

A TAXONOMIC REVISION OF THE MOSS GENERA
RHEGMATODON AND *MACROHYMENIUM*

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Specimens in the following herbaria were studied and I express my appreciation to the curators. The abbreviations are those recommended by the International Bureau of Plant Taxonomy and Nomenclature in *Index Herbariorum*, Part 1, 1974. NICH, FH, MO, MICH, NY, MPU, Z, HBG, B, LD, PE, O, S, L, GL, MANCH, BM, C, HIRO, H, BR, TENN, PC, FI, FLA, and JE. In several instances H-BROTH was used to indicate that the specimen was from the Brotherus collection housed at Helsinki.

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By

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The moss genera *Rhegmatodon* (Leskeaceae) and *Macrohymenium* (Sematophyllaceae) are revised on a worldwide basis. Two species, *Rhegmatodon declinatus* (Hook.) Bridel emend. Eakin and *Rh. polycarpus* (Griff.) Mitten emend. Eakin, are recognized for the genus *Rhegmatodon*. Four species, *Macrohymenium acidodon* (Mont.) Doz. and Molk. emend. Eakin, *M. mülleri* Doz. and Molk., *M. rufum* (Reinw. and Hornsch.) C. Muell. emend. Eakin, and *M. strictum* Bosch. and Lac. emend. Eakin, are recognized for the genus *Macrohymenium*. Keys to the species are included. Presented with each taxon is a complete list of synonymy, a taxonomic description and discussions on morphology and distribution. Standard notation of herbarium disposition is supplied for all specimens examined, and distributions of the taxa are based only on these specimens. Where available, information is given on the ecology of each taxon.

STATEMENT OF PROBLEM

The purpose of this investigation is to present a revision¹ of the moss genera *Rhegmadodon* and *Macrohymenium*. In the field of bryology today, there is a critical need for taxonomic revisions of many of the currently recognized genera. The relatively short history of modern bryology (less than 200 years) has produced more than a twenty-fold multiplication of genera. However, only a very few have been subjected to the scrutiny of a major revision and, of these few, most were revised before the 1930's. In spite of the many fine investigations since the turn of the century, bryological taxonomy remains in the 'alpha' state. Revisional bryology is well characterized by the idea, "the fields are white unto harvest, but the laborers are few." The need for revision appears even more critical when we realize that many of the current genera were established during a period when the philosophical concept of genus in Musci was undergoing tremendous changes in perspective.

Rhegmadodon and *Macrohymenium* were typical of the many genera needing revision, but at the same time offered features that made them particularly attractive for dissertation research. Both included a "manageable" number of species and there existed a good possibility of procuring nomenclatorial type specimens, so indispensable to revisional taxonomy. The decision to consider two genera, which are

¹See discussion about the definitions of *revision* and *monograph* in Appendix I (page 93).

currently assigned to two different families, was based on the fact that their histories are greatly intertwined. As late as 1898, Paris (*Index Bryologicus*) included all previously described species of the two genera under the name *Rhegmatodon*. This was fascinating to me, since even a beginning student of bryology would place these genera in two different groups on the basis of current generic and familial concepts.

The objectives of this study were

1. to collect, translate, and reevaluate all of the previous taxonomic literature with reference to these genera.
2. to provide a history of these genera with special reference to the changing concept of the genus within Musci as a whole.
3. to collect and critically reexamine all available type material on which previous taxonomic concepts were based.
4. to provide a revised taxonomic treatment of these genera based on type material and the greatest possible number of other collections.

This treatment includes complete descriptions of the genera and keys to their component species. The types are designated for all species, and their location noted. Collection data and herbaria citations have been given for all specimens examined. Discussions of previous taxonomic treatments, nomenclatorial changes, and synonymy are included. Distributions are presented for each species as recognized by the author. To date, no cytological, genetic, or ecological studies have been completed on these rare genera. None were attempted by this author due to the lack of fresh, living material.

There are two areas of background necessary for a proper understanding of the results and conclusions of this dissertation. The first involves an understanding of those basic taxonomic concepts revealing the underlying philosophy and assumptions of modern taxonomic research in bryology. It is important to specifically relate these ideas to the modern generic concept in Musci. Secondly, one must recognize that the thread of history relating *Rhegmatodon* and *Macrohymenium* is most meaningfully seen in the context of the overall historical fabric of taxonomic bryology.

HISTORY OF *RHEGMATODON* AND *MACROHYMENIUM*

The original specimen of *Rhegmatodon* was described as part of a collection of Nepalese mosses sent by Dr. Francis Buchanan Hamilton¹ to William J. Hooker. Hooker (1808) based his "*Musci Nepalenses*" on this collection. In error, he classified his specimen on the basis of a single row of peristome teeth; designating it as *Pterogonium declinatum* sp. n., a

*Pterogonium caule repente, foliis imbricatus ovatus
integerrimis mediotenus uninerviibus, capsulae declinata,
operculo incurvato* (Hooker, 1808, p. 309).

Had he seen the exostome, and following the generic concepts of his day, he would either have designated it a new species of *Hypnum*, or perhaps erected a new genus. He was clearly aware of its Hypnaceous appearance.

I have named this plant from its most obvious character, the drooping capsule, in which it differs from all the other species of this genus described by Hedwig or Bridel, and has, in consequence of it, so completely the appearance of a *Hypnum*, that no one would suspect its real family, without first examining it (Hooker, 1808, p. 310).

It seems strange that Hooker should have missed the exostome. According to Margadant (1968), Hooker was elected a Fellow of the Linnaean Society of London (1806) at 21 years of age on the basis of his discovery and

¹H. C. Gangulee in his *Mosses of Eastern India and Adjacent Regions*, gives some interesting historical anecdotes about those who have collected in eastern India. The collections of 1802-03, mostly from the Kathmandu valley of Nepal, were the first on the Indian subcontinent and earned for Hamilton the distinction of being the pioneer collector of bryophytes for this area.

description of *Bauxbaumia aphylla* in the British Isles. This moss also has a double row of peristome teeth which are not nearly as distinct as those of *Rhegmatodon*. In addition, W. J. Hooker was an accomplished illustrator and engraver. Nor was it a case of having seen poor material for the original specimen has both endostome and exostome. My only explanation is that he first viewed the specimen dry, in which case, the external teeth would not have been seen at low magnification. In *Rhegmatodon* the exostome teeth alternate with those of endostome and, when dry, are inflexed between them. This possibility is seen by comparing Hooker's illustration (Fig. 15:7-9) with a low magnification photograph of a dry capsule (cf. Fig. 1:2). We should recall that microscopic characters were not commonly used at this time and microscopes were generally poor. Nevertheless, he did draw the endostome at a higher magnification and it is still puzzling to me how he missed picking off a few exostome teeth.

With reference to the endostome he noted:

There will also be found under the microscope a strong peculiarity in the circumstance of the teeth of the peristomium being cleft in a very curious manner (Hooker, 1808, p. 310).

This peculiarity is in fact a central point in circumscribing the genus *Rhegmatodon*. His description is as follows:

Peristomium dentibus sedecim, suberectis, e capsulae membranâ interiore reticulatâ ortis, lineari-subulatis, luteis, transversè striatis, a basi ad medium longitudinalitèr fissis (Hooker, 1808, p. 310).

S. E. Bridel, in *Bryologia Universa* (1827), established the new genus *Regmatodon*¹, based primarily on this peculiarity of the peristome. The

¹Note that the original spelling of the name is *Regmatodon* and not *Rhegmatodon*. These two spellings are orthographic variants. However, while some weight should be given to the spelling of the original

name itself reflects the character, being formed from the two Greek words ρήγμα fissure, and οδούζ of the teeth. F. C. Kiaer (1882, p. 41) notes that Bridel "who only knew the plant from the Hooker description, also designated the peristome as simple." Thus, while Bridel did segregate the specimen as a new genus, he perpetuated Hooker's error.

The genus *Macrohymenium* with one species, *M. rufum*, was established by Carl Müller in 1847, based on three specimens previously described as *Leskea? rufa* Reinwardt and Hornschuch (1826), *Leskia mitrata* Dozy and Molkenboer (1844), and *Leskea acidodon* Montagne (1845). Müller was apparently strongly influenced in this decision by various characters of the leaves; as indicated by the first of his "essential characters."

The leaves ecostate formed from narrow prosenchymatous cells (ellipsoidal areolation), strongly concave, subplicate, at the base to both sides provided with several large yellow lateral cells, densely overlapping, subsecund. With the capsule mouth constricted. The peristome double; the outer: the 16 teeth from the oblong base provided with striae in the middle, traveculate, suddenly long cuspidate, bent inwards; the interior: the teeth just as many, much overlapping the very longest outer teeth, widest, cuspidate, membrane lacking, put together from quadrate large yellow cells, placed on the reddish membrane, scarcely canaliculate, tessellated, not perforated (Müller, 1847, col. 825).

Just three years later, however, when treating these same specimens in *Synopsis Muscorum Frondosorum*, he included his new genus under the concept of *Rhegmatodon*. He dealt with only three species; *Rh. declinatus* (Hook.) Brid., *Rh. orthostegius* Mont., and *Rh. rufus* C. Müller. The former two are *Rhegmatodon* in the modern sense, but *rufus* is a *Macrohymenium*. It may first be puzzling that Müller would dissolve a

author, I feel that Bridel's spelling is in error. The Greek word should have a rough breathing symbol over the letter *rho* indicating the presence of 'h' when the word is transliterated to English. The correct spelling is therefore *Rhegmatodon* (cf. Stearn, William, 1967, *Botanical Latin*, p. 263).

concept which just three years earlier had been so clear in his mind. Had he overlooked some important characters, or perhaps new and better specimens had come to light? Neither was the case. In fact, in expressing his concept of *Rhegmatodon* in this latter work, he did not even consider gametophytic characters. Note the following description from *Synopsis Muscorum Frondosorum*:

The calyptra dimidiate. The peristome double. The external teeth very short, trabeculate, hypnaceous; the internal upon a short, scarcely keeled, tessellated, as if perforated membrane, turning reddish, very long, for a long time rising above the external, scarcely keeled, with the longitudinal line gaping to undivided, furrowed, remotely articulated (Müller, 1850, p. 29).

There is no mention of the once predominant leaf characters in this latter description. The only gametophytic character used in this later classification is the nature of the costa.

This actually represents a shift in Müller's views regarding the relative importance of sporophytic versus gametophytic characters in the delimitation of genera. This example well illustrates the problem facing bryologists as a result of the dual nature of mosses. The difficulty of systematizing a double organism, i.e., one representing two distinct generations of the life cycle is discussed in Appendix I. This problem is in fact central in the history of the changes which have taken place in the concept of genus in mosses. This discipline-wide vacillation with regard to the selection of essential characters is reflected throughout the history of *Rhegmatodon* and *Macrohymenium*. Müller was obviously struggling with the problem in his treatment of the two genera. Hedwigian tradition emphasized the importance of the sporophyte. Müller at first breaks with this tradition by emphasizing various gametophytic characters and establishing the new genus

Macrohymenium. He then conservatively shifts his emphasis back to sporophytic characters which, in the case of these taxa, will unite them under the same generic concept. This is a characteristic trend in the classification of the two genera. Whenever the gametophytic leaf characters were emphasized, *Macrohymenium* and *Rhegmatodon* were separated. Emphasis on the sporophyte, especially the peristome characters, united the specimens. Dozy and Molkenboer (1848) in *Musci frondosi inediti archipelagi indici . . .*, attempted to refine the genus concept for *Macrohymenium* on the basis of two new species, *M. mülleri* and *M. serrulatus*. Again we find the major emphasis given to the shape and structure of the peristome; especially to the ratio of length between the endostome and exostome teeth. Some insight into their view of the limited importance of gametophytic characters is shown by the following:

Quadrate areoles to both sides at the wing of the leaves are not uniformly evident in all species, and therefore, they are seen to us not to be of great value, at least in explanation of the essential characters (Dozy and Molkenboer, 1848, p. 166).

Emphasis on the similarities of the peristome caused them to ignore the obvious lack of inflated alars in *serrulatum*. This further illustrates the principle stated above. However, in this case, Dozy and Molkenboer were dealing with two species of *Macrohymenium* and only one of *Rhegmatodon*; thus including both genera under the name *Macrohymenium*. In 1864, van der Bosch and van der Sande Lacoste continued Dozy and Molkenboer's work in *Bryologia Javanica*. They added one new species, *M. strictum*, and reclassified *M. serrulatum* as *Rhegmatodon serrulatus*. While they did not specify the reason for this move, a look at their

description of *Rh. serrulatum* implies greater stress on gametophytic differences.

A major revision of the two genera was undertaken by F. Kiaer in 1882, which essentially established the modern distinctions between *Rhegmatodon* and *Macrohymenium*. There has been very little change in the circumscription of these taxa since Kiaer. Later taxonomic changes revolved around the question of closeness of relationship between the two genera. Kiaer used mostly gametophytic characters to distinguish the genera but placed them in the same subfamily, *Macrohymenieae*, on the basis of their proportionately long endostome. He lists: *Rh. schotheimioides*, *Rh. filiformis*, *Rh. crizabanus*, *Rh. orthostegius*, *Rh. polycarpus*, *Rh. brasiliensis*, *Rh. secundus*, *Rh. declinatus*, and *Rh. serrulatus*. Under *Macrohymenium* he includes: *M. rufum*, *M. strictum*, *M. acidodon*, *M. nietneri*, *M. laeve*, *M. mülleri*, and *M. gracillimum*.

All of these species distinguish themselves (as a group-DAE) by means of the great inner peristome with the processes which are 2-4 times longer than the teeth (Kiaer, 1882, p. 10).

With the publication of Philibert's *Études sur le péristome* (1884-90) the peristome again was emphasized as the essential character in taxonomic bryology. The impact of Philibert on the classification of these genera is most clearly reflected by the treatment of these species by Paris (1898) in *Index Bryologicus*. All species of *Macrohymenium* were synonymized under the name *Rhegmatodon*. Twenty-one species are listed, apparently on the basis of this similarity in peristome structure. Gametophytic distinctions must necessarily have been entirely abandoned as generic criteria.

When Brotherus (1909), in Engler and Prantl's *Die Natürlichen Pflanzenfamilien* (1st edition), established the family Sematophyllaceae

on the basis of Mitten's (1869) Tribus 16, Sematophylleae, the stage was set for separating *Rhegmatodon* and *Macrohymenium*. Brotherus' family concept was later emended by Fleischer (1923), *Die Musci der Flora von Buitenzorg*, into four subfamilies: Clastobryoideae, Heterophylloideae, Sematophylloideae, and Macrohymenioideae. Brotherus (1925) followed this treatment in the second edition of Engler and Prantl.

Moving away from the overwhelming emphasis on the sporophyte, the essential characteristics of the family Sematophyllaceae (sensu Brotherus and Fleischer) are

1. costa absent, or short and bifurcated
2. alar cells enlarged
3. operculum long-rostrate.

Both of these authors gave little regard to the peristome and thus the sporophytic characteristics within the Sematophyllaceae are widely variable. This was the last major treatment of these taxa. Currently *Macrohymenium* is found as a subfamily of the Sematophyllaceae, and *Rhegmatodon* holds a similar position in the Leskeaceae. Subsequently, five new species have been described and I have found a great number of names *ex herbario*, which apparently have not been validly published.

Table 1. A Chronology of important dates and publications in the history of the genera *Rhegmatodon* and *Macrohymenium* including significant dates in the history of taxonomic bryology.

1741	Dillenius - <i>Historia Muscorum</i>
1753	Linnaeus - <i>Species Plantarum</i>
1781	Hedwig - <i>Fundamentum Hist. natural</i>
1801	Hedwig - <i>Species Muscorum</i>
1808	Hooker, W. J. - First specimen of <i>Rhegmatodon</i> ; described as <i>Pterogonium declinatum</i>
1819	Bridel, <i>Mantissa Muscorum</i>
1826	Bridel, <i>Bryologia Universa</i> - the establishment of the new genus <i>Rhegmatodon</i> based on Hooker's <i>Pterogonium declinatum</i>
1826-27	<i>Leskea? rufa</i> Reinwardt & Hornschuch
1836	<i>Bryologia Europaea</i> begun
1838	<i>Anhymenium polycarpon</i> Griff.
1839	<i>Leskea parvula</i> Hampe
1842	<i>Rh. orthostegius</i> Mont.
1844	<i>Rh. parvulus</i> Hamp.
1844	<i>Leskia mitrata</i> Dz. & Molk.; in <i>Muscorum Frondosorum-Novae Species ex Archipelago Indico et Japanio</i>
1845	<i>Leskea acidodon</i> Mont.
1847	<i>Macrohymenium rufum</i> Müller; the establishment of the new genus <i>Macrohymenium</i>
1848	<i>M. mülleri</i> Dz. & Molk; <i>M. serrulatum</i> Dz. & Molk; in <i>Musci frondosi inediti Archipelagi indici sive descriptio et adumbratio Muscorum Frondosorum in insulis Java, Borneo, Sumatra, Celebes, Amboina. . .</i>

- 1849 *Anhymenium polysetum* Griff.
- 1848-51 (50) Müller, *Synopsis Muscorum Frondosorum* - *M. rufum* changed to *Rh. rufum*
- 1854 *Bryologia Europaea*, Bruch, Schimper, & Guembel; completed
- 1856 *Clasmatodon parvulus* Hook. & Wils.
- 1859 Mitten's *Musci Indiae Orient*
- 1862 *Rh. brasiliensis* Müller
- 1855-70 (64) *Bryologia Javanica*, *M. strictum* Dz. & Molk.
- 1868 *Rh. kunzii* Müller *in schedula*
- 1869 Mitten's *Musci Austro-Americana*; *Rh. schlotheimioides* Spruce; Tribus Sematophylleae established
Hypnum minutum Mitten
Rh. nietneri Müller
- 1871 Bescherelle, *Prodromus Bryologiae Mexicanae*
Rh. filiformis Besch.
Rh. fusco-luteus Schimp
Rh. hypnoides Besch.
- 1872 *Rh. chryseus* Schimp.
- 1872 (73?) *M. laeve* Thw. & Mitten
- 1876-77 *Adumbratio florae muscorum*, Jaeger & Sauerbeck
First reference to *Rh. orizabanus*
- 1880 *M. acidodon* (part of *rufum* moved by Bescherelle)
Florule Bryologique de la Reunion
M. acidodon var. *acutissima* Besch.
- 1881 *Rh. filiformis forma major* (collection date of *in schedula* specimen of Bruch)
- 1882 *Rh. madagassus* Geheeb
Kiaer, revision of *Rhegmatodon* and *Macrohymenium*
Rh. secundus Kiaer
Rh. densus Schimp. *in schedula*
M. gracillimum Müll. *in litt.*
Rh. orizabensis Besch. *in schedula*
M. cuspidatum Mitt. *sedis incertis*
- 1884-90 Philibert, H. *Études sur le péristome*
- 1891 *Rh. feanus* Müller

- 1895 *Rh. palustris* Broth. *in schedula*
Rh. palustris var. *minor* *in schedula*
Rh. schlotheimioides var. *minor*
- 1897 *Rh. newtonii* Broth.
- 1898 Paris, *Index Bryoloicus* (all species of *Rhegmatodon* and
Macrohymenium under *Rhegmatodon*)
- 1904-05 *Rh. bornmülleri* Broth. *in schedula*
- 1905 *Rh. fissidens* Thériot *in schedula*
- 1907 *Rh. filirameus* Broth. *in schedula*
- 1909 *Rh. sinense* Thériot
- 1909 Engler & Prantl - 1st edition - made the family
Sematophyllaceae from Mitten's Tribe - Sematophylleae
- 1910 *Rh. pringlei* Cardot
- 1910-11? *Rh. mülleri* forma *pubea* Dixon *in schedula*
- 1910 *Rh. crassirameus* Cardot
- 1910 *Rh. cameruniae* Broth. (collection date)
- 1923 Fleisher, *Die Musci der Flora von Buitenzorg* (4 vol.)
Macrohymenioideae - one of four subfamilies of Sematophyllaceae
M. mitratum
M. wichurae Broth. *in schedula*
M. densirete Broth.
- 1924-25 *Musci*, Brotherus, in Engler and Prantl, *Die natürlichen*
Pflanzenfamilien 2nd edition
- 1924 *Rh. handelii* Broth.
- 1929 *Rh. declinatus* var. *minor* Broth.
Rh. novo-guinense Reimers
- 1932 *Manual of Bryology*, Verdoorn. Contains Dixon's
classification
- 1947 *Rh. brevicuspes* P. de la Varde and Leroy (collected 1936)
- 1955 *Rh. schwabei* Herzog

FAMILIAL AFFINITIES OF *RHEGMATODON* AND *MACROHYMENIUM*

There have been some comments in the literature suggesting that the genus *Rhegmatodon* be transferred from the Leskeaceae to its own monotypic family, the Rhegmatodontaceae (Crum, 1951, 1973). The apparent motivation for the suggestion is the unique peristome of *Rhegmatodon*. Brotherus, in the second edition of Engler and Prantl (1925), segregates *Rhegmatodon* in its own subfamily, the *Rhegmatodontoidae*, on the basis of the

Peristom weit unter der Mündung inseriert, das äussere veil kürzer.

Macrohymenium holds a parallel position with respect to the Sematophyllaceae. Brotherus separates this genus into its own subfamily, the *Macrohymenioideae*, on the basis of

Fortsätze 2-3 mal so lang als die Peristomzähne.

In both cases, the remaining genera of these families have peristomes in which the endostome is either the same length as the exostome or perhaps a little shorter or absent. These two genera stand alone in their respective families by virtue of an endostome 2-3 times longer than the exostome. However, this peculiarity of the peristome is not a sufficiently strong character to warrant such a transfer. With reference to some of the more recent discussions of the Leskeaceae and related families (Watanabe, 1972; Noguchi, 1972; Crum, 1973), all of the *Rhegmatodon* generic characters fit well into the family concept, with the exception of the ratio of endostome to exostome length. A

similar situation exists with respect to the relationship of *Macrohymenium* to the Sematophyllaceae. Although Seki (1968) did not specifically deal with *Macrohymenium* in his revision of the Sematophyllaceae of Japan, this genus fits very well into his revised concept of the family; again with the exception of the endostome to exostome ratio. Both in the case of *Rhegmatodon* and *Macrohymenium*, transfer to a monotypic family would be unnecessary and place too great an emphasis on this one peculiarity of the peristome. It is recommended that *Rhegmatodon* remain in the subfamily Rhegmatodontoideae of the Leskeaceae, and that *Macrohymenium* retain a similar position in the subfamily Macrohymenioideae of the Sematophyllaceae. Much more revisional work should be done with reference to the genera in these families before new families are proposed.

INFRAGENERIC RELATIONSHIPS IN *RHEGMATODON*

As previously noted (cf. p. 9), Kiaer accurately circumscribed the genus *Rhegmatodon* with reference to both gametophytic and sporophytic characters. Within *Rhegmatodon* he erected two sections, *Laevisetia* and *Scabrosetia*, which correspond to the two species of the present treatment. In the wake of Kiaer's revision, however, a proliferation of new species occurred on the basis of certain gametophytic characters, i.e., leaf shape, average leaf ratio and perichaetial leaves. In the present work each of these characters was tested, both in the type specimens and later collections. I attempted to use both gametophytic and sporophytic characters to delimit species and gave careful consideration to those characters used by previous workers. However, the traditional gametophytic characters were found either to be continuously variable or to represent ecotypic variants, and were thus set aside.

The morphological structures of taxonomic importance in *Rhegmatodon* are completely sporophytic. The only sure way to distinguish the two species is by examination of the endostome teeth, the seta and the walls of the exothecial cells. These three characters will be found in one of two discrete combinations, each characterizing one of the two species of *Rhegmatodon*. *Rh. declinatus* can be recognized by the combination 1) endostome teeth lacking dotting (Figs. 2:5, 4:12), 2) seta clearly rough from top to bottom (Fig. 4:3), and 3) cell walls

of the exothecium irregularly thickened, presenting a collenchymatous appearance (Fig. 4:13). *Rh. polycarpus* is characterized by 1) dense dotting of the endostome teeth (Fig. 5:1, 2), 2) a smooth seta (Fig. 5:3), and 3) the walls of the exothecial cells regularly thickened parallel to the central axis of the capsule, with the transverse walls appearing thinner (Fig. 5:23).

The taxonomic treatment of *Rhegmatorodon* by Brotherus (in Engler and Prantl, 1925) is based on F. C. Kiaer's revision of 1832, *Genera muscorum Macrohymenium et Rhegmatorodon revisa specieque nova aucta exposuit*.¹

Within Kiaer's and Brotherus' *Scabroseta*, species were differentiated by serrations on the leaf tips. This character proved to be a continuum, being highly variable, even within a single specimen. From specimen to specimen an examination of leaves from the branch tips revealed a continuum from those completely entire, to a few somewhat serrated, to those distinctly serrate (Fig. 4:5-1). In all cases, the leaves at the base of the branch were entire. To date no specimens of *Rh. polycarpus* with serrate leaves have been seen, though a slight tendency toward serration was noted (Fig. 5:9). Caution should be exercised in using this difference alone to distinguish species, as leaf serrations have been shown to be ecotypically variable (Briggs, 1965).

In section *Laevisetia*, Kiaer and Brotherus used leaf ratios (2-2.5:1 vs. 1.8:1) and leaf shapes (oval vs. oblong-oval) to distinguish species. Table 2 presents data taken primarily from type specimens for all the

¹For the purpose of comparison, translations of both these keys are presented in Appendix I.

species with smooth setae. This clearly shows a continuum of leaf ratios. The averages in Table 2 are based on an examination of a minimum of 20 individual leaves per specimen. No correlation exists between leaf length and ratio or ratio and shape. Figure 5:11-22 well illustrates the range of the continuous variables of size, shape, ratios, and secundity. The extent and degree of secundity varied even within the same specimen. For example, the three leaf tips shown in Fig. 5:7-9 are from the same specimen. Secundity cannot be used in *Rhegmatodon* as a discrete species marker. Developmental studies will probably show this character to be an ecotypic variable as has been shown for other mosses (Streeter, 1970). Similarly, the degree of filiformity in branches was found to be highly variable within single specimens, and was excluded as a marked species character. This character has also been shown to be an ecotypic variant of mosses in very moist microhabitats (Richards, 1967).

Several pictures of the exostome teeth have been included which clearly show two external plates backed by a single set of highly trabeculate plates (Fig. 2:1-3, 6-12). This was considered necessary since the well-known illustration by Dozy and Molkenboer (Fig. 15:4) is incorrect on this point. Their illustration represents only the interior set of trabeculate plates. The error has been widely circulated in that Brotherus chose this plate as his illustration of *Rhegmatodon* in *Die natürlichen Pflanzenfamilien* (1925). In this same drawing, the relative height of the endostomal and exostomal membranes is misrepresented. In the genus *Rhegmatodon*, the point of attachment of the endostome and exostome to their respective membranes is the same, i.e., the point of attachment for both the endostome and exostome

is an equal distance below the rim of the capsule. Dozy and Molkenboer drew this as if *Rhegmatodon serrulatus* was in fact a *Macrohymenium*, as they supposed. Both parts of the peristome are inserted below the rim of the capsule in *Rhegmatodon*.

The presence of paraphyllia in *Rhegmatodon* was first noted by Fleischer (1923) and subsequently by Brotherus (1925). However, no description accompanied these notations. These structures actually fit the concept of pseudoparaphyllia as presented by Ireland (1971). A comparison of Ireland's illustrations of pseudoparaphyllia with the pictures in Fig. 2:13-22 will document the similarity of structure. Furthermore, they are relatively sparse in *Rhegmatodon* by virtue of being restricted to branch and reproductive primordia on the branches.

One other character used by Kiaer and Brotherus was the presence of teeth on the margins of the inner perichaetial leaves (cf. Fig. 1:17). The consistency of this character was tested in several specimens by the examination of many perichaetia. The presence and number of teeth was not at all consistent, whether in the same specimen or in different specimens, supposedly of the same species. This character was also excluded.

DESCRIPTION OF THE GENUS *RHEGMATODON*

Regmatodon (*Rhegmatodon*) Bridel, Bryol. Univ. 2:294. 1827.

Pterogonium declinatum Hook., Trans. Linn. Soc. IX, t. 26, f. 3.

1808. TYPE: Dr. Francis Buchanan Hamilton, Nepal, 1802-03
(holotype, NY; isotypes, S, H, BM).

Plants slender to fairly robust, forming loose to dense mats, mostly dull or somewhat shiny, rigid, dark green or brownish. *Primary stems* prostrate, creeping, yellow to brownish, irregularly subpinnately and densely branched, rooting by means of radicles on the underside. *Stem leaves* small, usually absent, short, ovate-acute, entire, *alars* inconspicuous, marginal cells quadrate, the rest elliptical. *Branches* ascending to upright, terete, straight to curved, rigid, varying from short, thick and clavate to long, slender and of uniform diameter. *Pseudoparaphyllia* present but sparse. Branches densely foliose, leaves appressed and densely imbricate when dry, erect-spreading when wet, 0.5-1.7 mm long. *Leaves* broadly ovate, oblong-ovate to ovate-lanceolate, short acuminate, concave, completely entire to strongly serrate at the apex, margins weakly to strongly reflexed to base of short acumen. *Costa* single from a wide base, narrowing rapidly, disappearing at or somewhat above midleaf. Laminar cells oblong, arranged in oblique and longitudinal series, crowded, becoming subquadrate toward the margins and base of the leaf. Indistinctly bordered by a single

row of quadrate marginal cells with transverse walls at right angles to the margin. *Alars* undifferentiated. *Goniautoicous*. *Inner perchaetial leaves* erect, lanceolate, gradually acuminate, with either completely entire or crenately denticulate margins (Fig. 1:12-17). *Perichaetium* inserted near the base of the branch, budlike, somewhat open at the apex, *archegonia* shortly stipitate, cylindrical from an oval base, with numerous filiform paraphyses, a little longer than the archegonia (Fig. 1:8). *Perigonium* axillary, budlike, ovate, leaves somewhat round ovate, suddenly constricted into a short, wide, moderately obtuse acumen, concave, completely entire, ecostate, the cells loose, hexagonal-rhomboidal (Fig. 1:6, 9). *Paraphyses* filiform and numerous (Fig. 1:9). *Seta* either smooth or rough, 4.5-13.5 mm in length. *Capsule* erect to inclined, unsymmetric, straight to somewhat curved, slightly constricted below the mouth, especially when dry, oblong cylindrical to long cylindrical, 1.5-3.1 mm long, smooth, brown to reddish brown, sometimes substrumose at base, exannulate. *Exothecial cells* either collenchymatous or with regularly thickened longitudinal walls and thinner transverse walls. *Operculum* short, conic, acumen short, obtuse, 1/4-1/2 the length of the deoperculate capsule (cells regularly hexagonal). *Peristome* double, the sixteen teeth of the exostome lanceolate, obtuse, inflexed in the dry state, composed of a double series of cross-striolate external plates, and a single series of inner plates, trabeculate on the inner face (Fig. 2:1-3, 6-12). The sixteen processes of the *endostome*, well-developed, 2X longer than the *exostome* teeth, translucent, with or without dotting, split on midline from base to middle with one to three perforations in segments immediately above, appearing faintly to strongly bordered (Fig. 2:5). No cilia.

Spores yellow-green to olive, globose, papillose, 21-30 μm . *Calyptra* cucullate, smooth, somewhat longer than the operculate capsule.

KEY TO THE SPECIES OF RHEGMATODON

1. Seta rough from top to bottom; endostome teeth translucent and not dotted; the walls of the exothecial cells irregularly thickened, appearing collenchymatous. *Rh. declinatus*

1. Seta smooth from top to bottom; endostome teeth translucent and densely dotted; the walls of the exothecial cells regularly thickened longitudinally, the transverse walls appearing thinner. *Rh. polycarpus*

1. *RHEGMATODON DECLINATUS* (Hook.) Brid., Bryol. Univ. 2:204-205. 1827.

(Figure 4)

Pterogonium declinatum Hooker, Trans. Linn. Soc. Lond. 9:309-310, t. 26, f. 3. 1808. TYPE: Nepal, without precise locality, Francis Buchanan Hamilton, s.n. (holotype, NY; isotypes, S, H, BM).

Macrohymenium serrulatum Doz. & Molk., Musci Frond. Ined. Archip. Indici 6:170, t. 56. 1848. TYPE: Java, Mt. Patoeha, Korthals, s.n. (holotype, L; isotypes, S, H, BM, O, L, PC).
New synonymy.

Rhegmatodon serrulatus (Doz. & Molk.) Bosch. & Lac., Bryol. Jav. 2:111-112. 1864. New synonymy.

Rhegmatodon feanus C. Müell., Nuov. Giorn. Bot. Ital. 23:601. 1891. nom. nud. TYPE: Burma, Bhamo, *Feanus* 25 (holotype, FI).
New synonymy.

Rhegmatodon declinatus var. *minor* Broth., Symb. Sin. 4:94. 1929. TYPE: China, in Kwangtsaoba, S. W. Kweitschou, *Handel-Mazzetti* 10395 (holotype, H-BROTH; isotype, S). New synonymy.

Rhegmatodon schwabei Herz., J. Hatt. Bot. Lab. 14:66, f. 22. 1955. TYPE: Formosa, western Middletaiwan, "Tigerkopf," *Schwabe*, s.n. (holotype, JE). New synonymy.

Branch leaves 0.6-1.7 mm long, 0.3-0.7 mm wide, the average length to width ratios ranging from 2.2-3.0. Leaf margins range from completely entire to coarsely serrate, from midleaf to tip. Seta from 4.5 to 10.5 mm in length, 187-260 μ m wide, *conspicuously rough from top to bottom*. Vaginule 1.0-1.9 mm long. Capsule 1.5-2.4 mm long. *Exothecial cell*

walls with irregular thickenings giving a collenchymatous appearance. Endostome teeth translucent and lacking dotting. Endostome teeth are twice the length of the exostome teeth, ranging from 450-600 μm , while the exostome range from 200-300 μm .

Habitat: Usually on bark of fallen logs or trees, also on moist shady rocks. Mostly 500-1700 meters in altitude (rarely to 3000 meters).

Distribution: Formosa, China, Burma, India, Nepal, Borneo, Sri Lanka, Java, Thailand, and Malakka (Malay Peninsula), Sikkim, Assam (Fig. 6:2).

FORMOSA. Mt. Lu-Chang-Ta, Nao-liao to Kuei-shan, Wu-feng Hsiang, Hsinchu, on bark of log on roadside in hardwood forest, 1800 m, Wang 1562; upstream area of Luming Chi, Hung-yey Tsun, Yen-ping Hsiang, Taitung, on hardwood log lying on roadside in hardwood forest, 100 m, Wang 0903; upstream area of A-li-pu-tang Chi, Wang-mei Tsun Sin-yi Hsiang, Nantow, on large branch of broad-leaved tree in hardwood forest, 1200 m, Wang 1449 (NICH); Hsueh Shan Shan Mo, on fallen tree in hardwood forests just below Anma-shan, c. 2100 m, Iwatsuki & Sharp 3140; Hsueh Shan Shan Mo, 17 km, above Anma-shan at edge of logging area near Chungshueh-shan in a wet, n-facing ravine on a decaying log, c. 2500 m, Iwatsuki & Sharp 732a (NICH, TENN). Western Middletaiwan, Tigerkopf, Schwabe, s.n. (JE).

CHINA. Fukien Province, Buong Kang, Yenping, on mossy bark covering the whole base of a tree, 700 m, Chung B34 (NICH, FH, MICH, O, PE, S); on a mushroom log, 1000 m, Chung B117 (NICH, FH, MICH, O, BM); on a mushroom log in a bamboo forest, 3000 m, Chung B112 (FH, MICH, PE); on mossy rock, 700 m, Chung B48b, B52 (FH); on branch of madiellus, Chung B90 (FH, MICH); on rock, Chung B65, B68, B67a (FH, MICH); Chung B74a

(FH, MICH, O); *B90a* (MICH); Fukien Province, Kushan near Foochow, on a shady rock, 500 m, *Chung B173* (FH); on a moist shady rock, *Chung B245a* (FH, HBG, MICH). Province Kweitschou, austro-occid, ad viam Tschenning-Kuang-tsaoba, Yunnan in silva ad vic. Djitschangring pr. opp. Muyusse, substr. truncis viv. arb. frondos, c. 1050 m, *Handel-Mazzetti 10395* (S, H-BROTH). Province Kweitshou orient, prope oppidum Liping in silva mixta Nandjing-schan, ad arbores, c. 750 m, *Handel-Mazzetti 10981* (H). Province Kwangsi, Laoshan, Ling Yuin Hsine, *Cheo 1963* (FH). Yunnan, frontier of Burma, no collector cited, 1898 (H).

BURMA. Yunnan frontier, Niebolitz, 1911 (L, JE, PC). Bhamo, 3000', *Feanus 25* (FI).

SIKKIM. Yoksam, 1700 m, *U. Tokyo Bot. Exp. to E. Ind. 200244* (NICH, NY, L); *20046* (H); Himalaya, prope Kurseong, 1372 m, *P. Decoly & Schaul 2356* (BM, H).

ASSAM. Khasia, Myrung, *Griffith 212*, *Herb. E. India Co. 515* (BM).

INDIA. Dehra Dhoon, *Simla 717 (Griffith)* (NY, BM).

NEPAL. Without precise locality, *Buchanan, s.n.* (NY, S, H, BM).
Without precise locality, *Wallich, s.n.* (BM).

THAILAND. Payap, limestone massive Doi (Mt.) Chiegdao, hill ever-green forest, on fallen tree trunks, 98° 55' E 19° 25' N, *Touw 9063* (L).

EAST INDIES. Without precise locality, *Buchanan 1316* (S, BM).

BORNEO. Between Sosopodon and S. Kelinggen, foot of Mt. Kinabalu, on fallen trunk, 1350-1400 m, *Iwatsuki 1355* (NICH).

SRI LANKA. Central Province, *Müller 248* (H, PC).

JAVA. Mt. Patoeha, *Korthals, s.n.* (S, H, L). Mt. Gédé, *Gerker, s.n.*; Mt. Patoeha, *Korthals, s.n.* (L). Lignes i Habitus mest den fra Java in ag pedicelli Lenghe, Monte Patoeha, *Korthals* (O). Buitenzorg

an Baum, *Schiffner 11016* (S). Without precise locality, *Korthals, s.n.* (L, BM, S, PC). Without precise locality, no collector cited (H, S, BM, C). Natural Reserve, Tjibogo, rainforest, tree trunk in shade, 1480 m, *Soekar, 1949* (L). Tjibodas, Pentjuran mas on bark, *van der Wijk 1001* (L). Without precise locality, *Junghuhn, s.n.* (L).

MALAKKA. Bergland der Sakai, *Werner, 1913* (S, JE).

Rhegmatodon declinatus is clearly distinguished from *Rh. polycarpus* by its rough seta, the absence of dotting on the endostome teeth, and the collenchymatous appearance of the exothecial cell wall thickenings. It is unfortunate that no morphological characters of the gametophyte can be used to separate sterile specimens of the genus. Although no specimens of *Rh. polycarpus* having serrated leaf tips have been collected, I would caution against using this character alone to identify a specimen as *Rh. declinatus*. Although branch leaf characters fall within a continuum, the branch leaves of *Rh. declinatus* are, on the average, longer and more narrow than those of *Rh. polycarpus*. Similarly, the range of length for both the capsule and the seta is somewhat shorter in *Rh. declinatus*.

The holotype for *Rh. schwabei* Herz. was sterile. As only *Rh. declinatus* has been collected in Formosa, *Rh. schwabei* was placed under it.

While *Rh. polycarpus* is widely distributed in the New World, no collections of *Rh. declinatus* have yet been made from this part of the world. *Rh. declinatus* seems then to be restricted to the Old World tropics and subtropics.

2. *RHEGMATODON POLYCARPUS* (Griff.) Mitt., J. Linn. Soc. Bot. Suppl. 1:127. 1859. TYPE: Khasia, *Hooker and Thomson* 775 (lectotype, BM).

(Figure 5)

Anhymenium polycarpon Griff., Griff. muscolog. itin. Assamici, 1838 (Calcutta J. of Nat. Hist. 3:275, t. 16. 1843), Not. p. 471, Griff Icones plant. Asiat. 2: t. 97, f. 1. 1849. TYPE: Assam, Mumbree, *Griffith*, 1835 (not seen).

Rhegmatodon orthostegius Mont., Ann. Sc. Nat. Bot. ser. 2, 17:248. 1842. TYPE: India, Nilghiris, *Perrottet*, s.n. (lectotype, O; syntypes, BM, PC, NY, O). New synonymy.

Anhymenium polysetum Griff., Not. p. 472, 1849, Griff. Icones plant. Asiat. 2: t. 97, f. 2., 1849. *nom. inval.* TYPE: Assam, without precise locality, *Griffith*, s.n. (lectotype, NY).

Rhegmatodon brasiliensis Lindb. ex C. Müller, Bot. Zeit. 20:374. 1862. TYPE: Brazil, prov. Sao Paulo, Santos, *Lindberg*, 1854 (holotype, S; syntypes, O, BM, H). New synonymy.

Rhegmatodon schlotheimioides Spruce ex Mitt., J. Linn. Soc. Bot. 12:566. 1869. TYPE: Ecuador, Andes Quitenses, near Antombos of the river Pastasa, *Spruce* 1437 (holotype, NY-MITT; isotypes, MPU, O, S, BM, H, BR, PC). New synonymy.

Rhegmatodon filiformis Schimp. ex Besch., Mem. Soc. Sc. Nat. Cherbourg 16:231. 1872, et Besch. in Fourn., Mex. Pl. 1 (Crypt.): 43. 1872. TYPE: Mexico, Chinantla, *Liebmann*. 1841 (lectotype, C; syntypes, O, BM, H). New synonymy.

- Rhegmatodon orizabanus* Hamp. in Jaeg., Ber. S. Gall. Naturw. Ges. 1877-78:477. 1880 (Ad. 2:741) *nom. nud.* TYPE: Mexico, Mt. Orizaba, no collector cited, *s.n.* (lectotype, NY; syntype, BM).
- Rhegmatodon filiformis* f. *major* Bruch, in *schedula*, (holotype, BM). New synonymy.
- Rhegmatodon secundus* Kiaer, Forh. Vid. Selsk. Christiania 1882 (24): 38, 2 f. 5-7, 3 f. 1-5. 1883. TYPE: Malagasy Rep., Mt. Ankaratra, *Borgen*, 1887 (holotype, O; isotypes, S, NY, L, BM, C, H, BR, PC). New synonymy.
- Rhegmatodon orizabensis* Besch. in Kiaer, Forh, Vid. Selsk. Christiania 1882 (24): 37. 1883. *nom. nud. in synon.* Type not seen.
- Rhegmatodon densus* Schimp ex Kiaer, Forh. Vid. Selsk. Christiania 1882 (24): 37. 1883. TYPE: Mexico, Orizaba, *Mohr*, 1857 (lectotype, BM). New synonymy.
- Rhegmatodon palustris* Broth., Bih, K. Svensk. Vet. Ak. Handl. 21 Afd. 3(3): 64. 1895 *nom. nud. in synon.* TYPE: Brazil, prov. Minas Geräes, *Caldas, Mosen 365* (holotype, H; isotypes, Z, FH, S, BM). New synonymy.
- Rhegmatodon schlotheimioides* var. *minor* Broth., Bih. K. Svensk. Vet. Ak. Handl. 21 afd. 3(3): 64. 1895. TYPE: Brazil, without precise locality, *Cardot 38* (holotype, H). New synonymy.
- Rhegmatodon palustris* var. *minor* Broth., in *schedula*. TYPE: Brazil, without precise locality, *Binot, s.n.* (holotype, BR).
- Rhegmatodon newtonii* Broth., Bot. Jahrb. 24:281. 1897. TYPE:

Fernando Po, Pic Clarence, Newton, 1894 (holotype, H-BROTH; isotype, S). New synonymy.

Rhegmatodon filirameus Broth., *in schedula*, 1907. TYPE: Guatemala, Alta Verapaz, Coban, *Türckheim 6744* (holotype, H-BROTH; isotypes, FH, NY, LD, S, BM, PC, FI). New synonymy.

Rhegmatodon pringlei Card., *Rev. Bryol.* 37:58. 1910. TYPE: Mexico, Puebla, Tezuitlan, *Pringle 15285* (holotype, H; isotypes, FH, NY, LD, O, S, L, MANCH, BM, C, PC). New synonymy.

Rhegmatodon crassirameus Card., *Rev. Bryol.* 37:58. 1910. TYPE: Mexico, Morelos, Cuernavaca, *Pringle 15283* (lectotype, H; cotype 15310, NY). New synonymy.

Rhegmatodon cameruniae Broth., *in schedula*, 1910 (TYPE: Cameroon, Kamerunberg, Musalse, Bushwald, *Hintz*, 1910 (holotype, H-BROTH)). New synonymy.

Rhegmatodon handelii Broth., *Sitzungsber. Ak. Wiss. Wien Math. Nat. Kl. Abt. 1*, 133:578. 1924. TYPE: China, Yunnan, *Handel-Mazzetti 260* (holotype, H-BROTH; isotype, S). New synonymy.

Rhegmatodon brevicuspis P. Vard et Leroy, *Bull. Jard. Bot. Bruxelles* 18:182. 16. 1947. *hom. illegit.* TYPE: Africa, Tschibinda, *Leroy 227* (holotype, BR). New synonymy.

Branch leaves 0.5-1.3 mm long, 0.2-0.6 mm wide, the average length to width ratios range from 1.85-2.83. Leaf margins are completely entire with no serrations, weakly to strongly reflexed to base of the acumen. Seta from 5.5-13.5 mm in length, *smooth from top to bottom*. Vaginule 1.0-1.9 mm long. Capsule 1.9-3.1 mm long. *Exothecial cells*

with regularly thickened longitudinal walls; transverse walls appearing thinner. Endostome teeth translucent, densely punctate. Endostome teeth ranged from 470-620 μ m and exostome teeth ranged from 200-350 μ m.

Habitat: Usually on the bark of trees or fallen logs, occasionally on wet ground and rocks. Ranging from 1000-3048 m in altitude.

Distribution: Sikkim, Assam, India, China, Sri Lanka, Thailand, Malagasy Rep., Malawi, Guinea, Fernando Po, Cameroon, Mexico, Panama, Guatemala, Brazil, Bolivia, Burma (Fig. 6:1).

SIKKIM. Without precise locality, 2-4000', no collector cited, s.n. (NY). Punkabari, 2-4000' Kurz 2453 (H, BM). Himalaya, 2-4000', Kurz 276/5 (O). Without precise locality, 5000', King 114b (BM). Without precise locality 2-8000', King, 1894 (BR).

ASSAM. Moosai, Griffith, s.n. (O, H). Khasia, regio sub trop., 4000', JD Hooker and Thomson 775 (BM).

INDIA. Kumaon, NW Himalaya, Malkarzun, Askote district, 1388 m, Khan, Broth 1940 (NY, S, H, BM); Rolam River, 3048 m, Khan, Broth 1935 (O, H). Nilghiris, Perrottet 1644 (BM, NY); Perrottet, s.n. (NY, BM, O, PC); Montagne, s.n. (NY, BM, BR, L, O); prope Ootacamund, Weir 276/21 (NY, BM); Ootacamund, 7000', Gambleu 17260 (H); Coonor, trees, 5000', Gambleu 13013 (H). Nilghirebirge bei Coonor in Simsparkjungle an Baumen, 1950 m, Fleischer 511 (B, H, L). Eastern Nilghiris, Kotagiri, tree, 6500', Sedwick 757 (BM). Nilghiri Hills, Srinivasan 277 (HIRO). Palni (Pulney or Palm) Hills, Kodaikanal, Foreau, 1927 (FH); in groves along the Kodai road about 29th mile, c. 5900', Foreau 477 (FH); Kodai road, Foreau 199 (BM); Togaivarai Shola, 4500', Foreau 262/26 (F, BM); Perumalmai Shola, along torrent, 4500', Foreau 141/26 (BM); near Shembaganur, Pragasafuram, 6400', Foreau, 1957 (BR); 6700', Foreau, 1958 (TENN). Kodaikanal, on trees, 2400 m, Foreau and Roine 71 (MANCH,

PC, FH, O, H); Madura, Foreau, 1911 (BR); en Madure dans les Gathes, 7000'+, Andre 35 (PC); Andre, 1909 (BM).

BURMA. Yunnan frontier, Niebolitz, 1911 (JE).

CHINA. Yunnan, Pe yen tsin, auf Baumrinde, Ten, 1921 (FH, JE, S); Ten 9 (S); Ten, 1924 (H). Prope urbem Yunnanfu, in regionis calide temperatae, truncis viv. Quercuum ad templ. Helungtang, c. 1950 m, Handel-Mazzetti 260 (H, JE, S).

SRI LANKA. Without precise locality, Thwaites, s.n. (S); Thwaites 248 (S, BM, H). An Heinen in der Bathschlucht bei Hakgala, 1300 m, Herzog 139 (H, L); 138 (JE).

THAILAND. Payap, granitic massive Doi (Mt.) Inthanon, on branches of Quercuus in clearing, 98° 30' E, 18° 35' N, 1750 m, Touw 9845 (L). Payap, limestone massive Doi (Mt.) Chiengdao, deciduous forest on NNE slope, on tree trunks, 98° 55' E, 19° 25' N, 1000 m, Touw 8903 (L).

MALAGASY REP. Mt. Tsaratanana, 1200-2400 m, Bathie, 1924 (FH, S, JE, H, BR). Mt. Ankaratra, Borgen, 1877 (NY, O, BR, PC); Borgen, s.n. (NY, O, L, BM, C, H, S).

MALAWI. Vernoy Nyasaland, Lucheny Plateau, Mlange Mt., Mlange dist., on trunks of trees in dense forest shade, 1890 m, Brass 16537 (NY).

GUINEA. In jugo Danguina, 1100 m, Robegrin, s.n. (O, S, L, GL, H, BR, PC); 1800 m, Robegrin, 1843 (H).

FERNANDO PO. Pic Clarence, 2000 m, Newton, 1894 (S, H).

CAMEROON. Bamenda, Lake Bambaluwe, on tree trunks in montane forest, Richards R5250 (GL, L, BM). Victoria div., below Likonge, on stem in montane forest, 6500-7000', Richards R4264 (BM, L). Cameroon Mt., on trunks of fallen trees, 5000', Dunlap, 1926 (BM); on trunks of

trees near timberline, 7000', *Dunlap, s.n.* (BM).

MEXICO. Oaxaca, vor dem Pass oberh. Teotitlan in der Sierra, in epiphytenreichen Bergwald an Barke, 2100 m, *Düll 92* (MICH). Puebla, Tezuitlan, on wet banks, 7000', *Pringle 15285* (H, FH, NY, LD, O, S, L, MANCH, BM, C, PC); Tulancingo Road west of Huauchinango, bark of alder, 5000', *Sharp 887* (TENN); on *Carpinus*, 5000', *Sharp 913a, 911B* (TENN). Chinantla, *Liebmann, s.n.* (O, BM, C, H). Michoacan, vicinity of Morelia, Cerro Azul, 2300 m, *Arsene 4543* (FH, S). Morelos, near Cuernavaca, *Pringle 15283* (H), *15671* (S, MICH, PC), *15310* (NY). Chiapas, ditio San Cristobal, "Los Llanos" in silva quercuum, 2200 m, *Munch 7464* (NY, FH, H, BM); prope San Cristobal, "Los Llanos," in praeruptis umbrosis, 2500 m, *Munch 7462* (NY, BM, H); in montibus supra S. Cristobal, 2100 m, *Munch 7282* (H, PC); Cerro Hueytepec, near Las Casas, 8000', *Sharp 3283*, bark of oak, *Sharp 3283a, 3270*; between Las Casas and San Gregorio, on oak, 7500', *Sharp 4683, 4682a* (TENN); SW Jalisco slopes of La Ferreria, above Manantlan, on rotted log, oak forest, 6500', *Crum 1041* (MICH, S, TENN, NY). Guerrero, gorge below Ormiltemi, 30 km west of Chilpancingo, 6300', *Sharp 1149a* (TENN); Rancho del Cielo above Gomez Farias, Tamps., at the mine, fallen log, meso, partial shade, *Sharp 3618* (TENN). Orizaba, no collector cited, 1857 (NY); No. 68 (BM), *Borgeau, 1866* (PC). In planitic Orizabac in sylving ad 6500', *Mohr, 1856* (O). Without precise locality, no collector cited, 1865, (NY); without precise locality, *Liebmann, s.n.* (BM); Totutle, ad hunc ono pertinet fruches perfecti et caespes flaveferis, *Liebmann 8467* (C).

PANAMA. Chiriqui, El Volcan, 6500', *Llano, 1952* (HIRO); vicinity of El Boquete, 1000-1300 m, on tree trunk, *Maxon 4985* (NY).

GUATEMALA. Quetzaltenango, on oak, 7800', *Sharp 2063* (MO, TENN);

7700', *Sharp 2086* (TENN). Chimaltenango, on oak above Tecpam, 8300', *Sharp 2571* (TENN). Coban, Alta Verapaz, in arbore vetusta, 1310 m, *Türckheim, Broth 6744* (NY, FH, LD, S, BM, H, PC, FI).

BRAZIL. Caldis, *Lindberg*, 1854 (NY). Prov. Sao Paulo, rariss ad truncos arb. pu. silv. primae. propr opp. Santos, *Lindberg*, 1854 (O, S, BM, H). Prov. Minas Geräes, Serra de Caldos ad radices arb in suargine paludis, *Mosen 365* (NY, S, H, Z, FH).

BOLIVIA. Below Pelichuco, on rock, 3000 m, *Williams 2851* (NY, H, BM).

ECUADOR. Andes Quitenses, Antombos, Pastasa River, 5000', *Spruce 1441, 1437* (NY, MPU, O, S, BM, H, BR, PC).

Rhegmatodon polycarpus is readily distinguished by 1) highly dotted endostome teeth, 2) a smooth seta, and 3) exothecial cell walls regularly thickened longitudinally, with the transverse walls appearing thinner. The margins of the branch leaves are completely entire. The perichaetial leaf margins with or without teeth. The shape of the branch leaves is highly variable. The branches range from thick and clavate to filiform.

This species has a pantropical and subtropical distribution.

Table 2. Data on three traditional leaf characters formerly used to differentiate smooth-setaed Rhegmatodons.

Original Name	Herbaria	Average Leaf Ratio	Minimum Leaf Ratio	Maximum Leaf Ratio	Average Leaf Length	Minimum Leaf Length	Maximum Leaf Length	Average Leaf Width	Minimum Leaf Width	Maximum Leaf Width
<i>Rh. newtonii</i>	(H)	1.85	1.52	2.05	.985 mm	.728 mm	1.140 mm	.532 mm	.416 mm	.624 mm
<i>Rh. schlotheimioides</i> var. <i>minor</i>	(H)	1.89	1.50	2.35	.690 mm	.478 mm	.832 mm	.364 mm	.249 mm	.457 mm
<i>Rh. brasiliensis</i>	(H)	2.04	1.80	2.36	1.027 mm	.624 mm	1.206 mm	.503 mm	.353 mm	.561 mm
<i>Rh. brevicuspis</i>	(BR)	2.05	1.79	2.38	1.112 mm	.998 mm	1.260 mm	.540 mm	.436 mm	.624 mm
<i>Rh. filirameus</i>	(H)	2.08	1.79	2.42	.750 mm	.665 mm	.936 mm	.359 mm	.249 mm	.457 mm
<i>Rh. secundus</i>	(O)	2.08	1.78	2.45	1.112 mm	.873 mm	1.289 mm	.534 mm	.374 mm	.603 mm
<i>Rh. orizabanus</i>	(NY)	2.12	1.95	2.33	.877 mm	.728 mm	.936 mm	.413 mm	.312 mm	.478 mm
<i>Rh. schlotheimioides</i>	(NY)	2.18	1.81	2.69	.896 mm	.769 mm	1.040 mm	.420 mm	.374 mm	.478 mm
<i>Rh. cammeruniae</i>	(H)	2.19	1.91	2.46	.827 mm	.728 mm	.956 mm	.376 mm	.312 mm	.416 mm
<i>Rh. crassirameus</i>	(NY)	2.30	1.85	2.64	.967 mm	.832 mm	1.144 mm	.420 mm	.291 mm	.561 mm
<i>Rh. hypnoides</i>	(O)	2.33	2.06	2.47	.757 mm	.624 mm	.894 mm	.324 mm	.249 mm	.416 mm
<i>Rh. orizabanus</i>	(BM)	2.34	1.95	2.64	.902 mm	.769 mm	.936 mm	.391 mm	.332 mm	.478 mm
<i>Rh. densus</i>	(BM)	2.37	2.13	2.71	.688 mm	.520 mm	7.900 mm	.291 mm	.228 mm	.312 mm
<i>Rh. filiformis</i>	(C)	2.38	2.11	2.86	1.027 mm	.832 mm	1.185 mm	.434 mm	.312 mm	.540 mm
<i>Rh. orthostegius</i>	(BR)	2.38	2.15	2.65	1.114 mm	.728 mm	1.248 mm	.468 mm	.312 mm	.561 mm
<i>Rh. polycarpus</i>	(O)	2.38	2.17	2.64	1.154 mm	.936 mm	1.310 mm	.484 mm	.353 mm	.603 mm
<i>Rh. polysetus</i>	(NY)	2.42	2.13	2.76	1.025 mm	.894 mm	1.164 mm	.422 mm	.332 mm	.499 mm
<i>Rh. crassirameus</i>	(H)	2.45	2.22	2.75	1.052 mm	.832 mm	1.144 mm	.428 mm	.374 mm	.520 mm
<i>Rh. palustris</i>	(H)	2.46	2.18	2.93	.925 mm	.769 mm	1.040 mm	.376 mm	.312 mm	.457 mm
<i>Rh. handelii</i>	(H)	2.48	2.18	2.81	.859 mm	.665 mm	.956 mm	.345 mm	.270 mm	.416 mm
<i>Rh. brasiliensis</i>	(S)	2.48	2.17	2.88	1.092 mm	1.019 mm	1.164 mm	.438 mm	.375 mm	.478 mm
<i>Rh. polycarpus</i>	(NY)	2.53	2.33	2.84	1.110 mm	1.081 mm	1.248 mm	.438 mm	.353 mm	.499 mm
<i>Rh. pringlei</i>	(H)	2.55	2.25	2.84	.834 mm	.707 mm	.936 mm	.326 mm	.270 mm	.374 mm
<i>Rh. orthostegius</i>	(L)	2.58	2.14	3.05	.875 mm	.624 mm	1.081 mm	.339 mm	.270 mm	.395 mm
<i>Rh. filiformis</i> f. <i>major</i>	(BM)	2.83	2.18	3.14	1.027 mm	.915 mm	1.144 mm	.361 mm	.291 mm	.457 mm

DISTRIBUTION AND HABITAT OF THE GENUS *RHEGMATODON*

Rhegmatodon declinatus has only been collected from the tropics and subtropics of the Old World (Fig. 12:2). In contrast, *Rh. polycarpus* (Fig. 12:1) has a pantropical distribution ranging from Central and South America to Africa, Madagascar, India, and China. Unlike *Rh. declinatus*, *Rh. polycarpus* has not been collected in Indonesia and Malaysia. The ranges of these two species overlap in China (Yunnan), Sikkim (Himalaya), Assam (Khasia), Ceylon, and Thailand (Mt. Chiengdao). The areas of collection are characterized by altitudes of 650-1400 m.

The disjunctive distribution of *Rh. polycarpus* is similar to that of other moss genera such as *Pilotrichella*, *Squamidium*, *Lindigia*, *Braunia*, and *Dimerodontium*. Herzog (1926, 1932) uses the continental disjunctions of certain mainly austral families of vascular plants, with similar patterns of distribution in support of Wegener's (1924) theory of continental drift. The disjunctive distribution of *Rh. polycarpus* is very similar to that of *Leptodontium viticulosoides* and vars. (Zander, 1972).

Rhegmatodon is most often found at the middle and high altitudes in the mountainous regions of the tropics and subtropics. *Rh. declinatus* grows at lower altitudes than *Rh. polycarpus*. *Rh. declinatus* has been found on the bark of fallen logs or trees, and occasionally on moist shady rocks, most often between 500-1700 m. *Rh. polycarpus*, usually found between the altitudes of 1400-2500 m is also corticolous, but may be collected on wet ground and rocks.

DISPOSITION OF NAMES OTHER THAN SYNONYMS IN *RHEGMATODON*

The following list includes the names of *in schedula* specimens, as well as validly published specimens, where examination of the types showed them to belong to some other taxa than *Rhegmatodon*. Most of these specimens were collected in areas for which adequate keys are not available, and only a limited attempt was made to assign these taxa to genera. For the purpose of completeness, previous exclusions and transfers are included in this list.

Rhegmatodon bornmülleri Broth. *in schedula*, 1904. TYPE: Brazil, Cruz Alta, Colonia Nova Wurtemberg, Elsenau, in arboribus, 450 m., *Bornmüller* 6156 (holotype, JE: isotypes, B, S). This differed from *Rhegmatodon* by having no exostome and highly papillose, bifid endostome teeth. Most likely this is *Dunerodontium mendozense* Mitt.

Rhegmatodon chryseus Schimp *nom. nud. in synon.* = *Rozea chrysea* Besch. in Mem. Soc. Sc. Nat. Cher. 16:242. 1872. And Besch. in Fourn., Mex. Pl. 1 (Crypt.):48. 1872. TYPE: Mexico, no collector cited, *s.n.*

Rhegmatodon fissidens Thér., *in schedula*, 1905. TYPE: China, Prov. Kong Tiheau, *Carabrie* 3629 (holotype, H). Laminal cells all subquadrate. This is probably a *Leskea* sp.

Rhegmatodon fusco-luteus Besch., Mem. Soc. Sc. Nat. Cherbourg 16:232. TYPE: Mexico, Orizaba, Müller, *s.n.*, in herb.

Schimper (not seen) = *Platygyrium tuscoluteum* Card. cf.

Card, Rev. Bryol. 38:40. 1911.

Rhegmatodon minutus (Mitt.) Par., Ind. Bryol. 1109. 1898. TYPE:

Andes, Jameson, s.n., (not seen) \equiv *Helicodontium minutum*

(Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. 1876-77:225.

1878 (Ad. 2:291).

Rhegmatodon nietneri C. Müell., Linnaea 36:20. 1869. TYPE:

Ceylon, Nietner, s.n. (isotype, 0). The areolation of the

lamina was not like *Rhegmatodon*. I was unable to identify

this to genus.

Rhegmatodon parvulus Hamp. Icon. Musc. 2:14. 1844. TYPE: Georgia,

Eleenezar near Savannah River, no collector cited, s.n.,

(not seen) \equiv *Clasmatodon parvulus* (Hamp) Sull. in Gray,

Man. Bot. N.U. States ed. 2:660-5. 1856.

INFRAGENERIC RELATIONSHIPS IN *MACROHYMENIUM*

The taxonomic treatment of *Macrohymenium* by Brotherus (in Engler and Prantl, 1925) is based on F. C. Kiaer's revision of 1882, *Genera muscorum Macrohymenium et Rhegmatodon revisa specieque nova aucta exposuit*.¹ Kiaer based his key totally on gametophytic characters in order to include *M. sinense*. This specimen has subsequently been placed in the genus *Giraldiella*. Thus Brotherus also separated the various specimens of *Macrohymenium* on the basis of gametophytic characters.

In this present study, many of these characters are excluded. The following were found to be variable, varying even within the same specimen: denticulations on the margins of the perichaetial leaves, loose to densely imbricated leaves, and leaves heteromallous to homomallous.

Some gametophytic characters are useful in determining species of *Macrohymenium*, e.g., leaf size, shape, and areolation. *M. rufum* leaves are the smallest (.79-1.41 mm long) and widest (2.27) ovate and abruptly constricted to a short acumen (Fig. 8:13-18). In *M. acidodon*, branch leaves are small (.89-1.45 mm) (Fig. 9:10-13) and more narrow than *M. rufum* (2.77). *M. acidodon* can be differentiated from the other species by virtue of the uniform size of the leaf cells (Fig. 9:2,3,7, 9). Each of the other species has leaf cells which are much longer at

¹For the purpose of comparison, translations of both the keys from both works are presented in Appendix II.

the base and gradually shorter toward the tip. *M. mülleri* is the largest of the species, the leaves the longest (1.9-2.5 mm) and the most narrow (4.0) (Fig. 10:11-14). It also has more enlarged alar cells (12-20) (Fig. 10:19). The other species have from 6-9. *M. strictum* has slightly larger leaves (1.0-1.43 mm) than *M. acidodon* and can be distinguished by a sudden constriction to a long acumen (Fig. 11:2-3).

Brotherus did include one sporophytic character in his key, separating his six species into two equal groups on the basis of the seta plainly rough versus the seta set above with very low, broad warts. While some setae may appear rough when dry (Fig. 6:1), moistened setae of all species are smooth at the base and towards the top have a few low, broad projections (Fig. 6:11-12). Neither Kiaer nor Brotherus used the presence or absence of perforations in the endostome teeth as key characters. Probably, this was due to Kiaer's statement that he had found both perforate and imperforate endostome teeth on the same specimen. In every specimen examined during this study this character was discrete. The endostome teeth were either perforate or imperforate, and never differed within the same endostome.

Of the four species recognized in the present work, two have perforated endostomes and two are imperforate. The two species which have perforations are also quite different in the expression of the character. *M. mülleri* has very regular perforations in nearly every segment, producing a scalloped effect. *M. mülleri* also has the shortest peristome, the endostome ranging from 250-300 μ m and the exostome from 190-200 μ m (Fig. 10:1-3). The seta is moderately long (8-11 mm) and quite thin (130-150 μ m). On the other hand, *M. acidodon* has irregular perforations in the upper portion of the teeth, sometimes

nearly continuous (Fig. 9:4-5). The peristome is moderate in size, the endostome ranging from 350-500 μm and the exostome from 200-250 μm . The seta is 9-11 mm long and 115-180 μm wide. The endostomes of *M. rufum* (Fig. 8:4-5) and *M. strictum* (Fig. 11-4-5) are imperforate. The peristome of *M. strictum* is much larger (endostome, 550-750 μm ; exostome, 300-410 μm) than that of *M. rufum* (endostome, 440-600 μm ; exostome, 170-300 μm). The seta of *M. strictum* also is much longer (8-21 mm) and wider (200-374 μm) than that of *M. rufum* (6-6.5 mm long and 160-220 μm wide).

DESCRIPTION OF THE GENUS *MACROHYMENIUM*

Plants lustrous, yellow-brown to reddish green, in moderately compact, low sods, copiously fruiting. Pleurocarpous mosses, prostrate and rooting. The sporophytes lateral at base of the branches. *Goniautoicous*. Primary stems thin, stolon-like, zigzag, creeping, lacking a central strand, copiously branched. *Branches* typically simple, ascending, short, thick and round, straight to curved, densely foliose; leaves imbricate, heteromallous to somewhat homomallous. *Paraphyllia* or *pseudoparaphyllia* lacking. *Branch leaves* ecostate, concave, ovate-lanceolate, acuminate, with the leaf margins entire, more or less recurved. *Laminal cells* elongate, oval, walls incrassate osteoform with thin connecting areas between cells. *Alar cells* rectangular and quadrate, colored and somewhat inflated. *Leaves* .79-2.53 mm long, and .29-.66 mm wide. *Inner perichaetial leaves* large ecostate or faintly hinting of a costa, upright, sheathing, ovate-lanceolate, acuminate, or somewhat blunt. *Perichaetium* rooting. *Vaginule* small, oblong cylindric. *Perigonium* axillary, hidden between the stem and branch leaves, budlike, very small, 1/3 length of leaves. *Perigonal leaves* broadly ovate, acuminate, ecostate, entire. *Antheridia* many, pedicellate, short stipitate, oblong-cylindric, with small paraphyses sparse or lacking. *Perichaetium* axillary, inserted in the axils of the branchlets, budlike, many-leaved, and obscured between the leaves. The *archegonia* short, moderately robust, with very few short, filiform

paraphyses. *Setae* flexuous or twisted in the dry state, short to long, 6-21 mm, smooth at base, but with low hyaline protuberances below the capsule. *Capsule*, erect-inclined, constricted below the mouth, oblong, reddish brown. *Exothecial cell walls* irregularly thickened, appearing collenchymatous. *Operculum* conic rostrate, nearly equalling the capsule in length. *Peristome* double; *exostome* of 16, equidistant, erect-incurved teeth, inflexed in the dry state, broad at the base with two striated dorsal plates separated by a zigzag line, suddenly constricted to a long ciliate tip, the zigzag line continuing to the tip. Dorsal plates backed by a single row of trabeculate plates. *Endostome* of 16 teeth, from a low basal membrane, without cilia, the processes about 2X longer than the exostome teeth, keeled, entire, either perforate or imperforate on keeled midline. Membrane subplicate, tessellated. *Spores* globose and papillose, 15-27 μm in diameter. *Calyptra* cucullate.

Margadant (1959) posed a nomenclatorial problem with reference to the genus *Macrohymenium*. Fleischer (1923) synonymized *Leskea? rufa* Reinwardt and Hornschuch with *Acroporium braunii* (C. Müll.) Fleisch. Because *Leskea rufa* was an earlier collection than the type for *A. braunii* the name was changed to *Acroporium rufum* (Hornsch. and Reinw.) Fleischer. Fleischer said he had examined the type for *Leskea rufa* in the Berlin Herbarium. Believing this specimen to be the basionym for *Macrohymenium rufum*, the type species of the genus *Macrohymenium*, Margadant felt that this transfer threatened the nomenclatural standing of *Macrohymenium*. He therefore proposed that *Macrohymenium acidodon* (Mont.) Doz. and Molk. (1848) be designated the lectotype and the name *Macrohymenium* be conserved. All of this is based on the assumption that Carl Müller used *Leskea rufa* Reinwardt and Hornschuch as the type specimen for his new genus. There is good reason to believe that this was

not the case.

The original specimen of *Leskea rufa* was described in Nov. Act. Caes. Leop. 14: Suppl. 2: pp. 716-17. 1826. It was collected by Reinwardt on Mt. Malabar (Malabaria), Java. In 1847, when erecting the new genus, *Macrohymenium*, Müller cited three specimens in synonymy. The first was *Leskea rufa* Reinwardt and Blume, Java. This same citation is found in *Synopsis Muscorum Frondosorum* 2:30, 1850, when Müller dissolved *Macrohymenium* and moved *M. rufum* into the genus *Rhegmatodon* as *Rh. rufus*. In neither of these citations does Müller ever mention Malabaria. This suggests that his type for *M. rufum* was in fact based on another specimen. There are several facts which support this idea.

The original description of *Leskea rufa* Reinwardt and Hornschuch, states that the peristome was destroyed. Yet Müller's genus description contains a detailed description of both the endostome and exostome; neither of which could be mistaken for *Acroporium*.

Further support issues from the synonymy of Dozy and Molkenboer (1848) in which they list two specimens from Java; Blume and Reinwardt, Java, and a separate Reinwardt, Mt. Malabar.

Java: collegerunt Blume et Reinwardt, monente Müllero:
Malabaria: collegit Reinwardt (cf. Nov. Acta Acad. Caes.
Leop. 1. cit.). (Dozy & Molk., 1848, p. 167.)

Note that the first specimen was "collected by Blume and Reinwardt, with advice by Müller," while the Malabar listing only mentions Reinwardt as the collector, and by the accompanying citation gives clear indication that this second specimen is the *Leskea rufa* of 1826. Whenever the Mt. Malabar specimen is cited, Reinwardt's name is used alone, never in conjunction with Blume.

There is sufficient evidence to support the existence of a separate specimen from Java, collected by Blume & Reinwardt, on which the type

description of *M. rufum* is based. Fleischer, recognizing that the specimen from Mt. Malabar was actually an *Acroporium*, placed it in synonymy with *Acroporium braunii* without jeopardizing the nomenclatorial standing of *Macrohymenium*.

One other possibility exists. Müller may have described his new genus using a combination of characters from the three specimens in his synonymy. This would assume the Mt. Malabar collection to be the same as the Blume and Reinwardt collection. If so, his description of the peristome could only be that of *L. mitrata* since no perforations of the endostome are noted. *L. acidodon*¹ has definite perforations, for which reason it was taken out of synonymy and designated the type for *Macrohymenium acidodon* (1848). I recently received a collection of *Macrohymenium* from Jena (JE) which contained a specimen with the following data:

Rhegmatodon rufus mihi!

Java: Blume

Vereinigte Herbarien Karl Schliephaeke, Osterfeld und
Hermann Winter, Gotha.

This specimen is clearly a *M. rufum* and has two sporophytes in excellent condition. While there is no date, I believe this is the missing specimen of Blume and I am designating it as the lectotype for *M. rufum*.

If further evidence negates my argument, I recommend that *Leskia mitrata* Doz. and Molk. be designated the lectotype for *Macrohymenium rufum*.

For reasons stated above, *Leskia mitrata* Doz. and Molk., *Musci Frond. ex Archip. Indici*. 1844, p. 15; *Ann. des Sc. Nat.* 1844, p. 511, is the earliest described specimen of *Macrohymenium rufum* C. Müller.²

¹Assuming Müller saw the 1845 specimen of Doz. and Molk.

²Granting the above argument, this would be the proper citation for *M. rufum*.

KEY TO THE SPECIES OF *MACROHYMENIUM*

1. Endostome teeth with perforations in the keeled midline,
at least from mid-tooth to tip. 2
1. Endostome teeth with no perforations of the keeled midline
. 3
2. Perforations even, uniform, giving a scalloped ap-
pearance from the base to the tip; large branch
leaves (1.9-2.5 mm long) with long basal cells (12:1),
the cells gradually shortening to the tip (3:1)
. *M. milleri*
2. Perforations uneven, irregular, restricted mostly to
the upper half of the teeth, sometimes appearing bifid
at the tip; smaller branch leaves (0.9-1.5 mm long),
the cells of uniform size from the base to the tip of
the leaf (5:1 - 3:1). *M. acidodon*
3. Branch leaves lanceolate, gradually acuminate; peri-
chaetial leaves abruptly constricted to acuminate tip;
seta ranging from 8-21 mm in length. . . *M. strictum*
3. Branch leaves from a squarish base, widely ovate-lanceolate,
abruptly acuminate; some of the perichaetial leaves blunt;
seta ranging from 6-7 mm in length. . . *M. rufum*

1. *MACROHYMENIUM RUFUM* C. Müell., Bot. Zeit. 5:825. 1847. TYPE:

Java, without precise locality, *Blume and Reinwardt, s.n.* (lectotype, JE).

(Figure 8)

Leskea rufa Reinw. and Hornsch., Nov. Act. Acad. Caes. Leop. Carol. 14, p. 2 suppl. 1826, p. 716-717. TYPE: Java, Mt. Malabar, *Reinwardt s.n.* (not seen).

Leskea mitrata Doz. & Molk., Ann. Sc. Nat. 3 ser. 2. p. 311. 1844. TYPE: Sumatra, *Korthals, s.n.* (holotype, L). New synonymy.

Rhegmatodon rufus (Reinw. and Hornsch.) C. Muell., Syn. 2:30. 1850. TYPE: Java, *Blume and Reinwardt, s.n.*

Macrohymenium curvirostrum, Braun, in schedula. TYPE: Java, *Braun, s.n.* (holotype, BM). New synonymy.

Plants small, the leaves .79-1.41 mm long and .31-62 mm wide, with an average length to width ratio of 2.27. The leaves ovate and abruptly constricted into the acumen. The leaf cells longer at the base of the leaf (10-12:1), gradually shortening towards the tip (2-3:1). Six to nine inflated quadrate colored alar cells. Usually, one or two of the inner perichaetial leaves with a very blunt tip. Seta from 6-6.5 mm in length and 160-200 μ m in width. The endostome teeth lacking perforations on the midline. The endostome teeth ranging from 440-600 μ m, and the exostome teeth ranging from 170-300 μ m.

Habitat: On tree trunks in forests, epiphytic, usually found between 1500-2000 m, but occasionally up to 3030 m.

Distribution: Java, Sumatra, Borneo, New Guinea, Australia, Sri Lanka, Malagasy Rep.

JAVA. Tjibodas, mountain garden, *Meijer*, 1953 (L); *Nurta*, 1953 (L). Between Tjibodas and Tjihoerang, in *Eupaternia pallescens* plain at Koebang tree trunk in the sun, 1380 m, *Soekar* 2247 (L). Namtrong Djimter, Jeger Bentang, rainforest tree trunk in the sun, 1450 m, *Soekar* 3187 (L). G. Sindoro, rainforest, 2400 m, *Leeuwen* 8889 (L). Without precise locality, *Gerker*, *s.n.* (L); *Braun*, *s.n.* (L). Without precise locality, no collector cited, *s.n.* (BR). Without precise locality, *Blume*, *s.n.* (JE)

SUMATRA. Mt. Sogo, near summit, mossy forest, 2000 m, *Meijer* 6126 (L). *Korthals*, *s.n.* (L, H, O, S). West coast, Mt. Merapi, west side, Prim. forest on branch, *Waalkes* 2236 (L); 1700 m, Belukar, on trunk, *Waalkes* 2270 (L). Aek na Vli, near Toba Lake, in mixed forest on bark, 1400 m, *Wijk* 1870 (L). Without precise locality, no collector cited, *s.n.* (S, C).

BORNEO. E. Kutai, peak of B. papan, terr. Beul, on Magnoliaceae, 600-700 m, *Meijer* B1968 (L). N. Borneo, west coast res, Mt. Kinabalu, near Paka Cave, c. 9700', *Meijer* B11-903 (L).

NEW GUINEA. Star Mts. Mt. Antares, on rotten trunk of tree in rain forest, 1500 m, *van Zanten* 385b (BM). Eastern Highlands District, Arau, low on a tree in *Castanopsis*, oak forest, 1400 m, *Brass* 31976a (L). Sepik District, Ambunti Subdistrict, summit of Sunset, Mt. Hunstein, in elfin woodland on summit plateau, epiphytic on upper branches of small tree, c. 5000', *Hoagland and Craven* 10985 (L). Western Highlands District, Wabag area, Ranges south of Wabag, *Nothofagus* lower montane rain forest, corticous, 8000', *Robbins* 2859 (L).

AUSTRALIA. Queensland, Ravenshoe, *Watts* 660 (H).

SRI LANKA. Beim Stausee von Kandy, c. 55 m, *Herzog*, 1906 (BM).

MALAGASY REP. "Certainly from Madagascar," no collector cited, s.n. (BM).

M. rufum has the smallest and widest leaves of any of the species. The widely ovate leaves, with a short abrupt acumen, are easily recognized. The imperforate endostome is similar to that of *M. strictum* but smaller, and the seta is the shortest of all *Macrohymenium* species. *M. rufum* is the only species in which some of the inner perichaetial leaves are blunt.

2. *MACROHYMENIUM ACIDODON* (Mont.) Dzy et Molk., Musci Frond. Ined.

Archip. Indici 6:168. 1848.

(Figure 9)

Leskea acidodon Mont., in Ann. sc. nat. 1845, p. 96, t. 5, f. 4

and Syll. p. 19. 1845. TYPE: Réunion, no collector cited
s.n. (holotype, L).

Macrohymenium laeve Thwait. and Mitt., J. Linn. Soc. Bot. 13:317.

1873. TYPE: Ceylon, *Thwaites* 236 (holotype, NY-MITT; iso-
types, O, H-BROTH, PC, BM). New synonymy.

Macrohymenium acidodon var. *acutissima* Besch. ex Par., Ind. Bryol.

1108. 1898 *nom. inval. in synon. err. pro* M. a. fo. Besch.,
Ann. Sc. Nat. Bot. ser. 6, 10:292. 1880. TYPE: Madagascar,
Perville, s.n. (holotype, L; isotype, L, H-BROTH). New
synonymy.

Rhegmatodon madagassus C. Müell. ex Geh., Abh. Naturw. Ver. Bremen

7:211. 1882. TYPE: Madagascar. forest of Ambatondrazaka,
Rutenber, s.n. (holotype, O).

Rhegmatodon acidodon (Mont.) Par., Ind. Bryol. 1108. 1898.

Rhegmatodon laevis (Thwait. and Mitt.) Par., Ind. Bryol. 1109.

1898.

Rhegmatodon acidodon var. *acutissima* (Besch.) Par., Ind. Bryol.

1108. 1898.

Plants with leaves, .89-1.45 mm long, .29-.58 mm wide, with an
average length to width ratio of 2.77. *Leaf cells uniform in length
from the base to the tip of the leaf.* Six to eight golden-colored in-
flated quadrate alars. Perichaetial leaves slightly serrate, ecostate
or with a faint trace of a costa on some of the large inner leaves.

Seta from 9-11 mm in length, 115-180 μ m in width, slightly twisted, quite smooth at the bottom with hyaline protuberances toward top. *Endostome teeth perforated on their midline with uneven irregular perforations*. The perforations are mostly in the top half of the tooth, occasionally producing a bifid tip. Endostome teeth ranged from 350-500 μ m and the exostome teeth ranged from 200-250 μ m.

Habitat: On branches and rocks, 1800-2500 m.

Distribution: Malagasy Rep., Reunion, Seychelles, Sri Lanka, N. Borneo.

MALAGASY REPUBLIC. Forest of Ambatondrazaka, *Rutenberg*, s.n. (O); *Hildebrandt*, 1880. Without precise locality, no collector cited, s.n. (O, L); *Hildebrandt*, 1880 (L); *Perville*, 1879 (H, O).

RÉUNION. Without precise locality, *Lepervanche*, 1879 (O, BM, H, PC); no collector cited (O, L); *Richards* (BM); *De L'Isle* (PC); *Rodriguez* (PC); Plain au Cafres, *De L'Isle* (BM).

SEYCHELLES. Without precise locality, *De L'Isle* (PC).

SRI LANKA. An baumen beim Rambotta pass, c. 2000 m, *Herzog 115* (H, JE, L). Central Province, *Thwaites 236* (T, PC, NY, O, BM). An Baumen beim Tec von Nuwara Eliya, 1800 m, *Herzog*, s.n. (PC, S). Nuwara Eliya, rotting stump in jungle, *Binstead 183* (BM).

BORNEO. N. Borneo, West Coast Res. Mt. Tambuyokon, c. 15 miles NE of Kinabalu Peak, summit area on branches and rocks, c. 8000', *Meijer B11-378* (L).

M. acidodon differs from all other species by the uniform size of the leaf cells from base to tip. The endostome of *M. acidodon* is also uniquely perforated with irregular, uneven slits, mostly in the upper half of the precesses. This sometimes produces a bifid appearance.

3. *MACROHYMENIUM MÜLLERI* Doz. and Molk., Musci Frond. Ined. Archip.

6:168. 55. 1848. TYPE: Java, Mt. Gédé and Talaga-Bodas, Korthals, s.n. (cotypes, O, C, H, S, L). Borneo, Mt. Sakoembang, Korthals, s.n. (lectotype, L). Sumatra, Batang-Bessie, Korthals, s.n.

(Figure 10)

Rhegmatodon mülleri (Doz. and Molk.) C. Müell., Linnaea 36:21.

1869.

Macrohymenium mülleri forma *pubea* Dix., in schedula, 1909. TYPE:

Java, Mt. Pangerango, Palmer & Bryant 982a (holotype, BM).

New synonymy.

Plants large, the branches thick and curved, leaves 1.9-2.53 mm long and .42-.66 mm wide, with an average length to width leaf ratio of 4.0. Leaf cells at base much longer (10:1) than cells at the tip (3:1). Twelve to twenty inflated, colored, quadrate alar cells. Seta from 8-11 mm in length, 130-150 μ m in width. The endostome teeth perforated on the midline nearly the whole length with very uniform and regular perforations giving a scalloped appearance to the midline. Occasionally the tip of a tooth is bifid. Endostome teeth ranging from 250-300 μ m, the exostome teeth from 190-200 μ m.

Habitat: On trees and ravine in very moist forest, usually found at elevations from 1200-1800 m, but occasionally up to 3100 m.

Distribution: Java, Borneo, Malay Peninsula, and Malagasy Rep.

JAVA. Mt. Pangerango, 4-6000', Motley, 1906 (NY); 7-10,000', Motley, 1906 (BM); Palmer & Bryant 982a (BM). Prov. Preanger, In decliv. austral. montis Pangerango, in horto montano Tjibodas, Regio nubium,

± 1420 m, *Schiffner 12729* (S); in Cinchoneto, Daradjat prope Garut ad truncos putridos, Regio nubium, ± 1730 m, *Schiffner 12127* (L). Mt. Salak, Binnendijk (S, L). Rawa gajonggong Tjibeureum, plain of gajonggong, tree trunk in the sun, 1700 m, *Soekar, 1949* (L). West Java, Tjibodas, Mt. Gede, Batu gonggang, Nature reserve, in rain forest, on *Vernonia arborea* base of trunk, shadowed, 1600 m, *VanOostatroom 14235* (L). Without precise locality, *Schroted, 1927* (H).

BORNEO. In Sakoembang, *Korthals, s.n.* (L). Kinabalu, *Low, 1859* (BM); Below Kamborangah, ravine in wet montane forest, 6000', *Richards R5758* (L).

MALAY PENINSULA. Gunong Tahan, Pahang, *Ridley 1035* (BM).

MALAGASY REPUBLIC. Without precise locality, no collector cited, *s.n.* (S).

M. mülleri is distinguished from the other species of *Macrohymenium* by its large size, and its long, narrow leaves with many alar cells. The endostome of *M. mülleri* is differentiated by its peculiar pattern of perforations, and by its generally smaller peristome. Although *M. mülleri* is the most robust of all the species, it is marked by the smallest peristome and a very thin seta.

4. *MACROHYMENIUM STRICTUM* Bosch. and Lac., in Doz. & Molk., Bryol.

Jav. 2:114. 1865. TYPE: Borneo, Mt. Kinabalu, *Low*, s.n. ex herb. Hook (holotype, NY; isotypes, O, S, L).

(Figure 11)

Rhegmatodon strictus (Bosch. and Lac.). C. Müell., *Linnaea* 36:21. 1869.

Macrohymenium nova-guineense Reim., *Hedwigia* 69:129, 1929. TYPE: Nova Guinea neerlandica, Mt. Doorman, *Lam 1701* (not seen).
New synonymy.

Macrohymenium acidodon (Mont.) Doz. et Molk. *fo. longisetum*, in *schedula*. TYPE: Madagascar, Massif de L'Anjanaharibe, *Humbert, Capuron and Cours*, 1951 (holotype, PC). New synonymy.

Plants moderate to large, the leaves 1.0-1.43 mm long, and .37-.55 mm wide, with an average length to width ratio of 2.7. The leaves ovate-lanceolate with a long acumen. The leaf cells generally uniform in size over most of the leaf (3:1), much longer at the base (10-12:1). Eight to twelve inflated, quadrate, colored alars. All of the perichaetial leaves with acuminate tips. Seta from 8-21 mm in length and 200-372 μ m in width. Endostome twice as long as the exostome; endostome teeth not perforated. Endostome teeth ranging from 550-750 μ m; exostome teeth ranging from 300-410 μ m.

Habitat: On trees and ground in subalpine forests and open thickets, occasionally found 1000-2000 m, but usually above 3000 m and up to 4370 m.

Distribution: Malagasy Rep., Seychelles, Sri Lanka, Borneo, Sarawak, Sumatra, New Guinea, Australia, and the Philippines.

MALAGASY REP. Massif de L'Anjanaharibe (Pentes and Sommet Nord), a L'ouest D'Andapa Haute AndraMonta, Bassin de la Lokoho, nord-est, foret ombrophile sur gneiss et grantie, \pm 1000 m, *Humbert, Capuron and Cours*, 1951 (PC).

SEYCHELLES. Prés la baie Sainte Anne, no collector cited, *s.n.* (PC).

SRI LANKA. Nuewara Eliya, foot of tree by road, *Binstead 181* (BM).

BORNEO. Mt. Kinabalu, *Low, s.n.* (O, S, L, NY). North Borneo, West Coast Res., Mt. Tambuyokon, c. 15 miles NE of Kinabalu, *Meijer B11-473*; ultrabasic area, \pm 9000', *Meijer B10-242* (L). North Borneo, Kota Belud distr., one mile n. of Kamarangan camp on path to Paka Cave, Mt. Kinabalu, common on ground in turf under an open, scrubby growth, averaging 12' high, dominated by Ericaceae, Dacrydium and Phyllocladus, in fairly pure, abundantly fruiting tufts up to 9" diameter, moist and shady, deep humus over shallow, grey loam, 2750 m, *Wood 1539* (L).

SARAWAK. Without precise locality, *Oxford Exped. (1932) 1631* (BM).

SUMATRA. Sumatra occid, ad declif. occid. montis ignivomi Merapi, regio nubium, 1800-2050 m, *Schiffner 12724* (L, PC).

NEW GUINEA. Mt. Albert Edward, common on forest trees, 3680 m, *N. Guinea Exped. of Am. Mus. of Nat. Hist. 4431, 4438, 4439, 4435* (NY). Western Highlands, Kubor Range, Mt. Kinkain, on tree trunk, alpine shrubbery, 3580 m, *Vink 16178* (L). Western Highlands, Wabog Area, Sugarloaf Mt. area, montane rain forest, epixylic, 10,000', *Robbins 2805* (L). Eastern Highlands, Bismarck Ranges, Mt. Wilhelm, on trees in grove at base of Bogonota Ridge, SE of Lake Aunde of edge of valley floor, 11,000', *Weber and McVean B-32129* (LD, GL); Pindaude, Mt. Wilhelm trail, epiphytic on *Coprosma* sp. in alpine tussock grassland, locally common, 14,000',

Weber and McVean B-33522 (TENN); on dead wood in edge of subalpine forest 3700 m, Brass 29994 (L). NE Wilhelmina, top, epiphyte, 3650 m, Brass and Myer-Drees 9775 (TENN). Lake Habbema, enveloping branch in open thickets, 3225 m, Brass 9453 (L, TENN).

AUSTRALIA. Molanda, Queensland, Watts 623, 664 (H). Ravenshoe, Queensland, Watts 662, 657 (H).

PHILIPPINES. SE Mindanao, Todaya, Mt. Apo, on tree, 1220 m, Williams 2675 (NY, H).

M. strictum is distinguished by its larger leaves with a long, suddenly constricted acumen. It also has the largest peristome of any species. Though the imperforate endostome closely resembles that of *M. rufum*, it is differentiated by its much larger size. The seta is also much longer and more robust than that of *M. rufum*, and the perichaetial leaves more acuminate. *M. strictum* is a species growing at very high altitudes, usually above 3000 m, while *M. rufum* is found at lower altitudes, from 1700 m down to 600 m.

DISTRIBUTION AND HABITAT OF THE GENUS *MACROHYMENIUM*

Species of *Macrohymenium* have been collected only in the Old World tropics (Fig. 13:1-2; Fig. 14:1-2). The genus is essentially insular, occurring from the Malagasy Republic through Sri Lanka and Indonesia to northeastern Australia. Species of *Macrohymenium* are very similar in their distribution. Every species has been found from both Borneo and the Malagasy Republic, and all but one, *M. mülleri*, from Sri Lanka.

Although the species of *Macrohymenium* occupy areas very similar in latitude, the altitudinal ranges of each vary widely. *M. strictum* has been collected primarily above 3000 m. *M. acidodon* is found at relatively lower altitudes, 1800-2500 m, while *M. mülleri* is, for the most part, encountered between 1400-1700 m, but has been reported from as low as 600 m. *Macrohymenium* is primarily a corticolous genus, although a few specimens have been collected on rocks and soil. Collection data for most specimens are so scarce that it is difficult to be more precise in describing the habitat of the genus.

DISPOSITION OF NAMES OTHER THAN SYNONYMS IN *MACROHYMENIUM*

The following list includes the names of *in schedula* specimens, as well as validly published specimens, where examination of the types showed them to belong to some other taxa than *Macrohymenium*. Most of these specimens were collected in areas for which adequate keys are not available, and only limited attempt was made to assign these taxa to genera. For the purpose of completeness, previous exclusions and transfers are included in this list.

Macrohymenium cuspidatum Mitt. in Kiaer, Forh. Vid. Selsk.

Christiania 1882 (24): 45. 1883. TYPE: Assam, Mt. Khasia, Griffith (No. 212, Hb. Kew. No. 516 intermixed) (isotype, 0). *Index Muscorum* incorrectly attributes a new species, *Sematophyllum cuspidatum*, to Kiaer on the basis of this specimen. Actually, he notes that the peristome was destroyed by age and unknown to him, and that it perhaps belonged to the genus *Sematophyllum*. Having seen the specimen, I would agree.

Macrohymenium densirete Broth. in Fleisch., Musci Fl. Buiten-

zorg 4: 1192. 1923 *nom. nud. in synonym*. TYPE: not given
≡ *Clastobryum conspicuum* Fleisch.

Macrohymenium gracillimum C. Müll. ex Kiaer, Forh. Vid. Selsk.

Christiania 1882 (24): 19. 1883 *nom. inval.* TYPE: not given.

Macrohymenium kunzii C. Müll., *in schedula*, 1868. TYPE: India, Pegu, Yomah, Kunz 2939 (holotype, H). Broad bodies were present on this specimen. It is clearly in the Sematophyllaceae and probably in the Clastobryoideae.

Macrohymenium sinense Thér., Bull. Ac. Int. Geogr. Bot. 19:20. 1909. TYPE: China, Prov. Kweitschou, Lou-mong-touan, Fortunat, 1903 (holotype, S) = *Giraldiella levieri* C. Müll. *fid.* Reim., Hedwigia 71: 62. 1931. I have seen this specimen and agree.

Macrohymenium wichurae Broth. in Fleisch., Musci Fl. Buitenzorg 4: 1364. 1923 *nom. nud. in synonym.* TYPE: not given.

LEGENDS FOR THE FIGURES

To facilitate reference and comparison of the characters presented in Figures 1-11, the following standardized magnifications have been used:

Habits	X8	Spores	X466
Calyptrae	X30	Leaf tips	X164
Opercula	X30	Alar cells	X164
Endostome teeth	X125	Basal cells	X164
Exostome teeth	X125	Juxtacostal cells	X164
Exothecial cells	X164	Antheridia	X117
Setae	X117	Archegonia	X117
Perichaetia	X30	Portion of branch	X30
Vaginules	X30	Perichaetial leaves	X30
Pseudoparaphyllia	X164	Branch leaves	X30
		Perichaetial teeth	X164

The maps in Figures 12-14 show the distribution of the various species of *Rhegmatodon* and *Macrohymenium* on a world-wide basis. Only the locations of those specimens examined and verified by the author have been plotted. The base map is a modified Denoyer Semi-elliptical Projection.

Figures 15 and 16 contain the major published illustrations of these genera.

Figure 1: Pictures 1-18. *Rhegmatodon* spp. 1-3. Habit. 4-5. Operculae. 6. Perigonium. 7. Perichaetial Leaf Cells. 8. Archegonia and Paraphyses. 9. Antheridium and Paraphyses. 10. Capsule and Operculum. 11. Calyptra. 12-16. Perchaetial Leaves. 17. Perchaetial Leaf Tip with Tooth. 18. Exothecial Cells.

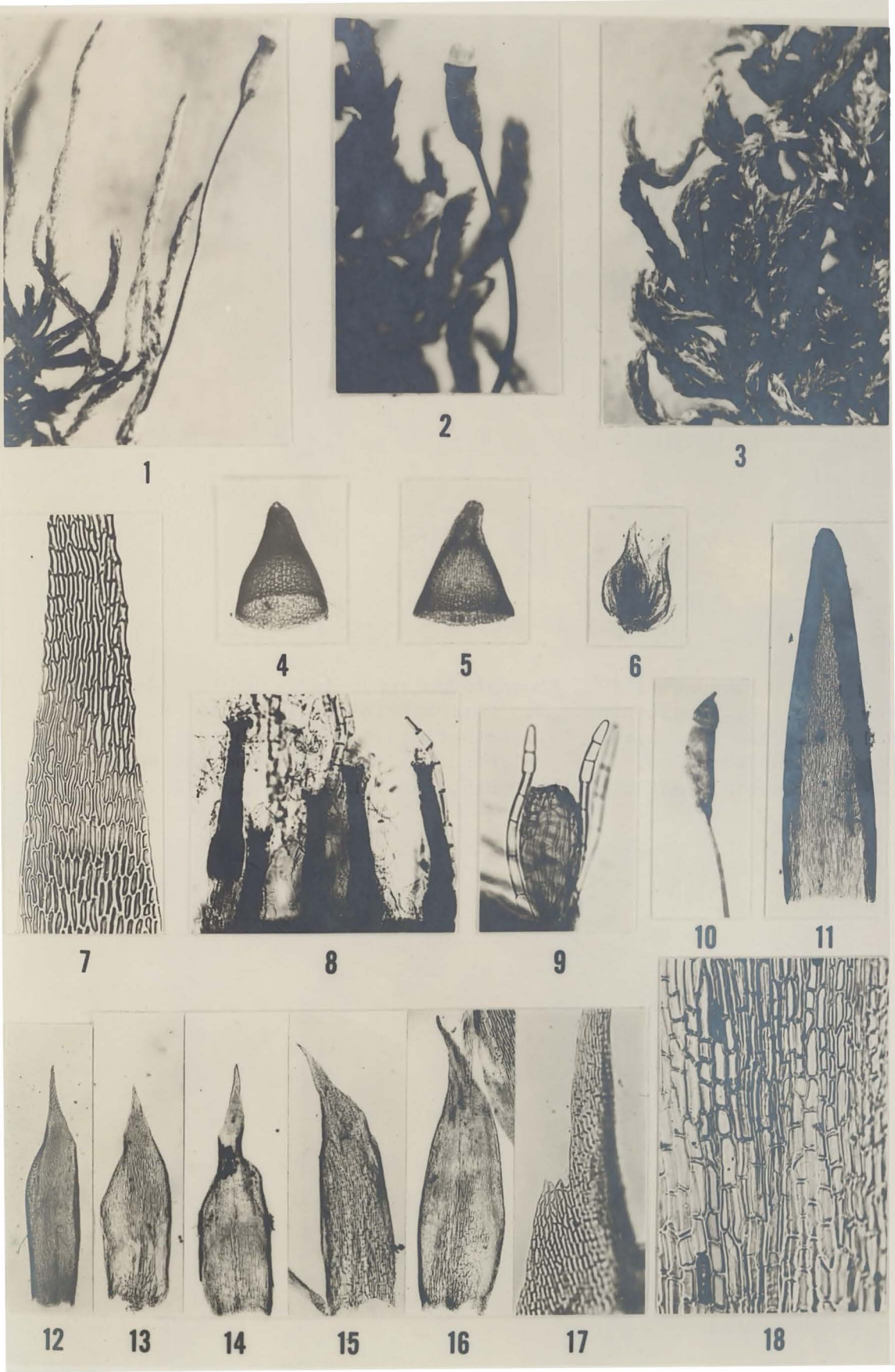
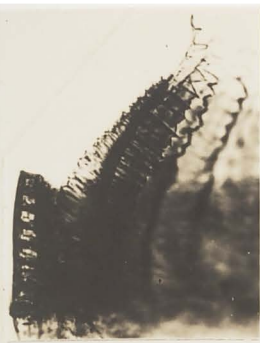


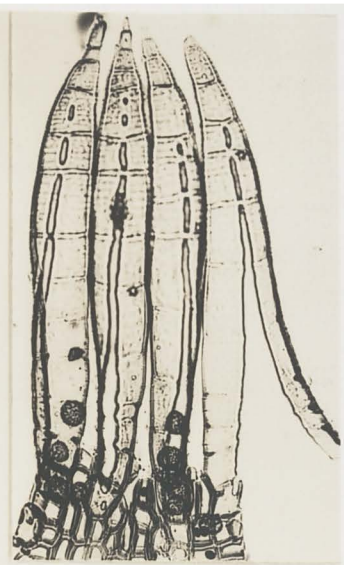
Figure 2: Pictures 1-22. *Rhegmatodon* spp. 1-2. Exostome Teeth on Capsule. 3. Exostome from Top. 4. Spores. 5. Endostome Teeth. 6-12. Exostome Teeth. 13-22. Pseudoparaphyllia.



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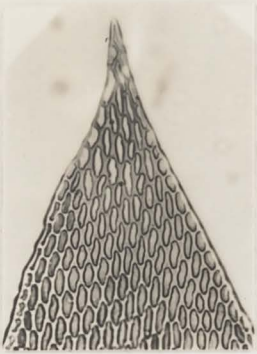


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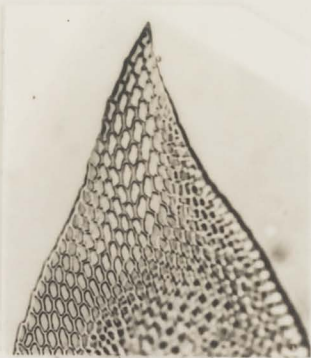


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Figure 3: Pictures 1-7. *Rhegmatodon* spp. 1-7. Leaf Cells.



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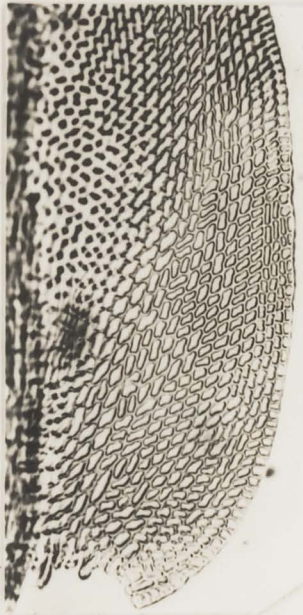
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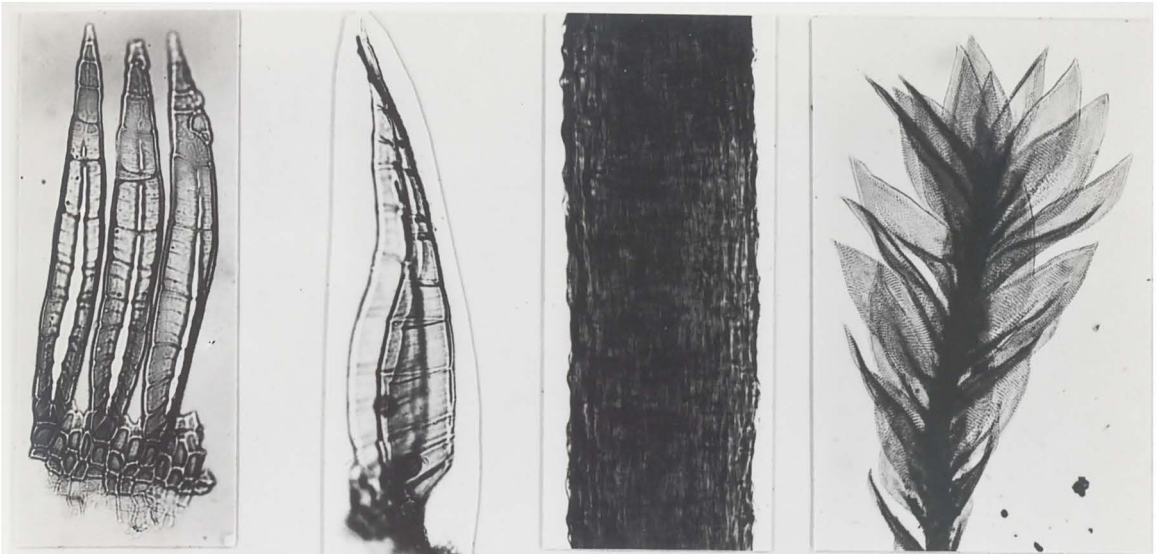


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Figure 4: Pictures 1-13. *Rhegmatodon declinatus*. 1-2. Endostome
Teeth. 3. Rough Seta. 4. Terminal Portion of Branch. 5-7. Leaf Tips.
8-12. Branch Leaves. 13. Exothecial Cells.

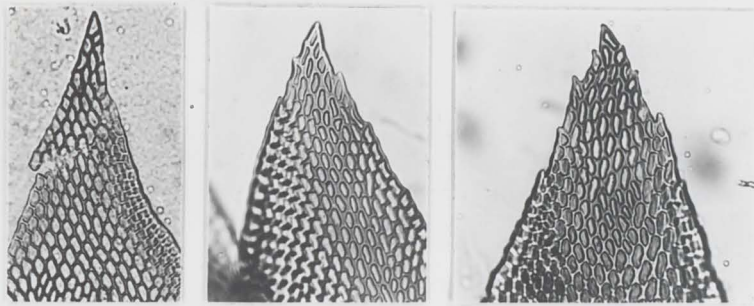


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Figure 5: Pictures 1-23. *Rhegmatodon polycarpus*. 1-2. Endostome
Teeth. 3. Smooth Seta. 4. Terminal Portion of Branch. 5-9. Leaf
Tips. 10-22. Branch Leaves. 23. Exothecial Cells.

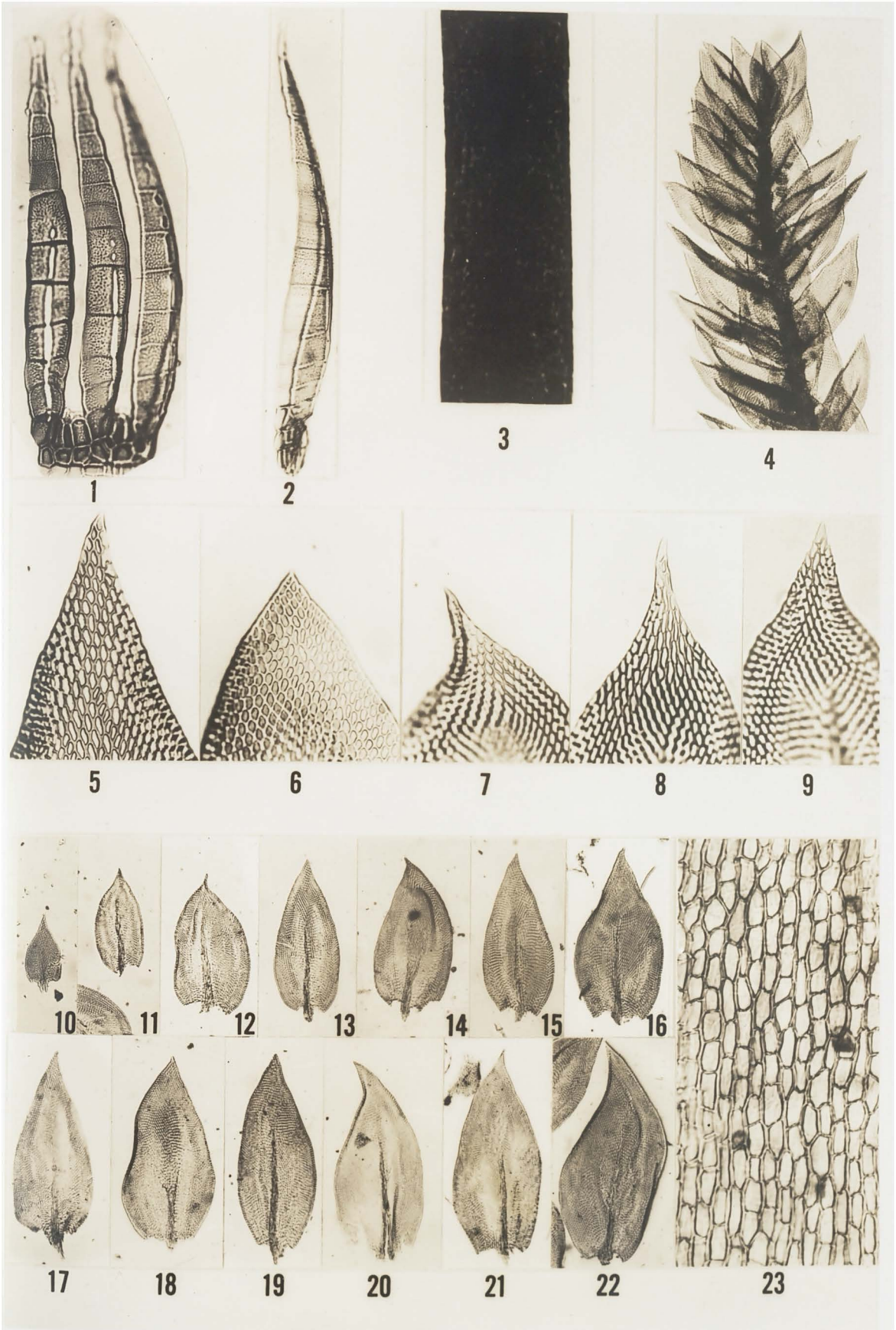


Figure 6: Pictures 1-14. *Macrohymenium* spp. 1-3. Habit. 4. Antheridia. 5-6. Alar Cells. 7. Perchaetium. 8. Perigonial Leaf. 9-10. Basal Leaf Cells. 11. Seta with Warty Projections. 12. Vaginule and Seta. 13-14. Basal Perichaetial Leaf Cells with Pores.

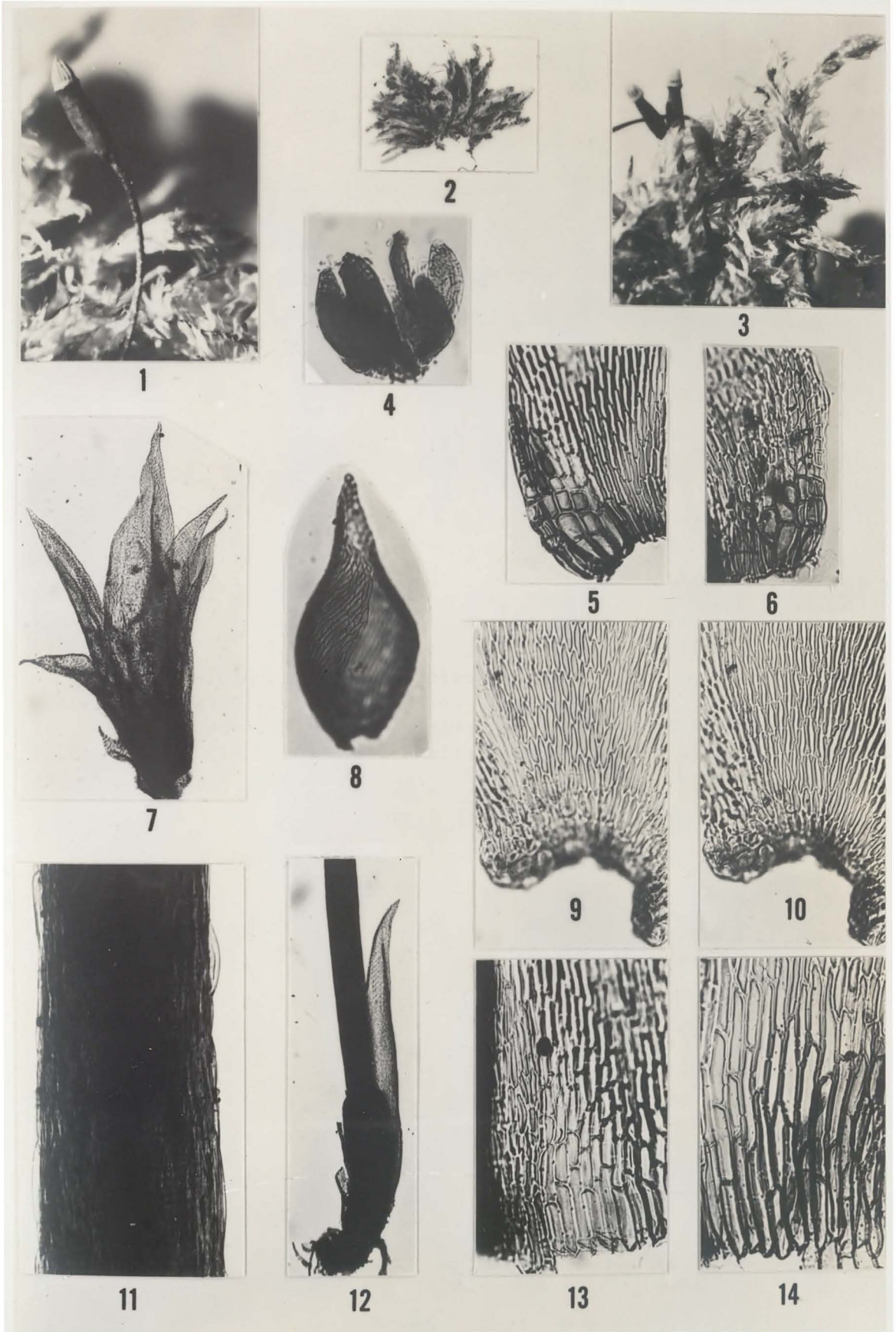


Figure 7: Pictures 1-15. *Macrohymenium* spp. 1-2. Endostome and Exostome Teeth. 3. Complete Endostome. 4. Spores. 5-8. Exostome Teeth. 9. Complete Exostome. 10-11. Calytrae. 12-14. Operculae. 15. Exothecial Cells.

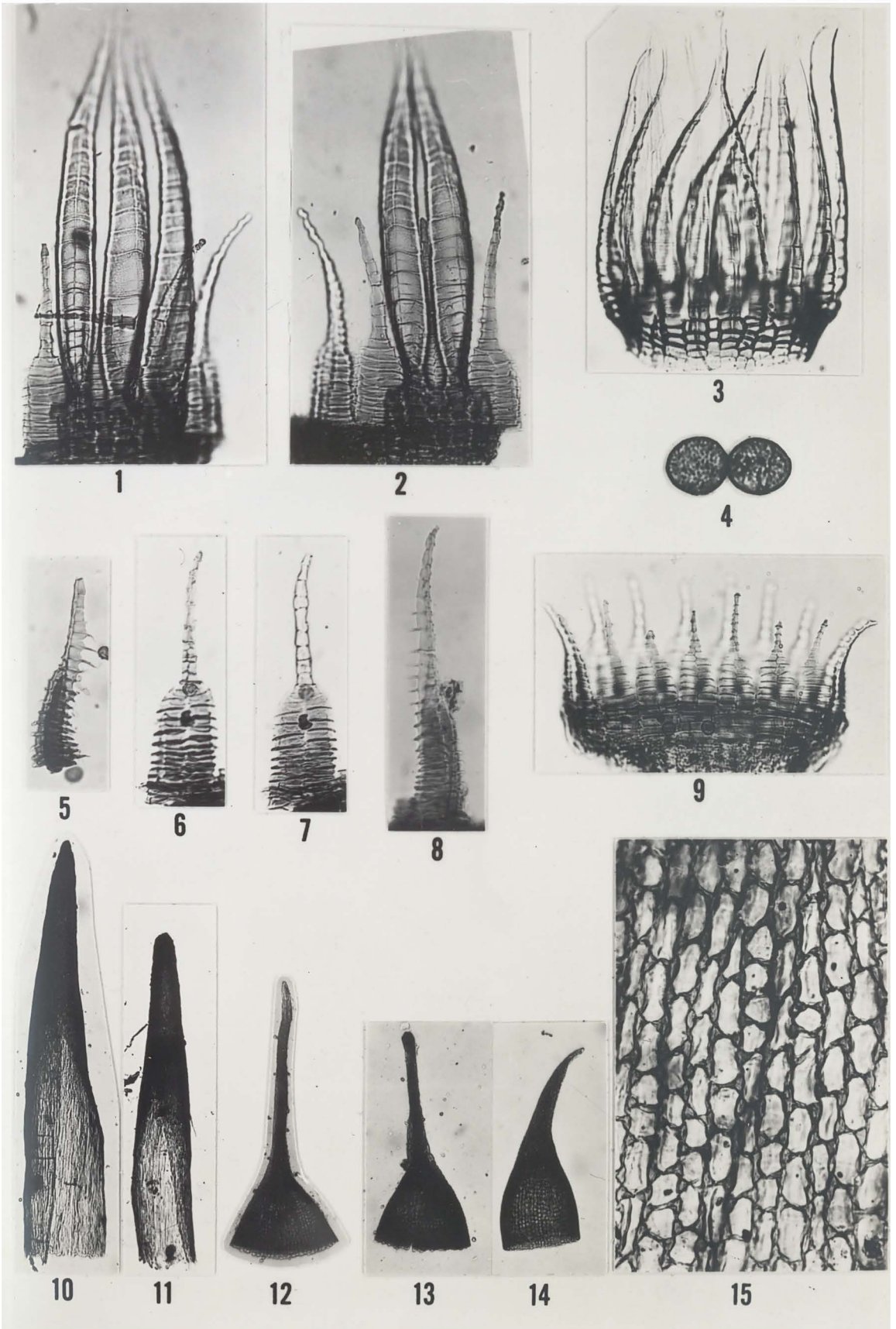
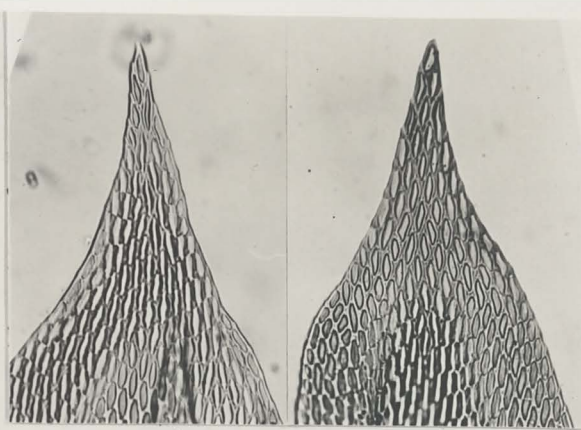


Figure 8: Pictures 1-19. *Macrohymenium rufum*. 1. Portion of Branch. 2-3. Leaf Tips. 4-5. Endostome Teeth. 6-7. Cells of Midleaf. 8-10. Perchaetial Leaves. 11-12. Cells of Leaf Base. 13-18. Branch Leaves. 19. Alar Cells.

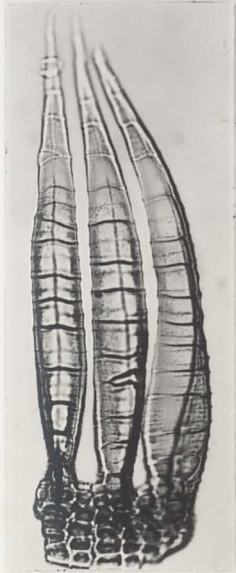


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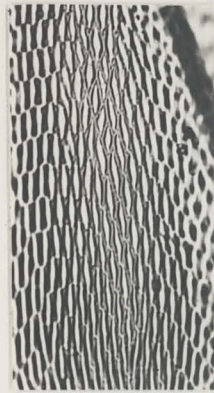
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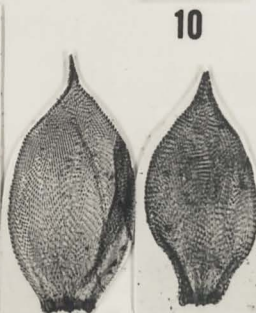


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Figure 9: Pictures 1-14. *Macrohymenium acidodon*. 1. Portion of Branch. 2-3. Leaf Tips. 4-5. Endostome Teeth. 6. Perchaetial Leaf. 7. Cells of Midleaf. 8, 14. Alar Cells. 9. Cells of Leaf Base. 10-13. Branch Leaves.

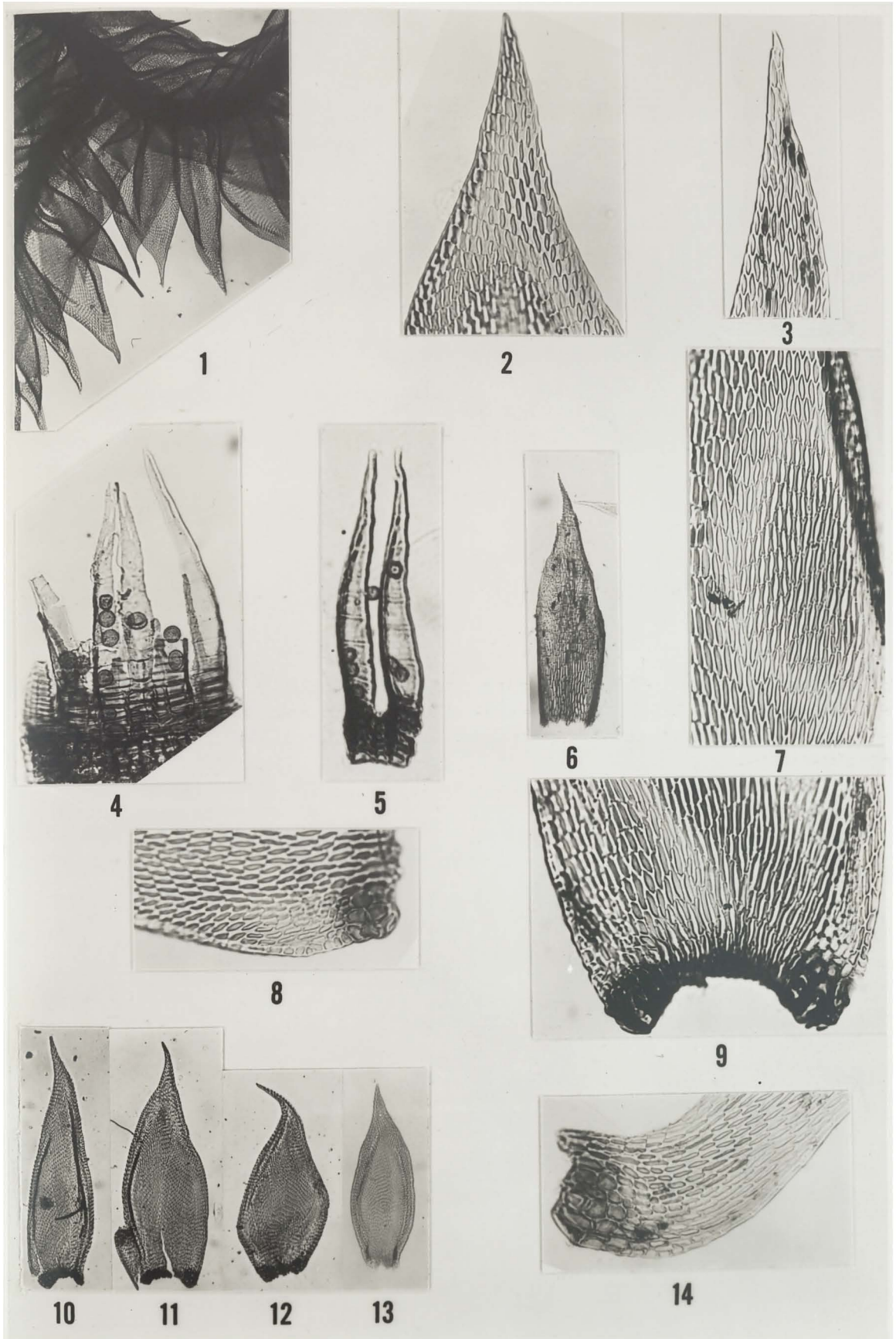


Figure 10: Pictures 1-16. *Macrohymenium müelleri*. 1-3. Endostome Teeth. 4-5. Leaf Tips. 6-7. Cells of Midleaf. 8-9. Cells of Leaf Base. 10. Perchaetial Leaf. 11-14. Branch Leaves. 15-16. Alar Cells.

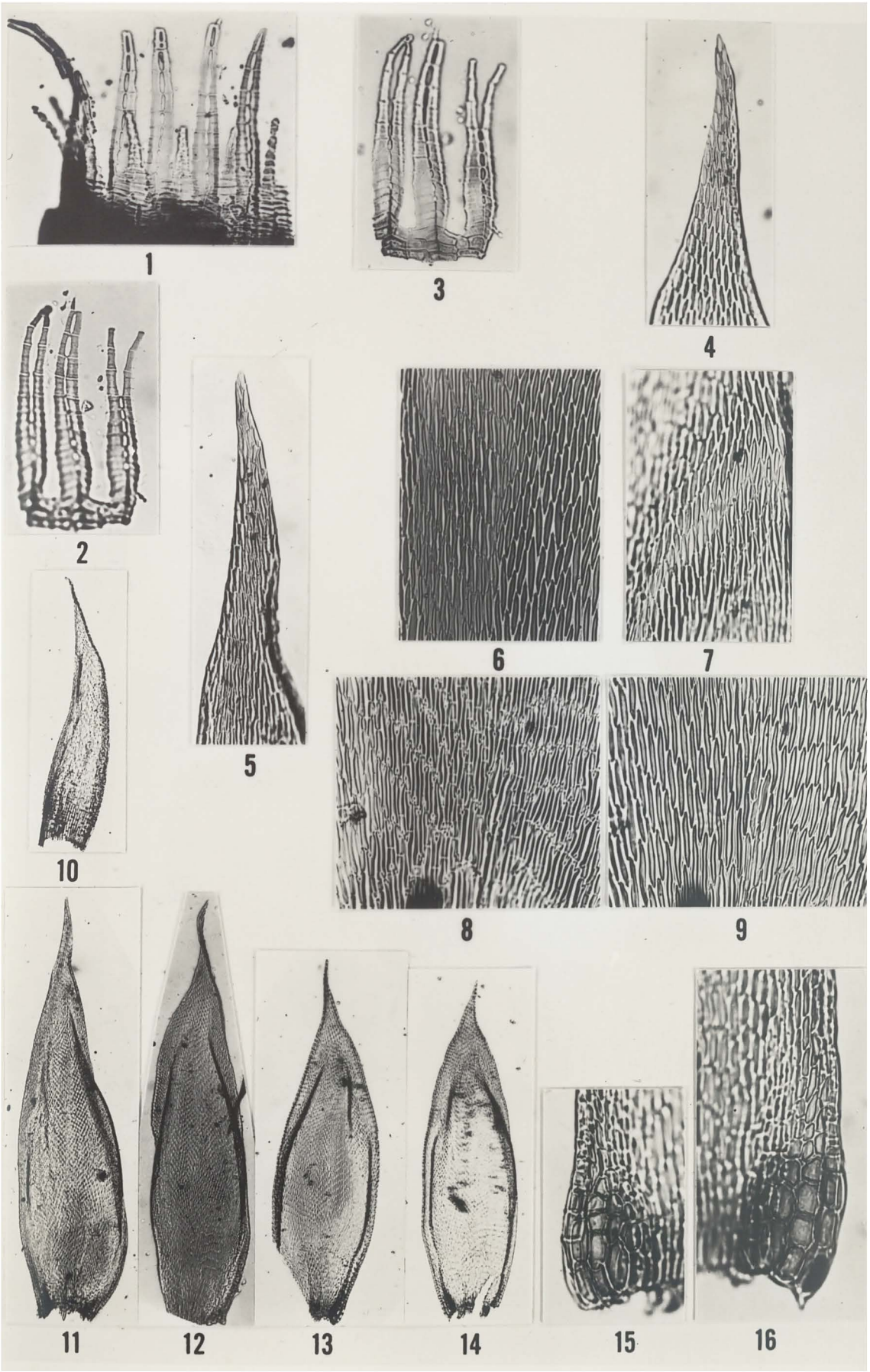


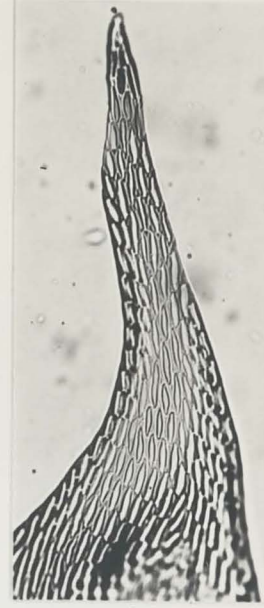
Figure 11: Pictures 1-14. *Macrohymenium strictum*. 1. Portion of Branch. 2-3. Leaf Tips. 4-5. Endostome Teeth. 6. Perchaetial Leaf. 7. Cells of Midleaf. 8-12. Branch Leaves. 13-14. Alar Cells.



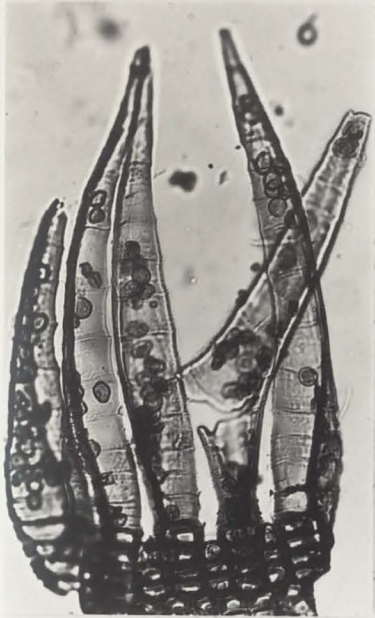
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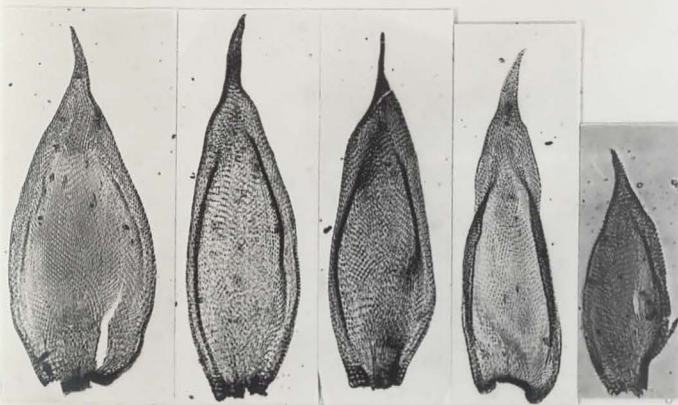
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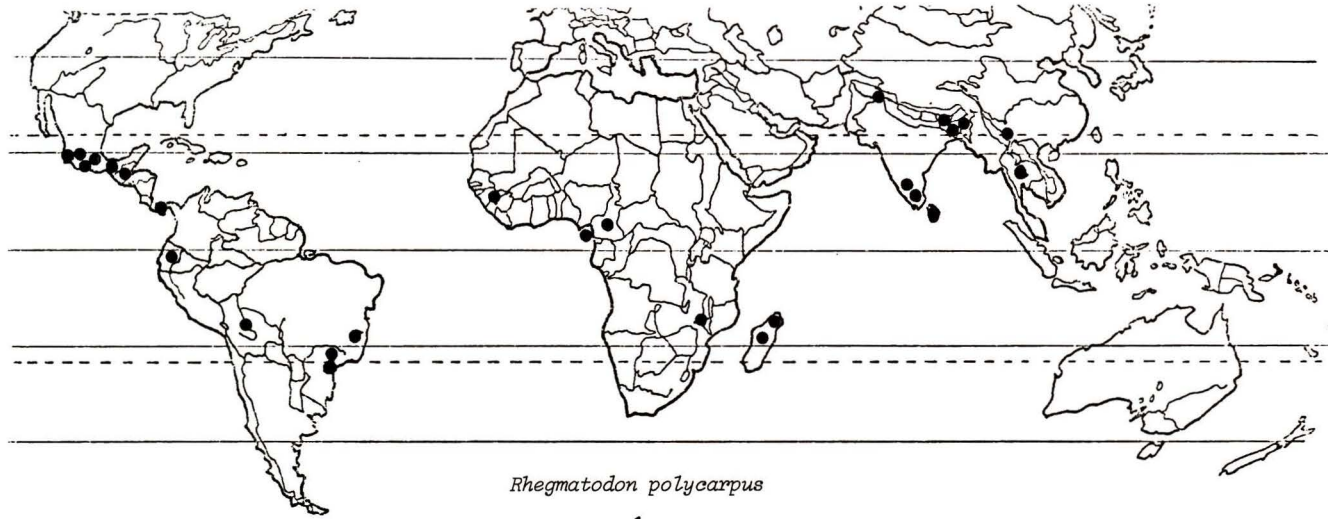
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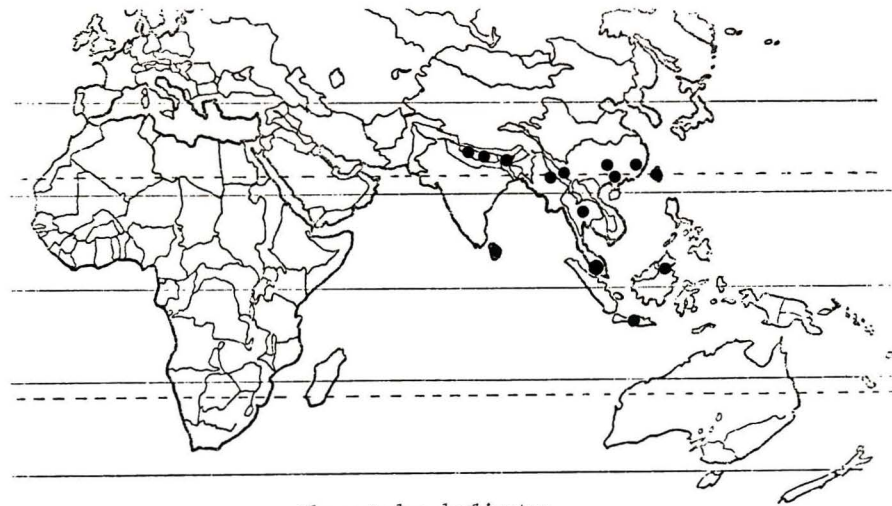
14

Figure 12: 1-2. Distribution of *Rhegmatodon* spp. 1. Distribution of *Rhegmatodon polycarpus*.
2. Distribution of *Rhegmatodon declinatus*.



Rhegmatodon polycarpus

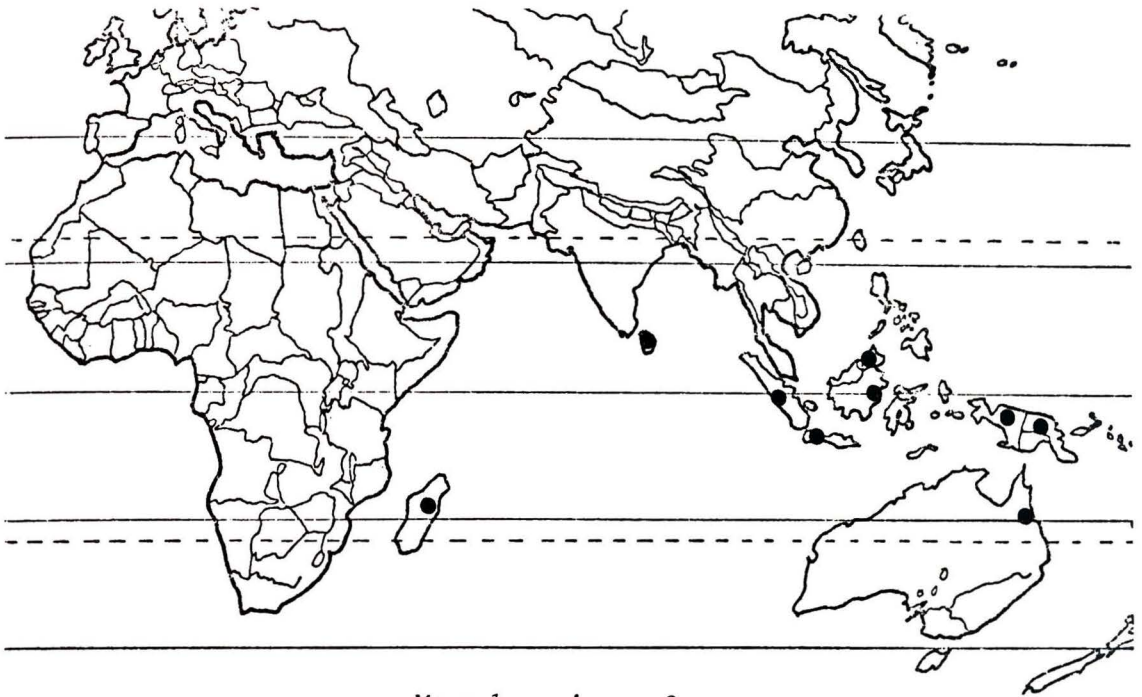
1



Rhegmatodon declinatus

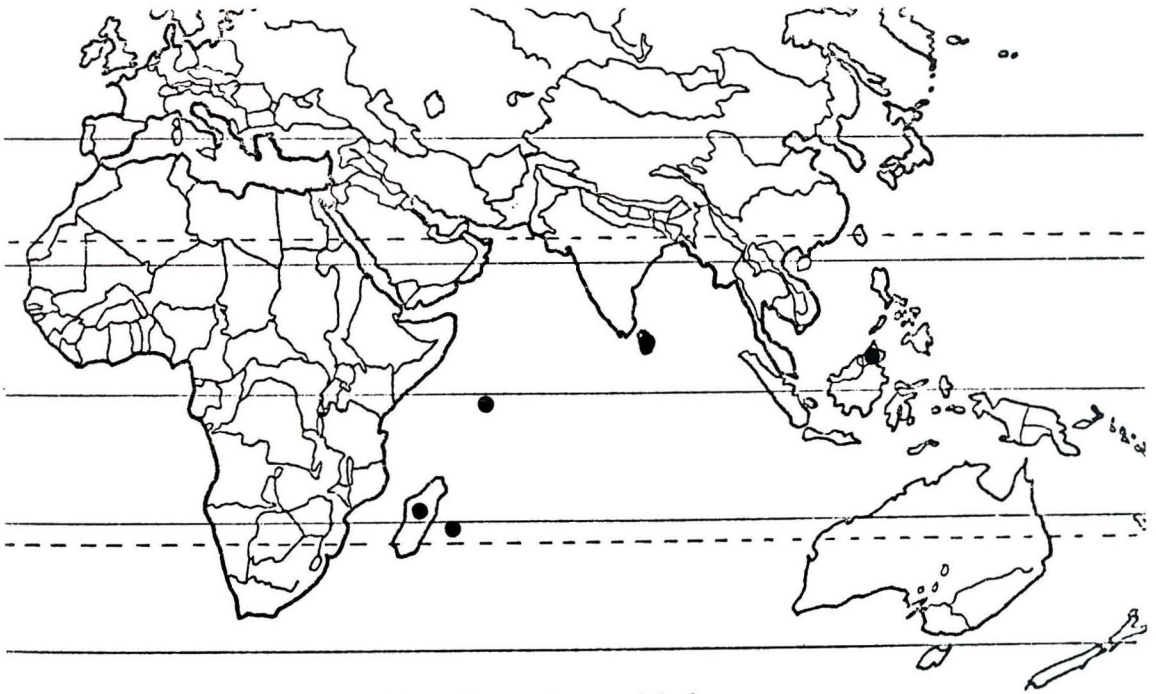
2

Figure 13: 1-2. Distribution of *Macrohymenium* spp. 1. Distribution of *Macrohymenium rufum*. 2. Distribution of *Macrohymenium acidodon*.



Macrohymenium rufum

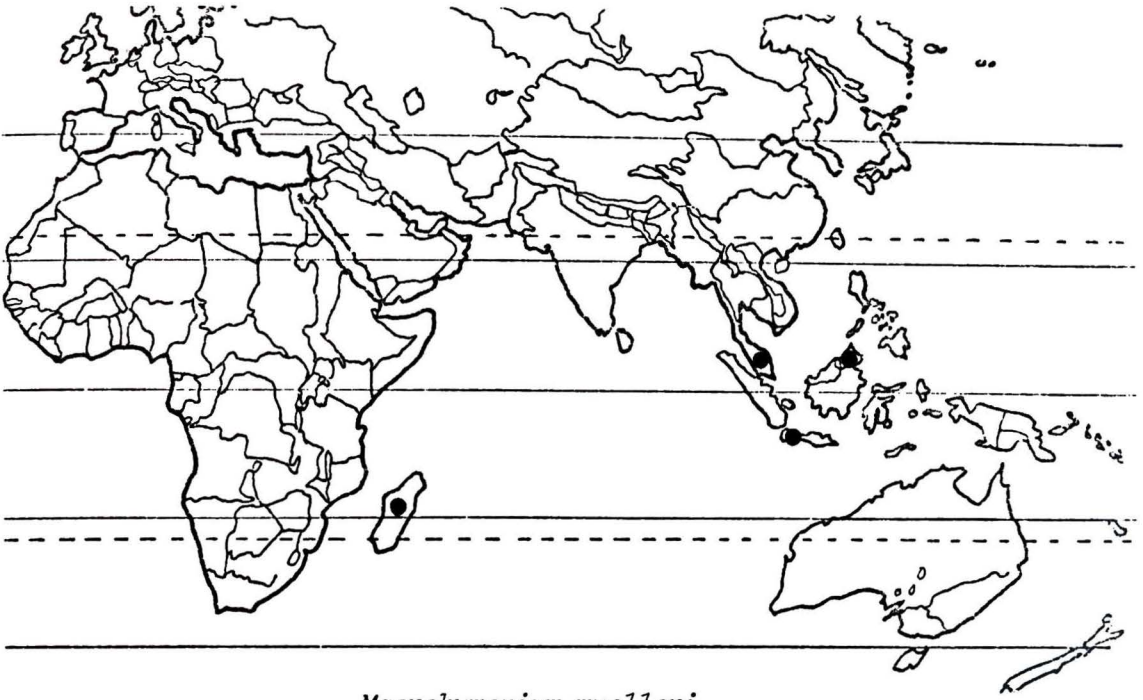
1



Macrohymenium acidodon

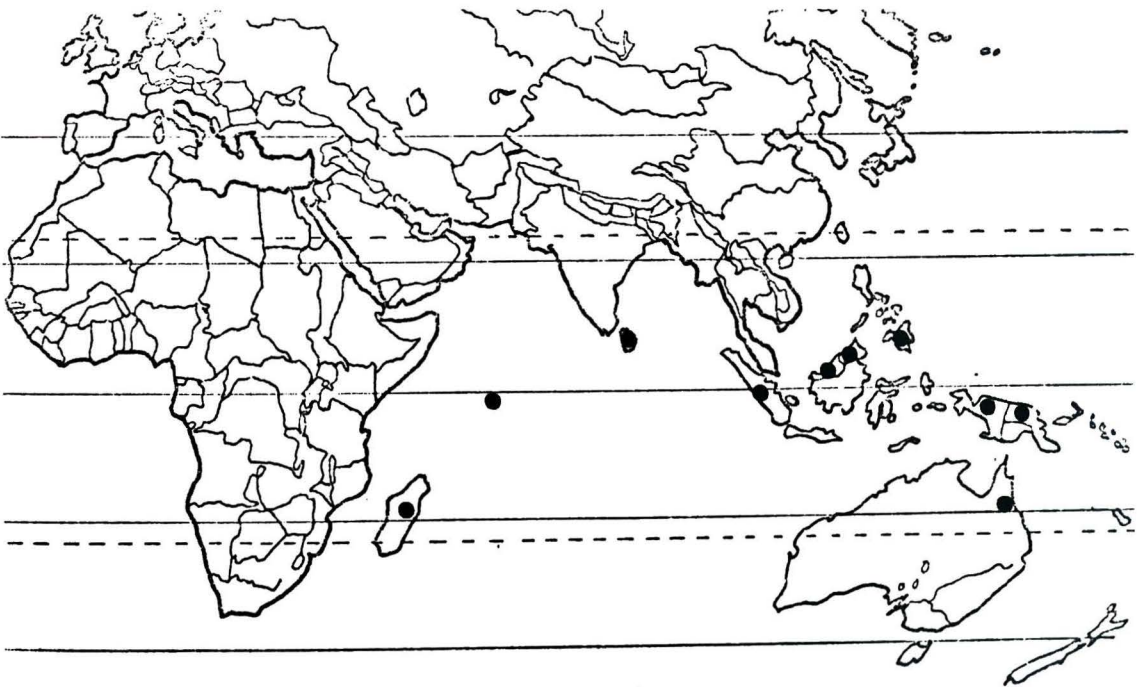
2

Figure 14: 1-2. Distribution of *Macrohymenium* spp. 1. Distribution of *Macrohymenium müelleri*. 2. Distribution of *Macrohymenium strictum*.



Macrohymenium muelleri

1



Macrohymenium strictum

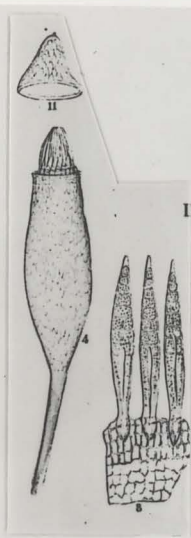
2

Figure 15: Pictures 1-9. Previous Illustrations of *Rhegmatodon*.

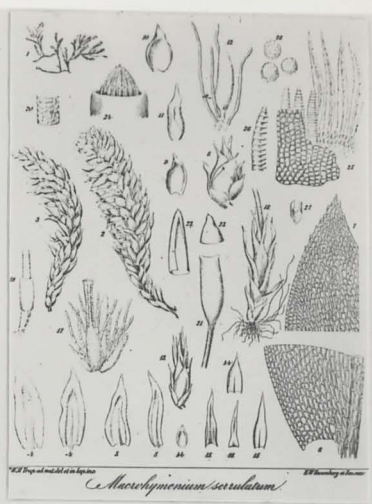
1. *Anhymenium polycarpon* Griff., Calcutta Jour. Nat. Hist. t. 16. 1843.
2. *Anhymenium polysetum* Griff., Icones Plant. Asiat. t. 97, f. 2. 1849.
3. *Macrohymenium serrulatum* Doz. & Molk. Musci Frond. Ined. Archip. Indici t. 56. 1848.
4. *Rhegmatodon serrulatus* (Doz. & Molk.) Bosch. & Lac., in A. Engler & K. Prantl, "Die natürlichen Pflanzenfamilien," Band 11, p. 298, f. 648. 1925.
5. *Regmatodon declinatus* (Hook.) Brid., Bryol. Univ. 2, t. 9.
6. *Regmatodon declinatus* (Hook.) Brid., Schwaegrichen, Species Muscorum Frondosorum, t. 204. 1827.
7. *Pterogonium declinatum* Hook., Trans. Linn. Soc. Lond. 9: t. 26, f. 3. 1808.
8. Enlargement of part of no. 7.
9. Original pencil drawings by Hooker found with the holotype (NY).



1

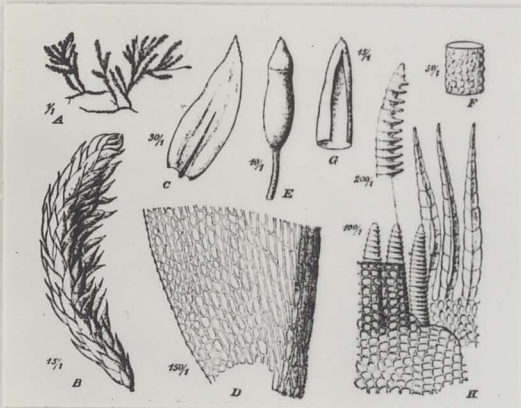


2

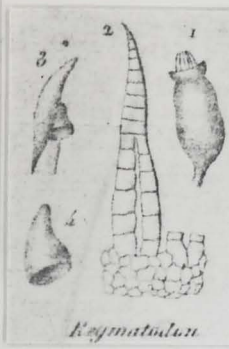


Macropodium serrulatum

3

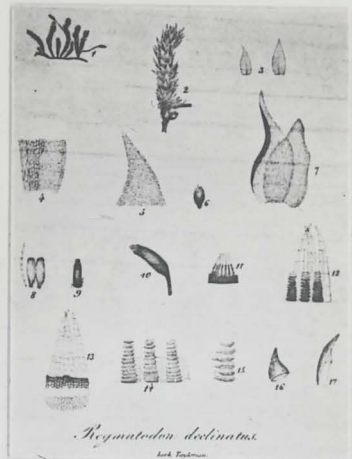


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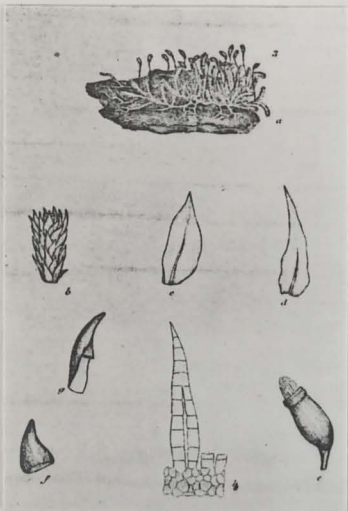
Reymatula

5

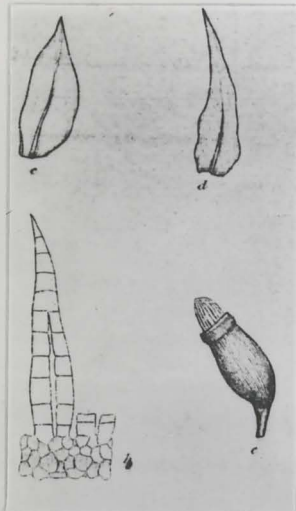


Reymatula declinata

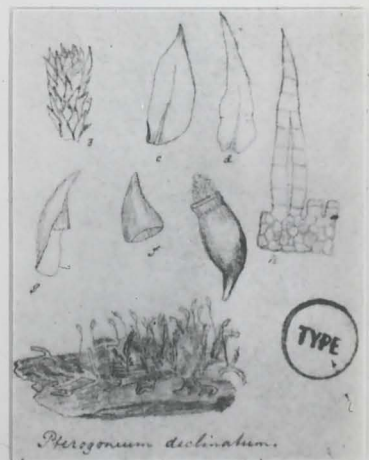
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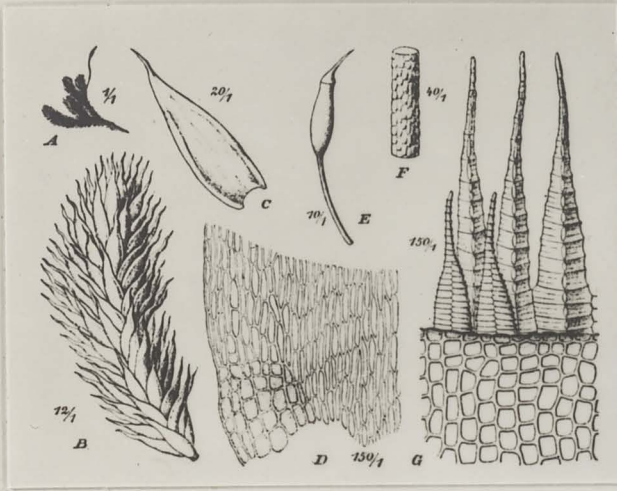


Phlegonum declinatum

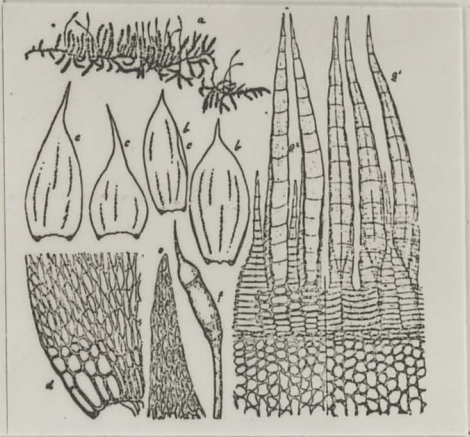
9

Figure 16: Pictures 1-6. Previous Illustrations of *Macrohymenium*.

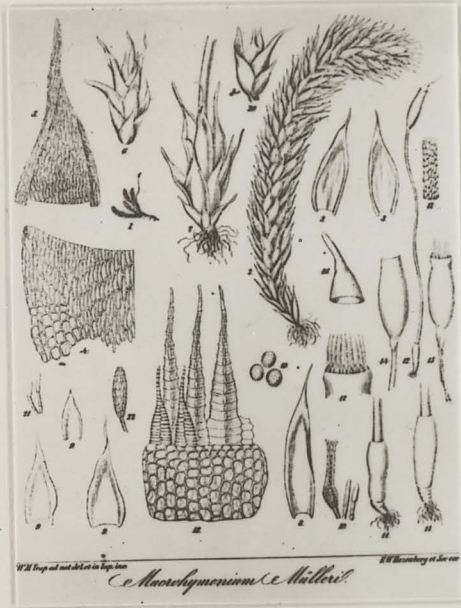
1. *Macrohymenium mülleri* Doz. & Molk., in A. Engler & K. Prantl, "Die natürlichen Pflanzenfamilien," Band 11, p. 445, f. 745. 1925.
2. *Macrohymenium mitratum* (Doz. & Molk.) Flsch., in Fleischer, Die Musci der Flora von Buitenzorg, 4: 1365, f. 221. 1923.
3. *Macrohymenium mülleri* Doz. & Molk., Musc. fr. ined. Archip. ind. pp. 167-68, t. 55. 1848.
4. *Macrohymenium rufum* Doz. & Molk., Musci fr. ined. Archip. ind. pp. 168-69, t. 54. 1848.
5. *Leskea acidodon* Mont., Ann. sc. nat. p. 96, t. 5, f. 4. 1845.
6. Original pencil drawings found with the holotype (L).



1



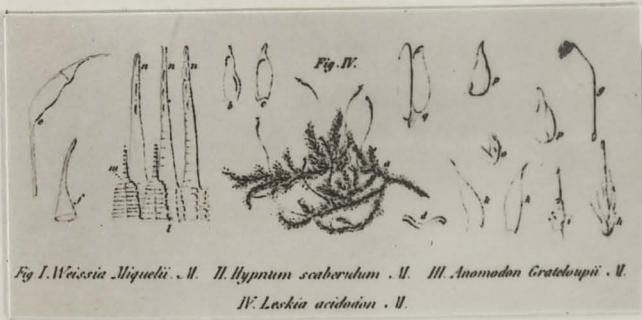
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APPENDIX I

HISTORICAL PERSPECTIVES IN TAXONOMIC BRYOLOGY

Modern classification is the end-product of a long series of decisions regarding the relative importance of certain characters as indicators of some "natural" relationship. Naturally, whatever biases or assumptions are used to determine these characters will be reflected in our final classification. This appendix is provided to supply some background with regard to the historical development of taxonomic bryology. The basic points to be covered are as follows

1. Bryology is a relatively new discipline, having begun in the modern sense with Hedwig only two centuries ago. This, and the fact that there are so few workers in the field, had slowed the growth of knowledge so that bryology is still in the exploratory and descriptive stages of taxonomy.

2. The current classification of mosses (Dixon) is the product of a long series of individual opinions and tradition with its roots deep in the folk science of various civilizations. A brief history of the ebb and flow of taxonomic opinion in bryology, especially with reference to the concept of the genus, suggests that each taxon is an abstraction in which we have assembled certain plants for the purpose of understanding and separated them from other groups.

3. Classification of mosses, like other plants, has been traditionally based on morphological or anatomical characters which are

readily observable by ordinary methods. Characters which require great time to discern are impractical for the purpose of putting a name on a plant.

4. The choice of critical characters in bryology is arbitrary, based on speculative logic of individual workers, because there is no fossil evidence to suggest what characters should be considered primitive or advanced.

Origins of the Generic Concept

From the beginning of time man has expressed a need to name and classify the various aspects of his sensory world. Even the dim light of prehistory reveals that, within the folk science of all civilizations, those botanical aspects of man's environment which were of greatest importance to his survival were distinguished and named.

An obvious example of this would be man's ability to discover and retain information about edible and non-edible plants. With increasing experience, finer distinctions would be required for plants previously included under the same name. Bartlett (1940) suggests that the original name then attained generic significance, as a basis for specific names. He gives "grass" as an example of this analytical process. "Many kinds of grass are so similar that we can hardly believe that the concept 'grass' was not more ancient than the distinction of particular kinds" (p. 349). On the other hand, some groupings undoubtedly arose when people noted previously unrecognized similarities and combined various plants which are superficially very dissimilar. Bartlett believed this to be the case for the generic concept of "fern."

On the contrary, the generic concept 'fern' is a technical one, depending upon close observation, so when we find a people of relatively low culture, such as the

Batak of Sumatra, defining extremely diverse plants as 'fern' pretty much as the modern botanist does, on the basis of a relatively obscure characteristic, namely, the leaf-borne sporangia, we feel sure that a genus has been set up by synthesis of things superficially very unlike. (Bartlett, 1940, pp. 349-350)

Thus, delimitation of various groups or taxa came about by one or both of these processes of analysis and synthesis.

This reasoning applies equally well to the description, naming, and classification of mosses. For instance, one would expect very inclusive grouping for those plants which were inconsequential in the day to day existence of a people. This is true for the Musci. Bartlett notes, from personal experience with the Batak of Sumatra, that *lumut*¹ suffices as an inclusive generic name for almost all moss-like plants. He further states that

Classification of *lumut* is hardly attempted, but the conspicuous *Leucobryum* has a generic name. The condition of their moss nomenclature is after all not so very different from that in scientific systematic botany before Dillenius. (Bartlett, 1940, p. 354)

The role of utility in the development of plant nomenclature is certainly not restricted to the Batak. The bryophytes have always been of limited value to man and therefore were not studied until fairly recently. An exception to this is *Sphagnum* whose utility has been recognized almost everywhere it is found. For this reason, it was so sufficiently defined in pre-Linnaean folk science that modern workers² have agreed to designate the beginning of this modern genus concept with Linnaeus' 1753 publication of *Species Plantarum*, starting point for the nomenclature of higher plants. Even today,

. . . bryophytes are almost totally free from economic involvements. Excepting the modest peat moss industry, the

¹Pardembanan dialect (a sub-Toba dialect) of Asahan, Sumatra.

²Third International Botanical Congress, Vienna, 1905.

small favor they find in a few Japanese gardens and their limited usefulness as packing materials for shipping live plants, mosses, and liverworts have no economic worth. (Anderson, 1974, p. 56)

Due to the purely academic nature of bryological studies, the starting point for the nomenclature of bryophytes, except for *Sphagnum* and the Jungermanniales, was designated¹ with the much later publication of Hedwig's *Species Muscorum* (1801). Closer examination permitted investigators of moss-like plants to segregate originally large inclusive genera into smaller genera and species. Steere (1947) indicates the extensiveness of this process by noting that the original 35 genera of Hedwig had multiplied to more than 700 genera by 1947. Thus, detailed analysis has been the most important process in the development of moss taxonomy.

History of the Concept of the Genus in Musci

In presenting a historical perspective of the changes which have taken place in the concept of genera of Musci, I have relied heavily on the classic presentations of Steere (1947), Florschütz (1960), Margadant (1968), and Dixon (1932).

The first book dealing explicitly with the mosses and liverworts was *Historia Muscorum* by Dillenius (1741). Twenty genera were described and, following the general concepts of his day, he included "every low-growing plant which was not clearly a flowering plant, fern or a fungus" (Margadant, 1968, p. I). In addition to hepatics, lycopods, lichens, and algae Dillenius was acquainted with six modern genera of mosses: *Sphagnum*, *Mnium*, *Fontinalis*, *Hypnum*, *Bryum*, and *Polytrichum*. Except for *Sphagnum*, these genera, while including some presently

¹Fourth International Botanical Congress, Brussels, 1910.

recognized species, were very broad and inclusive. *Bryum*, for example, included most of the mosses which grow in tufts and produce their sporophytes terminally (i.e., the acrocarpous mosses) while *Hypnum* was inclusive of those mosses which produce the sporophyte laterally and are generally mat-forming and prostrate (i.e., the pleurocarpous mosses). Dillenius made no attempt to show intergeneric relationships or to suggest a systematic arrangement.

In *Species Plantarum*, Linnaeus added two new moss genera, *Phascum* and *Splachum*, to the six of Dillenius. At the same time he restricted the term Musci to mosses more nearly in the modern sense. He did include, however, the hepatic genus *Porella*, some other hepatics under *Mnium*, and the fern ally *Lycopodium*. We should remember that Linnaeus was as significant to bryological nomenclature as he was to the rest of taxonomy, being the first to establish the universal use of binomials in nomenclature. Linnaeus also did not attempt to show a systematic arrangement of intergeneric relationships.

The next landmark in taxonomic bryology is the work of Johannes Hedwig. Perhaps the clearest indicator of his importance to bryology is the fact that his *magnum opus*, *Species Muscorum*, published posthumously by Schwaegrichen (1801) was chosen as the starting point for all legitimate nomenclature of Musci. This decision reflected a recognition of his careful observation and meticulous description of characters previously unknown or unappreciated. Florschütz has stated,

Hedwig was one of the best observers of his day. he used and improved the microscope which even at that time was sometimes considered as being unreliable. He developed a special preparation-technique and a technique for drawing magnifications by microscope. He was the first to publish very accurately the form and structure of the smallest organs of cryptogams. Several of these organs were already

known, but nobody had perceived them so exactly as Hedwig did. (Florschütz, 1960, p. ix)

In *Hedwigii Fundamenta Historiae Naturalis Muscorum Frondosorum* (1782) he included, for the first time in bryological literature, a key to genera. The key clearly shows Hedwig's concept of the relationships between these genera. The presence or absence of the peristome, the form and number of the peristome teeth, and the form of the male "flower" (perigonium), were the critical generic characters. In his final concepts he stressed the position of the male flower on the stem, rather than its form.

Species Muscorum includes a glossary of terms, key to genera (35), descriptions of many species, and 77 plates published originally as hand-engraved colored masterpieces.

A storm of controversy surrounded Hedwig's choice of characters, especially those microscopic details; viz, the male "flower." Steere (1947) records an interesting criticism of Hedwig's "*Stirpium Cryptogamicarum*" (1787-1797) by one A. Menzies (1798).

The laborious works of the celebrated and persevering Hedwig have, of late years, thrown much light upon the subjects of this natural order; but the general complaints against his new arrangement of it are, that his genera are too artificial, and that their characters are taken from parts so minute and difficult to examine, that they rather tend to perplex and discourage a young beginner in his investigations, than aid his pursuits in acquiring a scientific knowledge of this intricate tribe. While it can therefore be avoided, no generic or specific characters ought ever to be adopted, that cannot easily and distinctly be seen by the assistance of a single lens magnifier, such as botanists commonly carry in their pockets. (Steere, 1947, pp. 248-249)

This quote is particularly interesting because it reveals that most botanists or bryologists did not at this time make regular use of the microscope. The "minimal accessory equipment" used to accompany a

bryologist's sharp eyes was a hand magnifier. Only when the microscope became readily available were Hedwig's characters generally accepted.

This criticism is perhaps more clearly appreciated when we recall that Hedwig was the first to discover and describe the male "flower." His system was a vast improvement over earlier treatments of Musci. It is currently felt that Hedwig's system was too artificial in that it gave almost exclusive weight to the sporophyte (i.e., peristome characters) while largely ignoring gametophytic characters. This resulted in grouping under the same generic name many mosses with comparable peristomes, but completely dissimilar gametophytes. This does, in fact, represent one extreme facet of the systematic problem presented by plants which are composed of both the haploid and diploid generations, and where the sporophyte is persistently attached and at least somewhat dependent on the gametophyte. Nevertheless,

The main characters Hedwig used are still the very important characters for our present classification of the mosses. Although our delimitations of genera changed, the discovery of the importance of these characters came from the brilliant thoughts of this eminent bryologist. (Florschütz, 1960, p. xx)

In 1819 Sam Bridel published his *Mantissa Muscorum* as an apparent supplement to his earlier works on mosses. Although adopting Hedwigian classification, he did introduce two new characters; the position of the female flower (perichaetium) and various characters of the calyptra. This was considered a great improvement over characters of the male flower since both capsule position and the form of the calyptra are features which can be seen with the unaided eye. In this work, the terms *acrocarpi* and *pleurocarpi* were introduced for the first time as the two most important classes of his Section I, *Olocarpi*. These characters became the pivotal points of classification in Bridel's famous

two volume work, *Bryologia Universa* (1826). On the basis of variation in calyptra characters, Bridel proposed several new genera.

During the period 1811-1842, there appeared three supplements to "*Species Muscorum*." These were the work of Christian Friedrich Schwaegrichen, whose respect for his teacher is demonstrated by the fact that all three supplements appeared under the name of Hedwig. Schwaegrichen also proposed new genera.

The first bryologist to reintroduce the potential use of gametophytic characters in the classification of mosses was Carl Müller in his two volume, *Synopsis Muscorum Frondosorum*, 1848-1851. Mosses were divided into two classes; *Cleistocarp*i and *Stegocarp*i. The former included those mosses with sessile sporophytes, sphaerical to sub-sphaerical capsules with no definable mouth or peristome. The *Stegocarp*i included those forms with the sporophyte on a seta, \pm elongate, with an operculum, and a well-defined mouth and peristome. This latter class was divided into the *Acrocarp*i and *Pleurocarp*i, using leaf arrangement to delimit the still smaller groups of taxa. The sporophytic characters were then used to define genera. The use of leaf arrangement was not generally accepted by other workers, and thus his system was not adopted. One important contribution of this work should be noted. The various comprehensive treatments of mosses during the nineteenth century lacked a world-wide perspective, their taxonomic treatment reflecting a "local-flora" or regional outlook. Müller did attempt to compile in his work all of the known, described species of mosses to date. Even the monumental *Bryologia Europaea* (Bruch, Schimper, and Guembel, 1836-1854) did not present world-wide coverage of the Musci. *Bryologia Europaea* did establish a significant proportion of the generic names now in use in Europe and North America, many genera appearing for the first time

as segregates of some of Hedwig's mammoth genera. Such well-known generic names as *Thuidium*, *Pseudoleskea*, *Bracynthecium*, and *Amblystegium*, all cleaved from Hedwig's *Hypnum*, date from this time. The tremendous importance of this work is suggested by the fact that most authors during the following 40 years adopted Schimper's classification *in toto*. The descriptions of species and detailed illustrations are among the very finest in bryological literature. In 1855, Schimper attached his *Corollarium Bryologiae Europaea*, in which he classified all of the European species of Musci. Here Schimper elevated the terms *acrocarpi* and *pleurocarpi*, coined by Bridel (1819), by designating his two main orders *Musci acrocarpi* and *Musci pleurocarpi*.

Jaeger and Sauerbeck (1869-1878), in their *Adumbratio*, attempted a bibliographic treatment of all of the world's mosses, but simply intercalated the non-European genera into Schimper's system.

Two important anatomical studies were published within the last quarter of the nineteenth century which greatly influenced further innovations in the classification of Musci. *Grundlinien zu einer vergleichenden Anatomie der Laubmoose*, authored by Lorentz (1867-1868), aroused new interest in the importance of anatomical characters. He specially called attention to the usefulness of microscopic details in leaf cells. While leaf characters had been used prior to this time, both in *Bryologia Europaea* and many of Müller's publications, many look to Lorentz for the most persuasive argument of the correctness of this view. For example, Limpricht (1895) in his *Die Laubmoose* incorporates Lorentz's ideas within the older acrocarpous-pleurocarpous concept. (*Die Laubmoose* dealt only with European genera.)

The second important anatomical influence on the classification of mosses was Philibert's *Études sur la péristome* which appeared as

many separate papers in *Revue Bryologique* between the years 1886 and 1890. This work represents a magnificent investigation into the development and structure of the moss peristome. Philibert was able to identify certain basic kinds of peristomes within Musci, greatly increasing the feeling that the peristome reflected the phylogeny of the moss more clearly than the gametophyte. The occurrence of a similar kind of peristome in two taxa persuaded Philibert that they must be closely related. He could not conceive of such a complex structure as the peristome having evolved in two separate groups as the result of convergent evolution.

The feeling that peristome types are basic and dependable indicators of phylogenetic relationships is exemplified by the following statement from Dixon:

Certain basic principles at any rate may be recognized and utilized for taxonomic purposes. For one thing, it is quite clear that the main types of peristome among the Bryales are of great phylogenetic importance, and are more or less primitive, viz. the Nematodontae and the Arthrodontae, the latter divided into Haplolepideae and Diplolepideae. No part of our classification based on gametophyte characters must cut across these broad lines. (Dixon, 1932, pp. 402-403)

It would be an oversight to fail to indicate the great influence the theory of evolution had on moss taxonomy. The following statement by Dixon will suffice to indicate this point.

The gradual acceptance of the doctrine of evolution has placed all taxonomy on a new plane. Resemblances and differences between organisms mean something entirely different from what they meant before. It is the business of the taxonomist not only to tabulate and classify differences and resemblances, but so to classify them that the relationships between the organisms shall thereby be brought out. Resemblances may indicate relationship, but they may not. Wide apparent differences may suggest wide divergence of origin, but they may be only apparent, not fundamental ones. The taxonomist has to lay down a system which shall, so far

as possible, indicate the actual phylogenetic relationship of the plants with which he is dealing. (Dixon, 1932, p. 398)

During the period from 1900 to 1923, Max Fleischer published his four volumes on *Die Musci der Flora von Buitenzorg*. This work presented a system of classification which has been hailed as the most creative scheme of the twentieth century. It incorporates Philibert's peristome groupings, and the location of the sporophyte and various gametophytic characters. This is regarded as the first important treatment of the mosses from a non-European viewpoint and included a great number of new families, orders, and genera. With few alterations, this system is used among present-day bryologists. It was adopted by Brotherus in his treatment of the Musci in Engler and Prantl, *Die natürlichen Pflanzenfamilien* (2nd edition, 1925), and also was used as a basic outline of Dixon's classification, as presented in Verdoorn's *Manual of Bryology* (1932). It is the system which has been used as a basis for the present work.

Modern Taxonomic Bryology

In theory, modern taxonomists are "to lay down a system which shall, so far as possible, indicate the actual phylogenetic relationship of the plants with which he is dealing" (Dixon, 1932, p. 398). This is not possible in the case of mosses for several reasons. In view of the general acceptance of the theory of evolution, characters chosen to group taxa are to be selected because they are thought to best represent phylogenetic relationships, i.e., primitive vs. advanced characters. The selection of a character as primitive, however, must result from the examination of the only direct evidence available, i.e., the geologic record. In the case of mosses, this source of information is virtually

non-existent. The only bryophyte fossils, primarily hepatics, are nearly identical to extant forms.

Anderson remarked that,

Steere and Inoue (1972) (JHBL 35) . . . summed up the status of present-day taxonomic and evolutionary knowledge of bryophytes in a devastatingly frank statement. "Although there are many published papers discussing the species concept of bryophytes," they stated, "we still know little about the nature of species, and even the concept of taxonomic rank is not clearly understood." To this pessimistic appraisal, they might well have added that we know even less about the age of bryophytes, their evolutionary origins directions and rates. (Anderson, 1974b, p. 8)

Thus, any attempted phylogenetic groupings must at this time be recognized as purely speculative.

A further problem arises from the fact that each moss consists of two different plant generations; the gametophyte and sporophyte.

Mosses are unusually difficult to systematize because they present a double organism - a sporophyte plant that lives at least in part parasitically on a green gametophytic plant . . . If undue weight is placed upon characters derived from either generation alone, an artificial system like that of Hedwig's will be created. (Steere, 1947, p. 253)

Hedwig's system exemplifies the extreme of assigning almost complete weight to sporophytic characters. While no single system of classification can be noted to exemplify the other extreme, it is clear that grouping on the basis of gametophytic characters alone would be equally artificial. The third possibility is to classify mosses on the basis of some combination of gametophytic and sporophytic characters. Our current classification systems reflect this philosophy. But the selection of "critical" characters, representing both generations, is equally arbitrary in view of the absence of fossils. The classification of bryophytes, then, will always be open to the charge of artificiality unless definitive fossils are found.

Nearly all bryologists and vascular plant systematists agree that bryophytes are not ancestral to the vascular plants or their presumed fossil progenitors. It is also generally agreed that none of the three bryophyte classes recognized today are ancestral to any of the others. But popular and current as these views may be, they are based on speculative logic and not facts. There is no fossil evidence to relate bryophytes to either the green algae or the tracheophytes. . . . unless additional fossil material comes to light or some other fresh evidence is forthcoming, the subject is likely to remain, as Richards (1959) puts it, "a fascinating subject for speculation." (Anderson, 1974a, p. 78)

Delimitation of species is considered less arbitrary than the higher taxa, because the criterion of degree of interbreeding is added. Theoretically, species will be separated by nearly complete gaps in variability, and by "a complete or nearly complete barrier to interbreeding" (Cronquist *et al.*, 1972, p. 6). The disability to freely interbreed will maintain differences between populations and allow further divergence. Unfortunately, present knowledge is scant regarding the causes of variation, what factors produce barriers to interbreeding, and the role of asexual reproduction, etc., in reference to speciation.

The nature of many bryophyte species is poorly understood, principally because the causes of variation are not known. Thus, while the "species is ordinarily considered by taxonomists to be a real entity, existing in nature, which we recognize and describe but do not create," we can see why some workers "have considered it to be a mere creation of the mind, simply an aid to understanding or cataloging natural diversity" (Cronquist *et al.*, 1972, p. 6). The taxonomic categories above the rank of species have generally been recognized as convenient devices to show our concept of the degree of relationship among species.

All taxonomic groups are abstractions, in which we assemble, for purposes of understanding, certain individuals or groups of individuals, and separate these collectively from other groups. These groups are founded on the ensemble of similarities and differences, our efforts at analysis being aided by the fact that diversity among living things is not continuous but exhibits gaps of varying size . . .

The basic difficulty with taxonomic groups above the rank of a species is that the precise rank of a group is not inherent but is determined by individual opinion and by custom, which is the sum of a series of individual opinions . . . Where custom itself is divided . . . one chooses the course one prefers, and custom remains divided. (Cronquist *et al.*, 1972, p. 5)

As Anderson has said

. . . generic criteria are evasive in any group and especially in bryophytes . . . Bryophyte genera rest heavily on tradition, which is not always good science . . . (Anderson, 1974, p. 10)

Traditionally, the fundamental characters used in taxonomic classification are features of the external morphology of the organism. A predictable sequence of characters has been used since man first began to group plants. The most obvious characters of the plant, e.g., habit, flower color, leaf arrangement, etc., were first used for classification. Even today there is a feeling that genera of plants should be recognizable with little or no aid from magnifiers. Treating mosses in this manner would create very large, inclusive groupings.

Sometimes severe criticism is directed at taxonomists who only sparingly use cytological or chemical characters. However, one of the foremost concerns of taxonomy has been to provide a practical way for scientists and laymen alike to put a name on a specimen. Characters which are not easily observed are impractical for this purpose.

External morphology furnishes an amazingly large number of differences which can be readily observed and has consequently been the chief source of the characters by which taxonomic groups are recognized and defined. Anatomical, physiological, biochemical, and cytological characters are at least theoretically of equal importance

to the morphological ones. Indeed, all morphological as well as other differences arise eventually from biochemical ones. On the other hand, the acquisition of sufficient data from these other sources so that one can be sure he is dealing with features of groups rather than of mere individuals is so time-consuming as to be often impractical. Data from these sources tend to be concordant with data from morphology. In some cases in which morphology does not provide conclusive evidence of affinities, information from these other sources may tip the scales decisively to one side or the other. Not infrequently, however, when morphology is inconclusive, other data are equally ambiguous. (Cronquist *et al.*, 1972, p. 5)

With reference to vascular plants, Cronquist says that specific rank should not be applied to "plants of ordinary size which cannot be distinguished by sharp eyes with only minimal accessory equipment. One should not have to do an *Arbeit* to put a name on his specimen."

One further advance should be mentioned. Because of their small size, mosses were relatively unknown until the development of light microscopy. We must remember that the microscopes of Hedwig's day were not capable of the magnifications and resolution of modern optical instruments. In the introduction to Hedwig's "*Species Muscorum*," Florschütz (1960) comments that the microscope which Hedwig obtained from Schreber was a simple "Rheinthal" with a magnification of 50X. With this microscope he apparently did all of his investigations, although he was later able to boost the magnification to 170-290X. Magnification, however, does not tell the whole story. The most critical feature of a lens system is its ability to resolve. Certainly the resolution of Hedwig's lenses was considerably less than would be found in modern lenses providing equivalent magnification. The nineteenth century saw improvements in the grinding of lenses which eventually made it possible to resolve objects at some 2000 diameters (Gardner, 1965). This is the limit set by the wavelength of light itself. The first achromatic lenses to correct for chromatic aberration were not available until 1830, and the sub-stage condenser was not designed until 1870.

The significance of this to bryological taxonomy, of course, was the extension of our ability to view a new world of morphological characters which could be used to define and separate taxa. And as microscopes became "backpocket" tools of the biologist, microscopic characters were accepted more and more as critical taxonomic features of mosses.

Another important factor in the development of bryology and of the study of cryptogams in general, was that more and better microscopes became available. Microscopic details could be studied with greater precision and ease, and they began to play a more important role in the delimitation of species and other taxa. Life history studies became more accurate. This motivated an intensification of the work begun by Hedwig. (Margadant, 1968, p. II)

Today a similar situation exists with respect to the development of the electron microscope; both for transmission and scanning EM. Again the range of observable characters has been increased. Biochemical and cytogenetic techniques have added even further possible characterizations. However, these characters are not universally available, many times requiring days in preparation. The presence or absence of characters which can only be seen with a scanning electron microscope are at this time impractical for general use in keys. Perhaps if this new technology becomes as commonplace as light microscopy, these characters may supplant some of the larger traditional morphological characters.

Summary

The history of the generic concepts for *Rhegmatodon* and *Macrohymenium* can be fully appreciated only in the context of these overall changes. The taxonomic histories of *Rhegmatodon* and *Macrohymenium* span almost the entire history of bryology. Taxonomic concepts and opinions were continually changing as new and different specimens and characteristics

came to light. Corresponding changes were evidenced in the concepts of these two genera, as the influence of these new characteristics grew in the general taxonomy of bryophytes. I believe that the history of these genera presents a nearly perfect "case in point" to show the practical implications of these influences in the classification of mosses.

APPENDIX II

PREVIOUS KEYS TO THE SPECIES OF *RHEGMATODON*
AND *MACROHYMENIUM* BY BROTHERUS AND KIAER

Key to Species of *Rhegmatodon sensu* Kiaer (1882)

A. Laeviseta

The seta smooth, the operculum equalling 1/4-1/3 of the deoperculate capsule, the longitudinal walls of the external cells of the capsule thickened throughout, the processes distinctly punctulate. 1

B. Scabroseta

The seta scabrous, the operculum equalling nearly 1/2 of the deoperculate capsule, the walls of the external cells of the capsule interruptedly thickened, the processes smooth. 14

1. The branch leaves more narrow (2.00-2.58). 2

The branch leaves wide (1.82-1.85). 11

2. With the maximum width of the leaf a little above the base. . . 3

With the maximum width of the leaf a little below the middle. . 6

3. The branch leaves more loosely imbricated, the perichaetial leaves with the teeth solitary or very few coarsely serrate, distinctly costate. 4

Rh. schlotheimioides

The branch leaves densely appressed, the perichaetial leaves completely entire obsoletely costate. 5

Rh. filiformis

- With the margin of the perichaetial leaves provided with
teeth one to each. 7
6. *Rh. orizabanus*
- The perichaetial leaves completely entire or the margin erose-
denticulate. 8
- The branches at the apex attenuate, the branch leaves
(apical) homomallous, the costa extended to the middle.9
8. *Rh. orthostegius*
- The branches subclavate at the apex, thickened, the leaves
heteromallous, the costa extended above the middle. 10
- Rh. polycarpus*
- The branches nearly straight, the branch leaves heteromallous,
the processes indistinctly bordered. 12
- Rh. brasiliensis*
11. The branches curved, the branch leaves homomallous, the pro-
cesses distinctly hyaline-bordered. 13
- Rh. secundus*
- The branch leaves completely entire. 15
- Rh. declinatus*
14. The branch leaves at the apex finely serrate. 16
- Rh. serrulatus*

Key to Species of *Rhegmatodon* sensu Brotherus (1925)¹

I. (A) Seta smooth

A. (a) Branch leaves 2-2.5:1

1. (Aa α) Branch leaves oval

- a. (Aa α I) Branch leaves laxly appressed; inner involucreal leaves with serrated teeth

Rh. schlotheimioides Spruce

- b. (Aa α II) Branch leaves tightly appressed; inner involucreal leaves with entire margins; obscurely costate

Rh. filiformis Schimper

Rh. pringlei Card.

2. (Aa β) Branch leaves oblong - oval

- a. (Aa β I) Inner involucreal leaves with individual little teeth

Rh. densus Schimp.

- b. (Aa β II) Inner involucreal leaves with entire margins or crenately denticulate

- 1) (Aa β III1) Branches acuminate; the upper branch leaves bent to one side (homomallous); costa stopping at midleaf

Rh. orthostegius Mont.

- 2) (Aa β III2) Branches club-shaped, thickened; branch leaves not bent to one side; costa continuing past midleaf

Rh. polycarpus (Griff.) Mitt.

B. (Ab) Branch leaves about 1.8-1

1. (Ab α) Branches nearly straight; branch leaves not bent to one side

Rh. crassirameus Card.

¹The characters in parentheses were originally used by Brotherus in A. Engler and K. Prantl, "Die natürlichen Pflanzenfamilien." Ed. 2. 1925. 11:298-99. I have supplied my own outline form in the interest of clarity.

Rh. brasiliensis Lindb.

2. (Ab β) Branches curved; branch leaves bent to one side

Rh. secundus Kiaer

Rh. newtoni Broth.

II. (B) Seta rough

A. (Ba) Branch leaves with entire margin

Rh. declinatus (Hook.) Brid.

B. (Bb) Branch leaves serrate to the tip

Rh. serrulatus (Doz. et Molk.)

Key to Species of *Macrohymenium* sensu Kiaer (1882)

Macrohymenium gracillimum (C. Müll. in correspondence 1882), of Tahiti, with the cells of the leaves provided with alars round-quadrate, inflated, yellow, the rest is not know to me.

The Other Six Species

- The branch leaves wider (2.19) smaller. 2
1. *M. rufum*
- The branch leaves narrower (above 2.87) larger. 3
- The branch leaves very long (3.91). 4
3. *M. strictum*
- The branch leaves shorter (2.88-3.23). 5
- The perichaetial leaves denticulate. 6
5. *M. acidodon*
- The perichaetial leaves completely entire. 7
- The branch leaves loosely imbricated, outspread. 8
7. *M. nietneri*
- The branch leaves densely imbricated erect-spreading or spreading. 9
- The branch leaves heteromallous. 10
- M. laeve*
9. The branch leaves homomallous. 11
- M. mülleri*

Key to Species of *Macrohymenium* sensu Brotherus (1925)

Section I. *Leidontium* Broth. n. sect. ± slender plants. Peristome teeth smooth. The processes of the inner peristome broad, finely papillose, transparent. (6 species)

A. The seta above set with very low, broad warts.

Aa. The inner perichaetial leaves entire margined.

Aaa. Slender plants; the branch leaves nearly 2:1 *M. mitratum* (Doz. and Molk.) Fleisch. [*M. rufum* (Reinw. and Hornsch.) C. Müll.] Sumatra, Java, Queensl.

Aab. Less slender plants; the branch leaves very long, about 4:1 *M. strictum* Bryol. Jav., Borneo, Mindinao.

Ab. The inner perichaetial leaves denticulate: *M. acidodon* (Mont.) Doz. and Molk., Bourbon, Madagascar.; f. *acutissima* Besch. (*Rhegmatodon madagassus* Gêh. nach Kiaer), Madagascar, Seychelles.

B. The seta plainly rough; the inner perichaetial leaves entire margined.

Ba. The dry branch leaves loosely appressed, when moist spreading: *M. nietneri* (C. Müll.) Mitt., Ceylon.

Bb. The dry branch leaves densely appressed, when wet erect-spreading.

Bba. The branch leaves spreading on all sides: *M. laeve* Thwait. and Mitten., Ceylon.

Bbb. The branch leaves unilateral: *M. mülleri* Doz. and Molk. (Fig. 745), Sumatra, Java, Borneo.

Section II. *Trachydontium* Broth. n. sect. Robust plants. The peristome teeth papillose above. The processes of the inner peristome narrow, through a thick framework of papillae opaque. (1 species)

M. sinense Thér., Kweitschou.

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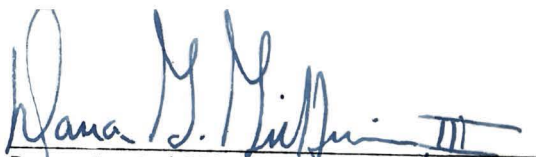
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BIOGRAPHICAL SKETCH


David Alvin Eakin was born February 21, 1945, in Bridgeport, Connecticut. He was graduated from Seneca High School, Louisville, Kentucky in June, 1962. He received the Bachelor of Arts with a major in Biology from the University of Louisville in Louisville, Kentucky, in January, 1967. He worked as a graduate teaching assistant at the University of Louisville, receiving his Master of Science in Biology in December, 1972. From September, 1971, until the present time he has pursued his work toward the degree of Doctor of Philosophy.

David Alvin Eakin is married to the former Lois Darlene Walker, and is the father of a daughter, Heather Rebecca, and a son, Jonathan David. He is a member of the American Bryological and Lichenological Society of America and the Association of Southeastern Biologists.

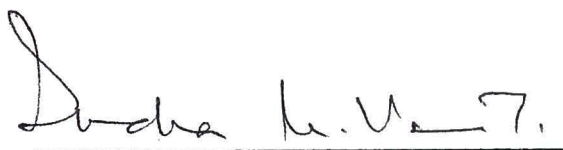
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Dana G. Griffin, III, Chairman
Associate Professor of Botany

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James W. Kimbrough
Professor of Botany

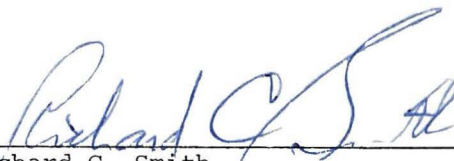
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


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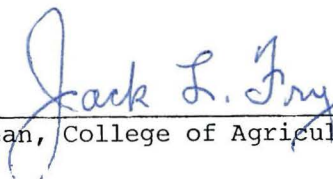
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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1976



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