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THE UNIVERSITY OF ALBERTA

A REVISION OF THE PANTROPICAL MOSS GENUS *LEUCOPHANES*

by

NORIS SALAZAR ALLEN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR IN PHILOSOPHY

IN

BRYOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL 1986

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A REVISION OF THE PANTROPICAL MOSS GENUS *LEUCOPHANES* submitted by NORIS SALAZAR ALLEN in partial fulfilment of the requirements for the degree of DOCTOR IN PHILOSOPHY in TAXONOMY (BRYOLOGY).

Dale H. Vitt

Supervisor

Diana Horton

Ruth A. Stockey

Harvey

External Examiner

Date 16 July 1986

To my parents and in memory of my grandmother Maria Silvestra who introduced and guided me into the appreciation of Nature and its many wonders.

ABSTRACT

The species of the pantropical genus *Leucophanes* are characterized by whitish-green appearance, mainly corticolous, turf-forming habit; multistratose structure of the leaf; production of leaf-tip gemmae, and short branching systems. A definition of leaf structure is based primarily on comparative morphology of young and adult leaves, perigonial bracts, and scale leaves of *Leucophanes* and those of the related genera *Exodictyon, Exostratum, Arthrocormus,* and *Syrrhopodon*. The leaf is a complex organ composed of a costa (with stereids, guide cells and hyalocysts) and a multistratose lamina. The multistratose lamina is considered to be composed of two sections, a basal unistratose, hyaline area and a multistratose section with a central layer of quadrangular chlorophyllous cells (living photosynthetic elements), the chlorocysts, arranged in a net-like pattern and surrounded, on each surface, by one or more layers of porose hyaline cells (devoid of protoplasm at maturity), the hyalocysts. Similarities in leaf structure with *Leucobryum* are the result of convergent evolution. Growth-habit and structural features displayed by the gametophytes of *Leucophanes* are considered adaptations for water retention. It is most likely that the life-form characteristic of the genus developed in relation to environmental stresses imposed by the corticolous habit in seasonally dry tropical forests.

Three subgenera, thirteen species and six subspecies are recognized. Important characters in defining these taxa include leaf apex, shape and arrangement of chlorocysts as observed in surface view, size and shape of hyalocysts, layers of hyalocysts in the multistratose lamina, pore size on the transverse walls, sexual condition, perichaetial leaves, and peristome and spore ornamentation.

Leucophanes is distributed in the tropical and subtropical areas of the world, particularly in central Africa, Malesia, Southern Japan Australia, the islands of the tropical Pacific and the Neotropics. There are two centers of species diversity, one in Africa and the other in Malesia and adjacent areas. Of these, Africa has the highest number of endemics with five species, while Malesia has two. The species are able to grow on both acidic and basic

substrata. An active radiation to littoral forests appears to have taken place in some species, e.g., *L. glaucum* and *L. octoblepharioides*, while others appear to be strictly elements of inland tropical rain forests.

Four [illegible]ges are recognized. The putative ancestor to all of them must have had costate leaves with a multistratose lamina composed of chlorocysts in a single, non-dissected layer, surrounded on each surface by one layer of hyalocysts, a broad, basal hyaline lamina, papillose-foveolate peristome and verrucate to gemmate spores. The lineage considered closest to the putative ancestor is that of *L. milleri*, *L. octoblepharioides*, and related species. It is characterized by having leaves with a single layer of hyalocysts on each side of the chlorophyllous layer and papillose-foveolate peristomes. The African lineage is considered to have evolved in isolation, from a common ancestor of *L. milleri* and *L. octoblepharioides*, developing the apotypies of long rectangular cells, retuse to strongly spinose apices and peristomes with the dorsal plates having longitudinal to semi-circular thickenings. *Leucophanes candidum* is considered to form a derived lineage by the development of unique apotypies. *Leucophanes glaucum* is considered as a derived lineage characterized by leaf cells with broad, curved end walls; costa strongly spinose abaxially to smooth; and a papillose peristome with papillae irregularly arranged or in more or less defined vertical rows.

The genus is hypothesized to have originated in Laurasia (Southeast Asia) as early as the Lower to Upper Cretaceous. Its present day distribution reflects not only its paleohistory but also its efficient dispersal capabilities.

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I. INTRODUCTION

Leucophanes is a pantropical genus with a concentration of species in the Old World, between 20 degrees north and south of the Equator. Its northernmost range extends to approximately 24-26 degrees north of the Equator and its southernmost to the Tropic of Capricorn. It is, at times, an important component of the lowland tropical vegetation occurring mainly as a corticolous epiphyte, particularly on palm trees.

In the Neotropical Region, the genus is distributed in South America, from central and southern Brazil to the Ecuadorian Andes and the Guianas; in Central America from Panama to Nicaragua and in the Caribbean from Trinidad to Puerto Rico. In Africa, the genus is reported in the forested areas of the West Coast from Liberia to Cameroon, through the Congo Basin to Tanzania with representatives in Madagascar, Comoro Islands, the Mascarenes, La Réunion, Mauritus, Rodriguez and the Seychelles.

In the Old World Region, the genus is distributed in Malaysia, Thailand, Vietnam, and northwest into Nicobar and Andaman Islands, Sri-Lanka and India with one report from Nepal. To the east it extends into southern Japan (Ryukyu Islands), Taiwan, the Philippines and to the south to Indonesia, Greater Sunda Islands: Sumatra, Java, Borneo, Celebes and Lesser Sunda Islands; Moluccas, New Guinea, Bismarck Archipelago, Australia, Solomon Islands, Vanuatu, New Caledonia and the islands of the tropical Pacific.

The present study is an attempt to:

1. Define the taxa in *Leucophanes* primarily on the basis of structure.
2. Clarify the genus taxonomically on a world-wide basis.
3. Delineate habitats for the taxa.
4. Correlate habitat, life-form and structure to evolution of adaptations to a corticolous habit.
5. Based on these data and correlations, propose a phylogenetic hypothesis of the relationships among the taxa as well as how the genus is interrelated with other groups in the Bryopsida. Particular attention is given to correlations with other members of the Calymperaceae and closely related families.

Historical Review

Since its description as a new genus (Bridel, 1827), 42 species names and 3 varietal ones have been validly published in *Leucophanes*. Of these, ten were proposed by C. Mueller. Bescherelle proposed five new species names, Brotherus three, while Fleischer published four species and one varietal name, and Cardot, Thériot and Renauld individually or jointly named six species and one variety. The remaining species and varietal names were proposed by Dixon, Dusén, Dozy and Molkenboer, Jaeger, Lindberg, Potier de la Varde, Mitten and the most recent one by Gangulee (1971). C. Mueller gave five specimens new names without descriptions (*nomina nuda*).

Bridel (1827), in his original description of the genus described three species: *L. octoblepharioides*, *L. squarrosum* and *L. fragile*. The first two remain within the modern concept of the genus with *L. squarrosum* as a *nomen invalidum* and conspecific with *L. candidum*. The third species, *L. fragile*, is a *Syrrhopodon* (*Syrrhopodon involutus* Schwaegr., *teste* W. D. Reese).

Schwaegrichen (1827), perhaps unaware of Bridel's new genus, described, two new species of *Syrrhopodon*. These were *S. candidum* and *S. glaucum*. Both species were placed in *Leucophanes* by Lindberg (1865) and Mitten (1859) respectively. In 1846, Dozy and Molkenboer described *L. korthalsii* from their Indonesian collections. This name was given varietal status by Fleischer (1900-1904), as *L. octoblepharioides* var. *korthalsii*.

Mitten (1863) described *L. unguiculatum* from a West African collection. A year later, C. Mueller described a specimen of *L. glaucum* as *L. albescens*. Lindberg (1865) described a disjunct population of the same species from the Antilles (Guadeloupe) as *L. guadalupense*.

From 1870-1900, twenty-two new species of *Leucophanes* were described. Of these, only five are recognized as valid taxonomic entities in this treatment. The species recognized are: *L. angustifolium* Ren. and Card. (1891); *L. molleri* C. Muell. (1886); *L. hildebrandtii* C. Muell. (1876); *L. rodriguezii* Ren. & Card. (1895) and *L. seychellarum* Besch. (1880), most of them from Africa.

In the 20th Century, thirteen new species and two varieties have been described. Of these, only three remain taxonomically recognized today. These are: *L. renauldii* Card. (1904); *L. serratulum* Fleisch. (1914); and *L. scabridens* P. Vard. (1935).

I have been unable to examine the type material of *L. scabridens* therefore, this species name is retained until the types can be reviewed (see Appendix 1).

Most descriptions of new species of *Leucophanes* have been based on a few variable structural characters of the gametophyte. A critical revision of specimens from different geographical localities has shown that some of the characters considered important in delimiting particular species are more variable than originally thought. *L. glaucescens*, for example, was distinguished from *L. subglaucescens* by the spinosity of the costal area. This character varies within plants of the same population and between leaves of the same plant. Dixon (1916) noted this variability in the above mentioned species, indicating also the need for a revision.

Of the 13 species of *Leucophanes* here considered as taxonomically recognizable, 12 were originally described under 41 names. The additional species, *L. milleri* is described as new. Types for 34 of the 42 names have been critically examined; another, *L. smaragdinum* can be placed in synonymy using additional criteria. The names not yet typified are listed in Appendix 1. In addition, 12 *nomina nuda* are known; five of these have been placed in synonymy by previous authors (Appendix 2).

Of the three varieties formerly described in the genus, none of them is given formal taxonomic rank in this treatment. Instead, six subspecies are recognized in the genus. These are *L. glaucum* subsp. *glaucum*, *L. glaucum* subsp. *nukahivense*, *L. glaucum* subsp. *vittii* and *L. octoblepharioides* subsp. *octoblepharioides* and *L. octoblepharioides* subsp. *meijeri* and *L. octoblepharioides* subsp. *whittieri*.

At the generic level and based exclusively on gametophytic characters, *Leucophanes* was first divided by C. Mueller (1874) into three sections (Table 1). These are:

1. **Section Trachynotus**. Plants in this section were characterized by their habit of erect, narrow

Table 1. Infrageneric taxa in *Leucophanes*

C. Muell. (1874)	C. Muell. (1901)	Cardot (1900)	Cardot (1915)	Salazar-Allen
Section Leionotus	**Section Leionotus**	**Section A**	**Section 1. Homodictya**	**Subgenus Leionotus**
L. candidum	*L. candidum*	*L. candidum*	*L. candidum*	*L. candidum*
(=L. recurvum)	*(=L. pucciniferum)*	*L. unguiculatum*	*L. unguiculatum*	
(=L. reinwardtianum)	*(=L. recurvum)*			
(=L. tetensii)	*(=L. reinwadtianum)*			
	(=L. tetensii)			
	L. glaucum			
	(=L. nukahivense)			
Section Trachynotus	**Section Trachynotus**	**Section B**	**Section 2. Heterodictya**	**Subgenus Trachynotus**
			Subsection Heterostrosica	
L. glaucum	*L. glaucum*	*L. glaucum*	*L. glaucum*	***L. glaucum***
(=L. albescens)	*(=L. albescens)*	*(=L. albescens)*	*(=L. albescens)*	
(=L. guadalupense)	*(=L. glauculum)*	*(=L. australe)*	*(=L. australe)*	
	(=L. guadalupense)	*(=L. beccarii)*	*(=L. beccarii)*	

Table 1. Continued.

C. Muell. (1874)	**C. Muell. (1901)**	**Cardot (1900)**	**Cardot (1915)**	**Salazar-Allen**
	(= *L. sordidum*)	(= *L. glauculum*)	(= *L. glauculum*)	
	(= *L. subglaucescens*)	(= *L. guadalupense*)		
Exostratum asperum	*Exostratum asperum*			
(= *L. asperum*)	(= *L. asperum*)			
(= *L. papillosum*)	(= *L. subscabrum*)	(= *L. nukahivense*)	(= *L. nukahivense*)	
E. blumei	*E. blumei*	(= *L. smaragdinum*)	(= *L. smaragdinum*)	
(= *L. blumei*)	(= *L. blumei*)	(= *L. sordidum*)	(= *L. sordidum*)	
(= *L. scabrum*)	(= *L. scabrum*)	(= *L. subglaucescens*)	(= *L. subglaucescens*)	
E. sullivantii	(= *L. arthrocormoides*)	*L. octoblepharioides*	*L. octoblepharioides*	
(= *L. hispidulum*)	*L. seychellarum*	(= *L. nicobaricum*)	(= *L. nicobaricum*)	
Section Tropinotus	**Section Tropinotus**	**Section C**	**Subsection Homostrosica**	**Subgenus Leucophanes**
L. octoblepharioides	*L. candidum*	*L. angustifolium*	*L. angustifolium*	*L. angustifolium*
(= *L. albo-nitens*)	(= *L. naumanni*)	(= *L. massartii*)	(= *L. massartii*)	*L. hildebrandtii*
L. glaucum	*L. glaucum*	(= *L. prasiophyllum*)	(= *L. prasiophyllum*)	*L. milleri*
(= *L. cuspidatum*)	(= *L. australe*)	(= *L. tahiticum*)	(= *L. tahiticum*)	*L. molleri*

Table 1. Continued

C. Muell. (1874)	C. Muell. (1901)	Cardot (1900)	Cardot (1915)	Salazar-Allen
L. vitianum (?)	(= *L. cuspidatum*)	*L. hildebrandtii*	*L. hildebrandtii*	[illegible]
	(= *L. glaucescens*)	*L. molleri*	*L. molleri*	[illegible]
	(= *L. guadalupense*)	(= *L. calymperaceum*)	(= *L. calymperaceum*)	*L. rodriguezii*
	L. hildebrandtii	(= *L. calymperatum*)	(= *L. calymperatum*)	*L. scabridens(?)*
	L. molleri	(= *L. cameruniae*)	(= *L. cameruniae*)	*L. serratulum*
	(= *L. calymperaceum*)	(= *L. denticuspis*)	(= *L. denticuspis*)	*L. seychellarum*
	(= *L. cameruniae*)	(= *L. horridulum*)	(= *L. horridulum*)	*L. unguiculatum*
	(= *L. obtusatulum*)	(= *L. lecomptei*)	(= *L. lecomptei*)	
	L. octoblepharioides	(= *L. obtusatulum*)	(= *L. obtusatulum*)	
	(= *L. albo nitens*)	*L. octoblepharioides*	*L. octoblepharioides*	
	(= *L. minutum*)	(= *L. albo nitens*)	(= *L. albo nitens*)	
	(= *L. nicobaricum*)	*L. rodriguezii*	*L. renauldii*	
	L. vitianum(?)	*L. seychellarum*	*L. rodriguezii*	
			L. seychellarum	

(?) Names for which no type material (or potential isotypes) have been available for critical examination leaves with a thick midrib that is strongly dentate on back.

This section included: *L. glaucum* (Schwaegr.) Mitt. (as *L. albescens, L. guadalupense*), and three species of *Exostratum* that Mueller classified in the genus *Leucophanes*. These are: *E. asperum* (Mitt.) L.T. Ellis (as *Leucophanes asperum and L. papillosum*), *E. sullivantii* (Doz. & Molk.) L.T. Ellis (as *Leucophanes hispidulum*) (Doz. & Molk.) Fleisch. var. *hispidulum* (Mitt.) Fleisch.) and *E. blumei (Mitt.) L.T. Ellis (as Leucophanes blumei* and *L. scabrum*).

2. **Section Leionotus**. Taxa in this section were characterized by having robust stems, forming tall turfs, leaves that bend outward at a sharp angle and smooth costa.

The species included here was: *L. candidum* (Schwaegr.) Lindb. (Mueller's *L. tetensii, L. reinwardtianum*) and *L. recurvum* Mitt.).

(3) **Section Tropinotus**. The species in this section were characterized by a small turf-forming habit, stiff upright leaves, with a smooth costa, and strongly keeled leaves.

Species included here were: *L. candidum* (as *L. vitianum*), *L. glaucum* (as *L. cuspidatum*) and *L. octoblepharioides* Brid. (also as *L. albo-nitens*).

In 1901, Mueller expanded the number of species included in each section. Thus, eleven species were placed in Section *Trachynotus*, four of these are presently recognized in the genus *Exostratum*; 20 species were included in Section *Tropinotus* and five in Section *Leionotus* (Table 1).

Cardot (1900) also divided the genus into three sections (Table 1). The structure of the leaf (expanded costa of Cardot), as observed in transverse section, was the main character for his classification. Of the three sections recognized by Cardot, only one, Section A, is equivalent to any of C. Mueller's, corresponding to his section *Leionotus*. The other sections (B and C) included species from both *Trachynotus* and *Tropinotus*. Cardot's classification is as follows:

(1) **Section A**. This section included species with a uniform structure of the leaf from base to apex, not only in the number of layers of cells, but also in the shape of the cells. Plants in this section have leaves that are, in Cardot's concept, "homostrôsique" (from *στρωσις*= layer).

that is, the leaf (or the expanded costa of Cardot) is composed of two layers of leucocysts from base to apex. They are also "homodictyée" (from δμοα = resemblance, δικτυον = plexus or net) that is homogeneous in their structure.

The species included in this section were: *L. candidum* (as *L. fusculum* C. Muell., *L. aciculare* C. Muell., *L. naumannii* C. Muell., *L. recurvum* Mitt., *L. tetensii* C. Muell. and *L. densifolium* Mitt.), and *L. unguiculatum*.

2. **Section B**. All the species included here have in common a leaf (expanded costa of Cardot) that is "hétérodictyée" (with a different structure at the base than at the apex) and "hétérostrôsique or subhétérostrôsique (abaxial side with numerous hyalocysts). The leaves are goitrous throughout their length, loosely overlapping, and have a fairly long hyaline lamina. The chlorocysts are thicker than in the previous section. A transverse section of the leaf is composed of two, at times three, layers of leucocysts on the abaxial surface; the hyalocysts on the adaxial side, rarely divide to form more than one layer. The chlorocysts are "hypercentrique" (closer to the adaxial surface) and numerous (5 to 8 on each side of the central stereid band), more or less rhombic and elongated along the longitudinal axis of the leaf. The central stereid band (stereome) and the margins are thicker than those of the species in the previous section.

The species included here were: *L. glaucum* (as *L. albescens* C. Muell., *L. australe* Broth., *L. beccarii* Broth. et Geh., *L. compactum* Broth., *L. guadalupense* Lindb., *L. glaucum* Mitt., *L. glauculum* C. Muell., *L. nukahivense* Besch., *L. pugionatum* C. Muell., *L. smaragdinum* Mitt., *L. sordidum* C. Muell., *L. subalbescens* Broth. and *L. subglaucescens* C. Mull.), and *L. octoblepharioides* (as *L. nicobaricum* C. Muell.)

3. **Section C**. The structure of the leaf in plants of this section is close to that of Section B. The leaf is "homostrôsique" throughout its length and the apex is more or less convex or plane as seen from the abaxial or adaxial surfaces respectively. The chlorocysts are "hypercentrique" at the base, nearly median at middle and "hypocentrique" (closer to the abaxial surface) at the apex. At base, the number of chlorocysts is reduced (as compared to Section B) to two [illegible]

side of the central stereid band and are elongated along the main axis of the leaf.

The species included here were: *L. angustifolium* Ren. & Card. (as *L. massartii* Ren. & Card., *L. prasiophyllum* Besch. and *L. tahiticum* Besch.), *L. hildebrandtii* C. Muell., *L. molleri* (as *L. calymperatum* C. Muell., *L. cameruniae* C. Muell., and *L. denticuspis* C. Muell., *L. horridulum* Broth., *L. lecomptei* Besch., *L. minutum* C. Muell. and *L. obtusatulum* C. Mull.), and *L. octoblepharioides* Brid. (also as *L. albo-nitens*).

Later, Cardot (1915) proposed to divide the genus into two sections: (1) Homodictya, including species with a leaf (expanded costa of Cardot) that is "homodictyée" and "homostrôsique" and, (2) Heterodictya, including species with a leaf that is "heterodictyée". This last section he subdivided into two subsections, Hétérostrôsica and Homostrôsica (Table 1). Subsection Hétérostrôsica is characterized by a leaf (expanded costa of Cardot) that is "hétérostrôsique" or "subhétérostrôsique" and the leaves keeled throughout. Subsection Homostrôsica is characterized by a leaf more or less "homostrôsique" ending in a convex area on the abaxial side, plane on the adaxial side.

At the family rank, *Leucophanes* has been closely associated with *Arthrocormus*, *Exodictyon*, *Exostratum*, *Octoblepharum*, *Cladopodanthus*, *Leucobryum*, *Ochrobryum*, and *Schistomitrium* (Table 2). Many of these relationships have been primarily based on the structure of the leaf. All these genera share the multistratose condition of the leaves. In transverse section, the leaf is composed of one layer of chlorophyllous cells (except for *Arthrocormus*, *Exodictyon* and *Exostratum*) surrounded by two or more layers of porose hyaline cells.

C. Mueller (1849, 1874, 1897, 1901), Cardot (1899, 1900, 1904, 1915) and Brotherus (1901), who followed Cardot's (1900) classification, included *Leucophanes* and all the other above mentioned genera in the Tribe or Family Leucobryaceae (Table 2). Even though Cardot (1900) recognized that, by peristomial characters, *Leucophanes* is closely related to *Syrrhopodon* rather than to *Leucobryum*, he maintained these genera within the same family.

Table 2 Historical synopsis of the classification of *Leucophanes* and related genera

C. Mueller (1849, 1874)	C. Mueller (1897)	Cardot (1899)	Cardot (1900)	C. Mueller (1901)
Tribe Leucobryaceae	Family Leucobryaceae	Family Leucobryaceae	Family Leucobryaceae	Gruppe Leucobryaceae
		Tribe 1. Leucophaneae	Tribe 1. Leucobryeae	
Cladopodanthus	*Cladopodanthus*		*Cladopodanthus*	*Leucobryum*
Leucobryum	*Leucobryum*	*Leucophanes*	*Leucobryum*	*Ochrobryum*
Schistomitrium	*Schistomitrium*		*Schistomitrium*	*Schistomitrium*
Arthrocormus	*Arthrocormus*		*Ochrobryum*	*Leucophanes*
Leucophanes	*Leucophanes*	Tribe 2. Leucobryeae	Tribe 2. Leucophaneae	*Arthrocormus*
Octoblepharum	*Octoblepharum*	*Cladopodanthus*	*Leucophanes*	
		Leucobryum	Section A	
		Schistomitrium	Section B	
		Ochrobryum	Section C	
		Tribe 3. Octoblehareae	Tribe 3. Octoblephareae	
		Leucobryum (=*Cardotia*)	*Leucobryum* (=*Cardotia*)	
		Octoblepharum	*Octoblepharum*	
		Tribe 4. Arthrocormeae	Tribe 4. Arthrocormeae	
		Arthrocormus	*Arthrocormus*	
		Exodictyon	*Exodictyon*	

Table 2. Continued.

Fleischer (1900-1904)	Cardot (1904)	**Brotherus (1908)**	Brotherus (1901)	**Cardot (1915)**
Reihe Dicranoideae				
Family Leucobryaceae	**Family Leucobryaceae**	**Family Leucobryaceae**	**Family Leucobryaceae**	**Family Leucobryaceae**
Euleucobryeae	**Tribe 1. Leucobryeae**		**Subfamily 1. Leucobryeae**	**Tribe 1. Leucobryeae**
Leucobryum	*Ochrobryum*	*Leucobryum*	*Cladopodanthus*	*Ochrobryum*
	Leucobryum		*Leucobryum*	*Leucobryum*
Schistomitrieae			*Ochrobryum*	**Sect. 1. Heterostrosica**
Cladopo[illegible]thus			*Schistomitrium*	**Sect. 2. Polystrosica**
Schistomitrium				**Sect. 3. Homostrosica**
Reihe Monocranoideae				
(hyophiloideae)				
Family Leucophanaceae	**Tribe 2. Leucophaneae**	**Family Leucophanaceae**	**Subfamily 2. Leucophaneae**	**Tribe 2. Leucophaneae**
Gruppe Leucophaneae				
Leucophanes	*Leucophanes*	*Leucophanes*	*Leucophanes*	*Leucophanes*

Table 2. Continued.

Fleischer (1900-1904)	Cardot (1904)	Brotherus (1908)	Brotherus (1901)	**Cardot (1915)**
				Sect. 1. Homodictya
				Sect. 2. Heterodictya
				Subsect. Heterostrosica
				Subsect. Homostrosica
Gruppe Octoblephareae	Tribe 3. Octoblephareae			
		Octoblepharum	Subfam. 3. Octoblephareae	**Tribe 3. Octoblephareae**
Octoblepharum	*Octoblepharum*	*Arthrocormus*	*Octoblepharum*	*Octoblepharum*
	Leucobryum (=Cardotia)	*Exodictyon*	*Leucobryum (=Cardotia)*	*Leucobryum (=Cardotia)*
Gruppe Arthrocormeae			Subfam. 4. Arthrocormeae	**Tribe 4. Arthrocormeae**
Arthrocormus			*Arthrocormus*	*Arthrocormus*
Exodictyon			*Exodictyon*	*Exodictyon*

Table 2. Continued.

Fleischer (1923)	**Brotherus (1924)**	Herzog (1926)	Crosby & Magill (1977)	**Edwards (1980)**
Reihe Dicranales			Order Syrrhopodontales	**Order Syrrhopodontales**
Unterreihe Leucobryineae				
Family Leucobryaceae	**Family Leucobryaceae**	**Family Leucobryaceae**	Family Calymperaceae	**Family Calymperaceae**
	Subfam. Leucobryoideae	**Leucobryoideae**	*Arthrocormus*	
	Cladopodanthus	*Cladopodanthus*	*Exodictyon*	*Calymperes*
Leucobryum	*Leucobryum*	*Leucobryum*	*Leucophanes*	*Calymperopsis*
	Ochrobryum	*Ochrobryum*	*Octoblepharum*	*Hypodontium*
	Schistomitrium	*Schistomitrium*	*Mitthyridium*	*Mitthyridium*
			Octoblepharum	*Syrrhopodon*
			Syrrhopodon	
Family Leucophanaceae	**Subfam. Leucophanoideae**	**Octoblepharoideae**	*Calymperes*	**Family Leucophanaceae**
Arthrocormus	*Leucophanes*	*Octoblepharum*	*Calymperopsis*	*Arthrocormus*
Exodictyon		*Leucobryum*	*Hypodontium*	*Exodictyon*
Leucophanes				*Leucophanes*
Octoblepharum				*Octoblepharum*
Leucobryum	**Subfam. Octoblepharioideae**			
		Arthrocormoideae	Order Dicranales	**Order Dicranales**
(=*Cardotia*)	*Leucobryum*	*Arthrocormus*	Fam. Dicranaceae	**Fam. Dicranaceae**
	Octoblepharum	*Exodictyon*	*Cladopodanthus*	
	Subfam. Arthrocormoideae	**Family Leucophanaceae**	*Leucobryum*	
	Arthrocormus	*Leucophanes*	*Ochrobryum*	
	Exodictyon		*Schistomitrium*	

Table 2. Continued.

Vitt (1982)	**Ellis (1985)**
Order Pottiales	
Family Calymperaceae	**Family Calymperaceae**
	Subfam. Leucophaneae
Arthrocormus	*Leucophanes*
Calymperes	*Exodictyon*
Calymperopsis	*Exostratum*
Carinafolium	*Arthrocormus*
Exodictyon	*Octoblepharum*
Hypodontium	
Leucophanes	
Mitthyridium	
Octoblepharum	
Syrrhopodon	
Order Dicranales	
Family Leucobryaceae	
Cladopodanthus	
Leucobryum	
Ochrobryum	
Schistomitrium	

Based on peristomial characters, Fleischer (1900-1904) separated *Leucophanes*, *Octoblepharum*, *Arthrocormus* and *Exodictyon* into a single family: the Leucophanaceae. *Leucobryum* and related genera were segregated into the family Leucobryaceae. These families were placed in different taxonomic "Reihes". *Leucophanes* was associated with the Syrrhopodontaceae and the Calymperaceae in the "Reihe" Monocranoideae (or Hyophiloideae). *Leucobryum* and related genera were placed close to the Dicranaceae and Fissidentaceae in the "Reihe" Dicranoideae (Table 2). Fleischer (1923) later changed his mind and included the Leucophanaceae and the Leucobryaceae in close association in the Dicranales (Table 2). Fleischer's first classification was overlooked for many years, perhaps, due to his later rearrangement of the genera or to the fact that peristome characters were not heavily weighted in determining relationships among various taxa, or both.

Brotherus (1908), following Fleischer (1900-1904), in a list of mosses from Samoa and the Solomon Islands segregated *Leucophanes*, *Arthrocormus*, *Exodictyon* and *Octoblepharum* into the family Leucophanaceae. *Leucobryum* was placed in a separate family the Leucobryaceae. In a later publication, Brotherus (1924) followed Cardot's (1900) arrangement of the genera and placed all of them in a single family, the Leucobryaceae, with *Leucophanes* segregated into the subfamily Leucophanoideae. *Arthrocormus*, *Exodictyon* and *Exostratum* were placed in the subfamily Arthrocormoideae, and *Octoblepharum* and *Leucobryum* (as *Cardotia*) in the subfamily Octoblepharoideae (Table 2).

Herzog (1926) placed *Leucophanes* in a monogeneric family the Leucophanaceae. *Arthrocormus*, *Exodictyon*, *Octoblepharum*, and *Leucobryum* and related genera, were placed in the Leucobryaceae (Table 2). No explanation was given for this arrangement.

Andrews (1947) proposed the elimination of the family Leucobryaceae. Based on the structure of the peristome and the anatomy of the leaf, he proposed the inclusion of *Leucophanes*, *Arthrocormus*, *Exodictyon* and *Octoblepharum* in the Calymperaceae. For *Leucobryum* and related genera, he proposed their placement in the Dicranaceae.

Crosby and Magill (1977) following Andrews (1947) included *Leucophanes* and related genera in the Calymperaceae. *Leucobryum* was placed in the Dicranaceae.

Edwards (1979), in his studies of the haplolepideous peristomes, included *Leucophanes*, *Octoblepharum* and *Exodictyon* in the Order Syrrhopodontales. He stated that the peristome of *Leucophanes* (based on *L. candidum* (Schwaegr.) Lindb.) is "typical of the Syrrhopodontales". In his discussion, Edwards also noticed the close structural relationship between the leaf base of *Exodictyon* and that of *Syrrhopodon*. He indicated, at the same time, that the multistratose condition of the leaf in *Leucophanes* and the other transferred genera is "unlike anything found in the Calymperaceae". Edwards (1980), based on the multistratose structure of the leaf with one or more layers of chlorocysts surrounded by hyalocysts (the so called leucobryoid leaf structure), suggested the retention of Fleischer's Leucophanaceae as a family separate from the Calymperaceae.

Crosby (1980), in grouping mosses into orders according to peristomal similarities, followed Edwards' ordinal arrangement within the haplolepideous Bryidae. Unlike Edwards (1980), Crosby placed *Leucophanes*, *Arthrocormus*, *Exodictyon* and *Octoblepharum* in the Calymperaceae rather than in the Leucophanaceae.

Vitt (1982b, 1984), like Edwards (1979) and Crosby (1980), suggested stressing peristomial similarities and placed *Leucophanes*, *Octoblepharum* and related genera in the Calymperaceae, and *Leucobryum* and related genera in the Dicranaceae (Table 2).

Ellis (1985) in his revision of *Exodictyon* proposed the inclusion of this genus as well as *Arthrocormus*, *Leucophanes* and *Octoblepharum* in the subfamily Leucophanoideae within the Calymperaceae. His classification is a modification of that which appeared in Brotherus (1924) (Table 2).

II. MATERIALS AND METHODS

NOMENCLATURE. One of the objectives of a taxonomic monograph is the clarification of the names of the taxa considered. Like Horton (1982), I believe that nomenclatural stability is one of the critical and fundamental aims of the taxonomist. I also believe that the International Code of Botanical Nomenclature (ICBN) (Voss et al., 1983) offers the guidelines for a taxonomic work of this type.

I have obtained and reviewed the original literature and protologues of all names, and the types of all basionyms have been examined, except the few for which I was unable to locate the type specimens. Bibliographic citations and abbreviations follow Index Muscorum (Wijk *et al.*, 1964, 1969).

Types not seen were: some specimens from C. Mueller's herbarium, e.g. *Leucophanes albescens*, which was destroyed during World War II. In other cases like *L. smaragdinum* Mitt. and *L. scabridens*, the type specimen could not be located (see also Appendix 1). For the Mueller types, potential type specimens were requested from other herbaria with which the authority was known to have exchanged materials. In the cases in which type specimens were not examined, a careful study of the material from the author's (or his colleagues') herbarium was pursued to arrive at the concept of the species in question.

In order to determine the existence of a Holotype or to select a Lectotype various steps were followed. First, a careful revision of the protologue was made and the basionym was listed. Potential type specimens were requested from the author's herbarium and others in which duplicates of his collections were or might have been deposited. If there was evidence (as far as we can presently verify) that a single specimen from the author's herbarium was used for the original description of the taxon, with no duplicates found in any other herbaria, this specimen was considered to be the holotype. For most taxa, various duplicates of the potential type material were present in other herbaria. I do not know if all the samples were part of a single specimen, later separated by the author (or some other person), or if the sample in the author's herbarium was the only one used to name the taxon. Thus, for these taxa, a lectotype was selected. Like Vitt (1980) and Horton (1982), I considered unnecessary the use of the term isolectotype for duplicates of the lectotype. All duplicates of the lectotype are considered isotypes. When various specimens (either from the same locality or from different ones) were used originally to designate a taxon, one of them was selected as the lectotype. The others were designated as isotypes or syntypes accordingly.

The 42 names originally recognized were validly published by 16 authorities. Ten of these names are from C. Mueller, three from Brotherus (herbarium now at H), one from Brotherus and Geheeb (H), five from Bescherelle (BM and PC), two from Bridel (B), two from Cardot (PC), two from Cardot and Thériot (PC), one from Dixon (BM), two from Dusén (S, NY), four from Fleischer (FH), two from Lindberg (H), one from Gangulee (BM), two from Mitten (NY), one from Potier de la Varde (PC), two from Renauld and Cardot (PC), and one from Jaeger (NY).

TAXONOMIC CONCEPTS. The classification of objects into taxa (taxonomic concept) is as old as the history of man. Even before the advent of early civilizations, man recognized groups of edible, medicinal and poisonous plants. This is what has been called "folk taxonomy" (Heywood, 1976) and it still exists in some tribal groups around the world. Classification implies a system of information storage and retrieval (Heywood, 1976). In the biological world, it is essential as a refer[illegible] the organisms with which the biologist works.

In botany and [illegible] species has been considered the basic evolutionary unit (Mayr *et al.* 1953; Ma[illegible] 1, to mention some). It is important in the sense that it represents a level of in[illegible] biological world (Mayr, 1957). Yet, as simple as these statements may sound, the species concept has been one of the most interesting and controversial problems in modern science and an extensive literature has been produced through the years covering the different aspects of it (Mayr, 1957; Simpson, 1961; Wiley, 1978, 1981 provide good reviews of it).

Two important figures in biology are associated with any discussion of the species concept: Linnaeus and Darwin. Linnaeus believed that the species were divinely created, constant and sharply delimited (have reality and objectivity)(Mayr, 1957). The taxonomic species concept of Linnaeus was based on structural characters including some knowledge of geographical distribution (Heywood, 1976). Linnaeus' species concept was not only morphological, but also typological. Thus, the type specimen was considered to represent the species.

The morphological-geographical species concept became widely successful through the years reaching its culmination towards the end of the nineteenth century. Separation of individuals (populations or groups of populations) was based on similarities among groups or entities coupled with morphological discontinuities. The success of the morphological species concept was due, in part, to the fact that the morphological units recognized would usually correspond to natural breeding populations (Davis & Heywood, 1973).

With Darwin and the advent of the evolutionary theory, a new conceptual framework was brought into taxonomy. Similarities between present day organisms were viewed as manifestation of common ancestry or common genetic background (Davis & Heywood, 1973; Heywood, 1976). Thus, according to this concept, species were considered groups of ancestor-descendant lineages each with its own tendencies and evolutionary roles. This evolutionary concept has been refined (Wiley, 1981) and is much use in systematics today.

The biological species concept is, perhaps, as old as the taxonomic one. Although the concept was a generalized opinion by the nineteenth century, botanists accepted it with apprehension, particularly those engaged in hybridization experiments (Raven, 1980). The biological species concept is based on the concept of interbreeding populations that are reproductively isolated from other such units. Mayr (1940, 1957, 1963, 1969, 1976) has been a leading proponent of this concept. According to this view, a species is a group of organisms sharing a common gene pool. Gene flow is responsible for maintaining the species integrity. Differentiation, therefore, is not possible unless species gene flow is stopped.

The biological species concept was initially adopted by plant systematists interested in evolution (Stebbins, 1950; Grant, 1957, 1971). Nevertheless, the application of the concept in botany has encountered many problems. Free interbreeding between populations cannot be taken loosely as a determinative measure for individual species (see for example, Anderson and Snider, 1982). There are many exceptions in bryophytes to the biological species concept. Anderson and Lemmon (1974) have demonstrated that gene flow distances for bryophytes may be very short. Thus, entities located many meters away may not frequently exchange genes, yet they may be morphologically indistinguishable. Also, geological events may disrupt populations into isolated entities that otherwise may remain morphologically identical. On the other hand, allopatric populations, occupying different geographical areas, may still interbreed when crosses are artificially made. Yet, these entities, in nature, may have diverged to such an extent that they are otherwise distinct. In other words, they share a particular set of apomorphies which define them as distinct entities even though breeding barriers have not yet developed. Thus, the fact that they have potential to freely interbreed should not be weighted singly to place both entities into a single species. In bryophytes, restricted gene flow with the production of hybrids or the study of meiosis in hybrids are not, by themselves, sufficient for taxonomic conclusions (Szweykowski, 1984). Added to this is the fact that many bryophytes exist in large unisexual populations that reproduce only by asexual means (Anderson, 1963; Longton & Schuster, 1983; Schuster, 1983; Szweykowski, 1984). Thus, for practical purposes, the biological species concept, useful for animals, is not operational in bryophytes (and many other plant groups as well); supplemental data from different methods should be compared. These methods must be as objective as possible and ideally an experimental approach ought to be involved. Experimental approaches may include crossing of individuals, transplants and growth under controlled environmental conditions. The data must be evaluated in the light of phylogenetic relationships of ancestral-descendant lineages to arrive at the concept of a species for a particular taxon. I, then, support a pluralistic approach to the species concept. Like Mishler and Donoghue (1982), I believe that each problem should be carefully and critically examined in the light of all possible gathered data to arrive at a concept of a species for that particular taxon. In this evaluation, phylogenetic relationships of ancestral descendant lineages, based on shared derived characters (synapotypies that delimit monophyletic groups) are of prime importance. The species thus defined, will be phylogenetically meaningful.

In this treatment of *Leucophanes*, my species concept is primarily based on structural features. It is my belief that it is essential for a systematic revision of this type to have a thorough knowledge of the structure of the taxa. This can be done by an extensive study of herbarium specimens. Field work is also essential in the understanding of any group. It is not a substitute for the study of structure, but a complement that gives a perspective of populations not possible to achieve with the study of herbarium material alone. I believe that species have a reality of their own in time and space. Species also have continuity in time which allows for phylogenetic reconstructions. It is in this framework that taxonomic and phylogenetic conclusions are dealt with in this treatment.

There have also been many controversies in relation to infraspecific categories. The category of subspecies was first used by Persoon (1805-1807). It did not have any geographical connotations but was used only as an intermediate category between the species and the variety (Davis and Heywood, 1973). The modern usage of subspecies follows closely that proposed by Du Rietz (1930) and Rothmaler (1944, 1954, 1955). Du Rietz (1930) defined the subspecies as: "a population of several biotypes forming a more or less distinct regional facies of a species". The restriction of the concept to major geographical races dates back to the early works of Wettstein (1896, 1898).

For Rothmaler (1944, 1954, 1955), the subspecies is a group of plants more or less separated by a group of characters and usually not genetically isolated. In this sense, various subspecies of a species may be continuously intergrading with each other. Subspecies clearly have a common origin as denoted by the many attributes they share in common.

The subspecific category has been widely used in zoology (Mayr, 1969; Simpson, 1961). It has been used for example for a taxon "characteristic of a particular geographical area of geological horizon" (Intern. Code of Zool. Nom., Art. 45, 1961). Traditionally, botanists have used both subspecies and variety (Davis and Heywood, 1973). In bryology, the subspecific category has been of limited usage when compared to variety. The common practice is to restrict its use to populations of various biotypes with a restricted geographical area or cytological sterility barrier that have an imperfect morphological differentiation (Crundwell, 1970a).

The taxonomic rank of variety has been widely used in botany, perhaps, imposed by the Linnean tradition as suggested by Davis and Heywood (1973). As with the case of the subspecies, the category of variety has been used in taxonomy for units of different ranks (Du Rietz, 1930; Davis and Heywood, 1973). Du Rietz (1930) proposed the use of variety for "a population of one or several biotypes, forming more or less distinct local facies of a species". In its modern usage it is widely applied to morphologically distinct populations (that may comprise several biotypes) with a restricted geographical area (Davis and Heywood, 1973). In this sense, varieties may be ecological, geographical, genetic or a combination of these. Bryologists have used the variety to circumscribe ecological variations as well as morphological variants that occur in a particular geographical area (see for example Buck, 1980). Crundwell (1970b) has proposed the use of infraspecific categories to stimulate the investigation of some variations that may be otherwise overlooked. In this treatment, the subspecific category will be recognized in the sense of Du Rietz (1930) and Rothmaler (1944, 1954, 1955).

In the present taxonomic treatment, some morphological variations have been useful in distinguishing populations of *Leucophanes*. For example, in *L. glaucum*, variations in peristome ornamentation segregate populations that are otherwise gametophytically indistinguishable. These populations have been recognized at the subspecific level. In *L. octoblepharioides*, there are populations in which more than one layer of hyalocysts are observed on the abaxial side of the leaf, at base. These populations were given varietal rank (*L. octoblepharioides* var. *korthalsii*) by Fleischer (1900-1904). The formation of the second layer of hyalocysts is variable among populations of this species and a range of intermediate forms are observed between the two structural variants. It is here considered that these variations are part of the structural plasticity of the species. Thus, populations with this type of variation are not given taxonomic recognition. Other populations of the same species from Borneo and Thailand have long setae and squarrose leaves with a costa that is covered, from base to apex, by a layer of hyaline cells. These features are constant and characteristic for these populations. Thus, plants with these characters have been given subspecific rank.

At the generic level, the first definition of this category was given by Linnaeus (1751) in his "Philosophia Botanica". The genus was conceived by him as a group of closely related species (Love, 1963).

In bryophyte taxonomy, generic concepts had rested a great deal upon tradition (Anderson, 1974). Recently, increasing cytological evidence, and critical evaluation of morphological data complemented by numerical (quantitative) methods have resulted in the segregation of some genera (Koponen, 1968; Smith, 1971; Horton, 1982; Frahm, 1983, Ellis, 1985).

I believe that an evolutionary approach to the concept of the genus (as with the species) will certainly help in providing some unifying guidelines. A critical analysis of discontinuities and variational patterns of genera within a given family, based on all data available, is a very important step in this direction (see also Frahm, 1982, 1983).

In the circumscription of the genus *Leucophanes*, as with the species, structural characters coupled with data from field observations were evaluated. Gametophytic and sporophytic characters (within certain degrees of variability) are typical for the genus (see taxonomic section on the Genus). The combination of these characters in *Leucophanes* is distinct from those occurring in *Exodictyon*, *Exostratum*, *Arthrocormus*, and *Octoblepharum*. No important discontinuities to these general morphological patterns have been observed to justify the proposal of an additional generic category. At the subgeneric level, three distinct species-complexes can be distinguished. These have been taxonomically recognized as the subgenera *Leucophanes*, *Trachynotus* and *Leionotus*.

DESCRIPTIONS. The descriptions are based on critical examination of herbarium specimens and where possible living material. A diagrammatic representation of the methodos followed in the measurement of different plant parts is given in Figs. 1-11. Size of the plants was measured under the stereomicroscope or with the naked eye. Leaf aspect was determined from dry and moist material. For leaf size, the plants were moistened in boiling water and leaves from the most distal part of the stem detached and mounted on a slide, a coverslip was placed with a slight pressure to flatten the leaves. Five leaves from each specimen examined were selected for measurements, using a stereomicroscope at a magnification of 120X for leaf length and, at 250X and 500X for leaf width. For species with strongly squarrose leaves, the length of the leaf was measured from insertion to the bent area and from the bent area to the apex (Fig. 2). Cell size was taken only for surface hyalocysts on the abaxial side of the leaf. For basal and median hyalocysts, 20 measurements per leaf were recorded (5 leaves per sample); for apical hyalocysts, 10 measurements. Length and width sizes of cell lumena were taken under a light microscope at a magnification of 400X. Transverse sections of the stem were taken from moist material under the stereomicroscope. These sections were mounted and measured under the light microscope at a magnification of 400X. Length of the hyaline lamina was taken from the leaf insertion to the uppermost hyaline cells and recorded as a fraction of the whole leaf length. The width of the lamina (in rows of cells) was determined from surface view and transverse sections. Length of the seta was recorded from its insertion to the vaginula to its attachment to the neck of the capsule. Twisting of the seta was determined, on face view, from dry material, counterclockwise twisting is referred to as dextrorse, clockwise twisting, sinistrorse. Capsule length included the operculum and urn unless otherwise stated. Exothecial cells from the center of the capsule were measured from material previously mounted in Hoyer's medium. Measurements of length and width of the lumen of exothecial and rim cells were carried out under the light microscope at 400X. Ten cells per capsule were measured. The number of capsules measured was dependent on the material available for examination. Length and width of the guard cells (5 measurements per capsule) and spore size (based on 50 measurements per capsule) were recorded from prepared slides mounted in Hoyer's and examined under a light

Figs. 1-11. Schematic representation of the methodology used in the measurement of plant parts. A = apex, B = midleaf, C = base, ad = adaxial surface, ab = abaxial surface, Ch = chlorocysts, Co = costa, De = dextrorse, Gc = guide cells, H = hylocysts, Hl = hyaline lamina, L = length, La = lacunae, Lc = length of capsule, Lo = length of operculum, Ls = length of setae, Lu = length of urn, Ml = multistratose lamina, S = stereids, Si = sinistrorse, W = width.

Figs. 1-2. Leaf habit.

Fig. 3. Chlorocysts in surface view.

Fig. 4. Hyalocysts in surface view.

Fig. 5-6. Transverse sections of leaves.

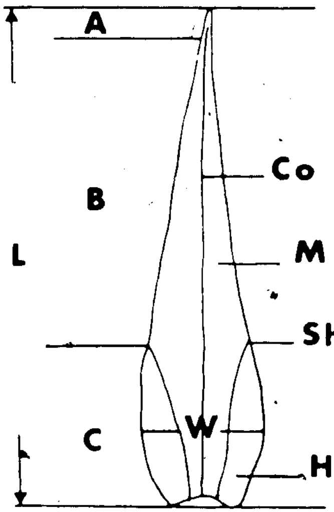
Fig. 7. Habit.

Fig. 8. Transverse sections of stem.

Fig. 9. Capsule.

Fig. 10. Sporophyte.

Fig. 11. Twisting of seta.



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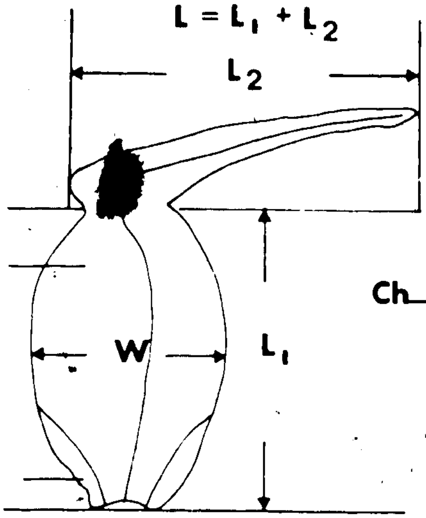

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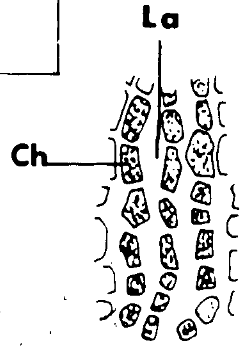

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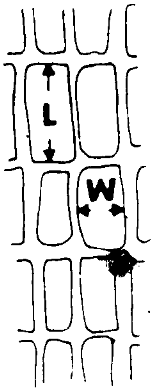

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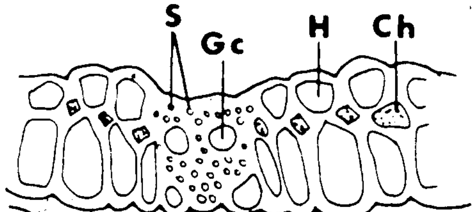

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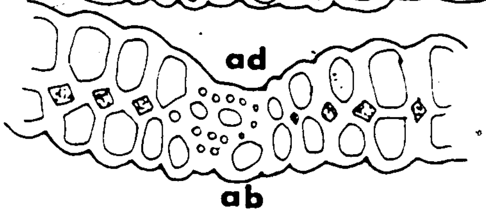

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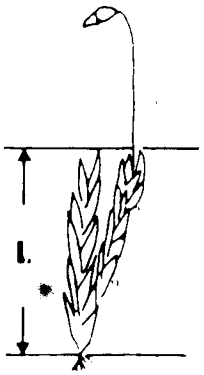

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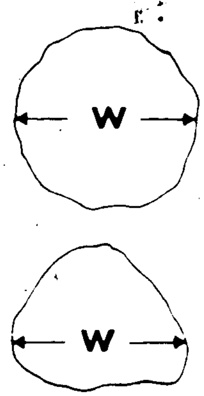

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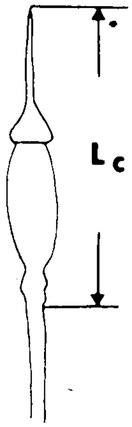

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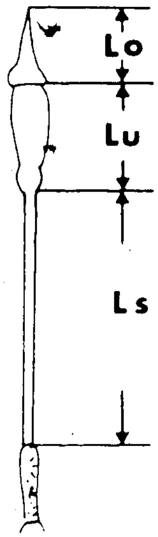

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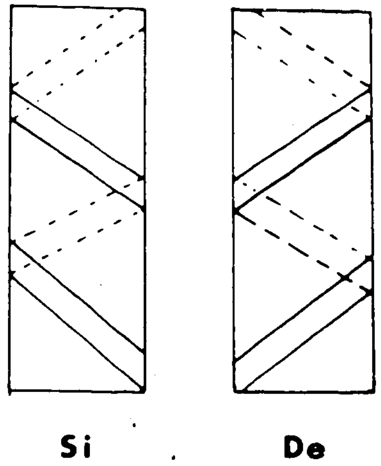

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microscope at 400X. Details and size of spore ornamentation were described from SEM micrographs.

LINE DRAWINGS AND SCANNING ELECTRON MICROGRAPHS. Photographs of plant habits were taken based on dried specimens. For calyptrae and capsules, drawings of dried samples were done under the stereomicroscope with the aid of a drawing tube. In other cases, a projecting microscope was used and line drawings of the magnified image were done. For the leaves and gemmae, line drawings were made on thoroughly moistened material placed on a slide with either the abaxial or adaxial surfaces down and compressed under a coverslip. Freehand, transverse sections of thoroughly moist leaves were mounted in water and Hoyer's medium (Anderson, 1954). Line drawings of freehand sections were done under a compound microscope with an attached drawing tube.

Specimens to be used for scanning electron microscopy (SEM) were selected from those studied with the light microscope to represent the variations observed in a particular taxon. The selected material was prepared for SEM as follows: (1) throroughly hydrated in distilled water (for capsules, in particular, after treatment in boiling water, they were left overnight to ensure complete penetration of water into the spore sac); (2) sectioned-freehand with a sharp razor blade (when applicable); (3) fixed in OsO_4 for 25-30 minutes; (4) thoroughly washed; (5) dehydrated through a 10, 20, 50, 75, 90, 95% sequence into absolute ETOH; (6) left overnight in 100% ETOH; (7) set through a 10, 20, 50, 75, 90, 95% sequence into 100% amyl acetate; (8) left overnight in 100% amyl acetate. The material was then critically point-dried and mounted in double-sided tape on stubs or in glue (Mikrostick) on stubs.

HABITAT. Information on habitat was derived mainly from the protologues, previous publications on the material revised and herbarium labels. Habitat information for the Caribbean, Panama and the Vanuatu collections was also gathered from field trips to these areas.

Measurements of bark pH were obtained for some specimens from Vanuatu and Panama. About 2-5 mg of air-dried bark were placed in distilled water and stirred for a few minutes. The solution was allowed to stand for at least twelve hours and readings were taken with a single probe Beckman Electromate meter.

For the Neotropical sample, pH determination was made from a single collection from Panama (Salazar, 3017). The plants have been growing in the laboratory for two years on a piece of branch from a *Virola* shrub. The bark was processed as above and the pH was measured. A second determination was made in the following manner: the piece of branch with the growing plants was thoroughly washed with distilled water and the pH of the leachate measured.

G[illegible]APHICAL DISTRIBUTION. Individual localities were plotted by a dot or half dot based on information obtained from specimens received on loan from various herbaria and from my own collections mainly from Panama, the Caribbean and Vanuatu. In some instances in which localities were close together, it has not been possible to retain clarity of representation. Based on the information available to me at the present time (April, 1986), I have attempted to plot as many taxa as occur in the Old World, India, Africa, New Guinea, Australia, the islands of the tropical Pacific and the Neotropics. Specimens cited in other publications have not been considered unless they were examined and their identification confirmed. For specimens with no specific locality, e.g. "Sumatra", "Java", a careful study was made of the collector's botanizing trip(s) as appear in his own, or his colleagues' publications. With this information, the approximate locality was plotted. Specimens from the following herbaria were used in plotting the distributions: ALTA, B, BM, C, CBG, EGR, FH, G, H, INPA, JE, L, M, MU, H.A. Miller personal herbarium (that will be transferred to MU), NY PC, PMA, S, TRTC, U and W. Particularly useful in determining the geographical range of taxa were the many collections from B, BM, CBG, EGR, FH, INPA, L, M, NY, PMA, S, U, W and H.A. Miller, personal herbarium. Worldwide maps (Goode homolosine equal area projection), and maps of Africa and New Guinea (Mercator projection) were used for plotting the geographical distribution of the taxa.

SPECIMENS EXAMINED. Citation of specimens examined represents a useful source of information that supplements the distributional maps presented. First, it gives information on the location of a particular sample(s) on which distribution dots were based. Secondly, it may also provide altitudinal notes important in documenting and defining the habitat ranges for species. Thirdly, it gives some indication of the total number of specimens examined that served as the basis for the descriptions presented. Finally, it may help interested researchers in requesting a loan of particular specimens to arrive at the taxonomist's concept of a taxon. Nevertheless, I have considered that the amount of space that specimen citations take in a publication and the time involved in compiling these records outweigh the purposes of citing them. Instead, I list, for each taxon, the number of specimens examined and annotated in each herbarium (number of specimens above 30 are rounded to the nearest five).

III. MORPHOLOGICAL DESCRIPTION

DIAGNOSIS. Plants of *Leucophanes* are characterized by a white-green to blue-green color; erect turf-forming habit (close to *Exodictyon* and *Arthrocormus*); the presence of epigametophytes (Salazar-Allen, 1985); leaves composed of a costa and a lamina with multistratose and unistratose areas, and the tips of the leaves bearing clustered gemmae or rhizoids. The capsule is exserted, cylindrical to ovoid with a short neck and phanerophore stomata. The peristome is haplolepideous with a prostome, and is composed of 16 orange-red, papillose to smooth teeth, that are slender to stout.

Plants of *Leucophanes*, particularly *L. candidum*, have been used by natives of Malaysia, as stuffing material for pillows. This is the only practical use of these plants known to me.

HABIT. Plants of *Leucophanes* are acrocarpous, unbranched or sparingly branched, in loose to compact turfs. Although sporophytes are terminal on the main shoot, the stem continues growth by subterminal innovations and also by short branching systems (epigametophytes) arising from a large superficial stem cell. Thus, the main stem branches sympodially. The short branching systems arise independently of the production of the sporophyte and develop sex organs. They also develop abundant rhizoids at the base and are easily detached from the main stem, hence acting in vegetative reproduction. The stem has also been observed to produce branches in groups of 2-3.

Individual plants vary in size and growth increments, perhaps yearly or according to seasonality of rain patterns are often observed. The tallest plants are observed in *L. serratulum, L. candidum and L. milleri*. Among the smallest are the Neotropical populations of *L. molleri*.

The phyllotaxis is essentially spiral, although leaf arrangements in five ranks have been observed in some populations of *L. candidum* from New Guinea. Within the genus, there is considerable variation in leaf size in different species. The largest leaves measure 7-8 mm while the smallest range from 2-4 mm. The growth habit and over-all color impression of the gametophyte are important features that define many species of *Leucophanes*. Important in *L. candidum* are the squarrose to erect, tumid leaves and robust habit. The blue-green to light green color, broad to narrow twisted leaves with sharply dentate to smooth costae, thick margins and oceanic distribution characterize *L. glaucum*. *Leucophanes angustifolium* is characterized by its whitish to light blue-green color, long, narrow, easily detachable leaves and a habit of loose turfs. The greenish-white to light blue-green color and the erect, narrow leaves are typical of *L. octoblepharioides*, while plants of *L. molleri* are characterized by their light-green delicate appearance, forming small turfs. *Leucophanes hildebrandtii* forms tall, compact turfs with stiff leaves. *Leucophanes renauldii* has a very distinct translucent aspect under the steroscope, with the large bulging hyaline cells clearly observable at low magnification. *Leucophanes serratulum*, on the other hand, is characterized by its robust habit with long, erect to semi-arcuate leaves, synoicous condition and abundant production of sporophytes. *Leucophanes unguiculatum* is distinguished by its coarse appearance with compact falcate-secund leaves.

STEM. The stem of *Leucophanes* in transverse section is more or less round to irregularly triangular and composed of a central medullar area of large cells that are isodiametric in shape, variable in size and have thin walls. These cells are surrounded by an outer cortex of one to two layers of cells that are smaller and have thicker walls than the medullary cells (Fig. 12). All the cells in the stem develop a reddish-brown pigmentation in their walls. There is no central strand. The younger, apical portions of the stem are lighter in color than the older basal parts.

AXILLARY HAIRS. Axillary hairs are present at the apex of the stem surrounding the apical bud (Fig. 13). They are unbranched, multicellular, hyaline structures variable in size and number of cells. The apical cell is larger than those below it and rounded at its apex. Axillary hairs have been found in all species studied, although no mention of their presence has been reported in the literature. Axillary hairs have been associated with the protection of the growing

Fig. 12. *L. candidum*. Transverse sections of stem and leaves. Scale = 100 um. (Schultze-Motel 3416, B).

Fig. 13-15. *L. molleri.* (Salazar 3017, ALTA, PMA).

Fig. 13. Apex with axillary hairs. Scale = 50 um.

Fig. 14. Leaf-tip gemmae. Scale = 20 um.

Fig. 15. Leaf-tip gemmae germinating into protonema. Scale = 100um.

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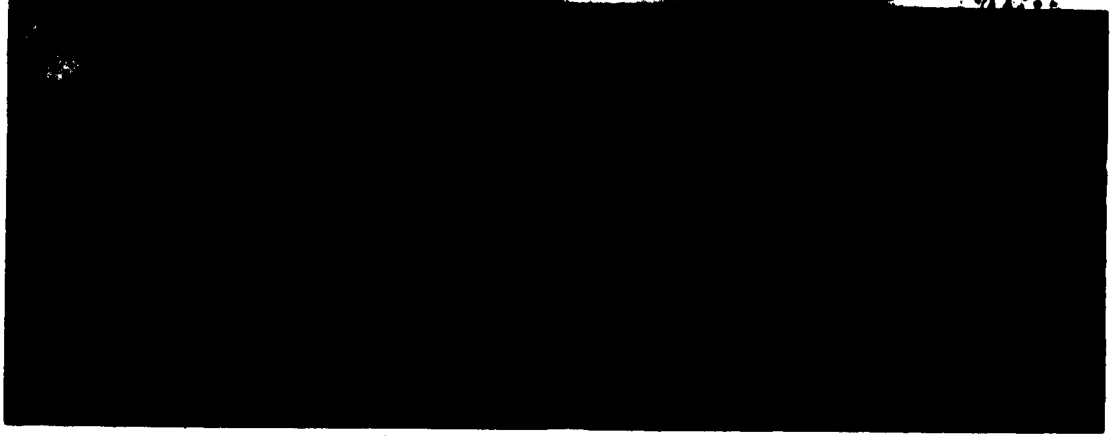


apices against drought by secreting mucilaginous substances (Schofield and Hébant 1984). As well, they have been particularly useful in the study of some acrocarpous groups (Saito 1975, Horton 1982). In *Leucophanes*, they are structurally similar and of no taxonomic value.

Mature leaves of ***Leucophanes*** **are not associated with axillary hairs, these disappearing** as the leaf matures. This disappearance has also been reported to occur in some pleurocarps (Buck 1980).

ASEXUAL REPRODUCTIVE STRUCTURES. The most characteristic diaspores in *Leucophanes* are leaf tip gemmae. The concept of gemma as compared to propagula, followed here is that of Schofield and Hébant (1984). Accordingly, gemmae are vegetative reproductive structures that develop a protonematic phase before producing leafy gametophytes. Propagula, on the other hand, develop an apical cell and are therefore considered small leafy gametophores. In all cases of observed germinating diaspores, a protonematic phase preceded the production of leafy gametophores.

All species, except for *L. candidum*, produce, clusters of gemmae at the leaf tips (Figs. 14, 15). These are long, clavate to elliptic-clavate in shape, with more or less thick, papillose walls. The number of chlorophyllous cells per gemma varies as does its size. Gemmae have been observed to germinate *in situ* (Fig. 15) or when detached. They can germinate from either their proximal or their distal ends. On detached gemmae germination is observed, whereas in those attached to leaves, germination takes place distally. The proximal region can be branched or unbranched (Fig. 30) and it is the narrowest section of the gemma except when distal portion is germinting. Asexually produced gametophores in early stages of development have been observed among clusters of gemmae. Even though the apex of the leaf is the main area for the production of gemmae, they can also be formed below the apex to midleaf, on adaxial and abaxial surfaces, particularly associated with the costal area. Ligrone (1984, 1985) has suggested that, perhaps, the regenerative capacity of the leaf will be mostly restricted to the chlorocysts in the costal area. This is based on the structural composition of these cells that contain spherical bodies apparently composed of ribosome-like particles. Frequency in the production of gemmae does not seem to be correlated with the absence or presence of sex organs as reported for some mosses (During, 1979; Une *et al.*, 1983) Although leaf gemmae are of frequent occurrence in most species, there is little mention of them in the literature.

Correns (1899) based his brief discussion of the brood bodies (gemmae) mostly on Dozy and Molkenboer's (1855-1870) latin descriptions of *L. octoblepharioides*, *L. candidum* and *L. hildebrandtii* rather than on examined material. He suggested that the descriptions "*caule fragilis*" for the first two species and *nervo in summo apice saepius incrassato et anomalo vel radiculoso*" for *L. hildebrandtii* possibly indicated, production of brood bodies.

Cardot (1900) mentioned very briefly the occurrence of leaf tip gemmae in *Leucophanes* and their development into leafy gametophytes: "...le stereome est fréquemment dilaté et propagulifière au sommet, et les qu'il porte donnent souvent naissance à de jeune plantules". Fleischer (1900-1904) gave a brief description of the "Brütkorpern" in *L. octoblepharioides*, *L. angustifolium* (as *L. massartii* Ren. and Card.) and *L. glaucum* (as *L. glaucescens* C. Muell.) as long, elliptical and shortly articulated ("kurzgliedrigen"). Andrews (1947) discussed the production of propagula in *Leucophanes* as a trait suggesting the relationship between this genus and the Calymperaceae in which they frequently occur. Roth's (in Andrews, 1947) unpublished drawings of the gemmae of *L. glaucum* (as *L. neocaledonicum* Card. and Thér.), *L. octoblepharioides* (as *L. nicobaricum*) , and *L. molleri* (as *L. horridulum* Broth. and *L. mittenii* Card.) are, perhaps, the earliest illustrations of these vegetative diaspores in *Leucophanes*.

Detached, short branching systems or epigametophytes, may also serve as vegetative propagules. These epigametophytes arise from superficial cells of the stem (and perhaps from gemmae too) apparently by a similar process to that which originates a propagulum. The epigametophytes develop into fully grown gametophytes and remain attached to the mother plant by an extensive rhizoidal system. These epigametophytes are readily detached and serve also as asexual propagants (for more details see Salazar-Allen, 1985).

Leucophanes leaves, particularly detached ones and those close to or buried in the substrata, have been observed to develop protonema and leafy gametophores, thus acting as another means of vegetative reproduction.

THE LEAF

1. THE CONCEPT OF THE LEAF STRUCTURE IN *LEUCOPHANES*

Leaf structure is of critical importance in the understanding of the biosystematics of *Leucophanes*. Traditionally, the leaves of *Leucophanes*, *Exodictyon*, *Arthrocormus*, *Octoblepharum*, *Leucobryum* and related genera, have been considered to be composed mainly of an expanded costa (De Notaris 1869, Cardot 1900). In these genera, the costa is thought to be represented by the multistratose structure of the leaf, with living chlorophyllous cells (chlorocysts) and dead, porose, hyaline cells (hyalocysts or leucocysts) in various layers and arrangements while the unistratose hyaline areas, at the sides of the leaf near the base, are considered the true lamina (Fig. 16). The chlorocysts of the leaf are living elements with abundant chloroplasts and thin or thick walls. They are the major photosynthetic elements of the leaf. The hyalocysts, at maturity, are devoid of protoplasm, have porate walls (Figs. 22-25) and may contain cyanobacteria and other organisms.

Bridel (1827), in the first description of *Leucophanes*, considered the leaves as characteristically costate "*folia luculentissime nervata*". Mueller (1843) followed Bridel's concept describing the leaf of *Leucophanes* as "*folia nervosa*". Morin (1893), in his studies of moss leaves, compared the origin of the midstereid band in *Leucophanes* to that of *Campylopus* (Dicranaceae). He suggested that the pattern of development indicated a common trait between these genera: "C'est un trait d'union avec *Campylopus*, ou le stereome se retrouve plus developpé et multiplié surtout dans sens de la largeur de la feuille".

The concept that the leaf is composed of the expanded costa was first proposed by De Notaris (1869) for *Leucobryum*: "*Folia enervia, vel si mavis, nervo latissimo depresso exarata*".

Figs. 16-21. C = costa, Ch = chlorocysts, H = hyalocysts, Hl = hyaline lamina, M = margin.

Fig. 16. *L. molleri*. Transverse section of leaf. Scale = 55 um. (Puerto Rico, Salazar 2958, PMA)

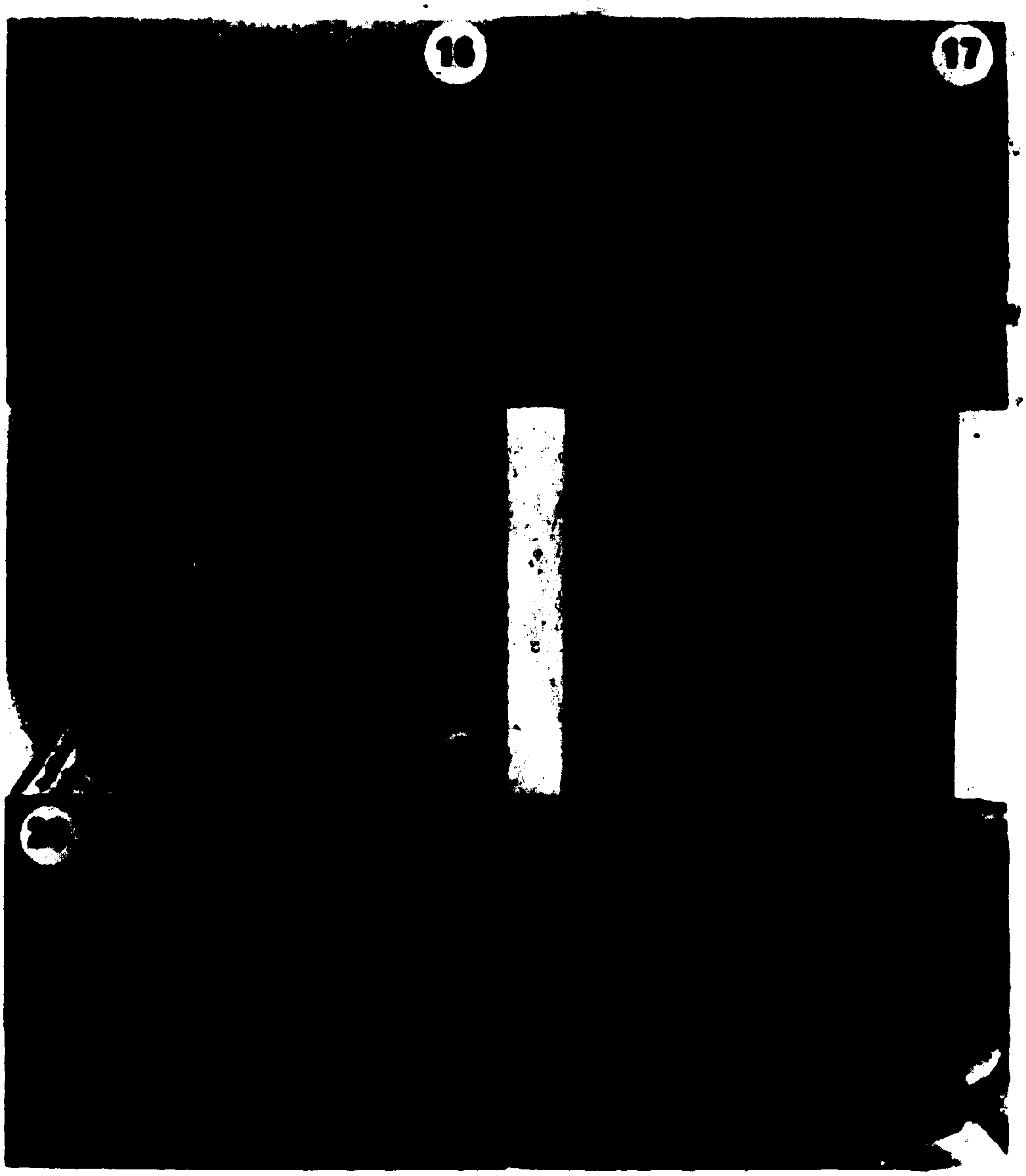
Fig. 17. *L. angustifolium*. Transverse section of leaf at base. Scale = 20 um. (Society Islands, Moore 6, B)

Fig. 18. *L. molleri*. Isolated hyaline areas at apex of leaf. Scale = 25 um. (Panama, Salazar 3017, ALTA, PMA).

Fig. 19. *L. hildebrandtii*. Spinose apex. Scale = 40 um. (Comoro Islands, Hildebrandt a. 1875, H).

Fig. 20. *L. molleri*. Apex with leaf-tip gemmae. Scale = 40 um. (Cameroon, Dusen 117, BM).

Fig. 21. *L. glaucum*. Transverse section of leaf at base. Scale = 20 um. (Australia, Bailey 651, BM).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Figs. 22-23. Pores on basal hyalocysts.

Fig. 22. *L. candidum*. Scale = 20 um. (Samoa, Schultze-Motel 3416, B).

Fig. 23. *L. molleri*. Scale = 20 um. (Salazar 3017, ALTA, PMA).

Fig. 24-25. Pores on apical hyalocysts. Scale = 20 um.

Fig. 24. *L. glaucum* (S. Andaman, Kurz 2546, BM).

Fig. 25. *L. molleri* (Brazil, Schiffner 699, H).

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This concept was adopted years later by various authors, among them Lindberg (1886), Braithwaite (1887-1905) and Husnot (1884-1890). Lorch (1894) on the bases of morphological studies, suggested that the multistratose area of the leaf in *Leucophanes* represented the expanded costa. In a later work (1931), he emphasized the physiological aspects of the leaf structure and proposed to regard the central area with stereids as the true costa. Cardot (1900), following De Notaris, indicated that the leaf in *Leucophanes* and related genera was mainly composed of the expanded costa. No developmental patterns were illustrated. Fleischer (1900-1904), in his description of *L. sertatulum*, pointed out the distinct costal character of the midstereid band, particularly at the leaf base, and used the term "pseudolamina" instead of costa for the multistratose section of the leaf: "...zeigt ebenfalls das M[illegible]m am Blattgrunde einen ausgesprochenen Rippencharakter (s.t II fig. 9) [illegible] den Ausdruck Rippe [costa] auf das ganze Blatt bezogen (soweit die merhschic[illegible]*cocysten* reichen) ganz vermeide und dafür schon in der Flora v. Buitenzorg die Beze[illegible]g *Pseudolamina* angewendet habe." He also questioned the application to the Leucophanaceae of the theory ("Rippentheorie") of the leaf as composed of the expanded costa: "Uberhaupt lässt diese Tatsache die ganze Rippentheorie der *Leucobryaceen*, besonders auf die *Leucophanaceen* angewendet, sehr zweifelhaft erscheinen." Ligrone (1985) proposed a hypothesis of the evolutionary development of the leaf in the Leucobryaceae (including *Leucophanes* and *Leucobryum*) from a "Pottioid and/or Dicranoid" ancestor. The multistratose condition was considered to have arisen, as proposed by Cardot (1900), by progressive enlargement of the costal area concomitant with a reduction of the lamina. The evolution of hyalocysts and chlorocysts in mosses with this type of leucobryalean leaf structure is considered to have been the result of an adaptation to relatively dry climatic conditions (see also Salazar-Allen, 1985). The leaf is thought to have evolved from a heterostrosic type (Cardot 1900) to a homostrosic type (Cardot 1900), this evolution related to a "restrictive" adaptation to more moist habitats.

Perhaps, the critical point involved in determining whether the leaf of *Leucophanes* is structurally composed of the expanded costa or whether it is a costate organ with a multistratose lamina is based on the concept of the costa and its ontogeny. The costa of a moss leaf has been defined as a specialized area that functions in support and translocation of water and dissolved substances (Hébant, 1977; Schofield & Hébant, 1984). Its structure may be rather simple or complex and at least four types of cells besides the epidermal ones have been described for it: stereids or supporting elements, hydroids or water conducting elements, parenchyma, and leptoids (Hébant, 1977; Schofield and Hébant, 1984). Not all of these elements occur in all moss leaves. Variation in the structure and composition of the costa are being used in recent systematic studies as a useful character in clarifying relationships between and within taxa (Hébant 1970 (1971), 1976, Smith 1971, Saito 1975, Peterson 1979, Horton 1982, among some). In *Leucophanes*, the central area of the leaf has this specialization in cell structure and function (Figs. 17, 26-29) and thus, in this sense, can be considered homologous to the costal area of most moss leaves. Ligrone (1984) indicated that the chlorocysts enclosed in the central stereid band ("pseudonerve" of Ligrone), unlike those of the adjacent leaf areas, contain small chloroplasts, numerous vacuoles, abundant lipid inclusions and occasional electron dense bodies of tightly packed ribosome-like particles. Thus, these cells appear to be homologous to the specialized parenchyma that occurs in the costal area of most moss leaves. These specialized parenchyma cells have been called "deuters", "duces" or "guide cells" (Lorentz, 1867-68), "eurycystes" (Morin, 1893) and "socii" (Lorentz, 1867-68). The stereids of the costa and marginal multistratose border in *Leucophanes* have a polilamellate structure with small pores (Ligrone, 1984). They may retain some protoplasmic material or be completely devoid of it at maturity.

Three approaches were taken to determine homologies of leaf structure. The first one included the study of the apical bud and young gametophores developing from gemmae and/or rhizoids. The second involved the study of perigonial bracts and, the third one, the study of scale leaves that occur at the base of the stem and subterminal innovations.

In *Leucophanes*, the apical bud consists of the apical cell and its immediate derivatives as well as the first differentiating leaves. The young differentiating leaf is composed of

Figs. 26-27. Transverse sections of the leaves.

Fig. 26. *L. rodriguezii*. Midleaf. Scale = 20 um. (Mauritius, Balfour, NY).

Fig. 27. *L. angustifolium*. Midleaf. Scale = 20 um. (Bourbon, Rodriguez, PC).

Fig. 28. *L. glaucum*. Base. Scale = 20 um. (Java, L).

Fig. 29. *L. molleri*. Midleaf. Scale = 20 um. (Ghana [Ashanti], Cummings a. 1895/6, H).

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unistratose quadrate chlorophyllous cells. Early in development, a central multistratose area of elongated cells, the central stereid band, differentiates at the leaf apex. Prolonged cell divisions in the central stereid band give rise to groups of cells that differentiate into layers of stereids on the abaxial and adaxial sides of the 2-4 central chlorophyllous cells (guide cells) (Morin 1893, Cardot 1900). This differentiation takes place basipetally. The adjacent areas develop a multistratose structure, with a central layer of chlorophyllous cells surrounded by one or more layers of hyaline cells. These areas narrow towards the base in a V-shaped configuration; that is, only the areas adjacent to the midstereid band are multistratose. The multistratification of the leaf is sometimes interrupted by the development of isolated hyaline areas on one or both sides of the central stereid band (Fig. 18). These hyaline areas are structurally similar to those that develop at the base of the leaf. In *Exodictyon* and *Exostratum*, Ellis (1985) has reported, above the leaf base, the presence of laminal hyalocysts distributed between groups of laminal chlorocysts . These laminal hyalocysts closely resemble the isolated hyalocysts areas found in some *Leucophanes* leaves. It appears that in *Leucophanes*, the development of a central stereid band and the multistratification of the adjacent areas are independent but simultaneous events.

Perigonial leaves in *Leucophanes* resemble young *Syrrhopodon* (*sensu Leucophanella*) leaves. In the genus *Leucophanella* (Fleischer, 1900-1904), now included in *Syrrhopodon*, the plants have leaves with a hyaline area that extends to near the apex. The distal portion is composed of a unistratose layer of chlorocysts. Perigonial leaves in *Leucophanes* are costate organs composed of a hyaline base that extends in a V-shape to near the apex. The innermost perigonial leaf does not develop the multistratose condition characteristic of other vegetative leaves. Instead, the upper fourth consists of a single layer of chlorocysts while the lower portion of the leaf is composed of one, at times, two, layers of hyalocysts. Subsequent perigonial leaves develop the three layered structure at the apex. The basal area remains hyaline and contains only hyalocysts.

Scale leaves at the base of the stem and subterminal innovations are structurally costate organs, the lamina composed of only hyaline cells in one or two layers and the margins have a more or less distinct unistratose layer of stereids. These scale leaves are similar to those observed in *Syrrhopodon, Calympheres* and related genera (Pottiaceae). Scale leaves are produced early in development. The first leaves (one or two) produced by the young gametophores or the apical bud of a subterminal innovation, develop into scale leaves.

The central stereid band of *Leucophanes* leaves varies in thickness and width. In some species like *L. octoblepharioides, L. candidum, L. agustifolium* and *L. molleri*, the stereid band is very narrow. It consists mostly of 2-4 guide cells and an abaxial layer(s) of stereids (Figs. 17, 27-29). In *L. milleri, L. serratulum* and *L. glaucum*, on the other hand, the central stereid band is thick, composed of 2-4 guide cells surrounded by layers of stereids that extend from the abaxial to the adaxial surfaces as in many other strongly costate moss leaves (Figs. 179, 465, 467).

The structure of the leaf in *Leucophanes*, with a central stereid band and multistratose areas of chlorocysts and hyalocysts is unique when compared to other members of the Calymperaceae and Pottiaceae. In *Exodictyon* and *Exostratum*, hyalocysts are produced in both the lamina and the costal area (Ellis, 1985). In some members of the Pottiaceae, Saito (1975) has reported the presence of large "parenchymatous cells" on the adaxial side of the costa. In transverse sections, these cells resemble, in size, the adaxial hyalocysts observed in the costal area of *Leucophanes*.

In *Exodictyon, Exostratum* and *Arthrocormus*, the costa is composed of a central layer of chlorocysts, 2-3 abaxial and adaxial layers of hyalocysts and an external layer of chlorocysts, this in *Arthrocormus*, surrounded by a layer of hyaline cells (Figs. 33-34). The lamina may consist of only hyaline cells or, in the uppermost regions, of chlorocysts and hyalocysts in alternate arrangements. In some species of *Leucophanes*, the central stereid band is surrounded by an irregular layer of chlorocysts in much the same way as in the costae of *Exodictyon* and *Exostratum*. In *Leucophanes*, external chlorocysts of this type have not been observed outside the central stereid band.

Fig. 30. Leaf-tip gemmae. Scale = 100 um. Figs. 31-32. Chlorocysts (Ch) and lacunae (La) as observed in surface view. Scale = 100 um. Ch = chlorocysts, Gc = guide cells, H = hyalocysts, S = stereids, P = pores.

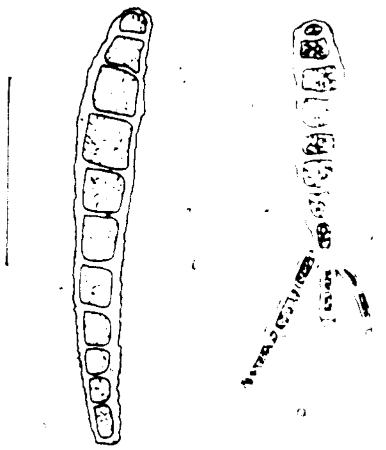
Fig. 31. *L. glaucum* (Bismarck Arch., Fleischer 406, L).

Fig. 32. *L. octoblepharioides* (Vanuatu, Salazar 3704, ALTA, PMA). Figs. 33-35. Transverse sections of the leaves. Scale = 100 um.

Fig. 33. *Arthrocormus schimperi* (Borneo, Meijer B12108, L).

Fig. 34. *Exostratum* sp. (New Guinea, Streimann 11264, CBG).

Fig. 35. *Leucophanes octoblepharioides* (New Guinea, Streimann 11699, CBG).



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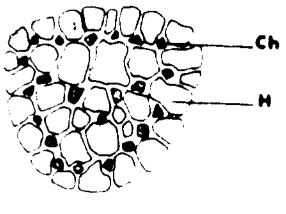

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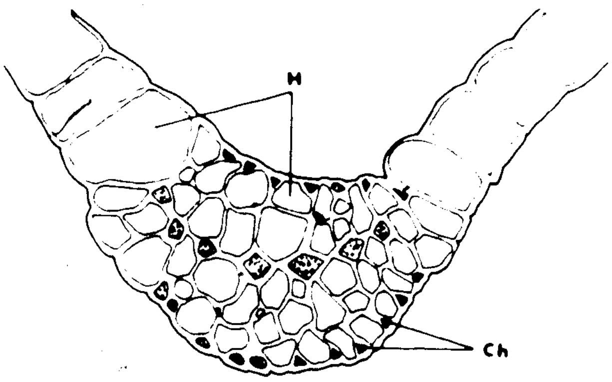

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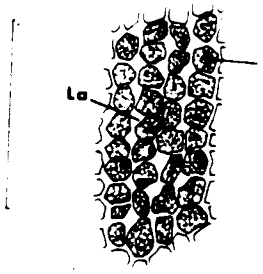

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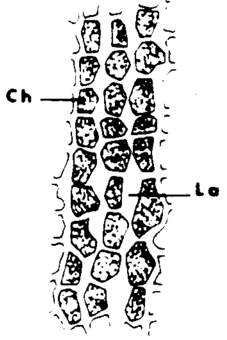

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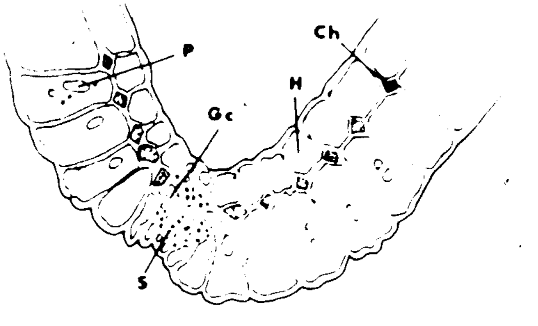

35

Duplication of adaxial and abaxial hyalocysts along the sides of the central stereid band occurs in some species of *Leucophanes*. This process appears to be independent of the developmental sequences that lead to the differentiation of the midstereid band.

In the Dicranaceae (e.g., *Campylopus* and *Paraleucobryum*), the multistratose condition of the leaf is considered to be the result of an expansion of the costal area (Morin, 1893; Cardot 1900; Frahm, 1982). This process includes proliferation of the median chlorocysts (e.g., in *Paraleucobryum longifolium* (Hedw.) Loesk. and *P. brasiliense* Broth.), duplication of dorsal hyalocysts (e.g., in the subgenus *Paraleucobryum*) and duplication of hyalocyst initials and their further development into stereids (e.g., in the subgenus *Campylopus*) (Frahm, 1982). Moreover, the expanded costa in the Dicranaceae is variable in structural details, even within a single genus (Frahm, 1982). It has been suggested that the multistratose structure of the leaf in some members of the Dicranaceae (e.g., *Campylopus*) arose independently many times (Frahm, 1982).

Expansion of the costa similar to that reported in some members of the Dicranaceae (*Paraleucobryum* and *Campylopus*), has not been observed in *Leucophanes*. In this genus, when the costa increases in thickness, it does so mostly by proliferation of stereids. Structurally and functionally, the central stereid band appears to be homologous to the costa of most moss leaves.

The multistratification of the leaf lamina is known to occur in various groups of mosses. These plants are frequently epiphytic or terrestrial in seasonally dry habitats. The multistratose lamina consists of 2-3 layers of chlorophyllous cells (except in some members of the Dicranaceae discussed above); in addition, a unistratose hyaline area may develop at the base of the leaf, e.g., in *Calymperes lonchophyllum Schwaegr., Calymperes venezuelanum* (Mitt.) Pittier ex Broth., *Timmiella anomala* (B.S.G.) Limpr. *Tortella fragilis* (Hook. et Wils.) Limpr. and *Tortula chisosa* Magill, Delgadillo et Stark.

In transverse section of the leaf in *Leucophanes* (and also in *Leucobryum*), every chlorocyst in the multistratose areas is surrounded by four hyaline cells; two of these cells are shared with the adjacent chlorocysts (Figs. 16, 17, 29). There appears to be a defined pattern of cell division and differentiation that results in the multistratification of the lamina. This pattern is either lost with further development of stereids or does not develop in the central stereid area. It appears that, in *Leucophanes*, the development of the central stereid band and the adjacent multistratose areas are independent events. Thus, in *Leucophanes*, the structure of the leaf is hypothesized to be mostly the result of a multistratification of the lamina, with the development of a central to subcentral layer of chlorocysts surrounded by one or more layers of porose hyalocysts. The leaf is considered to have retained the structural morphology and functionality of the costal area (a [illegible]typic condition) from its *Syrrhopodon*-type ancestor.

Based on the distinct differentiation of the central leaf area observed in some species of *Leucophanes*, which parallels structurally the costa of a moss leaf, and the potentiality of the lamina to become multistratose, I propose the following terminology for the *Leucophanes* leaf. The term costa (*sensu stricto*) is here proposed for the central area with stereids, guide cells, hyalocysts and, sometimes, an external layer of chlorocysts; multistratose lamina or pseudocosta for the adjacent regions of chlorophyllous and hyaline cells; and hyaline lamina for the all hyaline unistratose basal portion (Figs. 1, 2, 16). The leaf is thus considered a structurally complex organ composed of a costa, a multistratose and a hyaline lamina and two marginal stereid bands. The scale leaves and perigonial bracts are considered to have retained most of the plesiotypic characters of a *Syrrhopodon*-type ancestor; the outermost perigonial bracts developing the multistratose lamina (apotypy) characteristic of vegetative leaves. The *Leucobryum* leaf is considered an analogous structure and the result of convergent evolution.

2. LEAF STRUCTURE

Structurally, the leaf of *Leucophanes* can be divided into three sections: apex, midleaf, and base (Fig. 1). The apex includes the uppermost 200 um; the midleaf is that portion between the apex and the shoulders, and the basal area is considered to include the area below the shoulders to the insertion of the leaf to the stem. This lowermost section can be subdivided into two distinct laminar areas: the multistratose lamina (in transverse section, composed of a central layer of chlorophyllous cells surrounded by 2-4 layers of porose hyaline cells) and the hyaline lamina (composed of one, occasionally, two layers of hyalocysts). The hyaline lamina may extend beyond the shoulders of the leaf, one side longer than the other. The midleaf portion is composed of a multistratose lamina of chlorocysts and hyalocysts. All species of *Leucophanes* show some degree of asymmetry in their leaf structure (see below and also discussion on "Transverse Section" of the leaf). A distinct costa runs the length of the leaf. The costal area may be smooth (*L. candidum*) or it may be ornamented with spine-like processes (Figs. 148, 211, 414).

The leaves are spirally arranged around the stem; some plants have a densely foliose habit whereas others have a loose arrangement of leaves (Figs. 232, 273, 278, 321, 380, 443). The leaves are either narrow at the insertion and loosely attached to the stem, or vaginant with the broad basal area overlapping the stem. When dry the leaves are erect-patent to slightly spreading and strongly to slightly twisted above the hyaline area (Figs. 273, 443); marked differences in degree of contortion of the leaves are observed among species. The margins are serrate at the apex to near midleaf (one side of the lamina more serrate than the other) or smooth, straight to strongly undulate in some species, and more or less recurved particularly at the base. The costa forms a prominent keel on the abaxial surface of some leaves. Moist leaves are erect-patent to curved spreading and less twisted. The lamina is incurved to somewhat keeled and the margins straight to undulate, while in some species they are slightly recurved below the shoulders. The basal leaves of the stem are either smaller or longer than the uppermost ones. It appears that, at least in some cases, microenvironmental conditions influence their growth.

Scale leaves are observed at the base of innovations produced below the perichaetia and perigonia and also at the base of the stem. The first leaf or the first two leaves of the developing gametophore are scale leaves, composed only of hyaline cells in one or at times two layers. A costa occupies the center of the leaf. Subsequent leaves are multistratose with basipetal development of the multilayered condition.

Length and width of the leaves vary within individual species. This is particularly notable among those species with long leaves. *Leucophanes glaucum*, for example, has leaves that vary from 2.5 to 4(5) mm in length, varying in shape from more or less broadly lanceolate to very narrowly lanceolate. The apex is also variable within the same species. Scale leaves and young leaves in most species are acuminate while mature leaves may be broadly acute to apiculate(Figs. 91, 148), or long to short acuminate to truncate (Figs. 256, 257). In some populations of *L. molleri* the apex of mature leaves is bent backwards (Fig. 274).

Color of leaves is variable and it appears to [illegible] correlated with moisture and light conditions. Plants under shade, in concavities of palm rootlets for example, are darker blue-green than those in more exposed areas on the same trunk, that sometimes have a yellowish color. In some populations, the apex of the leaf develops dark-red pigmentation. Even though coloration may vary in plants growing on the same trunk, there is an overall color and habit impression of the vegetative plant that prevails. For example, *L. glaucum* has a blue-green to yellow-green shade and a tight turf forming habit, with erect to strongly twisted leaves. *Leucophanes octoblepharioides* has a light blue-green hue, but forms loose turfs with erect leaves that are more translucent than those of *L. glaucum* and less twisted.

CELL TYPES. Leaves of *Leucophanes* are composed of four basic cell types. These are: (1) Porose hyaline cells (hyalocysts or leucocysts); (2) chlorophyllous cells (chlorocysts); (3) guide cells, and (4) stereids. The terms chlorocysts and hyalocysts, are here used to designate the chlorophyllous and hyaline cells respectively. The terms were first introduced by Morin (1893) in his comprehensive study of moss leaves.

Each cell type recognized is described separately. Their association in the leaf is discussed under "Transverse Section".

1. *HYALOCYSTS*. The hyalocysts are at maturity non-living elements with resorption pores in

their walls. They may have cyanobacteria and other microorganisms in their lumena. They vary in shape from irregularly triangular to quadrate (Figs. 22, 358), to rectangular (Figs. 18, 23, 24, 299) or oblong to irregularly hexagonal (Figs. 304, 329, 330, 359, 360). Their size ranges from (12.5)25-60 um long X 7.5-30 um wide. Hyalocysts are wider at the leaf base, particularly along the costal area, than at midleaf (Figs. 258-260, 389, 391-395), and their walls vary from rectilinear to irregularly sinuose (Fig. 389-399). Hyalocysts of the hyaline lamina may develop collenchymatous thickenings.

In transverse section, the hyalocysts form one or more layers on each surface of the central chlorophyllous cells (Figs. 17, 21, 26-29, 297). Surface walls of hyalocysts as observed in transverse section, are concave to irregularly rectilinear to sinuous vermiform. Sinuous walls may serve to increase the surface area for water retention.

Pores on the surface walls are frequent and larger at the leaf base than at the apex or midleaf (Figs. 22-25). In *L. candidum*, *L. hildebrandtii*, and *L. molleri*, this condition is not observed. In these species, large pores are present both at the base and at the apex of the leaf. Size of the pores varies interspecifically and is not related to the length of the leaf. It is possible that resorption pores are the result of enzymatic digestion of the cell walls during differentiation. In *Syrrhopodon*, Allen *et al.*, (1984), have reported the presence of cellulase associated with the production of resorption pores.

2. *CHLOROCYSTS*. These cells are the photosynthetic elements of the leaf. In surface view, they are irregularly hexagonal to pentagonal, more elongated at the leaf base than at the apex. They are arranged in longitudinal rows below the lateral walls of the hyalocysts with 1-2 chlorocysts uniting these rows at the transverse walls thus, forming a reticulate pattern. Consecutive rows of chlorocysts are separated by broad or elongated areas here called lacunae (Figs. 31, 32, 298). The size and shape of these lacunae and of adjacent chlorocysts is characteristic for some species (e.g., *L. glaucum*). In transverse section, the chlorocysts are rhomboidal in shape, with walls varying in thickness. Chlorocysts have abundant discoid

chloroplasts. In young developing leaves, the chlorocysts are arranged in a rosette pattern. This arrangement is analogous to the circular patterns formed by the papillae of some peristomes.

In transverse section, each chlorocyst is surrounded by four hyalocysts. Two of these are shared with adjacent chlorocysts (Figs. 16, 17, 27-29). In some leaves, the continuity of the central chlorophyllous layer is interrupted by isolated areas of hyalocysts that are found near the apex of the leaf (Fig. 18).

3. *GUIDE CELLS*. These cells are structurally part of the costa. They vary in number from 2-4 and are continuous with the chlorophyllous layer (Figs. 26-29). In some species, e.g. *L. candidum*, they are constant in number from leaf base to apex. In other species, e.g. *L. glaucum* they vary from three to four at base to two at apex.

Guide cells are living elements structurally similar to chlorocysts. They vary in width, being either wider (Figs. 17, 27-29, 297, 382) or narrower (Figs. 99-411) than adajacent chlorocysts. This variation is related to the thickness of the costa. Ligrone (1984, 1985), has reported structural differences between the guide cells and adjacent chlorocysts (see discussion on the "Leaf Structure").

4. *STEREIDS*. These are elongated cells with thick, porate walls (Ligrone, 1984). Stereids are usually non-living elements at maturity (Hébant, 1971; Ligrone, 1985; personal observations). They form the leaf margins and majority of the costa (Figs. 16, 26, 28, 29). Stereids function as supporting elements for the leaf and perhaps, in maintaining a hydrated surface around the photosynthetic guide cells. The walls of the stereids may be orange-red to dark-red in some species most probably, the result of pigment deposition.

TRANSVERSE SECTION OF THE LEAF

1. LAMINA. Except for the hyaline lamina near the leaf base, and occasional hyaline portions near the apex, the lamina is multistratose. It is composed of a central to subcentral layer of

chlorocysts surrounded on each side by one or more layers of hyalocysts. In most species, the hyalocysts are taller on the abaxial surface at the leaf base, thus, the chlorocyst layer appears closer to the adaxial (ventral) surface (Fig. 5). This condition was called "hypercentrique" by Cardot (1900). At midleaf; the hyalocysts are equally tall on each surface and the chlorophyllous layer appears centrally located. At the apex, the adaxial layer of hyalocysts is taller and the chlorocysts appear closer to the abaxial (dorsal) surface. Cardot (1900) named this condition "hypocentrique" (Fig. 6).

Several characters observed in median transverse section of the leaf are important in distinguishing externally similar species. The layers of hyalocysts on each surface of the chlorophyllous cells vary characteristically between some species. In *L. candidum* the structure of the leaf is homogeneous from base to apex (Figs. 369, 371). It is composed of one layer of hyalocysts on each side of the chlorophyllous layer. Unlike *L. candidum*, the layering of hyalocysts is not a constant feature in *L. octoblepharioides*. In this species, some populations develop more than one layer of hyalocysts on the abaxial side of the leaf, at the base. In *L. angustifolium*, a proliferation of hyalocysts on the adaxial and abaxial sides of the costa is characteristic with 2-3 layers developing on each side of the chlorophyllous layer (Fig. 159). No other species develops this marked proliferation of hyalocysts.

The transverse section of the leaf in *L. glaucum* is characterized by 2-3 layers of hyalocysts on the abaxial side at the base, above which they form a single layer on each surface of the chlorocysts.

2. COSTA. The costa, in transverse section, is composed of 2-4 centrally located guide cells that are continuous with the chlorophyllous layer. These guide cells are surrounded on the adaxial and abaxial sides by stereids (Figs. 26-29, 35) and/or hyalocysts. The layers of stereids vary characteristically for some species. In *L. candidum*, for example, there are no adaxial stereid bands, whereas in *L. serratulum*, *L. glaucum* and *L. angustifolium* adaxial and abaxial layers of stereids develop. Thickness of the costa is related to an increase in the number of

stereids.

The costa may be located in a groove formed by the adjacent bulging hyaline cells (Fig. 28), particularly at the base; it may be completely superficial (Figs. 27, 29), or enclosed by hyaline cells (Figs. 26, 117-120, 297). These variations may be observed at different levels on the same leaf.

Stereids in the costal area may extend to both surfaces or they may be covered by hyaline cells. Particularly above the leaf base, the costa is usually covered by one or more (*L. angustifolium*) layers of hyaline cells on the abaxial and adaxial surfaces. These abaxial hyalocysts may have thin or thick walls or they may be bulging and with thin walls. In some taxa, e.g., *L. octoblepharioides* subsp. *meijeri* the hyaline cells are so inflated that the costa appears to be adaxially located (Figs. 116-120). At the apex of the leaf, some species have the costa prominent and occupying most of the leaf width. In other species, e.g., *L. candidum*, the costa is consistently narrow from leaf base to apex (Figs. 369-371).

3. **MARGINS**. The margins are composed of stereid cells in three or more rows and one to many layers. At the base, the stereids are unistratose; above the base, the margins increase in thickness and are composed of 3-5 layers of stereids in various rows. Serrations of the leaf are formed by projections of the marginal stereids and are either single or paired (Figs. 231, 277).

RHIZOIDS. Rhizoids are produced from superficial cells of the stem, particularly at the base. They also develop at the apices of the leaves and less frequently at their bases. They have been observed developing into protonema and leafy gametophytes, thus serving as another mean of asexual propagation. Gametophores developing *in situ* from rhizoids also serve to increase the density of the turfs and thus, enhance their water holding capacity.

SEXUAL CONDITION AND CYTOLOGY. All species of *Leucophanes* except *L. serratulum* are dioicous. Male and female plants are morphologically similar. Sexual dimorphism is here confirmed for the first time in *L. candidum*. Dwarf males as well as normal males have been observed in this species, thus, it can be considered pseudonanandrous (Une, 1985). Fleischer (1900-1904), in his description of *L. candidum*, suggested the occurrence of dwarf males: "Pseudautocisch?", "....♂.. Blüten Zwergmännchen?". Some species of *Leucophanes* are only known by their female gametophores, including *L. rodriguezii*, *L. unguiculatum* and the neotropical populations of *L. molleri*.

Perichaetia are terminal. For most species, perichaetial leaves are structurally similar to the vegetative ones. In *L. octoblepharioides*, *L. candidum*, *L. angustifolium*, *L. seychellarum* and *L. milleri* the innermost vegetative leaves, differentiate into perichaetial leaves covering the vaginula and proximal part of the seta. These leaves are smaller in size, lanceolate from a broad sheathing base and are hyaline for 2/3 of their length. The hyalocysts of the perichaetial leaves are usually broader and/or longer than those of vegetative leaves. In *L. candidum*, they have narrow, slit-like pores arranged in vertical rows (Fig. 354). Archegonia are found in groups of 5 to more than five. Perigonia are either terminal or lateral. Perigonial branches are bud-like in appearance with two to three differentiated perigonial leaves. Their size ranges from 0.9 to 2 mm long. The innermost perigonial leaf is oval, with a broad hyaline base that folds into a tubular enclosure around the antheridia. A chlorophyllous unistratose lamina occupies the upper one-fourth to one-fifth of the leaf. The next outer perigonial leaf has a much narrower base and the upper portion develops the multistratose condition typical of vegetative leaves. The third leaf, in a centrifugal sequence, is smaller than adjacent vegetative leaves and has a long hyaline base. Maturation of sex organs is not synchronous.

No chromosomal counts are known for the genus. Living materials collected in Fiji and the Vanuatu were at the tetrad or spore state and not useful in determining chromosomal numbers.

CALYPTRA. The calyptra is uniform throughout the genus. It is cucullate and non-plicate. Its size ranges from 1.2 to 4.0 mm long. Its color changes gradually from a dark red apex to a yellow lower portion. The calyptra can be divided into two areas, the rostrum and the cylinder. The rostrum is papillose at its apex, while the cylinder is smooth. The base of the cylinder varies within populations from entire to irregularly lacerate (Figs. 361-363). In populations of some species, e.g., *L. octoblepharioides*, and *L. serratulum*, the calyptra remains attached to the operculum at dehiscence.

SPOROPHYTE. The sporophytes in *Leucophanes* are terminal but they appear lateral by the production of subterminal innovations. In most species, they are exserted on a short to long seta produced singly from the perichaetia. *Leucophanes serratulum* is the only species in which more than one sporophyte per perichaetium has been observed.

SETA. The seta in all species of *Leucophanes* is exserted. Its size varies from 6-19 mm long, with the longest found in *L. candidum*. The color of the seta varies from a light orange in immature sporophytes to dark orange-red or dark-brown when mature. In some populations of *L. candidum*, a difference in color is observed in the mature seta with the distal portion lighter than the proximal. This variation appears to be random.

The seta is twisted sinistrorsely particularly above the middle portion. Fleischer (1900-1904) reported dextrorse twisting of the seta in *L. serratulum*, but I have been unable to confirm this condition. There is little interspecific variation in the diameter of the seta. In the specimens examined, the diameter remains constant throughout the length, increasing slightly at the junction with the capsule neck. In transverse section, the seta consists of a central area of parenchymatous cells surrounded by 1-2 layers of small thick-walled cells. The cells are progressively smaller and with thicker walls towards the periphery.

CAPSULE. In all species of *Leucophanes* the capsule is cylindrical, erect to subinclined, to nearly horizontal. Its size and general shape varies within populations and its length ranges from 1.2 mm to 3.5 mm long. The color is orange-red, becoming darker at the rim and neck. In some populations of *L. glaucum*, the capsules have shiny indentations, perhaps resulting from the collapse of the exothecial cells. The capsules are irregularly plicate to nearly smooth (Figs. 103-104, 122, 185, 362, 363, 428, 455, 458), with the plicae corresponding to longitudinal thickenings of the walls. In most species, there is a distinct constriction below the mouth (Figs. 103-104, 122, 141). A papillose short **neck** is differentiated in all capsules, the papillae extending to the distal portion of the seta. In one instance an anomalous production of two sporophytes fused to a single vaginula was observed in *L. hildebrandtii*. One of the capsules developed normally into a cylindrical structure whereas the other was short-spherical, unlike the species. The seta of the cylindrical capsule was flattened on the side facing the short sporophyte, while the seta of the spherical capsule was short and cygneous.

EXOTHECIAL CELLS. The exothecial cells are oblong to irregularly hexagonal. Their walls are rectilinear and thin to thickened longitudinally. Their size varies from (25)35.5 to 62.5(100.0) um long. Wall thickenings are related to longitudinal plications observed in the capsules. At the neck, the cells are smaller and the walls are thicker and papillose. The largest exothecial cells were observed in *L. milleri, L. serratulum* and *L. hildebrandtii*.

RIM CELLS. In all species of *Leucophanes* the rim cells are longitudinally oriented in 4-6 rows. They are 7.5-22.5 um in length, quadrate (1:1) to subquadrate (0.5:1), to short oblong (2:1). Their walls vary from very thin to slightly thicker. Their color is brown-red and darker than the exothecial cells. In some species, e.g., *L. glaucum*, they form uniform rows that are clearly distinguished at low m[illegible]

STOMATA. All species of *L*[illegible]*nes* are characterized by phaneropore stomata located on th[illegible]k of the capsule. They are composed of two to three guard cells with subsidiary cells undifferentiated (Figs. 108, 123, 316, 339). The shape of the guard cells varies, from arcuate oblong to irregularly pentagonal or hexagonal. The pore (ostiole) in most stomata is reduced [illegible] size by the inner wall thickenings of the subsidiary cells. The size of the guard cells varies from 12 to 20 um in length and the stomatal apparatus is generally 20-25 um in width. The number of stomata per capsule varies from 12-14 in all species except *L. serratulum* that has 22-24. The type and shape of the stomata in *Leucophanes* is similar to those found in the Calymperaceae (Egunyomi, 1982; Ellis, 1985).

OPERCULUM. The operculum is structurally similar in all species of *Leucophanes*. Its length varies from 0.9-1.2 mm. It is long rostrate, and more or less plane-convex and can remain attached to the calyptra at the time of dehiscence or fall independently.

PERISTOME. The arthrodontous, haplolepideous peristome of *Leucophanes* is composed of 16 teeth with more or less equally thickened dorsal and ventral plates (Figs. 44, 51, 54, 172). In some peristomes, the ventral plate is slightly thicker. These plates vary from strongly papillose to nearly smooth (Figs. 36-59). The papillae are capitate to globular, to short and club-shaped. They can be irregularly distributed throughout the plate (Figs. 37, 38, 39, 50) or arranged around central circular depressions (foveolae) (Figs. 41, 42, 43, 46). This pattern of circular depressions has also been observed in *Exodictyon*, *Exostratum*, and on the inner and outer plates of *Arthrocormus* (Ellis 1985; personal observations). Fleischer (1900-1904) in his illustrations of the peristome of *Syrrhopodon tristichus* Nees ex Schwaegr., indicated the presence of "Perforationem" on the dorsal and ventral plates. These "Perforationem" are similar although more irregular in outline than the circular depressions observed in the peristomes of *Leucophanes*.

Longitudinal to semicircular, to oval thickenings also occur in the peristomes of some *Leucophanes* species (Figs. 48-49); in others the dorsal plates have vertical striations (Figs. 53-55). These striations may develop scattered elongated to short papillae. I have observed similar striations on the dorsal peristomial plates of *Arthrocormus*. The degree of ornamentation is variable between teeth in the same peristome (Figs. 432, 434). Peristomes

Figs. 36-41. PERISTOME TYPES.

Figs. 36-40. *L. candidum*

Fig. 36. Outer surface of teeth at base with prostome. Scale=50 um. (New Guinea, van Zanten 277, L).

Fig. 37. Scale=10 um. (N. Borneo, Meijer B1248, L).

Fig. 38. Scale=50 um. (W. Borneo, Winkler 3097, L).

Fig. 39. Scale=10 um. (Ibid. 38)

Fig. 40. Inner surface of teeth. Scale=10 um. (Ibid. 37).

Fig. 41. *L. angustifolium*. Outer surface of teeth, papillose-foveolate. Scale=10 um. (Ternate, Beccari 110, L).


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Figs. 42-47. PERISTOME TYPES.

Figs. 42-44. *L. octoblepharioides* subsp. *octoblepharioides*. Papillose-foveolate. (Vanuatu, Salazar 3498, ALTA, PMA).

Fig. 42. Scale = 20 um.

Fig. 43. Scale = 10 um.

Fig. 44. Lateral view of teeth. Outer peristomial plate to the right. Scale = 10 um.

Fig. 45-46. *L. milleri*. Papillose-foveolate. (Micronesia, Dutton 63, MU).

Fig. 45. Scale = 50 um.

Fig. 46. Scale = 10 um.

Fig. 47. *L. hildebrandtii*. Papillose with longitudinal to semi-circular thickenings and foveolate areas. Scale = 20 um. (Comoro Islands, Hildebrandt a. 1875, G).

Figs. 48-53. PERISTOME TYPES.

Fig. 48. *L. molleri.* Oval thickenings on the outer peristomial plate. Scale = 10 um. (Yaptown, Miller & Whittier 8106, Type, MU)

Fig. 49. *L. renauldii.* Papillose with longitudinal thickenings. Scale = 20 um. (Mauritius, Balfour, NY)

Fig. 50-51. *L. glaucum* subsp. *glaucum*. Papillose with more or less defined longitudinal striations. (New Guinea, Beccari 138, L).

Fig. 50. Scale = 20 um.

Fig. 51. Lateral view of peristomial plates. Scale = 10 um.

Figs. 52-53. *L. octoblepharioides* subsp. *whittieri*. Papillose-striated. Prostome at base. (Yaptown, Miller & Whittier 1252, Type, MU).

Fig. 52. Scale = 20 um.

Fig. 53. Scale = 10 um.

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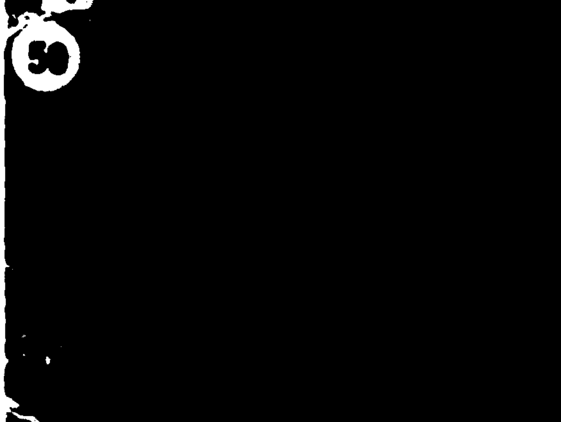

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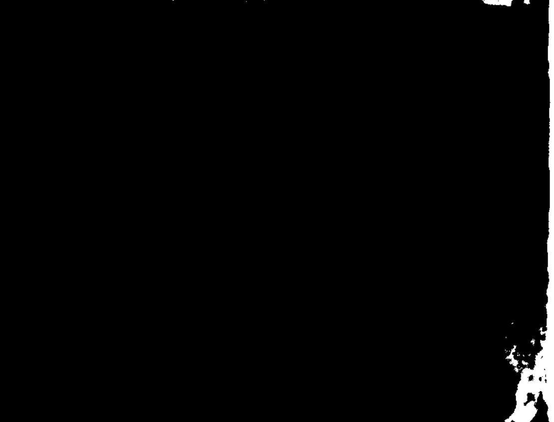

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Figs. 54-59. PERISTOME TYPES.

Figs. 54-55. *L. octoblepharioides* subsp. *whittieri*. (Yaptown, Miller & Whittier 1252 Type, MU).

Fig. 54. Lateral view of peristome. Scale = 10 um.

Fig. 55. Outer surface of teeth. Scale = 20 um.

Figs. 56-57. *L. seychellarum*. (Seychelles, Horne 696, BM).

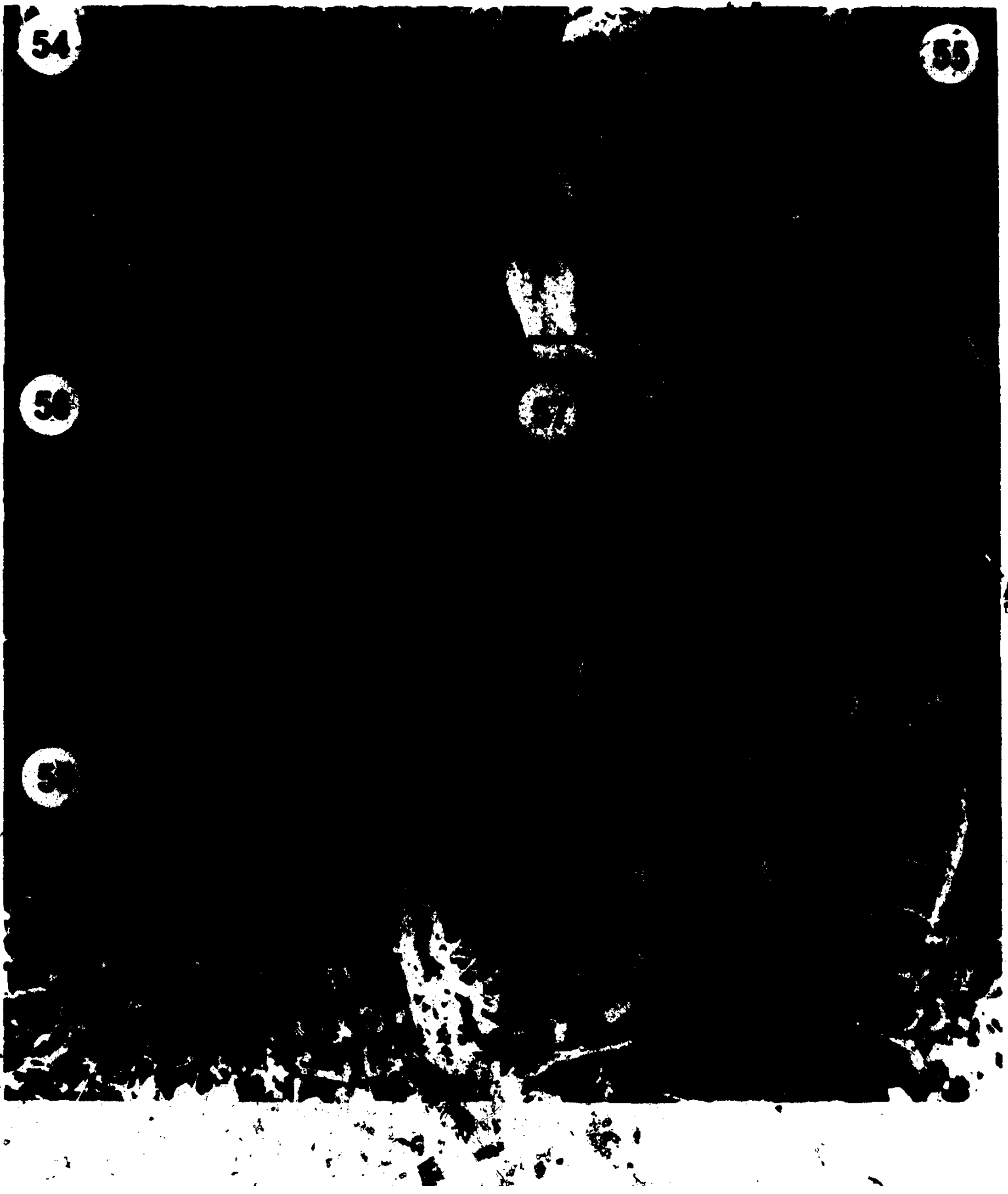
Fig. 56. Outer surface of teeth. Scale = 20 um.

Fig. 57. Inner surface of teeth, 2:3 pattern above base. Scale = 20 um.

Figs. 58-59. *L. glaucum* subsp. *vittii*. (New Guinea, Brass 21774, Type, FH).

Fig. 58. Outer surface of teeth. Scale = 20 um.

Fig. 59. Inner surface of teeth. Scale = 10 um.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with smooth to nearly smooth, dorsal and/or ventral plates also occur in *Leucophanes* (Figs. 56, 58-59). A hyaline prostome, 2-3 cells high is present in most species (Figs. 36, 56). Due to the lack of good peristome material it is difficult to observe the presence of a prostome in some species. Prostomes have also been reported for the peristomes of *Exodictyon*, *Arthrocormus* (Fleischer, 1900-1904; Ellis, 1985) and *Syrrhopodon tristichus* (Fleischer, 1900-1904).

According to the presence or absence and type of ornamentation as well as its distribution on the dorsal and ventral plates, six peristome types can be distinguished in *Leucophanes*. The first type is represented by *L. candidum*. Here, both the dorsal and the ventral plates are strongly papillose except at the apex where they are smooth. The papillae project strongly from the sides of the teeth and they are arranged in irregularly circular patterns. Trabeculae are prominent on both plates. A hyaline prostome 2-3 cells high is observed on the dorsal side of the teeth (Figs. 37, 39).

The second peristome type is represented by *L. octoblepharioides* and *L. milleri*. In these species, the peristome is densely papillose-foveolate (with central circular depressions) on both surfaces (Figs. 42-43, 45-46). Trabeculae are obscured by the strong papillosity of both plates. A prostome is also present on the dorsal side of the teeth. The third type is represented by *L. molleri* and *L. renauldii*. In this type, the dorsal plate is less papillose than the ventral plate and is composed of papillae and thick, bar-like ornamentations, oval to semi-circular or longitudinal in shape (Figs. 47-49). The fourth type is represented by *L. glaucum* (in part) and *L. octoblepharioides* subsp. *whittieri*. In this peristome type, the dorsal plates and sometimes the ventral plates, particularly at apex, have more or less defined longitudinal striations, ornamented with papillae (Figs. 50, 53, 55, 432). The ventral plates of these species are foveolate, with the depressions more or less defined. The fifth peristome type is represented by *L. seychellarum*. In this type, the outer peristomal plates are slightly smooth to papillose while the inner plates are strongly papillose. The teeth have a broad basal area covered by the prostome (Fig. 56). The sixth peristome type is represented by *L. glaucum* subsp. *vittii*. It is characterized by rather short, stubby teeth that are smooth on the dorsal and ventral plates

(Figs. 58-59).

SPORES. Descriptions of spore size and ornamentation in *Leucophanes* are known from as early as 1898 when Brotherus and Geheeb described and illustrated the spores of *L. beccarii*. The spores were described as "subangulatae, laeves, 0.015-0.020 mm". Fleischer (1900-1904), in his treatment of the various species of *Leucophanes* gave a description of size, color and ornamentation of spores for those species that bore sporophytes. The spores of *L. serratulum* were also described by Fleischer ([illegible]14). Nevertheless, spores have been of little use in the taxonomy of *Leucophanes*. Most species do not produce sporophytes readily, thus, the characters used to distinguish species are based on the structural morphology of the leafy gametophytes; also spores are very small and patterns of ornamentation are difficult to assess with light microscopy. In other moss taxa, spore morphology has been of limited use before the development of the electron microscope. Early light microscope work of McClymont (1954) and Erdtman (1957, 1965) suggested that the study of spore ornamentation might be a useful character in the taxonomy of mosses. Sorsa and Koponen (1973) using light microscopy and SEM, studied a number of species in the Mniaceae. They found considerable intraspecific variation in spore ornamentation and concluded that the most useful characters to distinguish spores in the family were size and thickness of the exine. These differences corresponded well to the subdivision of the family into Tribes proposed earlier by Koponen (1968). Vitt and Hamilton (1974), in an SEM study of the spores of eight species of *Encalypta* found that these species could be differentiated on the basis of spore morphology. They also used this character to segregate three major groups of species which corresponded to those proposed by Philibert (1889) based on peristome morphology. Horton (1981), in her revision of the Encalyptaceae indicated that although the correlations between spore-type and peristome-type are not absolute, the general groupings are quite close to those based on peristome. Saito and Hirohama (1974), in a comparative study of 19 species of 14 genera in the Pottiaceae found that spore ornamentation could not be correlated with other characters and, as such was of limited taxonomic value. Among the most comprehensive studies of moss spores was that of Boros and Járai-Komlódi (1975) on European mosses. Although based on light microscopy, the LO-analysis (L. from lux, light; O from obscuritas, darkness) of spore ornamentation is very detailed.

Most of the work carried out up to date is centered on species from the temperate zone; very little is known for tropical taxa. Studies of spore ornamentation are unknown for *Leucophanes* or any member of the Calymperaceae. Spores of ten species are here examined with light microscopy and SEM. Various samples were taken from open capsules thus, swelling and germination were observed (Figs. 81-87). It has been previously suggested for other moss taxa (Mogensen, 1978) that these processes alter the patterns of ornamentation. Nevertheless, I have considered it important to give a brief description of the type of ornamentation observed until further material is available for critical examination. The terms are those of Erdtman (1952, 1969), Boros and Járai-Komlódi (1975) and Kremp (1965).

The spores of *Leucophanes* are paraisopolar with a more or less distinct differentiation in structure and/or sculpturing of the two faces (Figs. 60-89). The shape varies from spheroidal to subtriangular (Figs. 84, 86, 88) and the size ranges from 10-20 um in diameter. The largest spores are found in *L. candidum* and *L. milleri*. Abortive spores have been observed in some species, e.g. *L. milleri* and *L. octoblepharioides*. These appear to be cases of spore mortality, perhaps related to the meiotic process as reported in other mosses (Mogensen, 1978; Horton, 1982).

In *Leucophanes*, two general types of spores can be distinguished under the SEM. These are, the verrucate to short baculate type, with the verrucae or short baculae more or less ornamented with granular depositions 0.1-0.2 um in diameter (Figs. 60-86) and the gemmate-verrucate type (Figs. 88-89). Variations are observed in the density and uniformity of the granular depositions. These have a distinct pattern in *L. octoblepharioides* (Figs. 66-69), and are coarser in *L. candidum* and *L. milleri* (Figs. 72-75). Deposition of additional granular to amorphous sculpturing material occurs on the surface of spores and the sporangium (Fig.

Figs. 60-65. SPORE TYPES.

Figs. 60-61. *L. glaucum* subsp. *glaucum*. (Rauwack, Gaudichaud 10, Type, G).

Fig. 60. Proximal face. Scale = 10 um.

[illegible]ail of ornamentation. Scale = 2 um.

[illegible] *glaucum* subsp. *vittii*. (New Guinea, Brass 21774, Type, FH).

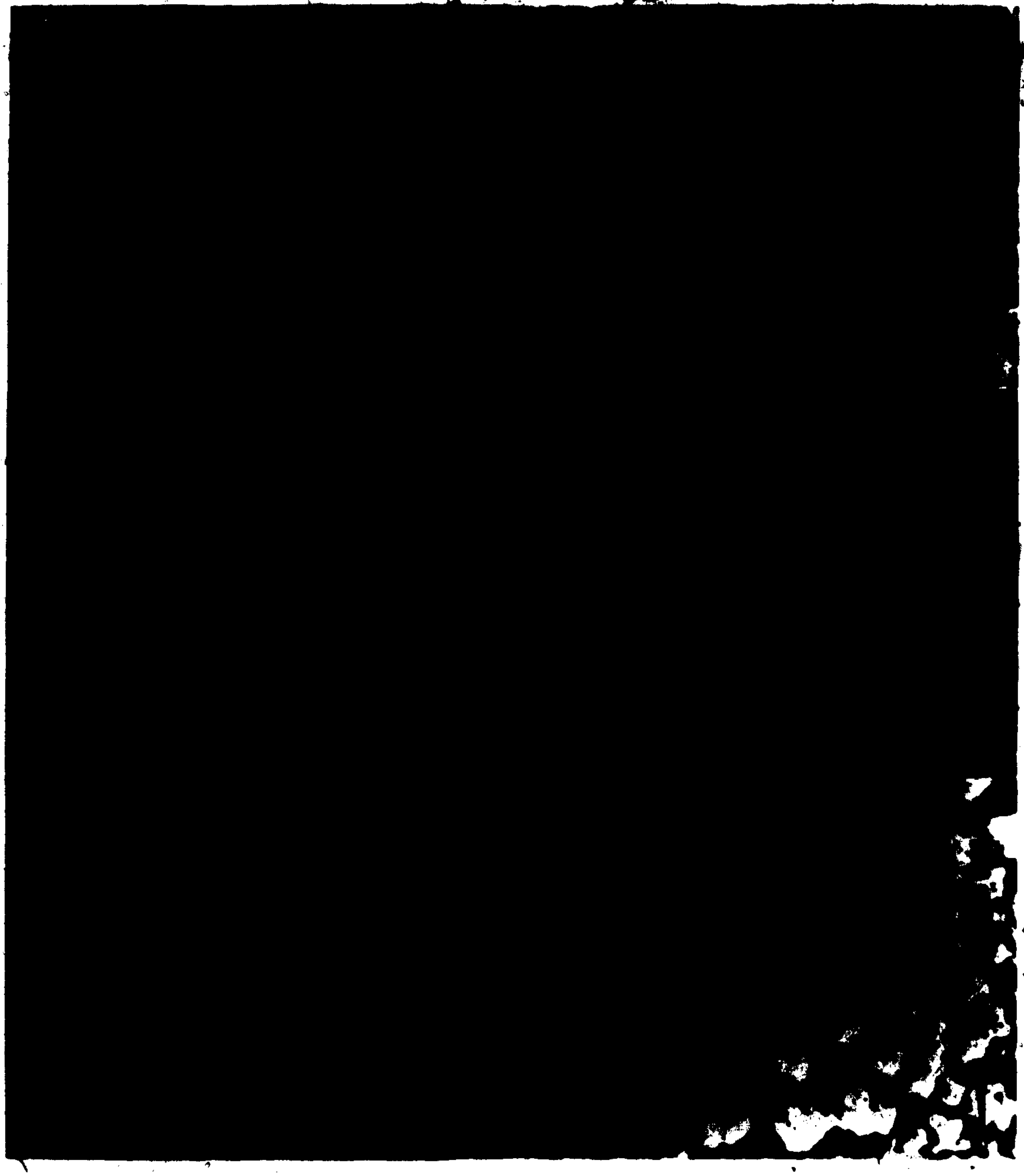
[illegible] 62. Equatorial face. Scale = 4 um.

Fig. 63. Detail of ornamentation. Scale = 1 um.

Figs. 64-65. *L. glaucum* subsp. *nukahivense*. (Marquesas, Jones 1107, L).

Fig. 64. Equatorial face. Paraisopolar. Scale = 4 um.

Fig. 65. Detail of ornamentation. Scale = 4 um.



Figs. 66-71. SPORE TYPES.

Figs. 66-69. *L. octoblepharioides* subsp. *octoblepharioides*. Paraisopolar. (Vanuatu, Salazar 3493, ALTA, PMA).

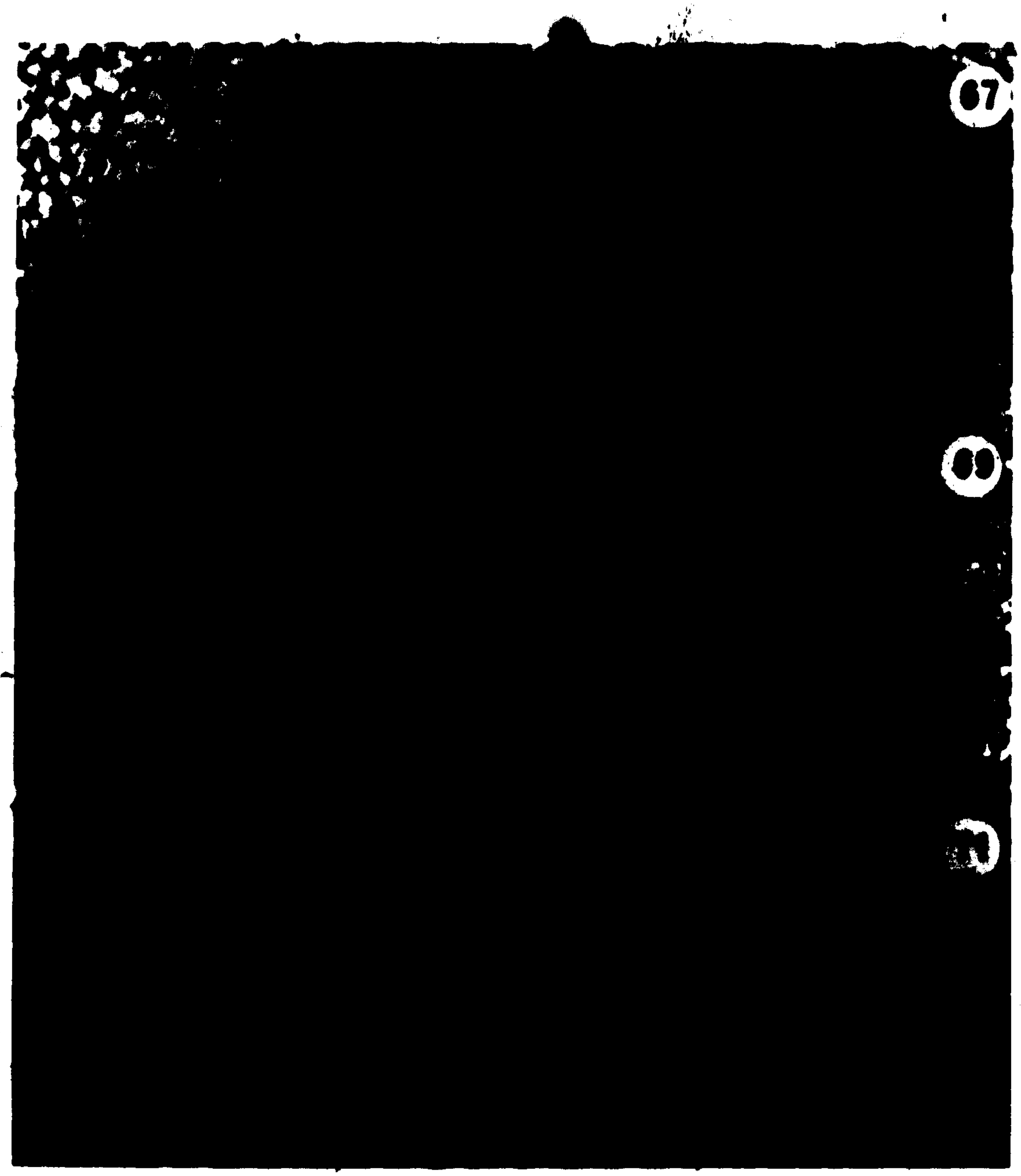
Figs. 66-67. Distal face. Details of ornamentation. Scale = 1 um.

Figs. 68-69. Proximal face. Scale = 1 um.

Figs. 70-71. *L. angustifolium*. Paraisopolar. (Ternate, Beccari 110, L).

Fig. 70. Proximal face. Scale = 4 um.

Fig. 71. Equatorial face. Scale = 1 um.



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Figs. 72-77. SPORE TYPES.

Figs. 72-75. *L. milleri*. Paraisopolar. (Micronesia, Dutton 63, MU).

Figs. 72-73. Equatorial face. Scale = 4 um.

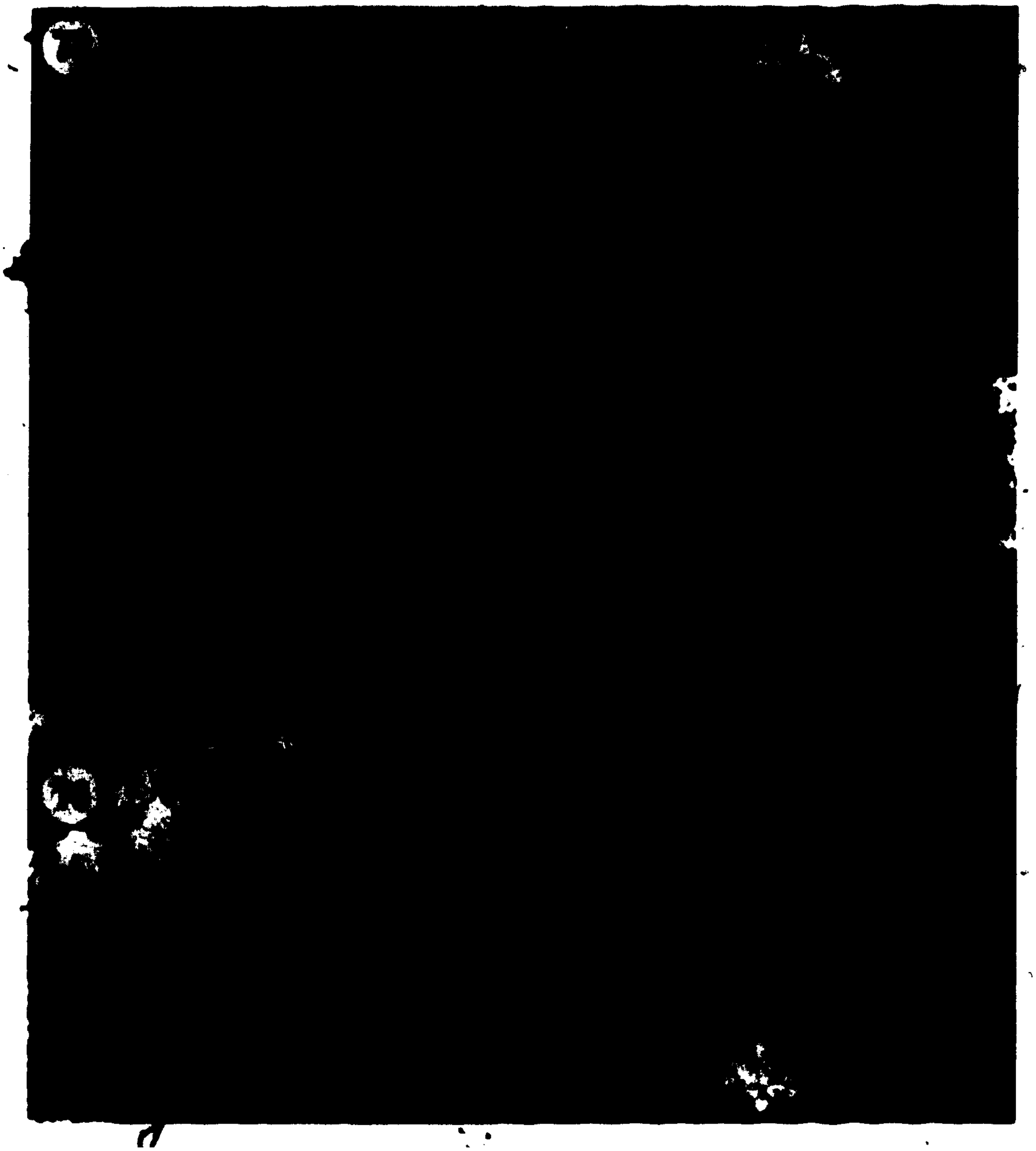
Fig. 74. Detail of ornamentation. Scale = 1 um.

Fig. 75. Distal face. Scale = 4 um.

Figs. 76-77. *L. candidum*.

Fig. 76. Equatorial face. (New Guinea, van Zanten 277, L).

Fig. 77. Distal face.



Figs. 78-83. SPORE TYPES.

Figs. 78-79. *L. seychellarum*. Paraisopolar. Scale = 4 um. (Seychelles, Horne 696, BM).

Fig. 78. Distal face.

Fig. 79. Proximal face.

Figs. 80-81. *L. serratulum*. Paraisopolar. Scale = 4 um. (New Guinea, Gjellerup 27, 27a, Type, FH).

Fig. 80. Equatorial face.

Fig. 81. Equatorial face of germinating spore.

Figs. 82-83. *L. hildebrandtii*. Paraisopolar. Scale = 10 um. (Comoro Islands, Hildebrandt a. 1875, Isotype, G).

Fig. 82. Equatorial face.

Fig. 83. Equatorial face with partial view of the less ornamented proximal face.

Figs. 84-89. SPORE TYPES.

Figs. 84-85. *L. molleri*. Paraisopolar. Scale=4 um. (Liberia, Linder 231, G).

Fig. 84. Proximal face.

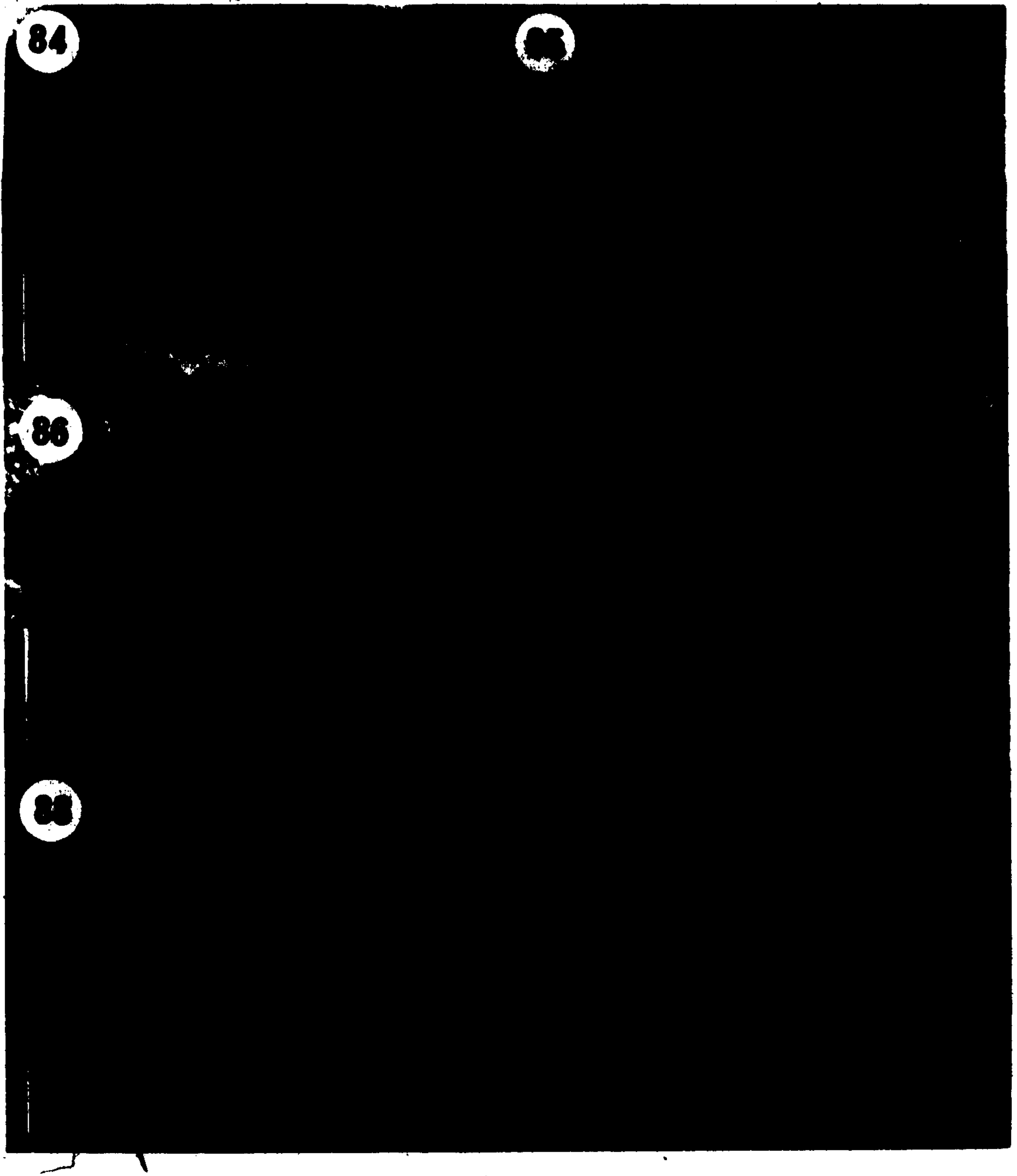
Figs. 85-86. Equatorial face.

Fig. 87. Germinating spore.

Figs. 88-89. *L. renauldii*. Verrucate-gemmate. Scale=4 um. (Mauritius, Balfour, NY).

Fig. 88. Distal face.

Fig. 89. Tetrads.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60). The spores of most species of *Leucophanes* appear to be atreme or inaperturate with no distinct trilete mark. In most species, the proximal face is less ornamented (Figs. 70, 83) and, with an irregular to elliptical smooth area (Figs. 84, 86), this perhaps, functioning as a leptome at gemination. In *L. renauldii*, unlike most species, the area with less processes is located on the distal face (Fig. 88-89).

Interspecific variation in spore ornamentation is considerable, particularly in *Leucophanes* subg. *Leucophanes* (Figs. 60-65). In this subgenus, some morphologically closely related species may differ considerably in spore ornamentation. In the African lineage, for example, spores of *L. hildebrandtii* are more similar to those of *L. molleri* than to spores of the morphologically related *L. renauldii*. In the mostly Southeast Asian-tropical Pacific species clades, two groups are distinguished based on spore ornamentation. The first group is characterized by spores with irregular and coarse granular depositions on the gemmae. The species included here are *L. serratulum*, *L. milleri* and *L. seychellarum*. These species are cladistically related (sister groups) (Fig. 481). The spore type of these species is also similar to that observed in *L. candidum* thus, suggesting an affinity between Subgenus *Leionotus* and Subgenus *Leucophanes*. The other spore group in Subgenus *Leucophanes* is represented by *L. octoblepharioides*. Spores of this species are basically verrucate to short baculate with granular depositions that are more symmetrically arranged than those of *L. milleri*, *L. seychellarum* and *L. serratulum*. Perhaps, this is a derived condition. In Subgenus *Trachynotus*, the spore ornamentation of *L. glaucum* subsp. *glaucum* with an irregular reticulate pattern appears to be similar to that of *L. glaucum* subsp. *vittii* rather than to *L. glaucum* subsp. *nukahivense* (Figs. 60-65). Additional material is needed to determine variations within and between populations to evaluate the usefulness of spore ornamentation in clarifying potential phylogenetic relationships.

IV. HABITAT OF *LEUCOPHANES*

Information on the habitats of species of *Leucophanes* is limited. Some herbarium labels give no information on specific localities (e.g., Celebes, Java) and practically no data on substrata, altitude or type of forest. Thus, the discussion on habitats is based on additional information from the following sources:

(1) Critical examination of the protologues and related literature.

(2) Field observations gathered from trips to Panama, Puerto Rico and Vanuatu.

(3) Information provided by colleagues who are familiar with the geography and vegetation of localities where *Leucophanes* has been collected, particularly in Southeast Asia.

(4) Information gathered from the literature on past and present distributions and characteristics of the tropical rain forests of the world.

Leucophanes is a corticolous epiphyte growing on living trees (palm, other angiosperms, and tree ferns), from the base to heights of 1-5 meters above ground level. On palm trees, particularly in coconut plantations along seashores and farther inland, *Leucophanes* (*L. glaucum* and *L. octoblepharioides*) has been observed growing at the bases of trees, in the rootlets and bulb areas. These areas, particularly the rootlet section, are frequently shaded by grasses and species of *Mimosa* and have accumulated soil in the crevices. These conditions, perhaps, provide a more moist and shaded microhabitat for the establishment and growth of *Leucophanes*. In theses habitats, *Leucophanes* is found in association with *Syrrhopodon*, *Calymperes*, crustose and foliose [illegible]ens. Old palm trees, particularly those in shaded, moist localities, frequently have their bark decomposed with tunnel-like cavities housing termites, ants, scorpions and sometimes woodspecies of beetles. In these trees, *Leucophanes* species have been observed to grow from the base to heights of about 5 m above ground level, many times on a very thin, fragile layer of bark. In these habitats it is frequently observed in association with species of *Syrrhopodon*, *Calymperes*, and members of the Sematophyllaceae, leafy hepatics, crustose and mucilaginous lichens.

In a study of three sites on the island Espiritu Santo (Vanuatu), the distribution of *Leucophanes glaucum*, at the bases of palm trees in coconut plantations shows strong association with the prevalent direction of the rain-laden winds. pH readings of six bark samples collected in association with *L. octoblepharioides* on Mt. Patliu (on the same island), are in the acid range of 3.5-5.5. In the island forests of Mt. Patliu, species of *Leucophanes* were observed growing on trees to heights of about 5 m above ground level.

Three species of *Leucophanes* grow on trees and rocks (e.g., limestone cliffs) along seashores. These are *L. candidum*, *L. octoblepharioides*, and *L. glaucum*. The most widespread of the three appears to be *L. glaucum* as indicated by the high frequency of occurrence of this species in collections from this area, when compared to those of *L. octoblepharioid*[illegible] *L. candidum*. These species are the only ones reported to occur in littoral forests subject to salt spray. These three species also grow in inland forests, on trees, decomposing logs, rocks and on soil.

Of the African species of *Leucophanes*, as early as 1896, Dusen indicated that: "The species of the genus *Leucophanes* are not particularly common in the Cameroon colony and, apparently, do scarcely ascend more than 1000 m up the mountain. They more specially seem to belong to the coast-district". All the localities known for *L. molleri* in Africa appear to be from inland rain forests. Comparative studies on the habitat and associations of *L. molleri* at the Luquillo Mountains in Puerto Rico, and two localities in Panama (Santa Fe, Veraguas, Santa Rita, Panama) indicate the occurrence of this species on palm trees and other angiosperms (e.g., *Virola* sp.) and also on tree ferns (*Cyathea*). In these habitats, it grows associated with species of *Syrrhopodon, Calymperes, Leucobryum, Octoblepharum*, pleurocarpous mosses, leafy hepatics (e.g., *Plagiochila*), filmy ferns (Hymenophyllaceae) and foliose lichens. A pH determination of a bark sample (*Virola* sp.) collected in Panama was 4.5. No seashore populations of *L. molleri* are known from the Neotropics.

Of the six species of *Leucophanes* reported for Africa, *L. hildebrandtii* and *L. angustifolium* appear to be the two with the widest altitudinal range, growing from the lowlands to elevations of about 2000 m. They have been collected on such substrata as the bark of angiosperms and tree ferns, decomposing logs, and rocks. All other species of *Leucophanes* in Africa and Southeast Asia appear to be corticolous epiphytes, with some of them also growing on decomposing bark. Species of *Leucophanes* are mostly elements of the lowland tropical rain forest, with some (*L. candidum*, *L. octoblepharioides*, *L. glaucum*, *L. hildebrandtii* and *L. angustifolium*) extending into montane forests.

Thus, the following conclusions and hypotheses on the ecology and distribution of *Leucophanes* can be derived from the information known to date.

(1) Plants of *Leucophanes* to grow on a wide range of substrata, although they are primarily corticolous epiphytes.

(2) *Leucophanes* species grow under acidic conditions, although some species may have a wider tolerance, growing on basic substrata (e.g., limestone). Perhaps, with more field studies, preferences at the specific level will be found.

(3) Some species of *Leucophanes*, particularly those of Africa, and some from Southeast Asia appear to be restricted to inland forests, while others like *L. glaucum*, *L. octoblepharioides* and *L. candidum* occur in littoral forests as well. Of these, *L. glaucum* appears to be the most widespread (and, perhaps, ecologically successful) species with a distribution in the littoral forest of the South Pacific.

(4) Species of *Leucophanes* are frequently associated with such closely related genera as *Syrrhopodon*, *Calymperes*, *Octoblepharum*, *Exodictyon*, *Exostratum* and *Arthrocormus*. They also grow in association with *Leucobryum* and various pleurocarpous mosses, leafy hepatics and lichens. In drier, more exposed habitats, *Leucophanes* is associated with *Syrrhopodon*, *Calymperes*, some xeric hepatics (e.g., *Frullania*), foliose and crustose lichens. In inland forests, perhaps, under more moist conditions, *Leucophanes* grows associated with species of the abovementioned genera and also *Exodictyon*, *Exostratum*, *Leucobryum*, various pleurocarpous mosses and leafy hepatics.

(5) The species of *Leucophanes* that are widespread in littoral forests appear to be pioneer

colonizers.

(6) I hypothesize that the success of species of *Leucophanes* as pioneers of the tropical islands of the Pacific Ocean is due to their ability to withstand prolonged periods of desiccation, these perhaps coupled with high light intensities and temperatures in some areas. The structure of the gametophyte (particularly the leaf), along with some physiological adaptations, growth-form, and life-strategies especially the change towards asexual means of reproduction, and perhaps, lack of competition, appear to be important factors in the successful colonization of littoral habitats by *Leucophanes*.

(7) Even though plants of *Leucophanes* are able to withstand prolonged periods of desiccation, they do not appear to be xerophytes. This is evidenced by the fact that they do not occur in xeric habitats such as exposed rock outcrops, sand dunes or arid soils. Thus, I hypothesize that the genus most probably originated in inland tropical rain forests, developing its structural and almost certainly physiological adaptations and life-mechanisms, in relation to selective forces brought about by its corticolous habit coupled with seasonally dry periods in the forest in which it grew. Thus, by being pre-adapted to withstand prolonged dry periods, *Leucophanes* was able to disperse and diversify into littoral habitats.

V. PLANT AND ANIMAL INTERACTIONS

Biological interactions between bryophytes and animals (particularly insects), algae, fungi and bacteria are known to occur in nature. They vary from mutualistic associations in which the partners derive more or less equal benefits to associations of semi- to complete parasitism (Redhead 1980, 1981). Endophytic and epiphytic associations of green algae and mosses have been reported since the early part of this century (see Reese, 1981 for a short review). Cyanobacteria, either as endosymbionts of mosses or as epiphytes are known to be the main nitrogen fixing organisms in the Arctic (Jordan et al., 1978). They have also been known to promote moss growth (Rodgers and Henriksson, 1976) and increase nitrogen uptake, e.g. in *Sphagnum* (Brasiler, 1980).

Species of *Leucophanes* have been observed to be associated with filamentous (Oscillatoriales) or non filamentous (Chroococcales) cyanobacteria. These appear between leaf tip gemmae and also on the gametophores, particularly in association with new growth. In some samples, the cyanobacteria form a blue-green band, clearly distinguishable with the naked eye. Cyanobacteria are found on the surface of the leaves and within the hyalocysts. They have not been observed in the chlorocysts. It is probable that these cyanobacteria function as an additional source of nitrogen, parallel to what occurs in *Sphagnum* (Brasiler, 1980).

Moss associated bacteria have been reported to have an influence on their growth (Spiess et al., 1971, 1976, 1981, 1982, 1984). Bacteria have been observed associated with leaf tip gemmae, but their taxa an[illegible]ffects on *Leucophanes* growth are unknown.

There is a growing literature on moss-fungi associations (Oherroja, 1971; Singer, 1975; Chopra et al., 1978; Watling, 1978; Grasso and Scheirer, 1981; Parke and Linderman, 1980; Rabitin, 1980; Redhead, 1980, 1981). Some fungi have been known to promote germination and growth in some mosses (Vaarama and Taren, 1959). The associations between fungi and mosses are parasitic or non parasitic (Redhead 1980, 1981). In many others the exact nature of their associationis still unknown (Singer, 1975; Grasso and Scheirer, 1981).

Fungal spores and hyphae have been observed in leaves and sporophytes of *Leucophanes*. Tixier (1969) related the structure of leaf-tip gemmae (Tixier's propagules) to that of some fungal spores, e.g., *Fusarum* and *Helmithosporium*. He suggested that this similarity could indicate an evolutionary continuity ("continuité") between mosses and fungi. [illegible] phae have been observed to penetrate the hyaline cells, most likely at the resorption pores. Unless living cells [illegible] are affected with a consequent damage to the living plant, I have considered these associations as exogenous and non parasitic.

Parasitic (endogenous) interactions have been observed in *L. angustifolium*. Leaves infected by fungi undergo localized tumor-like growth in which the fungi are contained. Apices are also areas succeptible to fungal infection. Swollen apices, and bleached, unhealthy looking plants are indications of fungal attack. In all instances in which the apices have been invaded, the plants look achlorotic and the leaves are readily detachable.

It is most likely that all of these plant associations may have some influence on the growth of *Leucophanes* under natural conditions. It has been very difficult to grow this moss in axenic culture, regardless of the different growth media and pH I used. Perhaps, some or all of the plant-moss associations related to *Leucophanes* are needed for their successful growth under laboratory conditions.

In relation to animal interactions, cylindrical to oblong pellets, formed by cut pieces of leaves have been frequently encountered in populations of *Leucophanes*. Matthey (1977) reported the use of cut moss gametophores for the construction of special pupating cells in some insects. Glime (1978) reported the use of moss parts in the construction of larval cases, these serving as camouflage devices for the insects. The foraging of moss parts by ants has also been documented (Plitt, 1907; Matthey, 1977; Loria and Herrnstadt, 1980). Mutualistic associations between beetles and bryophytes, "epizoic symbiosis", have also been reported (Gressit et al., 1966, 1968). Here the bryophytes are thought to provide camouflage for the insects and also make them distasteful to predators.

There has been no direct observation of animal predation on *Leucophanes*, although ants have been observed crawling over the turfs. It is most interesting to note that, in some palm trees, *Leucophanes* have been observed growing on the thin decomposed bark of tunnels inhabited by ants, scorpions or termites. Exoskeletons of mouth pieces and whole insects have been gathered from herbarium materials. A beetle of the family Bostrichidae has been collected among cut turfs. Members of this family are known to be wood-tunnel builders in tropical trees (G. Ball, personal communication).

Considering the richness of the tropical fauna, it is most likely that many animal groups, are responsible for the foraging of *Leucophanes* gametophores. It is probable that the water-holding capacity of the leaves is the critical factor in their selective use or, perhaps, their availability in a particularly restricted habitat for soft, pliable plant material or both.

VI. TAXONOMIC TREATMENT

LEUCOPHANES BRID.

Bryol. Univ. 1: 763. 1827. Type species: *L. octoblepharioides* Brid.

DISTINGUISHING FEATURES. *Leucophanes* is characterized by gametophores with a corticolous, turf-forming habit, whitish-green to blue-green in color; the stem sympodially branched and, also with short branching systems that develop into fully grown gametophytes while still attached to the parent plant (epigametophytes); leaves with a costa and a structurally complex lamina composed of two areas, a multistratose area with a central to subcentral layer of chlorocysts surrounded, on each surface, by one or more layers of hyalocysts and, a hyaline lamina composed only of hyaline cells; dioicous, except for one species, antheridial and archegoniate plants morphologically similar or male plants small and dwarf (*L. candidum*); sporophytes terminal, exserted, capsules erect to subinclined, with a papillose neck; the peristome with a prostome, 2-3 cell high, haplolepideous, of 16 orange-red teeth inserted in the mouth of the capsule, the teeth irregularly papillose to foveolate-papillose, or striated-papillose or with wide longitudinal to semicircular thickenings or smooth; spores 10-20 um in diameter, paraisopolar, verrucate to shortly baculate, verrucate-gemmate, to reticulate. The genus is distinguished from *Exodictyon*, *Exostratum*, *Arthrocormus* and *Octoblepharum* by the costate leaves, the costa, in transverse section, composed of 2-4 guide cells surrounded by stereids, these in turn, may be covered by a layer of porose hyaline cells on the abaxial and adaxial surfaces. Unlike the other genera, the lamina in *Leucophanes* is composed of a multistratose area and a hyaline basal portion.

DESCRIPTION. *Plants* 2-7 cm tall, whitish-green to blue-green or yellow-green, in dense to loose turfs. *Stem* orange-brown to orange-red, sparingly branched (sympodially) and with short branching systems that may develop into fully grown gametophytes while attached to the mother plant by rhizoids (epigametophytes), in transverse section round to irregularly triangular with a central area of large medullary cells surrounded by a layer of small cortical cells. ***Leaves*** (2.5)3.0-8.5(10) mm long, 0.3-0.8(0.9) mm wide, erect to squarrose above midleaf (e.g., *L. candidum*), loose to closely overlapping when dry; erect spreading to curve and squarrose when moist; long lanceolate from a broad to narrow base, keeled at base or through most of their length, plane above; acute, acuminate, mucronate, retuse or with a sharply dentate apex; in transverse section, the multistratose lamina composed of a central to subcentral layer of chlorocysts surrounded, on each surface, by 1-2(3) layers of hyalocysts; ***hyaline lamina*** 1/8-1/3 length of leaf from base, uni- to bistratose, 5-10 cells wide; ***margins*** plane, serrate in upper third with teeth single or in pairs, or margins smooth, straight to undulate or recurved; in transverse section uni- to multistratose; ***costa*** percurrent to shortly excurrent, enclosed in a groove formed by bulging hyalocysts or superficial, smooth to spinose on back at apex or in upper third; in transverse section composed of one layer of adaxial hyalocysts, 1-5 layers of adaxial stereids, 2 guide cells continuous with the chlorophyllous layer, 2-4 layers of abaxial stereids that may or may not be covered by a layer of hyalocysts, these with thin or thick walls or inflated; at base, in some species, costal stereids extend from adaxial to abaxial surfaces. ***Hyalocysts***, in surface view, on abaxial surface at base, rectangular to quadrate to hexagonal, with pores on surface and transverse walls; at midleaf rectangular to long or short hexagonal with surface pores narrow, slit-like and restricted to marginal hyalocysts; at apex, hyalocysts oblong rounded-quadrate or hexagonal with narrow to wide surface pores. ***Gemmae*** oblong to clavate composed of 6-9(10) cells, papillose, branched or unbranched at proximal end. ***Rhizoids*** orange-red, papillose.

Dioicous or synoicous, male and female plants growing intermixed or in separate turfs and structurally similar or with male plants small and dwarf (in *L. candidum*). ***Perichaetial leaves*** similar to vegetative ones or differentiated and mostly hyaline, archegonia in groups of five to more than ten, flask-shaped. ***Perigonial leaves*** differentiated, 2-3 in number, and completely covering the antheridia, ovate from a broad wing-like base, with a V-shaped hyaline lamina occupying the basal 2/3 to 4/5 of leaf and, a uni- to multistratose upper portion; antheridia in groups of five to more than five, paraphyses absent from both gametoecia.

Calyptra 1.2-3.8 mm long, cucullate, orange-red and papillose at apex, stramineous below. *Sporophytes* terminal, monosetous, seta exerted, 3.1-15 mm long, dark-orange to brown-orange, sinistrorse, smooth to slightly papillose on distal portion; operculum long, subulate rostrate; *capsule* 1.2-3.5 mm long, dark orange-red to brown-orange, darker at rim, erect to subinclined, cylindric to oblong-cylindric, slightly contracted under mouth, gradually narrowing to seta by a short neck; *exothecial cells* rectangular to quadrate with thin to thick walls (particularly the longitudinal walls); *rim cells* quadrate to rectangular with thin walls; *stomata* superficial on neck of capsule; *peristome* with a prostome 2-3 cells high, teeth orange-red inserted below rim of capsule, long or short lanceolate, strongly papillose on both plates with papillae in foveolate arrangements, or dorsal plate papillose-striated, or with longitudinal to semi-circular thickenings and ventral plate more or less foveolate or, peristome teeth smooth on both plates; trabeculae distinct. *Spores* 10-20(22.5) um in diameter, paraisopolar, granular to gemmate with bacula-type ornamentations projecting from the surface; under SEM strongly gemmate, to verrucate-gemmate to more or less reticulate.

HABITAT. Plants of *Leucophanes* are most commonly found as corticolous epiphytes on bark of palms and other angiosperms, on tree ferns, decomposing logs, rocks (siliceous or basic) and on soil. They have been observed growing from tree bases to approximately 5 meters above ground level. Members are important components of the littoral forest particularly in the islands of the tropical Pacific. Some species appear to be restricted to inland forests, while others are found in both, littoral and inland forests.

DISTRIBUTION. *Leucophanes* is distributed in the tropical and subtropical regions of the world. Its distribution coinciding with the major blocks of tropical rain forests. Seven endemics are recognized. Of these, five are from Africa, *L. hildebrandtii*, *L. rodriguezii*, *L. renauldii*, *L. seychellarum* and *L. unguiculatum*; the other endemics are from New Guinea, *L. serratulum*; and Micronesia, *L. millerii*.

KEY TO SUBGENERA OF LEUCOPHANES

1\. Laminar hyalocysts, in surface view, oblong with ± sinuose lateral walls and broad to narrow dove-tail end walls, longitudinal rows of chlorocysts above midleaf broad, 10-15 um wide with rounded to oval lacunae, transverse section of leaves heterogeneous with 2(3) layers of abaxial hyalocysts at base .... Subgenus *Trachynotus* (page 229)

1\. Laminar hyalocysts, in surface view, short or long hexagonal with ± rectilinear lateral and end walls, longitudinal rows of chlorocysts above midleaf narrow, 7.5-10(12.5) um wide with elongated lacunae, transverse section of leaves homogeneous from base to apex with one or more layers of hyalocysts on each side of the chlorophyllous layer or heterogeneous with 2(3) layers of abaxial hyalocysts at base 2

2\. Leaves tumid, squarrose-spreading to erect, acuminate, costa narrow and short excurrent, exposed abaxially, hyalocysts in surface view, short hexagonal, transverse section of leaves homogeneous throughout with one layer of hyalocysts on each side of the chlorophyllous layer ....Subgenus *Leianotus* (page 211)

2\. Leaves flattened to slightly tumid, ± spreading, erect, curved or falcate, acuminate, obtuse, or with an erose or incised apex, costa narrow or broad, percurrent to shortly excurrent, exposed or covered by hyaline cells abaxially, hyalocysts, in surface view, rectangular to hexagonal, transverse section of leaves homogeneous with one or more than one layer of hyalocysts on each side of the chlorophyllous layer or heterogeneous .... Subgenus *Leucophanes* (page 96)

KEY TO SPECIES AND SUBSPECIES OF *LEUCOPHANES*

1\. Plants robust, leaves tumid, squarrose -spreading to erect, closely vaginant, hyalocyst surface walls porate from base to apex; transverse section of leaves chlorophyllous layer, costa smooth . . . . *L. candidum*(page 212)

1\. Plants slender to robust, leaves flattened to slightly tumid, erect to irregularly curved, loosely to closely overlapping, hyalocyst surface walls porate mainly at base and apex, transverse section of leaves with one or more layers of hyalocysts or smooth . . . . (2)

2\. Midleaf cells rhomboid to oblong with ± straight walls, chlorocysts above midleaf narrow to + broad (1:1, 2-3:1), lacunae narrowly elongated to ± broad, transverse section of the leaf base with one or more layers of hyalocysts on each side of chlorophyllous layer . (3)

2\. Midleaf cells oblong to irregularly hexagonal with sinuose lateral walls and rounded bulging end walls, chlorocysts above midleaf broad (1:1, 1:2), lacunae short and broad, transverse section of leaf with more than one layer of hyalocysts on abaxial side of chlorophyllous layer . . . . *Leucophanes glaucum sensu lato* (14) (page 230)

3\. Leaves narrowly lanceolate (11-15:1), in transverse section with one or 2(3) irregular layers of hyalocysts on the abaxial and adaxial sides of chlorophyllous layer, pores on transverse walls narrow 2.5-5.0 um in diameter . . . . *L. angustifolium* (page 119)

3\. Leaves narrowly to broadly lanceolate (6-13:1), in transverse section with one layer of hyalocysts (in some populations of *L. octoblepharioides* two layers at base, on abaxial side) on each side of chlorophyllous layer, pores on transverse walls narrow or wide, 2.5 to more than 5.0 um in diameter . . . . (4)

4\. Costa ending in a truncate, spinose-erose apex, margins smooth . . . . (5)

4\. Costa percurrent in an acuminate or truncate, smooth apex, margins serrate or smooth . . (6)

5\. Leaves markedly shiny-translucent, mid- and apical hyalocysts, on abaxial side, short hexagonal, bulging . . . . *L. renauldii* (page 200)

5\. Leaves slightly translucent, mid- and apical hyalocysts, on abaxial side, oblong-hexagonal to irregularly rectangular, not inflated or slightly so . . . . *L. hildebrandtii* (page 192)

6\. Apex of mature leaves variable, acuminate to obtuse or incised, recurved, plants small to medium sized . . . . *L. molleri* (page 166)

6\. Apex of mature leaves acuminate to apiculate, straight, plants medium sized to robust . . . (7)

7. Plants robust, leaves broadly lanceolate, acuminate to apiculate, margins strongly serrate in the upper third or smooth .... (8)

7. Plants slender, leaves narrowly lanceolate, acuminate, margins serrate in the upper third . (9)

8. Leaves strongly curved to falcate-secund, apiculate (in some leaves the apiculus hook-like), margins smooth, dioicous .... *L. unguiculatum* (page 183)

8. Leaves squarrose from middle, acuminate, margins strongly serrate, synoicous .... *L. serratulum* (page 149)

9. Pores on transverse walls of hyalocysts 5.0 um or more in diameter, costa narrow, abaxially exposed or covered by inflated hyaline cells, margins when dry + plane to slightly recurved below shoulders ....(10)

9. Pores on transverse walls of hyalocysts mostly 2.5-5.0 um in diameter, costa wide, abaxially covered by a layer of hyaline cells, margins strongly revolute below shoulders .... *L. rodriguezii* (page 160)

10. Midleaf cells long-hexagonal with rectilinear to + curve end walls, peristome plates longitudinally striate and papillose ....*L. octoblepharioides* subsp. *whittieri* (page 114)

10. Midcells rectangular to hexagonal with rectilinear to ± curved end walls, peristome plates papillose, foveolate ....(11)

11. Plants slender to 3 cm high, leaves dull to translucent, loosely overlapping, spores granular, seta 6-8 mm long ....(12)

11. Plants slender to robust, 3-5 cm tall, leaves shiny, closely overlapping, spores grossly and irregularly baculate-gemmate, seta 8-18 mm long ....(13)

12. Leaves narrowly to broadly lanceolate, margins serrate, midleaf hyalocysts irregularly hexagonal to rectangular, in transverse section with curved to ± straight surface walls, peristome plates densely papillose, foveolate .... *L.octoblepharioides* subsp. *octoblepharioides*(page 102)

12. Leaves narrowly lanceolate, margins sharply serrate, midleaf hyalocysts rectangular, in transverse section with strongly concave surface walls, peristome dorsal plates ±

smooth, ventral plates papillose ....*L. seychellarum* (page 143)

13. Plants to 3 cm tall, leaves squarrose to curved-spreading, abaxial hyalocysts short hexagonal (1-2:1), inflated, covering the costa from base to apex .... *L. octoblepharioides* subsp. *meijeri* (page 109)

13. Plants to 5 cm tall, leaves erect, to curved-spreading, abaxial hyalocysts long rectangular (3-5:1), not inflated, costa exposed ....*L. milleri* (page 132)

14. Peristome dorsal plates papillose, with ± defined vertical striations ornamented with papillae; ventral plates strongly papillose; costa sharply spinose to nearly smooth.. *L. glaucum* subsp. *glaucum* (page 230)

14. Peristome dorsal plates faintly papillose to smooth at apex, ventral plates papillose to smooth; costa smooth or with few scattered teeth ....(15)

15. Peristome dorsal plates slightly papillose and articulated at base, smooth at apex, ventral plates papillose, spores sparsely granular with short baculate ornamentation projecting from the surface ....*L. glaucum* subsp. *nukahivense* (page 250)

15. Peristome dorsal and ventral plates smooth, unarticulated at base, spores finely granular .... *L. glaucum* subsp. *vittii* (page 254)

LEUCOPHANES SUBG. LEUCOPHANES

Lectotype: *Leucophanes octoblepharioides* Brid.

Section Tropinotus C. Muell., J. Mus. Godeffroy 3(6): 57. 58. 1874. *nom. illeg. incl. lectotyp. gen.= Leucophanes* Brid. sect. *Leucophanes.*

Section C. Cardot. Mem. Soc. natn. Sci. nat. Math. Cherbourg 32: 1-84. 1900.

Subsection Homostrôsica. Cardot. *in* Grand. Hist. Madag. 39: 148. 1915.

Plants 3-6 cm tall in loose to dense turfs; *stem* sparingly branched; *leaves* lanceolate from a broad or narrow base, erect spreading to + falcate and closely overlapping when dry, slightly spreading when moist, acuminate, acute, apiculate or retuse, keeled below, plane above; *hyaline* *lamina* occupying 1/5-1/3 length of leaf; *hyalocysts* rectangular to hexagonal, *chlorocysts* in surface view above midleaf with narrow to ± broad lacunae; *costa* narrow or broad, spinose at apex or smooth; *margins* serrate in upper 1/4-1/3 to smooth with 2-3 colored cells at insertion; transverse section of leaf with one or more than one layer of hyalocysts on each side of chlorophyllous cells. Dioicous, male and female plants similar, *perichaetial leaves* shorter and hyaline through most of their length or not differentiated; *seta* 4.4-7.2 mm long; *capsules* 1.7-2.6 mm long, cylindrical; *peristome* with a prostome 2-3 cells high; haplolepideous of 16 narrow to broadly lanceolate teeth, papillose-foveolate on both plates to smooth on dorsal plate or with semi-circular to longitudinal thickenings; *spores* 7.5-17.5(20) um, gemmate, under SEM gemmae ornamented with granular depositions.

Leucophanes octoblepharioides Brid.

Bryol. Univer. 1: 763. 1826. Types: "In insula Java unde clariss Nees v. Esenbeck habuit et humanissime in isum communicavit, et in regione Nepal Indiae ex Herbario Candolleano caespitose ad terram habitat."(Lectotype: "Java. Leg. Nees v. Esenbeck", B-Nees v. Esenbeck!; Isotype: BM-Hb. Nees!; Syntype: B-De Candolle!).

Syrrhopodon octoblepharis Nees ex Schwaegr., Spec. Musc. Suppl. 4: 311 a. 1842. Type: "In Java lectum misit Nees ab Esenbeck, praeses Soc. Leopold." (Lectotype: G-Hedw.-Schwaegr.!; Isotype: G-Hedw.-Schwaegr.!).

Leucophanes korthalsii Doz. et Molk., Musci Fr. Ined. Archip. Indici 3: 65. 23. 1846. Types: "Java: in monte Gede. Zippelius. Borneo: prope pagum Martapoëra. Korthals. Amboina: collegit Zippelius." (Lectotype: "*Syrrhopodon octoblepharis*" Nees. B. *flexirostrum*. Collegit G.W. Korthals Martapoera, pagum insulae Borneo". L-Lugd.Bat!; Syntypes: "Amboina". L-Lugd.Bat. (3 specimens)!).

Leucophanes albo-nitens C. Muell., J. Mus. Godeffroy 3(6): 58. 1874. Type: "Samoa-insulae, inter alios muscos parcissime, Savaii, Upolu et Tutuila. Leg. Dr. Ed. Graeffe". (Isotype: "*Leucophanes albo-nitens* C. M. Samoa insulae, Upolu ad Tofra. 1861, leg. E. Graeffe com. C. M., resp. Broth." S-Roth!).

Octoblepharum octoblepharioides (Brid.) Mitt., Rep. Sc. Voyage Challenger Bot. 1(4): 259. 1885. Type: "*Leucophanes octoblepharioides* Brid., Bryol. Univ., i.p. 763; C. Mull., Synopsis Musc. Frond., i.p. 82."

Leucophanes minutum C. Muell. in Geh., Biblioth. Bot. 13:2. 1889. Type: "Fly River (Branch), alliis muscis parcissime intermixtum leg. W. Bauerlen." (Type: not seen).

Leucophanes francii Card. et Ther., Diagnost. Esp. Var. Nouv. Mouss. 8.2. 1910. Type: "Hab. Forêt de Tao, de 100 a 600m." (Lectotype: PC-Ther.!; Isotype: BM-ex Ther.!; FH-ex Ther.!).

Leucophanes pungens Fleisch. ex Dixon., Proc. Linn. Soc. N.S. Wales 55(3): 268. 1930. Type: "M:. Fr. Arch. Ind. et Polynes., No. 405; Samoa, Ins. Savai'i, deter. Fleischer." (Lectotype: "Musci Frond. Archipelagi Indici et Polynesiaci. Serie IX (No. 401-450). 1906. 405 *Leucophanes (Tropinotus) pungens*. Fleisch. n. sp.." BM!; Isotypes: B!, BM (2 specimens)!, EGR!, G!, JE (2 specimens)!, L!, M!, NY!, S!).

Leucophanes nicobaricum C. Muell. ex Gangulee, Mosses of Eastern India and adjacent regions. Archidiales, Dicranales, Fissidentales. Fasc. 2. p. 438. 1971. Type: "Kurz lectum ad Ketchall Inseln in Nicobar Is. et positus in BM". (Lectotype: "Nicobar Ins. Katchall. 11/275. Leg. J. Kurz", BM!; Isotypes: B!, S!).

NOMENCLATURAL NOTE. The species was first described by Bridel (1826) based on two collections. One collection from Nees v. Esenbeck from Java and another from Nepal from De Candolle's herbarium. There is a question mark on the herbarium sheet besides the specimen from Nepal and a hand-written locality reading: "East Indies". There are no collections recorded from Nepal except for this one.

DISTINGUISHING FEATURES. *Leucophanes octoblepharioides* is characterized by its erect leaves, that are slightly spreading when dry and moist and narrowly lanceolate from a broad to ± narrow base as well; the leaves are broadly acuminate to acute, keeled below and plane above; the hyaline lamina occupies 1/5-1/3 the length of the leaf, and the costa is narrow; in transverse section the leaves have a single layer of hyalocysts on abaxial and adaxial sides of central chlorophyllous layer; the costa is exposed to completely covered the hyalocysts on the abaxial side. There are some populations of *L. octoblepharioides* that have two layers of hyalocysts on the abaxial side of the leaf at base.

DESCRIPTION. *Plants* to 3.5 cm tall, in dense or loose turfs, white-green when dry, light-green to blue-green when moist. *Stem* red to brown-red, (100.0)112.5-150.0(175.0) um in diameter, flexuose; in transverse section with a central area of large thin-walled medullary cells surrounded by a ± thick-walled cortex. Branching single or in 2-3's. *Leaves* 3.0-5.4 mm long, 0.4-0.9 mm wide, loosely overlapping (subvaginant), erect-patent and ± twisted when dry, slightly spreading when moist, narrowly lanceolate from a broad to ± narrow base, broadly acuminate to acute, ± keeled below, plane at apex, decurrent at costal area, with 3-4 red cells at insertion; in transverse section with one layer of quadrangular chlorocysts surrounded on each surface by one layer of hyalocysts (isolated cross-walls observed at base in some populations); *hyaline lamina* extending 1/5-1/8 (1/3) the length of leaf, 4-10 cells wide, uni- or bistratose; *margins* recurved below shoulders, irregularly serrate in upper 1/3-1/2, with one side more strongly serrate than the other, teeth single, in transverse section with 2-5 rows of stereids, uni- to multistratose; *costa* narrow throughout, percurrent, smooth to abaxially spinose at apex, partially to completely covered by hyalocysts on abaxial side from base to apex (see *L. octoblepharioides* subsp. *meijeri*); in transverse section with one layer of adaxial hyalocysts, 1-(2) layers of adaxial stereids or none at all, 2 guide cells continuous with the central chlorophyllous layer and 2-6 layers of abaxial stereids; *hyalocysts* in surface view on abaxial surface at base, 24.0-52.8 um long, 12.5-25.0 um wide, rectangular, rhombic-elongated, or quadrate; at midleaf (17.5)22.5-42.5(62.5) um long, (8.5)10.0-17.5(22.5) um wide, ± hexagonal to irregularly rectangular; at apex (16.5)20-48.5(52.5) um long, (6.3)8.3-15.0(20.0)um wide, irregularly hexagonal to rectangular; *pores* on surface walls single, wider at base, narrow and restricted to marginal hyalocysts at midleaf and apex, 1-2 on transverse walls at base, a single pore above. *Gemmae* variable in number of cells, finely papillose, clavate to oval-elongate in shape, branched or unbranched at base. *Rhizoids* brown-red to orange-red, finely papillose.

Dioicous, *perichaetial leaves* differentiated, 2.9-3.3 mm long, with a broad hyaline sheathing base covering vaginula and base of seta, archegonia in groups of five, to more than five. Male plants morphologically similar to female plants, in some populations slender and flexuose, with a nodose appearance due to perigonia; *perigonial leaves* three, antheridia in groups of more than five. *Calyptrae* 2.3-3.3 mm long, cylindrical, cucullate, red and papillose at apex, stramineous below, cylinder entire or irregularly lacerate. *Sporophytes* terminal, monosetous, setae 4.4-12.0 mm long, dark-red to brown-red, sinistrorse, ± papillose at neck, smooth; *opercula* 0.8-1.4 mm long, subulate-rostrate; erect to curved; *capsules* (1.5) 1.7-2.6 mm long, dark red, darker at rim, erect to subinclined, cylindric to oblong-elliptical, gradually narrowing to seta, apophysis papillose; *exothecial cells* 35.0-62.5(87.5) um long; (15.0)17.5-22.5(30.0) um wide, rectangular to quadrate, in longitudinal rows, with ± thick walls; at rim (10.0)12.5-22.5(25.0) um long, 7.5-12.5 um wide, short oblong to hexagonal, in 3-4(5) horizontal layers; *stomata* 20.0-25.0 um long, 20.0-22.5 um wide, 12-14 in number; *peristome teeth* 162.5-200.0 um long, orange-red, densely papillose on both surfaces, papillae clavate in circular arrangement, trabecula prominent on inner side. *Spores* 7.5-10.5(17.5) um in diameter, paraisopolar, densely verrucose to short-baculate, these with granular depositions.

HABITAT. *Leucophanes octoblepharioides* has been collected on trees, rotting logs, rocks and soil. It is reported to grow in inland and littoral forests throughout its range. It appears to have habitat preference (higher frequency of occurrence) for inland forests and grows with *L. glaucum*, *L. angustifolium*, *Exodictyon*, *Octoblepharum* and other members of the Calymperaceae.

DISTRIBUTION. This species has been verified from Australia; India; Southern Japan; Taiwan; S.E. Asia: Nepal, Malesia, Democratic Republic of Vietnam, Thailand; New Caledonia; the tropical Pacific: Guam, Samoa (Savai'i, Tutuila, Upolu), Society Islands (Raiatea, Moorea, Tahiti), Tonga Islands (Tofua); Micronesia and Vanuatu; Seychelles and Mauritius.

PHYLOGENETIC RELATIONSHIPS. In leaf structure *L. octoblepharioides* is closely related to the African species of *Leucophanes*, as well as the Indo-Pacific *L. milleri* and *L. candidum*. All these species have a single layer of hyalocysts on either side of the chlorophyllous layer. In peristome features, *L. octoblepharioides* is closely related to *L. milleri*, *L. angustifolium*, *L. seychellarum and L. serratulum* . In these species, the teeth are papillose on both plates, with capitate papillae arranged around central circular depressions (foveolae).

SPECIMENS EXAMINED. ALTA (3), B (21), BM (63), CBG (12), EGR (12), FH (30), G (9), H (3), L (92), M (9), MU (40), NY (15) PC (2), S (41).

Leucophanes octoblepharioides Brid. subsp. octoblepharioides

(Figs. 32, 35, 42-44, 66-69, 90-112, 146)

Type: *L. octoblepharioides* Brid.

DISTINGUISHING FEATURES. This subspecies is characterized by its habit of long, narrow to broad leaves, loosely overlapping; in transverse section with one or more than one layer of abaxial hyalocysts at base; the peristome distinctly papillose-foveolate; spores verrucate to short-baculate, the verrucae or baculae ornamented with granular depositions.

HABITAT. Plants of *L. octoblepharioides* subsp. *octoblepharioides* have been collected on the bark of angiosperms and tree ferns and on decomposing logs.

DISTRIBUTION. This subspecies has been collected throughout Malasia, Australia, New Guinea, Solomon Islands, Vanuatu and Fiji.

SPECIMENS EXAMINED. ALTA (1), B (1), BM (12), EGR (1), FH (3), G (4), L (17), M (2), NY (1), S (5).

Figs. 90-98. *L. octoblepharioides* subsp. *octoblepharioides*.

Fig. 90. Vegetative leaves. Scale = 1 mm (Taiwan, Sin 128, L).

Fig. 91. Apices. Scale = 100 um. (Samoa, Fleischer B1189, B).

Fig. 92-94. A[illegible]l hyalocysts of the leaf. Scale = 50 um.

Fig. 92. Base. (Java, Kurz iv. 61, M; Solomon Islands, Dissing 2807, L).

Fig. [illegible]. Mi[illegible] (New Guinea, van Zanten 568b, L; Java, Lectotype, B).

Fig. 94. Apex. [illegible], Lectotype, B; Solomon Islands, Dissing 2807, L).

Fig. 95. Transverse section of stem. Scale = 50 um.

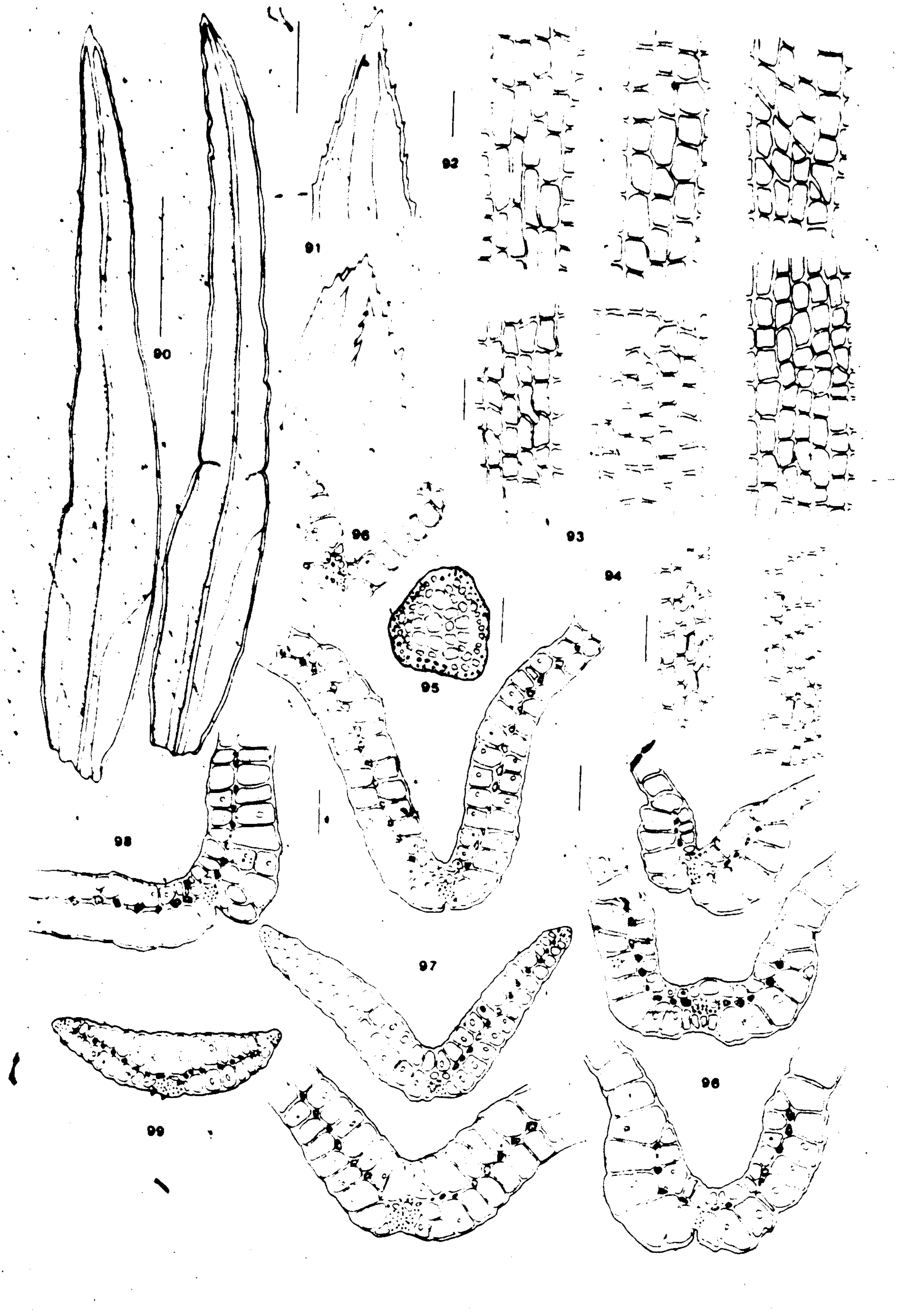
Figs. 96-99. Transverse sections of leaves. Scale = 50 um.

Fig. 96. Base. (Society Islands, Moore 71, BM; Java, Isotype, M; Sumatra, Wijk 1362, L; Kuala Lumpur, Wood 1276, BM).

Fig. 97. Midleaf. (Java, Fleischer 56, S; Fiji, Salazar 3716, ALTA, PMA; Java, Schiffner 10409, L).

Fig. 98. At end of lamina. (Java, Kurz, M).

Fig. 99. Apex. (Java, Fleischer 56, S).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Figs. 100-108. *L. octoblepharioides* subsp. *octoblepharioides*.

Fig. 100. Perigonium. Scale=0.5 mm. (Java, Fleischer 96, S).

Fig. 101. Perichaetial leaf. Scale=0.5 mm. (Ibid. 100).

Fig. 102. Calyptrae. Scale=0.5 mm. (Java, Fleischer a. 1898, S; Java, BM).

Fig. 103-104. Capsules. Scale=0.5 mm. (Java, Blume, L; Kuala Lumpur, Wood 1276, BM; Java, Holle, L; Java, L).

Fig. 105-108. Scale=100 um. (Kuala Lumpur, Wood 1276, BM).

Fig. 105. Transverse section of seta.

Fig. 106. Exothecial cells.

Fig. 107. Rim cells.

Fig. 108. Stomates.

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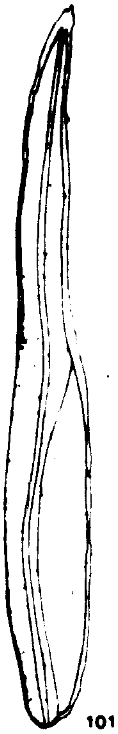

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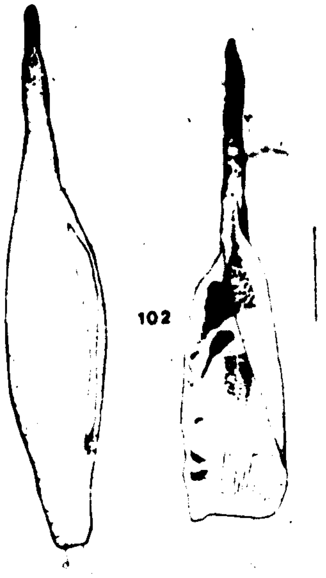

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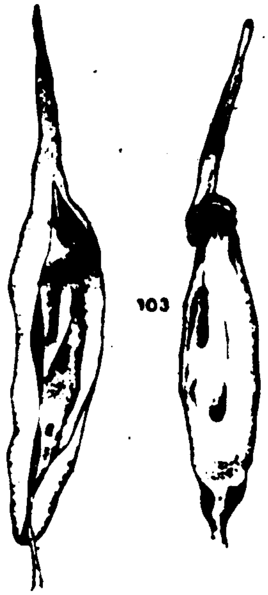

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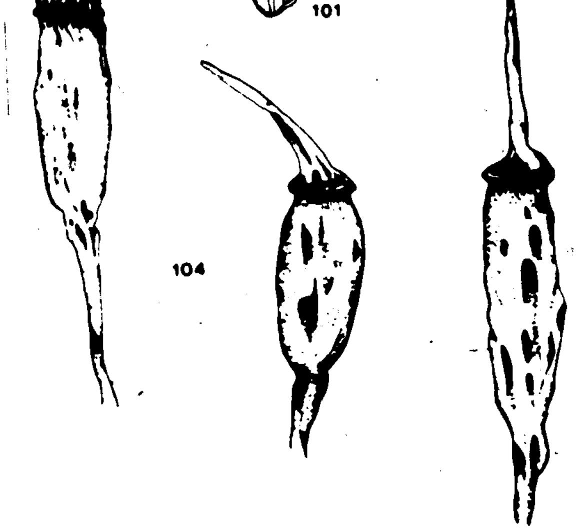

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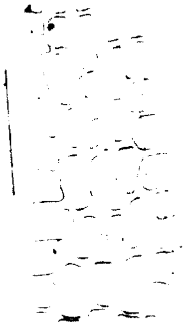

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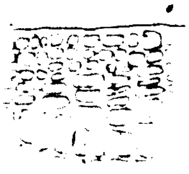

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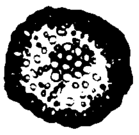

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Figs. 109-112. *L. octoblepharioides* subsp. *octoblepharioides*. Peristome papillose-foveolate. (Vanuatu, Salazar 3493, ALTA, PMA).

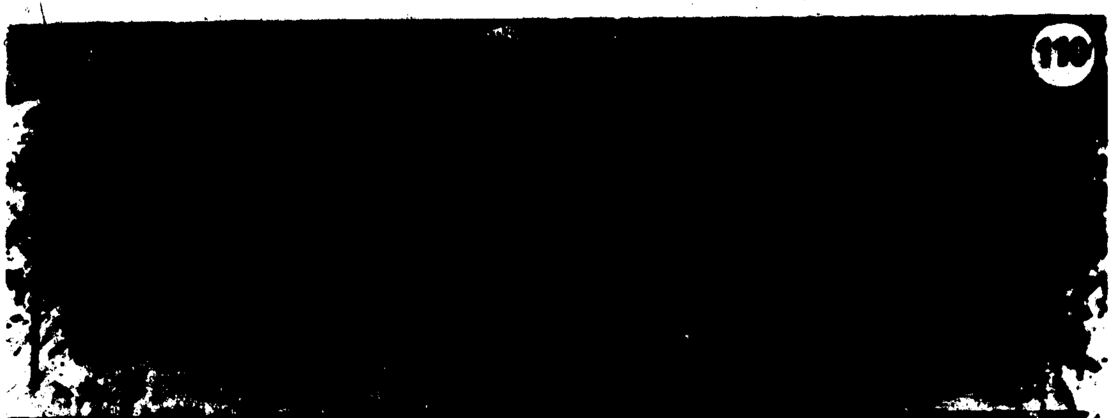
Fig. 109. Scale = 50 um.

Fig. 110. Scale = 20 um.

Figs. 111-112. Spore ornamentation.

Fig. 111. Scale = 4 um.

Fig. 112. Scale = 1 um.



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Leucophanes octoblepharioides Brid. subsp. **meijeri** Salazar-Allen *subsp. nov.*

(Figs. 113-130, 146)

Type: "West Borneo, Sarawak, limestone hill near Bau. Leg. W. Meijer. No. B12368. Dat. 6-1960." L!; Paratypes: W. Borneo, Sarawak, limestone hill near Bau. Leg. W. Meijer No. B12382. Dat. 6-1960, L!; W. Borneo, Sarawak, limestone hill near Bau. Leg. W. Meijer. No. B12386. Dat. 6-1960, L!; Borneo-East Borneo, E. Kutei, district Muaramuntai. Peak of Balikpapan (G. B[illegible]) [illegible]50 m alt. Coll. W. Meijer. No. B1421 a. dd. 3-7, 1952, L!; N. Borneo, Tawau K[illegible] [illegible]a River Forest Reserve. Leg. W. Meijer, No. B10755. dat. 9-1960, L!; 1200 Borneo, Sarawak, 1911. Native collector, L!, M!).

DISTINGUISHING FEATURES. This subspecies is characterized by its tall habit of long narrow, curve (arcuate) to squarrose leaves, in some populations (e.g. from Thailand) closely resembling those of *Exodictyon* and *Exostratum*; the leaves tumid by the inflated hyalocysts (less so than in *L. candidum*), in transverse section, with the costal area covered from base to apex by a layer of inflated hyaline cells; the seta 6.0-12.0 mm long and the spores paraisopolar, grossly verrucose to short-baculate. Under the SEM the verrucae or short baculae are composed of a thick column with irregular deposition of globular material at the distal end.

HABITAT. *Leucophanes octoblepharioides* subsp. *meijeri* has been collected on living trees, on sandstone and other rocks of unknown nature in the forest, and on soil.

DISTRIBUTION. This subspecies has been collected thoughout Indonesia, in Borneo, where it is reported from North Borneo in the Tawau River Forest Reserve; in East Borneo at the Peak of Balikpapan (G. Beratus), also in West Borneo, in Sarawak near Bau and at Bako National Park; in Java and, in Sumatra at Padang. This subspecies has also been collected in Sri Lanka, Figs. 113-126. *L. octoblepharioides* subsp. *meijeri.*

Fig. 113. Vegetative leaves. Scale=1 mm. (N. Borneo, Meijer B12368, Type, L).

Fig. 114-116. Abaxial hyalocysts of leaf. Scale=100 um. (Ibid. 113).

Fig. 114. Base.

Fig. 115. Midleaf.

Fig. 116. Apex.

Fig. 117-120. Transverse sections of the leaves. Scale=100 um. (Ibid. 113).

Fig. 117. Base.

Fig. 118. Apex.

Fig. 119. Midleaf.

Fig. 120. Above midleaf.

Fig. 121. Young calyptra. Scale=0.5 mm (capsule also). (Sarawak, native collector 1200, L).

Fig. 122-126. Sporophyte.

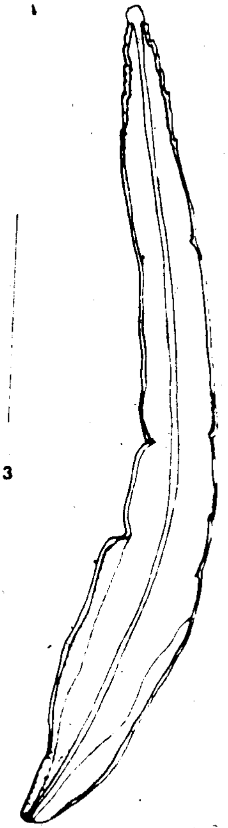
Fig. 122. Capsule. (Ibid. 113).

Fig. 123. Stomates. Scale=50 um. (Ibid. 121).

Fig. 124. Rim cells. Scale=50 um. (Ibid. 121)

Fig. 125. Transverse section of seta. Scale 50 um. (Ibid. 121)

Fig. 126. Exothecial cells. Scale=50 um. (Ibid. 121).



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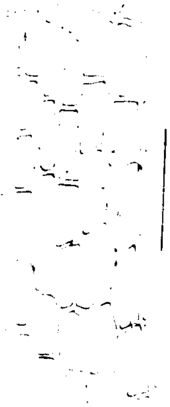

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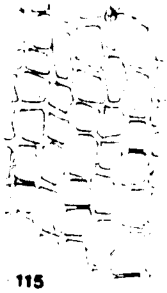

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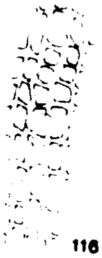

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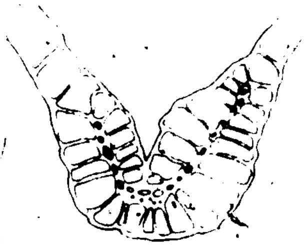

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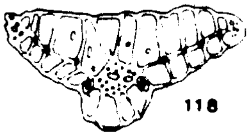

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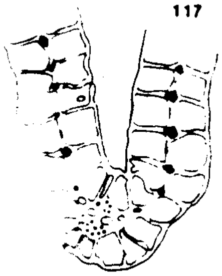

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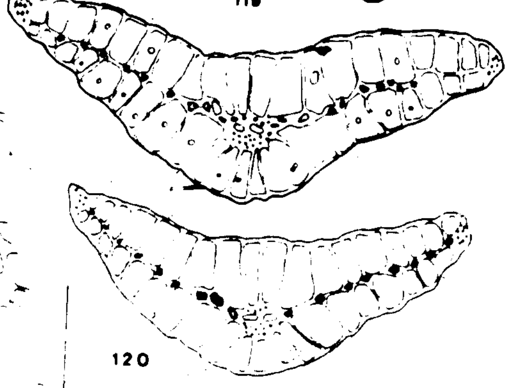

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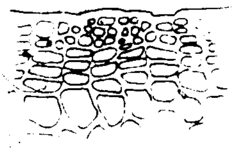

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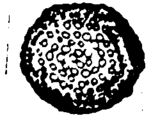

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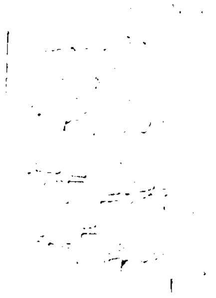

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Figs. 127-130. *L. octoblepharioides* subsp. *meijeri*. (Borneo, native collector 1200, M).

Fig. 127-128. Scale = 50 um.

Fig. 129. Outer surface of teeth. Scale = 20 um.

Fig. 130. Apex of calyptra. Scale = 50 um.

and Thailand.

SPECIMENS EXAMINED. BM (2), G (2), L (12), M (1), NY (1), S (1).

Leucophanes octoblepharioides Brid. subsp. whittieri Salazar-Allen *subsp. nov.*

(Figs. 52-53, 131-146)

Type: "Yap: Yaptown. Altitude 100-150 feet. Coll. H.A. Miller & H.O. Whittier. Date 17 August 1960. No.1252." MU!; Paratypes: "Yap: Yaptown. Altitude 100-150 feet Coll. H.A. Miller & H.O. Whittier. Date 17 August, 1960. No. 1230, 1254. MU!

DISTINGUISHING FEATURES. This subspecies is characterized by its whitish-green appearance, flexuose stem, leaves erect and slightly twisted with a broad hyaline base; in transverse section with a single layer of hyalocysts on each surface of the chlorophyllous layer, a narrow costa with two distinct guide cells; the peristome is papillose-striate.

HABITAT. Plants of this subspecies have been collected on the bark of angiosperms and tree ferns.

DISTRIBUTION. *Leucophanes octoblepharioides* subsp. *whittieri* is restricted to the islands of Micronesia,

SPECIMENS EXAMINED. MU (3)!

Figs. 131-145. *L. octoblepharioides* subsp. *whittieri*. (Yaptown, Miller & Whittier 1252, Type, MU).

Fig. 131. Vegetative leaves. Scale = 0.5 mm.

Fig. 132-134. Abaxial hyalocysts of leaf. Scale = 50 um.

Fig. 132. Base.

Fig. 133. Midleaf.

Fig. 134. Apex.

Figs. 135-137. Transverse sections of leaves and stem. Scale = 100 um.

Fig. 135. Base.

Fig. 136. Midleaf.

Fig. 137. Apex.

Fig. 138. Transverse section of stem.

Fig. 139. Perigonium. Scale = 0.3 mm.

Fig. 140. Calyptra. Scale = 0.5 mm.

Figs. 141-145. Sporophyte.

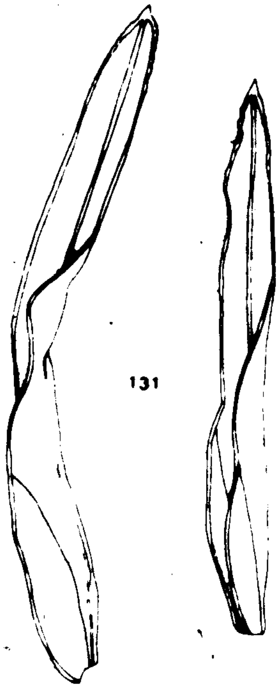
Fig. 141. Capsules. Scale = 0.5 mm.

Fig. 142. Exothecial cells. Scale = 100 um.

Fig. 143. Stomates. Scale = 100 um.

Fig. 144. Rim cells. Scale = 50 um

Fig. 145. Transverse section [illegible] Scale = 50 um.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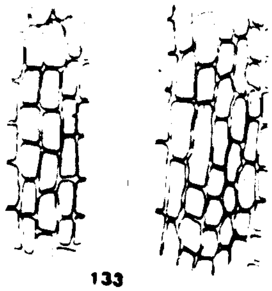
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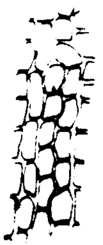
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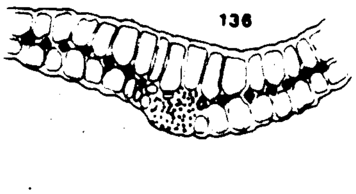
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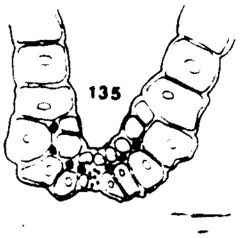
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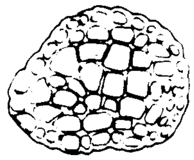
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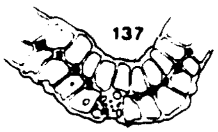
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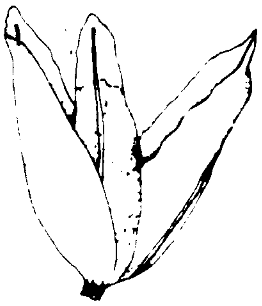
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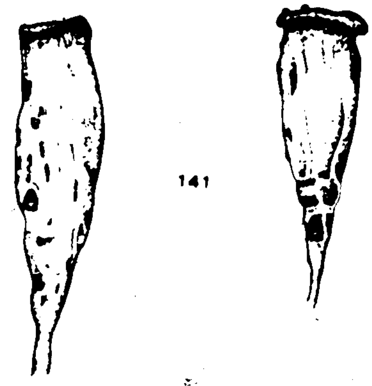
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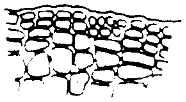
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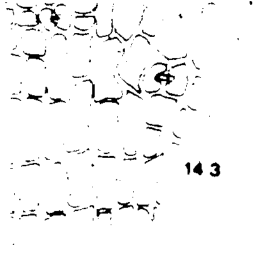
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Fig. 146. Distribution of *L. octoblepharioides.*

● Subspecies *octoblepharioides.*

◐ Subspecies *meijerii.*

⊖ Subspecies *whittieri.*

WORLD, HOMOLOSINE

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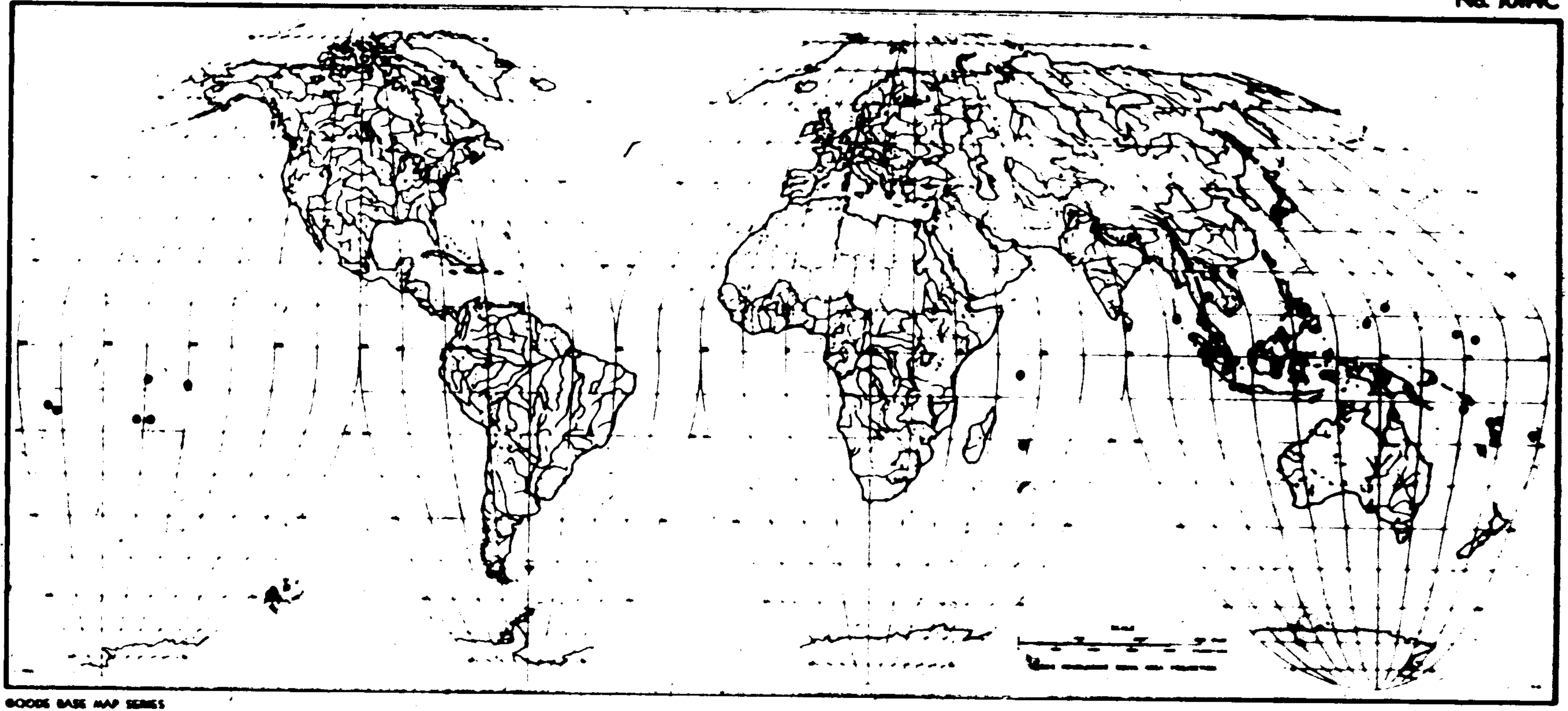


GOODE BASE MAP SERIES

Leucophanes angustifolium Ren. et Card.

(Figs. 17, 27, 41, 70, 71, 147-173)

Rev. de Bot. 9:395.1891. Type: "Hab. Bourbon. Leg. Rev. Rodriguez". (Lectotype: "Tronc pourris Bourbon. Rodriguez. 74c", PC-Ren!; Isotype: PC-Card, (2 specimens)!, S-ex Ren!).

Leucophanes denticuspis C. Muell. ex Dus., K. Svensk. Vet. Ak. Handl. 28(3): 16. a-b. Fig. 43. 1896. Type: "Habitat in Camerunia in truncis arborum, ubi prope Basse pagum m. Octobri a. 1890. Collecti Dusén". (Lectotype: "Ad Basse pagum Camerunia a P. Dusén, truncis arborum 29/x/1890." S-Dusén! Isotype: S!, M!).

Leucophanes massartii Ren. & Card., Rev. Bryol. 23: 99. 1896. Type: Java. "Forêt de Tjibodas; sterile (No. 1545). Leg. Massarti". (Lectotype: "Java: Forêt de Tjibodas. Leg. Massarti, 1895. No. 1545", PC-Card!; Isotype: PC-ex Ren!).

Leucophanes prasiophyllum Besch., Bull. Soc. Bot. France 45: 56. 1898. Types: "Tahiti. 4e herbor., No. 216; 8e herbor., No. 217. Leg. J. Nadeaud". (Lectotype: not selected; Isotype: "Mousses de Tahiti. Coll. No. 1. 216. *Leucophanes prasiophyllum* Besch. RRR. Tahiti. Leg. Dr. Nadeaud", S-ex Roth!; Syntype: not seen).

Leucophanes tahiticum Besch., Bull. Soc. Bot. France 45: 57. 1898. Types: "Tahiti. 2e herbor., No. 218; 3e herbor., No. 219 bis. Leg. J. Nadeaud". (Lectotype: "Nadeaud No. 219", BM-Besch!; Isotype: S!; Syntype: not seen).

Leucophanes mayottense Card., Bull. Herb. Boiss. ser. 2, 4: 113. 1904. Type: "Comores. Mayotte, Mont Sapéré (Marie; herb. Bescherelle, sub nom. *L. hildebrandtii* C. M.)".

(Holotype: PC!; Isotypes: H-Broth!, M-ex Corr!, NY-Mitt!, S-H. Moll!).

NOMENCLATURAL NOTES. There are three specimens from La Réunion (Bourbon) in PC. Two are from Cardot's herbarium and one from Renauld's. Two of the specimens have a handwritten (presumably Renauld's) number "74c", whereas the third one is not numbered. The selected lectotype has a hand-written label that reads on one side: "Tronc pourris", on the other side, "coussinets lacher, non bombes", one of the isotypes has a label that reads: "ad truncos putredos". The other isotype has only the locality, "Bourbon". Despite these differences in labelling, the three specimens appear to be part of a single collection and are treated as such in the lectotypification.

No potential type material of *L. prasiophyllum* was present among the types from BM. There is a specimen at S which corresponds to the protologue's locality and number. It is here considered a duplicate of the potential type, thus an isotype.

DISTINGUISHING FEATURES. *Leucophanes angustifolium* is characterized by loosely to densely foliose plants, with erect to curved leaves, costa percurrent to short excurrent, and slightly dentate on abaxial surface at apex. The leaves are long lanceolate, acuminate to rounded obtuse, erect to ± curved, plane at apex, keeled below; margins strong, serrate in upper third to half the length of the leaf, faintly serrate to smooth below; hyaline lamina, occupying the lower 1/6-1/3 of leaves; transverse section of leaf with a central to subcentral layer of chlorophyllous cells surrounded, on each side, by one or more layers of porose hyaline cells. These layers formed by irregular occurrence of transverse walls in the hyalocysts. Costal area naked at base or covered by a layer of abaxial hyalocysts; apical portion of costa enclosed by hyaline cells; in transverse section with 1-7 layers of abaxial stereids and 1-4 on adaxial side (stereids, at base, reaching both surfaces with no cover of hyaline cells).

L. angustifolium resembles *L. octoblepharioides* in the elongated narrow leaves, their narrow insertion, and their loose overlapping nature. *Leucophanes angustifolium*, though, has longer and narrower leaves, with a thicker costa and, in transverse section, the abaxial and adaxial layers of hyalocysts are multistratose. Renauld & Cardot (1891) pointed out the differences with *L. rodriguezii*: "Differe du *L. rodriguezii* C. Müll. de Bourbon par ses touffes lâches non bombées, ses tiges plus courtes, ses feuilles *étroite* finement acuminées aigues, à nervure *excurrente*, distinctement dentées dans la moitié supérieure et par le margo relativement plus large". In 1895, Renauld compared *L. angustifolium* with *L. hildebrandtii*: "Cette espèce se distingue aisément a premiere vue des *L. rodriguezii* C. Müll. et *Hildebrandtii* C. Mull. par ses feuilles plus allongées (5-7 mill., au lieu de 3 1/2 a 5 mil.), très aigues au sommet, et á marge denticulé". It can be added that *L. angustifolium* does not have the wide pores (more than 5 um in diameter) nor the erose, sharply spinose apex that characterize *L. hildebrandtii*.

DESCRIPTION. *Plants* to 3 cm tall, robust, densely foliate in compact turfs. *Stem* orange-brown, in transverse section 115.0-150.0 um in diameter, irregularly triangular to ± round with central area of large medullary cells surrounded by a layer of small cortical cells. *Leaves* (3.7)4.9-8.7(10.0) mm long, 0.4-0.7 mm wide, erect to curve above midleaf, loose to ± closely overlapping when dry; erect spreading to curve spreading when moist; long lanceolate, acuminate, from a narrow ovate base, keeled to 3/4 of its length, plane above; transverse section with a central layer of chlorocysts surrounded on each side by 1-2(3) layers of hyalocysts; *hyaline lamina* to 1/5-1/3(1/2) the length of leaf from base, uni- to bistratose, 5-9 cells wide; *margins* plane, serrate in upper third, teeth single or in pairs, in transverse section uni- to multistratose; *costa* percurrent, in surface view on adaxial side, concealed by multistratose nature of leaf, spinose on back at apex; in transverse section at base, costa located in groove formed by bulging hyaline cells or completely enclosed by them, composed of 1-2 layers of adaxial hyalocysts that cover 1-5 layers of adaxial stereids, two guide cells continuous with central chlorophyllous layer; 3-5(6) layers of abaxial stereids, exposed or covered by 1-2 layers of porose hyalocysts at base and at midleaf; *hyalocysts* in surface view on abaxial surface, at base, 20.0-37.5(54.0) um long, (12.5)15.0-22.5(27.1) um wide, rectangular to

Figs. 147-161. *L. angustifolium*. (Samoa, Schultze-Motel 3642, B; Seychelles, Erickson, S)

Fig. 147. Vegetative leaves. Scale = 1 mm.

Fig. 148. Apices. Scale = 75 um. (Samoa, Fleischer B1186, B; Japan, Iwatsuki 2892, EGR; Cameroon, Dusen, Type, S).

Fig. 149. Transverse section of stem. Scale = 100 um. (Samoa, Schultze-Motel 3375, L).

Figs. 150-152. Abaxial hyalocysts of leaf. (Ternate, Beccari 110, L).

Fig. 150. Base.

Fig. 151. Midleaf.

Fig. 152. Apex.

Figs. 153-159. Transverse sections of leaves. Scale = 100 um.

Fig. 153. At insertion. (Tahiti, Nadeaud 219, BM).

Fig. 154. Above 153.

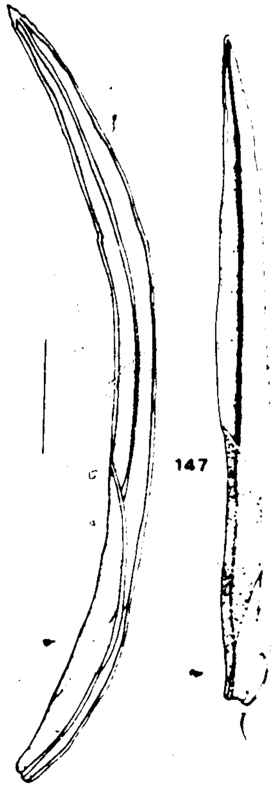
Fig. 155. Above 154.

Fig. 156-157. Base. (Fiji, Salazar 3723, ALTA, PMA).

Fig. 158. Apex. (Mayotte, Marie, M; Samoa, Schultze-Motel 3492, B; Java, Zippelius, L).

Fig. 159-160. Middle. (Nadeaud 216, S).

Fig. 161. Leaf-tip gemmae. (Java, J. Moller, L).



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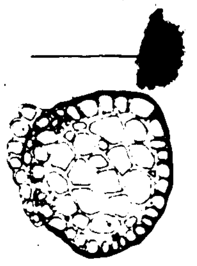

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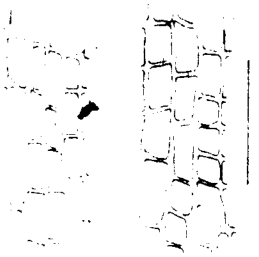

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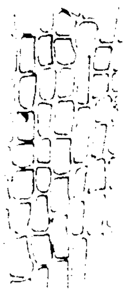

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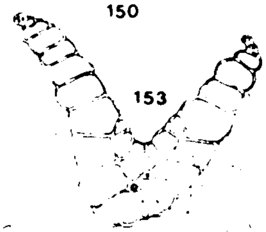

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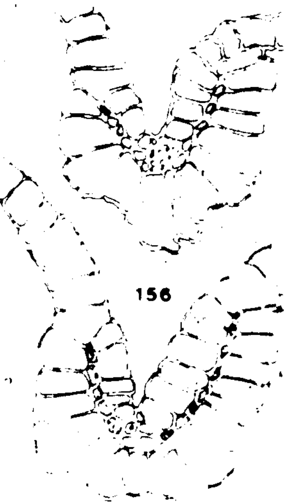

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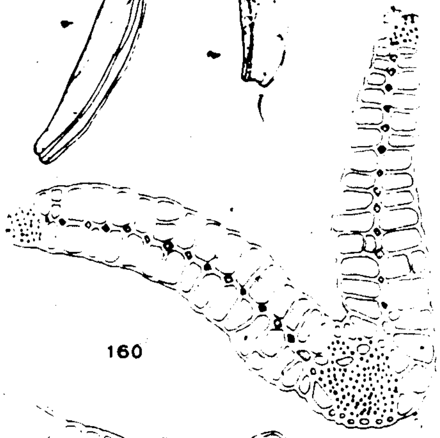

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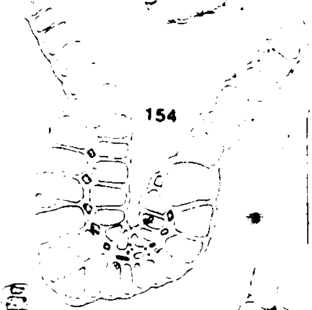

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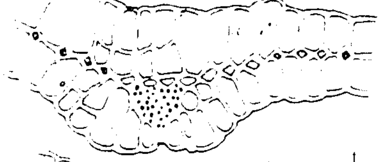

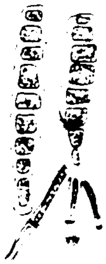

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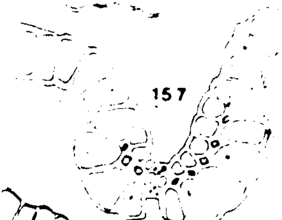

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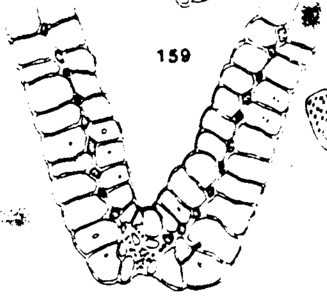

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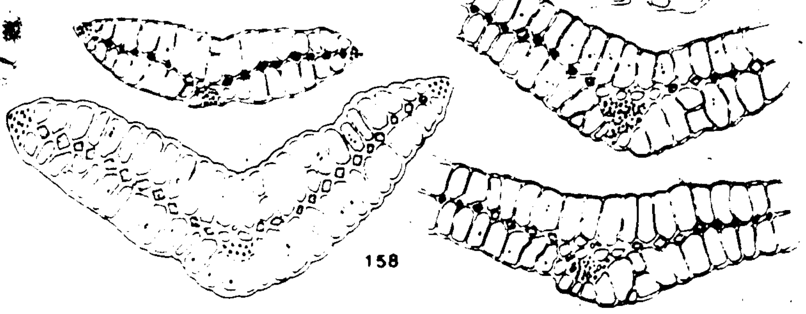

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Figs. 162-170. *L. angustifolium.*

Fig. 162. Perichaetial leaf. Scale = 0.5 um. (Ternate, Beccari 110, ALTA, PMA).

Fig. 163. Hyalocysts of perichaetial leaf. Scale = 50 um.

Fig. 164. Calyptra. Scale = 0.5 mm.

Fig. 165-170. Sporophyte. (Kuala Lumpur, Wood 2, BM).

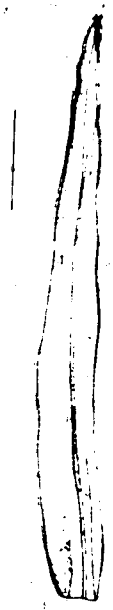
Fig. 165. Capsules. Scale = 0.5 mm.

Fig. 166. Transverse section of seta. Scale = 50 um.

Figs. 167-168. Exothecial cells. Scale = 100 um.

Figs. 169. Rim cells. Scale = 50 um.

Fig. 170. Stomates. Scale = 50 um.



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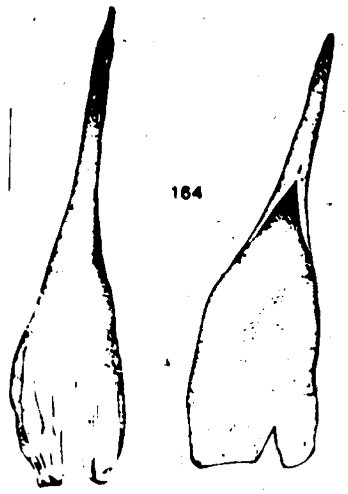

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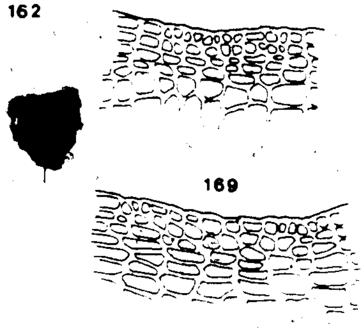

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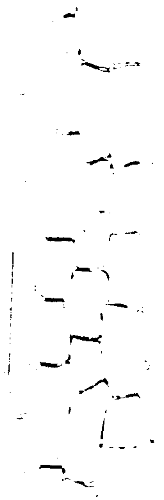

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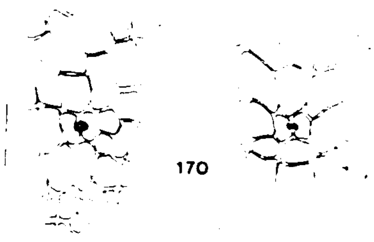

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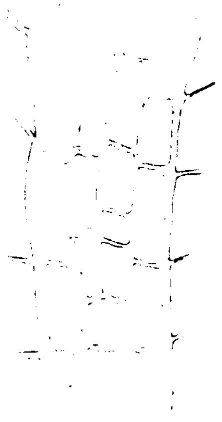

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Figs. 171-172. *L. angustifolium*. Peristome papillose-foveolate. Scale= 20 um. (New Guinea, Beccari 110, L).

Fig. 171. Outer surface of teeth.

Fig. 172. Lateral view of tooth.

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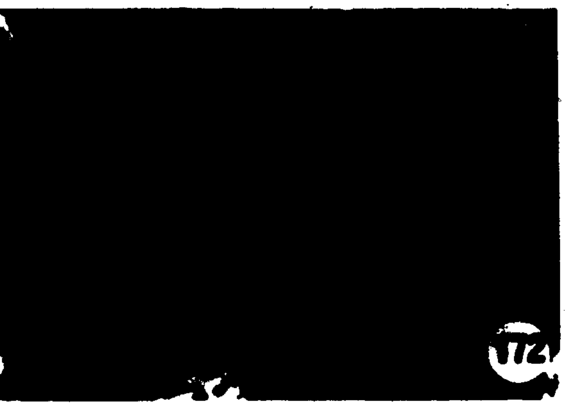

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quadrate to + hexagonal, bulging and wider on both sides of costa, longer at margins near insertion with few pores on surface walls; at midleaf, 20.0-41.5(56.8) um long, 10.0-25.8 um wide, rectangular to long or short hexagonal; at apex (7.5)12.5-17.5(25.8) um long, (4.3)7.5-12.5(17.5) um wide, oblong to rounded-quadrate. *Gemmae* oblong to clavate, composed of 6-9(10) cells, papillose, branched or unbranched at base. *Rhizoids* orange-red papillose.

Dioicous, female and male plants morphologically similar, though males tend to be more slender. *Perichaetial leaves* not differentiated. Archegonia in groups of 5 or more. *Perigonial leaves* differentiated, 0.9-1.7 mm long completely enclosing the antheridia, ovate from a broad overlapping base; antheridia terminal in groups of more than 5. *Calyptra* 2.5-2.7 mm in length, cucullate, red and papillose at apex, stramineous below. *Sporophyte* terminal, monosetous; *seta* 8.6-9.6 mm long, dark-orange to brown-red, sinistrorse, ± papillose at distal third, smooth below, in transverse section 75.0-112.0(125.0) um in diameter; *operculum*, 0.8-1.1 mm, long subulate rostrate, *capsule* 1.2 to 2.3 mm long, dark-red, darker at rim, erect to subinclined, cylindrical to oblong -cylindrical, gradually narrowing to seta through a short, papillose neck; *exothecial cells* (37.5) 50.0-95.0(100.0) um long, 17.5-22.5(27.5) um wide, rectangular to quadrate, in longitudinal rows, ± thin walled; *rim cells* 7.5-15.0 um long, 7.5-12.5 um wide ± hexagonal, in 4-5 horizontal layers; *stomata* superficial, 12-16 in number, restricted to neck of capsule, (12.5)20.0-25.0 um long; 20.0-25.0 um wide; *peristome teeth* 137.5-172.5 um long, yellow-orange, inserted under rim of capsule, strongly papillose on both plates, papillae capitate around central circular depressions. *Spores* 15.0-20.0 um in diameter, under SEM papillose on the distal face, nearly smooth on the proximal face.

HABITAT. *Leucophanes angustifolium* has been collected on rotten logs, on trees, and on rocks in moist forests from lowland to altitudes of ca. 2000 m. In Vanuatu and Fiji, *L. angustifolium* has been observed growing in lowland tropical rain forests on tree ferns, and dicotyledonous trees and shrubs.

This species has been observed in mixed collections associated with *L. octoblepharioides*, *L. glaucum* and *L. hildebrandtii*.

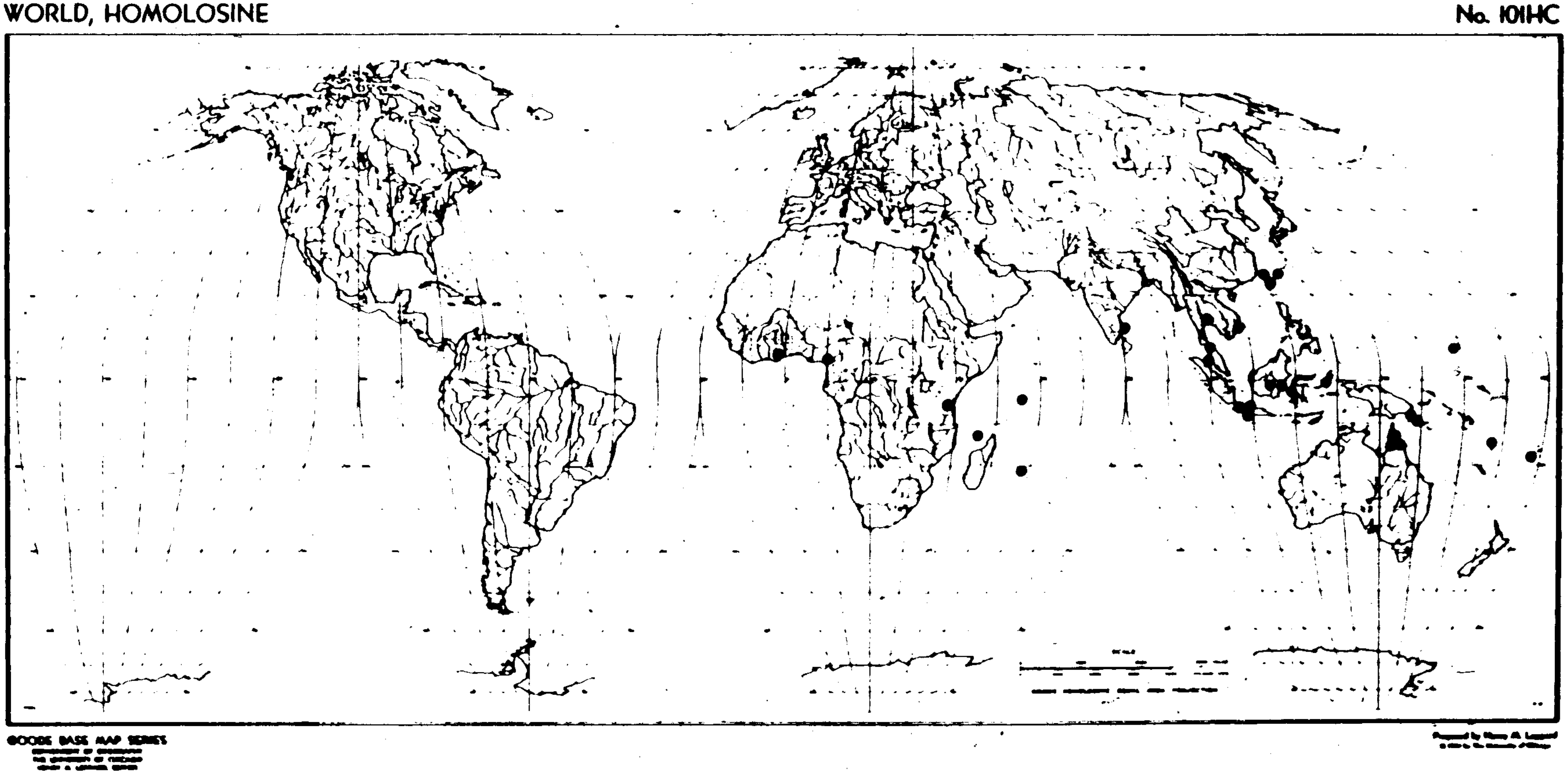
DISTRIBUTION. Australia; India; Japan (Ryukyu Islands); Taiwan; in S.E. Asia and the South Pacific in Malesia, Democratic Republic of Vietnam, Thailand, Society Islands (Tahiti), Samoa (Savaii, Upolu, Tutuila); Africa: Republic of Cameroon, Ghana, Republic of Tanzania, Comoro Islands (Mayotte), La Réunion, and Seychelles (Mahé).

PHYLOGENETIC RELATIONSHIPS. *Leucophanes angustifolium* is closely related to *L. octoblepharioides* in habit and leaf cell size. Leaves of *L. angustifolium* are longer and narrower (apotypies) than those of *L. octoblepharioides* and the pores are smaller in size (apotypy). In some populations, pores on transverse walls are few and slit-like. It is here considered that *L. angustifolium* is derived from a *L. octoblepharioides*-like ancestor, the multistratose condition (apotypy) of the leaf developing later in evolution.

VARIATIONAL PATTERNS. Variations in number of cells on each layer are observed in many specimens of *L. angustifolium*. Some leaves have mostly a single layer on each surface with scattered transverse walls at base and a more pronounced multistratose condition above middle. In others, the multistratose condition is found throughout the leaf giving it a thicker appearance.

There is also a trend related to the costal area. In some populations, the costal area is exposed at base and covered by hyalocysts at middle. Other populations have the costa covered at insertion, and above middle to apex (in here is included the former *L. tahiticum* Besch.). There are populations of intermediate forms with the costa covered to different degrees and also a variable multistratose condition. No formal taxonomic rank has been given to these modifications.

Fig. 173. Distribution of *L. angustifolium*.


WORLD, HOMOLOSINE
No. 101HC
GOODE BASE MAP SERIES

SPECIMENS EXAMINED. ALTA (4), B (20), BM (8), DUKE (1), EGR (4), FH (13), L (23), NY (7), PC (8), S (19).

Leucophanes milleri Salazar-Allen, *sp. nov.*

(Figs. 45-46, 174-195)

Holotype: "Palau. Forested Hills behind Cocoa Plantation Babelthuap, Ngatpang. Altitude 400-500 feet. Coll. H.A. Miller, No. 8106." MU!; Isotype: MU!. Paratypes: "Palau: Babelthuap, above Ngatpang, in forest. Alt. 600 feet. Coll. Lee S. Dutton, No. 63, MU!; "Palau: Forested hills behind cocoa plantation, Babelthuap, Ngatpang. Alt. 400-500 feet. Coll. H.A. Miller No. 8087, 8130, 8136, MU!; Palau: Summit of Island Eastern Koror. Alt. ca. 300 feet. Coll. H.A. Miller, No. 8266, MU!).

Plantae robustae dense et late caespitosae albo-virides (in sicco stramineae, sericeo-nitentes); caulis erectus ad 6 mm altus, foliatus; folia (4.5)5-8.5 mm longa et 0.5-0.8 mm lata, arcuata, in sicco arte imbricata, patentia ubi humida, lanceolata, acuminata, carinata ad basim, in sectione transversali stratum cellularum chlorophyllarum utrinque strato cellularum hyalocystarum circumdatum; margine recurvo ad basim, parum serrulato, cellulae hyalocystae usque 27.6-56.0 X 15.6-30.0 um ad basim folii et (16.6) 20.0-42.7 X 8.5-145.3 um ad apicem folii. Dioicum, folia perichaetialia cum lamina angusta-lanceolata, hyalina usque apicem. Archegonia numerosissima, plantae masculinae non visae. Sporogonia terminalia, seta 7.1-10.0 mm alta, sinistrorse, rubro-fusca; peristomii simplices, dorsaliter et ventraliter foveolati lanceolati; sporae 10.0-15.0(17.5) um.

DISTINGUISHING FEATURES: *Leucophanes milleri* is characterized by its robust, overlapping, foliose habit, with long abaxial hyalocysts; in transverse section, with one layer of hyaline cells on each surface of the chlorophyllous layer; sporophytes with a long capsule and seta (to 10 mm long), the peristome of narrow elongated teeth distinctly foveolate on both plates; spores short-baculate, the bacula-like processes ornamented with granular depositions and projecting distinctly from the spore surface.

DESCRIPTION. ***Plants*** robust to 6 cm tall, shiny, densely foliose. ***Stem*** orange-brown, branching single, in transverse section, rounded to irregularly triangular, 192.0-200.0 um in diameter with large medullary cells surrounded by one layer of cortical cells. ***Leaves*** (4.5)5.0-8.5 mm long, 0.5-0.8 mm wide, curve and closely overlapping when dry, slightly spreading when moist, lanceolate, keeled 3/4 of their length, plane above, in transverse section with a single layer of chlorophyllous cells surrounded, on each surface, by one layer of hyalocysts, ***hyaline lamina*** 1/7-1/5 the length of leaf, 8-10 cells wide, unistratose; ***margins*** recurved below, ± plane above, sharply serrate at apex, teeth single; with 1-9 rows of stereids, uni- to multistratose wider at insertion and with 2-3 orange-red, incrassate cells, ***costa*** percurrent, abaxially spinose in upper 1/4; in transverse section with 1-2 layers of adaxial stereids, 2 guide cells continuous with the central chlorophyllous layer, 4-5 layers of abaxial stereids, covered, at apex, by a layer of hyaline cells; ***hyalocysts*** in surface view, on abaxial side, at base, 27.6-56.0(68.8) um long, 15.6-30.0 um wide, longer and narrower near margins, quadrate to rectangular; at middle 22.5-55.7(63.0) um long, 10.0-20.5(24.0) um wide, oblong to irregularly long hexagonal; at apex, (16.6)20.0-42.7 um long, 8.5-14.3 um wide, rectangular to oblong or irregularly hexagonal, some with round bulging end walls. ***Gemmae*** clavate to elliptical, tapering to insertion, papillose, variable in number of cells. ***Rhizoids*** orange-red, papillose.

Dioicous, ***perichaetial leaves*** two, the innermost small, narrow-lanceolate to 3.5 mm long, with a hyaline area that extends to near apex, a second leaf longer but with a broad hyaline lamina; archegonia in groups of more than ten. Male plants not seen. ***Calyptra*** 1.9-2.5 mm long, cucullate, orange-red at apex, light yellow below. ***Sporophyte*** terminal, monosetous,

Figs. 174-186 *L. milleri*.

Fig. 174. Vegetative leaves. Scale = 1.5 mm. (Yaptown, Miller & Whittier 8106, Type, MU).

Fig. 175-177. Abaxial hyalocysts of leaf. Scale = 100 um (also for stem section). (Micronesia, Dutton 63, MU).

Fig. 175. Base.

Fig. 176. Midleaf.

Fig. 177. Apex. (Ibid. 175-177 & Type)

Fig. 178. Transverse section of stem. (Ibid. 175-177).

Figs. 179-181 Transverse section of leaves. Scale = 100 um.

Fig. 179. Base. (Ibid. 175-177).

Fig. 180. Midleaf. (Type).

Fig. 181. Apex. (Ibid. 177).

Fig. 182. Perichaetial leaf. Scale = 0.5 mm. (Ibid. 175-177).

Fig. 183. Hyalocysts of perichaetial leaf. Scale = 50 um.

Fig. 184. Calyptra. Scale = 0.8 mm. (Type).

Figs. 185-186. Sporophyte. (Type).

Fig. 185. Urn. Scale = 0.8 mm.

Fig. 186. Exothecial cells. [illegible] = 100 um.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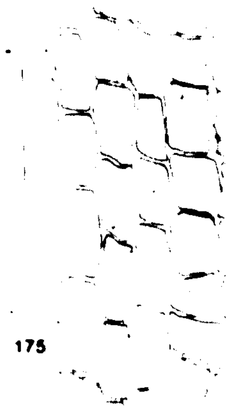
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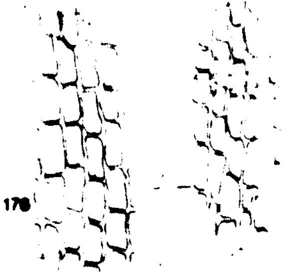
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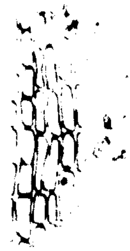
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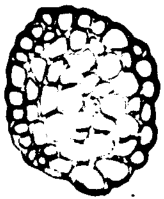
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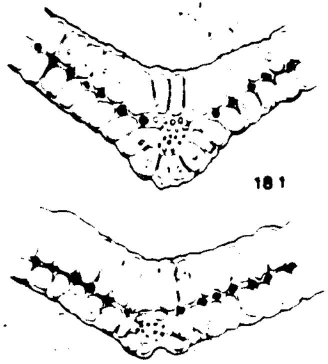
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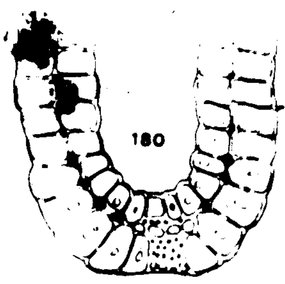
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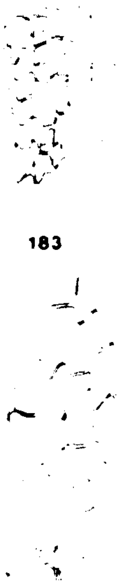
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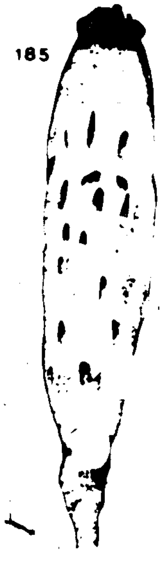
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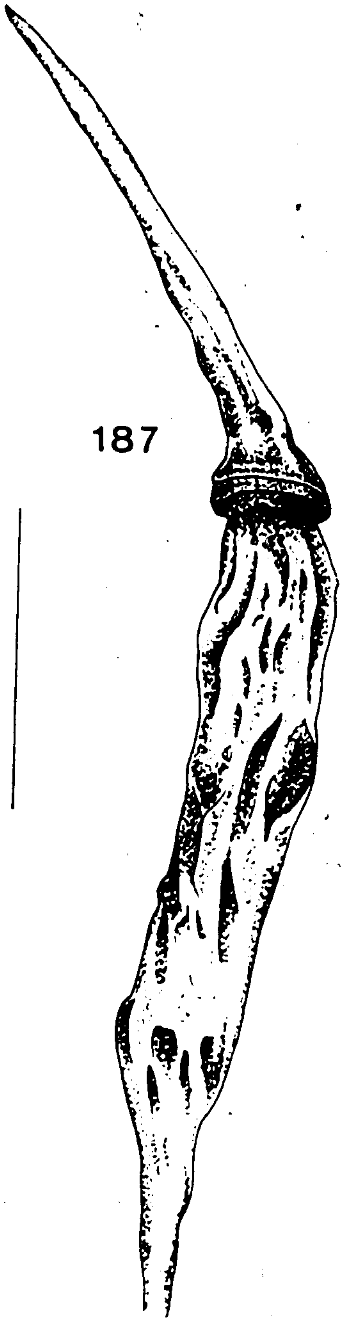
Figs. 187-190. *L. milleri.* (Yaptown, Miller & Whittier 8106, Type, MU).

Fig. 187. Capsule. Scale = 0.8 mm.

Fig. 188. Rim cells. Scale = 50 um.

Fig. 189. Stomates. Scale = 50 um.

Fig. 190. Transverse section of seta. Scale = 50 um.



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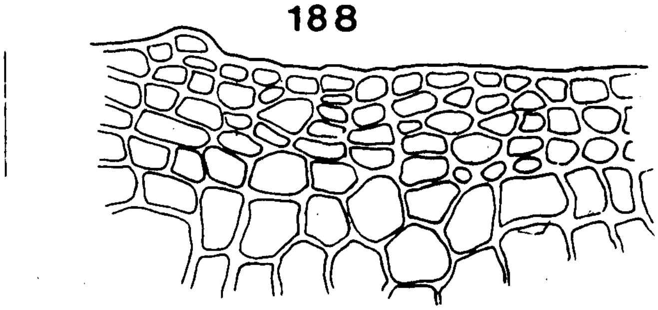

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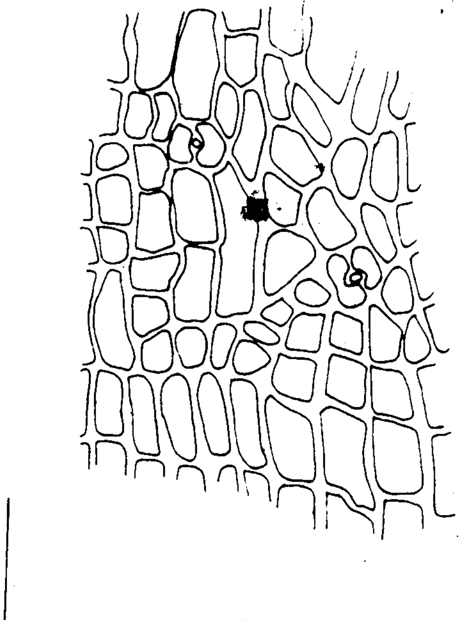

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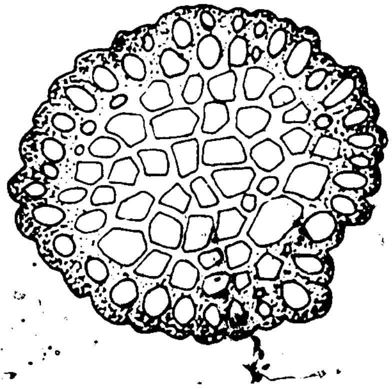

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Figs. 191-194. *L. milleri.* Peristome papillose-foveolate. (Micronesia, Dutton 63, Type, MU).

Figs. 191-192. Peristome, outer surface. Scale = 50 um.

Figs. 193-194. Detail of peristome teeth. Scale = 20 um.


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seta 7.1-10 mm long, red to brown-red, sinistrorse, papillose at distal end; *operculum* 0.7-0.9 mm long, subulate rostrate; *capsule* 2.0-2.6 mm long, orange-red to brown-red, erect to inclined, gradually narrowing to seta when dry; *exothecial cells* (19.3)41.2-89.2(99.0) um long, 14.8-35.3(44.5) um wide; *rim cells* 9.3-24.1 um long, 4.8-8.0(12.8) um wide, in 4-5 narrow, horizontal rows; *stomata* 15-27.5 um long, 22.5-25.0 um wide, 18-20 in number; *peristome* with a prostome 2-3 cells high, the teeth 185.0-190.0 um long, orange-red, inserted, foveolate papillose on both plates, papillae clavate, projecting from the margins, trabeculae clearly distinguished on both plates. *Spores* 10.0-15.0(17.5) um in diameter, spherical to irregularly triangular, paraisopolar, papillose-baculate, under SEM, papillae ornamented with granular depositions, and projecting from surface of spores.

HABITAT. This species has been collected on angiosperm trees in the forested areas of Belau (Palau Islands).

DISTRIBUTION. This species appears to be endemic to Micronesia. It is known only from Belau (Palau Islands).

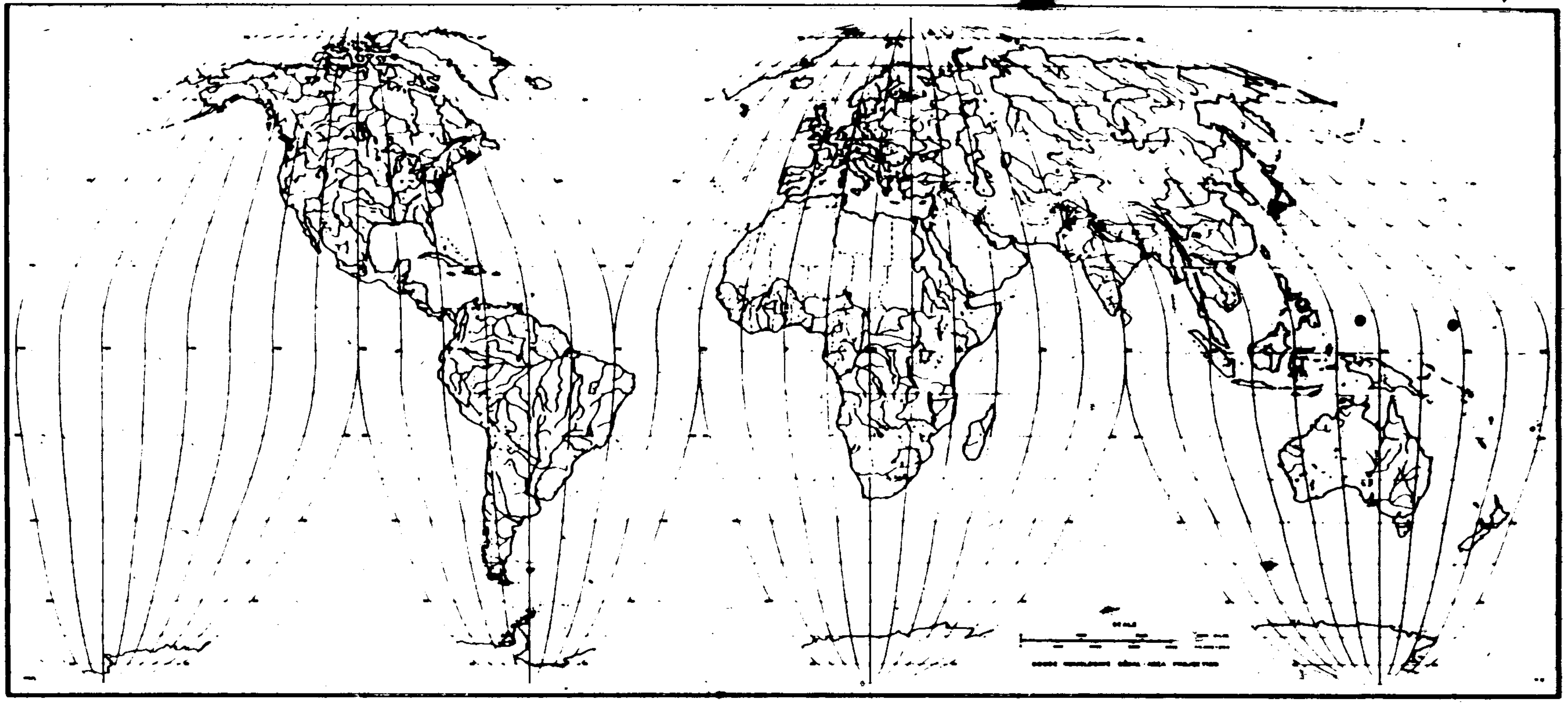
PHYLOGENETIC RELATIONSHIPS. *Leucophanes milleri* is closely related to *L. octoblepharioides*. It shares with it the symplesiotypies of the leaves, in transverse section, composed of a single layer of hyalocysts on each side of the central chlorophyllous layer, a costa with two guide cells and the strongly foveolate peristome teeth. It differs from *L. octoblepharioides* in its robust habit, shiny appearance, densely foliose stem with the leaves closely overlapping and in spore ornamentation.

SPECIMENS EXAMINED. MU (9).

Fig. 195. Distribution of *L. milleri*.

WORLD, HOMOLOSINE

No. 101HC



GOODE BASE MAP SERIES
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Leucophanes seychellarum Besch.

(Figs. 56-57, 78-79, 196-217)

Ann. Sc. Nat. Bot. ser 6, 9:337. 1880. Type: "Iles Seychelles: Mahé, G. de L'Isle." (Lectotype: BM-Besch!, Isotype: BM!).

NOMENCLATURAL NOTE. There are two specimens at BM that correspond to the description given in the protologue. One specimen from Bescherelle's herbarium is pasted on the same card with two other specimens from a collection by Verville. The second specimen appears in a separate herbarium sheet with a handwritten note: "Bescherelle's handwriting? Type?". The first specimen has been selected as the Lectotype and the second appears to be a duplicate of the type specimen, and so, has been considered an Isotype.

DISTINGUISHING FEATURES. *Leucophanes seychellarum* is characterized by its long narrow stiff leaves, erect when dry, slightly spreading when moist, with sharp to minutely dentate margins, the prominent and sharply serrate costa and its bulging hyalocysts with strongly concave surface walls; the dorsal hyalocysts, in transverse section at apex, are so inflated that the chlorocysts layer is closer to the abaxial surface.

DESCRIPTION. *Plants* to 2 cm tall, in compact turfs, whitish-green to brown-green. *Stem* dark orange to red-brown, 100.0-112.5 um in diameter, in transverse section ± triangular to circular with large medullary cells surrounded by a layer of small ± thick-walled cortical cells, branching sympodial. *Leaves* 2.2-5.5 mm long, 0.1-0.5 mm wide, stiff, erect-patent to ± curved sideways, when dry, slightly spreading when moist, narrowly lanceolate, acuminate, keeled through most of their length, plane above, in transverse section, with central layer of chlorophyllous cells surrounded, on each surface, by one layer of inflated hyalocysts; *hyaline*

Figs. 196-210. ***Leucophanes seychellarum.***

Fig. 196. Vegetative leaves. Scale = 1 mm. (Seychelles, Waterfall 1910, BM).

Figs. 197-198. Abaxial hyalocysts of leaf. Scale = 100 um.

Fig. 197. Base. (Ibid. 196 & G. de L'Isle, Type, BM).

Fig. 198. Midleaf. (Type).

Fig. 199. Apex. (Ibid. 197).

Fig. 200. Transverse section of stem. Scale = 50 um. (Seychelles, Waterfall 1910, BM).

Figs. 201-205. Transverse sections of leaf. Scale = 100 um.

Fig. 201. Base. (Ibid. 197).

Fig. 202. Midleaf. (Ibid. 197).

Fig. 203. Apex. (Ibid. 197).

Fig. 204. Perichaetial leaf. Scale = 0.5 mm. (Seychelles, Horne 696, BM).

Fig. 205. Hyalocysts of perichaetial leaf. Scale = 100 um.

Figs. 206-210. Sporophyte. (Ibid. 204).

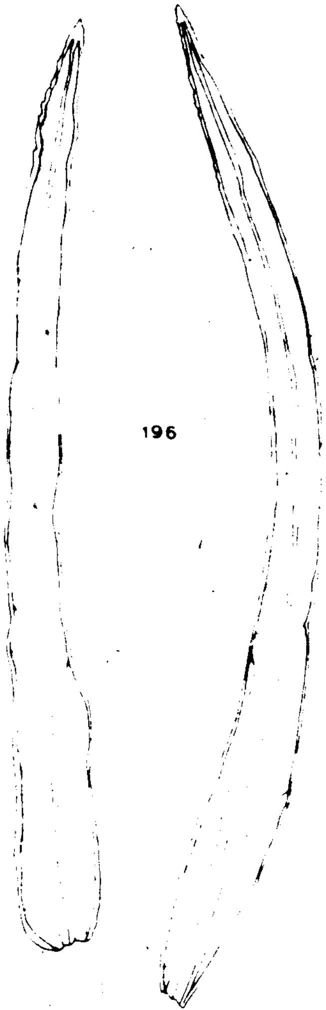
Fig. 206. Urn. Scale = 0.5 mm.

Fig. 207. Exothecial cells. Scale = 50 um.

Fig. 208. Stomates. Scale = 50 um.

Fig. 209. Transverse section of seta. Scale = 50 um.

Fig. 210. Rim cells. Scale = 50 um.



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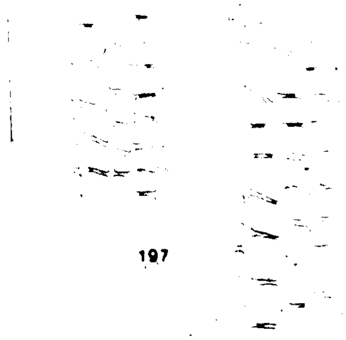

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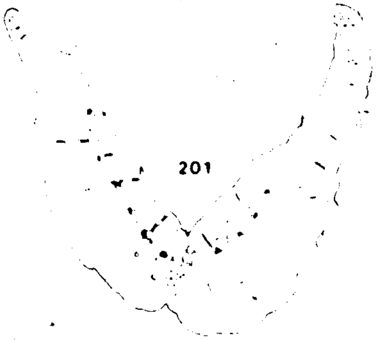

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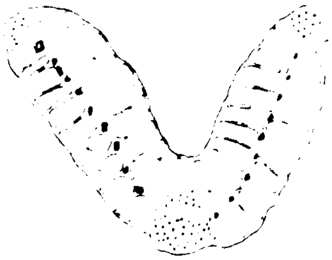

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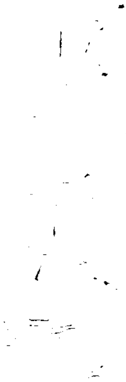

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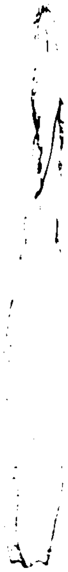

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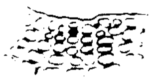

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Figs. 211-216. *L. seychellarum* (Seychelles, Horne 696, BM).

Fig. 211. Pores on abaxial hyalocysts at apex. Scale = 50 um.

Fig. 212. Peristome. Scale = 50 um.

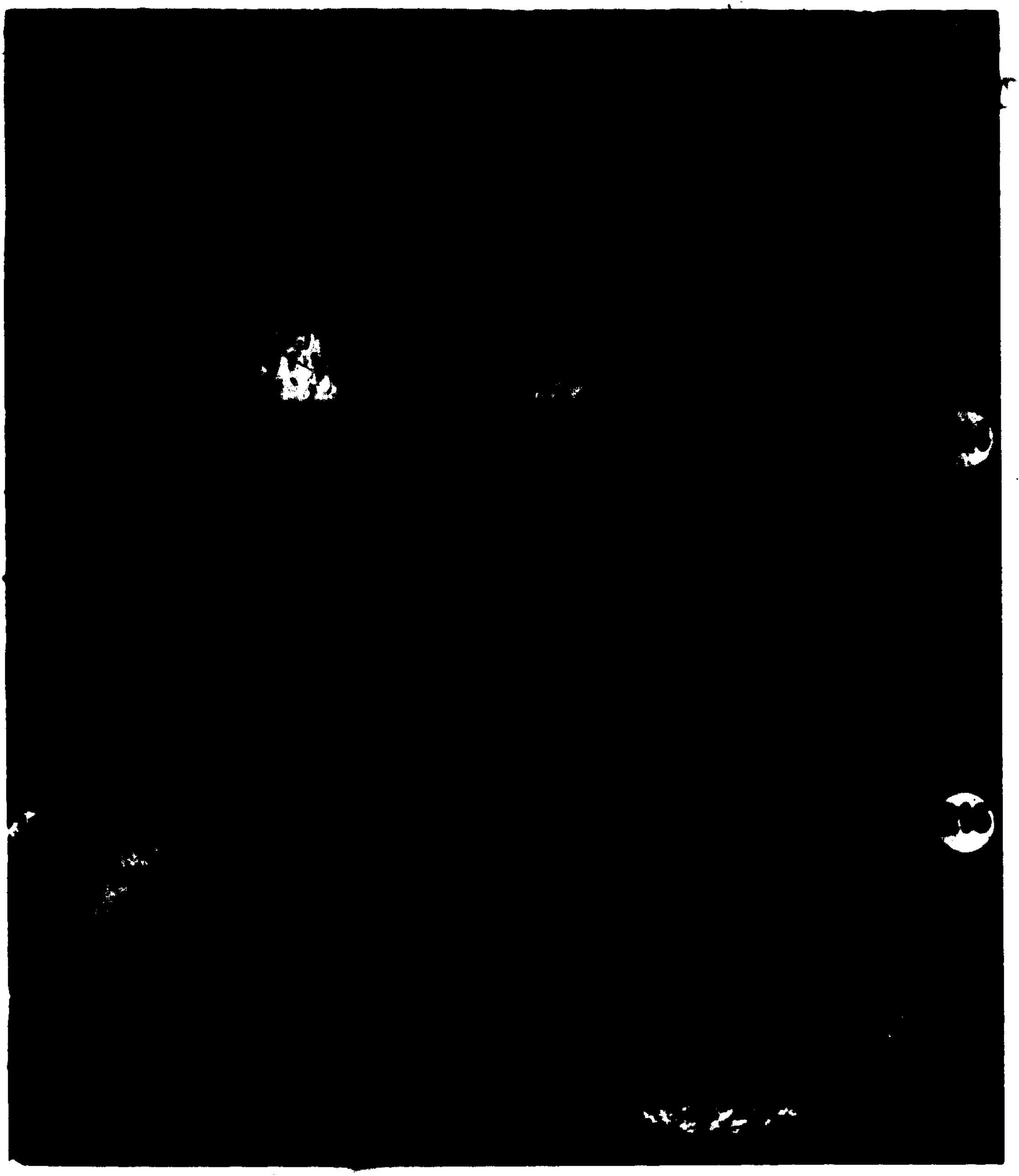
Fig. 213. Outer surface of peristome. Scale = 20 um.

Fig. 214. Inner surface of peristome. Scale = 20 um.

Fig. 215-216. Spore ornamentation. Scale = 4 um.

Fig. 215. Equatorial face.

Fig. 216. Proximal face.



lamina to 1/3-1/2 the length of leaf from base, unistratose, 5-8 cells wide; *margins* recurved from shoulders to base, plane above with 3-5 rows of stereids, uni- to multistratose, minute to sharply serrate to shoulder, particularly female plants, teeth single; *costa* strong, percurrent, abaxially spinose at apex, the teeth in rows, in transverse section with one layer of hyaline cells, 1-2 layers of adaxial stereids, two guide cells and 2-6 layers of abaxial stereids; *hyalocysts* in surface view, on abaxial side, at base (22.5)30.0-35.0(70) um long, 12.5-27.5 um wide rectangular to quadrate; at midleaf, (17.5) 25.0-50.0 um long, (10) 12.5-20.0 um wide, rectangular at apex, (15.0) 17.5-37.5 (42.5) um long, 10.0-12.5 um wide, rectangular to quadrate; hyalocysts with few pores on surface walls at base. *Gemmae* fusiform to clavate, papillose, variable in number of cells, tapering to base. *Rhizoids* orange-red, warty-papillose.

Dioicous, female gametophores with strongly dentate leaves otherwise similar to male gametophores, *perichaetial leaves* to 2.8 mm long with a lamina that extends to near apex; archegonia in groups of 5 to more than 5 per perichaetium. *Perigonial leaves* two, oval with a broad sheathing base covering the antheridia, these in groups of 10 or more than 10; adjacent vegetative leaves shorter and with a hyaline lamina that extends to 3/4 the length of leaf from base. *Calyptra* 1.7 mm long (one measurement only), cucullate, red and papillose at apex, stramineous below. *Sporophyte* terminal, monosetous; *seta* 4.4-6.0 mm long, brown-red, sinistrorse, smooth; *operculum* subulate-rostrate; *urn* 0.9-1.2 mm long, cylindrical, to oblong-elliptical, tapering to seta by a short neck, darker at rim and at insertion, erect; *exothecial cells* [illegible]5-55.0(62.5) um long, 12.5-22.5 um wide, rectangular to oblong hexagonal, to quadrate, thin-walled; *rim cells* 12.5-25.0 um long, 6.3-10.0 um wide, short-rectangular to quadrate, thin-walled, in 3-4 horizontal rows; *stomata* superficial in lower portion of capsule and at neck, 17.0-25.0 um long, 25.0-32.5 um wide, 14-16 in number; *peristome teeth* orange-red, dorsal plates smooth to slightly papillose, ventral plates papillose, inner and outer plates of equal thickness. *Spores* (10) 12.5-15.0 um in diameter, oval to spherical, papillose, under SEM surface ornamented with irregular granular depositions.

HABITAT. This species has been reported as a corticolous epiphyte, particularly in the inland forests of Mahé. Although some collections appear to be from higher elevations ("Morne Seychellois, Congo Rouge", Norkett s.n. 10 Oct. 1973) no altitudinal data is given on the labels.

DISTRIBUTION. All the specimens examined are from the island of Mahé. It is considered that this species is endemic to the Seychelles.

PHYLOGENETIC RELATIONSHIPS. Structurally, *L. seychellarum* is markedly similar to *L. octoblepharioides* and *L. angustifolium*. The leaves in their dry habit superficially resemble those of *L. hildebrandtii* but unlike it, the leaf margins are strongly serrate and the apex is not spinose-erose. Size and shape of hyalocysts and transverse section of the leaves also resemble those of *L. serratulum*.

SPECIMENS EXAMINED. BM (3), M (1), NY (2).

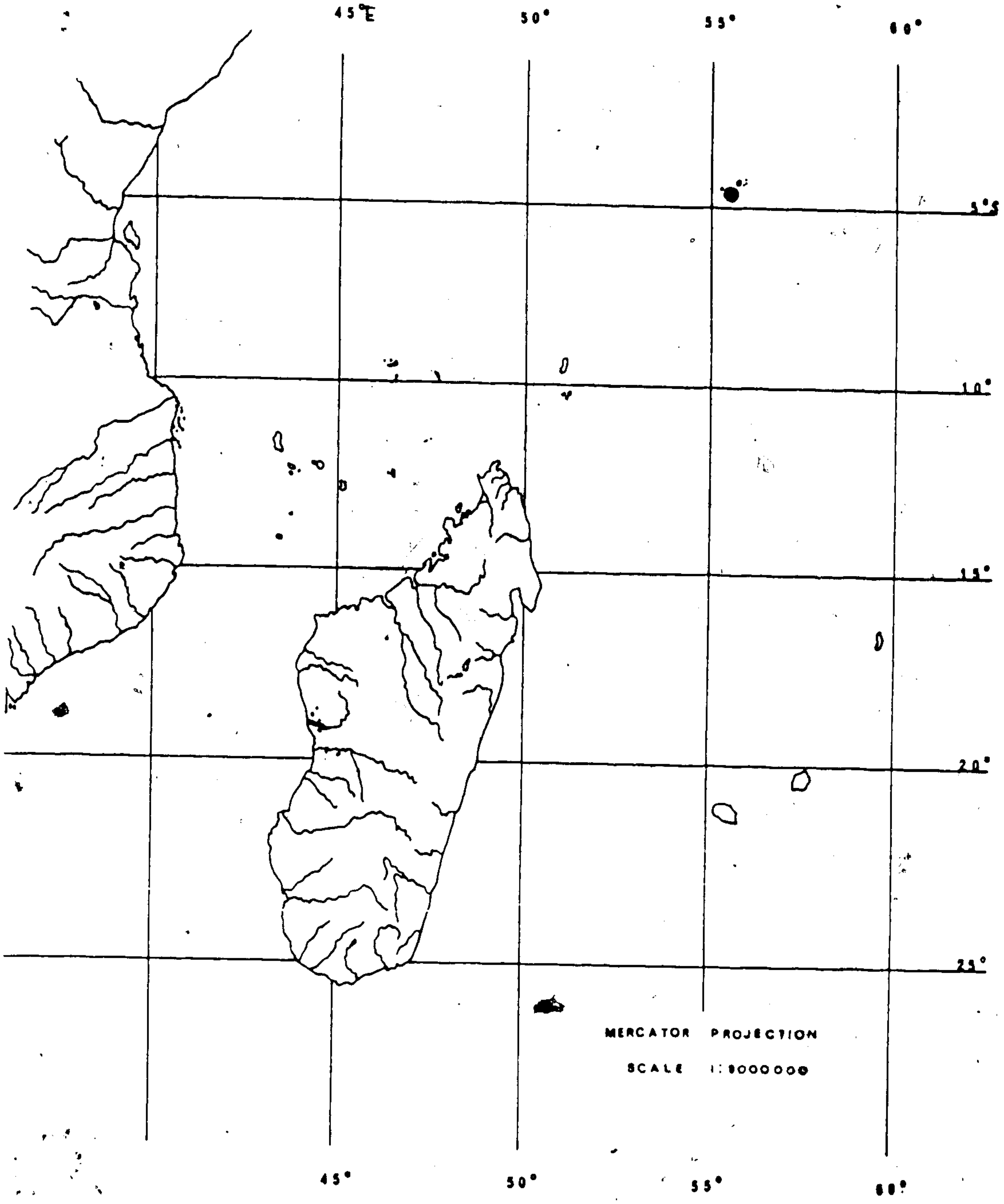
Leucophanes serratulum Fleisch.

(Figs. 80-81, 218-233)

Nov. Guinea 8(4): 741. 120. 1914. Type: "Niederländisch Neu-Guinea: Biwak Hollandia an der Nordküste au der Humboldt-Bay (deter. Gjellerup juli 1910). No. 27 ii. 27a." (Lectotype: "Holl.-Neu Guinea auf (illegible) Holz bei Hollandia. Leg. Gjellerup 27a", FH-Fleisch!; Syntype: "Niederl. Neu-Guinea. Hollandia. Leg. Gjellerup", FH-Fleisch!; Isosyntype: NY!, L!).

NOMENCLATURAL NOTE. There are three specimens in FH that correspond to the

Fig. 217. Distribution of *L. seychellarum*.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description of the protologue. Of these, two are labelled "27" and "27a". The specimen originally labelled "27a" has been corrected in red pencil to read "27" while one of the specimens labelled "27" has been relabelled "27a". The two specimens now under "27" appear to be part of the same collection. One of these specimens, the sample originally labelled "27a" was selected as the lectotype for the species, its duplicate as the isotype.

DISTINGUISHING FEATURES. *Leucophanes serratulum* is characterized by a robust, densely foliose habit; leaves, closely overlapping when dry, ± spreading when moist, distinctly falcate; margins sharply serrate at apex with single or double teeth; the calyptra covering capsule at dehiscence; its synoicous condition is unique within the genus.

This species resembles *L. candidum* in its robust, tall, densely foliose habit and also in the transverse section of the leaves having one layer of hyalocysts on each surface of the central chlorophyllous layer. Unlike *L. candidum* the margins in *L. serratulum* are strongly serrate, the costal area is prominent and spinose on back.

DESCRIPTION. *Plants* to 6 cm tall, in densely foliose turfs, whitish glossy when dry, whitish-green when moist. *Stem* reddish-brown, erect, flexuose, branches in pairs; transverse section of the stem, 237.5-275.0 um in diameter with large medullary cells with ± thick walls, surrounded by a cortex of small thick-walled cells. *Leaves*, 4.3-6.1 mm long, 0.7-0.9 mm wide, closely overlapping at base, spreading above middle when dry, distinctly falcate when moist, lanceolate to oblong lanceolate tapering to an acuminate to acute apex, keeled throughout, in transverse section with a single layer of rhomboid-shaped chlorocysts surrounded, on each side, by one layer of hyalocysts, these with rounded surface walls; *hyaline lamina* to 1/4-1/5 the length of leaf, 3-5 cells wide, *margins* revolute, in transverse section with 2-3 rows of stereids uni- or multistratose, narrower at base, strongly serrate with single or paired teeth; *costa* strong, excurrent, abaxially spinose throughout, teeth in rows, exposed on adaxial surface from base to apex, in transverse section composed of a single layer of adaxial hyalocysts, 2-5 layers

Figs. 218-230. *L. serratulum* (New Guinea, Gjellerup 27, 27a, Type, FH).

Fig. 218. Vegetative leaves. Scale = 1 mm.

Figs. 219-221. Abaxial hyalocysts. Scale = 100 um.

Fig. 219. Base.

Fig. 220. Midleaf.

Fig. 221. Apex.

Fig. 222. Transverse section of stem. Scale = 100 um.

Fig. 223-225. Transverse section of leaves. Scale = 100 um.

Fig. 223. Base.

Fig. 224. Apex.

Fig. 225. Midleaf.

Fig. 226. Calyptra. Scale = 0.5 mm.

Fig. 227-230. Sporophyte.

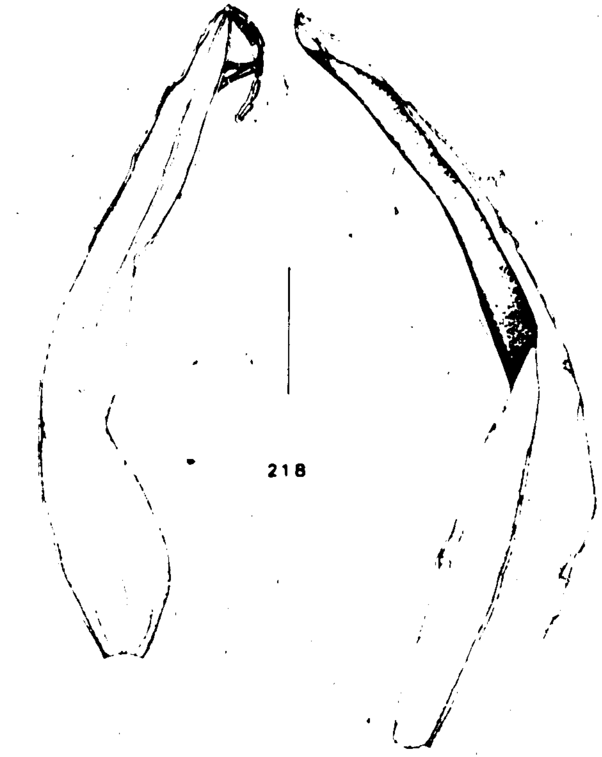
Fig. 227. Capsules. Scale = 0.5 mm.

Figs. 228-230, scale = 100 um.

Fig. 228. Rim cells.

Fig. 229. Exothecial cells.

Fig. 230. Stomates.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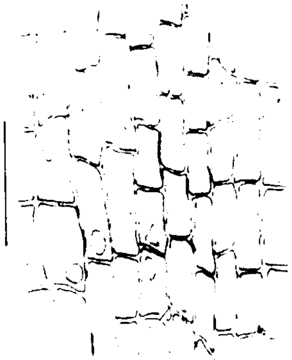
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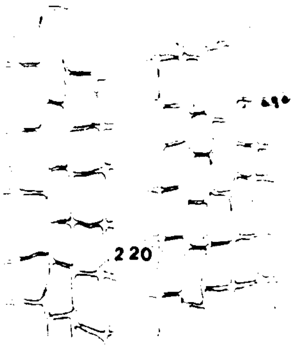
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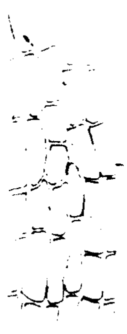
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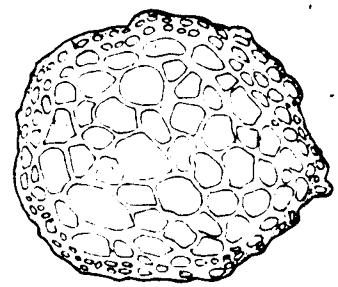
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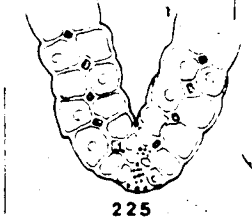
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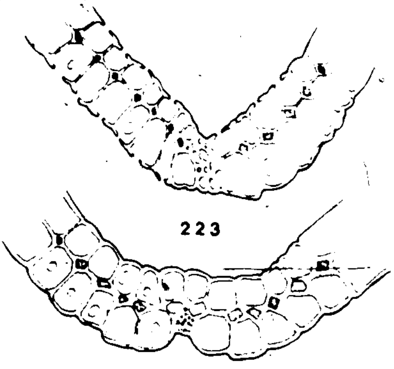
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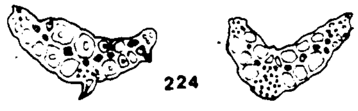
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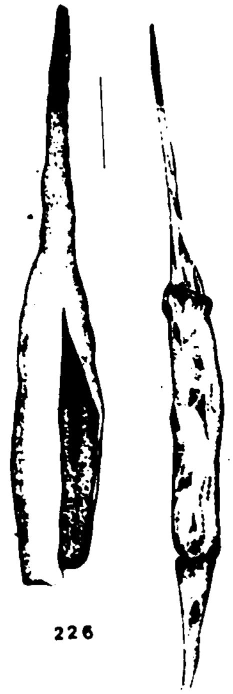
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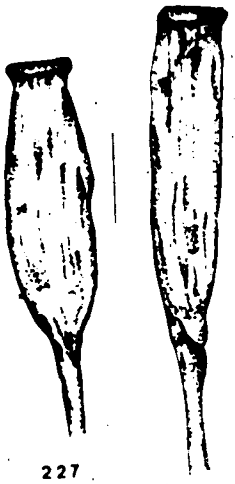
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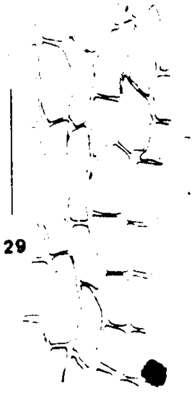
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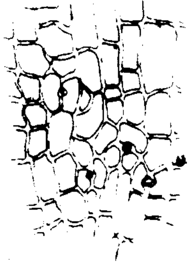
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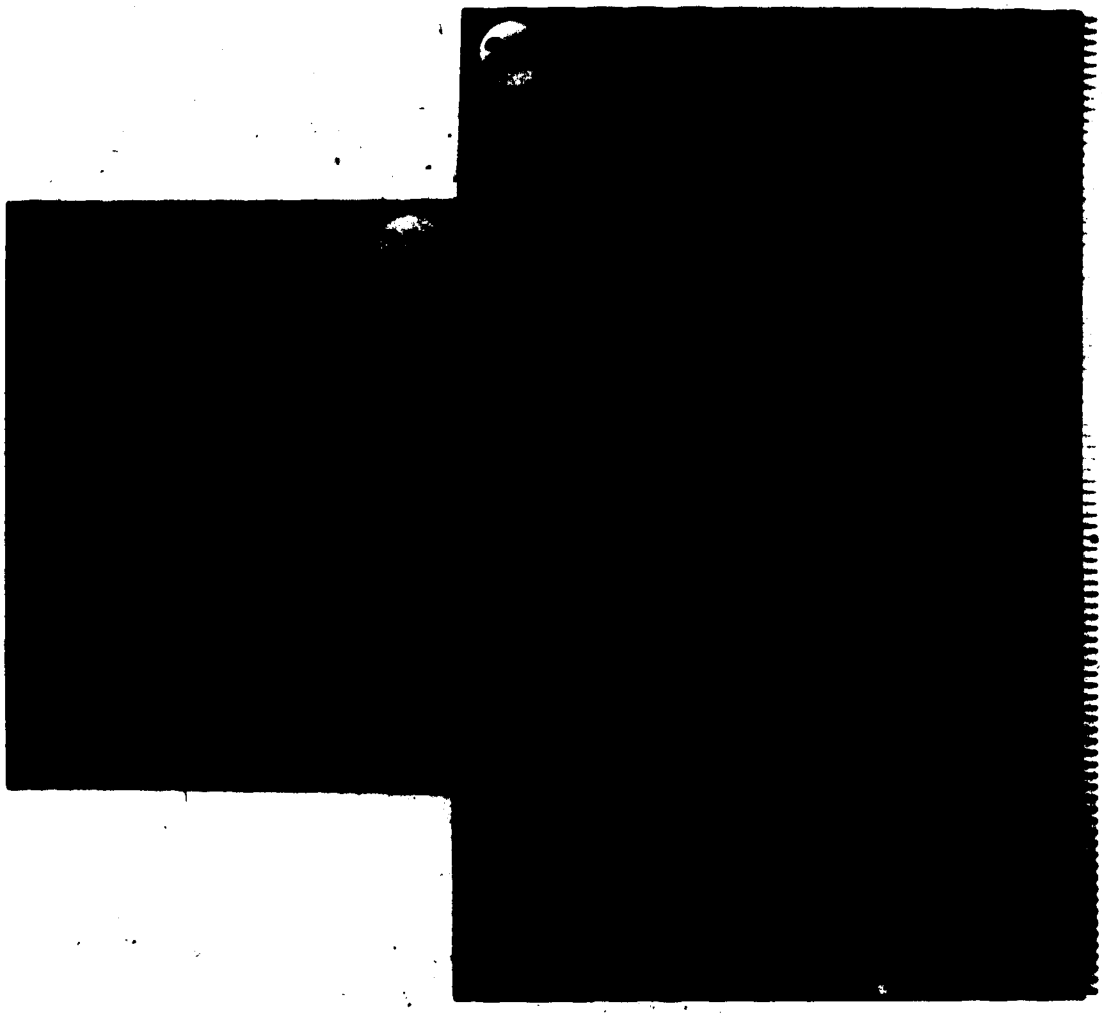
Figs. 231-232. *L. serratulum* (New Guinea, Gjellerup 27, 27a, Type, FH).

Fig. 231. Pores on apical hyalocysts, adaxial surface. Scale = 20 um.

Fig. 232. Habit.



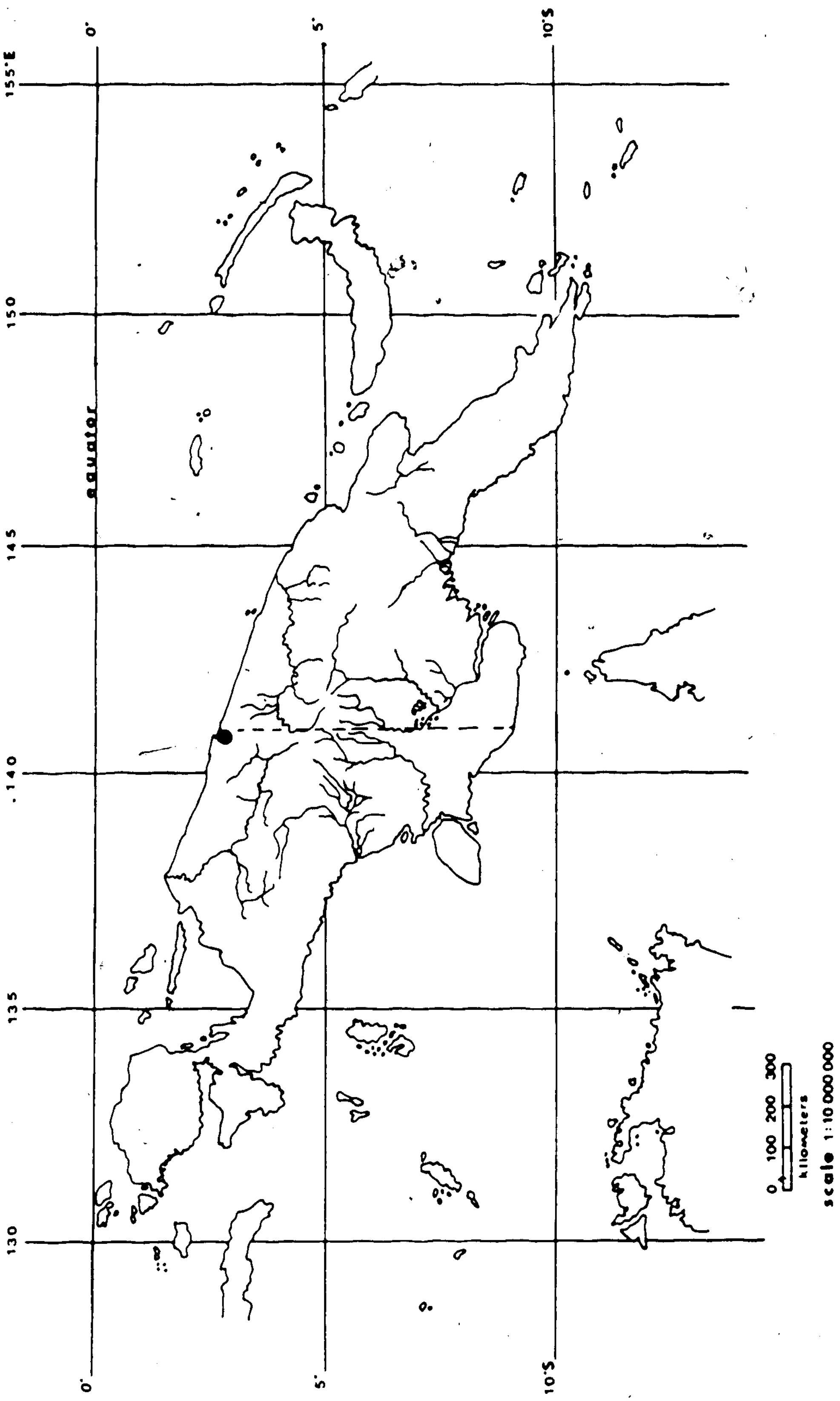
of adaxial stereids, 2 guide cells continuous with central chlorophyllous layer, and 2-5 layers of abaxial stereids, at base, near insertion, stereids forming a continuous band from abaxial to adaxial surfaces, or restricted to abaxial side of guide cells; *hyalocysts* in surface view, on abaxial side, at base, 25.0-55.0(62.5) um long, 20.0-25.0 um wide, rectangular to quadrate to hexagonal; at midleaf 25.0-37.5 um long, 12.5-17.5 um wide, rectangular to irregularly hexagonal; at apex, 22.4-44.2 um long, 8.8-20.5 um wide, oblong to quadrate; pores on surface walls single, few at base and apex. *Gemmae* not observed. *Rhizoids* red-brown, papillose.

Synoicous, gametangial leaves not differentiated, archegonia and antheridia numerous; *calyptra* cucullate, red and papillose at apex, stramineous below, remaining attached to capsule after dehiscence; *sporophyte* terminal, mono- or polysetous; *seta* 6.0-8.0 mm long, orange-red, sinistrorse, faintly papillose throughout; *operculum* 1.2-1.3 mm long, subulate rostrate; *capsule* 1.4-1.8 mm long, red to orange-red, darker at rim, oblong-cylindrical, smooth, erect to subinclined, gradually contracted to seta when moist, abruptly so when dry, irregularly constricted under mouth when old and dry; *exothecial cells* 25.0-67.5(82.5) um long, 15.0-25.0 um wide, rectangular, thin-walled, *rim cells* 10.0-25.0 um long, 5.0-15.0 um wide irregularly hexagonal to quadrate; *stomata* superficial in lower portion of urn, 22.5-27.5 um long, 22.5-30.0 um wide, 22-28 in number; *peristome teeth* 87.5-100.0 um long, orange-red to red-brown, both plates strongly papillose-foveolate with capitate papillae, inner plate slightly thicker than outer plate, prostome 2-4 cells high. *Spores* 12.5-20.0(30.0) um, oval to spherical, papillose under SEM verrucate to short-baculate with granular ornamentations over the verrucae or short baculae.

HABITAT. The only report is from the type specimen that was collected on dead wood.

DISTRIBUTION. This species is only known from the Type collection from Humboldt Bay, West Irian (New Guinea), Indonesia. It appears to be endemic to this area.

Fig. 233. Distribution of *L. serratulum*.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PHYLOGENETIC RELATIONSHIPS. Structurally, *L. serratulum* appears to be closely related to *L. milleri*, *L. octoblepharioides* and *L. seychellarum*. The hyalocysts are rectangular and with rectilinear walls; the leaves, in transverse section, have a single layer of hyalocysts on each side of the chlorophyllous layer and, the surface walls of the hyalocysts are strongly convex. The peristome with its plates strongly papillose-foveolate is closer to that of *L. octoblepharioides* and *L. milleri*.

SPECIMENS EXAMINED. FH (3), L (1), NY (1).

Leucophanes rodriguezii Ren. & Card.

(Figs. 26, 234-251)

Bull. Soc. R. Bot. Belg. 33(2): 113. 1895. Type: "Hab. Bourbon (Rodriguez).- (Renauld, *Musci masc. mad. exsicc.*, no. 110)." (Isotypes: S-*ex* Ren!, FH-*ex* Ren!, W-*ex* Ren!).

NOMENCLATURAL NOTE. The species was first named by C. Mueller in a letter. Renauld and Cardot (1895) validly published it giving a comparative description of the new species to that of *L. hildebrandtii*. Two specimens from Renauld's herbarium are in Farlow Herbarium (FH), another one is in Stockholm (S) and a fourth one in Wien (W). The sample in S has a hand-written label with the *exsiccata* number ("No. 110") mentioned in the protologue. Its habit also resembles *L. hildebrandtii* somewhat with which it was compared. The specimen in W also have the *exsiccata* number on the label although this is written in a different color of ink, perhaps added later. The other two specimens from FH do not have a number on their label but they appear to be duplicates of the samples in S and W. Since no potential type material from Paris (PC) has been examined, a lectotype cannot be selected. The four specimens studied are here considered duplicates of the potential type, hence isotypes.

DISTINGUISHING FEATURES. *Leucophanes rodriguezii* is characterized by its habit of compact turfs, erect leaves, stiff to flexuose when dry and moist, strongly keeled throughout, goitrous at base with wavy margins, recurved 2/3 to 3/4 of their length; costa strong and thick; leaves in transverse section, with a single layer of hyalocysts on each side of the central chlorophyllous layer, hyalocysts with small pores to 2.5 um in longest diameter; costa enclosed by hyaline cells above midleaf.

DESCRIPTION. *Plants* to 3 cm tall in dense compact turfs. *Stem* orange-red, erect, branching sympodial, in transverse section, 137.5-172.5 um in diameter, ± round with large thin-walled cortical cells surrounded by a layer of small epidermal cells. *Leaves* 3.6-4.7 mm long, 0.5-0.7 mm wide, erect, stiff looking and loosely overlapping when dry, slightly spreading when moist; lanceolate, acute to acuminate, keeled throughout to ± plane at apex (at times reflexed), transverse section with a central layer of chlorophyllous cells surrounded, on each surface by one layer of porose hyalocysts; *hyaline lamina* extending 1/4-1/5 the length of the leaf from base, uni- to bistratose, 2-4 cells wide; *margins* undulate, recurved below midleaf, plane above, serrate in upper third, teeth single; 3-4 orange-colored cells at base; *costa* strong, percurrent, spinose at apex with small teeth, in transverse section with one layer of adaxial hyalocysts, 1-2 layers of adaxial stereids, two large guide cells continuous with chlorophyllous layer, 2-4 layers of abaxial stereids (stereid layers extending to both surfaces at base). From midleaf to apex, costa is covered by one layer of abaxial hyalocysts; *hyalocysts* in surface view on abaxial side at base, 25.0-42.5 um long, 20.0-30.0 um wide, irregularly hexagonal to short rectangular to quadrate, at midleaf (12.5) 15.0-40.0 um long, 12.5-17.5 um wide; at apex 15.0-27.7 um long, 7.5-12.5 um wide; few hyalocysts with pores on surface walls at base, all with a narrow pore, 2.5 um (longest diameter) on their transverse walls; *gemmae* not seen; *rhizoids* papillose, orange-red.

Dioicous, *perichaetial leaves* not differentiated, archegonia in groups of five to more than five. Male plants and sporophytes not seen.

Figs. 234-246. *L. rodriguezii.*

Fig. 234. Vegetative leaves. Scale = 1 cm. Mauritius, Crosby 5612, L; Bourbon, Rodriguez, Isotype, W).

Fig. 235. Apices. Scale = 200 um. (Bourbon, Rodriguez, Isotype, W).

Figs. 236-238. Abaxial hyalocysts. Scale = 100 um.

Fig. 236. Base. (Bourbon, Rodriguez, Isotype, S, W).

Fig. 237. Midleaf. (Bourbon, Rodriguez, Isotype, S).

Fig. 238. Apex. (Ibid. 236).

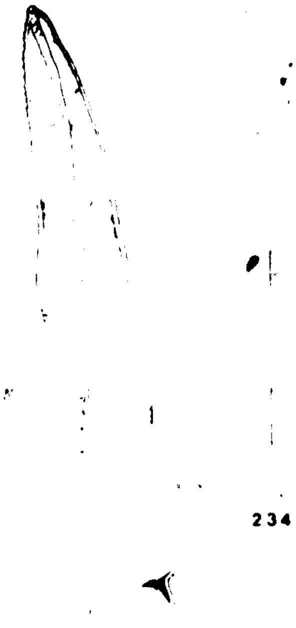
Fig. 239. Transverse section of stem. Scale = 100 um. (Mauritius, Crosby 5612, L).

Figs. 240-246. Transverse section of leaves. Scale = 100 um.

Figs. 240-242. Base. (Ibid. 234).

Figs. 243-244. Apex. (Mauritius, Balfour, NY; Isotype, W)

Figs. 245-246. Midleaf. (Ibid. 239).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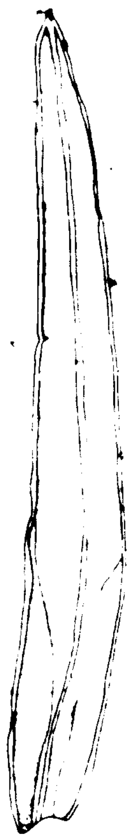
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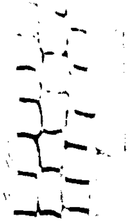
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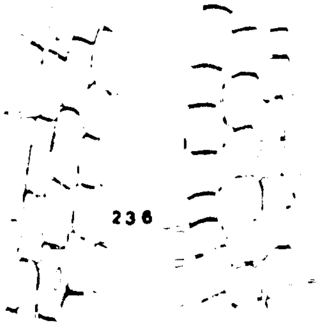
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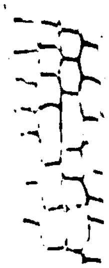
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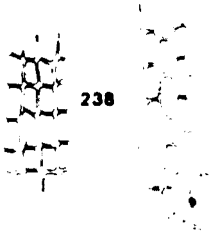
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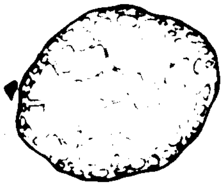
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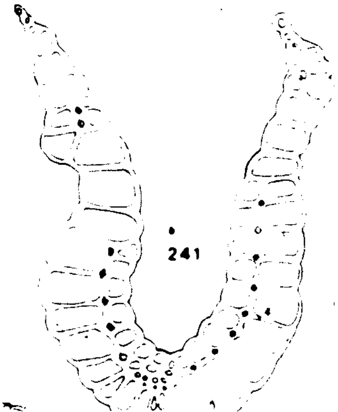
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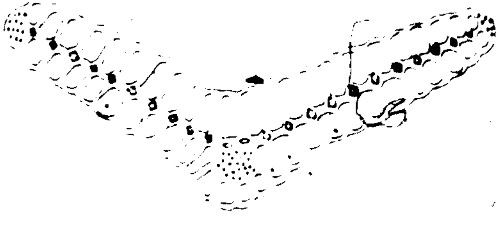
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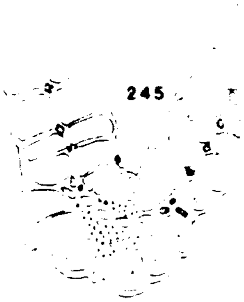
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Figs. 247-250. *L. rodriguezii.*

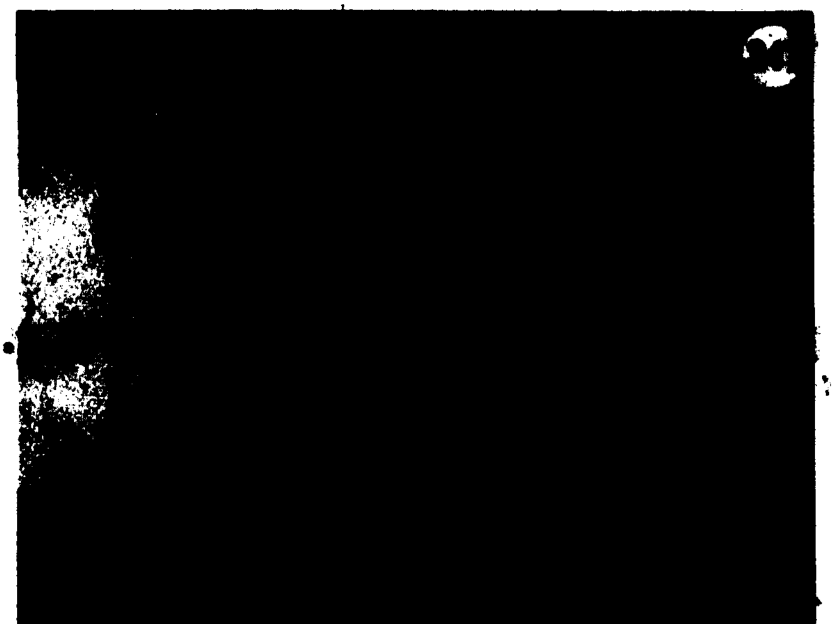
Fig. 247. Habit. (La Reunion, Rodriguez, Isotype, FH)

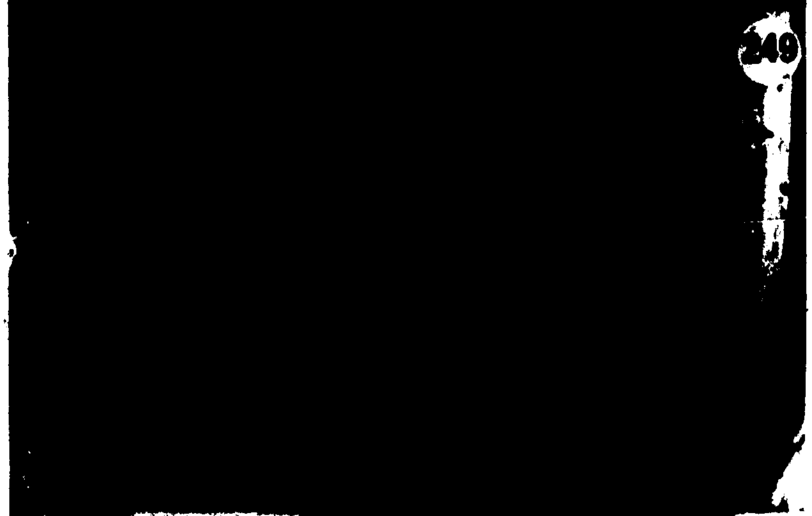
Fig. 248-249. Pores on abaxial hyalocysts. Scale = 50 mm. (Bourbon, Rodriguez, Isotype, S).

Fig. 248. Apex.

Fig. 249. Base.

Fig. 250. Transverse section of leaf at middle. Scale = 20 um.





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HABITAT. The only information on the habitat is from a specimen in W. It was collected on rotten logs. This species has been observed, in mixed collections, associated with *L. angustifolium*.

DISTRIBUTION. This species appears to be endemic to La Réunion (Bourbon); Malagasy Republic, Tananarive; and Mauritius.

PHYLOGENETIC RELATIONSHIPS. *Leucophanes rodriguezii* in leaf cell shape and in the single layer of porose hyalocysts on each side of the central chlorophyllous layer is very close to *L. octoblepharioides*. *L. rodriguezii* though, has broader leaves, strongly keeled, with reflexed margins and, unlike most specimens of *L. octoblepharioides* the costa is strong and covered, at midleaf, by a layer of hyaline cells. The pores on transverse walls of the leucocysts are narrow and small when compared to those of *L. octoblepharioides*. *Leucophanes octoblephariodes* var. *meijeri* differs from *L. rodriguezii* in having a narrower costa that is enclosed, from base to apex, by a layer of inflated hyaline cells. It is considered that *L. rodriguezii* is a segregate of *L. octoblepharioides* having developed in isolation (insular speciation) perhaps in recent times.

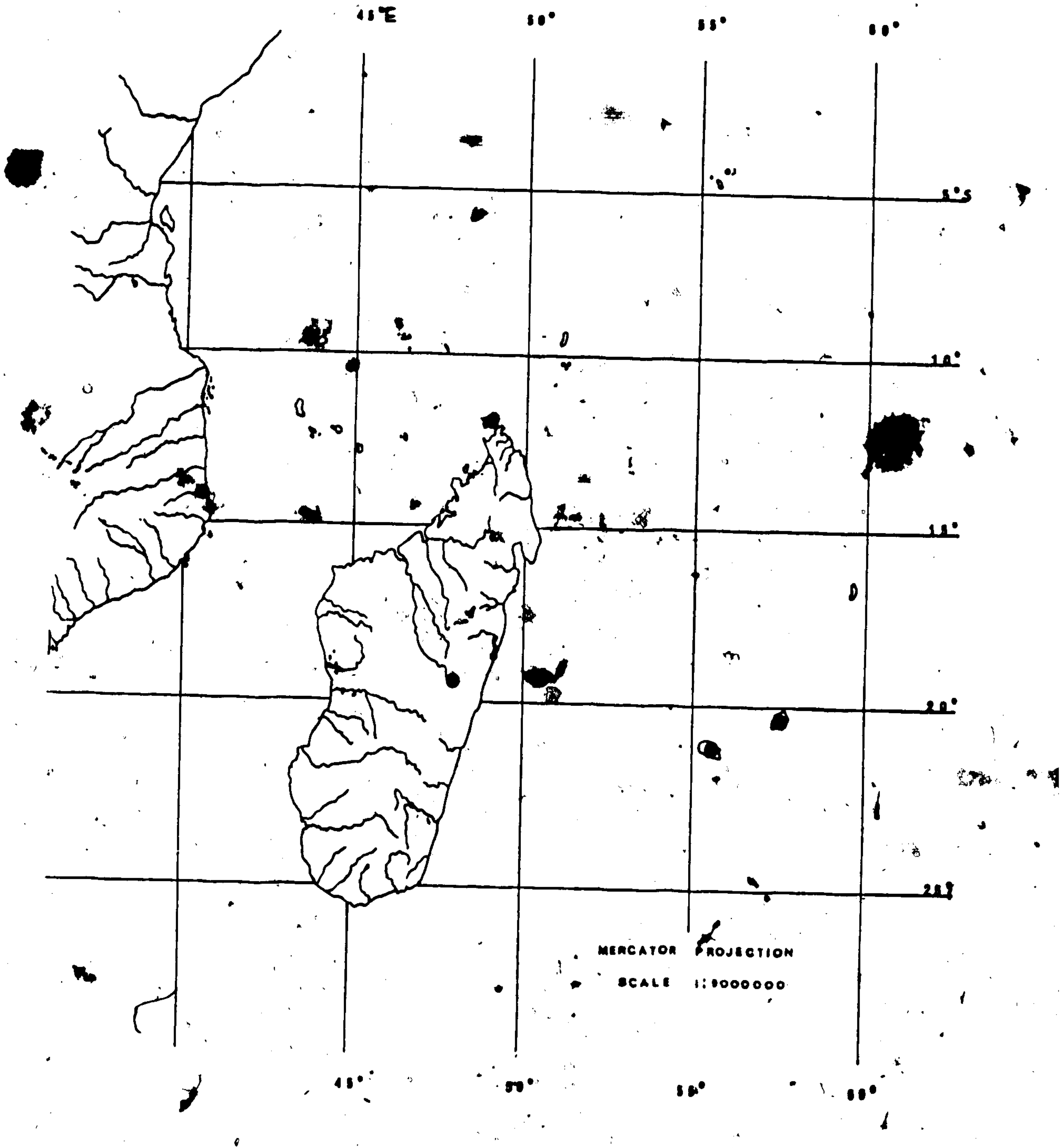
SPECIMENS EXAMINED. BM (1), FH (2), G (1), L (2), NY (3), S (2).

Leucophanes molleri C. Muell.

(Figs. 13-15, 16, 18, 20, 23, 29, 48, 84-85, 252-286).

Flora 69: 285. 1886. Type: "Patria Africa occid. trop. Insula S. Thomé, encostas do Pico; 1900 alt. inter *Thamnium molleri* frustula perpauca inveni." (Lectotype: "Afr. occ., ins. S. Thomé 1885." H-Broth!; Isotype: S-Roth!)

Fig. 251. Distribution of *L. rodriguezii.*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Leucophanes lecomptei Besch., J. de Bot. 9: 221. 1895. Type: Gabon. French Congo: "Mousse récoltee aussi par M. Thollon, sur les arbres, dans la forêt de Mayumba". (Lectotype: BM-Besch!; Isotype: BM-Besch!).

Leucopha[illegible]cam[illegible]iae C. Muell. ex Dusén., K. Svensk. Vet. Ak. Handl. 28(3): 15a. i. Plate [illegible] 1896. Type: "In Cameruniae in truncis ramisque arboru[illegible] prope Batoki pagum 14 m. [illegible] c.fr. vetustis et ad Love emporium m. Majo a. 1891 c.fr. legi." (Lectoty[illegible]toki, trad. 14/10, 90. No. 117, S-Dusén!; Isotype: NY-Uggla (2 specimens)!; Syntype: S!).

Leucophanes calymperaceum C. Muell. ex Dusén., K. Svensk. Vet. Ak. Handl. 28(3): 17 a-b. Plate 00, Fig. 39. 1896. Type: "Habitat in Camerunia in truncis ramisque arborum, ubi ad Bomanan pagum 670 m. supra mare m. Decembri a. 1890 legi." (Lectotype: "Africa occ., [illegible]amerunia ad Bomanan pagum c. 670 m.s.m. in truncis arb. Decembr. 1890. P. Dusén", S-Dusén!; Isotypes: S-Dusén!, H-Broth!).

Leucophanes obtusatulum C. Muell. ex Dusén, K. Svensk. Vet. Ak. Handl. 28(3): 17. a-e, Plate 00, Fig. 40. 1896. Type: "Habitat in Camerunia in truncis arborum, ubi ad Ekundu Ndene emporium et ad Ndian emporium m. Martio a. 1892 legi". (Lectotype: Kameron, Ekundu N'dene 3 (1892). Leg. P. Dusén. No. 766", S-Dusén!; Isotypes: BM-ex Dusén (2 specimens)!, NY- Uggla (3 specimens)!, S-Dusén (3 specimens)!; Syntypes: S-Dusén!, NY-Uggla!; M!.

Leucophanes calymperatum C. Muell., Malpighia 10: 570. 1896. Type: "Prope Georgetown ad cataractas "Marshall falls" fluvii Mazaruni a. Cl. J. Quelch collecti." (Type not seen).

Leucophanes horridulum Broth., Bull. Misc. Inf. Kew. 136-137. 1898. Type: "Ashanti, Cummings." (Lectotype: "Ashanti Expedition 1895/6. Leg. H. S. Cummings", H-Broth!;

Isotypes: S!, BM!).

Leucophanes brasiliense Broth., Denck. Akad. Wiss. 83: 279. 1924. Type: Brazil, "Sao Paulo. Prope Raiz da Serra; ad arbores in silva primigenia; 20-50 m s.m. (699). In silvaticis ad Rio Mambu; in districtu urbis Conceiçao de Itanhaen; ad arbores ca. 100 m s.m. (1434)." Leg. Schiffner. (Lectotype: "Brasilia. Prov. Sao Paulo. In silvaticis ad Rio Mambu in districtu urbis Conceiçao de Itanhaen; cca. 100 m.s.m. ad arbores. vi. 1901, Lgt. V. Schiffner", H-Broth!; Isotype: BM!; Syntype: BM!).

Leucophanes mittenii Card. in Par., Ind. Bryol. ed. 2, 3: 192. 1905. Basionym: *Octoblepharum angustifolium* Mitt. J. Linn. Soc. Bot. 12: 110. 1869. Type: Ecuador, "Andes Quitenses, fl. Napo, Villa[illegible]io." (Lectotype: "Andes Quitenses, Fl. Napo, Villavicenzio. Leg. Jameson", NY-Mitt!; Isotype: FH-Bartr!, S!).

NOMENCLATURAL NOTE. Of the nine names known for the species, five were originally assigned by C. Mu[illegible]er. Two of these, *L. molleri* and *L. calym*[illegible]re validly published by Mueller and the other three by Dusén. *L. molleri* is the oldest legitimate name for the species and thus, has priority over the rest (ICBN, Art. 11).

Leucophanes brasiliense first described by Brotherus from a specimen from Brazil is structurally similar to the African populations of *L. molleri*. [illegible]therus in his description of the species indicated this fact: "L. calymperaceo C. Mull.: e Camerunio valde affinis." It appears that Brotherus gave more weight to the geographical location of the specimen than its structural affinities in erecting a new species for the Neotropics.

DISTINGUISHING FEATURES. *Leucophanes molleri* is characterized by its narrow, slender, flexuose to erect-stiff leaves, slightly spreading when dry and moist; narrowly lanceolate, acute to rounded obtuse, to emarginate or ± obcordate, apex bent backwards in some specimens, leaves keeled below, ± plane above, with 3-4 red-orange colored cells at insertion; hyaline lamina occupying 1/3-1/2 the length of the leaf; transverse section with one layer of hyalocysts on the abaxial and adaxial sides of the central chlorophyllous layer; costa narrow, exposed throughout to covered by hyaline cells above midleaf.

DESCRIPTION. *Plants* to 4 cm tall in loose to dense tufts, white-green when dry, light green when moist. *Stem* red to brown-red, flexuose, in transverse section (100)112.5-162.5 um in diameter with large medullary cells surrounded by one layer of thick-walled cortical cells. *Leaves* 3.0-5.3 mm long, 0.4-0.5 mm wide, loosely overlapping, erect and ± twisted above midleaf when dry, slightly spreading when moist, narrowly lanceolate, broadly acute to rounded obtuse to ± truncate to emarginate, or ± obcordate, apex recurved in some specimens, with 3-4 red-colored cells at insertion; in transverse section with one layer of hyalocysts on each side of chlorophyllous layer; *hyaline lamina* to 1/3-1/2 the length of leaf, 4-8 cells wide uni- to irregularly bistratose; *margins* serrate at apex, in transverse section with 1-4 rows of stereids uni- to multistratose; *costa* narrow throughout, percurrent, exposed on abaxial surface from base to apex or covered above midleaf by a layer of hyaline cells, in transverse section with one layer of adaxial stereids or none, 2 guide cells continuous with central chlorophyllous layer and 3-4 layers of abaxial stereids; *hyalocysts* in surface view, at base 34.9-61.6(65.5) um long, 19.3-38.2 um wide, quadrate to rectangular; at midleaf 27.1-63.3(82.5) um long, 10.6-25.6 um wide, rectangular; at apex 9.1-24.6 um long, 5.0-11.8 um wide quadrate, oblong quadrate to rectangular, pores on surface walls single more numerous at base, narrow at midleaf and restricted to marginal hyalocysts. *Gemmae* variable in number of cells, papillose fusiform, clavate, elliptical or slenderly ovate, branched or unbranched at base. *Rhizoids* orange-red, verrucose-papillose.

Dioicous, *perichaetial leaves* not differentiated, archegonia in groups of more than 5; *perigonial leaves* two, antheridia in groups of 10 to more than 10. *Calyptra* cucullate, red and papillose at apex, stramineous below. *Sporophyte* terminal, monosetous, *seta* variable in length

Figs. 252-272. *L. molleri*.

Fig. 252. Vegetative leaves. Scale = 1 mm. (Cameroon, Dusén, BM; Dusén 766, BM).

Fig. 253. Transverse section of stem. (Scale = abaxial hyalocysts). (Cameroon, Dusén 955; S).

Figs. 254-255. Habit. Scale = 2 mm. (Liberia, Lin[illegible] 231, G).

Figs. 256-257. Apex variation. Scale = 75 um. (Ghana [Ashanti] Cummings, H; São Tomé, a. 1885, S; Cameroon, Dusén 117, BM; Dusén a. 1890, S; Panama, Salazar 2983, ALTA, PMA).

Figs. 258-260. Abaxial hyalocysts. Scale = 100 um.

Fig. 258. Base. (Dusén a. 1892, S; Panama, Salazar 2983, PMA).

Fig. 259. Midleaf. (Cameroon, Isotype, BM; Ghana [Ashanti] Cummings, H).

Fig. 260. Apex. (Cameroon, Dusén 766, BM; Panama, Salazar 2983, PMA).

Figs. 261-265. Transverse sections of leaves. Scale = 100 um.

Fig. 261. Apex. (Cameroon, Dusén 766, S; Dusén a. 1890, S).

Figs. 262-263. Base. (Cameroon, Dusén 117, BM; Dusén 766, BM).

Fig. 264. At end of hyaline lamina. (Cameroon, Dusén a. 1890, S).

Fig. 265. Midleaf. (Cameroon, Dusén a. 1890, S).

Fig. 266. Sporophytes. Scale = 0.5 mm. (Cameroon, Dusén 955, S; Dusén 117, BM; Liberia, Linder 231, S).

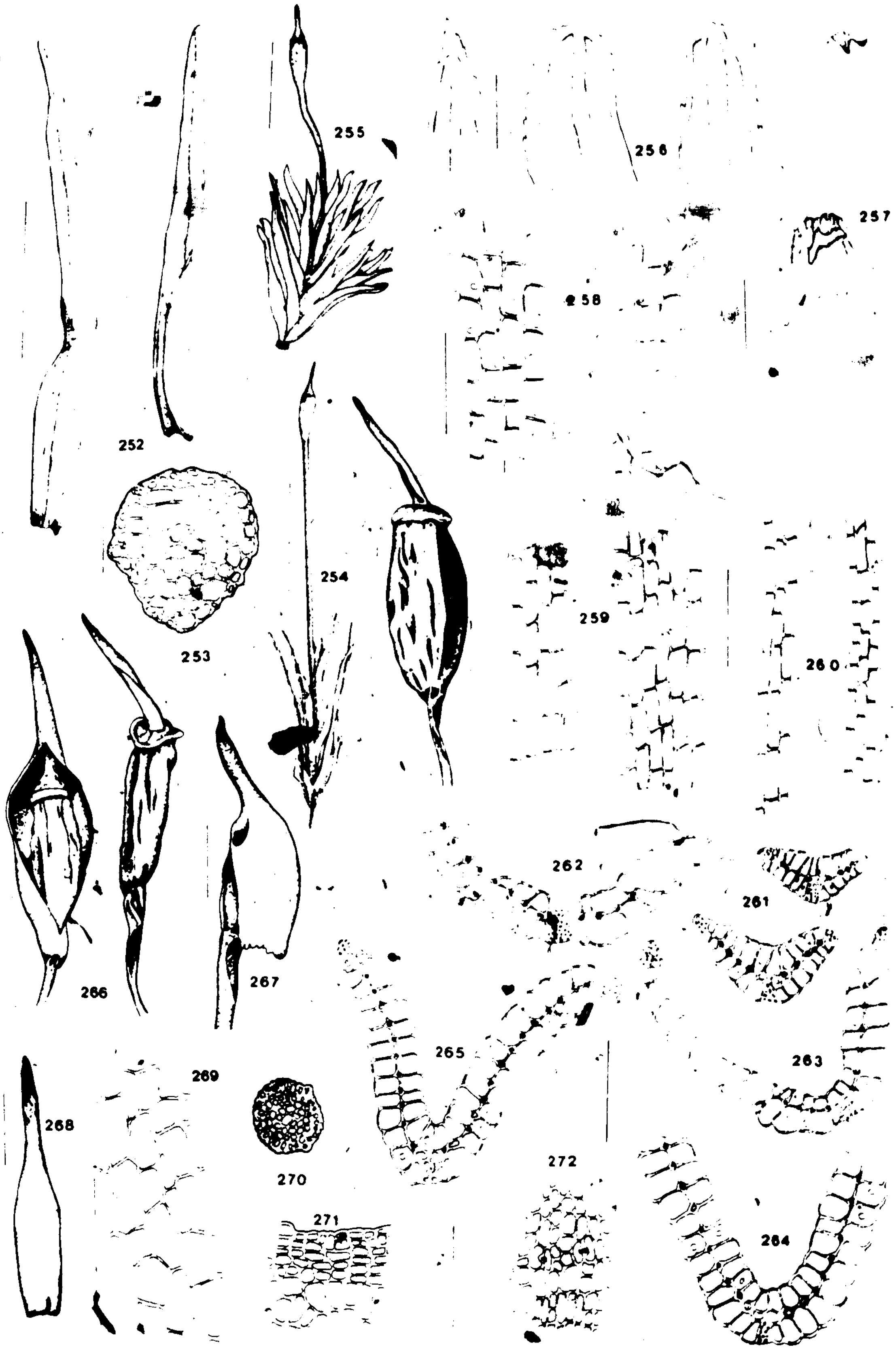
Figs. 267-268. Calyptra. Scale = 0.5 mm.

Fig. 269. Exothecial cells. Scale = 100 um.

Fig. 270. Transverse section of seta. Scale = 50um.

Fig. 271. Rim cells. Scale = 100 um.

Fig. 272. Stomates. Scale = 100 um.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Figs. 273-278. *L. molleri.*

Fig. 273. Habit. Scale = 5 mm. (Panama, Salazar 3017, ALTA, PMA).

Fig. 274. Apex with pores on abaxial hyalocysts. Scale = 20 um. (Zaire, Cummings, BM).

Fig. 275. Apex with leaf-tip gemmae. Scale = 20 um. (Cameroon, Dusen 117, S).

Figs. 276-277. Pores on abaxial hyalocysts. Scale = 20 um.

Fig. 276. Base. (São Thomé, Type, H).

Fig. 277. Apex. (Cameroon, Dusén 117, S).

Fig. 278. Habit. (Cameroon, Dusén 955, H).

Figs. 279-283. Peristome of *L.* [illegible]

Figs. 279-281. Outer surf[illegible] thickenings. Scale = 50 um. (Cameroon, Dusén 955, S; Dusén a. 1890, S).

Fig. 281. Scale = 20 [illegible] Dusén, a. 1890, S).

Fig. 282. Detail of thickenings on peristomial teeth. Scale = 2 um. (Cameroon, Dusén 117, S).

Fig. 283. Inner surface papillose-foveolate. Scale = 20 um. (Ibid. 282).

Figs. 284-285. *L. molleri*. Outer surface of peristome as observed under the compound microscope. Scale = 20 um. (Cameroon, Dusén 117, BM).

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to 7 mm long, 75-87.5 um in diameter, red to brown red, sinistrorse, smooth; ***operculum*** to 0.6 mm long, subulate-rostrate; ***capsule*** (1.8)2.1-2.3 mm long, dark orange-red, darker at rim erect to horizontal, cylindrical to oblong elliptical, gradually narrowing to the seta; ***exothecial cells*** 25-70 um long, 12.5-25(35) um wide, rectangular to quadrate to short oblong, ± thin-walled; at rim 12.5-25 um long, (5)7.5-12.5 um wide, short oblong to hexagonal in 4-5 horizontal layers, ***stomata*** 17.5-37.5 um long, 20-37.5 um wide, 16-20 in number; ***peristome*** with hyaline prostome of 3-4 cells high, teeth 145-154 um long, orange-red, lanceolate, outer surface with single row of plates at base, these irregularly papillose, papillae arranged in ± circular ornamentations or with semi-circular to longitudinal thickenings; inner surface bulging papillose, papillae arranged in ± circular configurations. ***Spores*** 10-15 um in diameter, spherical to oval, paraisopolar, densely verrucate at the distal surface, the proximal surface less ornamented.

HABITAT. This species has been collected on the bark of trees (at the base and main trunk), and on decomposing logs. It is mostly a member of the lowland tropical rain forest. It has been collected from sea level to ca. 1200 m. Dusén (1896) indicated that: "The species of the genus *Leucophanes* are not particularly common in the Cameroon colony and, apparently, do scarcely ascend more than 1000 m up the m[illegible]. They more specially seem to belong to the coast district." In the Neotropics, most of the collections examined are from inland tropical rain forests below 500 m.

DISTRIBUTION. *Leucophanes molleri* is distributed in Africa, from the East Usambara Mountains in Tanzania to the west into Zaire, Sao Tomé island, Cameroon, Ghana, Ivory Coast and Liberia. In the Neotropics it is reported in South America from Brazil to the Guianas and in Ecuador; in the West Indies form Trinidad and Puerto Rico, and, in Central America from Panama to Costa Rica and Nicaragua.

Fig. 286. Distribution of *L. molleri.*

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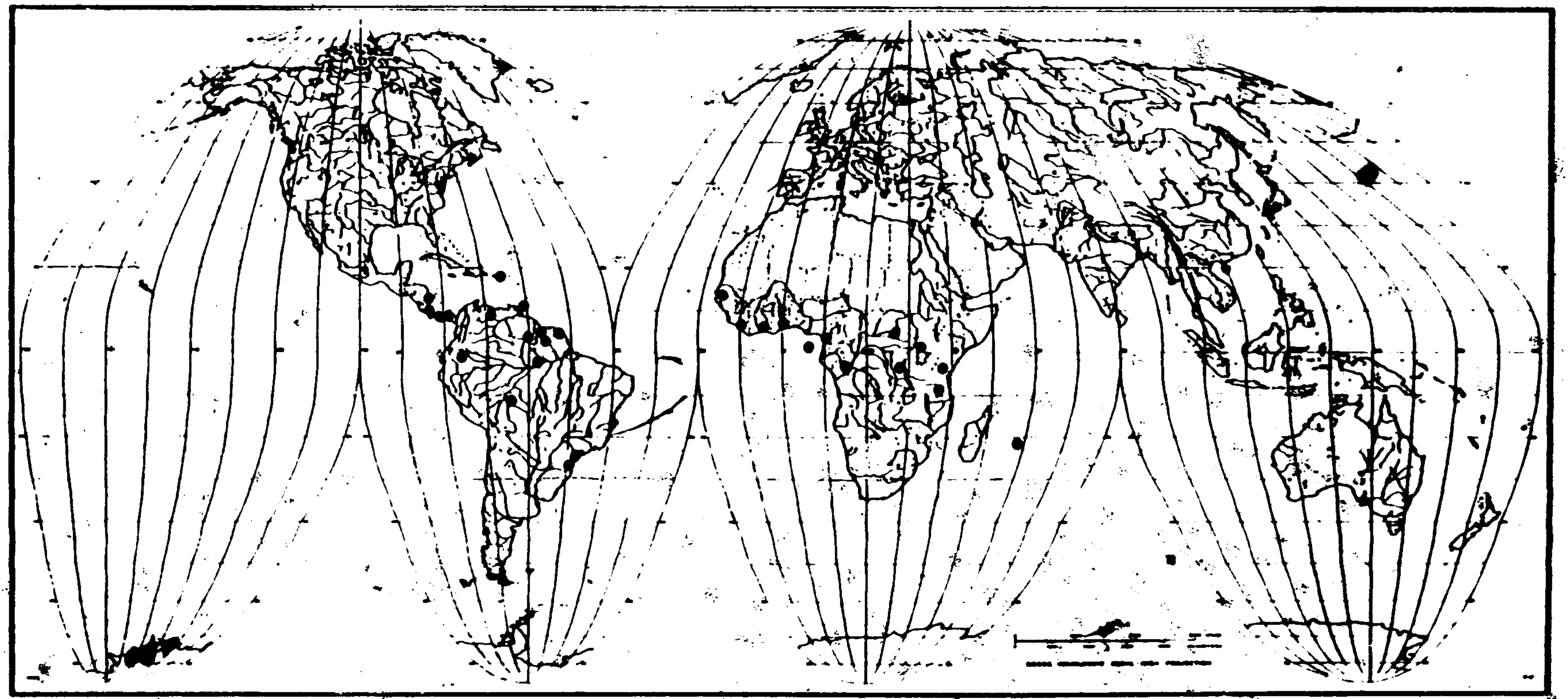

GOODE BASE MAP SERIES
[illegible]

Prepared by Henry M. Leppard
[illegible]

PHYLOGENETIC RELATIONSHIPS. *Leucophanes molleri* is closely related to *L. octoblepharioides* and *L. hildebrandtii* in having the symplesiotypies of a single layer of hyalocysts on each side of the chlorophyllous layer and a narrow costa. It differs from *L. octoblepharioides* in its flexuose, hyaline translucent looking leaves and the truncate to ± obcordate recurved apex and in peristome ornamentation. *Leucophanes hildebrandtii* differs from *L. molleri* in its strongly spinose-erose apex and shorter midleaf cells. *Leucophanes molleri* and *L. hildebrandtii* share the apotypic features of peristome ornamentation with gross, bulging elliptical to semicircular patterns on the outer plates.

SPECIMENS EXAMINED. ALTA (3), BM (10), FH (5), G (7), H (8), INPA (3), L (2), M (1), NY (12), PMA (15), S (18), SP (3), U (15).

Leucophanes unguiculatum Mitt.

(Figs. 287-300)

J. Linn. Soc. Bot. 7: 150. 1863. Type: "Prince's Island, at the base of Oil Palms, Barter." (Lectotype "Bark of oil palms Princes Is. Barter", NY-Mitt!; Isotypes: BM-Hook. (3 specimens)!, Welw!, G-ex Welw!, S!).

NOMENCLATURAL NOTE. The type collection is represented by a robust sample glued to a card and three small samples in envelopes. Of the samples in envelopes, two have labels with the type locality, the third sample has a handwritten note, presumably from Mitten, reading: "Leaf obtuse with a recurved minute mucro margin everywhere evident (illegible) entire, cells alike", and on the foldings of the envelope: "Niger Vogel". The three specimens in envelopes are thus, part of two different collections. Mitten (1863) cited "Niger, Vogel" as a distinct locality for other mosses listed in the same publication in which *Leucophanes unguiculatum* was described. The specimens with the type locality are considered duplicates of the Type, hence

Isotypes. The specimen from "Niger Vogel" is considered a separate collection, perhaps a Syntype.

DISTINGUISHING FEATURES. ***Leucophanes unguiculatum*** is characterized by its robust, densely foliose habit; the leaves falcate secund, broadly lanceolate from a tightly overlapping base (vaginant), channelled throughout; margins ± serrate at apex, smooth below, cuspidate to retuse; tranverse section of the leaves with a central layer of chlorocysts surrounded on each surface by one layer of porose hyalocysts; the costa smooth, excurrent into a curved (hook-like) apiculum or a short mucro; in transverse section with the abaxial layer of stereids covered by one layer of hyalocysts.

L. unguiculatum resembles superficially *L. candidum* in the robust habit, the densely foliose stem and the + curved to falcate secund leaves. The most distinct differences between the two are microscopic. In *L. unguiculatum* the lamina above the broad basal area is narrower, the margins are smooth and the apex is characteristically cuspidate to retuse with the costa percurrent into a hook-like apiculum or a short mucro. Leaf cells in *L. unguiculatum* are longer and narrower than in *L. candidum*. Unlike the latter, no sporophytes have been observed for *L. unguiculatum*.

Mitten (1863) first [illegible]w attention of its resemblance with other species of *Leucophanes*: "A little more robust than *L. glaucus* or *L. octoblepharioides*, from the more densely inserted leaves". ***Leucophanes glaucum*** (Schwaegr.) Mitt. has the compact foliose appearance but it is less robust than *L. unguiculatum*, the leaves have a strong spinose costa, abaxially exposed, are clearly acuminate and have a sharply serrate upper margin. A microscopic observation of *L. glaucum* will suffice to set it apart from *L. unguiculatum*. Sporophytes are also known for *L. glaucum*.

DESCRIPTION. *Plants* to 3 cm tall, robust, densely foliose, in compact turfs. *Stem* brown-red, sparingly branched, in transverse section + round 137.5-212.5 um in diameter with

Figs. 287-296. *L. unguiculatum*. (Principe Island, Type, Barter, NY).

Fig. 287. Vegetative leaves. Scale = 1 mm.

[illegible]8. Apices. Variations. Scale = 75 um.

[illegible]. 289. Transverse [illegible]le = 100 um.

Figs. 290-292. Abaxial hyalocysts. Scale = 100 um.

Fig. 290. Apex.

Fig. 291. Midleaf.

Fig. 292. Base.

Figs. 293-296. Transverse sections of leaves. Scale = 100 um.

Fig. 293. At end of hyaline lamina.

Fig. 294. Base.

Fig. 295. Midleaf.

Fig. 296. Apex.

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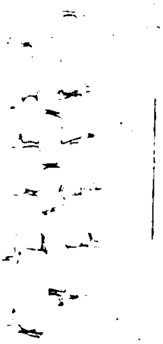

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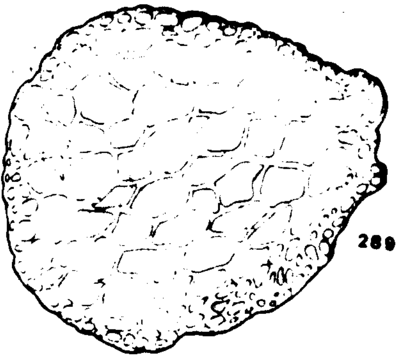

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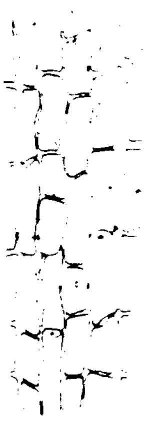

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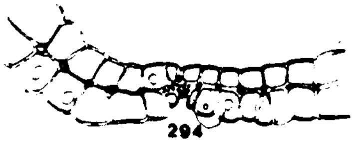

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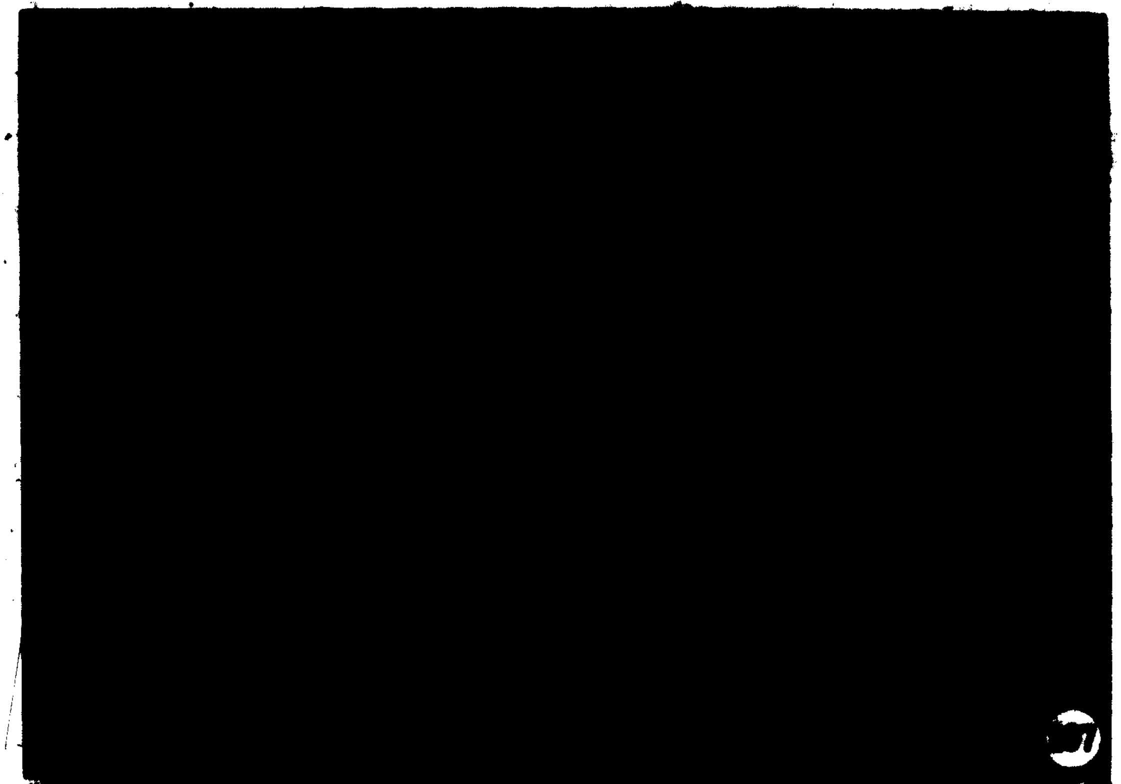
Figs. 297-299. *L. unguiculatum*. (Principe Island, Type, Barter, NY). Ch = chlorocysts, Gc = guide cells, H = hyalocysts, La = lacunae.

Fig. 297. Transverse section of leaf at end of lamina. Scale = 20 um.

Fig. 298-299. Leaf cells. Scale = 20 um.

Fig. 298. Chlorocysts and lacunae.

Fig. 299. Abaxial hyalocysts at midleaf.



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large thin-walled cells surrounded by a cortex of small thick-walled cells. *Leaves* 3.2-5.4 mm. long, 0.6-0.9 mm. wide, closely overlapping, ± falcate secund to stiff flexuose, curved when dry, spreading when moist, lanceolate from a broad base, cuspidate, rounded obtuse to retuse, channeled throughout; in transverse section with one layer of adaxial hyalocysts, a central layer of chlorocysts, and a single layer of abaxial hyalocysts; *hyaline lamina* to 1/3 length of leaf, unistratose; *margins* narrow, smooth except for the most apical portion that is slightly dentate; in transverse section, composed of 3-4 rows of stereids in 1-4 layers; *costa* strong, smooth, excurrent into a hook-like apiculum or short mucro; in transverse section with one layer of adaxial hyalocysts, 1-(2) layers of stereids, two guide cells continuous with chlorophyllous layer, 2-4 layers of abaxial stereids surrounded by an external layer of hyalocysts; *hyalocysts* in surface view, on adaxial side at base, 22.5-75.0 um long, 17.5-25.0 um wide, quadrate to rectangular; at midleaf 30.0-72.5 um long, 15.0-25.0 um wide; at apex 15.0-37.5(50.0) um long, 12.5-17.5 um wide, marginal hyalocysts porose on surface walls from base to apex. *Gemmae* not seen. *Rhizoids* dark orange-red, papillose.

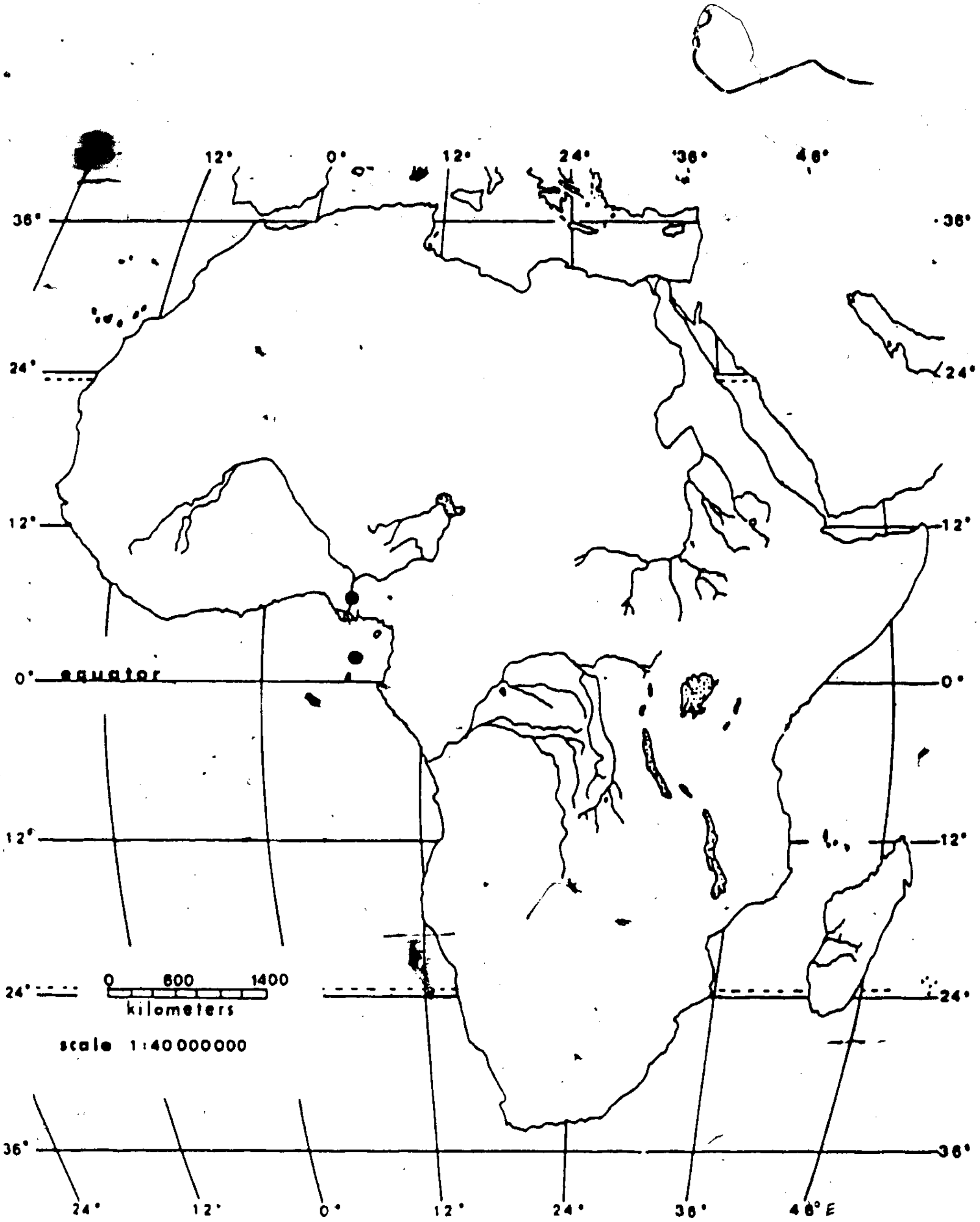
Dioicous, perichaetial leaves not differentiated, archegonia in groups of more than five. Male plants and sporophytes not seen.

HABITAT. The species has been collected as a corticolous epiphyte on oil palm trees.

DISTRIBUTION. *Leucophanes unguiculatum* appears to be an endemic species of West Africa. The only collections known are from Principe Island and River Niger.

PHYLOGENETIC RELATIONSHIPS. *Leucophanes unguiculatum* shares with *L. octoblepharioides*, *L. candidum* and most of the African species of *Leucophanes* the symplesiotypy of a single layer of hyalocysts on each side of the chlorophyllous layer. With *L. candidum* it also shares the robust habit and densely foliose stem. Of all the species to which it can be related, I believe it is very close to *L. molleri* sharing the apotypies of the long

Fig. 300. Distribution of *L. unguiculatum*.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rectangular hyalocysts of the leaf and the retuse to incised apex with enlarged hyaline cells.

SPECIMENS EXAMINED. BM (4), G (1), NY (4), S(1).

Leucophanes hildebrandtii C. Muell.

(Figs. 47, 82-83, 301-324)

Linnaea 40: 234-235. 1876. Type: "Comoro-insula Johanna, c. 900 met. elevationis, ad truncos arborum praesertim filicum in sylva umbrosa, Junio-Aug. 1875. Leg. Hildebrandt." (Lectotype: "Comoro-Insula Johanna. 1875, leg. J. Hildebrandt. Hb. C. Müll.", H-Broth!; Isotype: G-ex Duby!, NY-Jaeg!, S-Angst!).

DISTINGUISHING FEATURES. *Leucophanes hildebrandtii* is characterized by its tall, stiff habit, its leaves + curved to erect, long lanceolate, translucent, smooth margined, acuminate to broadly obtuse tips and the costa expanded to form a sharply dentate-erose apex.

DESCRIPTION. *Plants* to 6 cm tall in dense to loose turfs, light-green when moist, glaucous-green when dry. *Stem* dark orange-red, 92.5-137.5 um in diameter; in transverse section with a medulla of large cells intermixed with smaller ones, these surrounded by a layer of small cortical cells. *Leaves* 3.2-5.7 mm long, 0.4-0.6 mm wide, translucent, erect, stiff to curved, loosely overlapping when dry, erect to recurve-spreading when moist; long lanceolate from an oblong to elliptical base, apex broadly obtuse erose to more or less acuminate, at times, recurved; keeled below, plane at apex; transverse section of leaf with a central to subcentral layer of rhomboidal to irregularly triangular chlorocysts, surrounded, on each surface, by one layer of hyalocysts; *hyaline lamina* occupying 1/4-1/3 the length of leaf from base, uni- to

Figs. 301-316. *L. hildebrandtii.*

Fig. 301. Vegetative leaves. Scale=1 mm. (Comoro Islands, Hildebrandt a. 1875, Type, G).

Fig. 302. Calyptra. Scale=0.5 mm (Ibid. 301).

Figs. 303-306. Abaxial hyalocysts. Scale=50 um. (N. Uluguru Mts., Pócs 6464/BO, G; Ile Maurice Bouvier, G).

Fig. 303. Base.

Figs. 304-305. Midleaf.

Fig. 306. Apex.

Figs. 307-311. Transverse sections of leaf and stem. Scale=50 um. (Ibid. 303).

Figs. 307. Base.

Fig. 308-309. Midleaf.

Fig. 310. Apex.

Fig. 311. Transverse section of stem (Ibid. 301).

Figs. 312-316. Sporophyte. (Ibid. 301).

Fig. 312. Transverse section of seta. Scale=50 um.

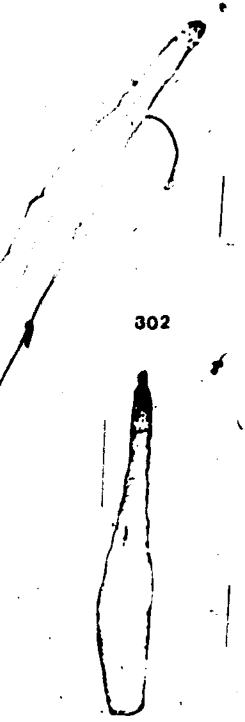
Fig. 313. Capsule. Scale=0.5 mm.

Fig. 314. Exothecial cells. Scale=50 um.

Fig. 315. Rim cells. Scale=50 um.

Fig. 316. Stomates. Scale=50 um.

301



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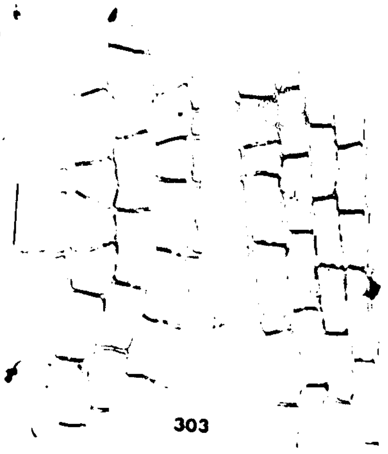

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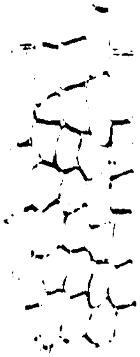

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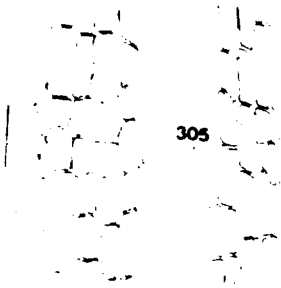

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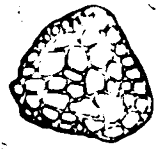

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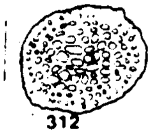

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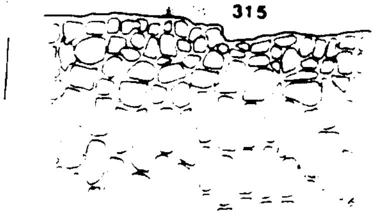

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Figs. 317-320. *L. hildebrandtii* (Comoro Islands, Hildebrandt a. 1875, Type, G).

Figs. 317-318. Variations in peristome ornamentation, outer surface. Scale = 20 um.

Fig. 319. Transverse section of two teeth; inner surface next to spore. Scale = 4 um.

Fig. 320. Spores, equatorial face. Scale = 4 um.

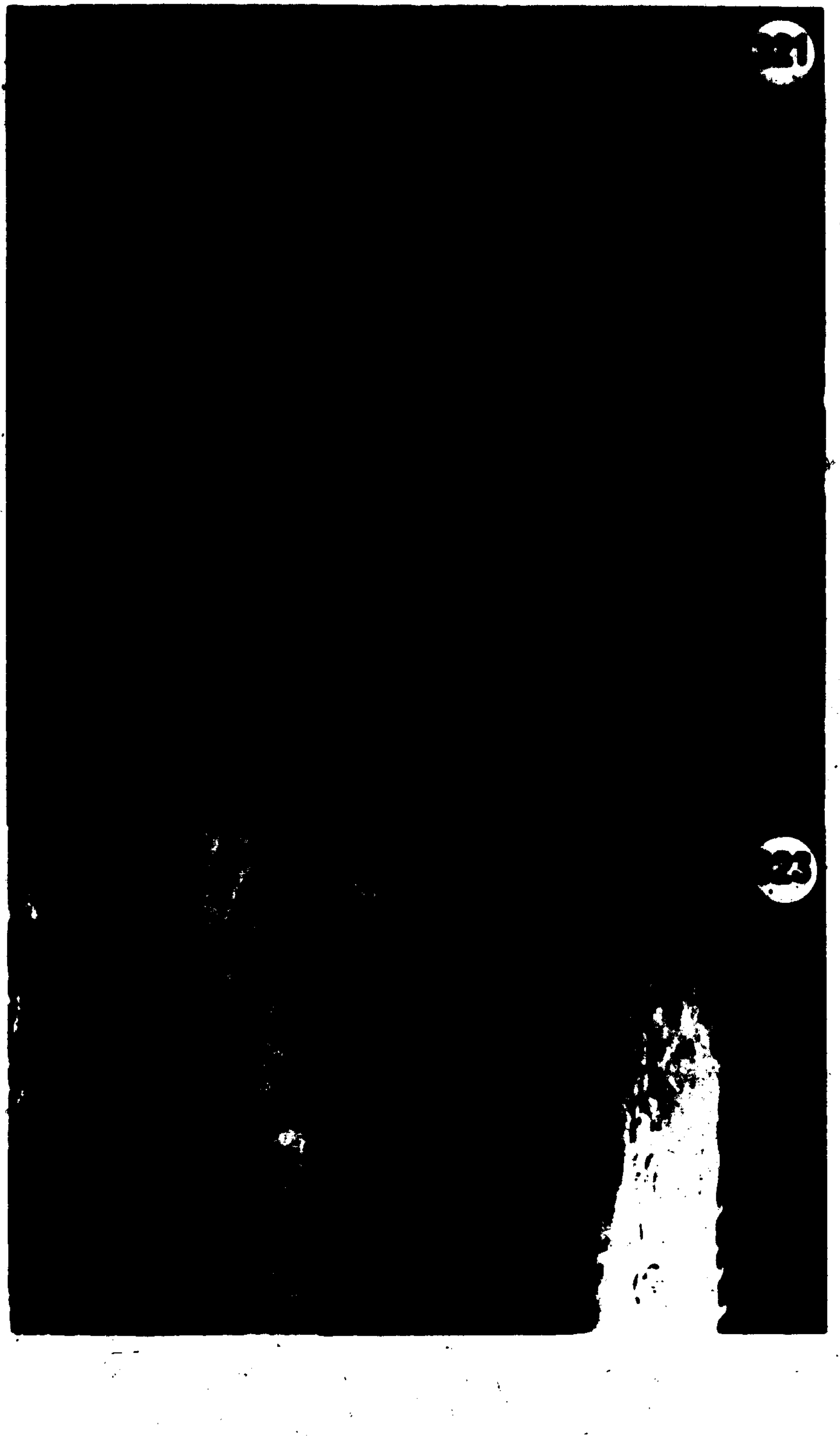

319

Figs. 321-323. *L. hildebrandtii.*

Fig. 321. Habit. (Uluguru Mts., Pócs 6464/BO, G).

Fig. 322. Pores on abaxial hyalocysts at apex. Scale = 50 um. (Comoro Islands, Hildebrandt a. 1875, Type, H).

Fig. 323. Spinose apex. Scale = 50 um. (Ibid. 322).



irregularly bistratose, 5-7 cells wide; *margins* strong, smooth to near apex, in transverse section with 1-6 rows of stereids unistratose at base, multistratose above; *costa* strong, occupying most of apex and excurrent into a sharp spinose-erose tip, in transverse section with one layer of adaxial hyalocysts, 1-2 layers of stereids, 2-3 guide cells and 2-3 layers of abaxial stereids, at base, stereids extending from abaxial to adaxial surfaces, above midleaf the costal area covered by a layer of hyaline cells; *hyalocysts* in surface view, at base, 12.5-45.8(67.5) um in length, 12.5-25.0(32.5) um in width, rectangular, quadrate, some oblong-triangular, larger near costa, with few pores on surface walls, at midleaf 25.0-47.5(60.0) um long, 12.5-20.0 um wide, more or less hexagonal to rectangular, at apex, 17.5-33.5(40.0) um long, 7.5-12.5 um wide, rectangular to oblong. *Gemmae* oblong, densely papillose. *Rhizoids* red-orange, papillose.

Dioicous, male and female plants morphologically similar. *Perichaetial leaves* not differentiated, archegonia in groups of 5. *Perigonial leaves* three, closely enveloping the antheridia, these in groups of more than 10. *Calyptra* 1.2-1.9 mm long, cucullate, smooth, red at apex gradually becoming orange-yellow below, cylinder entire. *Sporophyte* terminal, *seta* 4.4-5.2 mm long, 0.1-0.2 mm wide, orange-red sinistrorse, smooth; *operculum* 0.5-0.7 mm long; *capsule* 1.2-1.3 mm long, dark orange to orange-red, erect to subinclined, oblong cylindrical to cylindrical, gradually contracted to seta when moist, sharply so when dry, papillose at neck, somewhat constricted under mouth when old and dry; *exothecial cells* 27.5-57.5 um long, 12.5-25.0 um wide, irregularly rectangular to quadrate, with ± thick to thin walls, at rim 7.5-22.5 um long, 10.0-12.5 um wide, darker in color, irregularly quadrate to shortly hexagonal in 3-4 horizontal rows; stomata 22.5-25.0 um long, 20.0-29.5 um wide, 10-14 in number; *peristome* orange-red, lanceolate, outer surface with a single row of plates at base these bulging and strongly papillose, inner surface with two irregularly defined plates at base, densely papillose, papillae arranged in ± circular configurations. *Spores* 12.5-15.0(17.5) in diameter, spherical to oval, ± triangular, paraisopolar, under SEM densely verrucate on the proximal surface, slightly ornamented on the distal one.

HABITAT. This species is reported as a corticolous epiphyte, also on granitic rock and on soil near streams.

DISTRIBUTION. *Leucophanes hildebrandtii* has been collected in the forests of the Comoro Islands (Anjouan), Mauritius; Malagasy Republic (Farafangana forest); and in eastern Tanzania (Uluguru mountains). This species appears to be an element of the inland tropical rain forest, particularly at elevations of 800 m to over 1000 m.

PHYLOGENETIC RELATIONSHIPS. *Leucophanes hildebrandtii* shares with *L. molleri* and *L. octoblepharioides* the plesiomorphies of a single layer of hyalocysts on each side of the chlorophyllous layer and size of pores on the transverse walls. It also shares with *L. molleri* the stiff, translucent looking leaves and the apotypy of peristome ornamentation. It differs from *L. octoblepharioides* in the strongly spinose-erose apex and smooth margins. The costa in *L. hildebrandtii* is enclosed, above midleaf, by a layer of abaxial hyaline cells like *L. molleri*, *L. angustifolium* and *L. rodriguezii*. Unlike *L. angustifolium* there is no proliferation of adaxial or abaxial hyalocysts and pores on the transverse walls are larger. This last character also distinguishes it from *L. rodriguezii*.

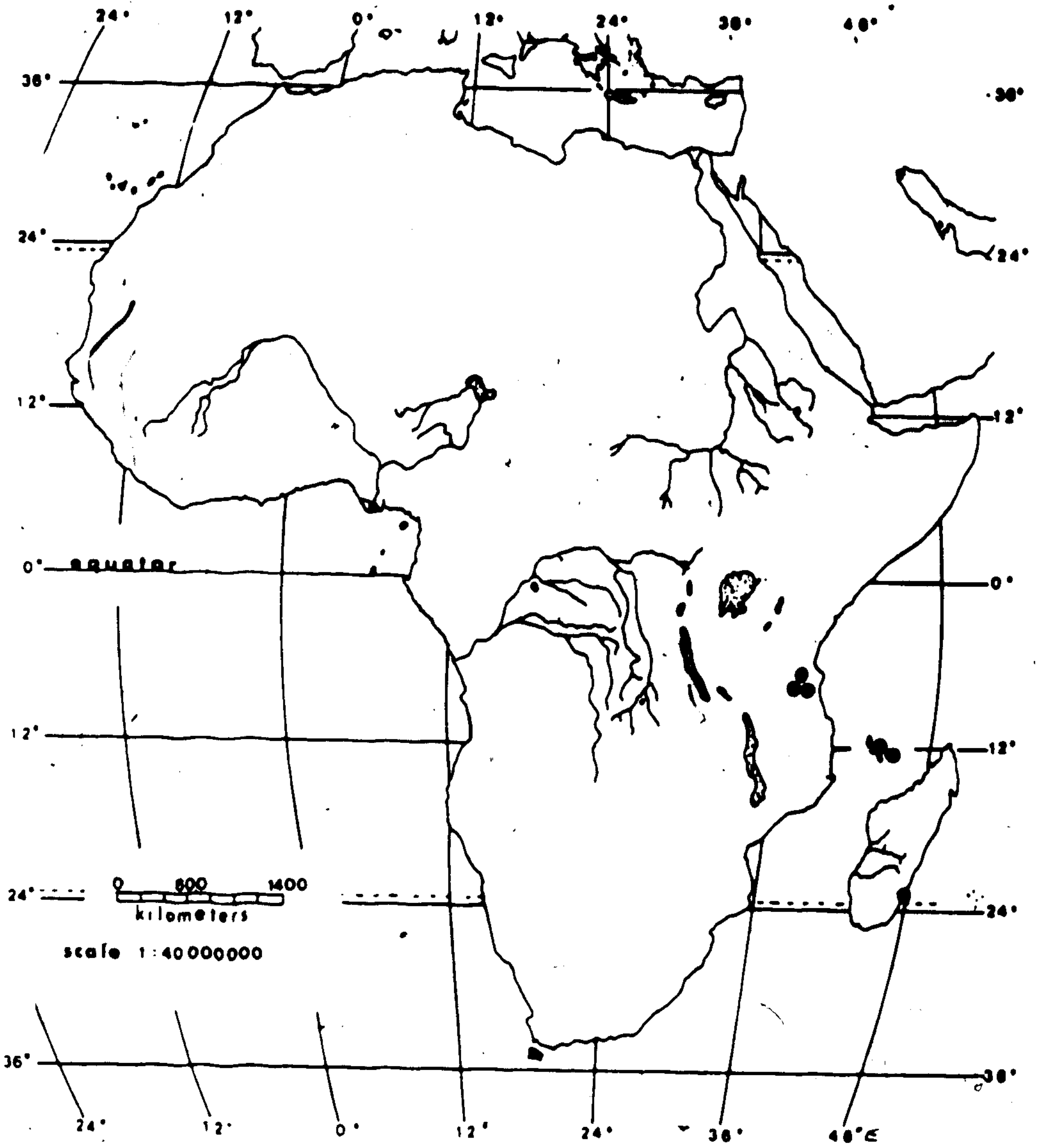
SPECIMENS EXAMINED. ALTA (2), FH (1), G (14), H (8), L (2), M (1), NY (5), S (3).

Leucophanes renauldii Card.

(Figs. 88-89, 325-345)

Bull. Herb. Boiss. ser 2, 4: 115. 1904. Types: "Madagascar. Forêt d'Alakaty (Perrot frères); cercle de Fort Dauphin: district de Mahinpoana (Herb. G. Paris)." (Lectotype: "Madagascar: Cercle de Fort Dauphin District de Mahinpoana no. 563, Com. et Paris 1900", PC-Card!;

Fig. 324. Distribution of *L. hildebrandtii.*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Syntype: PC-Card!).

DISTINGUISHING FEATURES. *Leucophanes renauldii* is characterized by its small size (to 7 mm tall), shiny translucent appearance, its leaves erect to curved, broadly acuminate to obtuse, with spine-like projections forming an erose apex. Hyalocysts are short and broadly hexagonal to wide rectangular, inflated and with large surface pores. The costa is exposed or covered by hyalocysts, these with a narrow pore on their transverse walls. Cardot (1904) in comparing this species with *L. hildebrandtii* indicated: "Diffiere du *L. Hildebrandtii* C. Müll. avec lequel on l'a confondu, par sa petite taille, ses feuilles plus petites, a denticulation apicale moins forte, ses leucocystes supérieures plus courtes, careés, brièvement rectangulaires ou hexagonales, et ses chlorocystes en général distinctement hypercentrique près du sommet".

DESCRIPTION. *Plants* in small turfs to 7 mm tall. *Stem* orange-red to orange-brown, unbranched; in transverse section (75.0)87.5-100.0(112.5) um in diameter, ± triangular with large central medullary cells, surrounded by a layer of small cortical cells. *Leaves* (2.5)3.0-5.0 mm long, 0.3-0.6 mm wide, erect to curved, loosely overlapping when dry, erect to curve spreading when moist; long lanceolate from a narrowly ovate to elliptic base, acuminate (particularly young basal leaves) to obtuse-erose at apex; concave at base, plane above, lamina with inflated hyalocysts enclosing the costa at midleaf; transverse section with a central layer of chlorophyllous cells, surrounded, on each surface, by one layer of porose hyalocysts; *hyaline lamina* occupying 1/3 length of leaf from base, uni- to irregularly bistratose, 4-6 cells wide; *margins* smooth or with few teeth at apex, in transverse section with 1-3 rows of stereids, uni- to multistratose; *costa* strong and excurrently erose at apex, exposed in a groove formed by the adjacent, inflated, hyaline cells, at apex, surrounded by an abaxial layer of large hyaline cells; in transverse section with a layer of adaxial hyalocysts, 1-2 layers of adaxial stereids, two guide cells continuous with the central chlorophyllous layer, and 2-3 layers of abaxial stereids. *Hyalocysts*, in surface view, at base, (20.0)37.5-50.0(57.5) um long, (15.0)20.0-30.0 um wide, Figs. 325-340. *L. renauldii.*

Fig. 325. Vegetative leaves. Scale = 1 mm. (Madagascar, Perrot, PC).

Figs. 326-331. Abaxial hyalocysts. Scale = 100 um. (Type & Mauritius, NY).

Figs. 326-328. Base.

Fig. 329. Midleaf.

Figs. 330-331. Apex.

Figs. 332-336. Scale = 100 um.

Fig. 332. Transverse section of stem. Scale = 100 um.

Figs. 333-336. Transverse sections of leaves. Scale = 100 um. (Type & Mauritius, NY).

Fig. 333. Base.

Figs. 334-335. Midleaf.

Fig. 336. Apex.

Figs. 337-340. Sporophyte. (Mauritius, NY).

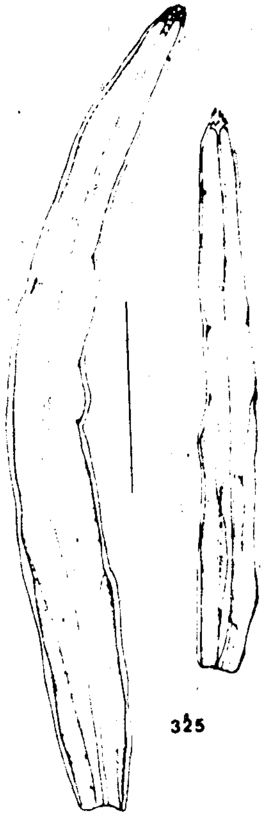
Fig. 337. Capsule. Scale = 0.5 mm.

Figs. 338-340. Scale = 100 um.

Fig. 338. Exothecial cells. Scale = 100 um.

Fig. 339. Stomates. Scale = 100 um.

Fig. 340. Rim cells. Scale = 100 um.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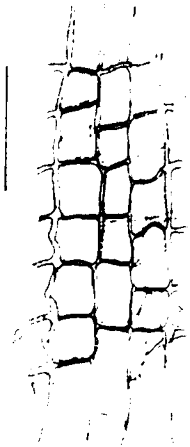
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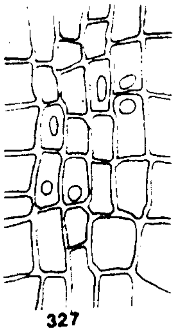
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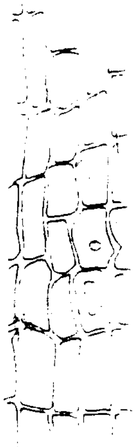
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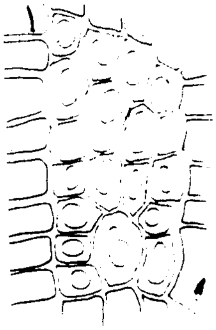
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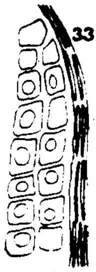
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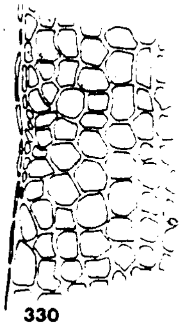
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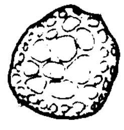
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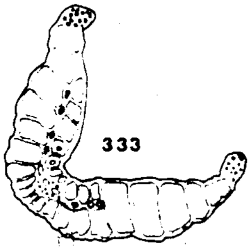
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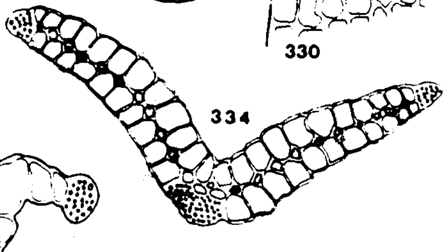
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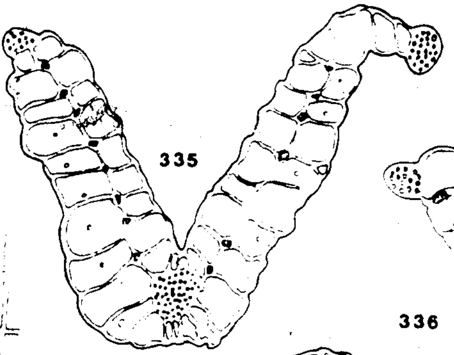
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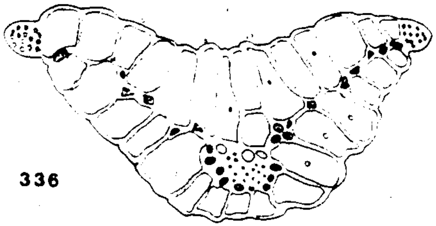
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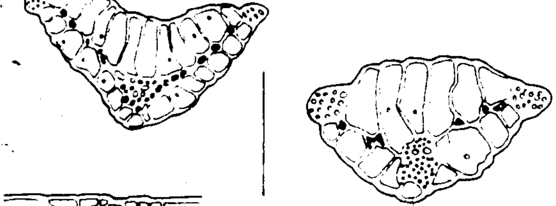


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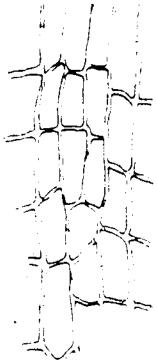
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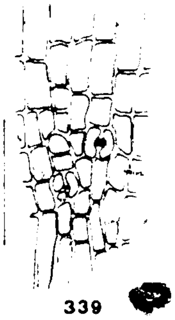
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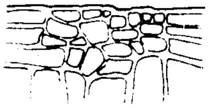
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Figs. 341-344. *L. renauldii.* (Mauritius, NY).

Fig. 341. Basal hyalocysts, abaxial side. Scale = 20 um.

Figs. 342-345. Peristome papillose-foveolate.

Fig. 342. External surface. Scale = 20 um.

Figs. 343-344. Internal surface.

Fig. 343. Scale = 20 um.

Fig. 344. Scale = 4 um.


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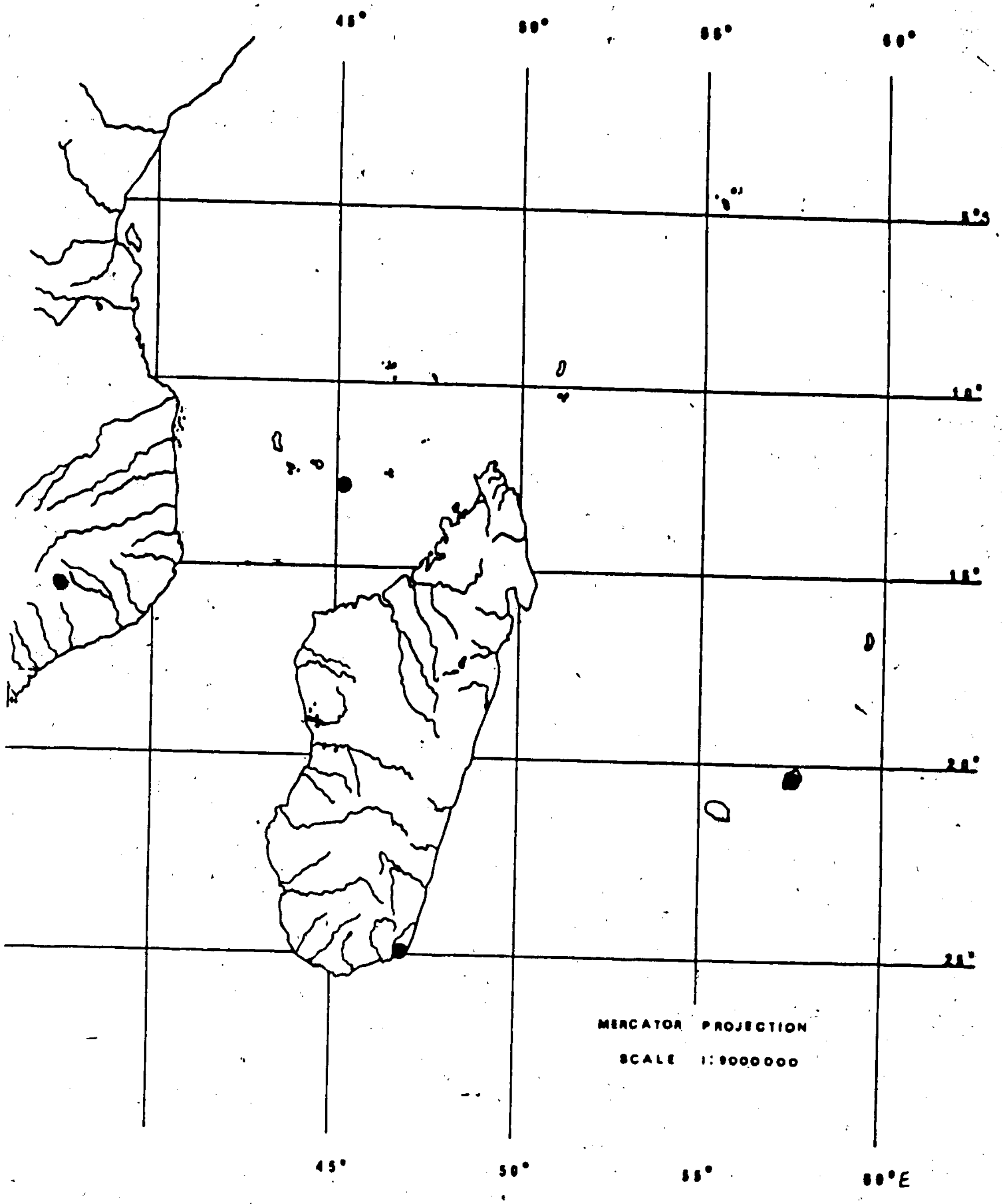
broad hexagonal to irregularly quadrate; at midleaf, (17.5)20.0-37.5 um long, 20.0-25.0(27.5) um wide, short hexagonal; at apex, (17.5)20.0-30.0(37.5) um long, (7.5)17.5-20.0(25.0) um wide, quadrate to oblong. *Gemmae* not seen. *Rhizoids* orange red, warty papillose.

Dioicous, perichaetial leaves not differentiated, archegonia in groups of five. Male plants not seen. *Calyptra* not seen. *Sporophyte* terminal, monosetous, seta 3.1-5.2 mm long, dark-orange to brown-orange, slightly papillose below the neck but otherwise smooth, in transverse section 73-75 um in diameter with a central layer of hyaline cells surrounded by one to two layers of thick-walled cells; *operculum* 0.6 mm (one measurement only) long, subulate rostrate; *capsule* 1.4-1.5 mm long, dark orange red, erect, cylindric, gradually narrowing towards the seta through a short papillose neck; *exothecial cells* 37.5-62.5(70.0) um long, 12.5-25.0 um wide, oblong to irregularly hexagonal; *rim cells* 10.0-25.0 um long, 7.5-20.0 um wide, irregularly quadrate to short oblong; *stomata* superficial, 10-12 in number, 22.5-25.0 um long, 22.5-25.0 um wide; *peristome teeth* 100-112.5 um in length, orange-red, inserted under the rim, strongly papillose on both plates, with central circular depressions. *Spores* 12.5-17.5 um in diameter, paraisopolar, papillose, under SEM gemmate to verrucate.

DISTRIBUTION. *Leucophanes renauldii* has a very restricted distribution. It has been collected in the forests of Madagascar at "Cercle de Fort Dauphin" in the District of Mahinpoana, and from an unknown locality "Alakaty"; also from the French Territories of the Comoro Islands. It appears to be endemic to these areas.

PHYLOGENETIC RELATIONSHIPS. *Leucophanes renauldii* is closely related to *L. hildebrandtii* in its habit, in the leaves with an erose, sharply spinose apex, in transverse section, with one layer of hyalocysts on each side of the chlorophyllous layer, and in the size of the pores on the transverse walls of the hyalocysts. Unlike *L. hildebrandtii*, but like *L. candidum*, surface pores of the hyalocysts in *L. renauldii* are large and numerous.

Fig. 345. Distribution of *L. renauldii.*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It is my feeling that *L. renauldii* was derived from a common ancestor to the widely spread *L. octoblepharioides* by reduction in the size of the leaf cells accompanied by (or perhaps the result of) an increase in volume (inflated hyalocysts). A better understanding of the phylogenetic relationships of *L. renauldii* will be greatly dependent on the critical examination of further collections.

SPECIMENS EXAMINED. FH (1), G (1), H (1), L (1), NY (1), PC (3).

LEUCOPHANES SUBG. LEIONOTUS (C. Muell.) Salazar-Allen *stat. nov.*

Lectotype: *Leucophanes candidum* (Schwaegr.) Lindb.

Section Leionotus C. Muell., J. Mus. Godeffroy 3(6): 57. 58. 1874.

Section A. Cardot. Mem. Soc. natn. Sci. nat. Math. Cherbourg 32: 1-84. 1900.

Subsection Homostrôsica. Cardot, *in* Grand. Hist. Madag. 39: 148. 1915.

Plants to 7 cm tall, in dense turfs; *stem* erect, foliose, sparingly branched or branches in 2-3(4); *leaves* broadly lanceolate, squarrose to erect and closely vaginant when dry, slightly spreading when moist, acuminate to acute, curved throughout, with 2-3 colored cells at insertion with stem; *hyaline lamina* narrow and short; *hyalocysts* + hexagonal, *chlorocysts* in surface view above midleaf with narrow, elongated lacunae; *costa* narrow and smooth; *margins* serrate at apex to smooth; transverse section of leaf with one layer of hyalocysts on each side of chlorophyllous layer from base to apex.

Dioicous, *perichaetial leaves* shorter with a wide tubular base covering base of seta, hyaline through most of their length; *hyalocysts* oblong-hexagonal and with pores in longitudinal rows, male plants similar to female or dwarf; *seta* to 11 mm long; *capsules* 2.4-3.5 mm long, cylindrical; *peristome* with a prostome 2-3 cells high, haplolepideous of 16 teeth; *spores* 17.5-20 (22.5) um, densely verrucate to short-baculate, the verrucae or baculae ornamented with granular depositions.

Leucophanes candidum (Schwaegr.) Lindb.

(**Figs. 12, 22, 36-40, 76-77, 346-383**)

Basionym: *Syrrhopodon candidus* Schwaegr., Spec. Musc. Suppl. 1. Vol. 2(2): 105. t. (183) 182. Figs. 1-8. 1827. Type: "Legit in insula Iapania, cl. Prof. Reinwardt." (Lectotype: "Ex insula Iapania? di-Reinwardt (illegible) *Dicrano Reinwardti* Horns. lit. b. *Leucophanes squarrosum* Brid. hbor. Amboina." G-Hedw-Schwaegr!; Isotypes: BM-Hook!, BM-Wilson!, G!).

Leucophanes squarrosum Brid., Bryol. Univ. I: 764. 1827. Type: "In insula Amboine unde clar. Dumont D'Urville retulit et communicavit caespitose ad terram habitat. Donata specimina fructu carebant". (Holotype: "Dicranum Amboina. Amboine. Dumont d'Urville. Paris 1825." B!)

Syrrhopodon candidus Hornsch., Acad. Caes. Leop. Nova Acta 14: 701 (1826) 1829. *Nom. illeg. incl. spec. prior.*

Didymodon sphagnoides Harv [illegible] Bo[illegible] 2: 4. 1840. *Nom. illeg. incl. spec. spec. prior.* (*Syrrhopodon candidus* Schw[illegible]*hanes candidum* (Schwaegr.) Lindb.

Leucophanes reinwardtianum C. Muell., Syn. Musc. Fr. 1: 82. 1848. *Nom. illeg. incl. spec. prior.* (*Syrrhopodon candidus* Schwaegr., 1827).

Leucophanes densifolius Mitt., Bonplandia 9: 366. 1861. Type: Viti Levu. "Seemann inter No. 862; Milne in Hb. Hook." (Type not seen).

Leucophanes candidum (Schwaegr.) Lindb., Oefv. K. Vet. Ak. Foerh. 21: 602. 1865.

Octoblepharum recurvum Mitt., J. Linn. Soc. 10: 179. 1868. Type: "Upolu, on trees. No. 104. Rev. T. Powell." (Lectotype: NY-Mitt!; Isotypes: BM (2 specimens)!; G-Davies!, NY-Mitt. (2 specimens)!; NY!).

Leucophanes recurvum (Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. 1871-72: 317. 1873, (Ad. 1: 165)(*Octoblepharum*, 1868).

Octoblepharum densifolium (Mitt.) Mitt., *in* Seem. Fl. Vit. 387. 98h. 1873 (*Leucophanes*, 1861).

Leucophanes tetensii C. Muell., J. Mus. Godeffroy 3(6): 57. 1874. Type: "Patria Pelew-Seu Palaus-insulae: Capit. Tetens." (Lectotype: BM-*ex* C. Muell!; Isotypes: BM-Hampe!, JE (2 specimens)!, M!, S-Angstr!, S-Roth!).

Leucophanes naumannii C. Muell., Bot. Jahrb. 5: 85. 1883. Type: "Nova Guinea. Leg. Naumann n.s." (Type not seen).

Leucophanes candidum (Schwaegr.) Lindb. var. *densifolium* (Mitt.) Dix., Ann. Bryol. 7: 23. 1934. (*Leucophanes*, 1861).

NOMENCLATURAL NOTE. In 1827, Bridel erected the genus *Leucophanes* and described three species: *L. octoblepharioides*, *L. squarrosum* and *L. fragile*. The second name *L. squarrosum* is a later taxonomic synonym for *L. candidum*. Schwaegrichen's (1827) publication of *Syrrhopodon candidus* appeared few months before Bridel's (Margadant, 1968). This is also indicated by Schwaegrichen (1842) in the last part of his discussion of *Syrrhopodon* *octoblepharis* Nees, when he compared this species with species of *Leucophanes*. He indicated that of the three species described by Bridel, two were previously published by him: "Offero hic primum *octoblepharin*, *squarrosum* est Syrrhopodon *candidus* supplem. mei II. 2. 105. t. 182., *fragilis* est Syrrh. *rigescens* eiusdem suppl. II. 103. t. 181., iam anno 1927 descriptus, ut vidi in herbario Bridelii". Thus according to the rules of priority Schwaegrichen's name is the valid epithet for the species. But, since the species belongs in the genus *Leucophanes*, Lindberg's combination *L. candidum* (Schwaegr.) Lindb. is the correct name and *Syrrhopodon candidus* the basionym.

DISTINGUISHING FEATURES. *Leucophanes candidum* is characterized by its robust plants with stems to 7 cm tall, densely foliate, lustruous white-green, to beige-green to yellow-green, leaves tumid by inflated hyalocysts, squarrose above middle to falcate secund or erect, tightly covering stem (vaginant), channeled throughout; transverse section with a single layer of hyalocysts on each side of chlorophyllous layer, costa narrow with 1-3 layers of stereids on abaxial surface and one to none on adaxial side, pores on transverse walls of hyalocysts large; seta to 2 cm long.

DESCRIPTION. *Plants* to 7 cm tall in dense, robust turfs, lustruous whitish-green. *Stem* orange-red, erect, sparsely branched, in transverse section more or less round, 125-200 um wide, the central area composed of large, parenchymatous cells, abruptly changing into small thick-walled cortical cells. *Leaves* 3.0-7.3 mm long, 0.7-1.4 mm. wide, closely overlapping stem with their bases, in 5 or more rows, squarrose spreading above midleaf to erect patent or falcate secund when dry, slightly spreading when moist, broadly lanceolate, curved throughout, with 3-4 orange-colored basal cells; transverse section with a central layer of chlorocysts surrounded on each side by one layer of hyalocysts; *hyaline lamina* narrow, extending to 1/8-1/9 the length of leaf from base, unistratose, 1-3 cells wide; *margins* ± undulate, smooth to slightly serrate in upper third, teeth single or paired, in transverse section uni- to

Figs. 346-357. *L. candidum*.

Figs. 346-348. Vegetative leaves. Scale = 1 mm. (New Guinea, Djamhari 425, L; Philippines, Ramos 23745, L; New Guinea, van Zanten 277, L).

Figs. 349-352. Perichaetial leaves. (Malaya, Robbins 3701, L; Samoa, Krauss 1295, L).

Fig. 349. Scale = 0.5 mm.

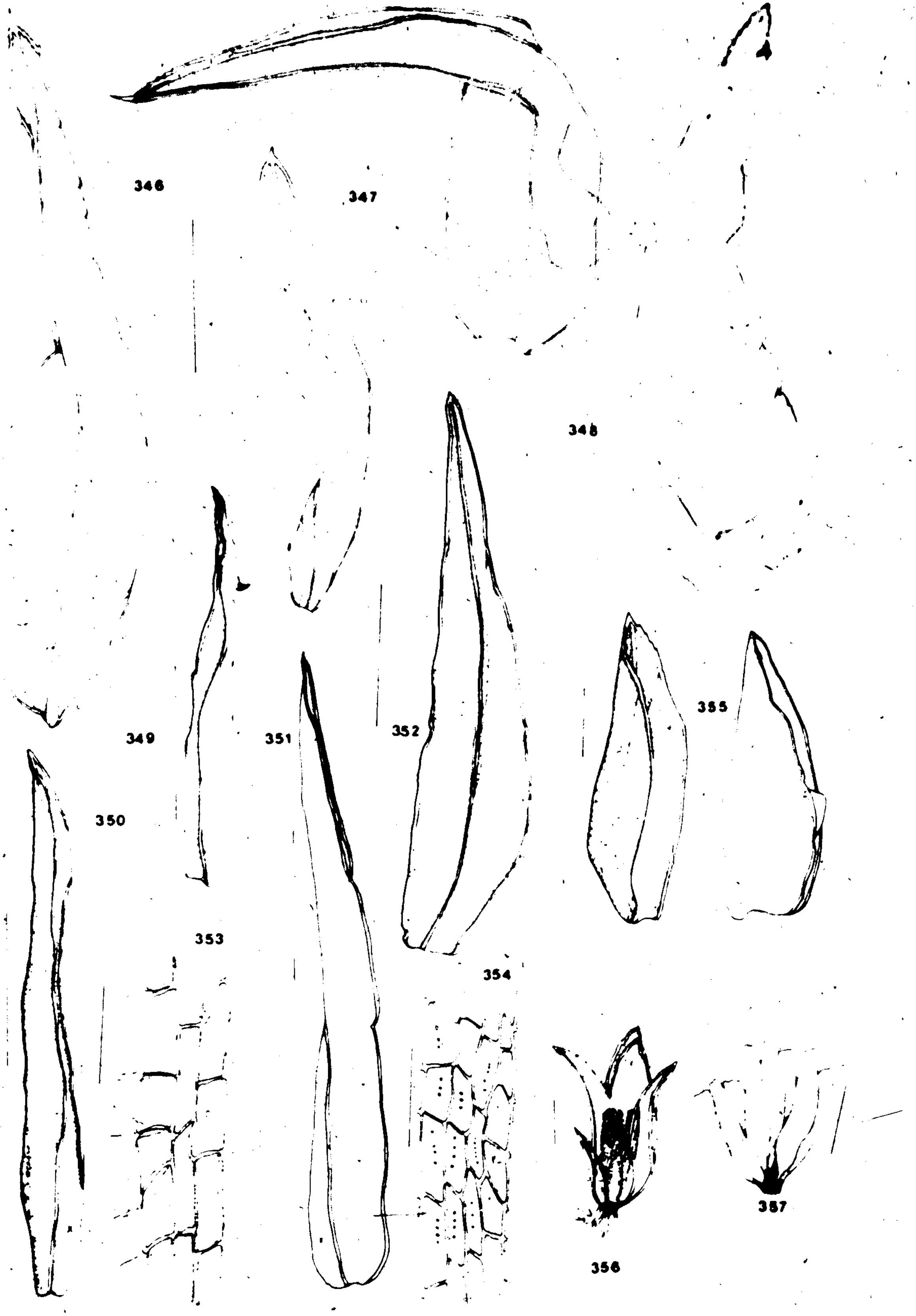
Figs. 350-352. Scale = 0.8 mm.

Figs. 353-354. Basal hyalocysts of perichaetial leaves at X. Scale = 100 um.

Fig. 355. Perigonial leaves. Scale = 0.2 mm. (Philippines, Hale & Banaag 25079, L).

Fig. 356. Dwarf male. Scale = 0.2 mm. (Ibid. 355).

Fig. 357. Antheridia. Scale = 200 um. (Ibid. 355).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Figs. 358-368. *L. candidum*. Abaxial hyalocysts. Scale = 50 um.

Fig. 358. Base. (Philippines, Foxworthy a. 1906, S; Sumatra, Teysmann, L).

Fig. 359. Midleaf. (Philippines, Foxworthy a. 1906, S; Teysmann, L).

Fig. 360. Apex. (Philippines, Foxworthy a. 1906, S; Ramos 23745, L).

Fig. 361. Calyptrae. Scale 0.5 mm.

Figs. 362-368. Sporophyte.

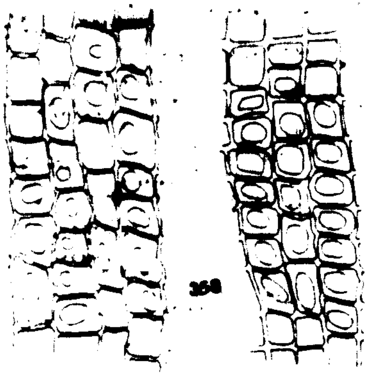
Fig. 362-363. Capsules. Scale = 0.5 mm. (Philippines, Ramos 23745, L).

Fig. 364. Transverse section of seta. Scale = 50 um. (N. Borneo, Meijer B12498, L).

Fig. 365. Exothecial cells. Scale = 100 um. (New Guinea, Darbishire & Hoagland 8358, B; Teysmann, L).

Fig. 366. Rim cells. Scale = 50 um. (New Guinea, Darbishire & Hoagland 8358, B; 8050, B).

Fig. 367-368. Stomates. Scale = 50 um. (Sumatra, Teysmann, L).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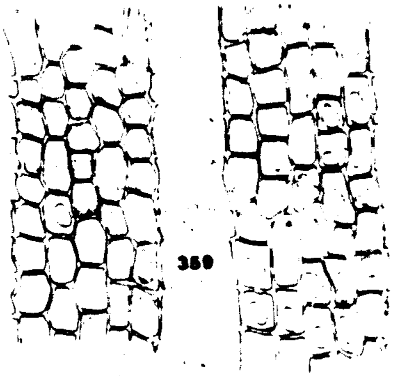
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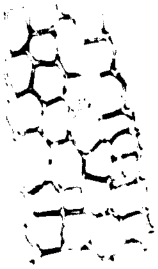
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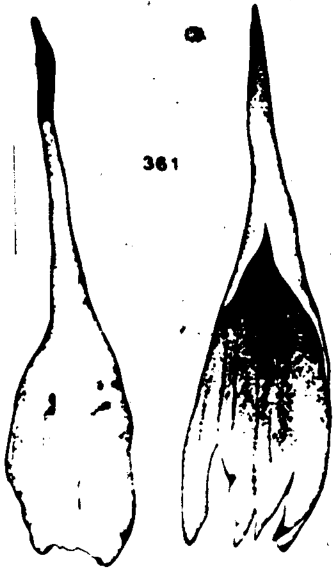
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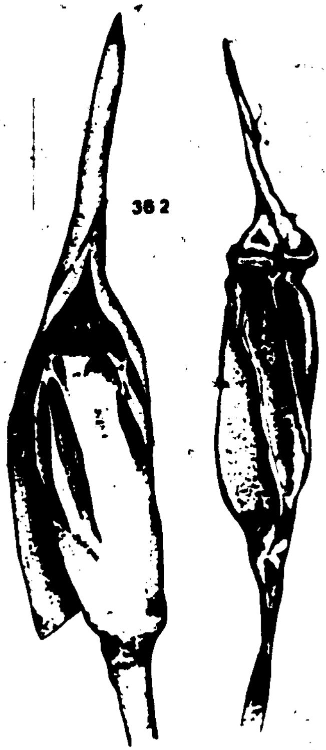
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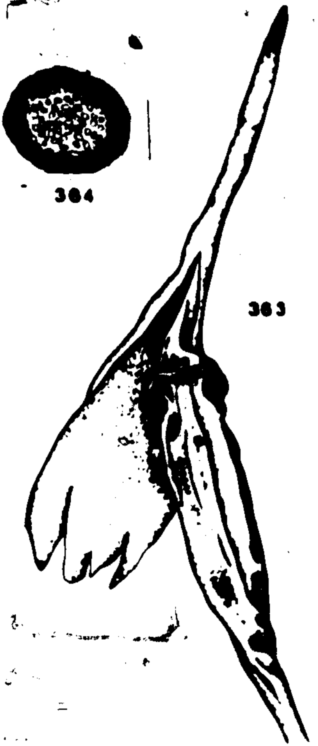
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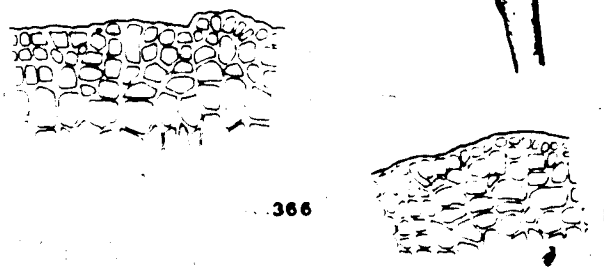
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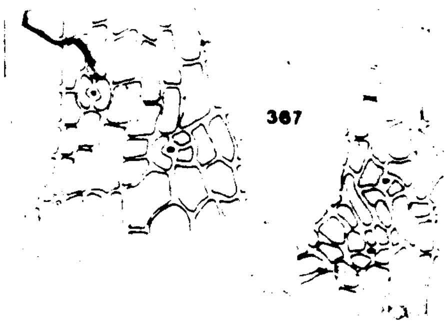
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Figs. 369-374. *L. candidum.* Scales = 20 um.

Fig. 369. Transverse section of stem and leaves. (Schultze-Motel 3416, B).

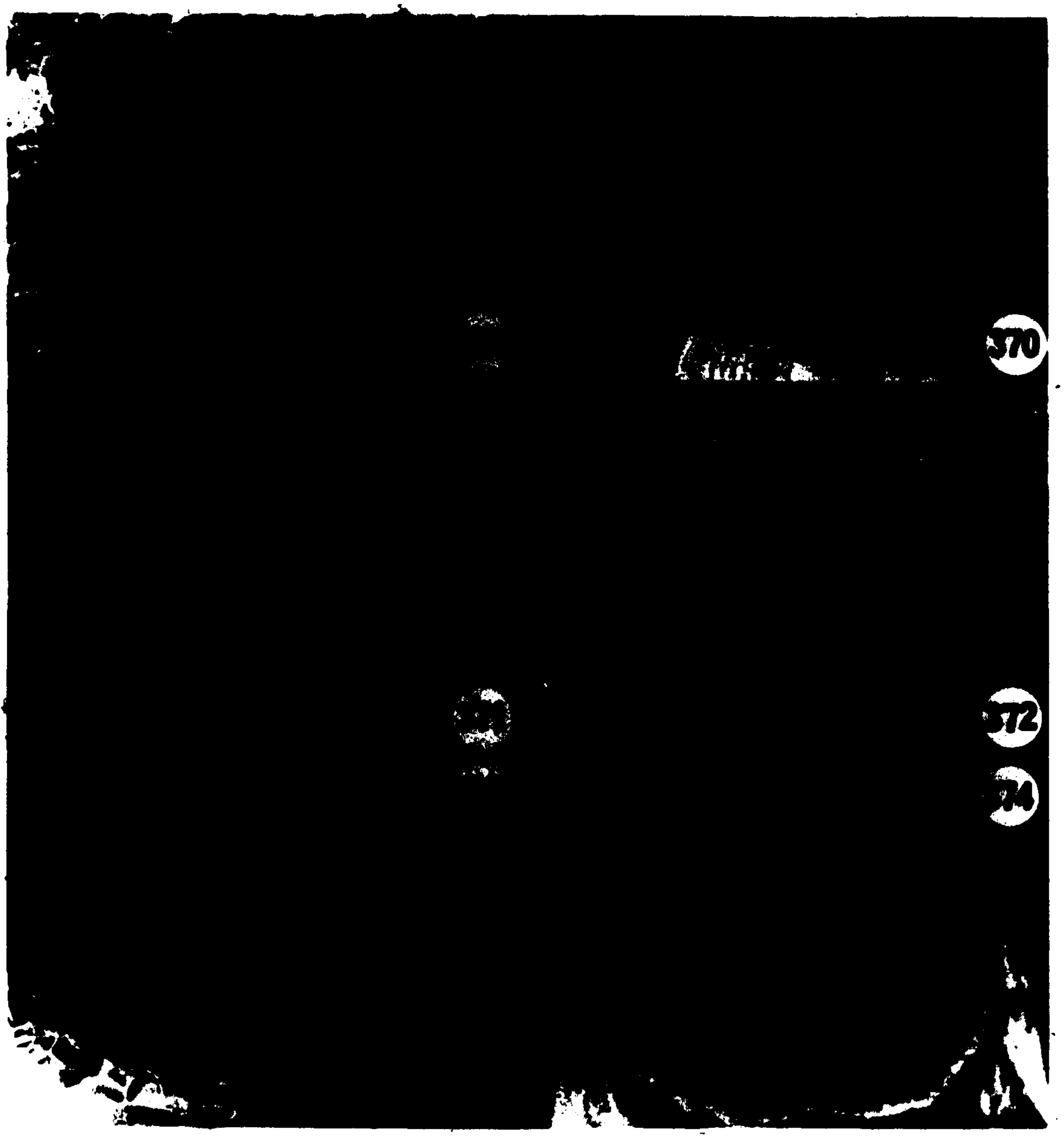
Figs. 370-372. Leaf.

Fig. 370. Surface pores on abaxial hyalocysts. (Brunei, Richards 57/7, L).

Fig. 371. Transverse section at apex. (Schultze-Motel 3416, B).

Fig. 372. Surface pores on basal hyalocysts. (Ibid. 372).

Figs. 373-374. Peristome. (New Guinea, van Zanten 277, L).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Figs. 375-378. *L. candidum.* Peristome.

Figs. 375-376. Outer surface. Scale=20 um. (N. Borneo, Meijer B1248, L).

Fig. 377. Inner surface. Scale=10 um. (W. Borneo, Winkler 3097, L).

Fig. 378. Lateral view of teeth, outer surface to the right. Scale=10 um. (New Guinea, van Zanten 277).


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Figs. 379-382. ***L. candidum.***

Fig. 379. Outer surface of peristome under light microscopy. Scale=25 um. (New Guinea, Darbishire & Hoagland 8358, B).

Fig. 380. Habit. (Philippines, Ramos a. 1915, L).

Fig. 381. Lateral view of peristome tooth and prostome. Scale=25 um. (Ibid. 379).

Fig. 382. Transverse section of leaf at base. Scale=20 um. (Iapania?, Reinwardt, BM)

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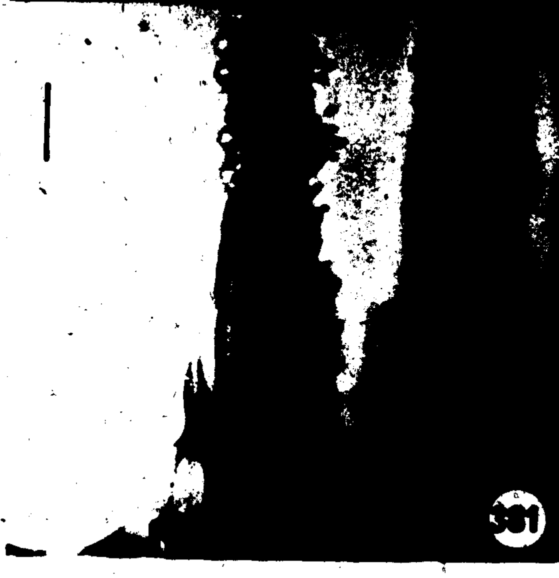

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multistratose; *costa* percurrent to shortly excurrent, smooth, in transverse section composed of one layer of adaxial hyalocysts, two guide cells continuous with central chlorophyllous layer and 1-3 layers of abaxial stereids; *hyalocysts*, in surface view, on abaxial surface, at base, 25-50(62.5) um long, 20-37.5 um wide, rectangular to short hexagonal to oblong triangular, at midleaf 25.0-45.0(62.5) um long, (17.5)20.0-25.0(30.0) um wide, oblong hexagonal; at apex 20.0-42.5 um long, (12.5)20.0-25.0(37.5) um wide oblong hexagonal. *Gemmae* not seen. *Rhizoids* orange-red, densely papillose.

Dioicous, archegonia in groups of 5 or more, *perichaetial leaves* erect, loosely overlapping to 4.6 mm. long and 0.4 mm wide with long tubular base, tightly covering basal portion of seta, mostly hyaline to near upper 1/3, hyaline cells with narrow vertically seriate pores. Male plants slender and smaller (to 2 1/2 cm tall); dwarf males present. *Perigonial leaves* three with a broad sheathing base. Innermost perigonial leaf hyaline throughout except for upper 1/4 that has a unistratose layer of chlorocysts. *Calyptra* cucullate 2.6-4.0 mm long, red at apex, stramineous below, papillose in upper portion, smooth below. *Sporophyte* terminal, appearing lateral by innovations; *seta* to 1.1 cm. long, light orange to dark brown-red, sinistrorse, smooth; in transverse section 92.5-100.0 um in diameter; *operculum* long rostrate 1.3-1.4 mm long; *capsule* 2.4-3.5 mm. long brown-red to orange-red, darker at rim, cylindrical to oblong cylindrical, gradually narrowing to seta by a papillose neck, slightly constricted at mouth; *exothecial cells* 25.0-112.5 um long, 20.0-27.5 um wide, oblong to irregularly hexagonal; *rim cells* 10.0-25.0 um long, 7.5-15.0 um wide, rhombidal-hexagonal to rectangular to quadrate or oval, in 4-5 horizontal layers; *stomata* superficial, 12-14, 20.0-27.5(32.5) um long, (20.0)25.0-27.5(37.5) um wide; *peristome* with a prostome 2-3 cells high, teeth 200-250 um long, orange-red, inserted under rim of capsule, strongly papillose on both surfaces, dorsal plate at apex of teeth smooth to nearly smooth; trabeculae clearly seen although narrow, papillae clavate to capitate. *Spores* 17.5-20.0(22.5) um in diameter, paraisopolar, granular, under SEM densely verrucate to short-baculate.

HABITAT. *Leucophanes candidum* is epiphytic on trees, rocks (limestone, sandstone, lava boulders and fragmented volcanic rock), decomposing logs and on soil. It has been reported from limestone cliffs along sea shore (Royen #5456, New Guinea) to inland tropical rain forests at altitudes of 1000 meters. It has been observed in mixed collections with *L. candidum*, *L. glaucum*, and *L. octoblepharioides*.

DISTRIBUTION. This species is distributed in Malesia, northern Australia New Guinea, Solomon Islands and and the islands of the tropical Pacific.

PHYLOGENETIC RELATIONSHIPS. *Leucophanes candidum* is closely related to *L. unguiculatum* and *L. octoblepharioides*. The transverse section of the leaf with one layer of inflated hyalocysts on each surface of the chlorophyllous layer, the hyalocysts with large pores on their transverse walls and the narrow costa are characters shared with *L. unguiculatum*. The size and shape (hexagonal with linear walls) of the hyalocysts are similar to those of *L. octoblepharioides* subsp. *meijeri*.

The peristome of *L. candidum* is densely papillose somewhat like *L. octoblepharioides*, although it does not have the foveolate pattern characteristic of the latter species and it is more articulated at the base. Unlike *L. octoblepharioides*, there is a trend in the peristome of *L. candidum* to become smooth at the apex. Smooth peristome plates are observed in some species like *L. seychellarum* and in *L. glaucum* subsp. *vittii*.

The combination of apotypies: tumid leaves, closely vaginant, squarrose spreading to falcate secund or erect, and the lack of leaf-tip gemmae are unique for this species.

VARIATIONAL PATTERNS. *Leucophanes candidum* is morphologically a very plastic species. Variations in leaf orientation are observed within individual stems, the basal leaves being squarrose whereas the upper ones are erect-patent, the reverse pattern also occurs. There appears to be no geographical correlation with populations exhibiting these variations nor is

Fig. 383. Distribution of *L. candidum*.

WORLD, HOMOLOSINE

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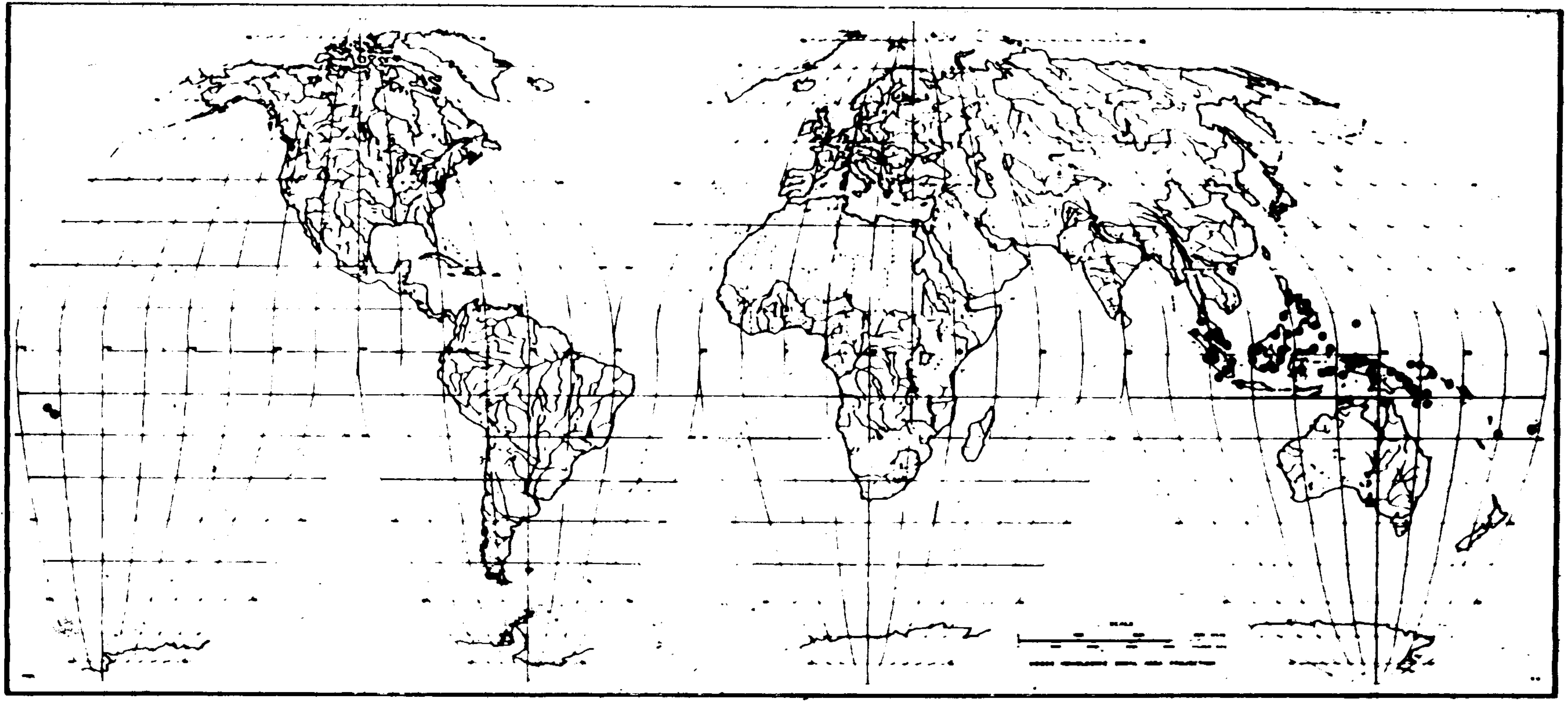

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there a significant number of specimens with critical ecological data to correlate habitat conditions and variations in growth-forms. It is my feeling that various factors may be responsible for the variations observed. Among these are: (1) A heterogeneous gene pool, (2) incomplete dominance, (3) pleiotropic genes affecting common developmental processes, (4) growth-form being affected by many genes, a case of polygenic inheritance, and (5) developmental or epigenetic constraints related to microhabitat conditions. Growth experiments, under controlled environmental conditions, will certainly give some information as to the possible causes underlying these variations in growth-form.

SPECIMENS EXAMINED. B (29), BM (67), CBG (4), EGR (2), FH (6), G (29), H (2), L (179), M (19), NY (31), PC (1), S (72), U (15).

LEUCOPHANES SUBG. TRACHYNOTUS (C. Muell.) Salazar-Allen *stat. nov.*

Lectotype: ***Leucophanes glaucum*** (Schwaegr.) Mitt.
Section Trachynotus C. Muell., J. Mus. Godeffroy 3(6): 57. 58. 1874.
Section B. Cardot. Mem. Soc. natn. Sci. nat. Math. Cherbourg 32: 1-84. 1900.
Subsection Heterostrosica Cardot, *in* Grand. Hist. Madag. 39: 148. 1915.

Plants 4 cm tall in densely foliose turfs, *stem* sparingly branched or branching in 2-3; *leaves* lanceolate from a narrow to broad base, strongly twisted to flexuose and loosely overlapping when dry, slightly spreading and less twisted when moist; acuminate, ± keeled throughout, hyaline lamina occupying 1/3-1/2 length of leaf; *hyalocysts* rectangular to irregularly hexagonal with strongly sinuose walls; *chlorocysts* in surface view above midleaf with short-oval lacunae; *costa* broad, strongly spinose to smooth in upper 1/3; transverse section of leaf with 2 layers of abaxial hyalocysts at base. Dioicous, male and female plants similar, *perichaetial leaves* not differentiated, *seta 5-8(15) mm long; capsules* 1.4-2.3 mm long, cylindrical, *peristome* with a prostome 2-3 cells high, haplolepideous of 16 papillose-striated to smooth teeth; *spores* 17-22.5

um, under SEM verrucate with a ± distinct reticular pattern or with scattered verrucae.

Leucophanes glaucum (Schwaegr.) Mitt.

Basionym: *Syrrhopodon glaucus* Schwaegr., Spec. Musc. Suppl. 2(2): 103. 181. 1827. Type: "In insula Rauwack Moluccarum et cum Octoblepharo albido in insulis Marianis cl. Gaudichaud." (Lectotype: " *Syrrhopodon glaucus*. Insula Rauwack. Moluc. (illegible). 1819. Gaudichaud no. 10." G-Hedw-Schwaegr!; Isotypes: G-Hedw-Schwaegr. (4 specimens)!, BM-Wilson (2 specimens)!, L-Mont!; syntype: G-Hedw-Schwaegr!).

Leucophanes cuspidatum C. Muell. Syn. 1: 83. 1849 *nom. illeg. incl. spec. prior* (*Syrrhopodon glaucus* Schwaegr., 1827) = L. glaucum (Schwaegr.) Mitt.

Leucophanes glaucum (Schwaegr.) Mitt., J. Linn. Soc. Bot. Suppl. 1: 25. 1859 (*Syrrhopodon*, 1827).

Leucophanes albescens C. Muell., Bot. Zeit. 22: 347. 1864. Type: "Pulo Penang Indiae Orientalis: Didrichsen Exp. transatlantica Danica. J. Lange." (Isotypes: "Original! Puloc-Pinang" FH-Fleisch!; BM- 2 specimens!, S!).

Leucophanes guadalupense Lindb., Oefv. K. Vet. Ak. Foerh. 21: 608. 1865. Type: "... in ins. Guadeloupe Antillarum legit Rev. Forsstrom." (Lectotype: "Guadeloupe. Leg. Rev. Forsstrom" NY!; Isotypes: S!).

Leucophanes smaragdinum (Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. 1877-78: 391. 1880 (Ad. 2: 655). Type: "Viti. Seemann inter No. 863." Not seen.

Leucophanes sordidum C. Muell., Forschungsr. Gazelle Bot. 4(5): 50. 1889. (*Leucobryum sordidum* C. Muell., 1883 hom illeg.). Type: "Nova Guinea. *Leucobryum* (Trachynotus) *sordidum* n. sp. (Isotypes: "New Guinea, (illegible) der Mc. Clear Bay an Baumen in Bergwalde. Dr. Naumann 18/vi.1875. JE!; FH-Fleisch!).

Leucophanes australe Broth., Oefv. Finsk. Vet. Soc. Foerh. 33: 96. 1891. Type: "*Leucophanes* (Tropinotus) *australe* Broth. in Bailey l.c.p. 96 (nomen solum). Patria Queensland, Freshwater Creek, Trinity Bay, ubi ad corticem arborum plantam femineam sterilem anno 1889 legit F.M. Bailey (n. 651)." (Lectotype: "651. *Leucophanes* (Tropinotus) *australe* Broth. Queensland Bellenden Ker Range, 1889, leg. M. Bailey." H-Broth.!; Isotypes: BM (3 specimens)!, FH!, S!).

Leucophanes bogoriense Fleisch., Musci Fl. Buitenzorg 1: 177. 1904. Type: "An Baumen im botanischen Garten von Buitenzorg entdeckt (F)." (Lectotype: FH!; Isotypes: FH!, JE!, S!).

Leucophanes glauculum C. Muell. ex Fleisch., Musci Fl. Buitenzorg 1: 181. 1904. Type: "von Bismarck-Archipel." (Lectotype: "Bismark Archipel. 1894. Leg. W. Micholitz, det. C. Muell." H-Broth!; Isotypes: L!, FH!).

Leucophanes neocaledonicum Card. et Ther., Diagn. Esp. Var. Nouv. Mouss. 8: 2. 1910. Type: "Forêt de Tao, de 100 a 610 m." (Holotype: "Nelle. Caledonie, reg. sept. a environs de Tao, 100 m. leg. Franc. Janvier 1910." PC!; Isotypes: PC!, FH-Fleisch!, G!, M!).

DISTINGUISHING FEATURES. *Leucophanes glaucum* is characterized by the densely foliose habit, the leaves erect, broad to narrow lanceolate, acuminate, contorted, keeled, with irregularly undulate margins, in transverse section, with the central chlorophyllous layer surrounded, at base, by 2-3 layers of abaxial hyalocysts and one layer on the adaxial side, above the base a single layer of sinuose-walled hyalocysts on each surface; the costa, abaxially, sharply spinose to nearly smooth, spinosity of the costa variable among leaves in the same plant.

DESCRIPTION. *Plants* robust to 4 cm. tall, in dense compact to loose turfs, glaucous-green to blue-green or browninsh-green. *Stem* dark orange-red to brown-red, branching monopodial, in transverse section round to irregularly triangular (100.0)137.5-150.0(167.5) um in diameter with large medullary cells surrounded by one layer of small, ± thick-walled cortical cells. *Leaves* 2.5-4.0(5.0) mm. long, 0.4-0.8 mm wide, straight to contorted when dry, slightly spreading and less twisted when moist, broad to narrow lanceolate tapering to an acuminate apex that terminates in a single cell, keeled throughout, narrow at insertion, in transverse section with a single layer of chlorophyllous cells surrounded, at base, by 1(2) layers of adaxial hyalocysts and 2-3 layers of abaxial ones; *hyaline lamina* 1/3 to 1/2 the length of leaf, uni- or bistratose; *margins* recurved below shoulders, plane above, with 1-5 rows of stereids, uni- or multistratose, irregularly serrate near apex or in upper third, teeth single or paired; *costa* strong, percurrent, abaxially spinose in upper 1/2 to 1/3 to ± smooth, teeth in rows, in transverse section with one layer of adaxial hyaline cells, 1-2 layers of adaxial stereids, 2-4 chlorophyllous guide cells continuous with central layer of chlorocysts, 1-4 layers of abaxial stereids covered by a layer of small, thick-walled hyalocysts; *hyalocysts* in surface view, on abaxial side, at base, (15.0) 27.5-50.0 (52.5) um long, 15.0-30.0 um wide, quadrate to rectangular, to irregularly hexagonal; at midleaf, 20.0-50.0 um long 12.5-20.0 um wide, oblong with sinuose lateral walls and concave bulging end walls; at apex, 10.0-32.5 um long, 5.0-15.0 um wide, irregularly quadrate to oblong. *Gemmae* fusiform-clavate, elliptical or slenderly ovate, tappering to base, papillose, variable in number of cells, branched or unbranched at base. *Rhizoids* orange-red papillose.

Dioicous, *perichaetial leaves* not differentiated, archegonia in groups of more than five. *Perigonial leaves* two to four to 0.9-1.3 mm long, ovate with a broad overlapping base that encloses the antheridia. *Calyptra* 1.5-2.4 mm long, cucullate, red and papillose at apex, stramineous below. *Sporophyte* terminal, monosetous, *seta* 5-15 mm long, red to brown red, sinistrorse, more or less papillose on the distal third, in transverse section 87.5-100.0(112.5) um wide; *operculum* 0.6-1.2 mm long, subulate rostrate; *urn* 0.8-1.4 um long, orange-red to brown-red darker at rim, erect to horizontal, cylindric to oblong elliptical, gradually narrowing to seta when moist, abruptly constricted when dry; *exothecial cells* 25.0-85.0 um long, 15.0-25.0 um wide, rectangular to quadrate oblong, thin-walled to + thickened longitudinally; *rim cells* 12.5-20.0 um long, 7.5-12.5 um wide, quadrate to short hexagonal, in 4-5 horizontal layers; *stomates* superficial, (17.5)20.0-25.0 um long, (12.5)20.0-25.0(37.5) um wide (10)12-14(18) in number, restricted to neck of capsule, *peristome* with a prostome 2-3 cells high, the teeth 80.0-115.0 um long, orange-red, inserted under the rim of the capsule, papillose to nearly smooth. Dorsal plate of teeth, with longitudinal striations ornamented with papillae, ventral plate irregularly foveolate or teeth with few to no papillae on both surfaces. *Spores* 17.0-22.5 um in diameter, spherical to oval, paraisopolar, papillose, under SEM gemmate to reticulate.

HABITAT. This species has been collected at the base and the trunk of trees, on decomposing logs, rock and soil. The species appears to occur in both acidic and basic rock substrata. It is most possible that, with an extended field study of different populations, habitat preferences may be determined, adding more information that will serve in the ellucidation of this morphologically complex species.

DISTRIBUTION. *Leucophanes glaucum* is distributed from India to Malesia, Japan, northestern Australia, Vanuatu, New Caledonia, the islands of the tropical Pacific and a disjunct population in Guadeloupe (West Indies).

PHYLOGENETIC RELATIONSHIPS. *Leucophanes glaucum* is closely related to *L.*

octoblepharioides in gametophytic and sporophytic character-states. The heterodictyee (Cardot, 1900) condition of the leaf with 2(3) layers of hyalocysts on the abaxial surface at base, pore size and midleaf cells with irregularly undulate lateral walls are shared with some populations of *L. octoblepharioides*. It also shares with this species the foveolate peristomal plate.

It is here proposed that *L. glaucum* evolved from a *L. octoblepharioides* type ancestor by proliferation of abaxial hyalocysts at base, and the development of strong rounded end walls and undulated lateral walls on the mid- and apical hyalocysts. The peristome is also considered to have evolved from a *L. octoblepharioides* type by a decrease in papillosity and development of irregularly defined longitudinal striations.

VARIATIONAL PATTERNS. *Leucophanes glaucum* is an extremely variable (plastic) species. Leaf shape, for example, may vary within the same plant, the lowermost leaves may be narrow and elongated, the uppermost ones wider and shorter. The costa is rather prominent in most members of the species particularly those of *L. glaucum* subsp. *glaucum*. Costal ornamentation of leaves within members of one population and also within a single individual vary considerably; some leaves have a strongly serrate costa whereas others have few to nearly no teeth. The aspect of the leaves (degree of contortion) is also variable. Populations from the Ellice Islands and Nuku-Hiva (Marquesas Islands) have stiff-looking leaves while those of Indonesia, SE Asia, Solomon Islands and Vanuatu tend to be strongly contorted. Sterile specimens can be readily identified to the specific category, but due to the extreme overlapping of morphological features, subspecific ranking is more difficult to determine unless sporophytes are produced.

It is my feeling that with additional field work and the critical examination of further collections bearing information on the ecology of this species, microhabitat preferences may be determined which will provide valuable information for the clarification of this morphologically plastic species.

SPECIMENS EXAMINED. ALTA (5), B (37), BM (82), EGR (3), FH (56), G (48), H (62), Je (2), L (114), M (18), MU (18), NY (42), PC (3), S (63), TRC (4), U (3).

Leucophanes glaucum (Schwaegr.) Mitt. subsp. **glaucum**

(Figs. 50-51, 60-61, 384-445, 478)

Leucophanes glaucum (Schwaegr.) Mitt.

Leucophanes beccarii Both. et Geh., Biblioth. Bot. 44: 6. 5. 1898. Type: [illegible] No. 138, Septembr. 1872, in reichlichen, schönen Fruchträschen". (Lectotype: "[illegible]a: Andai, Sept. 1872. G. R. O. Beccari." H-Broth!; Isotypes: FH (2 specimen[illegible], S!).

Leucophanes glaucescens C. Muell. ex Fleisch., Musci Fl. Buitenzorg 1:178. 23. 1904. Type: "Ferner Ost. Indien (ex Herb. Brit. Mus.) c. fr. (Kurz). (Isotype: FH-Fleisch!).

Leucophanes subglaucescens C. Muell. ex Dix., J. Linn. Soc. Bot. 43: 296. 1916. Type: "Timorlaut, 1891, leg. Micholitz, No. 8, herb. Brotherus in Herb. Kew." (Lectotype: BM-Broth!; Isotypes: BM-Broth!, FH-Fleisch. (2 specimens)!, S (2 specimens)!).

DISTINGUISHING CHARACTERS. *L. glaucum* subsp. *glaucum* is characterized by its strongly papillose peristome, the dorsal plate with irregular vertical striations ornamented with papillae and irregularly defined central circular depressions; the ventral plate densely papillose and foveolate. Variations in pattern of striations and papillosity of the dorsal plate are observed between teeth of the same peristome. Spores oval to spherical, paraisopolar, reticulate to densely verrucate.

Figs. 384-395. *L. glaucum* subsp. *glaucum*.

Figs. 384-385. Vegetative leaves. Scale=1 mm. New Guinea, Beccari, H; Bailey 1899, H; Marshall Islands, Horowitz 9669, G; Mioko, Fleischer, 406, FH).

Fig. 386. Apices. Scale=45 um.

Fig. 387. Young leaf. Scale=0.3 mm. (Australia, Bailey 1889, H).

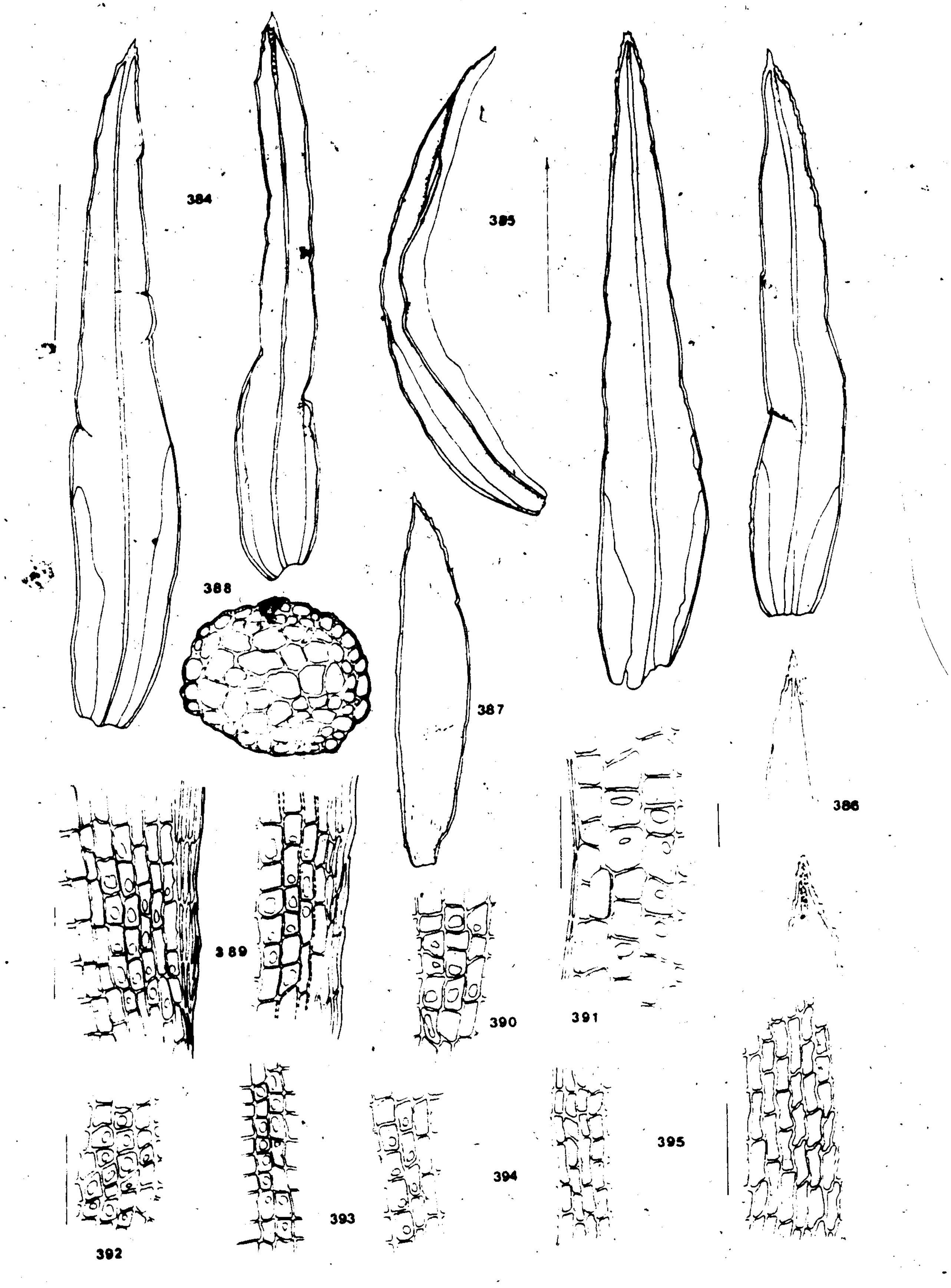
Fig. 388. Transverse section of stem. Scale=100 um. (Andaman, Kurz 2546, BM).

Fig. 389-395. Abaxial hyalocysts. Scale=100 um.

Figs. 389-393. Base. (Vanuatu, Salazar 3702, ALTA, PMA; Shortlands, H; Marshall Islands, Horowitz 9669, G).

Fig. 391. Hyalocysts next to costal area. (Micronesia, Herbst & Alberton 2777.0, B).

Figs. 394-395. Midleaf. (New Guinea, Beccari, H; Samoa, Schultze-Motel 4484, B).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Figs. 396-411. *L. **glaucum*** subsp. ***glaucum***. Scale = 100μm.

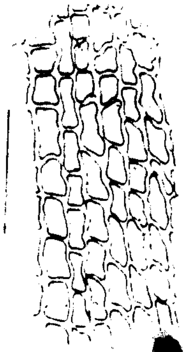
Figs. 396-399. Abaxial hyalocysts. (Java, Fleischer, FH; Solomon Islands, Milne 597, BM; Louisiades, Micholitz 232, L).

Figs. 396-397. Midleaf.

Figs. 398-399. Apex. (New Caledonia, 16831, H; Bismarck Arch., Fleischer 406, FH; New Guinea, Beccari, H; Samoa, Schultze-Motel 4484, B).

Figs. 400-411. Transverse sections of leaves at base. Scale = 100 um. (Borneo, Ooschot 1870, L; Caroline Islands, Forsberg 26094, L; Shortlands, Rechinger, H; Caroline Islands, Fosberg 26218, L; New Guinea, Beccari, H; Java, J. Moller, L; Bismarck Arch., Fleischer 406, L; Thailand, Touw 1147, NY; Java, S).

Fig. 410. Anomalous development of additional margin on the adaxial surface of costa. (Java, S).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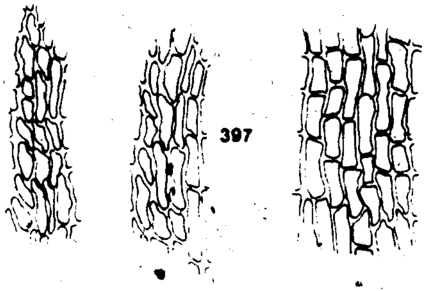
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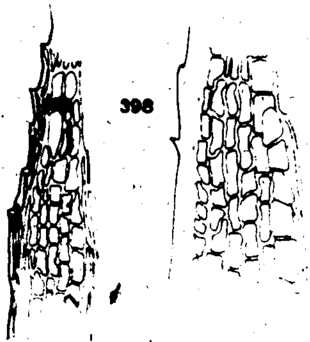
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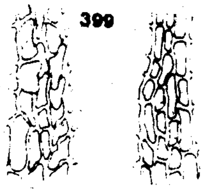
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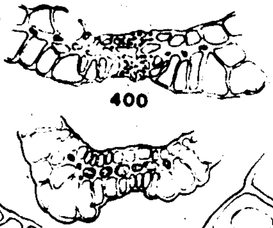
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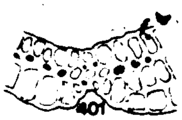
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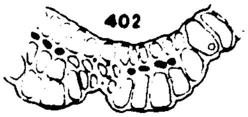
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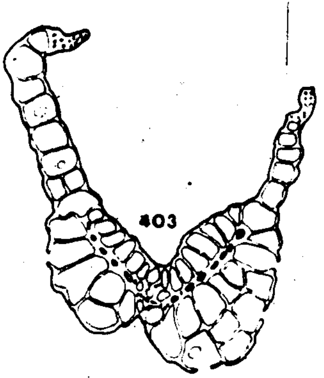
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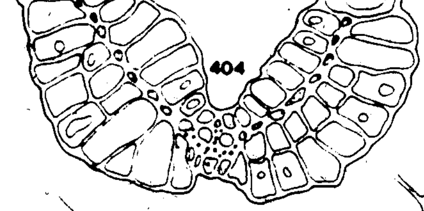
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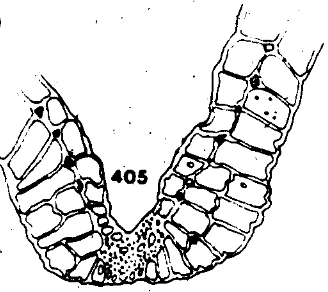
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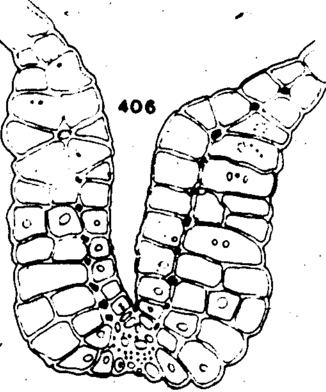
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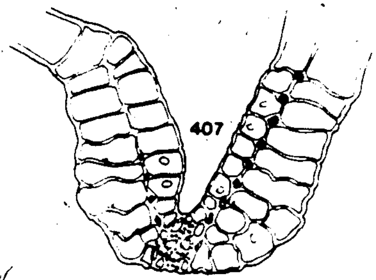
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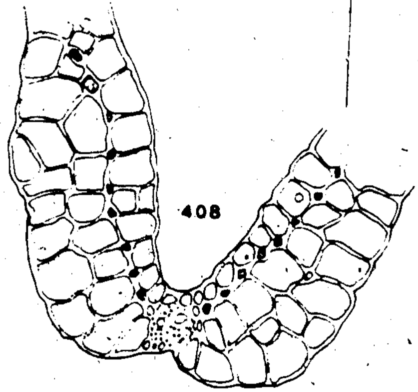
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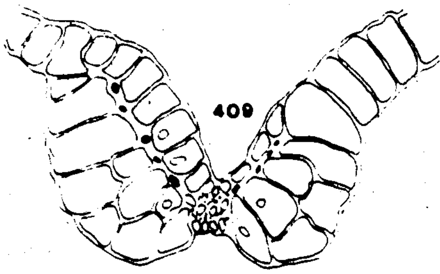
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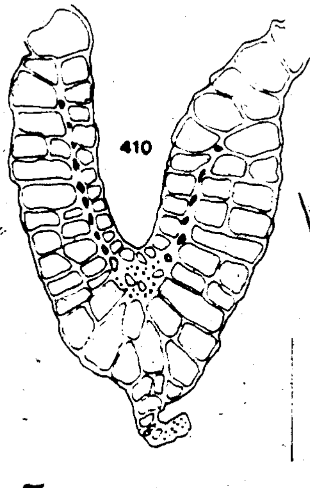
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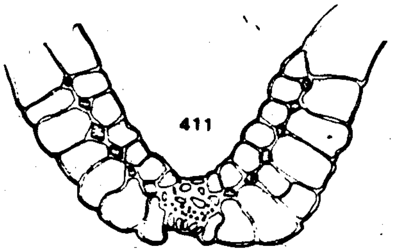
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Figs. 412-427. *L. glaucum* subsp. *glaucum*. Transverse sections of leaves. Scale = 50 um.

Figs. 412-414. Midleaf. (Micronesia, Whittier & Miller 1127, G; New Guinea, Beccari 138, H; New Guinea, Micholitz, L).

Figs. 415-417. Apex. (New Guinea, Beccari 138, H; Shortlands Ins., Rechinger a. 1905, H).

Fig. 418. Leaf-tip gemmae. Scale = 100 um. (Philippines, Robinson, H; Bismarck Arch., Fleischer 406, B; Australia, Weber B-31884, S).

Fig. 419. Perigonial leaves. Scale = 0.5 um. (Australia, Gribble a. 1894, G).

Fig. 420. Perigonium. Scale = 3.5 mm. (Ibid. 419).

Fig. 421. Branching of male plants. Scale = 3 mm. (Ibid. 419).

Fig. 422. Perichaetial leaf. Scale = 2.3 um.

Fig. 423. Calyptra. Scale = 1 mm. (New Guinea, Beccari 138, FH).

Fig. 424, 427. Rim cells. Scale = 50 um. (New Guinea, Beccari 138, H).

Fig. 425. Exothecial cells. Scale = 50 um. (Ibid. 424).

Fig. 426. Stomates. Scale = 50 um. (Ibid. 424).

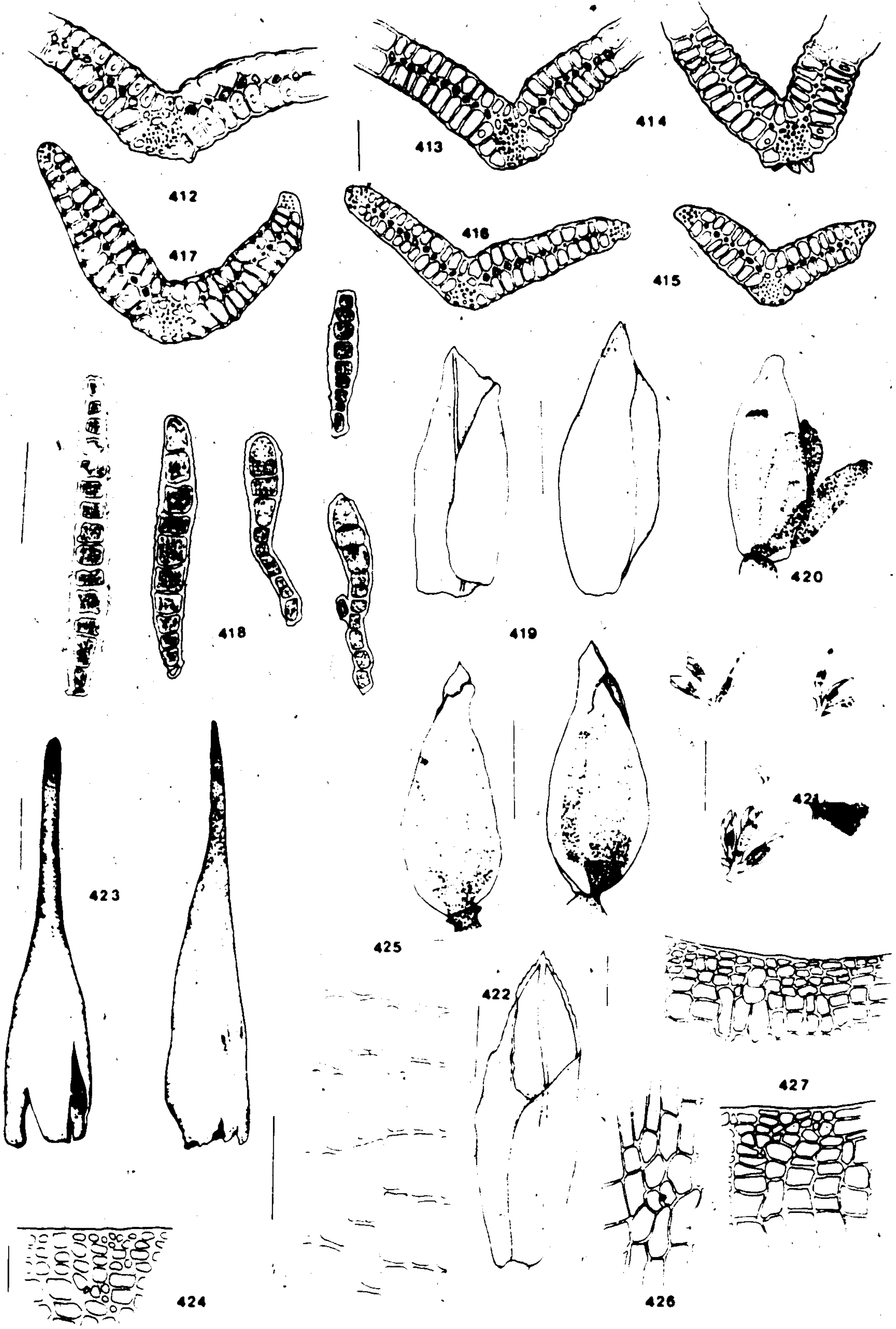
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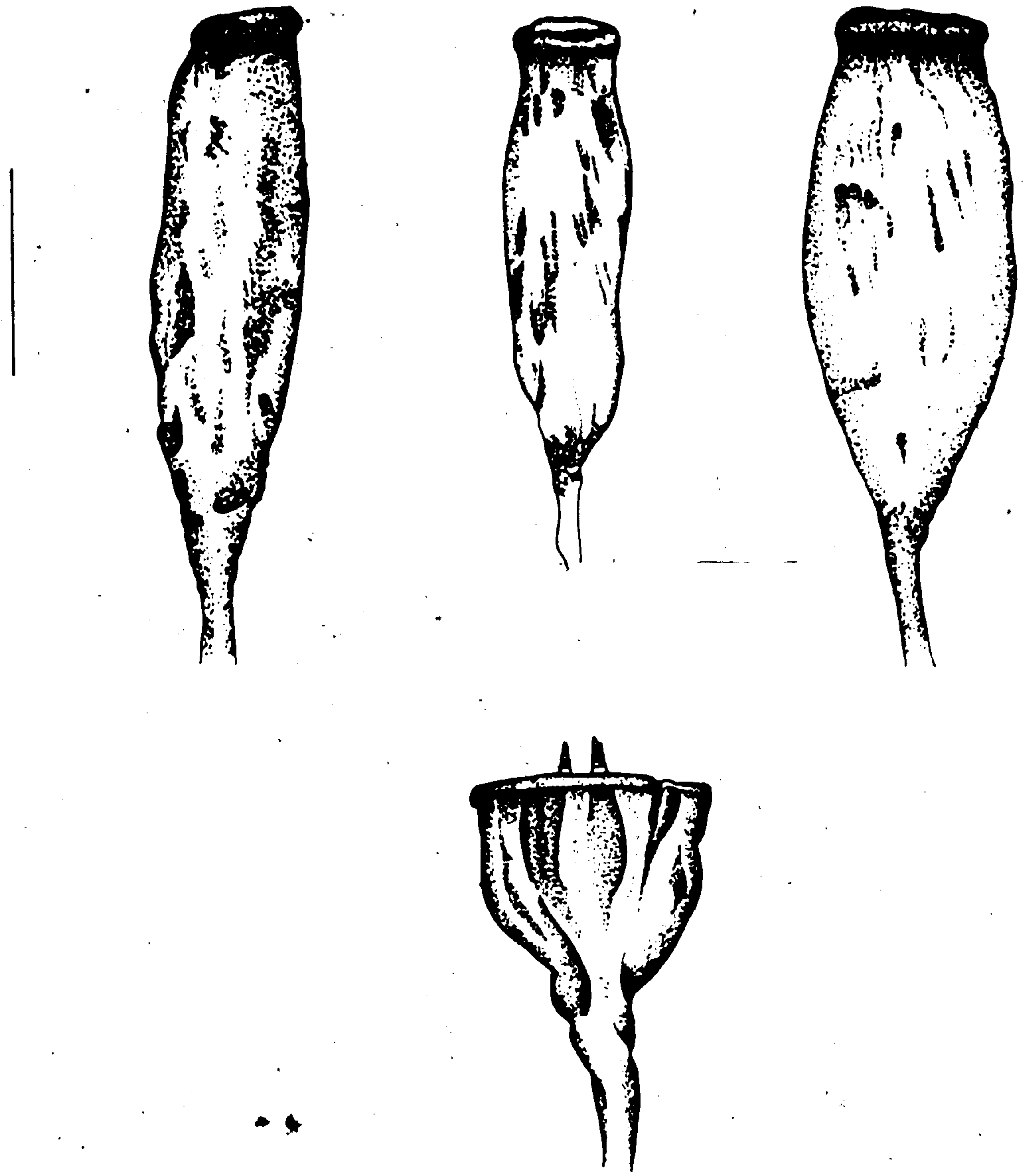
Fig. 428 *L. **glaucum*** subsp. ***glaucum***. Sporophytes. Scale = 0.5 mm. (New Guinea, Beccari 138, H; Micronesia, Whittier & Miller 1145, G).



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Figs. 429-434. *L. glaucum* subsp. *glaucum*.

Figs. 429-430. Pores on abaxial hyalocysts. (Banda Neira, Visser, L).

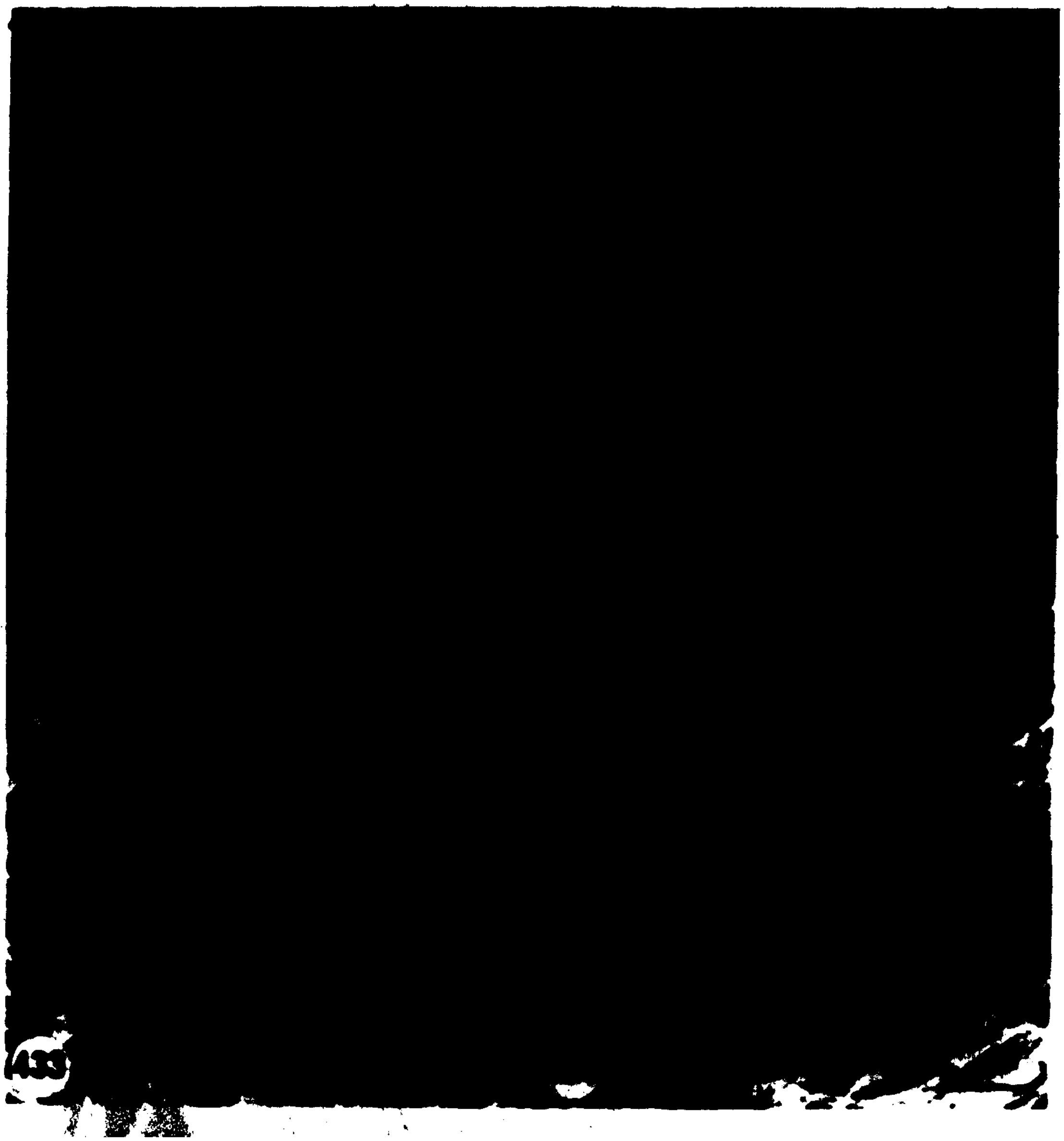
Fig. 429. Base.

Fig. 430. Apex.

Figs. 431-434. Peristome, papillose-striate. (New Guinea, Beccari 138, H).

Fig. 431. Scale = 50 um.

Fig. 432-434 Scale = 10 um.



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Figs. 435-440. *L. glaucum* subsp. *glaucum*. Peristome papillose-striate.

Fig. 435-439. Scale = 1 mm. (New Guinea, Beccari 138, H).

Fig. 437. Outer surface of peristome. (Banda Neira, Visser, L).

Fig. 438. Apex of tooth. (Ibid. 437).

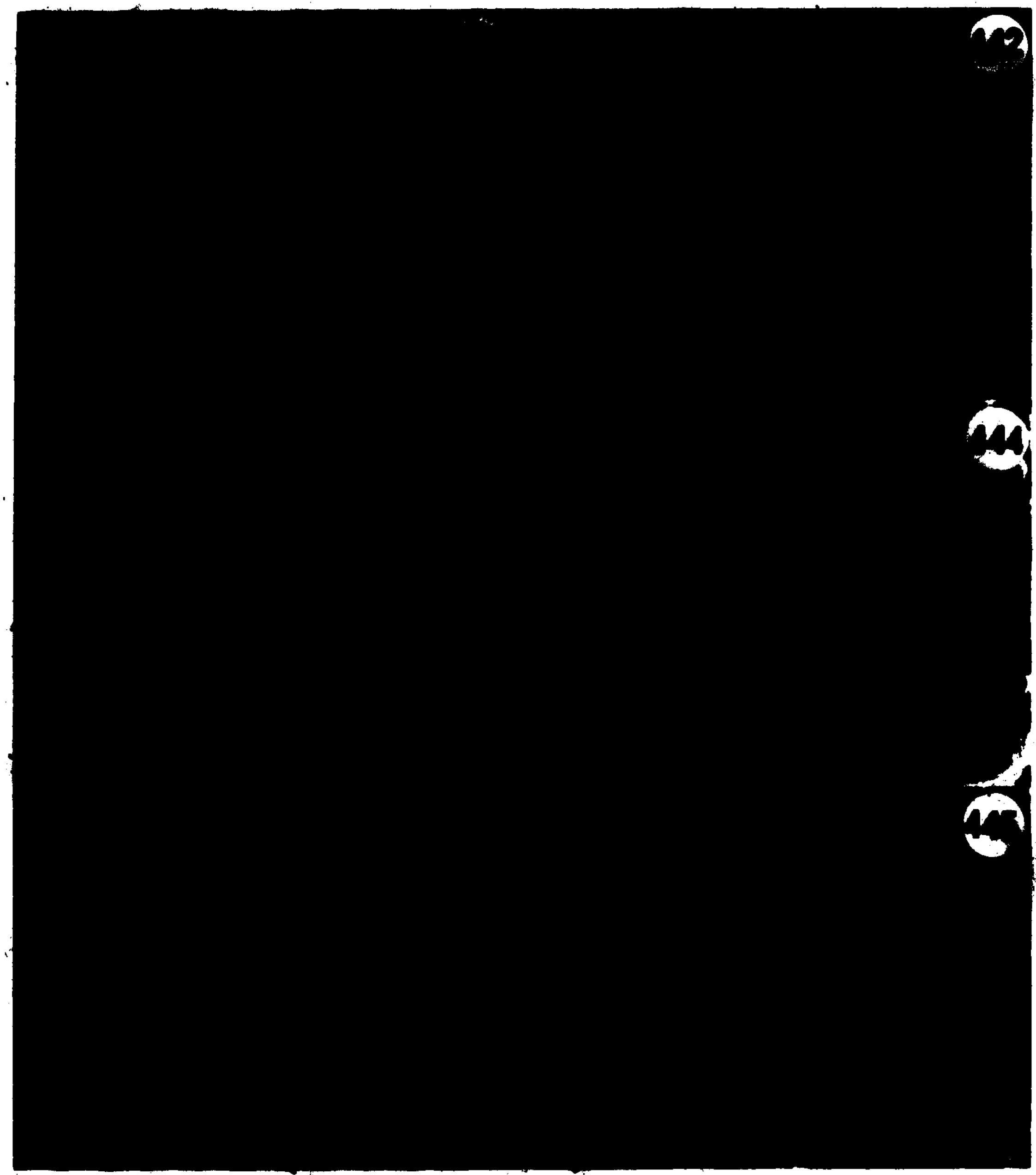
Fig. 439-440. Outer surface of teeth. Scale = 20 um. (Ibid. 437).

Fig[illegible]1-445. *L. glaucum* subsp. *glaucum*.

Figs. 441-442. Lateral view of (Micronesia, Whittier & Miller 1145, G). peristome, outer surface on the left. Scale=4 um.

Fig. 443. Habit. Scale=4 mm. (Pinang Ins., Deschamps, S).

Fig. 444-445. Spores. Scale=4 um. (New Guinea, Beccari 138, H; Banda Neira, Visser, L).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HABITAT. This subspecies is a corticolous epiphyte.

DISTRIBUTION. This subspecies is distributed in Southeast Asia, Australia, New Guinea and the islands of the tropical Pacific.

SPECIMENS EXAMINED. B (1), BM (2), FH (7), G (8), H (6), L (6), NY (1), S (1), U (1).

Leucophanes glaucum (Schwaegr.) Mitt. subsp. **nukahivense** (Besch.) Salazar-Allen *comb. et stat. nov.*

(Figs. 64-65, 446-460, 472-475, 478)

Leucophanes nukahivense Besch., Ann. Sc. Nat. Bot. ser. 7, 20: 20. 1894. Type: Sur une roche, dans la vallée d'Avao, à Taiohaë. (Jardin)". BM-Besch!; Isotypes: BM-Schimp!, G!, L!).

Syrrhopodon speciosus Schimp. in Jard., Bull. Soc. Linn. Normandie ser. 2, 9: 263, 264. 1875 *hom. illeg.* = *Leucophanes nukahivense* Besch. *fid.* Par., Ind. Bryol. 766. 1897.

Leucophanes nukahivense Besch. var. *theriotii* Card. ex Thér., Bull. Ac. Int. Geogr. Bot. 20: 97. 1910. Type: "Hab. Ile Maré (Loyalty), forêt claire, alt. 50 m., leg. Delord." (Holotype: "Ile Maré (Loyalty); forêt claire, alt. 50 m. Leg. Delord, 6 oct. 1909." PC-Thér!; Isotypes: FH-Fleisch!, G!, JE!, L!, M (2 specimens)!).

NOMENCLATURAL NOTE. The type specimen of this subspecies was collected by Jardin and sent to Schimper for identification (Jardin, 1875). Schimper named it *Syrrhopodon speciosus* although no description of the specimen was published. Bescherelle (1894) changed the name to

Leucophanes nukahivense indicating that: "J'ai dû, en transportant le *Syrrhopodon speciosus* dans le genre *Leucophanes*, changer le nom spécifique donné par Schimper, ce nom ayant été dejà employé par M.Ch. Mueller pour désigner une spèce de *Leucophanes* de Java (Sinops. Musc. I, p. 84) qu'il a placées depuis dans le genre *Schistomitrium* (Id. II, p. 537)." Thus, *Syrrhopodon speciosus* is an illegitimate homonym (Art. 64.1 of the International Code of Botanical Nomenclature, 1983).

DISTINGUISHING FEATURES. *L. glaucum* subsp. *nukahivense* is characterized by tall (to 4 cm), densely foliose turfs, leaves erect, stiff-looking, concave throughout; costa with few teeth on abaxial surface to smooth, margins undulate and irregularly recurved; peristome of articulated teeth, dorsal plate slightly papillose to smooth, ventral plate papillose, spores 13.5-17.5 um in diameter, paraisopolar, verrucate, the verrucae ornamented with granular depositions.

HABITAT. Plants of this subspecies have been collected on bark of angiosperm trees.

DISTRIBUTION. This only confirmed reports for this subspecies are from the Marquesas and the Loyalty Islands.

SPECIMENS EXAMINED. BM (1), L (1), S (1).

Figs 446-460. *L. glaucum* subsp. *nukahivense*. (Marquesas, Jones 1107, L).

Fig. 446. Vegetative leaves. Scale = 1 mm.

Figs. 447-449. Abaxial hyalocysts. Scale = 100 um.

Figs. 447-448. Base.

Fig. 449. Midleaf.

Fig. 450. Apex.

Figs. 451-454. Transverse sections of leaves. Scale = 100 um.

Figs. 451-452. Base.

Figs. 453. Apex.

Fig. 454. Midleaf.

Figs. 455-456. Scale = 0.5 mm.

Fig. 455. Capsule. Scale = 0.5 mm.

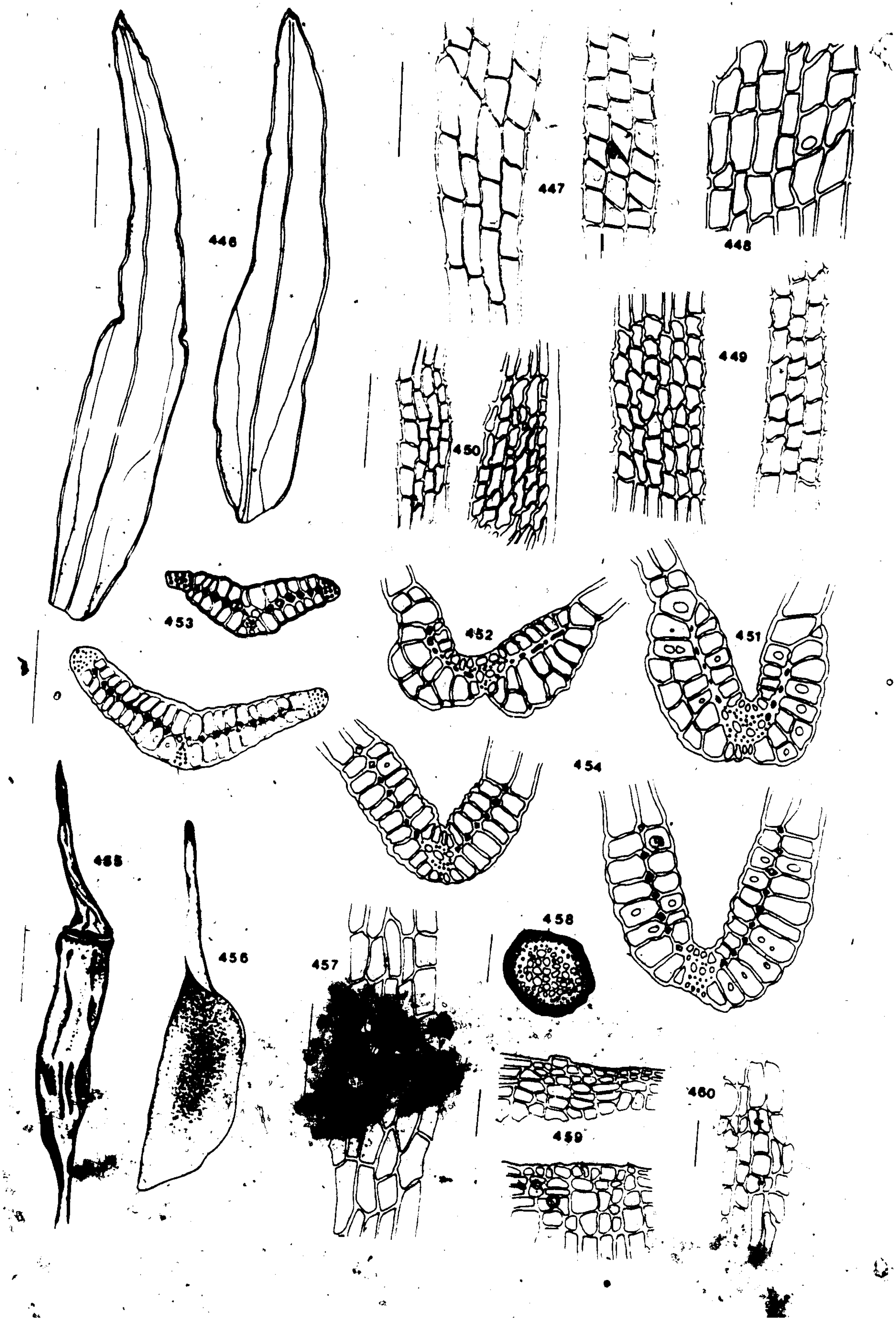
Fig. 456. Calyptra. Scale = 0.5 mm.

Fig. 457. Exothecial cells. Scale = 100 um.

Fig. 458. Transverse section of seta. Scale = 50 um.

Fig. 459. Rim cells. Scale = 50 um.

Fig. 460. Stomates. Scale = 50 um.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Leucophanes glaucum (Schwaegr.) Mitt. subsp. **vittii** Salazar-Allen

(Figs. 58-59, 62-63, 461-471, 476-478)

Type: "Plants of Papua Milne Bay District. Base of coconut palm, 2 m. Menapi, Cape Vogel Peninsula. Collected L. J. Brass on the 4th Archbold Expedition to New Guinea (March-November 1953), No. 21774." FH!

DISTINGUISHING FEATURES. *Leucophanes glaucum* subsp. *vittii* is characterized by its flexuose habit, loosely contorted leaves and the peristome of short (less than 100 um long), smooth teeth.

HABITAT. This subspecies is a corticolous epiphyte.

DISTRIBUTION. This subspecies appears to be endemic to New Guinea.

SPECIMENS EXAMINED. FH (1).

Figs. 461-471. *L. glaucum* subsp. *vittii*. (New Guinea, Brass 21774,type, FH).

Fig. 461. Vegetative leaves. Scale = 0.5 mm.

Figs. 462-464. Abaxial hyalocysts. Scale = 50 um.

Fig. 462. Base.

Fig. 463. Midleaf.

Fig. 464. Apex.

Figs. 465-467. Transverse sections of leaves. Scale = 100 um.

Fig. 465. Base.

Fig. 466. Apex.

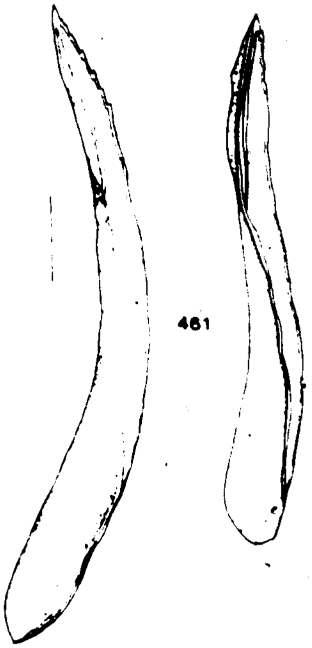
Fig. 467. Midleaf.

Fig. 468. Capsule. Scale = 0.5 mm

Fig. 469. Calyptra. Scale = 0.5 mm.

Fig. 470. Exothecial cells. Scale = 50 um.

Fig. 471. Rim cells. Scale = 50 um.



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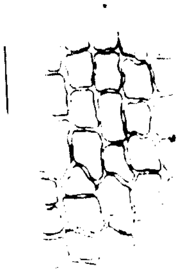

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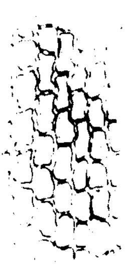

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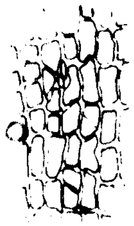

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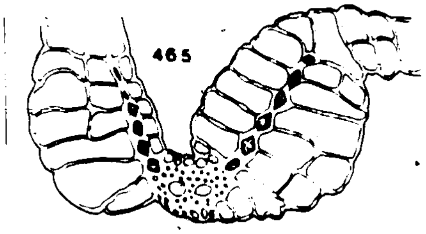

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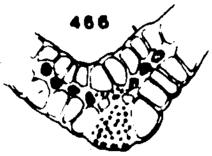

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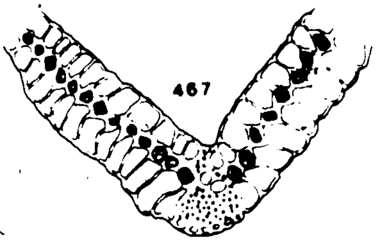

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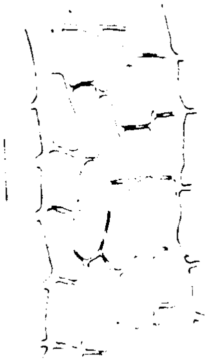

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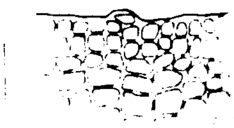


471

Figs. 472-477. *L. glaucum* subsp. *nukahivense*, and *L. glaucum* subsp. *vittii*.

Figs. 472-475. *L. glaucum* subsp. *nukahivense*. (Marquesas, Jones 1107, L).

Fig. 472-73. Peristome, external surface.

Fig. 472. Scale = 50 um.

Fig. 473. Scale = 20 um.

Fig. 474. Peristome. Inner surface. Scale = 20 um.

Fig. 475. Spore ornamentation. Scale = 2 um.

Figs. 476-477. *L. glaucum* subsp. *vittii*.

Fig. 476. Scale = 50 um. (New Guinea, Brass 21774, FH).

Fig. 477. Scale = 2 um.

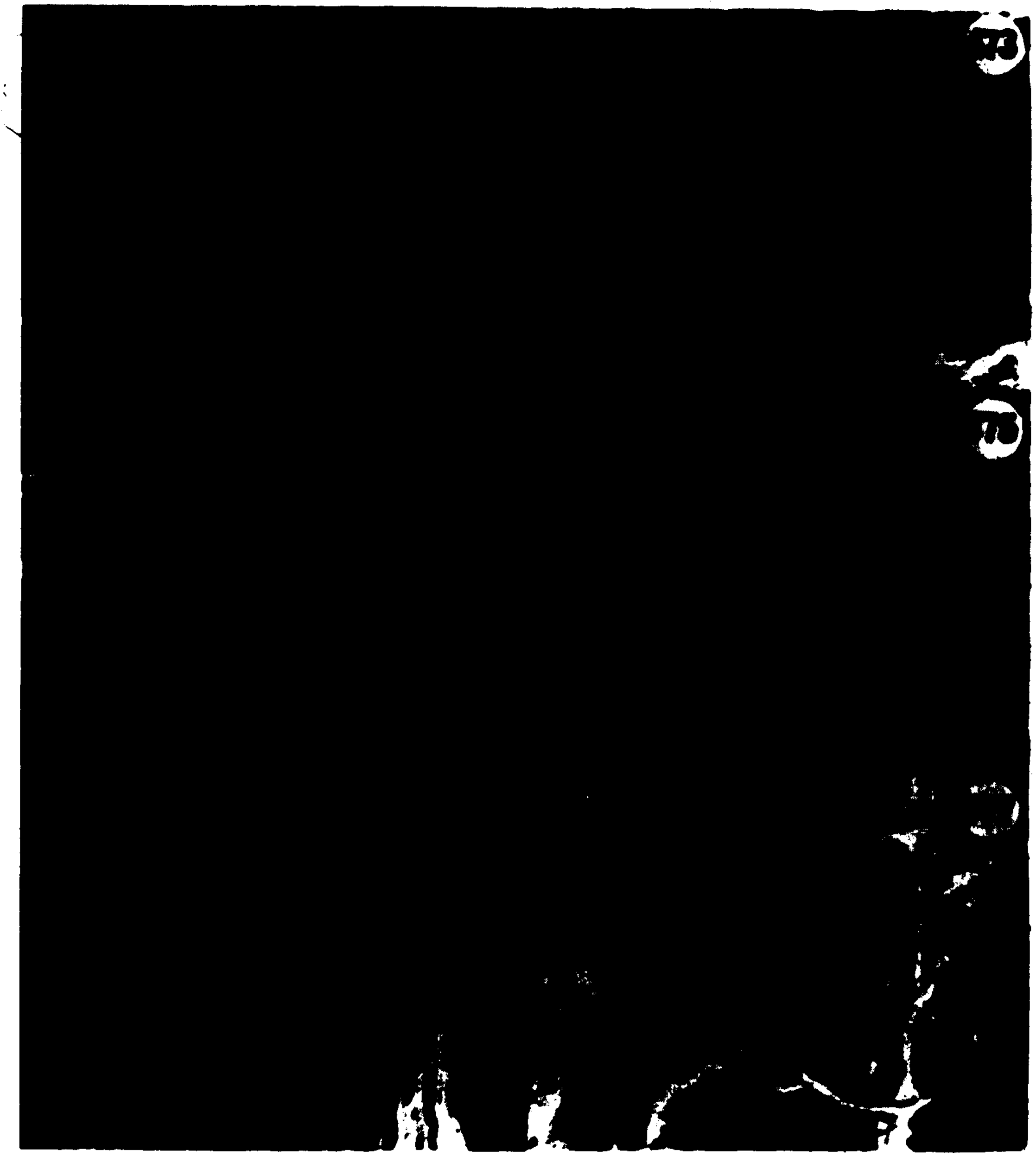
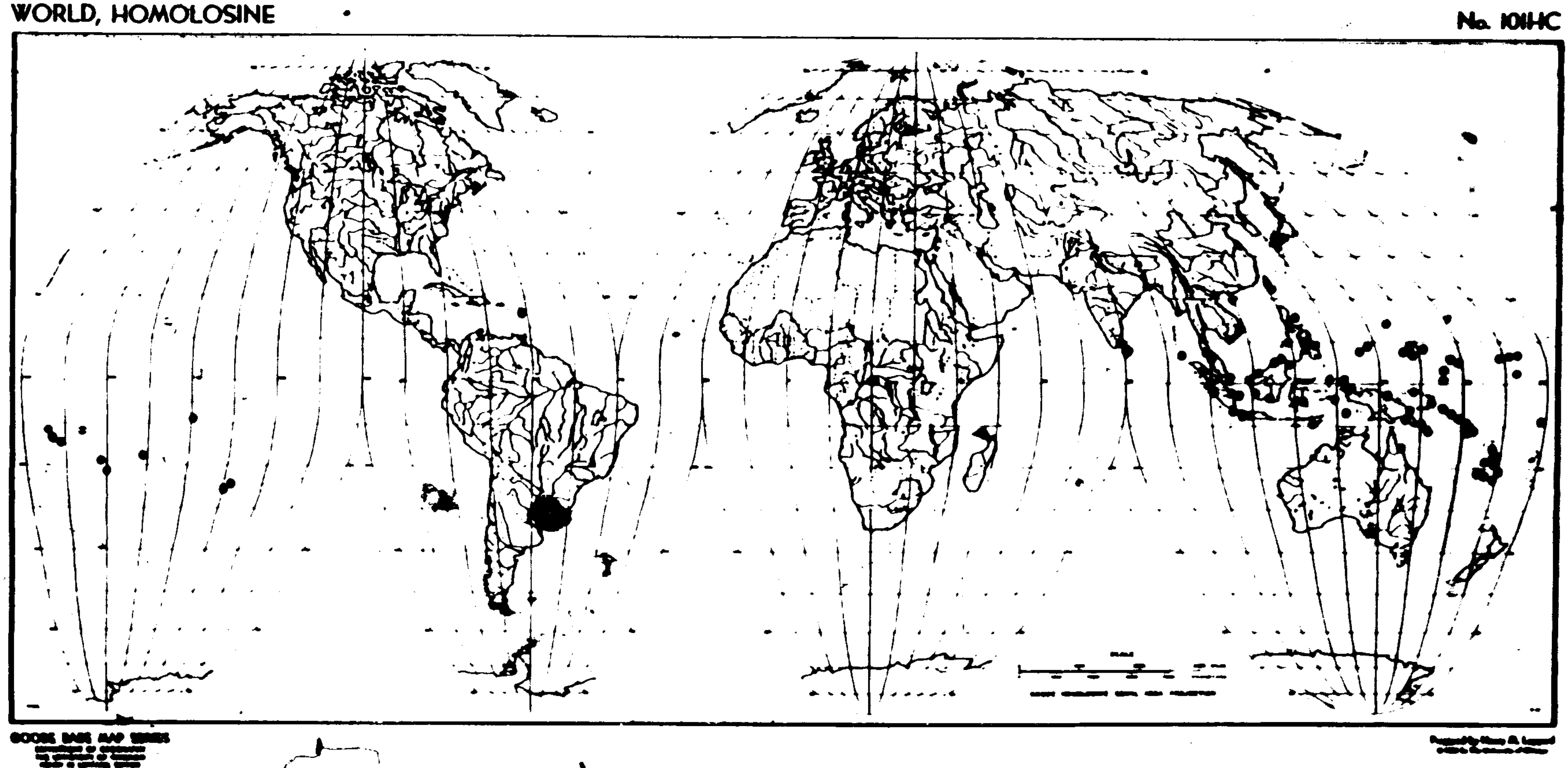


Fig. 478. Distribution of *L. glaucum*.

- ● Subspecies *glaucum*.
- ● Subspecies *nukahivense*.
- ◐ Subspecies *vitii*.


WORLD, HOMOLOSINE
No. 101HC
GOODE BASE MAP SERIES

VII. EVOLUTIONARY ASPECTS

1. RELATIONSHIPS OF *LEUCOPHANES* WITH OTHER MEMBERS OF THE CALYMPERACEAE

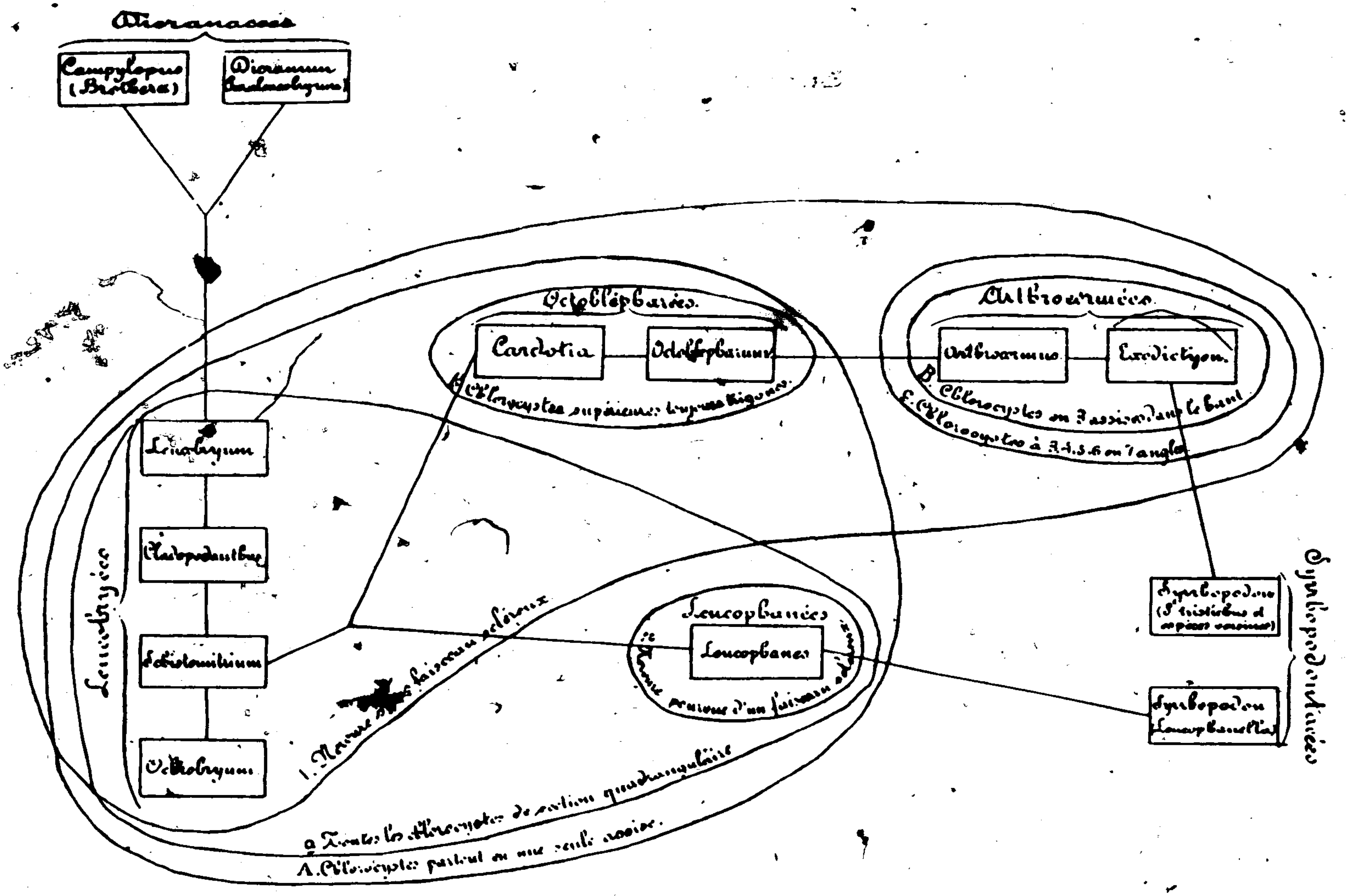
1. The Gametophyte. *Leucophanes*, in gametophytic and sporophytic characters, is markedly similar to *Exodictyon*, *Exostratum*, *Arthrocormus*, *Octoblepharum*, and *Syrrhopodon*. All these genera are acrocarpous, turf-forming mosses, with the stem having no central strand. The leaf structure, except in *Syrrhopodon*, consists of one or more layers of chlorophyllous cells surrounded by two or more layers of hyalocysts, the so called "leucobryoid" leaf structure. In *Exodictyon* and *Exostratum*, the multistratose condition of the leaf is the result of an expansion of the costa, concomitant with the loss of stereids (Cardot 1900, Ellis 1985). It appears that in *Arthrocormus* and *Octoblepharum*, the same process may have taken place in the formation of their leaf structure.

The leaf in *Leucophanes* has a distinct costa composed of guide cells, stereids and hyalocysts. In some species, e.g. *L. rodriguezii*, the costal area is surrounded by a layer of chlorophyllous cells, thus, resembling very closely the costal structure of *Exodictyon* and *Exostratum*. The lamina is a complex structure composed of two areas, a multistratose section of chlorocysts and hyalocysts and a hyaline area of only hyalocysts. The leaf structure in *Leucophanes* is unique for the genus and it appears that it originated independently of that of the other genera.

Scale leaves and perigonial leaves in *Leucophanes* are similar to those found in *Syrrhopodon*. The calyptrae in most species of *Leucophanes* is long persistent and may remain attached to the capsule after dehiscence as occurs in *Calymperes* and *Syrrhopodon*. Thus, the various gametophytic characters observed in *Leucophanes* indicate a close ancestral relationship with *Syrrhopodon*.

Cardot (1900) (Fig. 479), based mainly on gametophytic features, particularly leaf structure, suggested a close relationship between *Leucophanes* and *Syrrhopodon* (*sensu Leucophanella*). He indicated that in both genera the transverse section of the stem is similar,

Fig. 479. Cardot's proposed relationships among members of the Leucobryées, Octoblepharees, Leucophanées and Arthrocormées with the Syrrhopodontacées (*Syrrhopodon*) and Dicranacées (*Campylopus, Dicranum*).


Dicranacées
Campylopus (Brothera)
Dicranum
Leucobryacées
Leucobryum
Cladopodanthus
Schistomitrium
Ochrobryum
Octoblepharées.
Cardotia
Octoblepharum
C. Chlorocystes supérieurs trigones.
Arthrocormées.
Arthrocormus
Exodictyon.
B. Chlorocystes en 3 assises dans le bord
E. Chlorocystes à 3.4.5.6 en l'angle
Leucophanées
Leucophanes
Nervure pourvue d'un faisceau de stéréides
1. Nervure [illegible] faisceaux stéréides
2. Toutes les Chlorocystes de section quadrangulaire
A. Chlorocystes partout en une seule assise.
Syrrhopodontacées
Syrrhopodon (S. tristichus et espèces voisines)
Syrrhopodon Leucophanella

that is without a central strand and with a peripheral layer of cells that differ from the cortical ones only in size. The structure of the costa and margins are also very similar. The peristome, in both species, he described as non-dicranoid. *Exodictyon* and *Exostratum* were structurally related to *Syrrhopodon tristichus* Nees and closely related species. Andrews (1947) like Cardot (1900), proposed a close relationship between *Syrrhopodon (sensu Leucophanella)* and *Leucophanes* suggesting a homology between the hyalocysts of the cancellinae in *Syrrhopodon* and the basal hyalocysts of *Leucophanes*. He also indicated the structural similarities between the margins and the costa of these two genera. *Arthrocormus* was closely related to *Octoblepharum*. The major difference between these genera being the 2-3 layers of chlorocysts in the leaf of *Arthrocormus* as opposed to the single layer in *Octoblepharum*. For *Exodictyon*, Andrews (1947) suggested a close relationship with *Syrrhopodon*.

2. The Sporophyte. Sporophytically, *Leucophanes* is also very similar to *Exodictyon*, *Exostratum*, *Syrrhopodon* and *Arthrocormus*. All these genera have peristomes that are more or less papillose. In *Exodictyon* and *Exostratum*, Ellis (1985) reported (and personal observations) the occurrence of ridge-shaped thickenings, sometimes branched or anastomosing that may form simple or compound papillae. He has also reported central circular depressions on the teeth of *Exodictyon incrassatum*, on the dorsal plates of *E. dentatum* and, the ventral plates of *Exostratum sullivantii* and *E. blumei*. Ornamentations similar to those described by Ellis for the peristomes of *Exodictyon* and *Exostratum* have been observed in *Leucophanes*. More or less defined central circular depressions, here called foveolae, are present on one or both plates on the peristomal teeth of species of *Leucophanes*.

The peristomes of *Arthrocomus* (*A. schimperi* Dz. & Molk.) available for critical examination are papillose-striate, with coarse vertical striations on the dorsal plates and foveolate areas on the dorsal and ventral plates. Vertically striated plates similar to those of *Arthrocormus* have been observed in the highly derived lineage of *Leucophanes* subg. *Trachynotus* and in *L. octoblepharioides* subsp. *whittieri*. The peristomes of *Syrrhopodon* available for examination (e.g., *S. ciliatus* (Hook.) Schwaegr.) are densely papillose, the papillae branched, irregularly anastomosing and with more or less distinct foveolate areas. Fleischer (1900-1904) illustrated the peristome of *Syrrhopodon tristichus* Nees ex Schwaegr.; the central area of the dorsal plate has irregular depressions called "perforationem". These are similar to the foveolate areas observed in *S. ciliatus, Leucophanes* and some species of *Exodictyon*. Reese (1977) reported transverse striations on the papillose peristome teeth of *S. cryptocarpos* Doz. & Molk. Transverse striations have not been observed on the peristomes of species of *Leucophanes, Exodictyon, Exostratum, Arthrocormus* or *Octoblepharum*. Of the other genera in the Calymperaceae, Edwards (1979) has indicated that the peristome of *Hypodontium* is structurally closely related to that of *L. candidum*. *Hypodontium* has a peristome o[illegible] exostome teeth that are frequently shed with the operculum and 16 endostome teeth that have an irregular 2:3 pattern. The peristome in *Leucophanes candidum* is composed of a prostome of 32 segments (observed at the bases of the teeth), 16 simple teeth with a poorly developed 2:3 pattern. Thus it has a peristomial formula of (4":)2":'2(-3) (Edwards, 1979). It also appears that, at least, in some species, parts of the prostome may be shed with the operculum. The peristome of *Octoblepharum* differs in some structural details from those of other genera in the Calymperaceae. It consists of simple teeth with no trabeculae on the dorsal and ventral plates and the primary peristomial layer (PPL) has occasional variations in cell structure that are restricted to the bases of the teeth. Thus it has a peristomial formula 2(-3)":"2 z for a single tooth. Fleischer (1900-1904) indicated the presence of a prostome in the peristome of *O. albidum* Hedw. I have observed that in some populations of *O. albidum* the dorsal plates are strongly striated, the striations irregularly anastomosing unlike those observed in *Leucophanes* subg. *Trachynotus* and *Arthrocormus*.

Thus, based on the comparative structure of the gametophyte and sporophyte the following phylogenetic relationships can be postulated:

1. The sister-group of *Leucophanes* includes *Exodictyon, Exostratum, Arthrocormus* and *Octoblepharum*; the out-group, *Syrrhopodon* and related species.

2. *Leucophanes* shares with its sister-group the multistratose condition of the leaf with chlorocysts and hyalocysts. The leaf structure in these two groups appears to have arisen independently, perhaps by different developmental processes.

3. [illegible] structure between *Leucophanes* and *Syrrhopodon* could be postulated [illegible] of the perigonial leaves in *Leucophanes*. Basal hyalocysts of the pe[illegible] leaves in this genus appear to be homologous with hyalocysts of the cancellinae of *Syrrhopodon*.

4. Similarities at the peristomal level indicate affinities with both the sister group and the out-group. The plesiotypic condition of strongly papillose-foveolate peristome characteristic of some species of *Syrrhopodon*, *Exodictyon* and *Exostratum* is observed in the less derived members of *Leucophanes* subg. *Leucophanes*. The development of striations in the highly derived members of *Leucophanes* subg. *Trachynotus* is shared with species of *Arthrocormus*.

5. The presence of a distinct costa (symplesiotypic character), scale and perigonial leaves similar to *Syrrhopodon* suggest an ancestral relationship with members of this genus. Thus, the putative ancestor of *Leucophanes* and related genera must be sought in members of the genus *Syrrhopodon*.

6. Comparative developmental studies on leaf structure and monographic revisions of *Arthrocormus* and *Octoblepharum* are needed to propose a more defined scenario of the phylogenetic relationships between *Leucophanes* and its sister-group as well as its out-group.

7. Peristomial characters indicate that *Leucobryum* and related genera are not phylogenetically closer to *Leucophanes* but to the Dicranaceae. The leaf structure in *Leucobryum* is considered to have evolved independently, a case of convergent evolution.

2. RECONSTRUCTED PHYLOGENY OF THE SPECIES OF *LEUCOPHANES*

A systematic revision is not complete unless a careful evaluation of the char[illegible] used to define the taxa is performed. Many systematic studies, particularly in the last three decades, have emphasized the phylogenetic evaluation of characters used in formulating a phylogenetic hypothesis of the evolution of particular taxa. The phylogenetic hypothesis, thus derived, can be tested, modified or reevaluated in light of additional information (Wagner 1984). In bryophytes, from the early work of Koponen (1968) in the Mniaceae, others have followed in utilizing a phylogenetic approach. Among these are studies by Vitt on *Orthotricum* (1971[72]), *Macrocoma* (1982), *Macro*[illegible]*m* (1983) and *Seligeria* (1976); Vitt *et al.* (1985a, 1985b) on *Macromitrium* Delgadillo's (1975) treatment of *Aloinella* and *Crossidium*; Peterson's (1979) revision of the North American Dicranaceae; Shaw's (1980) treatment of the North American *Pohlia*; Buck's (1980) generic revision of the Entodontaceae; Bremer's treatment of *Schistidium* (1981); Horton's (1981) revision of the En[illegible] Churchill's (1981, 1985) studies of the Grimmiaceae and *Scouleria* respectively; Mishler and Churchill's (1984) proposed phylogeny of the bryophytes; Ellis' (1985) treatment of *Exodictyon* and *Exostratum*, Fife's (1985) generic revision of the Funariaceae and Rohrer's (1985) studies on Hylacomniaceae.

Character selection is of critical importance in the delimitation of the taxa to be evaluated. Characters selected in *Leucophanes* were based on their relative stability in the genus and their complexity (e.g., peristome structure). Complex characters are less likely to have evolved more than once and thus are less obscured by multiple parallelisms. Since no fossil record is known for the genus or closely related genera, character selection was based on the study of extant taxa. Out-group comparisons, with other genera of the Calymperaceae, particularly *Syrrhopodon, Calymperes, Exodictyon* and *Exostratum* were made to determine the polarity of character evolution (transformation series). In addition to out-group comparisons, the major evolutionary trends determined for the

Bryopsida (Edwards 1979; Crosby 1980; Vitt 1982b, 1984), particularly the haplolepideous, acrocarpous mosses, were also critically examined. All this information served as the primary basis for classifying characters as plesiotypic (ancestral) or apotypic (derived).

Twenty-two characters were selected for the phylogenetic evaluation of the species. The characters selected were assigned numerical values. The generalized or non-divergent (plesiotypic) state was given a value of zero (0), the derived (apotypic) state a value of one (1); intermediate states were considered as 0.5 and highly specialized as 2. Particularly important among the characters selected is peristome type and ornamentation.

The general evolutionary trend in the peristome of the Bryopsida has been postulated to be from a diplolepideous to a haplolepideous peristome, to the presence of rudimentary layers or the nearly complete lack of peristome. The diplolepideous condition is considered to be the most ancestral (plesiotypic), the other two, being derived from it (Crosby 1980; Vitt 1982b, 1984).

In *Leucophanes*, all the species have an arthrodontous haplolepideous peristome. Six types can be recognized on the basis of plate ornamentation (see section on Peristome). The evolutionary trends proposed for the peristome of *Leucophanes* is considered to have been from the strongly papillose-foveolate type to the striate and smooth types. Ornamentation on the plates is considered to have evolved from the plates being strongly papillose to becoming less papillose and striate or smooth. There is also variation in the organization of the papillae, from individual groups with no definite pattern to papillae partially fused into regular patterns or rim-like concretions around central circular depressions. Another type of ornamentation, perhaps also derived from the fusion of individual papillae is represented by longitudinal to semicircular thickenings. This last pattern is particularly characteristic of the African species of *Leucophanes*. A peristome similar to that of *L. octoblepharioides* is here proposed to represent the ancestral condition from which the other types were derived by reduction, fusion and perhaps suppression or loss of papillae concomitant with a shortening of the teeth.

The study of the external structure of spores has been used to distinguish between species and also to derive potential phylogenetic relationships (Horton, 1982). Due to the paucity and poor preservation of many samples available for critical examination and, the lack of comparative material of species from the sister group and the out-group, spore ornamentation is not used in the phylogenetic evaluation of *Leucophanes*. The peristome and other characters, with their evolutionary directions and variability are discussed below in alphabetical sequence. The distribution of apotypic and plesiotypic characters is indicated in Table 3. The calculated patristic relationships of the species of *Leucophanes* is illustrated by the use of a Wagner Dendrogram. The methodology for phylogenetic analyses follows that of Wagner (1952, 1962a, 1962b,1969, 1980, 1984). Sister group relationships and cladistic distances are illustrated by the use of a Hennig Cladogram according to Hennig (1965, 1966). The characters and their evolutionary directions are as follows:

Character A. Leaf size. Two states: plesiotypic, leaves medium size (L/W ratio= 7:1); apotypic, long, narrow leaves (L/W ratio= more than 8:1). This state is often correlated with leaf orientation particularly in *L. glaucum*.

Character B. Leaf orientation. Three states: plesiotypic, straight to flexuose; apotypic, (B) contorted to strongly twisted either individually or in spiral arrangement, and (B') squarrose to falcate-secund.

Character C. Leaf curvature. Two states: plesiotypic, leaves canaliculate to slightly keeled; apotypic, leaves strongly keeled to goitrous.

Table 3. The plesiotypic (-) and apotypic 0.5, 1, 1.5, 2, states of 22 characters selected in reconstructing the phylogeny of 13 species of <u>Leucophanes</u>. Numbers in parenthesis indicate character reversals.

CHARACTERS AND THEIR STATES	Octoblepharioides/ Octoblepharioides	Octoblepharioides/ Meijeri	Octoblepharioides/ Whittieri	Angustifolium	Seychellarum	Milleri	Serratulum	Rodriguezii	Molleri	Unguiculatum	Hildebrandtii	Renauldii	Scabridens	Candidum	Glaucum/glaucum	Glaucum/nukahivense	Glaucum/vittii
A Leaf size (ratio L:W). Medium 7:1, long 8-more:1	0.5	0.5	0.5	1	1	1	(2)	0.5	1	(2)	1	1	1	-	0.5	0.5	0.5
B Leaf orientation. Straight-flexuose/contorted-Squarrose to falcate secund	-	0.5	-	-	-	-	1	-	-	2^{B^1}	-	-	-	2^{B^1}	1	0.5	1
C Leaf curvature. Canaliculate to slightly keeled, strongly keeled to goitrous	0.5	0.5	0.5	0.5	0.5	0.5	1	1	-	1	-	-	0.5	1	1	1	1
D Marginal orientation. Straight to slightly recurved; strongly recurved to undulate.	0.5	0.5	0.5	-	0.5	0.5	-	1	-	-	-	0.5	-	-	1	1	1
E Margin Orientation. Serrate to dentate/smooth	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-

Table 3. (Continued)

CHARACTERS AND THEIR STATES	Octoblepharioides/ Octoblepharioides	Octoblepharioides/ Meijeri	Octoblepharioides/ Whittieri	Angustifolium	Seychellarum	Milleri	Serratulum	Rodriguezii	Molleri	[illegible]tum	[illegible]dtii	Renauldii	Scabridens	Candidum	Glaucum/glaucum	Glaucum/nukahivense	Glaucum/vittii
F Leaf apex. Acute to acuminate/ retuse to incised/spinose-erose	-	-	-	-	-	-	-	-	1	1	2	2	-	-	-	-	-
G Apex orientation. Straight/recurved.	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-
H Shape of lacunae. Oval/elongated	1	1	1	1	1	1	1	0.5	1	1	1	1	1	1	-	-	-
I Shape of midleaf hyalocysts. Hexagonal to rectangular/long rectangular/ short hexagonal.	-	-	-	-	-	-	-	-	1^{I}	1^{I}	-	$2^{I'}$	-	-	-	-	-
J Hyalocysts end walls. Straight/rounded	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
K Frequency of surface pores. Few at base and apex/many throughout	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
L Size of pores on cross-walls. 5:0-7.5/2.5-5 narrow slit-like	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-	-	-

Table 3. (Continued)

CHARACTERS AND THEIR STATES	Octoblepharioides/ Octoblepharioides	Octoblepharioides/ Meijeri	Octoblepharioides/ Whittieri	Angustifolium	Seychellarum	Milieri	Serratulum	Rodriguezii	Molleri	Unguiculatum	Hildebrandtii	Renauldii	Scabridens	Candidum	Glaucum/glaucum	Glaucum/nukahivense	Glaucum/vittii
M Layers of hyalocysts on each surface of chlorocysts. One or more than one abaxially (M)/more than one on both surfaces (M')	0.5^M	-	-	$2^{M'}$	-	-	-	-	-	-	-	-	-	-	1^M	1^M	1^M
N Length of costa. Percurrent/excurrent	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-
O Costal ornamentation. Smooth/s[illegible]	0.5	0.5	0.5	0.5	1	0.5	1	0.5	-	-	0.5	0.5	0.5	-	1	-	-
P Gemmae. Present/absent	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-
Q Sexual condition. Dioicous/synoicous	-	-	-	-	-	-	1	?	-	?	-	-	?	-	-	-	-
R Sexual dimorphism. Male and female plants similar/dwarf males present	-	-	-	-	-	-	-	?	-	?	-	-	?	1	-	-	-
S Perichaetial leaves. Not differentiated/ Differentiated.	[illegible]	1	1	1	1	1	-	?	-	?	-	-	?	1	-	-	-

Table [illegible] (Continued)

CHARACTERS AND THEIR STATES

	Octoblepharioides/ Octoblepharioides	Octoblepharioides/ Meijeri	Octoblepharioides/ Whittieri	Angustifolium	Seychellarum	Milleri	Serratulum	Rodriguezii	Molleri	Unguiculatum	Hildebrandtii	Renauldii	Scabridens	Candidum	Glaucum/glaucum	Glaucum/nukahivense	Glaucum/vittii
Seta length. T Long/short	1	0.5	1	0.5	1	-	0.5	?	1	?	1	1	?	-	1	1	1
Peristome. U Both plates papillose/ one plate less papillose (U)/Smooth (U')	-	-	1^U	-	1^U	-	-	?	[illegible]^U	?	1^U	1^U	?	-	1^U	1^U	$2^{U'}$
Type or ornamentation. V Papillose-foveolate/papillose-striated (v)/ papillose with semi-circular thickenings (V')/Smooth (V")	-	-	1	-	-	-	-	?	1.5V'	?	1.5V'	1.5V'	?	-	1V	1V	2V"
	5.5 A C D H M O S T	5 A B C D H O S T	7 A C D H O S T U V	7.5 A C H L M' O S T	8 A C D H L O S T U	4.5 A C D H O S	7.5 (A) B C H O [illegible]	4.5 A C D H L O	8.5 A F G H I' T U V'	11 (A) B' C E F G H I P	9 A E F H O T U V'	11.5 A D E F H I' O T U V'	3 A C H O	8.5 B C H K N P R S	9.5 A B C D J M O T U V	8 A B C D J M T U V	10.5 A B C D J M T U' V"

Character D. Marginal orientation. Two states: plesiotypic, straight to slightly recurved; apotypic, strongly recurved to undulate.

Character E. Margin ornamentation. Two states: plesiotypic, serrate to dentate; apotypic, smooth to nearly smooth.

Character F. Leaf apex. Three states: pleisotypic, leaf acute or acuminate; apotypic, apex retuse to incised; apex spinose-erose. The retuse to incised apex appears to have arisen by degeneration of the most apical cells, while the spinose-erose one appears to be the result of an apical expansion of a strongly spinose costa.

Character G. Apex orientation. Two states: plesiotypic, apex straight; apotypic, apex recurved. This character is closely related to Character F. Leaves with retuse to incised apex are usually recurved. This is particularly observed in African species of *Leucophanes*.

Character H. Shape of lacunae between contiguous rows of chlorocysts above midleaf. Two states: plesiotypic, lacunae short-rhomboidal the size of 1(2) chlorocysts or less; apotypic, lacunae elongated, oblong, 2-3 (or more) chlorocysts long.

Character I. Shape of midleaf abaxial hyalocysts (surface view). Three states; plesiotypic, leaf cells rectangular to irregularly hexagonal (ratio 5-7:1); apotypic, (I) leaf cells long rectangular (ratio 8:1 or more), to (I') short and irregularly hexagonal (ratio 1:1, 2:1).

Character J. Hyalocyst end walls. Two states: plesiotypic, straight to nearly straight walls; apotypic rounded to broadly dove-tailed. Cells with rounded end walls may appear sporadically in some groups characterized mostly by rectilinear walls.

Character K. Frequency of surface pores on the hyalocysts. Two states: plesiotypic, few at base and apex; apotypic, many throughout the leaf.

Character L. Size of hyalocyst pores on the transverse walls. Two states: plesiotypic, pores 5.0-7.5 um in diameter, oval, elliptical or nearly circular; apotypic, pores 2.5-5 um in diameter, narrow and slit-like.

Character M. Layers of hyalocysts on each surface of the chlorophyllous layer. Three states: pleisotypic, a single layer of hyalocysts on each surface; apotypic, more than one layer abaxially at base and a third state with hyalocysts proliferating on the adaxial and abaxial surfaces of the central chlorophyllous layer.

Character N. Length of the costa. Two states: plesiotypic, ending just below the apex or at the apex (percurrent); apotypic: excurrent.

Character O. Costal ornamentation. Two states: plesiotypic, smooth; apotypic, abaxially dentate to serrate.

Character P. Leaf-tip gemmae. Two states: plesiotypic, gemmae present; apotypic, gemmae absent.

Character Q. Sexual condition. Two states: plesiotypic, dioicous; apotypic, monoicous.

Character R. Sexual dimorphism. Two states: plesiotypic, male and female plants morphologically similar; apotypic, production of dwarf males.

Character S. Perichaetial leaves. Two states: plesiotypic, perichaetial leaves similar to vegetative leaves; apotypic, perichaetial leaves differentiated, with a long hyaline base covering the vaginula and lower portion of the seta.

Character T. Seta length. Two states: plesiotypic, long seta from 7-10 mm. or more; apotypic, short seta, less than 7 mm long.

Character U. Peristome. Distribution of ornamentation on the plates. Three states: plesiotypic both plates papillose; apotypic, (U) one plate less papillose than the other and, (U') both plates smooth.

Character V. Type of peristomal ornamentation. Four states: plesiotypic, papillose-foveolate; apotypic: (V) papillose/striated, (V') papillose with longitudinal to semi-circular thickenings, and the fourth state, (V'') smooth.

Based on the study of herbarium and living material, and the phylogenetic analysis of 22 characters and their states, three major species-complexes or lineages are distinguished in *Leucophanes* (Fig 480, 481). I have taxonomically recognized these lineages at the subgeneric level. Thus, three subgenera are proposed, *Leucophanes*, *Leionotus* and *Trachynotus*. Subgenus *Leucophanes* as stated in the ICBN (1983) (Art. 22.1) includes the type species for the genus, that is *L. octoblepharioides*. For the other subgenera, the earliest validly published names are those proposed by Mueller (1874) for Sections Leionotus and Trachynotus (Table 1). Although they have no priority at the Subgeneric rank, I have decided to retain them instead of creating new names. Subgenus *Leucophanes* includes two distinct clades. The first clade includes *L. angustifolium, L. milleri, L. octoblepharioides, L. rodriguezii, L. serratulum* and *L. seychellarum*; the second clade *L. hildebrandtii, L. molleri, L. renauldii* and *L. unguiculatum*. Subgenus *Leionotus* includes one species, *L. candidum* and subgenus *Trachynotus* includes *L.*

ig. 480. Wagner Dendrogram of the phylogenetic relationships among species of ***Leucophanes***, as determined by an analysis of selected character-states and their evolutionary trends.

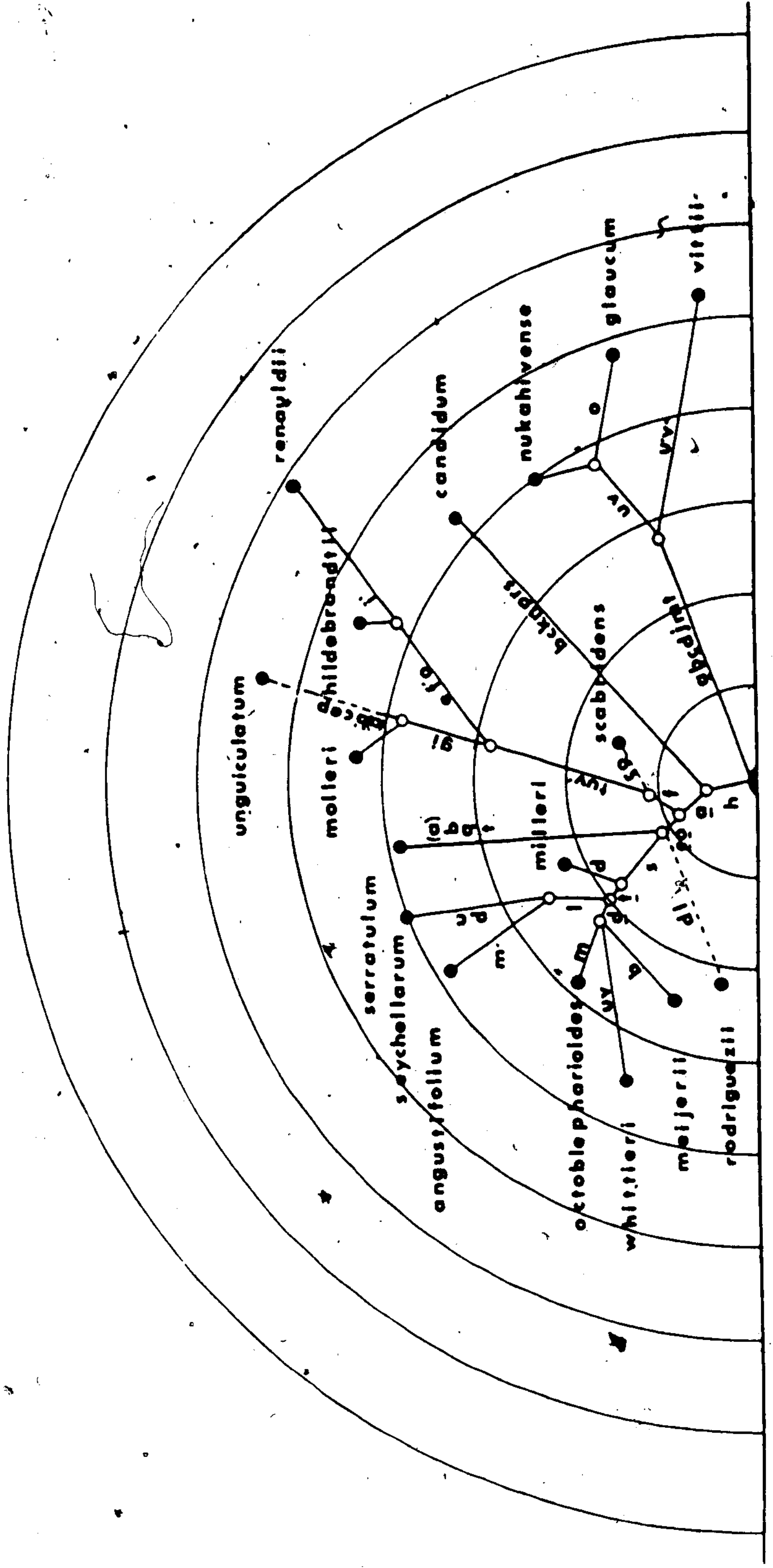
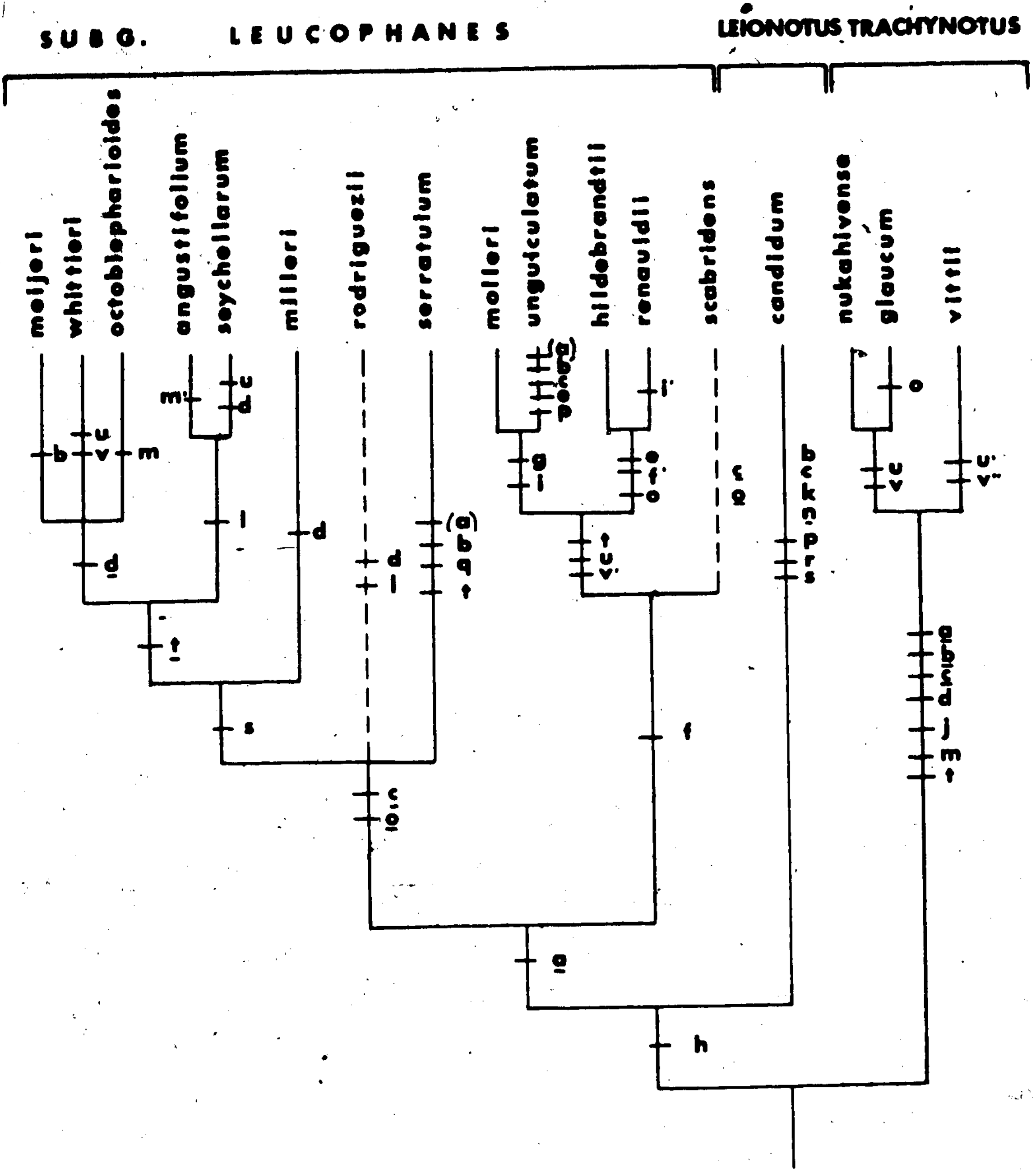

vitelli-
glaucum
nukahivense
candidum
renauldii
hildebrandtii
unguiculatum
molleri
scabridens
milleri
serratulum
seychellarum
angustifolium
oktoblepharioides
whittieri
meijerii
rodriguezii

Fig. 481. Hennig cladogram illustrating the relationships among the species of *Leucophanes* as determined by an analysis of character-states and their evolutionary trends.


SUBG. LEUCOPHANES
LEIONOTUS
TRACHYNOTUS
meijeri
whittieri
octoblepharioides
angustifolium
seychellarum
milleri
rodriguezii
serratulum
molleri
unguiculatum
hildebrandtii
renauldii
scabridens
candidum
nukahivense
glaucum
vittii
b
u
v
m
m'
u
d
d
l
d
t
s
d
l
(a)
b
q
t
c
o
(a)
b
c
e
g
i
i'
e
f'
o
t
u'
v'
f
b
c
k
n
p
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s
o
u
v
u'
v''
a
b
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d
j
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t
a
h

glaucum. The phylogenetic relationships of these subgenera are proposed as follows.

SUBGENUS *LEUCOPHANES*

1. The *L. angustifolium*, *L. milleri*, *L. octoblepharioides*, *L. serratulum*, *L. rodriguezii*, and *L. seychellarum* lineage.

All of these species are more or less similar in gametophytic and sporophytic characters. The transverse section of the leaf is composed of a central layer of chlorocysts surrounded, on each surface, by one layer of hyalocysts. In some populations of *L. octoblepharioides* and in *L. angustifolium*, hyalocysts on the abaxial side of the leaf at base proliferate to form two irregular layers. In *L. angustifolium*, additional layers of hyalocysts develop on the adaxial surfaces; this is considered apotypical for this species. Some populations of *L. angustifolium* have a single layer of hyalocysts through most of their leaf length, this condition perhaps suggesting the ancestral state. The peristome of the four species in this lineage is composed of 16 slender, strongly papillose-foveolate teeth with a prostome 2-3 cells high.

In this species group, *Leucophanes octoblepharioides* appears to be closely related to *L. angustifolium*. Intermediate forms of *L. angustifolium* approach very closely the habit and leaf structure of *L. octoblepharioides*. Despite the presence of these intermediates, the two species are quite distinct through most of their range. Both species have also been observed in mixed collections; in such, each species retains its characteristic pattern of structural features. Moreover, while *L. angustifolium* occurs in inland forests, *L. octoblepharioides* grows in both inland and littoral forests; also, the former species has a much wider geographical distribution extending from Southeast Asia and the tropical Pacific to Africa. I consider that *L. octoblepharioides* is an older species, that originated in lowland tropical rain forests and is, at the present time, actively radiating into littoral areas in the islands of the tropical Pacific and perhaps also in Asia (e.g., Japan). *L. angustifolium* is here considered to be derived from a *L.*

octoblepharioides- type ancestor of inland forests.

Leucophanes rodriguezii and *L. seychellarum* are closely related to *L. octoblepharioides* in the transverse section of their leaves. *Leucophanes seychellarum* resembl[illegible]*gustifolium* in its long, narrow leaves although the margins and costa are mo[illegible]y dentate. The peristome teeth also differ from *L. angustifolium* and *L. octoblepharioides* in having p[illegible] dorsal plates and papillose ventral plates. The dentate apex and spinose costa of *L. seychellarum* are morphologically similar to those of *L. serratulum*. *Leucophanes rodriguezii* in its strongly recurved, keeled leaves resembles members of *L. glaucum*, but the size and shape of its hyalocysts are closer to those of *L. octoblepharioides*. Structurally, *L. milleri* is very close to *L. octoblepharioides*. It has a more robust habit and it has retained the plesiotypic character of a long seta. In spore ornamentation, *L. milleri* is closely related to *L. serratulum* and *L. seychellarum*. All these species have grossly verrucate to short-baculate spores with irregular deposition of granular material. *Leucophanes seychellarum* and *L. milleri* appear to have been derived in insular isolation from a *L. octoblepharioides*-type ancestor. *L. serratulum* is the only synoicous species in *Leucophanes*. The leaves with strongly dentate margins, a spinose costa and, rectangular hyalocysts with very concave surface walls are similar to those of *L. seychellarum*. The peristome is strongly papillose-foveolate suggesting close affinities with *L. octoblepharioides* and related species.

2. The *L. molleri*, *L. unguiculatum*, *L. hildebrandtii* and *L. renauldii* lineage.

In habit and other characters these four species are markedly similar to one another. All four have leaves that, in transverse section, have one layer of hyalocysts on each surface of the central layer of chlorocysts (a symplesiotypy); the peristome is papillose with bar-like thickenings that are more or less rectilinear or are arranged in semi-circular configurations, to peristomes with nearly smooth teeth (e.g. *L. hildebrandtii*). No sporophytes are known for *L. unguiculatum*, but the long-rectangular hyalocysts of the leaves and the curved retuse apex with large cells are similar to those observed in *L. molleri*.

It seems that these four African species arose from a *L. octoblepharioides*-type ancestor; *L. molleri* and *L. unguiculatum* diverging early by the development of long rectangular cells while another branch gave rise to the putative ancestor of *L. hildebrandtii* and *L. renauldii*.

SUBGENUS *TRACHYNOTUS*

The *Leucophanes glaucum* lineage.

These species appear to be closely related to members of the Subgenus *Leucophanes*. The size of hyalocysts and the presence of two layers of hyalocysts on the abaxial side of the leaf at base are shared with some populations of *L. octoblepharioides* and *L. angustifolium*. The peristome with the inner plates papillose-foveolate, also suggests an ancestral relationship with members of Subgenus *Leucophanes*.

Of the three subspecies, *L. glaucum* subsp. *glaucum* and *L. glaucum* subsp. *vittii* are very similar in spore structure. Both have spores that are densely verrucate, with fusion of ornamentation that give the spore a reticulate-type pattern. Spores of *L. glaucum* subsp. *nukahivense* are sparsely papillose and strongly isopolar when compared with those of the other two subspecies. Unlike the spores, the peristomes of *L. glaucum* subsp. *glaucum* and *L. glaucum* subsp. *nukahivense* appear to be closely related. The peristome of the latter subspecies consists of articulated, sparsely papillose teeth closely resembling, at the base, the teeth of *L. glaucum* subsp. *glaucum*. The peristome of *L. glaucum* subsp. *vittii* consists of short, stubby, smooth teeth. This subspecies is thought to have developed its peristomal structure by a reduction in size of the teeth concomitant with a loss of papillae and striations, perhaps, in relation to adaptations to drier habitats. The gametophytes in this subspecies are small, with flexuose leaves that have short laminar hyalocysts with collenchymatous walls.

SUBGENUS *LEIONOTUS*

The *Leucophanes candidum* lineage.

This species represents a lineage in itself perhaps diverging early from the common ancestor shared with Subgenus *Leucophanes*. The transverse section of the leaves, with one layer of hyalocysts on either side of the chlorophyllous layer, the irregularly papillose-foveolate peristome and spore ornamentation suggest close affinities with members of Subgenus *Leucophanes*. *Leucophanes candidum* is a very distinct, although plastic species. The following combination of characters: tumid leaves, hexagonal and inflated hyalocysts, narrow costa, peristome strongly papillose and irregularly foveolate, and spore size, clearly separate this species from the rest.

Hypothetical Ancestor

By examining the different evolutionary trends presented in the Wagner Dendrogram, it is possible to derive a hypothetical ancestor to all species of *Leucophanes* and, also correlate the major divergences to the evolution of important characters as they occur in different lineages or clades. The ancestor of the genus is thought to have been similar in habit and structure to plants of *L. milleri* and *L. octoblepharioides* (particularly those populations with a single layer of hyalocysts on each side of the chlorophyllous layer). The plants were probably tall, the stem without a central strand, the leaves lanceolate (7-8:1), acuminate, with leaf-tip gemmae, serrate margins and, smooth to nearly smooth costa; the leaf lamina composed of two areas, a wide hyaline basal area and a multistratose area of chlorocysts and hyalocysts. The central chlorophyllous layer is thought to have been composed of many rows of chlorocysts in a single non-dissected layer (without lacunae between consecutives rows of chlorocysts), and surrounded, on the abaxial and adaxial surfaces by one layer of porose hyalocysts. The hyalocysts are thought to have been short quadrate shape with rectilinear walls. The plants were dioicous, with perichaetial leaves similar to vegetative ones, archegonia in terminal groups of more than five; the antheridia also terminal, surrounded by 2-3 perigonial bracts, these with a broad hyaline base and a multistratose apex particularly the most internal ones, antheridia in groups of five or more. A single sporophyte was born at the apex of the stem, exserted on a long seta, the capsule erect to subinclined with basal stomates, the neck undifferentiated; the peristome with a distinct prostome and 16 inserted, haplolepideous, densely papillose teeth, the papillae branched or unbranched without a distinct pattern or irregularly arranged around circular depressions, transverse walls (trabeculae) were present but obscured by papillae. The spores were verrucate with granular deposits irregularly distributed on the surface of the verrucae. This hypothetical ancestor is thought to have been a corticolous epiphyte of inland tropical rain forests. Its structural and, most certainly, physiological adaptations developing in response to environmental stresses posed by the corticolous habit, perhaps, coupled with seasonally dry periods in the forests in which it grew.

Of the various divergences that have occurred in the genus, perhaps one of the earliest could be related to the elongation of ancestral quadrate hyalocysts and chlorocysts, this elongation maybe, related to the dissection of the chlorophyllous layer into a reticulum. At the same time, or perhaps later in evolution, hyalocysts on the leaves of members of Subgenus *Trachynotus* developed sinuose lateral walls and bulging curved ends; these adaptations increasing the surface area for water retention without a marked increase in leaf size.

At the peristomal level, three major divergences, related to peristome ornamentation, appear to have taken place. Two of these occur in members of the Subgenus *Trachynotus*. One of this divergences (V) is characterized by the development of irregular striations on the peristomal plates (this character also developed in *L. octoblepharioides* subsp. *whittieri*, a member of Section *Leucophanes*) while the second one (V") is characterized by the absence of ornamentation on the peristomal plates (smooth peristome) concomitant with a reduction in the size of the teeth. The third divergence occurred in members of Subgenus *Leucophanes* most of which are characterized by the ancestral foveolate peristome type. Members of the African lineage of *L. molleri*, *L. hildebrandtii* and *L. renauldii* developed coarse longitudinal to semi-circular thickenings (V') on the peristomial plates with also a tendency for development of smooth dorsal plates.

The putative ancestor from which *Leucophanes* was derived must be sought in members of the genus *Syrrhopodon*. This ancestor is hypothesized to have had a peristome of strongly papillose teeth with irregularly defined foveolate areas, a prostome 2-4 cells high and costate leaves having a lamina composed of two areas, a basal hyaline portion and an upper chlorophyllous area, this perhaps irregularly bistratose.

3. GEOGRAPHICAL HISTORY OF *LEUCOPHANES*

Leucophanes is distributed in the tropical and subtropical regions of the world, from Asia to Africa, the Neotropics and the islands of the tropical Pacific. Its distribution coincides with the extent of the three great blocks of tropical rain forest in the world. The northernmost geographical localities of *Leucophanes* are in Nepal and southern Japan (Ryukyu Islands). The tropical forest of Nepal is considered to be the region where the tropical rain forest reaches farther from the Equator than anywhere else (Liu and Yu 1980, Whitmore 1982, 1984). The southernmost locality of *Leucophanes* is on the Henderson Island of southeastern Polynesia.

Two centers of species diversity can be distinguished; one is centered in Malesia and areas adjacent to the tropical Pacific, the second one is in Africa. Malesia is a very rich floristic region. It has been estimated that it contains approximately 25,000 species of flowering plants, nearly 10% of the world's flora that is known (van Steenis, 1971). Modern-day Malesia is a result of the collision of the Australian-New Guinean plate with Laurasia between 3 to 15 million years ago (Audley 1980, Audley *et al.*, 1981b; Whitmore, 1984). The close proximity of both plates allowed relatively rapid migration of Gondwanian and Laurasian elements north and south of their previous ranges (Whitmore, 1981,1982). Africa, Madagascar and some of the islands of the Indian Ocean (e.g., the Seychelles), were part of Gondwana (Audley, 1980; Audley et al. 1981b).

Five species of *Leucophanes* have their distribution centered in Malesia, Australia and the Pacific islands. These are: *L. candidum*, *L. glaucum*, *L. milleri*, *L. octoblepharioides*, and *L. serratulum*. The species centered in Africa are: *L. hildebrandtii*, *L. molleri*, *L. renauldii*, *L. rodriguezii*, *L. scabridens*, *L. seychellarum* and *L. unguiculatum* . *Leucophanes angustifolium* is the only species that is found in both centers of diversity although it appears to be more widespread in Malesia (Fig.173).

Among the species distributed in Malesia are those with the greater number of plesiotypic characters. These include *L. octoblepharioides* and *L. angustifolium*, as well as some of those considered to have many derived characters like *L. candidum*, *L. glaucum* and *L. serratulum*.

All the species distributed in Africa are considered to have been derived from a putative *L. octoblepharioides*-type ancestor and they appear to be closely. The Neotropical outliers, *L. molleri* and the disjunct population of *L. glaucum* are considered to have been derived from the African and Southeast Asian relatives respectively. *Leucophanes molleri* is thought to have arrived in the Neotropics via long distance dispersal. This event, perhaps a recent one (mid to late Tertiary), taking place after the splitting of Africa and South America. *Leucophanes glaucum* is most possibly an introduced species. It has been documented that ornamental and fruit trees (e.g., *Mangifera indica L.*), and herbs were introduced from Asia into the West Indies in the last half of the eighteenth century (Howard, 1975). It is possible that tree trunks covered with mosses, among these *Leucophanes glaucum* might have been transported and planted in Guadeloupe. No populations of *L. candidum* or *L. glaucum* have been reported for Africa.

Based on: (1) the distributional patterns of species of *Leucophanes*, (2) their life-mechanisms, among these, the abundant production of vegetative propagules coupled, in some species, with the loss of the male gametophores, and (3) comparative studies of distributional patterns of other bryophytes (for a recent review of the literature see Schuster 1983), I hypothesize that the genus most probably originated in Southeast Asia, in the area of the Malay Peninsula and adjacent Sunda Islands (Greater Sunda Islands) when these Laurasian land masses were still separated from Gondwanaland and its derived land, i.e. Australian-New Guinean plate. Populations of *Leucophanes* dispersed south into Australia, New Guinea and islands of the Sahul Shelf as this plate approached Laurasia, and also after the consolidation of Malesia. The distribution of the genus in the tropical Pacific is considered, at least in part, a more recent dispersal event.

Geological, paleomagnetic and paleontological data from Laurasian Southeast Asia indicate that this region has been in tropical to subtropical areas through most of its history (Stauffer, 1974). The Gondwanian-derived flora appears to have been composed of cool temperate elements as observed by the strongly marked rings in woody stems and the paucity of taxa (Kobayashi and Shikama 1961, Flenley 1979, Schuster 1983). Thus, prevalent tropical to subtropical conditions in Southeast Asia, somewhat altered by more or less drier climatic fluctuations, would allow ample time for diversification of forest elements to take place. The presence in Malesia of the species considered to have retained most of the plesiotypic character-states, that is *L. octoblepharioides*, and its closest apotypic sister group *L. angustifolium* as well as the presence of highly derived sister groups like *L. candidum* (only known for this area) and *L. glaucum* tend to support this hypothesis.

Three major factors have been important in the geographical distribution of *Leucophanes* south of its former range. These are: (1) the switch in reproductive mechanisms (perhaps brought about by past climatic fluctuations) with the abundant production of asexual propagules coupled with (2) its diversification into coastal areas (perhaps ecologically more exposed, drier habitats), and (3) the proximity of other continental areas to the Sunda Shelf in the late Tertiary. The consolidation of Malesia created an insular filter bridge between Laurasia and the Australian-New Guinean plate that allowed for the differential migration of many taxa into these areas.

Studying the widespread distribution of *Leucophanes* in some islands of the tropical Pacific, a recent long distance dispersal event, it is not impossible to envisage a similar event by which the putative ancestor(s) of the African species arrived in that continent. The dispersal of this ancestor might have been through a tropical corridor that existed in the near East during the late Mesozoic to early Tertiary or via the Indian Ocean or both. Many relationships that exists between the vascular flora of Indo-Malaysia and Africa can be attributed to simple or direct migrations between tropical and subtropical areas of Southeast Asia, India and Africa during the early Tertiary (Raven 1972). Thus, present day African populations of *Leucophanes* are considered remnants of a once continuous distribution extending from Southeast Asia to Africa through the tropical corridor of the Near East. The continuity of this tropical corridor was severed during the glaciation events of the late Tertiary that brought about the development of the deserts of Arabia and the Near East (Raven, 1972; Raven & Axelrod, 1974). If populations of *Leucophanes* were widely distributed in Africa and Southeast Asia before the late Tertiary, and considering the proposed low rate of evolution of unisexual taxa, that theoretically, would need more than 50-60 million years for the evolution of distinct species (Schuster 1983), I hypothesize that *Leucophanes* differentiated as a distinct genus, perhaps as early as the Lower to Upper Cretaceous period. Its present day distribution reflects not only its paleohistory but also its high dispersal capabilities. The high species endemism in the African taxa may be a reflection of their isolation from their Indomalayan putative ancestors.

Leucophanes serratulum, the only synoicous species, is considered a neoendemic. Its distribution in the New Guinean lowlands of Humboldt Bay, an area developed after the Pliocene collision of the Australian-New Guinean plate with Laurasia, su[illegible]ts a recent origin.

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APPENDIX 1

NAMES FOR WHICH NO TYPE SPECIMENS HAVE BEEN LOCATED

Leucophanes calymperatum C. Muell., Malpighia 10:570. 1896. Type: "Prope Georgetown ad cataractas "Marshall falls" fluvii Mazaruni a. cl. J. Quelch collecti".

Leucophanes minutum C. Muell. in Geh., Biblioth. Bot. 13:2. 1889. Type: "Fly River (Branch), alliis muscis parcissime intermixtum leg. W. Bauerlen".

Leucophanes naumannii (C. Muell.) C. Muell., Forschungsr. Gazelle Bot. 4(5):51. 1889. Basionym: *Leucobryum naumannii* C. Muell., Bot. Jahrb. 5: 85. 1883. Type: "Nova Guinea. Leg. Naumann n.s."

Leucophanes prasiophyllum Besch., Bull. Soc. Bot. France 45:56. 1898. Syntype: "No. 217. Leg. J. Nadeaud".

Leucophanes pucciniferum C. Muell., Bot. Jahrb. 5: 85. 1883. Type: "*Leucophanes* (Leionotus) *pucciniferum*. Inter omnes congeneres *L. vitiano* mihi proximum, sed foliis apice repandolimbatis puccinigeris distincte albide mucronatis longe diversum. (Anachoretes)."

Leucophanes rodriguezii Ren. & Card., Bull. Soc. R. Bot. Belg. 32(2): 113. Type: "Hab. Bourbon (Rodriguez).-(Renauld, *Musci masc. mad. exsicc.*, no. 110)."

Leucophanes scabridens P. Vard., Rev. Bryol. Lich. 8:52. 1. 1935. Type: "Hab. Forêt de Mayumbe, 150 km N.E. Mayumba (Leg. Dubois, comm. Hemery) Ghenyounga - Piti Masango - Sacamicandra - Mzocou - Nzoumou (Leg. LeTestu)".

Leucophanes smaragdinum (Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. 1877-78: 391. 1880 (Ad. 2:655). Type: "Viti. Seeman inter No. 863".

Leucophanes tahiticum Besch., Bull. Soc. Bot. France 45:57. 1898. Syntype: "No. 219 bis. Leg. J. Nadeaud".

Leucophanes vitianum C. Muell., J. Mus. Godeffroy 3(6): 58. 1874. Type: "Fidschi-insulae, Ovalau, ad basin *Rhizogonii setasi* in cacumine montis Tana-lailai, 2000 alt.: Dr. Ed. Graeffe. Dcbr. 1864 parcissime legit.

APPENDIX 2

NOMINA NUDA IN *LEUCOPHANES*

Leucophanes aciculare C. Muell., Gen. Musc. Fr. 86. 1900. = *L. candidum* (Schwaegr.) Lindb. *fid.* Card. in Fleisch., Nov. Guinea 8(2):741. 1914.

Leucophanes apiculatum Hamp. in C. Muell., Gen. Musc. Fr. 86. 1900.

L. arthrocormioides C. Muell. in Card., Rev. Bryol. 26:7. 1899 = *Exodictyon arthrocormioides* Fleisch.

Leucophanes blepharioides Schimp. in Jard., Bull. Soc. Linn. Normandie ser. 2, 9:264-265. 1875.

Leucophanes compactum Broth. in C. Muell., Musc. Fr. 86. 1900.

Leucophanes expallescens Card., Mem. Soc. Sc. Nat. Cherbourg 32:35. 1901.

Leucophanes fusculum C. Muell. in Geh., Biblioth. Bot. 44: 5. 1898. *nom. nud. in synon.* = *L. reinwardtianum* C. Muell. *fid.* Geh. l.c. ≠ *L. candidum* (Schwaegr.) Lindb. *fid.* Fleisch. Musci Fl. Buitenzorg 1: 183. 1904.

Leucophanes octoblepharis Kindb., Enum. Bryin. Exot. 92. 1889 = ? *L. octoblepharioides* Brid.

Leucophanes pugionatum C. Muell., Gen. Musc. Fr. 86. 1900.

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