyllia as unique synapomorphies to distinguish the true pleurocarpous clade (Hypnales, Hookeriales, and Leucodontales), from the acrocarpous and pleurocarpous clade (Bryales). The "pleurocarpous" taxa within the Bryales were defined as having axillary branching.

Subsequently, Hedenäs (1994) considered cauline versus axillary branches in a phylogenetic analysis of selected pleurocarpous taxa, and he observed that both cauline and axillary branch position occur in pleurocarps. He concluded that branch position was too variable to be informative. Beside the variability, many pleurocarps have densely foliate axes, which may preclude the determination of an axillary versus cauline position (e.g., *Spiridens flagellosus*).

A single type of lateral branch development has been described for mosses, whether cauline or axillary in position (Berthier 1972; Chamberlain 1980 - *Fissidens;* Crandall 1969 - *Fontinalis*; *Leucoloma* pers. observ.). The ultimate position of a lateral branch is determined by the amount of cell elongation and number of cell divisions between the branch primordium and the leaf above it, and the primordium may be displaced to an axillary position of the leaf below it (e.g., *Funaria hygrometrica, Hypnodendron marginatum*).

The terms used for growth form have been intermixed with life form, perichaetial position, and branching patterns or types. The separation of the terms into distinct categories facilitate understanding of the them (see Terms).

Branching Patterns

Fragile subapical or lateral innovations have been described as "epigametophytic plants" in *Leucophanes* (Salazar-Allen, 1985). Transverse sections have shown a basal constriction of the branches at the attachment to the main axis, and this constriction causes the branches to be fragile and easily detached. The fragile or tenuous nature of the branches has led to their interpretation as epigametophytic. Until now, the origin of these branches has not been well understood. These epigametophytic plants are derived from loosely attached, fragile, deciduous branches. This type of fragile branching is common in *Leucoloma* (e.g., *L. holstii*) and has been reported for other genera in the Dicranaceae (Newton & Mishler 1994). These branches form either a sympodial pattern from subapical innovations or a monopodial branching pattern from lateral innovations not associated with a terminal perichaetium (e.g., *Leucophanes hildebrandtii* and *L. octoblepharoides*). In *Leucoloma*, the sequence of branch development is from a nonprotruding lateral primordium, to a protruding primordium, to an immature branch with juvenile leaves, to a mature, branch that is fragile.

Sympodial branching has been misinterpreted as monopodial in a number of revisionary studies (e.g., Horton 1982; Lewinsky 1993). In both *Encalypta* and

Orthotrichum, the subapical innovations develop a chain of primary modules that form the primary branch system, which is a sympodial pattern.

Some authors have associated branching patterns with perichaetial position: acrocarpy with sympodial branching, and pleurocarpy with monopodial branching (De Luna 1995). Although there is a general correspondence, the terms should be considered separately, for both types of branching occur in plants with all types of perichaetial positions (Figs.IV.1,2). Sympodial branching is not restricted to subterminal innovations, rather it is formed by a chain of branches of the same hierarchy (e.g., basal innovations in *Climacium dendroides*). As well, monopodial and sympodial branching occur together within a single species (e.g., *Hylocomium splendens*, *Leucoloma dichelymoides*).

A system for analyzing the hierarchy of branches in mosses was presented by Mishler and De Luna (1991). The structural organization of an individual moss includes the shoot, branch, modular, and metamer (at the cellular level) systems. These ontogenetic components provide useful tools for analyzing gametophyte structure. Meusel (1935) was the first person to provide a comprehensive survey of branching patterns in mosses and little has followed in the interim. Branching patterns in mosses have been little studied and warrant further investigation to evaluate the evolutionary significance of these patterns.

Perichaetial Positions

Bridel (1819) classified species based on the position of the perichaetium. The terms *acrocarpi* and *pleurocarpi* were introduced by Nees von Esenbeck et al. (1823). In Latin, the terms mean terminal and lateral fruit, respectively (Stearn 1983). Mitten (1859) was the first to question the phylogenetic significance of acrocarpy and pleurocarpy, and established a classification based primarily on peristome characters. The primary divisions, *acrocarpi* and *pleurocarpi*, were also rejected by Fleischer (1902-1923) and replaced by peristome criteria.

Pleurocarpy (*sensu lato*) has been recognized as a feature, independently derived within the separate lineages of mosses (Brotherus 1924-1925; Cavers 1911;

Crosby 1980, Crum & Anderson 1981; Dixon 1932; Mitten 1859). In the most recent synopsis of the Bryopsida, Vitt (1984) designated the following families to have independently derived "pleurocarpy": Calymperaceae, Fissidentaceae, Gigaspermaceae, Leucobryaceae, Pleurophascaceae, Pottiaceae, Rhizogoniaceae, and Spiridentaceae. The Hookeriales, Hypnales, and Leucodontales were defined as completely pleurocarpous (true pleurocarpy). Crum has viewed the Orthotrichales as the transitional order between acrocarpous and pleurocarpous orders (Crum & Anderson 1981). The occurrence of pleurocarpy within so many disparate lineages (Vitt 1984) has prompted a re-examination of the definition of pleurocarpy and its distribution within mosses.

Superficially, the distinction between acrocarpy and pleurocarpy is not obvious for all taxa (De Luna 1990; Mitten 1859, p. 3). Some prostrate mosses have been misclassified initially as pleurocarps (*Leucoloma* Bridel 1827; *Sclerodontium* Crum 1986), but later determined as acrocarps (*Hedwigia ciliata* De Luna 1990; *Rhacocarpus purpurascens* this paper). Prostrate acrocarps that have laterally displaced, terminal perichaetia due to subperichaetial branching, have been termed pseudo-pleurocarpous. Vitt (1984) referred to the Orthotrichineae as an acrocarpous suborder with a pseudo-pleurocarpous condition in some of the genera. Two genera referred to as pseudo-pleurocarpous, *Macromitrium* and *Schlotheimia*, are cladocarpous (see below). Proctor and Smith (1995) defined *Cinclidotus* as a "pseudo-pleurocarpous" genus, even though Smith (1978) described the Cinclidotoideae as cladocarpous. Thus, the distinction between cladocarpy and acrocarpy has remained unclear in publications. Pseudo-pleurocarpy is a growth form modification and does not represent a distinct perichaetial position. It is proposed here that this term be dropped to avoid further confusion. A similar term that has been applied to the Hedwigiaceae and Orthotrichaceae is "pseudoakrocarp" (Meusel 1935, p. 266), although a formal definition of the term has not been found.

Cladocarpy is another term that has been used for perichaetial position. It was designated as one of six classes for the perichaetial position in *Sphagnum* and

Archidium (Bridel 1826). Mueller (1949) did not use *cladocarpi* as a formal division, although he designated several taxa within the subclass of acrocarpous taxa as cladocarpous, and stated that some pleurocarpous taxa often approach cladocarpy. As well, Schimper (1860) did not use cladocarpy as a formal division of mosses. In an artificial classification of the genera, Lesquereux and James (1884) used the term cladocarpi for *Fontinalis, Dichelyma* and *Cryphaea*. Fleischer (1904-1923) used the term cladocarp with reference to mosses that produce terminal perichaetia on lateral branches. Commonly, cladocarpy has been defined as a type of pleurocarpy (Frey 1971; Magill 1990; Mishler & De Luna 1991).

The distinction remains unclear between cladocarps and acrocarpous taxa with basitonous branches that produce terminal perichaetia. The Rhizogoniaceae were included within the concept of pleurocarpy (*sensu lato*) by Buck and Vitt (1986), whereas Koponen (1988) considered them an acrocarpous family. Koponen (1988) interpreted the perichaetial position of taxa in *Pyrrhobryum* sect. *Pyrrhobryum* as acrocarpous. These taxa develop terminal perichaetia on branches of determinant sterile shoots or branches of other fertile shoots (see cladocarpy in Terminology). Buck and Vitt (1986) described the family as pleurocarpous based on the interpretation of "non-terminal perichaetia", because the primary axis does not terminate with perichaetia.

Additional confusion exists between cladocarpy and pleurocarpy. Cladocarpy is commonly referred to as perichaetia on short lateral branches and pleurocarpy as perichaetia lateral. If the only difference between cladocarpy and pleurocarpy is the length of the lateral branch, when is there sufficient branch development to determine a cladocarp? For example, Lawton (1971) defined pleurocarpy as "having archegonia and later seta and capsule on short side branches and not at the apices of stems or branches" (e.g., *Homalothecium megaptilum* and *Hylocomium splendens*). Her definition of cladocarpy, "having fruit terminal on short lateral shoot", is difficult to differentiate from her definition of pleurocarpy. Dixon (1924) noted the difficulty of many pleurocarpous mosses with perichaetia that "appear to be terminal on very short lateral" branches. He explained that examination of the axis will show that it is "only an elongation of the perichaetium, originating in a lateral bud on the stem, containing the archegonia; the elongation taking place after fertilization...". This difference warrants clarification.

This difficulty in distinguishing cladocarpy from pleurocarpy is exemplified by the following: True pleurocarps (*sensu* Buck & Vitt 1986) are typified by lateral perichaetia, that lack branch elongation. Hand sections through the lateral perichaetial axes of species of *Aerobryidium, Daltonia, Drepanocladus, Hypnum, Leucomium, Neckera, and Rhytidiadelphus* show minimal development below the unfertilized perichaetium. Yet in some cladocarpous species, the perichaetial axes of *Anoectangium aesitivum, Fissidens cristatus*, and *Mielichhoferia bryoides* are extremely reduced. The question remains, are the perichaetial axes of true pleurocarps developmentally the same as cladocarps with extremely reduced axes, or is the reduced axis length an example of convergent evolution (Tables IV.1,2; Terms)?

Hedenäs (1994) defined a pleurocarpous, diplolepideous moss as "a diplolepideous moss...where the sporophytes are inserted on shortened and laterally inserted, specialized, perichaetial branches, with only more or less specialized leaves (perichaetial leaves)". He does not distinguish cladocarpy. This is evident from his character analysis where he defines perichaetial position as having two states: "archegonia terminal on shoots or on apparently undifferentiated branches (0) or archegonia on short specialized branches (always with more or less strongly modified perichaetial leaves) (1)". His classification of *Schlotheimia*, coded as state (0 or 1), indicates that he considers it polymorphic - cladocarpous and pleurocarpous (Hedenäs 1994, p. 235). My examination of *S. appressifolia, S. robusticuspis, S. serricalyx*, and *S. torquata* indicates that all of these species are cladocarpous. The perichaetia are terminal on lateral branches of the primary axis and have subperichaetial innovations. In Hedenäs' analysis, acrocarpy and cladocarpy are coded as the same state.

With respect to the evolution of acrocarpy, cladocarpy, and pleurocarpy, a number of conceptual differences are present. Vitt (1984) described a "hypothetical, primitive Bryalean moss" as acrocarpous and interpreted pleurocarpy as an "derived" condition, whereas Miller (1971) was noncommital. Cladocarpy has been inferred as a transitional state between acrocarpy and pleurocarpy (Crum & Anderson 1981; De Luna 1995 - the use of ordered character states; Hedenäs 1994). Elsewhere, cladocarpy has been defined as a specialized type of pleurocarpy (Mishler & De Luna 1991).

Several questions arise from the current usage of terminology of perichaetial position 1) Is pleurocarpy distinct from cladocarpy? 2) Is cladocarpy related to acrocarpy? 3) Should cladocarpy be recognized as a distinct category of perichaetial position? 4) Are there any attributes of cladocarpy, acrocarpy, or pleurocarpy that have been overlooked as distinguishing features? and 5) Are there any evolutionary implications based on the distribution of the perichaetial types within the Bryopsida?

Terms

The terms related to moss structure and perichaetial position can be classified into four categories: life form, growth form, branching pattern, and perichaetial position (Table IV.1). The amended definitions presented here are based on the examination of specimens cited in Table IV.2. These categories provide a system pf terms that can be applied independently to each species examined.

Life Form

Life form is the overall organization of growth form, branching pattern, general assemblage of individuals, and modification of a population by the environment (e.g., cushions, turfs, wefts; Table IV.1). There is a diverse range of moss life forms that have an integral relationship with their microhabitat (During 1990; Mägdefrau 1982; Richards 1984). For example, cushions are compact tufts of erect stems that commonly form in dry, exposed habitats (e.g., *Grimmia anodon*, on rock outcrops). The density of the stems provides protection against desiccation of the individual plants (During 1990). Thus, the aggregate population functions as a single life form providing an adaptation to its xeric habitat. Environmental modification of the life form of a population is evident in *Hylocomium splendens*, which forms prostrate wefts under mesic forest conditions or erect turfs in exposed, tundra habitats (During 1990;

Schofield & Hébant 1984). Life form is the overall structure of a group of individuals occurring in a specific habitat.

Growth Form

Growth form is the structural architecture of the individual moss plant (Table IV.1). The structure of an individual plant can be analyzed as a hierarchy of modules (Fig. IV.1; Mishler & De Luna 1991). A module is the product of a single apical meristem (White 1984).

The direction of growth in mosses is varied and depends on factors such as gravity, phototropism, and substrate. Orthotropic taxa have erect growth, whereas plagiotropic taxa have prostrate growth. Ascending stems are an intermediate direction. Horizontal growth, defined as perpendicular on vertical substrates, is common for epiphytic mosses in the tropics (e.g., *Rutenbergia* on tree trunks, *Daltonia* on bamboo stems). Within taxa classified as pendulous ("drooping", e.g., Meteoriaceae), some species have downward, outspreading stems (e.g., *Leucoloma sanctae-mariae, Neckera pennata*). The direction of growth may change during the maturation of an individual plant.

In certain mosses, the stems are unbranched (e.g., *Leptobryum pyriforme*; Fig. IV.1a), while other mosses develop simple branched stems by one to several subapical innovations for continued growth (e.g., *Dicranum, Grimmia, Orthotrichum*; Fig. IV.1b). Some mosses produce subapical whorls of branches (e.g., *Philonotis fontana*; Fig. IV.1c). Mosses with complex branch development (cladotaxies) produce lateral, secondary branches at either irregular or regular intervals (e.g., *Amblystegium* spp., *Cinclidotus fontinaloides*, respectively) or pinnate branches (e.g., *Ptilium crista-castrensis*). *Heterocladium macounii* is tripinnate, developing a hierarchy of four branch levels. The frequency of branch primordia does not necessarily imply the development of branches. In acrocarpous or cladocarpous species naked primordia or innovations with the initial juvenile leaf development are usually visible, when the leaves are removed from a stem or branch (*Leucoloma, Macromitrium*). In pleurocarps, the lateral primordia develop immediately into branches or lie dormant as buds or primordia along the axes (e.g., *Climacium, Neckera*). The distribution of the primordia or buds varies between taxa, resulting in diverse cladotaxies (Fig. IV.1; Koponen 1982). The branch length can be highly variable within a species (e.g., *Racomitrium lanuginosum*, Tallis 1959) or follow a predictable pattern (e.g., *Ptilium*). Physiological factors have a direct effect on the patterns of development, maturation of branches, and ultimately growth form (Chopra & Kumra 1988).

Basitonous and acrotonous branching are two specialized branch positions (Table IV.1). Mosses with basitonous branches develop branches at the proximal end of a module (e.g., *Rhizogonium novae-hollandiae*; Bryineae - Fig. IV.3), whereas mosses with acrotonous branches have branch development restricted to the distal end of a module (e.g., *Orthotrichum* spp.; Figs. IV.1a-c).

Branching Patterns

Two basic patterns of branching are sympodial and monopodial; each consisting of a hierarchy of modules (Table IV.1). A sympodial pattern has a chain of connected modules from the same level of branch hierarchy. For example, a primary branch system consists of a series of primary modules. A primary module is the first axis of a gametophore, or it is the product of a lateral initial that forms the primary branch system (Figs. IV.1a-g). The sympodial pattern occurs in acrocarps, cladocarps, and pleurocarps at various levels of the branch hierarchy (Meusel 1935; Figs. IV.1b,g; 2a-h,n).

The most common sympodial pattern in acrocarps is the primary branch system, derived from subapical innovations. The apical meristem of a primary module is consumed in the production of the archegonia, or vegetative if the apical cell has been damaged. *Leucoloma albo-cinctum* develops a single subapical innovation, whereas *L. sanctae-mariae* commonly has two subapical innovations that form the primary branch system.

In pleurocarps, the terminus of a primary module is vegetative (Figs. IV.1f; 2d,h,l,p). A common sympodial branching pattern in pleurocarps is from the development of a lateral initial that develops a functional primary module. Examples of pleurocarpous species that can develop sympodial branching include *Climacium dendroides, Hylocomium splendens* (Fig. IV.1f), and *Thuidium matarumense* (Touw 1976). These species also have monopodial branching (see below).

Sympodial branching often occurs in secondary branch systems in some cladocarpous species (Fig. IV.1g). Chamberlin (1980) observed up to five, repeated secondary modules in *Fissidens cristatus* that form a sympodial pattern. Lateral branches with terminal perichaetia produce subapical innovations that in turn produce innovations below the terminal perichaetia (e.g., *Macromitrium loamense*, Fig. IV. 4h).

In monopodial branching, the branches are produced along the main axis by subsidiary, lateral innovations (Table IV.1, Figs. IV. 1h, 2i-p). These lateral branches form a series of unconnected 2° or 3° modules along a 1° or 2° module, respectively, whereas sympodial branches are a chain of connected modules of the same hierarchical level. Pinnately branched taxa are elegant examples of monopodial branching (e.g., *Ptilium crista-castrensis*). Bipinnate or tripinnate branches in Thuidiaceae are examples of secondary and tertiary monopodial branches (Fig. IV.1h).

Monopodially branched axes are common in pleurocarpous mosses, yet are not restricted to them. In monopodial development, leaf size is not interupted at the branching points along the supporting axis. Examples of monopodial branching in acrocarpous and cladocarpous taxa include: Dicranaceae: *Dicranoloma blumei, Dicranum scoparium, Leucoloma holstii, L. dichelymoides, L. humbertii, Leucophanes candidulum*; Fissidentaceae: *Fissidens* spp.; Grimmiaceae: *Racomitrium lanuginosum*; Pottiaceae: *Cinclidotus fontinaloides;* Rhacocarpaceae - *Rhacocarpus purpurascens*; and *Bryowijkia ambigua* (Fig. IV.2).

Perichaetial Positions

Acrocarpy, cladocarpy, and pleurocarpy are the three perichaetial positions in mosses. The definitions are presented in Table IV.1. The schematic illustrations of acrocarps (Figs. IV.1a-d; 2b,f,j,n), cladocarps (Figs. IV. 1g; 2c,g,k,o), and pleurocarps (Figs. IV.1f; 2d,h,l,p) illustrate a range of growth forms, but are not exhaustive.

In some acrocarpous mosses, a single subapical innovation develops and laterally displaces the terminal perichaetium (Figs. IV.1e; 2f). These sympodially branched, prostrate acrocarps possess a chain of primary modules, each terminating with a perichaetium (e.g., *Hedwigia ciliata, Racomitrium canescens, Rhacocarpus purpurascens*). Confusion with pleurocarpy is clarified by the heteroblastic leaf series along the single chain of primary modules (Berthier 1972, Mishler & De Luna 1991). At the base of each primary module, a series of juvenile leaves is present that indicates the development of a new branch. These leaves are generally reduced in size and differ morphologically from mature leaves. These subperichaetial branches are easily removed for the examination of the juvenile leaves. In contrast, pleurocarps have a branch system that has lateral perichaetia along a single module, with an uninterrupted leaf series. The leaf series does not change size or shape at the fruiting points.

The similarity between pleurocarpy to cladocarpy is that the apical meristem of the primary module (or axis) continues to grow during the production of the perichaetia at the terminus of lateral meristems (Table IV.1). However, distinction between cladocarpy and pleurocarpy is found in the sequence of leaf development on the perichaetial branch. In cladocarps, the lateral innovation initially develops juvenile leaves at the base of the branch, followed by a series of mature leaves that grade into perichaetial leaves and terminates with the production of archegonia (Fig. IV. 4i). The development of the juvenile leaves through mature leaf development is the same on a vegetative or perichaetial branch of cladocarps. The terminal development of the perichaetial leaves and perichaetium is equivalent to that in acrocarps.

In true pleurocarps, the sequence of leaf development is modified. The lateral innovation develops juvenile leaves that are morphologically different from the juvenile leaves of a vegetative branch (Fig.IV. 5). The transition from juvenile leaves to the perichaetial leaves is typically abrupt. The lack of elongation between the leaf nodes is in contrast to those of the vegetative branches. The perichaetial leaves and archegonia develop at the terminus of the innovation as in acrocarps and cladocarps, and the result is the production of lateral perichaetial branches (or buds - Ireland, 1982) along the primary module, that appear sessile (Fig.IV. 4a,b). The perichaetial leaves are typically enlarged and strongly differentiated from the mature vegetative leaves; as well the perichaetial branch is commonly swollen. These features differentiate vegetative branches from perichaetial branches in pleurocarps (Fig. IV.4a).

In the development of an apical meristem a lateral meristem (innovation), each metamer (*sensu* Mishler & De Luna 1991) produces a lateral branch initial cell (Berthier 1972). In cladocarpous taxa, primordia develop from the branch initials below the perichaetium that either remain dormant or develop further lateral branching (e.g., *Bryowijkia ambigua, Cinclidotus fontinaloides, Cryphaea exigua, Fissidens taxifolius, Macromitrium longifolium, Mesotus celatus, Pyrrhobryum spinneforme, Racomitrium lanuginosum*; Figs.IV. 4c-i). The dormant primordia (pale patches or protuberances of small meristematic cells) or dormant buds are visible along the axes. Abundant rhizoid development at the base of the perichaetial branch in cladocarps occurs often.

In true pleurocarps (e.g., *Hypnum, Hookeria*, and *Brachythecium*), the perichaetial branches have lateral branch initials that do not develop primordia below the perichaetia, and therefore lack subperichaetial branches (Figs.IV. 4a-b). The lateral innovations in pleurocarps have truncated branch development in which the perichaetium develops from a lateral bud (Dixon 1924). This pattern of development is termed paedomorphosis, or specifically progenesis - a process of heterochrony that exhibits an early cessation of growth in the descendent (Mishler & De Luna 1991). Heterochronic processes that alter rates of development provide potential for new phenotypes that are dramatically different from those of ancestors (Rothwell 1987). The distinctive features of pleurocarpous perichaetial branches are 1) the development of juvenile perichaetial leaves that are morphologically different from juvenile leaves of vegetative branches (Fig. IV. 5); 2) the lack of primordia or branching below the perichaetium (Fig. IV.4); 3) the appearance of swollen fertile branches in comparison to the vegetative branches; and 4) a general lack of rhizoid development at the base of the lateral perichaetial innovation.

Genera that have representative species for each of the combined categories - direction of growth, branching pattern, and perichaetial position are designated (Fig.

IV.2). Previously, these categories have been interpreted as linked, however no strict correlation occurs between any two terms. Therefore, pleurocarps are not restricted to a prostrate growth form, nor do acrocarps only have sympodial branching. A schematic diagram representing each possible combination of branching pattern, direction and perichaetial position is presented (Figs. IV.2a-p). Thus an independent assessment of growth form, branching pattern, and perichaetial position is advocated to evaluate the structural elements of a taxon for potential systematic value.

Implications of the revised system of Terms

The terms commonly used for the structural organization of mosses has been classified and amended. When defined precisely, these terms can be evaluated as potential synapomorphies for phylogenetic analyses. For example, what is the pattern of distribution for the multistate character, perichaetial position? Although the phylogenetic arrangement of the Bryopsida suborders (excluding Tetraphidales, Polytrichales, and Archidiineae) is provisional, and not meant as a rigorous cladistic analysis, it is used here as a framework for 14 major suborders of mosses (Vitt 1984, figs. 28,29). Subsequent modifications and interpretations of the phylogenetic relationships of the diplolepideous mosses have been recently published (Buck & Vitt 1986; De Luna 1995; Hedenäs 1994). Using the amended definitions presented here, the following hypotheses are proposed: 1) acrocarpy is the plesiomorphic state, with the Funariineae as the basal group (outgroup comparison: Polytrichales, Tetraphidales, and Andreaopsida; Vitt 1984); 2) cladocarpy has evolved independently within selected taxa of at least 11 distinct families (Table IV.2); and 3) pleurocarpy is restricted to the Hookeriineae, Hypnineae, and Leucodontineae (These lack any acrocarpous taxa (De Luna 1990, 1995; see below)).

Several implications follow from these proposals:

1) Buck and Vitt (1986) defined the Rhizogoniineae to include the Rhizogoniacanae and the Racopilacanae. After examination of representative species of *Racopilum* and *Hypopterygium*, I agree with Koponen (1988) that the Racopilanae should be classified in the pleurocarpous clades (as Vitt 1984). The Rhizogoniacanae

consists of the Rhizogoniaceae and the Spiridentaceae (Buck & Vitt 1986). Koponen (1988) interpreted the Rhizogoniaceae as acrocarpous, not pleurocarpous. Cladocarpy occurs in genera of the Rhizogoniaceae, with the perichaetia terminal on lateral, basitonous to acrotonous branches (Koponen 1988). *Pyrrhobryum spiniforme* and *Rhizogonium novae-hollandiae* have subperichaetial primordia and branching, that indicate cladocarpy. The Spiridentaceae and Hypnodendraceae are interpreted here as pleurocarpous. Brotherus (1909) placed *Spiridens* near *Bescherellia* and *Cryptopus*. This relationship should be reconsidered. With the removal of the Racopilacanae, Spiridentaceae and the Hypnodendraceae (Buck & Vitt 1986), the Bryales represent an acrocarpous-cladocarpous clade, concordant with the Dicranales, Fissidentales, Funariales, Grimmiales, Pottiales, and Orthotrichales.

2) *Rhacocarpus purpurascens* previously has been classified as a pleurocarp (Brotherus 1925; De Luna 1995; Vitt & Buck 1984). It is a prostrate acrocarp, with a monopodially and sympodially branched axis (Fig. IV.2f). Hence, the systematic position of the monotypic Rhacocarpaceae should be re-evaluated and its relationship to the Hedwigiaceae reconsidered.

As well, *Bryowijkia ambigua* has been classified as a pleurocarp and removed from the Hedwigiaceae (Hedwigiaceae - Brotherus 1925, Trachypodiaceae - De Luna 1995, Vitt & Buck 1984). The rationale for removing *Bryowijkia* from the Hedwigiaceae was based partially on a pleurocarpous interpretation (De Luna 1995) and its lack of subperichaetial branching (Vitt & Buck 1984). Vitt and Buck (1984) excluded it from all acrocarpous mosses based on profuse branching and from the Orthotrichaceae based on the lack of subperichaetial branching, elongate leaf cells, and differentiated alar cells. However, the perichaetia are terminal on well developed branches and subperichaetial branching is evident (Fig. IV. 4i). Consequently, *Bryowijkia ambigua* is a cladocarpous species that has a creeping primary axis and densely foliate, highly branched secondary axes with terminal perichaetia on tertiary branches. The dimorphic, primary versus secondary branch leaves, the densely papillose leaf cells, strong single costa, profusely branched plants without pseudoparaphyllia, densely foliate branches, and cladocarpy comply with the Orthotrichales. Therefore, a re-evaluation of the phylogenetic relationship of this genus should be considered.

3) *Cryphaea* (*Acrocryphaea* and *Dendrocryphaea* included) has a minimum of 11 cladocarpous species within the Leucodontineae (Table IV.2). It should be noted that the Hedwigiaceae and the Orthotrichaceae, two acrocarpous or acro-cladocarpous lineages, were once included within the Leucodontineae (Fleischer 1904-1923). Two explanations for the occurrence of cladocarpous taxa within predominantly pleurocarpous lineages are possible - 1) the Cryphaeaceae are basal within the Leucodontineae and the suborder is basal within the pleurocarpous lineages. This interpretation would support an evolutionary sequence: acrocarpy → cladocarpy → pleurocarpy; or 2) the cladocarpous taxa within the Cryphaeaceae were derived from pleurocarpous ancestors: acrocarpy → pleurocarpy → cladocarpy. Detailed phylogenetic analyses of the family and suborder will determine which evolutionary hypothesis is applicable for the cladocarps within the Cryphaeaceae. The results from De Luna (1995) suggest that *Cryphaea* represents a more derived genus within the Leucodontineae. As well, Vitt (1984) and Buck and Vitt (1986) have considered the placement of the Cryphaeaceae well within pleurocarpous families.

The data matrix of De Luna (1995) includes several critical taxa for testing perichaetial position. A re-analysis of De Luna's (1995) data matrix with perichaetial position recoded for *Rhacocarpus*, *Bryowijkia*, and *Cryphaea* (Table IV.2), indicates 3 reversals for this character.[2] Two interpretations of his cladogram are possible - 1) The

---

[2] A re-evaluation of the phylogenetic position of *Cryphaea glomerata*, *Bryowijkia ambigua* and *Rhacocarpus purpurascens* was made using DeLuna's data matrix (41 characters and 36 taxa) including his 6 ordered characters with the following modification - the perichaetial position was recoded for according to Table 2. The data were analyzed using Phylogenetic Analysis Using Parsimony (PAUP) version 3.1.1 (Swofford 1993). The initial heuristic search using an unmodified data set produced 1036 equally most parsimonious trees, with a length of 185 (CI= 0.218 for the strict and semistrict concensus trees), compared with De Luna's results of 288 equally most parsimonious trees (185 steps, CI=0.319). A second search with the perichaetial position recoded for *Cryphaea*, *Bryowijkia* and *Rhacocarpus* resulted in 36 equally most parsimonious trees of 188 steps. The semistrict and strict concensus trees had a CI = 0.874. The

position of these taxa is phylogenetically correct, thus the genetic control(s) determining perichaetial position is (are) less stringent than considered here, with reversals commonly occurring. Although, these reversals weaken the rationale to order the character states (De Luna 1995); or 2) the position of these taxa is not phylogenetically correct, and should be re-evaluated.

4) The distribution of perichaetial position within the 14 major clades of Bryopsida (Vitt 1984), shows three basic patterns: 1) 11 acrocarpous-cladocarpous lineages; 2) 2 pleurocarpous lineages; and 3) one cladocarpous - pleurocarpous lineage. Within the predominantly acrocarpous lineages, (e.g., Grimmiineae), a single genus can have two species with different perichaetial positions - acrocarpy versus cladocarpy (*Racomitrium canescens* and *R. lanuginosum*, respectively). As well, cladocarpy has evolved independently in four disparate (or non-sister group) genera of the acrocarpous Pottioideae (Pottiaceae): *Anoectangium*, *Ganguleea*, *Molendoa*, and *Pleurochaete* (Zander 1993). The development of cladocarpy from acrocarpy has apparently occurred repeatedly in unrelated lineages and at various taxonomic ranks (Fig. IV.3).

An alternative hypothesis that should be considered is the evolution of pleurocarpy directly from acrocarpy (Fig. IV.3). Both cladocarpy and pleurocarpy have vegetative apices on the primary axis and produce lateral innovations with terminal perichaetia. The control of branch length in these two groups may be the result of different developmental constraints (in cladocarpy - reduction, or in pleurocarpy - paedomorphosis, the "immediate" development of the perichaetium). Differences in the shape and the cellular arrangement of the apical cell region has been observed in

---

strict concensus tree produced was concordant with De Luna's strict concensus tree. A third search was run with the multistate character - perichaetial position as an unordered character. The results were 28 equally most parsimonious of 187 steps. The strict concensus tree had CI = 0.91, the semistrict tree was CI = 0.919.

The results from reanalysing De Luna's matrix with only the modified perichaetial position suggests that the character has 3 reversals. By unordering the character the length of the tree is shortened and the number of most parsimonious trees was reduced to 28. From this test of the perichaetial position there seems to be little evidence to order the character.

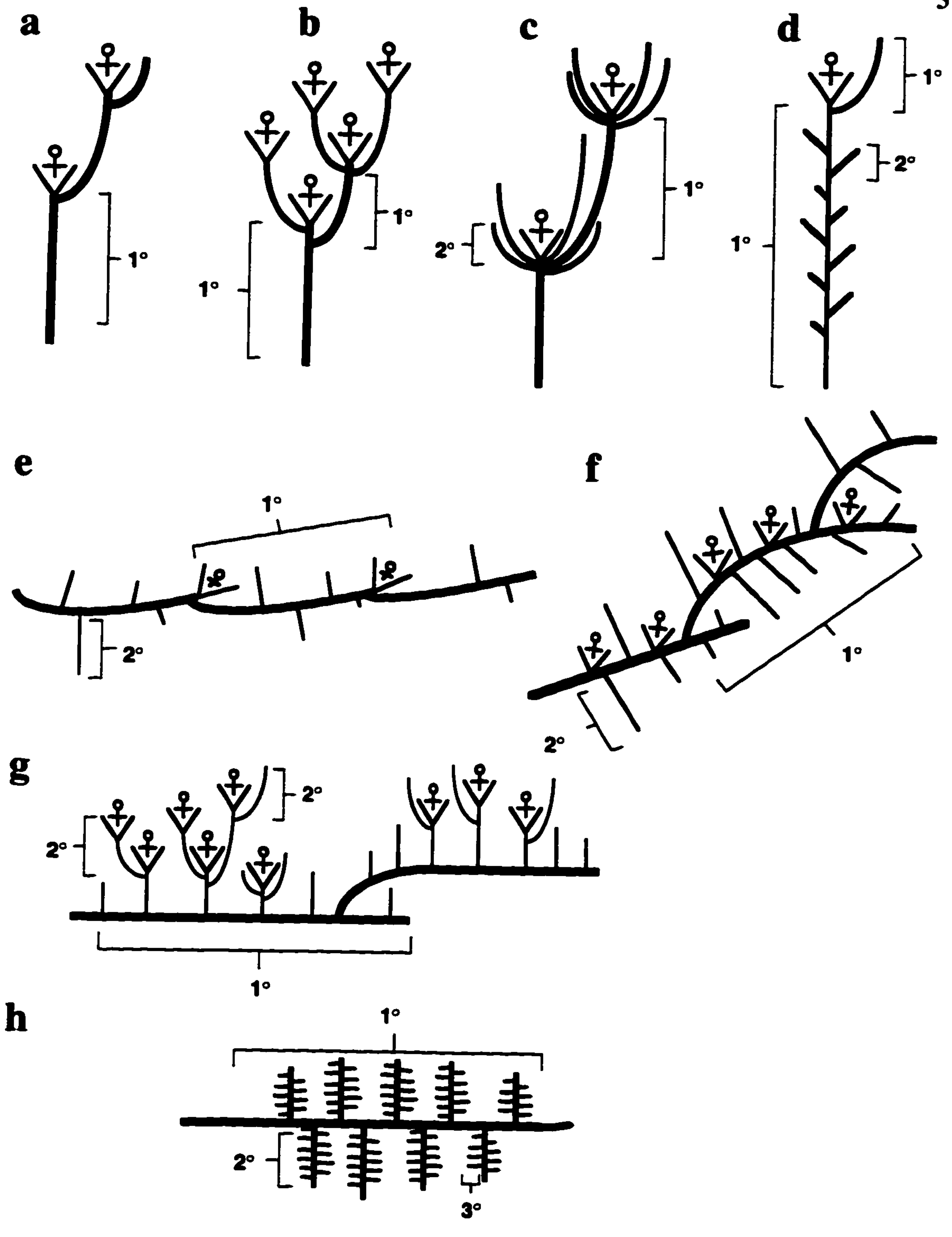
acrocarpous and pleurocarpous taxa (Frey 1971,1974). Developmental studies of the perichaetial branches in strongly reduced cladocarps and pleurocarps are needed to further clarify the distinctions. The phylogenetic position of the cladocarpous species in the Cryphaeaceae is central to the question of evolution of pleurocarpy. Therefore in choosing an outgroup for the pleurocarpous mosses, both acrocarpous and cladocarpous species should be considered. Detailed systematic analyses, such as on the subfamily Pottioideae (Zander 1993), are needed to evaluate the possible evolutionary pathways for perichaetial position.

Conclusions

A consistent use of terms regarding growth form, branching pattern, and perichaetial position provides a foundation for improved systematic analyses. The terms are classified into four distinct categories to emphasize independent assessment.

The classification of the terms for the structure of mosses and the amended definitions of perichaetial position in mosses present a framework for a more rigorous assessment of the structural organization of mosses. These will provide more robust characters in future phylogenetic analyses. The clarification of three distinct perichaetial positions may provide useful insights regarding the evolutionary relationships between mosses. Unless strict definitions of terms are applied, the terms may lack critical phylogenetic information.

Figure IV.1.a-h. Branching patterns, sympodial (a chain of modules) or monopodial (a series of unconnected modules along a supporting module), with modular components (1°) and perichaetial positions (♀) indicated: - a. sympodial, 1° modules develop from a single subapical innovation - acrocarp (terminal perichaetia). - b. sympodial, 1° modules from 2 subapical innovations - acrocarp. - c. sympodial, 1° modules develop from a single subapical innovation; monopodial, 2° modules determinant, from several subapical innovations (fasiculate) - acrocarp. -d-e. sympodial, 1° modules develop from a single subapical innovation; monopodial, 2° modules determinant lateral branches - acrocarps - f. sympodial, 1° modules develop from a single lateral innovation, 1° modules have vegetative apices; monopodial, 2° modules determinant lateral branches - pleurocarp (perichaetia terminal on lateral innovations). - g. sympodial, 1° modules develop from a single lateral innovation and have vegetative apices; sympodial; 2° modules from subapical innovations; monopodial, 2° modules from lateral innovations on 1° module - cladocarp (perichaetia terminal on lateral branches). - h. monopodial, 2° and 3° modules from lateral innovations on 1° or 2° module respectively.


a
b
c
d
1°
1°
1°
2°
1°
1°
1°
2°
e
f
1°
2°
1°
2°
g
2°
2°
1°
h
1°
2°
3°

	DIRECTION	PERICHAETIAL POSITION		
		acrocarpy	cladocarpy	pleurocarpy
SYMPODIAL	orthotropic	Funaria Fissidens Orthotrichum Leucoloma	Cinclidotus Anoectangium Fissidens	Hylocomium Hypnodendron Climacium
	plagiotropic	Hedwigia Sclerodontium Leucoloma Plagiomnium	Macromitrium Fissidens Mesotus	Hylocomium Thuidium
MONOPODIAL	orthotropic	Leucoloma Racomitrium Leucophanes Dicranum	Fissidens Racomitrium	Hylocomium Cratoneuron Calliergon
	plagiotropic	Leucoloma Dicranoloma Rhacocarpus	Macromitrium Fissidens Racomitrium Bryowijkia	Ptilium Hypnum Neckera Thuidium

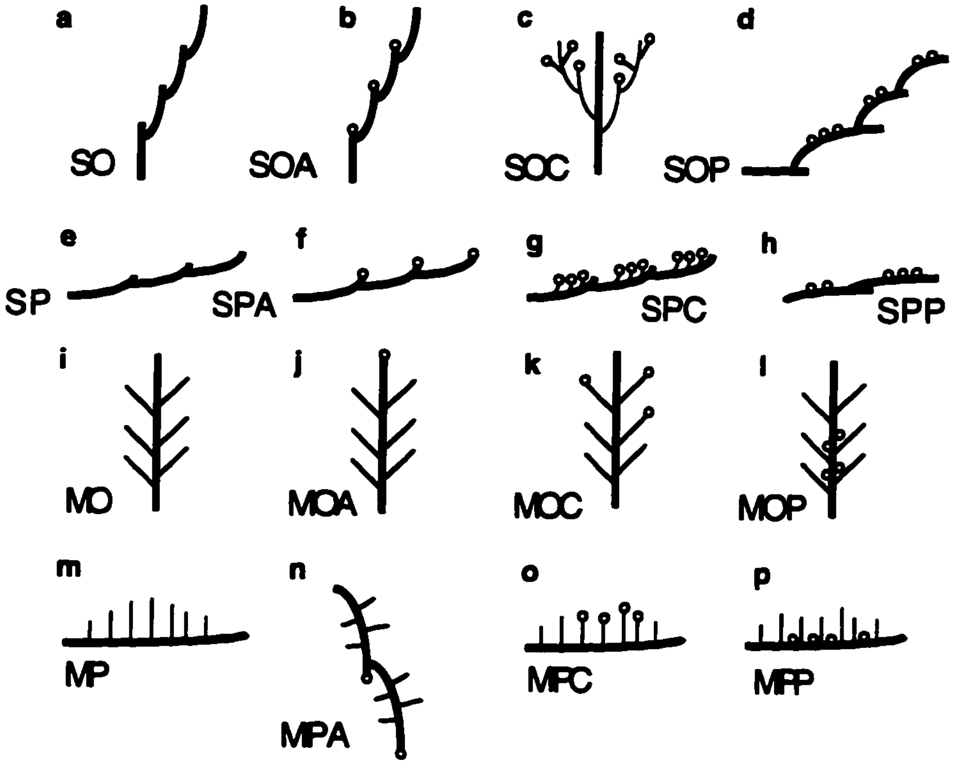


Figure IV.2. a-p. Genera that have species with the various combinations of direction of growth, branching pattern and perichaetial position. - a-p. S - sympodial; M - monopodial; O - orthotropic; P - plagiotropic; A - acrocarpous; C - cladocarpous; P - pleurocarpous.

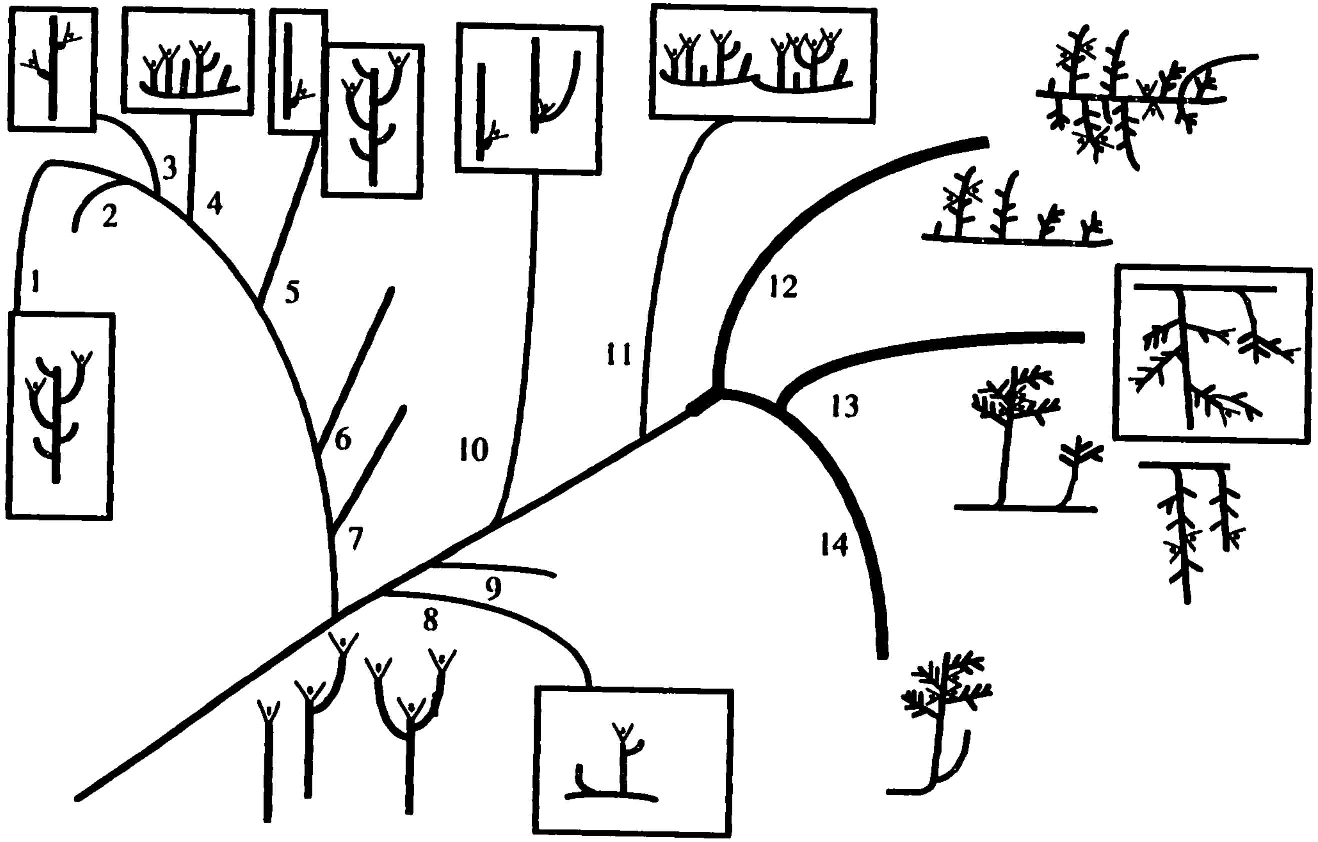


Figure IV. 3. A proposed cladogram based on Vitt (1984) and Buck and Vitt (1986), illustrating the 14 major lineages of arthrodonous mosses. The boxes indicate lineages where cladocarpous taxa occur. The thickened line indicates the pleurocarpous lineages. The thinner lines represent the acrocarpous lineages. The corresponding taxa for the numbered lineages are as follows: 1 - Grimmiineae, 2 - Seligeriineae, 3 - Fissidentineae, 4 - Dicranineae, 5 - Pottiineae, 6 - Encalyptineae, 7 - Buxbaumiineae, 8 - Funariineae, 9 - Splachnineae, 10 - Bryineae, 11 - Orthotrichineae, 12 - Hypnineae, 13 - Leucodontineae 14 - Hookeriineae.

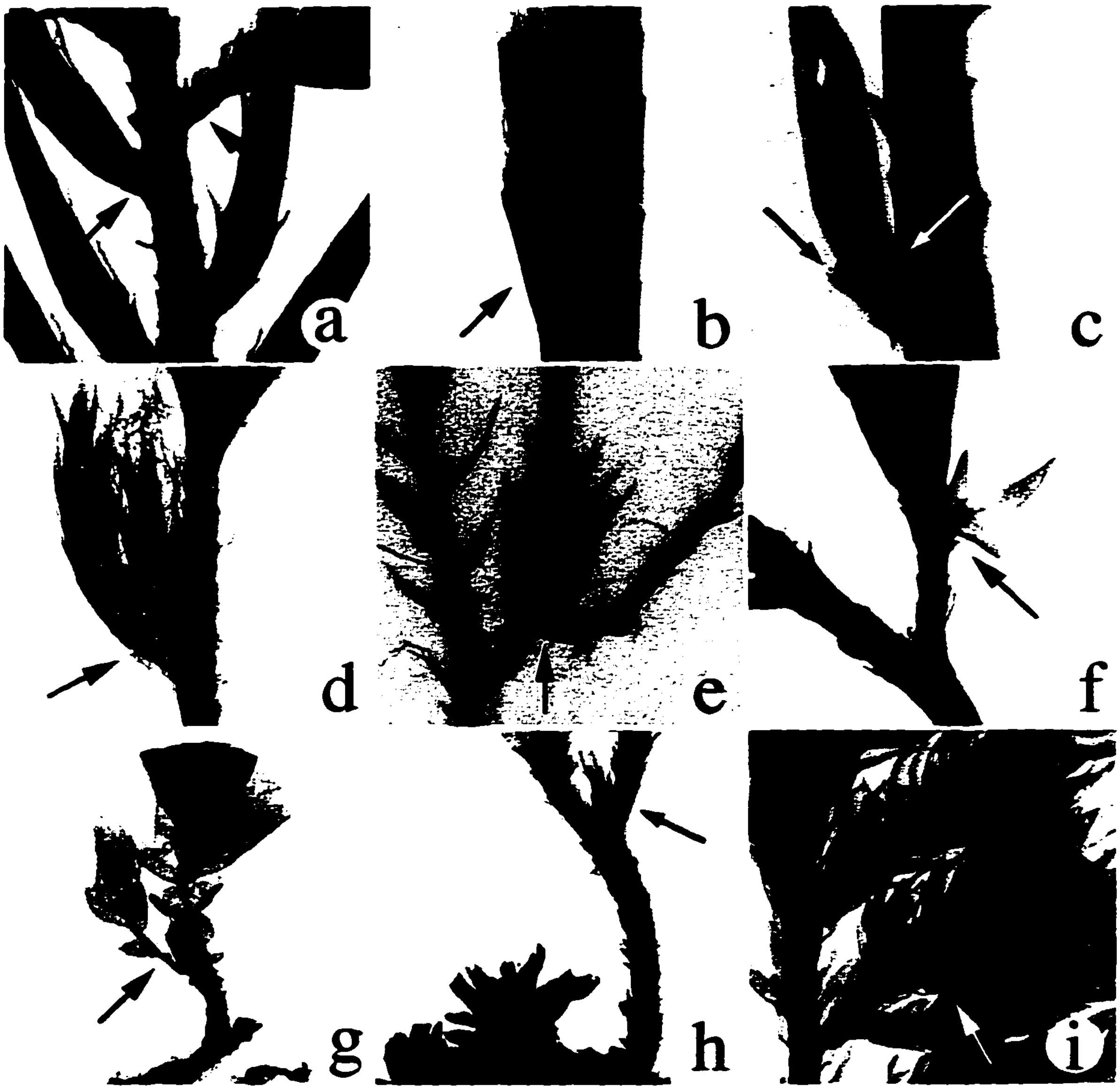


Figure IV. 4. Perichaetial position. Specimen citation for each species is found in Table IV.2.a - b. Pleurocarpy. a -*Dozya japonica*, left arrow indicates perichaetial innovation lacking subperichaetial primordia or branches. c - i . Cladocarpy. c -*Fissidens cristatus*, black and white arrows indicate subperichaetial primordia buds early in development. d - i. Black or white arrow indicates subperichaetial branches. d -*Anoectangium aestivum*.e -*Mielichhoferia bryoides*.f - *Cinclidotus fontinaloides*. g -*Pleurophascum grandiglobum*. h -*Macromitrium loamense*. i - *Bryowijkia ambigua*.

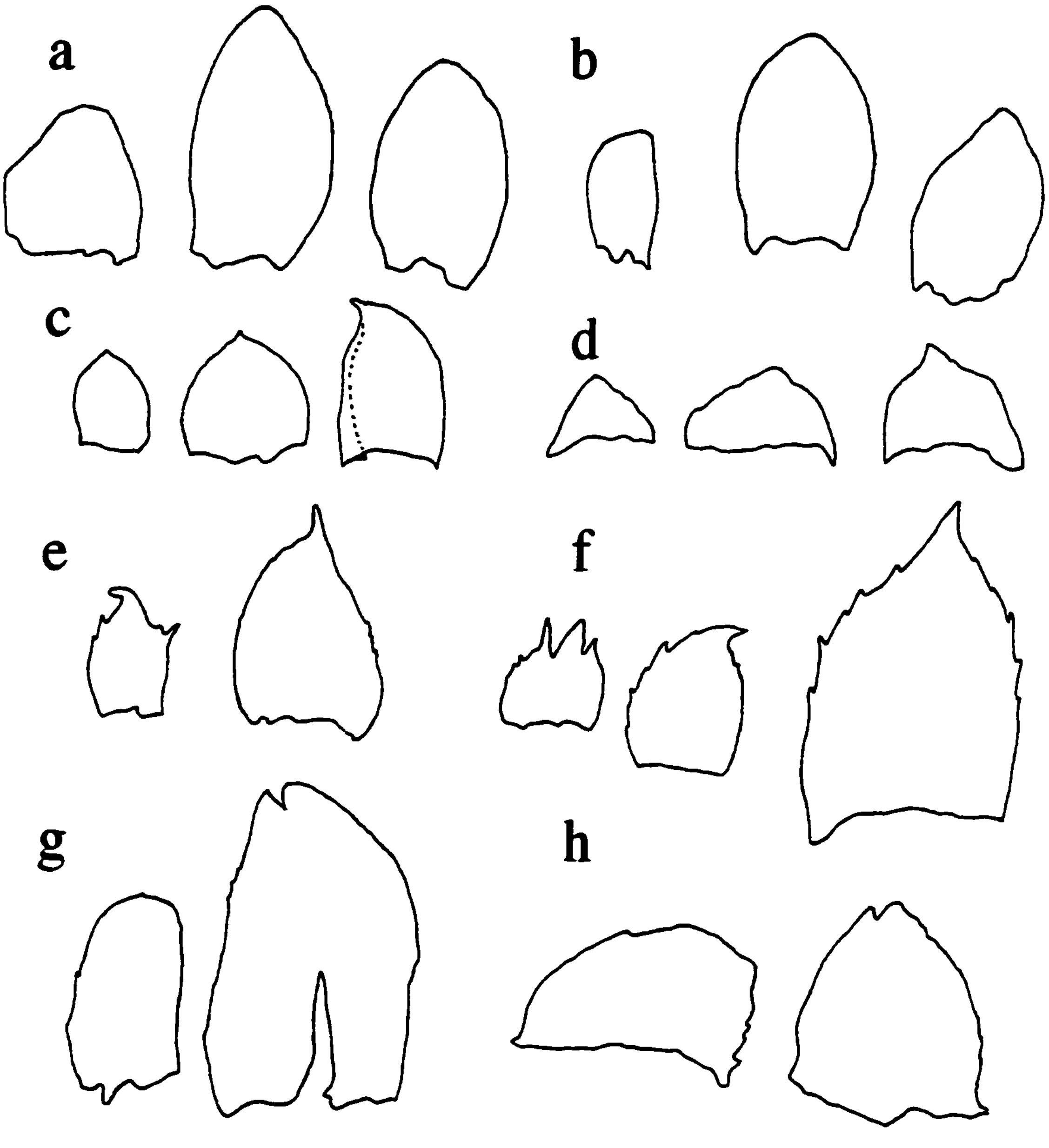


Figure IV. 5. Juvenile Leaves. a,c,e,g - Leaves of vegetative branches. b,d,f,h - Leaves of perichaetial branches. a - b cladocarpous, *Cryphaea tasmanica* (*Vitt 29343* ALTA); c - d pleurocarpous, *Porothamnium stipitatum* (*La Farge-England 6326* ALTA); e - f pleurocarpous, *Bescherellia elegantissima* (*Koponen 33971* ALTA); g - h pleurocarpous, *Aerobryidium sub-piligerum* (*La Farge-England 5359*) ALTA).

Table IV.1. The revised classification and definitions of terms related to life and growth form, branching pattern, and perichaetial position.

I. LIFE FORM

The structure of an assemblage of individual shoots, branching pattern, and direction of growth, with modification by its habitat (e.g., cushion, turf, dendroid, mat, weft, pendant, tail).

II. GROWTH FORM

The structure of an individual shoot, including direction of growth, with the length, frequency, and position of branches.

A. DIRECTION OF GROWTH

a. orthotropic: primary axes with erect growth
b. horizontal: primary axes growing perpendicular to vertical substrates
c. plagiotropic: primary with prostrate growth
d. pendulous: primary axes with downward outspreading or pendent growth

B. BRANCH FORM

a. Length
b. Frequency
c. Position
    1) basitonous: branches formed at the proximal end of a module
    2) acrotonous: branches formed at the distal end of a module
    3) axillary: branches positioned distinctly in the leaf axils
    4) cauline: branches positioned between the leaves

III. BRANCHING PATTERN

A. SYMPODIAL

A branch system that consists of a chain of connected modules of the same level of hierarchy. It occurs at different levels within the branch level hierarchy. Each connected module is defined by a heteroblastic series of leaves.

B. MONOPODIAL

A branch system that consists of a module with independent (or unconnected), subsidiary modules (lateral branches) of a different level of the branch hierarchy, derived along the main axis. Along the supporting module, an uninterrupted series of leaves is evident at each branch node.

IV. PERICHAETIAL POSITION

A. ACROCARPY

A *single* perichaetium is produced at the terminus of the primary module of the branch system. Subperichaetial primordia may develop for continued growth.

B. CLADOCARPY

One or more perichaetia are produced per primary module of the branch system. The primary modules terminate in vegetative growth. The perichaetia are produced at the terminus of lateral branches (secondary or tertiary modules) that have subperichaetial branch primordia or developed branches. Fertile branches do not appear swollen and differentiated from vegetative branches. The juvenile leaf development at the base of fertile branches is morphologically similar to that of a vegetative branches.

C. PLEUROCARPY

One or more perichaetia are produced per primary module of the branch system. The primary modules terminate in vegetative growth. Perichaetia are produced along the primary module or secondary modules at the terminus of lateral innovations that lack subperichaetial branch primordia or developed branches. Perichaetial leaf development is +/- immediate. Fertile branches commonly appear swollen and differentiated from vegetative branches. Juvenile leaf development on the perichaetial branches is morphologically different from that of the vegetative branches.

Table IV.2. List of species examined. All La Farge-England specimens are from the private herbarium of C. La Farge-England, the remaining are from ALTA, unless otherwise indicated.

FAMILY	SPECIES	SPECIMEN
ACROCARPOUS TAXA		
Bryaceae		
	Leptobryum pyriforme	*Peterson 4548*
	Mielichhoferia macrocarpa	*La Farge-England 5186*
Bartramiaceae		
	Bartramia halleri	*La Farge-England 3537*
	Bartramia pomiformis	*La Farge-England 4144*
	Bartramia sticta	*La Farge-England 4121*
	Leiomela africana	*La Farge-England 5342*
Calymperaceae		
	Leucophanes candidum	*Tan & Tandang,* 82-09
	Leucophanes hildebrandtii	*Pócs & Kornas 6531/E*
	Leucophanes octoblepharoides	*Vitt 33433a*
Dicranaceae		
	Dicranoloma blumei	*Weber & McVean B-34890*
	Dicranum scoparium	*Ireland 21330*
	Leucoloma dichelymoides	*La Farge-England 5960*
	Leucoloma fontinaloides	*La Farge-England 6328*
	Leucoloma holstii	*La Farge-England 5525*
	Leucoloma humbertii	*La Farge-England 6325*
	Leucoloma sanctae-mariae	*La Farge-England 6103*
	Sclerodontium clavinerve	*Petics s.n.* FH
	Sclerodontium pallidum	*Schofield 51446*
Ditrichaceae		
	Distichium capillaceum	*Vitt 34153*
Encalyptaceae		
	Encalypta procera	*Vitt 33836*
	Encalypta spathulata	*Vitt 35445*
Fissidentaceae		
	Fissidens bryoides	*Olsson 18/483*
Funaricaeae		
	Funaria hygrometrica	*Turner 9773*
Grimmiaceae		
	Racomitrium canescens	*MacFadden s.n.*
	Racomitrium ericoides	*Horton 5643*
Hedwigiaceae		
	Hedwigia ciliata	*La Farge-England 5255*
	Hedwigidium imberbe	*Cleef 6942*
Mitteniaceae		
	Mittenia plumula	*Fife 7079*
Mniaceae		
	Cryptopodium bartramioides	*Vitt 29618*
	Leucolepis menziesii	*La Farge-England 8125*
	Mnium spinulosum	*Handke s.n.*

Plagiomnium ciliare	*Churchill 9350*
Rhizomnium glabrescens	*La Farge-England 8138*
Rhizomnium punctatum	*Florin s.n.*
Orthotrichaceae	
Orthotrichum lyellii	*La Farge-England 8124*
Orthotrichum obtusifolium	*Vitt 15158*
Orthotrichum speciosum	*Vitt 13779*
Zygodon cf. microtheca	*La Farge-England 8097*
Zygodon gracillimus	*Bartlett 15148*
Pottiaceae	
Leptodontium viticulosoides	*Zander 1972*
Rhacocarpaceae	
Rhacocarpus purpurascens	*Griffin PV-1292*
Timmiaceae	
Timmia bavarica	*La Farge 308a*
Splachnaceae	
Tayloria hornschuchii	*La Farge-England 3829*

CLADOCARPOUS TAXA

Bryaceae	
Mielichhoferia bryoides	*Fife 7269*
Dicranaceae	
Mesotus celatus	*Fife s.n., ex* CHR 103959
Cryphaeaceae	
Acrocryphaea gardneri	*Wright 150*
Acrocryphaea coffeae	*Clayton B-390*
Acrocryphaea robustum	*De Sloover 18.717*
Cryphaea dilatata	*Vitt 27229*
Cryphaea exannulata	*Vitt 27416*
Cryphaea exigua	*De Sloover 18.555*
Cryphaea fasiculosa	*López 8697*
Cryphaea filiformis	*Buck 7899*
Cryphaea glomerata	*Allen & Magill 4702*
Cryphaea orizabae	*Larsen, Santisuk & Warncke 2719*
Cryphaea tenella	*Vitt 28067*
Dendrocryphaea tasmanica	*Vitt 29343,29400*
Erpodiaceae	
Venturiella sinensis	*Noguchi 117*
Fissidentaceae	
Fissidens adianthoides	*La Farge-England 3540*
Fissidens cristatus	*Schofield 53205*
Fissidens taxifolius	*La Farge-England 3484*
Gigaspermaceae	
Gigaspermum repens	*Oliver, Tolken & Venter 649*
Grimmiaceae	
Racomitrium lanuginosum	*Schofield 93253*
Orthotrichaceae	
Macromitrium loamense	*Hegewald 7458*
Schlotheimia appressifolia	*Weir 72*, NY LT!
Schlotheimia robusticuspis	*Schofield 64722, Ule 1417* H-Br LT!
Schlotheimia serricalyx	*Ule 902* H-Br LT!

Schlotheimia torquata	*Allen 11949,Vital & Buck 11441,Yano 1237*
Ulota magellanica	*Schäfer-Verwimp & Verwimp s.n.*
Pleurophascaeae	
Pleurophascum grandiglobum	*Vitt 29235*
Pottiaceae	
Anoectangium aestivum	*Vitt 19766*
Cinclidotus fontinalioides	*De Sloover 45.168*
Ganguleea angulosa	*Vital & Buck 20053*
Molendoa sendtneriana	*Vitt 10939*
Rhizogoniaceae	
Hymenodontopsis streimannii	*De Sloover 46.780*
Pyrrhobryum spiniforme	*La Farge-England 5375, 5377*
Rhizogonium dozyanum	*Ando*, Oct. 24, 1976
Rhizogonium novae-hollandiae	*Vitt 10360*
(?)	
Bryowijkia ambigua	*Larsen, Santisuk & Warncke 2877*
PLEUROCARPOUS TAXA	
Amblystegiaceae	
Calliergon giganteum	*Steere 15507*
Campylium stellatum	*Vitt 23943*
Cratoneuron filicinum	*La Farge-England 3491*
Drepanocladus aduncus	*Hermann 26506*
Brachytheciaceae	
Kindbergia oreganum	*La Farge-England 8141*
Eurhynchium pulchellum	*La Farge-England 2957*
Climaciaceae	
Climacium dendroides	*Moxley 103*
Cryphaeaceae	
Cryphaea borneensis	*van Zanten 57*
Cryphaea patens	*Frahm*, 23.3.79
Cyptodontopsis obtusifolia	*Susuki 1612*
Cryptopodiaceae	
Bescherellia elegantissima	*Koponen 33971*
Fontinalaceae	
Dichelyma capillaceum	*Ley 961*
Dichelyma japonica	*Toyohara s.n.*
Fontinalis neomexicana	*Naas, May 14/17*
Hookeriaceae	
Daltonia angustifolia	*La Farge-England 5360*
Hookeria luscens	*La Farge-England 8143*
Hookeriopsis papillosulum	*La Farge-England 5752*
Lepidopilidium attenuatum	*La Farge-England 5823*
Hylocomiaceae	
Hylocomium splendens	*La Farge-England 2873*
Rhytidiadelphus loreus	*La Farge-England 8137*
Hypnaceae	
Hypnum hamulosum	*Vitt 5474*
Leucomium sp.	*La Farge-England 5527, 5823*
Ptilium crista-castrensis	*La Farge-England 5051*

Hypnodendraceae	
Hypnodendron marginatum	*Schofield 49036, Vitt 29689*
Hypnodendron spininerve	*Schofield 49052*
Hypopterygiaceae	
Hypopterygium novae-seelandiae	*Vitt 8281*
Leptodontaceae	
Pseudocryphaea flagellifera	*Frahm 1997*
Leucodontaceae	
Alsia californica	*Schofield 76048a*
Dozya japonica	*Mizutani 13730*
Leucodon julacea	*Vitt 33710*
Meteoriaceae	
Aerobryidium subpiligerum	*La Farge-England 5359*
Meteorium miquelianum	*Streimann & Tamba 12210*
Neckeraceae	
Neckera douglasii	*La Farge-England 2876*
Neckera pennata	*Harms & Wright 25782-G*
Porothamnium bigelovii	*La Farge-England 8132*
Porothamnium stipitatum	*La Farge-England 6326*
Plagiotheciaceae	
Isopterygium elegans	*La Farge-England 8135*
Plagiothecium undulatum	*La Farge-England 8130*
Racopilaceae	
Racopilum convolutaceum	*Vitt 27429*
Spiridentaceae	
Spiridens balforianus	*Gardner s.n.*
Spiridens flagellosus	*Fleischer 1162*
Spiridens muelleri	*Vitt 28480*
Spiridens reinwardtii	*De Sloover 42.867*
Thuidiaceae	
Claopodium crispifolium	*La Farge-England 8129*
Heterocladium macounii	*La Farge-England 8140*
Abietinella abietina	*Redfearn 36411*
Thuidium tamariscinum	*La Farge-England 3448*

Bibliography

Akiyama, H. & N. Nishimura. 1993. Further studies on branch buds in mosses; "pseudoparaphyllia" and "scaly leaves". Journal of Plant Research 106: 101-108.

Berthier, J. 1972. Recherches sur la structure et le développment de l'apex du gamétophyte feuillé des mousses. Revue Bryologique et Lichénologique 38: 421-551.

Bridel, S.E. 1819. Muscologiae Recentiorum Supplementum Pars IV. Seu Mantissa naturae normam melius instituta et muscologiae recentiorum accomodata. Gothae.

_______. 1826-27. Bryologia universa seu Systematica ad Novam Methodum Dispositio, Historia et Descriptio omnium Muscorum Frondosorum Hucusque cognitorum cum Synonymia ex Auctoribus Probatissimis. Volumen Primum; Volumen Secundum. Leipzig.

Brotherus, V.F. 1901-1909. Musci (Laubmoose). III. Unterklasse Bryales. II. Spezieller Teil, pp. 277-1246. In A. Engler & K. Prantl (eds.), Die Natürlichen Pflanzenfamilien 1(3,I,II). Leipzig.

_______. 1924-1925. Musci (Laubmoose). Unterklasse Bryales: II Spezieller Teil. 10 Band, 1 Hälfte, pp. 143-478; 11 Band, 2 Hälfte, pp. 1-542. In A. Engler & K. Prantl (eds.), Die Natürlichen Pflanzenfamilien. Leipzig.

Buck, W. R. & D. H. Vitt. 1986. Suggestions for a new classification of pleurocarps. Taxon 35: 21-60.

Cavers, F. 1911. The inter-relationships of Bryophyta. The New Phytologist 9-10: 1-200.

Chamberlin, M. A. 1980. The morphology and development of the gametophytes of *Fissidens* and *Bryoxiphium* (Bryophyta). M.Sc. Thesis, Southern Illinois University, Carbondale.

Chopra, R. N. & P. K. Kumura. 1988. Biology of Bryophytes. New Delhi.

Crandall, B. J. 1969. Morphology and development of branches in leafy Hepaticae.

Beihefte zur Nova Hedwigia 30: 1-261.

Crandall-Stotler, B. J. 1984. Musci, hepatics, and anthocerotes - an essay on anologues, pp. 1093-1129. In R. M. Schuster (ed.) New Manual of bryology, Vol. 2. Nichinan, Japan.

Crosby, M. R. 1980. The diversity and relationships of Mosses, pp. 115-129. In R. J. Taylor & A. E. Leviton (eds.), The mosses of North America. Pacific Division, American Association for the Advancement of Science. California Academy of Science, San Francisco.

Crum, H. A. 1986. A survey of the moss genus *Sclerodontium*. Hikobia 9:289-295.

______ & L. E. Anderson. 1981. The Mosses of Eastern North America. Vol. 1. Coloumbia University, New York.

De Luna, E. 1990. Developmental evidence of acrocarpy in *Hedwigia ciliata* (Musci: Hedwigiaceae). Tropical Bryology 2: 53-60.

______. 1995. The circumcription and phylogenetic relationships of the Hedwiiaceae (Musci). Systematic Botany 20: 347-373.

Deguchi, H. 1978. A revision of the genera *Grimmia, Schistidium,*and *Coscinodon* (Musci) of Japan. Journal of Science of the Hiroshima University Series B, Div. 2 (Botany) 16: 121-256.

Dixon, H. N. 1924. The Student's Handbook of British mosses. Eastbourne.

______. 1932. The Classification of Mosses, pp. 397-412. In F. Verdoorn (ed.) Manual of Bryology. The Hague.

During, H. 1979. Life strategies of bryophytes: a preliminary review. Lindbergia 5: 2-18.

______. 1990. Clonal growth patterns among bryophytes, pp. 153-176. In J. van Groenendael & H. de Kroon (eds.), Clonal growth in plants: regulation and function. The Hague.

Fleischer, M. 1904-1923. Die Musci der Flora von Buitenzorg (zugleich Laubmoosflora von Java). Vols. 1-4. Brill, Leiden.

Flowers, S. 1973. Mosses: Utah and the West. Brigham Young University Press, Provo, Utah.

Frey, W. 1971. Blattenwicklung bei Laubmoosen. Dissertation Tübingen, pp. 463-556. Lehre.

______. 1974. Vergleichende entwicklungsgeschichtliche Untersuchungen an Laubmoosblättern als Beitrag zur Systematik der Laubmoose. Bulletin de la Société Botanique de France 121: 29-34.

Giesenhagen, K. 1910. Mosstypen der Regenwälder. Annales du Jardin botanique de Buitenzorg, Supplement 3: 711-790.

Gimingham, G. H. & E. M. Birse. 1957. Ecological studies on growth form in bryophytes. I. Correlations between growth form and habitat. Journal of Ecology. 45: 533-545.

Hedenäs, L. 1994. The basal pleurocarpous diplolepidous mosses. A cladistic approach. The Bryologist 97: 225-243.

Horikawa, Y. & H. Ando. 1952. A short study on growth-forms of bryophytes and its ecological significance. Hikobia 1: 119-129.

Horton, D. G. 1982. A revision of the Encalyptaceae (Musci) with particular reference to the North American taxa Part I. Journal of the Hattori Botanical Laboratory 53: 365-418.

Ireland, R. R. 1971. Moss pseudoparaphyllia. The Bryologist 74: 312-330.

______. 1982. Moss flora of the Maritime Provinces. Publications in Botany, no. 13. National Museum of Natural Sciences, Ottawa.

Iwatsuki, Z. 1960. The epiphytic bryophyte communities in Japan. Journal of the Hattori Botanical Laboratory 22: 159-348.

Koponen, T. 1982. Rhizoid topography and branching patterns in moss taxonomy. Nova Hedwigia 71: 95-99.

______. 1988. The phylogeny and classification of Mniaceae and Rhizogoniaceae (Musci). Journal of the Hattori Botanical Laboratory 64: 37-46.

La Farge-England, C. 1996. Growth form, branching pattern, and perichaetial position in mosses: cladocarpy and pleurocarpy redefined. The Bryologist 99: 170-186.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. Nichinan, Miyazaki, Japan.

Lesquereux, L. & T. P. James. 1884. Manual of Mosses of North America. Boston.

Lewinsky, J. 1993. A synopsis of the genus *Orthotrichum* Hedw. (Musci, Orthotrichaceae). Bryobrothera 2: 1-59.

Mägdefrau, K. 1982. Life forms of bryophytes, pp. 45-58. In A. E. J. Smith (ed.), Bryophyte Ecology, London.

Magill, R. E. 1990. Glossarum Polyglottum Bryologiae: A multilingual glossary for bryology. Monographs in Systematic Botany from the Missouri Botanical Garden 13: 1-297.

Meusel, H. 1935. Wuchsformen und Wuchstypen der europäischen Laubmoose. Nova Acta Leopoldina Neue Folge 3: 123-277.

Miller, H. A. 1971. An overview of the Hookeriales. Phytologia 21: 243-252.

Mishler, B. D. & E. De Luna. 1991. The use of ontogenetic data in phylogenetic analyses of mosses. Advances in Bryology 4: 121-167.

Mitten, W. 1859. Musci Indiae Orientalis. An enumeration of the mosses of the East Indies. Journal of the Proceedings of the Linnean Society (London), Botany Supplement 1: 1-171.

Mueller, C. 1948. Synopsis Muscorum Frondosorum omnium hucusque cognitorum. Pars prima. Berolini.

Nees von Esenbeck, C. G., Fr. Hornschuch, & J. Sturm. 1823. Bryologia Germanica, oder Beschreibung der in Deutschland und in der Schweiz washsenden Laubmoose. Erster Theil. Nürnberg.

Newton, A. E. & B. D. Mishler. 1994. The evolutionary significance of asexual reproduction in mosses. Journal of the Hattori Botanical Laboratory 76: 127-145.

Nishimura, N. 1985. A revision of the genus *Ctenidium* (Musci). Journal of the Hattori Botanical Laboratory 58: 1-82.

Proctor, M. C. & A. J. E. Smith. 1995. Ecological and systematic implications of branching patterns in bryophytes. Monographs In Systematic Botany from the Missouri Botanical Garden 53: 87-110.

Richards, P. W. 1984. The ecology of tropical forest bryophytes, pp. 1233-1270. In R. M. Schuster (ed.), New Manual of Bryology. Vol. 2. Nichinan, Japan.

Rothwell, G. W. 1987. The role of development in plant phylogeny: a paleobotanical perspective. Review of Paleobotany and Palynology 50: 97-114.

Salazar-Allen. 1985. The life-form and presence of epigametophytic plants in the genus *Leucophanes*. The Bryologist 88: 94-97.

Schimper, W. P. 1860. Synopsis muscorum europaeorum praemissa introductione de elementis bryologicis tractante. Vol. 1. Introductio I-CLIX, Vol. II. Speciarum descriptio. Stuttgartiae.

Schofield, W. B. & C. Hébant. 1984. The morphology and anatomy of the moss gametophore, pp. 627-657. In R. M. Schuster (ed.), New Manual of Bryology, Vol. 2. Nichinin, Japan.

Smith, A. E. J. 1978. The Moss Flora of Britain and Ireland. Cambridge.

Stark, L. R. 1985. Phenology and species concepts: a case study. The Bryologist 88: 190-198.

Stearn, W. T. 1983. Botanical Latin. London.

Swofford, D.L. 1993. Phylogenetic analysis using parsimony, ver.3.1.1. Computor program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Tallis, J. H. 1959. Studies in the biology and ecology of *Racomitrium lanuginosum* Brid. II. Growth, reproduction and physiology. Journal of Ecology 47: 325-350.

Touw, A. 1976. A taxonomic revision of *Thuidium*, *Pelekium*, and *Rauiella* in Africa south of the Sahara. Lindbergia 3: 135-195.

Vitt, D. H. 1984. Classification of Bryopsida, pp. 696-759. In R. M. Schuster (ed.), New Manual of Bryology,. Vol. 2. Nichinan, Japan.

______ & W.R. Buck. 1984. The familial placement of *Bryowijkia* (Musci: Trachypodaceae). Brittonia 36: 300-306.

White, J. 1984. Plant metamerism, pp. 15-47. In R. Dirzo & J. Sarukhán (eds.), Perspectives on Plant Population Ecology. Sunderland, Mass.

Zander, R. 1993. Genera of the Pottiaceae: mosses of harsh environments. Bulletin of the Buffalo Society of Natural Sciences 32: 1-378.

Zomlefer, W. 1993. A Revision of *Rigodium* (Musci: Rigodiaceae). The Bryologist

96: 1-72.

Chapter V

CONCLUSIONS

> "If systematics is an indispensable handmaiden of other branches of research, it is also a fountain head of discoveries and new ideas" (Wilson 1988)

The most recent study of the Madagascan moss flora was made by Renauld and Cardot (1915). Subsequently an updated list of species has been compiled (Crosby et al. 1983). *Leucoloma* represents 5% of the total estimated moss flora of Madagascar and the East African islands, the second largest moss genus for the region (Crosby et al. 1983, Frahm 1985). A systematic revision of *Leucoloma* indicates that 46% of the species are endemic to Madagascar and the East African islands and 68% of the species are endemic to the Afro-Madagascaren region. The pattern of high endemism in Madagascar is shared by numerous taxa that have undergone a species explosion within the Madagascar region (e.g., Baobabs, Didieraceae, Lemurs, and Tenrecs). *Leucoloma* is primarily a genus of forest habitats: lowland, montane, to elfin forests, including humid to dry forests of tropical regions. It forms a conspicuous element of the epiphytic biomass in montane and elfin forests of the East African forest archipelago Pócs (1980) and the eastern forests of Madagascar. Satellite imagery has monitored the alarming decrease in forest habitat in Madagascar since the 1950's (Sussman et al. 1994). Tropical rainforests represent a major source of biological diversity and are the most severely threatened ecosystems of the world (Campbell 1990, Wilson 1988). It is crucial that the biodiversity of these rich ecosystems be stuidied and not eclipsed by more fashionable research (e.g., genetic engineering).

Leucoloma represents a relatively derived genus within the subfamily Dicranoideae (unpublished data). Evolutionary trends of reduction (sporophyte) and amplification (papillae development) are well represented within the genus. The morphological expression of characters in mosses is constrained by their small stature, which often results in increased homoplasy at higher phylogenetic levels of analysis (e.g., ordinal - Goffinet 1996 per. comm., supraordinal - Hedenäs 1995, family - Zander 1993). Despite this constraint, the morphological analysis has provided a number of taxonomically and phylogenetically significant characters. These include sporophyte features such as seta length and color; number of layers of thickened cells in transverse section of the seta; the orientation of the cells in transverse section of the capsule wall; and peristome reduction and ornamentation (including with variation in peristomial thickening, e.g., OPL). Informative gametophytic characters that have not previously been used include: the costa in transverse section with stereid band and guide cell variation; variation in the development of transitional cells between the costa and lanimal cells; cell lumina shape; alar region enlarged or reduced with various cell wall thickenings; papillae variation including distribution, prominence, density and shape; branching patterns including monopodial, perpendicular branches.

The revision of *Leucoloma* resulted in a 17% reduction of species for the genus from 134 to 112 species. Five new species have been described, 2 have been transferred to the genus from *Dicranoloma*, and 1 has been re-recognized as a distinct species. This does not include an additional 13 taxa, yet to be published as new taxa or synonymised with existing taxa. The completion of the species level revision of subgenus *Syncratodictyon* will result in a further decrease in species for the genus, although I do not expect that the decrease will equal the projected 50-80% decrease that has been found for other tropical moss genera.

The terms for morphological characters including growth form, branching pattern, and perichaetial position have been inconsistently used in the literature. This spurred a review of the terms and a classification of the terms into separate categories in order to analyse a specimen with accuracy and consistency. By providing independent terms, the diagnosis of a species can be more consistent and perhaps provide characters that are phylogenetically informative at various levels of analysis.

The morphological data have provided the basis for the phylogenetic analysis to establish a working hypothesis of the infrageneric relationships. A new infrageneric classification has been produced and a hypothesis for examining the evolution of the genus based on the infrageneric distribution patterns.

The phylogeny of *Leucoloma* provides a framework for the conservation of the genus (Hedenäs 1996). The distribution of a number of species (e.g., *L. crosbyi*, *L. marojeziense*) is restricted to a single locality. Restricted distribution within the isolated high mountain regions of the island may be the result of under collection or endemism. Further collecting efforts are needed to modify these distribution patterns or support them. Recent recommendations for the expansion of protected areas for the diversity of the Madagascan ecosystem have been proposed (Nicoll & Langrand 1989). The diversity of the bryophyte flora was not included in their survey. *Leucoloma* occupies a broad altitudinal and forest type range that may prove instrumental for conservation recommendations for the Madagascan forest bryophytes.

The geographical distribution of the genus shows that the center of diversity remains in Madagascar as a marked pattern. Both plesiomorphic and apomorphic taxa occur in this region. Three out of 8 sections are endemic to Madagascar and 7 out of 8 sections have their highest diversity in Madagascar. Half of the species occur in the Madagascan region and new species are not uncommon to find. With Madagascar designated as the most threatened ecosystem of the world, and defined as one of the richest, yet most poorly collected biotas (Campbell 1990), *Leucoloma* represents a diverse genus that is severely threatened. The purpose here is not to just insure the survival of a single moss genus, but to emphasize that *Leucoloma* represents a pattern of diversity that is dependent on the survival of the forests of Madagascar, as do an unknown number of other organisms.

The revisionary studies of *Leucoloma* have stimulated questions and topics for further research that include the following: 1) Given a completed species revision and based on the phylogeny of the infrageneric taxa, what Madagascan - Mascaren localities are critical for the conservation of the genus?

2) Subgenus *Syncratodictyon* remains heterogeneous. Will a species level revision further strengthen the relationships of the infrageneric taxa?

3) Subgenus *Leucoloma* and subgenus *Syncratodictyon* are distinguished primarily by the reduction of the sporophyte in subgenus *Leucoloma*. The basal taxon

of subgenus *Syncratodictyon*, section *Dicranoidea*, remains heterogeneous retaining plesiomorphic gametophytic characters of *Dicranoloma*, and sporophytic characters of both subgenus *Leucoloma* and subgenus *Syncratodictyon*. Will a phylogenetic analysis at the species level clarify the affinities of the individual species of the section?

4) Further research on pleurocarpy, cladocarpy and acrocarpy is needed to assess the whether there is a difference in the sequence of development of the reduced branches of cladocarps and the perichaetial innovations of pleurocarps. Is there a fundamental difference between pleurocarpy and cladocarpy or is is simply a continuum as Hedenäs suggests (Hedenäs, per. comm. 1996)?

5) The observation of fused peristomial layers (outer-primary-inner, OPL-PPL-IPL) in *Leucoloma amblyacron* emphasizes that we do not know how varied the haplolepideous peristome is in mosses. Does fusion occur commonly as a result of reduction in many distinct lineages of the Haplolepideae, as Edwards (1979) suggests? As well, the extent of variation in number of cells of the inner peristomial layer is not known. Since the peristome has traditionally been used for the classification of mosses, and provides key morphological characters, further research is needed to explore developmental variation in the major lineages.

6) The phylogeny of *Leucoloma*, based on morphology, provides a hypothesis of relationship that can be further tested or expanded, utilising other data, such as molecular or developmental.

7) What is the variation of papillae in mosses? Are the thickenings over the interluminal walls in transverse section the same as the papillae centered over the cell liumina. Three genera are now identified with the "cell wall" papillae: *Racomitrium*, *Leucoloma* and *Mesotus*. These genera represent distinct clades, thus the character is shown to be independently derived.

8) Rhizoidal distribution in Dicranales has been reported as taxonomically significant. The occurrence on alar cells is unique to *Leucoloma*. The extent of expression in subgenus *Syncratodictyon* needs to be documented.

9) Two species were found to be both autoicous and dioicous. The factors

controlling the expression of sexuality in mosses needs further research. Is a species genetically restricted to a single expression or are there physiological and ecological factors that control the expression?

Bibliography

Campbell, D.G. 1990. Rates of botanical exploration in Asia and Latin America; similarites and dissimilarities with Africa. Proceedings of the twelfth plenary meeting of AEFAT. Hamburg, September 4-10, 1988. Mitteilungen aus dem Institut für Allgemeine Botanik 23 a: 155-168.

Crosby, M.R., W. Schultze-Motel, & U. Schultze-Motel. 1983. Katalog der Laubmoose von Madagaskar und den umliegenden Inseln. Willdenowia 13: 187-255.

Edwards, S.R. 1979. Taxonomic implications of cell patterns in haplolepideous moss peristomes, pp. 317-356. In: G.C.S. Clarke & J.G. Duckett (eds). Bryophyte Systematics. Academic Press, London.

Frahm, J.-P. 1985. Afrkanische *Campylopus*-Arten (Dicranaceae, Musci). Bryophytorum Bibliotheca 31: 1-219.

Hedenäs, L. 1995. Higher taxonomic level relationships among diplolepidous pleurocarpous mosses - cladistic overview. Journal of Bryology 18: 723-781.

______. 1996. How do we select species for conservation? Anales del Instituto de Biología de la Universidad Nacional de México, Ser. Bot. 67: 129-145.

Nicoll, M.E. & O. Langrand. 1989. Madagascar: Revue de la conservation et des aires protégées. World Wide Fund for Nature, Gland, Suisse.

Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru mountains (Tanzania, East Africa). Acta Botanica Academiae Scientiarum Hungaricae 26: 143-167.

Renauld, F. & J. Cardot 1915. Les mousses de Madagascar. In A. Grandidier & G. Grandidier (eds.). Histoire Physique, Naturelle et Politique de Madagascar (Mousses) 39: 1-560.

Sussman, R.W., G.M. Green, & L.K. Sussman. 1994. Satelite imagery, human ecology, anthropology, and deforestation in Madagasacar. Human Ecology 22: 333-354.

Wilson, E.O. 1988. The biological diversity crisis: A challenge to science. Acta Universitatis Upsaliensis Symbolae Botanicae Upsalienses 28: 5-12.

Zander, R. 1993. Genera of the Pottiaceae: mosses of harsh environments. Bulletin of the Buffalo Society of Natural Sciences 32: 1-378.