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A REVISION OF THE MALESIAN SPECIES OF *DICRANOLOMA* (DICRANACEAE, MUSCI)

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ABSTRACT. A revision of the Malesian species of *Dicranoloma* (Ren.) Ren. is presented. In order to clarify the circumscription of *Dicranoloma* a cladistic analysis was performed, including also species of *Dicranum* Hedw. and selected other genera. The number of informative characters that could be found was limited. The trees obtained are very sensitive to slight changes in the data matrix or choice of the outgroup. Both *Dicranoloma* and *Dicranum* are resolved as paraphyletic, the latter being more basal. *Braunfelsia* Par., the Dicnemonaceae and a clade containing *Mesotus* Mitt., *Sclerodontium* Schwägr. and *Leucoloma* Brid. appear to have been derived from *Dicranoloma* stock.

Despite its paraphyletic nature, *Dicranoloma* sensu Renauld (1901, 1909) was accepted. The genus is characterised by the presence of a limbidium and single-layered alar patches.

For the Malesian region 15 species are accepted in *Dicranoloma. Dicranoloma armitii* (C. Müll.) Par. and *D. fragile* Broth. are transferred to *Cryptodicranum* and *Dicranum* respectively. One new name, *Dicranum psathyrum* Klazenga (for *Dicranoloma fragile*), and two new combinations, *Dicranoloma bartramianum* (B.H. Allen) Klazenga and *D. cutlackii* (Norris & T. Kop.) Klazenga, are made. *Dicranum assimile* Hampe f. *major* Fleisch., *Dicranoloma euryloma* Dix. var. *rugifolium* Bartr., *D. brachyphyllum* Nog. and *D. havilandii* Broth. var. *latifolium* Van Zanten are synonymised with *D. assimile* (Hampe) Ren. *Dicranoloma novoguineense* Broth. & Geh. is synonymised with *D. billardierei* (Brid. ex Anon.) Par. *Dicranoloma braunfelsioides* Herz. is synonymised with *D. blumei* (Nees) Ren. *Dicranum laevifolium* Broth. & Geh., *Dicranoloma hemineuron* Dix. and *D. spiniforme* Bartr. are synonymised with *Dicranoloma braunii* (C. Müll. ex Bosch & Lac.) Par. *Dicranum brevisetum* Dozy & Molk. var. *angustum* Lac., *Dicranoloma defoliatum* Froehl. and *D. damanhurii* Tan & Mohamed are synonymised with *D. brevisetum* (Dozy & Molk.) Par. *Dicranoloma formosanum* Broth. is synonymised with *D. dicarpum* (Nees) Par.

Important characters to distinguish species are found in the absence or presence of a central strand in the stem, the areolation of the upper lamina, the anatomy of the costa and the number of sporogones per perichaetium.

Five species of *Dicranoloma* are endemic to New Guinea, *D. cutlackii* (Norris & T. Kop.) Klazenga occurs in New Guinea and in the Moluccas and *D. havilandii* Broth. is endemic to Mt. Kinabalu on Borneo. Seven species are widespread in Malesia. Most of these have occasionally been found in continental South East Asia as well. *Dicranoloma braunii* (C. Müll. ex Bosch. & Lac.) Par. and *D. brevisetum* (Dozy & Molk.) Par. are also found in India and Sri Lanka and the former is also widespread in the Pacific. *Dicranoloma billardierei* (Brid. ex Anon.) Par. is widely distributed in Africa, South America, the Antarctic Islands, Australasia and Malesia. *Dicranoloma dicarpum* (Nees) Par. is widely distributed in Australasia and also occurs in New Guinea and Taiwan. *Cryptodicranum armitii* has an East Malesian distribution. *Dicranum psathyrum* is a species of the Indian subcontinent and continental South East Asia also occurring on Luzon.

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Within Malesia all species of *Dicranoloma* grow at high altitudes, in the submontane forest zone or higher. Four species are also found in monsoon areas. All species are facultative epiphytes, but some are more commonly epiphytic than others.

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INTRODUCTION

Dicranoloma Ren. (Ren.) is a large genus of mosses distributed mainly in the Southern Hemisphere. Most of its members are very similar to members of the Northern Hemisphere genus *Dicranum* Hedw. The phytogeographic region Malesia, including Malaysia, Brunei, Indonesia, the Philippines, Papua New Guinea, and the Solomon Islands, is the region richest in species.

A world-wide revision of *Dicranoloma* is not available and neither are revisions for any of the major phytogeographic regions. Some local floristic-taxonomic treatments for the Malesian region have been published in the last two decades (Tan & Koponen 1983; Tan 1989; Akiyama 1990; Norris & Koponen 1990). Moreover, Eddy (1988) treated the genus for his "Mosses of Malesia". These treatments, however, do not cover all the described taxa and do not agree in their synonymies.

In the present study the Malesian species traditionally placed in *Dicranoloma* have been revised. Type specimens or original specimens of all published names were studied, as far as they could be located. Additional specimens were obtained from the following herbaria: BISH, B, BM, CBG, EGR, FH, G, GRO, H, H-BR, JE, KLU, L, MO, NY, PC, PE, S, SAN, SAR and W. Furthermore, some fieldwork has been done in order to study the variation in the field.

A cladistic analysis was performed in an attempt to clarify the relationships between *Dicranoloma* and other genera of the Dicranoideae, as the circumscription of *Dicranoloma* is not clear and a major change has recently been proposed (Norris & Koponen 1989, 1990).

HISTORY

The name *Dicranoloma* was first used by Renauld (1898) in his "Prodrome de la flore bryologique de Madagascar et des Comores", in which he divided *Leucoloma* Brid. into three subgenera: subg. *Dicranoloma*, subg. *Leucoloma* ["*Euleucoloma*"], and subg. *Dicnemoloma*. *Leucoloma* subg. *Dicranoloma* was created in order to accommodate species formerly belonging to *Dicranum* Hedw. possessing a differentiated limbidium, but differing from typical *Leucoloma* by the homogeneity of the lamina cells between the costa and the limbidium. Renauld (1909) credited C. Müller Halle and Bescherelle for already having moved species possessing a limbidium from *Dicranum* to *Leucoloma*, but no published evidence for this could be found. Initially, eight species were accommodated in subgenus *Dicranoloma*, distributed over two sections. *Leucoloma platyloma* (Besch.) Ren. and *L. formosum* (Besch.) Ren., nom. nud. from New Caledonian, *L. serratum* Broth. and *L. austroscoparium* Broth. from Queensland, and *L. sumatranum* Broth., nom. nud., from Sumatra were placed in sect. *Scoparioidea* Ren. whereas the African species *L. drepanocladium* (C. Müll.) Kindb., *L. dichotomum* (P. Beauv.) Ren. and *L. scopareolum* (C. Müll.) Ren. were placed in sect. *Oncophoroidea* Ren. The only difference between the sections is in the shape of the capsule, which is distinctly strumose in sect. *Oncophoroidea*, but scarcely or not at all strumose in sect. *Scoparoidea*.

While Renauld's treatment mainly concerned Madagascan species, Brotherus (1901) applied the same classification world-wide and made the necessary new combinations. It became evident that the majority of the Southern Hemisphere species formerly classified in *Dicranum* should be placed in *Leucoloma* subg. *Dicranoloma*.

In that same year, Renauld (1901) elevated the three subgenera to the genus level. This time Paris (1904) made most of the necessary new combinations in the second edition of his Index Bryologicus. In his "Essai sur les Leucoloma", Renauld (1909) presented a more detailed account of the morphology and classification of *Leucoloma*, *Dicranoloma*, and *Dicnemoloma* (*Sclerodontium*). He made some more new combinations in *Dicranoloma* and raised the sections *Scoparioidea* and *Oncophoroidea* to subgenera. Again it was Brotherus (1924) who gave a world-wide overview in the second edition of "Die natürlichen Pflanzenfamilien".

In "Index Muscorum" (Van der Wijk et al. 1962, 1969) 120 species of *Dicranoloma* were accepted, 37 of which occur in Malesia. Since then eight more species have been validly published, three of which are Malesian. Moreover, two New Guinean species have been described in *Dicranum* or have been transferred to it (Allen 1987a, Norris & Koponen 1990).

Dozy & Molkenboer (1848) published the genus *Megalostylium*. Only one species, *M. brevisetum*, originally described under the illegal homonym *Dicranum brevisetum* Dozy & Molk., was contained in this new genus. The genus was not adopted in important works like "Bryologica Javanica" (Bosch & Van de Sande Lacoste in Dozy & Molkenboer, 1858) and "Die Musci der Flora von Buitenzorg" (Fleischer 1904). Instead, *D. brevisetum* was retained in *Dicranum*. Later, Brotherus (1901) and Paris (1904) placed the species in *Leucoloma* subg. *Dicranoloma* and in *Dicranoloma* respectively. The genus *Megalostylium* was initially accepted in "Index Muscorum" (Van der Wijk et al. 1964), but this was corrected in the Addenda (Van der Wijk et al. 1969), where *Dicranoloma brevisetum* (Dozy & Molk.) Par. was accepted.

Bartram (1938) described *Cryptodicranum* for a new species from Bougainville, which later was found to be conspecific with *Dicranoloma armitii* (C. Müll.) Par. (Bartram 1942). The genus *Cryptodicranum* was accepted in "Index Muscorum", but was dismissed by Tan (1989) who returned *C. armitii* to *Dicranoloma*.

Herzog (1909) described *Werneriobryum* to accommodate the New Guinean moss *W. geluense*. He mentioned a number of character states which in his opinion point to a relationship of *Werneriobryum* with the Dicnemonaceae: a dicranoid peristome, large alar cells, a creeping stem and conspicuously large spores. Some characters like the presence of a limbidium, the single costa and the high sheathing perichaetium supposedly carried on a short lateral shoot would not fit *Dicnemon* badly. However, affiliation to the Dicnemonaceae was discarded, based on the habit which is not at all like in the Dicnemonaceae, the absence of a central strand, the aggregated sporogones and, most importantly, the unicellular spores. Therefore, Herzog proposed that the genus should be placed in a family of its own, the Werneriobryaceae. Brotherus (1924), without discussion, placed *Werneriobryum* in the Dicnemonaceae. In his revision of the Dicnemonaceae, Allen (1987c) accepted only two genera in the family, *Dicnemon* and *Eucamptodon*. *Werneriobryum* was synonymised with *Dicranoloma* (Allen, 1986b).

When Renauld published *Dicranoloma* it was not yet necessary to designate a nomenclatorial type. Williams (1913), following Canon 15 of the American Code of Botanical Nomenclature (Bull. Torrey Bot. Club 34: 172. 1907) chose the first species listed by Renauld (1898), *D. platyloma*, as a lectotype.

Norris & Koponen (1989) proposed to restrict *Dicranoloma* to a few northeastern Australian and New Caledonian species (see next section). Overlooking Williams' (1913) publication, they selected another lectotype, *Leucoloma serratum* Broth. from northeastern Australia.

Margadant & Geissler (1995) correctly pointed out that *Megalostylium* has priority over *Dicranoloma* and proposed to conserve the name *Dicranoloma* and to conserve *Leucoloma serratum* as its conserved type. It should be noted that *Dicranoloma brevisetum* is not part of *Dicranoloma* in the restricted sense of Norris & Koponen and thus there is no need to conserve *Dicranoloma* if their circumscription is accepted.

Systematic Status and Phylogeny of *Dicranoloma*

Introduction

In this chapter a cladistic analysis of *Dicranoloma* and putative allies will be described and discussed. Such an analysis was deemed necessary to elucidate the problematic delimitation of *Dicranoloma* from *Dicranum* and explore the possibilities of a phylogenetic classification of its species. The confounded literature on the delimitation of *Dicranoloma* from *Dicranum* is summarised in this introduction.

Renauld (1909) already wrote that one might be inclined to include *Dicranoloma*, as a subgenus, in *Dicranum* from which it only differs by the hyaline leaf border and a difference in geographical distribution. *Dicranoloma* has a largely Gondwanan distribution, whereas *Dicranum* is largely holarctic. Renauld admitted that in some species the border is so narrow and ill marked that it may be difficult to discern. In these cases assignment to either *Dicranoloma* or *Dicranum* is doubtful and he doubted whether some species that Brotherus (1901) had classified in *Dicranoloma* would not be better placed in *Dicranum*. He argued, however, that even if unclarity remains in the classification of a few species, this is insufficient as an argument against maintaining *Dicranoloma* as a genus, because only a few species are difficult to classify and because many other, widely accepted, genera have no clear boundaries either.

Brotherus (1901, 1924) too emphasised the geographic distribution of the species. Thus, some tropical species, e.g. *Dicranoloma braunii* (C. Müll. ex Bosch & Lac.) Par. and *D. armitii* (C. Müll.) Par., are placed in *Dicranoloma*, despite the fact that they do not possess a differentiated leaf border. Nevertheless, *Dicranoloma fragile* Broth., a species that lacks a limbidium and, moreover, is restricted to the Northern Hemisphere, is classified as a *Dicranoloma* in the second edition of 'Die naturlichen Pflanzenfamilien' (Brotherus 1924). In its first edition it had been classified as a *Dicranum* (*Dicranum fragile* Hook.).

Subsequent treatments have been floristic rather than taxonomic and, if they commented on the taxonomic status of *Dicranoloma* at all, merely mentioned that the genus is difficult to separate from *Dicranum* (cf. Dixon 1913, Robinson 1967, Tan & Koponen 1983, Eddy 1988, Tan 1989) or that the genus is in need of revision (cf. Tan, 1989). Some authors have tried to bring up additional characters, but have not been very specific in this. Thus, Scott & Stone (1976), describing Australian *Dicranoloma*, mentioned the tendency of Dicranolomas to be robust plants, an apparent difference between the genera in the colour and texture of cell contents, and slight differences in the structure of the peristome and in the general size and morphology of the capsule. In a revision of the Japanese species, Takaki (1966) mentioned a very narrow costa, numerous strongly sinuose basal juxtacostal cells and moreover describes the peristome as reduced which is not at all typical for *Dicranoloma*. Ramsay (1985), referring to the above authors, stated that the size and structure of the peristome is the most reliable character.

A serious challenge was put forward by Norris & Koponen (1989, 1990). They argued that, although *Dicranoloma* does include species with a prominent, clearly demarcated limbidium, at least as many species essentially have no limbidium at all, and, moreover, *D. billardierei* may show "either extreme of limbidium development" and species of *Dicranum* such as *D. scoparium* frequently show a hint of a limbidium. The other above-mentioned characters were likewise discarded. They proposed that the majority of the species traditionally placed in *Dicranoloma* should be placed in *Dicranum* and, in their treatment of the Dicranaceae for their series on the Bryophytes of the Huon Peninsula (Norris & Koponen 1990), they provided the necessary new nomenclatural combinations for the New Guinean species.

They furthermore proposed that the name *Dicranoloma* should be used for 2 northeastern Australian and 4 New Caledonian species only, choosing the northeastern Australian *Dicranoloma serratum* (Broth.) Ren. to be the lectotype, thereby overlooking that *Dicranoloma* had earlier been lectotypified by Williams (1913). In doing so, they claimed to follow Renauld's intent with *Dicranoloma*, interpreting the fact that *Dicranoloma* was first erected as a subgenus in *Leucoloma* as "a signal that we should choose a species superficially similar to *Leucoloma* as now understood". The species included in the newly circumscribed *Dicranoloma* all have an extremely strong limbidium that may constitute as much as nearly one-half of the leaf width. Norris and Koponen (1989) listed a few other characters of the lectotype which are quite usual in *Leucoloma*, but unusual in *Dicranoloma* (sensu Renauld). These are: "a broad and well-demarcated costa on leaves which are often caducous to their bases; and a short seta often exceeded by the perichaetial leaves". It should be noted that the fact that Norris & Koponen wrongly lectotypified the genus has no influence on the circumscription of *Dicranoloma*, as the lectotype selected by Williams, the New Caledonian *Dicranoloma platyloma* (Besch.) Ren. in Par., although not mentioned by Norris & Koponen, would certainly qualify as a member of *Dicranoloma* in their restricted sense.

Frahm (1993) agreed with Norris & Koponen that the terrestrial subantarctic species of *Dicranoloma* (sensu Renauld) cannot be clearly distinguished from species of *Dicranum* and observed the phytogeographic significance of the fact that *Dicranum* has become a genus with a bicentric rather then holarctic distribution and *Dicranoloma* a genus with a tropical distribution. He proposed to amend the circumscription of *Dicranoloma* as to include all tropical epiphytic species. The genus in his view would be characterised by several adaptations to an epiphytic life form, specifically often pendent growth, absence of a central strand in the stem, longer leaves with a border of narrow cells and smaller sporophytes. Although Frahm is vague about exactly which species should be included in *Dicranoloma*, the fact that the one species he did recommend for inclusion, *D. billardierei*, is not a tropical species and lacks some of the characters that should characterise *Dicranoloma*, suggests that the definition of the genus has not become much clearer in recent decades.

Material and Methods

Taxa included

As monophyly of *Dicranoloma* could not be made plausible prior to the analysis, species of both *Dicranum* and *Dicranoloma* had to be included in the ingroup. A number of additional genera of which a possible close relationship with *Dicranoloma* has been postulated in literature were also included. However, as the number of potentially informative characters was found to be very small, not all species could be included and a selection had to be made.

In order to represent groups in the analysis one can follow either an exemplar approach in which one or a few representative species of each group are selected, or a compartmentalisation approach (cf. Mishler 1994) in which "composite taxa" that are given the character states which are either the most plesiomorphic in the group, or the most common, or are based on the character states of all taxa in the group, are created. A drawback of the exemplar approach is that, even when care is taken that the taxon selected is basal in the clade represented, within-group variation is not fully represented (Mishler 1994). The compartmentalisation approach on the other hand has the disadvantage that the "composite taxa" may have a combination of character states that does not occur in any member of the group (cf. Kenrick & Crane 1997). In both methods monophyly of the taxa is assumed and thus a priori knowledge about the relationships within the groups is required and the delimitation of the groups should be clear, which is not the case in most of the groups included in the analyses. Therefore, it was preferred to select just one or more taxa from each formal or informal group.

Among the Malesian species traditionally placed in *Dicranoloma* six informal groups have been recognised during the revision. Three groups are all characterised by the absence of a central strand in the stem. The first group, containing only *Dicranoloma armitii* (C. Müll.) Par. is characterised by a very strong costa that constitutes almost the entire upper part of the leaf, a lamina that is abruptly contracted above the basal part, immersed capsules, and peristome teeth with the outer plates thicker than the inner ones.

The second group contains *Dicranoloma brevisetum* (Dozy & Molk.) Par., *D. braunii* (C. Müll. ex Bosch & Lac.) Par., *Dicranum cutlackii* Norris & T. Kop. and *Dicranoloma steenisii* Klazenga. It is characterised by absence of a central strand, a strong costa, aggregated sporogones with relatively short setae, and a typically dicranoid peristome, i.e. with the inner plates thicker than the outer ones. *D. steenisii* has a nerve similar to *D. armitii* and was initially aligned with that species (Klazenga 1996), but based on peristome characters has been moved to this group. This group is represented in the analysis by *D. brevisetum.*

The third group contains *Dicranoloma geluense* (Herz.) B.H. Allen and *Dicranum bartramianum* B.H. Allen, two species that were initially classified in the Dicnemonaceae, in *Werneriobryum* Herz. and *Eucamptodon* Mont. respectively, but have been transferred to the Dicranaceae by Allen (1986b, 1987a). Both have very wide leaves with a very weak costa that lacks abaxial teeth and produce gemmae born at the tips of rhizoids. Norris & Koponen (1990) expressed the view that future study of the generic limits in their newly expanded *Dicranum* would probably lead to reinstatement of the genus *Werneriobryum*, which should accommodate at least these two species. *D. geluense* represents this group in the analysis.

The remaining three groups all posses a central strand. The fourth group comprises *Dicranoloma billardierei* (Brid. ex anon.) Par. and *D. blumei* (Nees) Ren. and is distinguished by the presence of scattered prorate cells (rather than teeth) on the abaxial surface of the costa. The sporogones are almost always solitary, the cortical cells of the stem thick-walled, and the alar cells mostly not inflated. *Dicranoloma billardierei* is chosen to represent this group. *D. billardierei* also occurs outside Malesia and is the most widespread of all Dicranolomas.

The fifth group comprises *Dicranoloma assimile* (Hampe) Ren., *D. arfakianum* (Geh.) Par., *D. havilandii* Broth., *D. rugifolium* Bartr., *D. reflexum* (C. Müll.) Par., *D. dicarpum* (Nees) Par. and *D. daymannianum* Bartr. and is characterised by the presence of rows of teeth on the abaxial side of the costa. The sporogones are mostly aggregated, the cortical cells of the stem mostly thin-walled, and the alar cells mostly inflated. *Dicranoloma daymannianum* is often linked with *D. fragile* from the next group, because of its caducous leaf tips and the presence of rhizoidal gemmae, but I find it more similar to *D. rugifolium*, which also has caducous leaf tips. *Dicranoloma assimile* and *D. dicarpum* represent this group in the present analysis. The latter species also occurs outside Malesia in Australia, New Zealand, and Taiwan.

The sixth group contains only *Dicranoloma fragile* Broth. and is characterised by small size, caducous leaf tips, absence of a limbidium, and wide costa, with little internal differentiation, i.e. with all cells approximately equally large.

Many of the Australasian and Oceanian species of *Dicranoloma* are easily placed in one of these informal groups, more specifically the fourth and fifth ones. From the species that cannot be placed in any of the groups, the following ones have been included in the analysis: *D. menziesii* (Tayl.) Ren. (occurring in Australia, New Caledonia, New Zealand, southern South America and Subantarctic Islands), *D. serratum* (Broth.) Ren. and *D. austroscoparium* (Broth.) Par. (northeastern Australia), *D. eucamptodontoides* (Broth.) Par. (Tasmania), *D. platyloma* (Besch.) Par. (New Caledonia), and *D. rugosum* (Hook.) B.H. Allen (Society Islands). The choice of species has been such as to cover as much as possible of the variation present in *Dicranoloma*. With the inclusion of *D. serratum*, *D. austoscoparium* and *D. platyloma* the variation in *Dicranoloma* sensu Norris & Koponen (1989) is covered. The New Caledonian species not included in the analysis are very similar to *D. platyloma*, if specifically different at all. Similarly, all species I know from South America, Africa, and the Subantartic Islands are quite similar to either *D. menziesii* or *D. billardierei.*

As a word-wide treatment of *Dicranum* is lacking, two current, partly compatible, infrageneric classifications have been used to select species for the analysis. These classifications are juxtaposed in table 1. The sectional classification of Nyholm (1986) for the northern European species and adopted for North American species by Bellolio-Trucco & Ireland (1990) is the most detailed one, but many species occurring outside these areas cannot be assigned to a section without stretching the boundaries of some sections or describing new ones. Brotherus' (1924) subgeneric classification, recently adopted by Gao & Cao (1992) for the Chinese species, is less detailed, but can be used world-wide.

Among the European and North American species one or two species from each section were selected. The choice of taxa from each of the sections has been inspired by availability of material, especially complete specimens, rather than taxonomic considerations. Two additional species from Southeast Asia that belong to subg. *Dicranum* but are not easily assigned to a section were included. From subg. *Pseudochorisodontium*, *D. gymnostomum* from Southeast Asia and *D. johnstonii* from East Africa were selected. Neither the Asian species of subg. *Crassidicranum* nor the few Central and South American and very few Oceanian species that are best placed in subg. *Dicranum* were included in the data matrix.

Additional genera included are: *Leucoloma* Brid., *Sclerodontium* Schwaegr., *Braunfelsia* Par., *Brotherobryum* Fleisch., *Parisia* Broth., *Chorisodontium* (Mitt.) Broth., *Mesotus* Mitt., *Dicnemon* Schwaegr. and *Eucamptodon* Mont.

Leucoloma, *Sclerodontium* (as *Dicnemoloma*) and *Dicranoloma* once formed the subgenera of a larger *Leucoloma* (Renauld 1898, 1901). A cladistic analysis by La Farge-England (1998) demonstrated monophyly of and a sister group relationship between *Leucoloma* and *Sclerodontium*. *Dicranoloma* was used as one of the outgroups. The species of *Leucoloma* included in the present analysis, *L. molle* (C. Müll.) Mitt. and *L. mittenii* Fleisch. represent the two major subdivisions of La Farge-England's infrageneric classification of *Leucoloma*, subg. *Leucoloma* and subg. *Syncratodictyon* Ren. respectively.

Table 1. Comparison of the classifications by Brotherus 1924 and by Nyholm 1986 with the species included in the present cladistic analysis. For further explanation see text.

Brotherus' (1924) classification	Nyholm's (1986) classification	Species included in the analysis
Dicranum Hedw. subg. *Dicranum*	*Dicranum* Hedw. sect. *Dicranum*	*D. scoparium* Hedw. *D. polysetum* Sw.
	sect. *Spuria* B.S.G.	*D. spurium* Hedw
	sect. *Fuscescentiformia* Kindb.	*D. fuscescens* Sm.
	sect. *Muehlenbeckia* Peterson	*D. muehlenbeckii* B.S.G.
	sect. *Elongata* Hag.	*D. elongatum* Schleich. ex Schwaegr.
	?	*D. lorifolium* Mitt. *D. kashmirense* Broth.
subg. *Crassidicranum* Limpr.	sect. *Crassinervia* Roth.	*D. fulvum* Hook.
subg. *Pseudochorisodontium* Broth.	—	*D. gymnostomum* Mitt. *D. johnstonii* Mitt.
Orthodicranum Loeske	sect. *Montana* Hartm.	*D. montanum* Hedw.

Of the two species recognised in *Sclerodontium*, *S. pallidum* (Hook.) Schwaegr. was included in the analysis because that is the only one of which all characters could be scored.

A possible relationship between *Dicranoloma* and the genera *Braunfelsia*, *Brotherobryum* and *Parisia* has been postulated by Allen (1984, 1986a). *Braunfelsia* has never been revised. In a recent treatment of the genus for the Malesian area Eddy (1988) recognised four species that are very similar and questionably distinct. *Braunfelsia dicranoides* (Dozy & Molk.) Broth. was included in the analysis.

Brotherobryum and *Parisia* were revised by Allen (1984, 1986a). Four species are recognised in *Brotherobryum*, of which three are endemic to New Guinea and one has also been found on Sulawesi and Borneo. *Brotherobryum macgregorii* (Broth. & Geh.) Fleisch. was included in the analysis. All three species recognised in *Parisia* are endemic to New Caledonia and *Parisia neocaledonica* Broth. represents the genus.

Chorisodontium is a genus of South American and Subantarctic mosses. Apart from a very strong costa, that widens some distance from the base, and multicellular spores, they are very similar to species of *Dicranoloma* or *Dicranum*. *Chorisodontium aciphyllum* (Hook.f. & Wils.) Broth. was included in the analysis.

The monotypic genus *Mesotus* was excluded from the Dicnemonaceae by Allen (1987b). *Mesotus* shares rhizoids arising from the lamina and multicellular spores with the Dicnemonaceae, but possesses a reduced dicranoid peristome and was placed in the Dicranaceae in a subfamily of its own. Allen (1987b) considers it to be most closely related to *Sclerodontium*. The only species recognised in the genus is *M. celatus* Mitt.

Eucamptodon and *Dicnemon* together make up the family Dicnemonaceae Fleisch. ex Broth. The Dicnemonaceae are characterised by a very elaborate asymmetrical peristome with shorter teeth at one side of the capsule, rhizoids arising from the lamina, and wedge-shaped multicellular spores. The Dicnemonaceae have been included in the analysis because they are postulated to have arisen from *Dicranoloma* stock (Allen 1987c). *Dicnemon* is distributed in Papua New Guinea, New Caledonia, Vanuatu, eastern Australia, and New Zealand, and comprises 13 species, of which the New Guinean *D. novae-guineae* (Dix.) B. H. Allen was included in the analysis. *Eucamptodon* has two species, one of which occurs in eastern Australia, New Caledonia, and Norfolk Island, the other in southern South America. The former, *E. muelleri* Hampe & C. Müll., was included in the study.

Outgroups

The choice of an outgroup is a difficult one, as virtually nothing is known of the relationships between the genera in the Dicranaceae. At the same time, because no unique character states are present in either *Dicranum* or *Dicranoloma*, and many character states occur in many other genera of the Dicranaceae, the choice of the outgroup has a strong influence on the outcome of the analysis.

Current classifications recognise 4 to 7 subfamilies within the Dicranaceae. Walther (1983) recognised subfamilies Rhabdoweisioideae, Dicranelloideae (or Anisothecioideae), Campylopodioideae, Paraleucobryoideae and Dicranoideae. Frey et al. (1995) split off the Cynodontioideae from the Rhabdoweisioideae and included the Leucobryoideae, which in other classifications form a family of their own. Allen (1994) synonymised the Paraleucobryoideae with the Campylopodioideae. An additional subfamily, the Mesotoideae was described by Allen (1987b) to accommodate *Mesotus celatus*.

Dicranoloma, *Dicranum*, *Leucoloma* and related genera together make up the largest group within the Dicranoideae. The next, far smaller element in the subfamily is the *Holomitrium* group, containing *Holomitrium* Brid., *Eucamptodontopsis* Broth., *Schliephackea* C. Müll. and *Macrodictyum* (Broth.) Hegew. The *Holomitrium* group has a circumtropical distribution. Only *Holomitrium* occurs outside South and Central America. The Australasian *Holomitrium perichaetiale* (Hook.) Brid. was selected as one of the outgroups.

Another outgroup was chosen from the genus *Symblepharis* Mont. *Symblepharis* is a member of the Dicranoideae, but neither part of the *Dicranum-Dicranoloma-Leucoloma* group nor of the *Holomitrium* group. In habit *Symblepharis* is superficially similar to *Holomitrium*, but differs, among other things, by its bifid peristome teeth. Within the Dicranoideae *Symblepharis* stands out because it is autoicous and lacks differentiated alar cells. *Symblepharis* occurs in Asia and America. The species used as an outgroup is *S. vaginata* (Hook.) Wijk & Marg.

Since *Dicranum and Dicranoloma* are negatively characterised, i.e. by lacking character states that are diagnostic for other genera, they may well be basal in the Dicranoideae. Therefore, an additional outgroup was chosen from outside the Dicranoideae. Although very little is known of the relationships between the Dicranoideae and the other subfamilies of the Dicranaceae, subf. Campylopodioideae seems most closely related to the Dicranoideae. The presence of differentiated alar cells might then be considered a synapomorphy of these two subfamilies (three if subfamily Paraleucobryoideae is recognised). In a phenogram published by Frahm (1991) the genus *Orthodicranum* (the only member of the Dicranoideae included) appears to be most similar to the Campylopodioideae and Paraleucobryoideae. No members of the Dicranoideae were included in a cladogram in the same publication. From the Campylopodioideae, a species of *Dicranodontium*, *D. uncinatum* (Harv.) Jaeg., was chosen as an outgroup, as most other genera possess a very derived costal anatomy which cannot be compared with the one in the ingroup.

Analyses were performed with either *Holomitrium* or *Symblepharis* or *Dicranodontium* as outgroup. Moreover analyses were performed with *Dicranodontium* as outgroup and either *Holomitrium* or *Symblepharis* or both added to the ingroup.

Characters

The character matrix used for the analysis is given in table 2. The characters and states are explained below. Character states are numbered (1), (2) etc. A higher number does not necessarily indicate a more apomorphic state. Character coding of the individual species was based on the study of herbarium specimens (listed in the appendix) and literature (table 3). As it proved impossible to find sufficient discrete characters that could be easily coded, some continuous characters were used. None of the proposed coding procedures for continuous characters (reviewed by Chappill 1991) have been used as they always lead to characters with a large number of states that have very strong influence on the outcome of the analysis. Therefore, also within continuous characters only a few character states were recognised. Multi-state characters were treated as unordered unless otherwise indicated. A more detailed description of the morphology is given in the Morphology section.

1. Plants either without (1) or with the potential to develop dwarf males (2). As *Symblepharis* is autoicous, this character has been coded as inapplicable for *Symblepharis*.
2. Growth form erect (1) or pseudo-creeping (2). In pseudo-creeping plants the basal part of the primary axis is prostrate and the end ascending, the innovations starting as prostrate again. In *Mesotus* the axis is creeping, with strong branches that are ascending and bear gametangia. As *Mesotus* is the only genus with this growth form which need not have evolved through a pseudo-creeping growth form, this character has been coded as a gap for *Mesotus celatus*. *Leucoloma molle* and some species of *Dicranoloma* may be pendulous, but they start as erect plants and become pendulous when the stem gets long.
3. Stem tomentose (1) or naked (2).
4. Gemmae arising near the tips of rhizoids absent (1) or present (2). These rhizoidal gemmae are found in *Dicranoloma fragile* and *D. geluense*. Gemmae arising near the base of the rhizoids are found in *D. brevisetum*, but as this is the only species included in the analysis possessing this kind of gemmae this character has not been included, because it would be uninformative.
5. Central strand of the stem present (1) or absent (2).
6. Cortical cells in the stem thin-walled (1) or thick-walled (2).

Table 2. Data matrix. A dash indicates that the character is inapplicable; a question mark indicates that the character state is unknown. Character numbers refer to characters listed in the text.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Outgroup																																			
Dicranodontium uncinatum	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	3	1	2	3	4	2	2	1	1	3	1	1	1	2	2	1	1	1	2	1
Symblepharis vaginata	—	1	1	1	1	1	1	1	—	—	2	1	3	1	1	1	1	1/3	2	3	1/2	2	1	1	4	1	1	?	1	1	1	1	2	2	1
Holomitrium perichaetiale	2	1	1	1	1	1	1	1	1	2	1	1	3	1	2	1	1	3	3	2	1/2	2	2	1	4	1	1	1	1	2	1	2	1	4	1
Ingroup																																			
Braunfelsia dicranoides	2	1	1	1	1	2	1	1	1	3	1	2	1	1	1	1	1	3	1	1	1	1	2	1	4	1	1	1	1	3	3	—	—	—	1
Brotherobryum macgregorii	2	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	3	2/3	4	1/2	2	2	1	4	1	1	1	1	1	2	2	1	4	1
Chorisodontium aciphyllum	1	1	1	1	1	2	1	1	1	1	1	1	3	1	1	1	1	3	3	4	1	2	1	1	4	1	1	2	2	1	1	1	1	3	1
Dicnemon novae—guineae	1	2	1	1	2	2	1	2	1	3	1	1	1	1	1	1	2	—	—	—	—	—	2	1	3/4	1	2	2	1	1	1	1	2	2	2
Dicranoloma armitii	2	1	1	1	2	2	1	1	1	2	2	1	3	1	1	1	1	1	3	4	2	2	1	1	1	2	1	2	1	2	1	1	2	1	1
Da. assimile	2	1	1	1	1	1	1/2	1	1	2	2	2	2	1	1	1	1	1	2	1	1	1	1	2	4	1	2	2	1	2	1	1	1	3	1
Da. austroscoparium	2	1	1	1	1	2	1	1	1	1	2	3	1	1	1	1	1	1	1/2	1	1	1	1	1	3	1	1	2	1	1	1	1	1	3	1
Da. billardierei	2	1	1	1	1	2	1	1	1	1/2	2	2	1	1	1	1/3	1	2	1	1	1	1	1	1	4	1	2	2	1	1	1	1	1	3	1
Da. brevisetum	2	1	1	1	2	2	1	1	1	1	2	2	1	1	1	1	1	1	2	1/2	1	1	1	2	2	2	1	2	1	1	1	1	1	2	1
Da. dicarpum	2	1	1	1	1	1	2	1	1	2	2	2	2	2	1	1	1	1	2/3	3	1	1	1	2	4	1	2	2	1	2	1	1	1	3	1
Da. eucamptodontoides	?	1	1	1	1	2	1/3	1	1	1	1	2	1	1	1	1	1	3	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Da. fragile	2	1	1	2	1	1	1	1	1	2	2	1	3	1	1	1	1	1	3	—	1	1	1	2	4	1	1	2	1	2	1	1	1	1/2/3	1
Da. geluense	2	1	1	2	2	2	3	1	1	2	1	2	1	1	1	1	1	3	1	1	1	1	1	2	3	1	1	2	1	3	1	1	1	3	1
Da. menziesii	2	1	1	1	1	2	1	1	1	1	2	2	3	1	1	1	1	2	3	4	1	1	1	1	3/4	1	1	2	1	1	1	1	1	3	1
Da. platyloma	2	1	1	1	1	2	1	1	1	2	2	3	3	1	1	1	1	1	2/3	2	1	1	2	1	3/4	1	2	2	1	1	1	1	1	3	1
Da. rugosum	2	1	1	1	1	1	3	1	1	1	1	2	1	1	1	1	1	3	2	2	1	1	2	2	3/4	1	1	2	1	1	1	1	1	2/3	1
Da. serratum	2	1	1	1	1	1	1	1	1	1	2	3	3	1	1	1/3	1	1	2	1	1	1	1	1	3	1	1	2	1	1	1	1	1	3	1
Dicranum elongatum	1	1	1	1	1	1	1	1	1	2	1	1	3	1	1	1	1	2/3	3	2	1	1	1	1	4	1	1	1	1	2	1	1	1	1	1
Dm. fulvum	1	1	1	1	1	1	1	1	1	1/2	1/2	1	3	1	1	2	1	2	3	2	1	1	1	1	4	1	1	1	1	1	1	1	1	1	1
Dm. fuscescens	1	1	1	1	1	1	3	1	2	2	2	1	3	1	1	2	1	2	2/3	2	1	2	1	1	4	1	2	1	1	1	1	1	1	3	1
Dm. gymnostomum	?	1	1	1	1	1	1	1	2	2	2	1	1	1	1	3	1	2	3	2	1	1	1	1/2	4	1	1	1	1	1	3	—	—	3	1
Dm. johnstonii	?	1	1	1	1	1	1	1	2	1	2	1	1	1	1	1	1	1	2	1/2	1	1	1	1	4	1	1	2	1	3	2	1	1	1	1
Dm. kashmirense	?	1	1	1	1	1	1	1	1	1/2	2	1	1	1	1	1	1	1	2	1	1	1	1	1	4	1	2	2	1	3	1	1	1	3	1
Dm. lorifolium	?	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	1	2	3	1	1	1	1	4	1	1	2	1	3	1	1	1	3	1
Dm. montanum	1	1	1	1	1	1	1	1	1	2	2	1	3	1	1	2	1	2	2	1	1	1	1	1	3	1	1	1	1	2	1	1	1	3	1
Dm. muehlenbeckii	2	1	1	1	1	1	1	1	2	2	1/2	1	3	1	1	1/3	1	2	2/3	2	2	2	1	1	4	1	2	1	1	1	1	1	1	3	1
Dm. polysetum	2	1	1	1	1	1	4	1	2	2	2	1	1	1	1	1	1	1	2/3	2	1	1	1	2	4	1	2	2	1	3	1	1	1	3	1
Dm. scoparium	2	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	1	3	3	1	1	1	1	4	1	2	2	1	3	1	1	1	3	1
Dm. spurium	2	1	1	1	1	1	3/4	1	2	2	2	1	3	1	1	2	1	2	3	2/4	1	2	1	1	4	1	2	1	1	2	1	1	1	3	1
Eucamptodon muelleri	2	2	1	1	2	?	1	2	1	3	1	1	1	1	1	1	2	—	—	—	—	—	2	1	2/3	1	1	2	2	1	1	2	2	4	2
Leucoloma molle	1	1	2	1	2	2	1	1	1	1	2	2	3	2	1	2	1	3	2	2	1	1	1	1	2	2	1	2	2	3	1	1	2	3	1
L. mittenii	1	1	2	1	2	2	1	1	1	1	1	2	3	2	1	2	1	3	2	2	1	1	1	1	4	1	1	1	2	3	1	1	2	3	1
Mesotus celatus	2	—	1	1	2	2	3	2	1	1	2	2	3	1	2	2	1	3	2	2	1	1	1	1	1	1	1	?	2	1	2	1	2	1	1
Parisia neocaledonica	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	—	—	—	—	—	2	1	4	1	1	?	1	1	2	1	?	1	1
Sclerodontium pallidum	1	2	2	1	2	2	1	1	1	1	1	2	3	1	2	2	1	3	2	2	1	1	1	1	3/4	—	2	2	2	3	1	1	2	3	1

Table 3. Literature consulted for assigning or checking character states of species of the genera mentioned.

Brotherobryum	Allen 1984
Chorisodontium	Frahm 1981, 1989; Hyvonen 1991
Dicnemonaceae	Allen 1987b
Dicranum	Nyholm 1986; Bellolio-Trucko & Ireland 1990
Leucoloma	La Farge-England 1998
Mesotus	Allen 1987a
Parisia	Allen 1986a
Sclerodontium	Crum 1986; La Farge-England 1998
Holomitrium	Hegewald 1978; Ramsay 1986; Allen 1990, 1994
Symblepharis	Salmon 1898; Eddy 1988; Allen 1994
Dicranodontium	Frahm 1997

7. Leaves smooth (1), plicate (2), or rugose (3).

8. Rhizoid initials in leaf lamina absent (1) or present (2).

9. Alar patches single-layered (1) or multi-layered (2). This character is deemed diagnostic at the sectional or subgeneric level within *Dicranum*. Multi-layered alar patches are found in subg. *Pseudochorisodontium* and most species of subg. *Dicranum*.

10. Alar cells never inflated (1), inflated in most collections (2), or collenchymatous (3). As understood here, inflated alar cells are cells that have changed from the original quadrate to rectangular shape, as can be observed in very young leaves, to a round or elliptical shape and are much enlarged. Inflated alar cells always have thin walls. Within *Dicranoloma* the character correlates with the informal groups recognised above, some groups typically possessing alar cells that are often inflated and others having alar cells that are not.

11. Leaf margin entire (1) or serrate (2).

12. Limbidium absent (1), present (2), or present and very wide (3). An extra state has been included for the extremely strong, more than 10 cell rows wide, limbidium present in *Dicranoloma platyloma*, *D. serratum* and *D. austroscoparium*, i.e. those species included in *Dicranoloma* by Norris & Koponen (1989). The character is interpreted as a continuous one and was treated as ordered.

13. Lamina cells in the upper half of the leaf similar to the basal ones (1), conspicuously different from the basal ones and oblong to linear (2), or conspicuously different from the basal ones and isodiametric to oblong (3).

14. Differentiated upper lamina cells descending along the costa absent (1) or present (2). Upper lamina cells which descend along the costa are found in *Leucoloma* and in *Dicranoloma dicarpum*. Within *Leucoloma* the development of juxtacostal bands varies, the juxtacostal bands being more distinct in for instance *L. molle* than in *L. mittenii*.

15. Differentiated upper lamina cells descending along the margins absent (1) or present (2).

16. Upper lamina cells smooth (1), papillose (2), or prorate (3).

17. Costa present (1) or absent (2). For taxa that lack a costa the next few characters (18–22) are inapplicable.

18. Abaxial side of costa with 2(–4) rows of teeth (1), with scattered prorate cells (2), or smooth (3).

19. Guide cells either 2(–3) (1), or 4–5(–7) (2), or (7–)8 or more (3). Rather than following Renauld's (1909) typification of the costal anatomy, costal anatomy was subdivided into four charac-

ters (19–22). Although there is some overlap between the states, character states could mostly be easily determined. This character was treated as ordered.

20. Stereids absent, scattered or in one layer at most (1), in 1–2 layers (2), in 3–5 bundles (3), or in 4 or more layers (4). This character was treated as unordered, as the order that should be given to states 3 and 4 is unknown.

21. Adaxial epidermis not differentiated (1) or differentiated (2). The epidermis is considered differentiated if the peripheral cells have conspicuously larger lumina than the adjacent stereids. This character and the next one are partly functionally correlated with the former two characters, because a very narrow costa with few stereids cannot have a differentiated epidermis, and one cannot speak of differentiation between layers when only one layer is present at both sides of the guide cells.

22. Abaxial epidermis not differentiated (1) or differentiated (2).

23. Perichaetial leaves only slightly longer than the stem leaves and not conspicuously sheathing (1), or at least 1.5 times as long as the stem leaves and conspicuously sheathing (2). In the latter case the sheathing part may reach the capsule or at least halfway the seta when the seta is long.

24. Sporogones solitary (1) or aggregated (2). Species with aggregated sporogones are rare in *Dicranum* and more common in *Dicranoloma*. No taxonomic significance is given to this character in *Dicranum*. Species with solitary and aggregated sporogones are grouped in the same section or subgenus. Among the Malesian species of *Dicranoloma* this character is correlated with other characters.

25. Seta length <2 mm (1), 2–6 mm (2), 6–12 mm (3), or >12 mm (4). Although a continuous character, with no distinct gaps between the states, it could be easily coded for most species, especially when the distribution of seta length within species is considered as well. When no decision could be made between two states, which mainly occurred between states 3 and 4, the character was coded as polymorphic. This character was treated as ordered.

26. Seta in transverse section with 2 to several of the outer layers thick-walled, cortical cells from the centre towards the periphery gradually becoming smaller and more incrassate (1), or with one peripheral layer of thick-walled cells bordering on thin-walled medulla cells (2). This character, adopted from La Farge-England (1998), is of significance in the infrageneric classification of *Leucoloma*. The latter condition is considered a synapomorphy of subg. *Leucoloma* (La Farge-England 1998). However, among the species included in the analysis the same condition is found in *Dicranoloma brevisetum* and *D. armitii*. This character has been coded as inapplicable for *Sclerodontium*, because in this genus a unique condition is found with two layers of thick-walled cells bordering on thin-walled medulla cells.

27. Capsules straight to slightly curved (1) or arcuate (2). The character is rather variable within *Dicranoloma*, and even within some species. Most species of *Dicranum* have arcuate capsules. The presence of erect capsules has been one of the reasons to distinguish the genus *Orthodicranum* from *Dicranum* (cf. Allen 1998).

28. Exothecial cells in cross section with the longest axis parallel to the capsule wall, the lumen rectangular to quadrate or trapezium-shaped or lentil-shaped and the inner wall distinctly thinner than the lateral and outer walls (1) or with the longest axis perpendicular to the capsule wall, the lumen quadrate to rectangular or keyhole-shaped and with about evenly incrassate walls (2). This character has also been used in the analysis by La Farge-England (1998) who distinguished a third character state for *Sclerodontium* in which the exothecial cells are more or less quadrate in cross section. After a study of this character for the taxa included in the present analysis, it was judged better to distinguish only two character states, grouping *Sclerodontium* with the taxa in which the longest axis is the one parallel to the capsule wall. La Farge-England coded her outgroups, *Dicranoloma* and *Dicranum*, as having the longest axis perpendicular to the capsule wall, which is true for *Dicranolo-*

ma but within *Dicranum* only for sect. *Dicranum*, the Asian species belonging to subg. *Dicranum* and *D. johnstonii*, all other species of *Dicranum* having the longest axis running parallel to the capsule wall.

29. Stomata present (1) absent (2). The absence of stomata in the theca wall has been used to separate the subfamily Campylopodioideae from the subfamily Dicranoideae (Brotherus 1924). However, stomata are absent in some members of the Dicranoideae as well.

30. Annulus persistent (1), deciduous (2), or not differentiated (3). This character is of some significance in the sectional classification of *Dicranum*, section *Dicranum* lacking a differentiated annulus and the other sections having one which, depending on the section, may be either persistent or deciduous. All species of *Dicranoloma* that could be studied have a differentiated annulus. So few capsules of *Dicranoloma geluense* were available that I did not venture to sacrifice one, but according to Allen (1986b) an annulus is absent. Among the Malesian species the persistent or deciduous condition of the annulus coincides with the informal groupings identified above, the annulus being deciduous in the group around *D. assimile*, and in *D. armitii* and *D. fragile*, and persistent in the remaining three groups.

31. Peristome teeth complete (1), reduced (2), or absent (3). The peristome teeth are considered reduced when they are either very short or are very thin and transparent, and lack ornamentation. For the taxa which lack a peristome, characters 32 to 34 have been coded as inapplicable.

32. Peristome teeth split at least down to the middle (1) or entire (2).

33. Peristome teeth with ventral plates thicker than dorsal ones (1) or with thicker dorsal plates (2). The typical dicranoid peristome has inner plates and trabeculae thicker than outer ones. In *Leucoloma*, *Sclerodontium*, *Mesotus*, the Dicnemonaceae, and *Symblepharis* it is the other way around.

34. Outer face of the peristome teeth smooth (1), striate below (2), striate with cross-connections between the striae (striolate-pitted) (3) or papillose (4). In *Parisia*, *Mesotus* and *Dicranum johnstonii* there is a correlation between a reduced peristome and the absence of ornamentation, but in other species, e.g. *Dicranoloma armitii* and *Dicranum fulvum*, well-developed and smooth peristomes occur and still others, e.g. *Brotherobryum macgregorii* have reduced and at the same time papillose peristome teeth.

35. Uniform, wedge-shaped, multicellular spores absent (1) or present (2). The special spores described are found in *Eucamptodon* and *Dicnemon*. Other types of multicellular spores are found in *Mesotus* and *Chorisodontium*. In *C. aciphyllum* exactly the same situation was found as described by Frahm (1989) for *C. mittenii* (C. Müll.) Broth., i.e. a mixture of brown unicellular spores, green unicellular spores up to twice as large as the brown ones and green multicellular spores that have germinated and consist of 2–4 cells. *Mesotus* has massive endosporic protonemata, which vary in size, shape and cell number within a single capsule, depending on the time of division The spores that divide first form the smallest protonemata (Allen 1987b). As the types found in *Chorisodontium* and *Mesotus* are autapomorphies they have not been added as character states. The character has not been coded as unicellular versus multicellular since the different types of multicellular spores have probably been derived independently from unicellular ones.

Analytical protocol

For the cladistic analysis of the data the computer programme PAUP (version 3.1.1; Swofford 1993) was used. Heuristic search strategies were employed because the number of taxa in the data matrix, and hence the number of possible trees, was too large to attempt an exhaustive search. This involved building starting trees using random addition of taxa followed by branch swapping using tree bisection-reconnection (TBR). The number of replicates was set to 100.

Bremer support (Bremer 1988, Källersjö et al. 1992) values were calculated from trees up to five steps longer than the most parsimonious ones. Bremer support of a clade is defined as "the difference in length between the considered tree and the shortest tree lacking that group" (Källersjö et al. 1992). Because the maximum number of trees that can be kept (32767) was insufficient, trees were obtained by performing TBR branch swapping on the most parsimonious trees until memory was full. As the Bremer support values were not based on all trees up to five steps longer than the shortest ones, they may be overestimated. A bootstrap (Felsenstein 1985) was tried in PAUP, but was not finished, as already after the first few replicates the memory was full. Other ways to obtain bootstrap estimates were not tried, as high values were not expected for any of the branches.

In order to reduce the number of trees obtained, successive weighting (Farris 1969) was applied. The rationale behind this is that characters that better fit the most parsimonious reconstructions obtained under equal weights, or at least some of them, should be given higher weights than those with worse fit. Usually the rescaled consistency index, rc (Farris 1989), of the character for the reconstruction on which it fits best is used to calculate weights, but Carpenter (1994) and Goloboff (1991) recommend weighting on the consistency index, ci. The weighting procedure is to be reiterated until the weights of the characters and hence the trees obtained do not change anymore. A property of this method is that a new set of trees is produced that is not necessarily a subset of the one obtained with equal weights and in that case contains trees that are longer than the most parsimonious trees (MPT's) when measured against the equally weighted data.

Successive weighting was attempted using ci and rc. Weights were obtained by multiplying the maximum values of these indices by 1000 and rounding the resulting values to the nearest integer.

Results

The results of the analysis performed, in terms of the length of the shortest trees obtained, numbers of MPT's, ensemble consistency index (CI) and ensemble retention index (RI) are given in table 4.

With equally weighted characters only the analyses with *Dicranodontium* as outgroup (3a) and the one with *Dicranodontium* as outgroup and *Symblepharis* included in the ingroup (3c) yielded reasonably well-resolved consensus trees. The number of trees obtained from these two analyses and the topology of the trees are the same, except that in the latter analysis *Symblepharis* has been inserted in the cladogram. The consensus tree of analysis 3c is given in figure 1.

The majority of the species of *Dicranoloma* is included in a clade that moreover contains *Mesotus*, *Sclerodontium*, *Leucoloma*, *Braunfelsia* and the Dicnemonaceae. All species of *Dicranum* are excluded from this clade. Within this *Dicranoloma* clade a clade containing *D. assimile* and *D. dicarpum* branches off first, followed by *D. platyloma*. Next to branch off is a clade containing *D. brevisetum* and the genera *Mesotus*, *Sclerodontium* and *Leucoloma*. *Dicranoloma brevisetum* is sister group of a clade containing the three other genera. Within the latter clade *Sclerodontium* and *Leucoloma* again form a monophyletic

Table 4. Analyses performed with indication of outgroup and number of taxa in ingroup, as well as length of the shortest tree(s) (L) resulting from the PAUP analyses performed, numbers of trees obtained (N), ensemble consistency index (CI) and ensemble retention index (RI). Analyses were performed with equal weights after which successive weighting on consistency index (ci) and rescaled consistency index (rc) was applied. For results after successive weighting values for the statistics when weighted against the equally weighted data are given between brackets.

Analysis no.	Outgroup	No. of taxa in ingroup	Results of analyses: equal weights	successive weighting on ci	successive weighting on rc
1.	*Holomitrium*	35	L: 154	L: 50989 (155)	L: 25864 (156)
			N: 1194	N: 1	N: 9
			CI: 0.331	CI: 0.405 (0.329)	CI: 0.452 (0.327)
			RI: 0.607	RI: 0.661 (0.603)	RI: 0.768 (0.599)
2.	*Symblepharis*	35	L: 154	L: 51005 (155)	L: 5532 (156)
			N: 1194	N: 3	N: 27
			CI: 0.331	CI: 0.419 (0.319)	CI: 0.456 (0.327)
			RI: 0.598	RI: 0.686 (0.594)	RI: 0.762 (0.590)
3a.	*Dicranodontium*	35	L: 156	L: 50993 (156)	L: 25263 (159)
			N: 75	N: 10	N: 145
			CI: 0.327	CI: 0.386 (0.327)	CI: 0.450 (0.321)
			RI: 0.604	RI: 0.632 (0.604)	RI: 0.780 (0.592)
3b.	*Dicranodontium*	36	L: 161	L: 50989 (162)	L: 26133 (163)
		(35+*Holomitrium*)	N: 2061	N: 1	N: 81
			CI: 0.317	CI: 0.391 (0.315)	CI: 0.432 (0.313)
			RI: 0.600	RI: 0.617 (0.596)	RI: 0.738 (0.593)
3c.	*Dicranodontium*	36	L: 160	L: 51004 (160)	L: 24851 (163)
		(35+*Symblepharis*)	N: 75	N: 10	N: 145
			CI: 0.319	CI: 0.379 (0.319)	CI: 0.442 (0.313)
			RI: 0.595	RI: 0.626 (0.595)	RI: 0.776 (0.584)
3d.	*Dicranodontium*	37	L: 165	L: 50992 (166)	L: 25896 (168)
		(35+*Symblepharis*,	N: 2432	N: 1	N: 4
		Holomitrium)	CI: 0.309	CI: 0.381 (0.307)	CI: 0.453 (0.304)
			RI: 0.591	RI: 0.646 (0.588)	RI: 0.766 (0.581)

group. A clade containing *D. austroscoparium* and *D. serratum* branches off next, followed successively by *D. menziesii* and *D. billardierei*. What is left is a polytomy containing *D. eucamptodontoides*, *D. geluense*, *D. rugosum* and a clade containing *Braunfelsia* and the Dicnemonaceae. The Dicnemonaceae are resolved as a monophyletic group.

Of the species of *Dicranoloma* excluded from the *Dicranoloma* clade, *D. armitii* was placed at the base of the cladogram and *D. fragile* among species of *Dicranum*.

The species of *Dicranum* form a paraphyletic group basal to the *Dicranoloma* clade. A clade containing *D. kashmirense*, *D. johnstonii*, *D. lorifolium*, *D. polysetum*, and *D. scoparium* is the sister group of the *Dicranoloma* clade. Within this clade *D. kashmirense* is

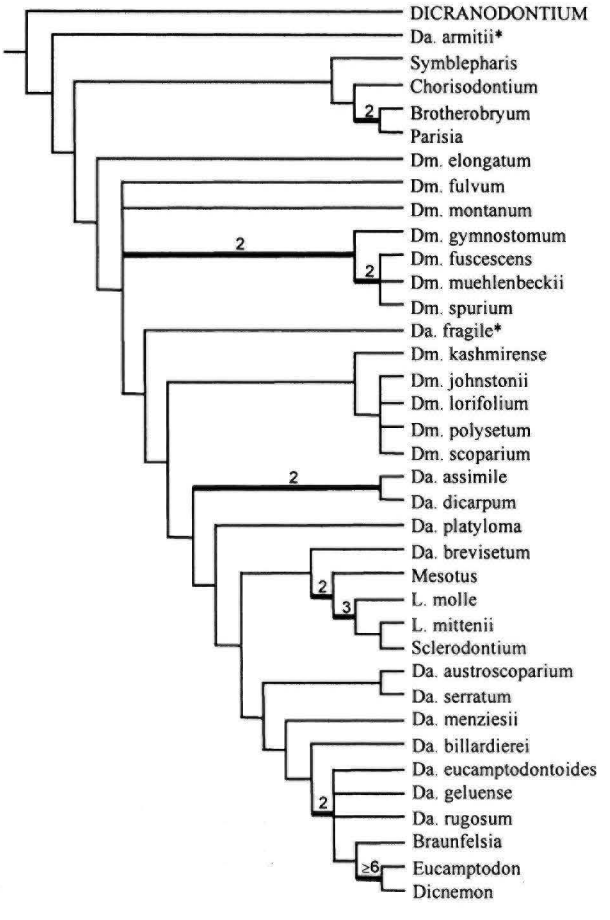

Fig. 1. Consensus tree of analysis 3c, outgroup *Dicranodontium*, *Symblepharis* included in ingroup, equal weights, based on 75 equally most parsimonious trees of 160 steps, CI 0.319, RI 0.595. Figures above thickened internal branches indicate Bremer support. Internal branches that are not thickened have Bremer support 1, i.e. they collaps in the consensus tree based on all trees up to 1 step longer than the shortest trees. Da. stands for *Dicranoloma*, Dm. for *Dicranum*. *) *Dicranoloma armitii* and *D. fragile* were, after the analysis, transferred to *Cryptodicranum* and *Dicranum*, respectively.

the most basal species. The relationships between the other species are unresolved. Another, more basal, clade is formed by *D. gymnostomum*, *D. muehlenbeckii*, *D. fuscescens*, and *D. spurium*. Within this clade the latter three species again form a clade in which the relationships are unsolved. *Dicranoloma fragile* is interposed between these two clades. *D. elongatum* is the most basal species within the *Dicranum* grade. The position of *D. montanum* and *D. fulvum* is unresolved. In different trees they are either placed at the base of the *D. gymnostomum-D. spurium* clade or more basal in the *Dicranum* grade, successively branching off immediately after *D. elongatum*.

The remaining genera included in the analysis form a clade at the base of the cladogram, branching off immediately after *Dicranoloma armitii*. Within this clade *Symblepharis* is the most basal taxon. *Brotherobryum* and *Parisia* together form a monophyletic group.

The Bremer support is low for most internal branches (see Fig. 1), the majority of the clades collapsing when trees one step longer than the most parsimonious trees are included in the consensus. A few internal branches have Bremer support 2, a single branch has Bremer support 3. Only the Dicnemonaceae are well-supported, having Bremer support 6 or higher.

The analyses with either *Holomitrium* or *Symblepharis* as outgroup (1 and 2 respectively) and the analyses with *Dicranodontium* as outgroup and *Holomitrium* or *Holomitrium* and *Symblepharis* included in the ingroup (3b and 3d respectively) yielded almost completely unresolved consensus trees. The clades supported are essentially the same as the ones with Bremer support 2 or higher from analysis 3c (see Fig. 1). The analysis with *Holomitrium* as outgroup moreover groups *Dicranoloma rugosum* and *Braunfelsia* and groups *Dicranum elongatum*, *D. fulvum*, *D. montanum*, and *D. gymnostomum* with the *Dicranum muehlenbeckii-D. fuscescens-D. spurium* clade. In the analyses in which *Holomitrium* is included in the ingroup (3b and 3d), this species is always grouped together with *Brotherobryum*.

Successive weighting

Successive weighting, especially on ci, proved very effective in reducing the numbers of trees. Successive weighting on ci always yielded fewer MPT's than successive weighting on rc. In the analysis with *Dicranodontium* as outgroup (3a) and in the analysis with *Dicranodontium* as outgroup and *Symblepharis* included in the ingroup (3c), successive weighting on rc yielded more trees than the analysis with equally weighted characters.

Trees obtained after successive weighting on ci in all cases are shorter than the ones obtained after successive weighting on rc when weighted against the equally weighted data. Trees obtained after successive weighting on ci are as long as or 1 step longer than the most parsimonious trees obtained under equal weights while trees obtained after successive weighting on rc are 2 or 3 steps longer.

The trees obtained from analyses 3a and 3c after successive weighting on ci again are identical (apart from the inclusion of *Symblepharis* in the latter) and are subsets of the sets of trees obtained with equal weights. The basal polytomy in the *Dicranum*-grade has been resolved. *Dicranum montanum* and *D. fulvum* are placed at the base of the clade otherwise containing *D. gymnostomum*, *D. muehlenbeckii*, *D. fuscescens*, and *D. spurium*. *D. montanum* is the basal taxon in this clade. Within this clade, moreover, *D. fuscescens* and *D. spurium* are resolved as sister taxa. Within the polytomy containing *Dicranum johnstonii*, *D. polysetum*, *D. scoparium*, and *D. lorifolium* the latter two species form a clade.

In all other cases trees obtained after successive weighting are longer than the trees obtained with equal weights when calculated against the unweighted data. Most of them support a *Dicranoloma* clade from which all species of *Dicranum* are excluded. Successive weighting on both ci and rc in the analysis with *Holomitrium* as outgroup and on rc in the analysis with *Symblepharis* however yielded trees in which the positions of *Dicranum* and *Dicranoloma* are reversed. In these trees the species of *Dicranum* form a clade that also contains *Dicranoloma fragile*. The species of *Dicranoloma* and the other genera otherwise included in the *Dicranoloma* clade form a paraphyletic group basal to the *Dicranum* clade. Within the *Dicranoloma* grade *D. menziesii* is the most basal taxon. The *Dicranoloma assimile-D. dicarpum* clade is the sister group of the *Dicranum* clade.

Trees obtained after successive weighting in the remainder of the analyses may show several differences with the ones described above for analysis 3c. The most important are the following. In many cases the Dicnemonaceae are placed outside the *Dicranoloma* clade as a sister group of *Dicranoloma armitii*. *Parisia* is often placed within the *Dicranoloma* clade, either as the sister group of *Braunfelsia*, or of *D. rugosum*, or of the Dicnemonaceae, or in a polytomy with *D. eucamptodontoides*, *D. geluense*, *D. rugosum*, and *Braunfelsia*. In one case *D. menziesii* is excluded from the *Dicranoloma* clade and placed at the base of a clade otherwise containing *Chorisodontium*, *Holomitrium*, and *Brotherobryum*. In another case *D. armitii* is included in the *Dicranoloma* clade interposed between *D. brevisetum* and the *Mesotus-Sclerodontium-Leucoloma* clade. *Dicranoloma platyloma* mostly forms a monophyletic group with *D. austroparium* and *D. serratum*. Finally, *D. geluense* and *D. rugosum* are sometimes interposed between *D. brevisetum* and the *Mesotus-Sclerodontium-Leucoloma* clade.

Discussion

The use of different outgroups and the inclusion in or exclusion from the ingroup of one or a few taxa strongly affected the number of trees, the resolution in the consensus tree and the topology. Several earlier authors observed the same effects (cf. Zander 1993, Zomlefer 1993, Hedenäs 1997, Lewinsky-Haapasaari & Hedenäs 1998). Hovenkamp (1999) demonstrated that changing a single entry in a data matrix may lead to huge differences in numbers of trees and in resolution, a fact probably experienced by many other taxonomists who discovered a mistake in their data matrix after the analysis has been performed.

The consensus tree obtained from analysis 3c was chosen to optimise the characters upon (Fig. 2), as analysis 3c is one of the two analyses with reasonable resolution in the consensus tree and of these two the one containing most taxa.

Goloboff (1993) argued that weighting should be considered an integral part of cladistic analysis. Carpenter (1988, 1994) on the other hand argued that reweighting of characters should be performed when the data set is to some degree ambiguous, ambiguity being measured by the number of trees obtained from the equally weighted data set. Hovenkamp's (1999) findings however indicate that obtaining one most parsimonious tree or only a few may give a wrong impression of unambiguity of the data. The purpose of weighting not being only to reduce the number of trees, but also to obtain a better estimate of the true phylogeny, the decision to reweight characters should therefore be made independently of the results of the equally weighted analysis (Hovenkamp 1999).

Successive weighting may lead and in the present study in many cases did lead to a set of trees that is not a subset of the set obtained with the equally weighted data. Turner & Zandee (1995) criticised Goloboff's method of parsimony analysis with implied weights, and implicitly successive weighting, among others because of this property. Although their arguments were immediately refuted by Goloboff (1995), the choice between trees from analyses with equally weighted characters and those obtained by analyses with differently weighted characters is arbitrary.

In studies with known phylogenies by Farris (1969) successive weighting almost always improved the estimate of the true tree and the strongest concave function always correctly estimated the true tree even when the number of unreliable characters was very much higher than that of the reliable ones. The analyses by Farris, however, included a constant number of reliable, fully congruent characters. When using real data, we may reasonably expect the successive weighting procedure to produce a good estimate of the true phylogeny only when the data set contains a substantial number of cladistically reliable, congruent characters (Farris 1969). This last observation also applies to analysis with equal weights.

Figure 2 shows the consensus tree of analysis 3c with equal weights, on which character state changes have been optimised. Only two characters are fully congruent with the tree. These characters support small groups of taxa that do not even belong to *Dicranoloma* or *Dicranum*. The stem (3) changes from tomentose (1) to naked (2) on the branch supporting the *Sclerodontium-Leucoloma* clade. Regular wedge-shaped multi-cellular spores (35 : 2) originate on the branch supporting the Dicnemonaceae. Two state changes in multistate characters occur only once in the trees. The *Dicranoloma assimile-D. dicarpum* clade is supported by elongate to linear upper lamina cells that are conspicuously shorter than the basal ones (13 : 2) and the clade containing *Braunfelsia* and the Dicnemonaceae is supported by collenchymatous alar cells (10 : 3). Weighting on ci does not lead to more characters being consistent with the tree. In the trees obtained after successive weighting on rc character 12 (limbidium) is congruent. In these trees the branch supporting the *Dicranoloma* clade, in which *Parisia* is included and from which the Dicnemonaceae are excluded, is supported by the presence of a limbidium. A clade containing *Dicranoloma austroscoparium*, *D. serratum* and *D. platyloma* is supported by an extremely well-developed limbidium consisting of more than 10 cell rows. The above-mentioned characters, sometimes with the exclusion characters 10 and 12 are also consistent with the trees obtained after successive weighting in the other analyses. In some trees character 17 (costa presence) is congruent with the tree, the absence of the costa being a synapomorphy for a monophyletic group containing *Parisia* and the Dicnemonaceae.

Despite the very low number of congruent characters the ensemble consistency index is within the range that could be expected from the study of Sanderson & Donoghue (1989) albeit in the lower part. In fact, Hedenas (1998) observed that the ensemble consistency indices of most of the analyses of pleurocarpous mosses evaluated by him are in the lower part of that range. The same applied to the single study of acrocarpous mosses he evaluated. The often observed higher amounts of homoplasy in mosses were attributed to a possibly higher frequency of very similar but non-homologous states of characters in mosses than in other organisms, or alternatively a lower level of understanding of morphological structures in mosses than in for instance higher plants, a possibly higher frequency of reversals or oscillations in mosses than in other groups, and the relative scarcity of unambiguous qualitative characters because of which bryologists may have to resort more often to quantitative characters (Hedenas 1998).

Considering the very low number of congruent characters and low tree stability, judging from the Bremer support values and the high sensitivity to slight changes in the taxa included, the value of the tree shown as a reconstruction of the phylogeny may be disputed. However, the relationship between support values and corroboration has not been explored and tree stability is not an aim of cladistic analyses (Kluge 1997). Low stability may not be a reason to reject the most parsimonious trees, as they are the best one can get with the

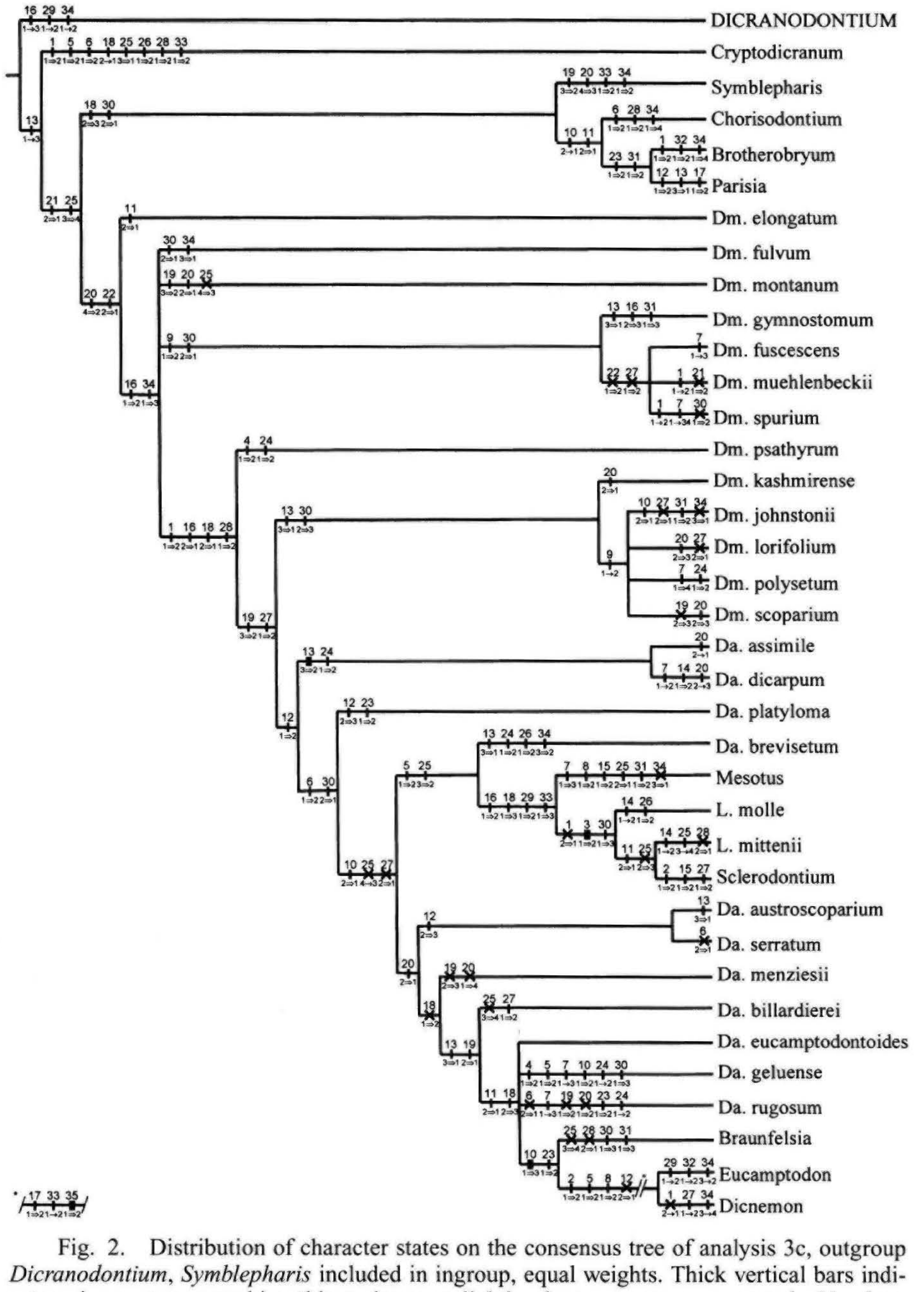

Fig. 2. Distribution of character states on the consensus tree of analysis 3c, outgroup *Dicranodontium*, *Symblepharis* included in ingroup, equal weights. Thick vertical bars indicate unique synapomorphies, thinner bars parallel developments, crosses reversals. Numbers above the symbols denote characters, figures below state changes. Double-shafted arrows indicate unambiguous character state changes, single-shafted arrows ambiguous ones. Ambiguous character state changes are optimised using delayed transformation (DELTRAN; Swofford 1993).

available data. As a depiction of morphological similarities and differences the obtained consensus tree is very useful. The following discussion is based on the tree shown in figs. 1 and 2, taking into account some of the most striking alternative topologies from other analyses.

Systematic implications

In a strictly cladistic classification, which only allows monophyletic groups, *Dicranoloma* cannot be maintained next to *Dicranum*. Both genera are paraphyletic, *Dicranum* being more basal than *Dicranoloma*. On the other hand, sinking *Dicranoloma* into *Dicranum* would not make *Dicranum* monophyletic. To obtain this many other genera would have to be sunk in *Dicranum*, which would not lead to a clearer classification. The best solution would be to split the large paraphyletic genera *Dicranum* and *Dicranoloma* into smaller, monophyletic groups, but the results of the present analysis do not yet allow this. First the diversity in the non-Malesian species of *Dicranoloma* and especially in *Dicranum* needs to be critically analysed.

Classification of Dicranoloma

I have chosen to maintain *Dicranoloma* in the circumscription of Renauld (1901, 1909). As such it is supported as a grade from which *Braunfelsia*, *Leucoloma*, *Sclerodontium*, *Mesotus*, and the Dicnemonaceae have been derived. In some of the other analyses also *Parisia* is resolved as being derived from *Dicranoloma*. The taxa in this grade are distinguished from all species of *Dicranum* by the possession of a differentiated leaf border and from most species of *Dicranum* by the single-layered alar patches. All species of *Dicranum* that can be possibly confused with *Dicranoloma* have multi-layered alar cells. This observation had already been made by T.-B. Engelmark (pers. comm.). Some species not included in the analysis lack a limbidium but still have to be assigned to *Dicranoloma*, as they are very similar to species that do have a limbidium and are therefore considered to be closely related. Among the Malesian species these are *D. braunii* and *D. bartramianum*, which are closely related to *D. brevisetum* and *D. geluense* respectively. The limbidium is interpreted to be secondarily absent in these species. In *D. braunii* a limbidium has been found in one collection among almost a thousand collections examined. Both species form large plants and have single-layered alar patches. All species of *Dicranum* with single-layered alar patches form small plants. Inclusion of *D. braunii* and *D. bartramianum* in the ingroup in analysis 3c did not affect the topology and confirmed close relationships with resp. *D. brevisetum* and *D. geluense*.

Dicranoloma sensu Norris & Koponen (1989) is resolved as polyphyletic in the trees from analysis 3c, but as monophyletic in some of the other analyses when the characters are weighted. It is not easily separable from their expanded *Dicranum*. The species included are solely characterised by an extremely strong limbidium, but some of the excluded species, e.g. *D. havilandii* Broth. and *D. rugosum* possess a limbidium almost as strong. Recognising the width of the limbidium as a separate character state may already have put too much weight on this feature. Of the other characters mentioned by Norris & Koponen, which might support a close relation to *Leucoloma* and the distinction from *Dicranum*, some are not present in all species, while others are present in excluded species as well.

In this context it may be useful to explore Renauld's intent with *Dicranoloma*, as Norris & Koponen (1989) derived from the fact that *Dicranoloma* was first classified as a subgenus in *Leucoloma* that Renauld meant *Dicranoloma* to be close to *Leucoloma*. Therefore, they selected a species they consider close to *Leucoloma* as a lectotype for their minimised *Dicranoloma*. In his account of the history of *Leucoloma*, Renauld (1909) wrote that K. Müller Halle and Bescherelle had already transferred limbate species of *Dicranum* to *Leucoloma* before he divided *Leucoloma* into subgenera (Renauld 1898). Although I could not find written evidence that this is indeed the case, Renauld must have thought they had done that and therefore, by placing these species in a subgenus of their own, must have wanted to emphasise the differences between these species and the other species of *Leucoloma*. In his 'Essai sur les Leucoloma' Renauld (1909) listed several differences between *Dicranoloma* on the one side and *Leucoloma* and *Dicnemoloma* (*Sclerodontium*) on the other: lamina uniform in *Dicranoloma*, but differentiated in chlorophyllose and membranaceous tissue in *Leucoloma* and *Dicnemoloma*; central strand present in *Dicranoloma*, but absent in *Leucoloma* and *Dicnemoloma*; costa very variable in *Dicranoloma*, but uniform in the other two genera. Renauld did not further discuss the differences between these three genera and merely stated that the first character alone is sufficient to separate them. The second character later proved not to be diagnostic.

Renauld had considerably more difficulty separating *Dicranoloma* from *Dicranum*. The only difference he found was the presence of a limbidium in *Dicranoloma*, which, he admitted, may be very narrow or even absent. He even considered the possibility of sinking *Dicranoloma*, as a subgenus, in *Dicranum*. From this he was kept by the almost non-overlapping geographical distribution of the two genera. He considered that the two genera might have been derived from a common ancestor. He did not discuss the phylogenetic relationships between *Dicranoloma* and *Leucoloma*. From the above it may be concluded that, although Renauld (1898) initially triggered the transfer of many species that are today placed in *Dicranoloma* from *Dicranum* to *Leucoloma*, which was eventually done by Brotherus (1901), he considered *Dicranoloma* to be closer to *Dicranum* than to *Leucoloma*.

Of the initial eight species Renauld (1898) classified in subgenus *Dicranoloma*, *Leucoloma serratum* Broth. and *L. austroscoparium* C. Müll. ex Broth. are the ones accepted in *Dicranoloma* by Norris & Koponen (1989). *Leucoloma platyloma* (Besch.) Ren. has a very strong limbidium and is very similar, probably even conspecific, with the New Caledonian species listed by Norris & Koponen (1990). *Leucoloma formosum* Besch. ex Ren. is an invalid name, based on one of the syntypes of *D. platyloma*. *Leucoloma sumatranum* Broth. ex Ren. is a synonym of *Dicranoloma assimile* (Dixon 1932). *Leucoloma drepanocladium* (C. Müll.) Kindb., *L. dichotomum* (P. Beauv.) Ren. and *L. scopareolum* (C. Müll.) are all conspecific with *D. billardierei* (Poitier de la Varde 1943 (as a variety), and Dixon 1916, respectively). In his 1909 publication Renauld listed many more species of *Dicranoloma* than the initial eight. He largely agreed with the list of species that Brotherus (1901) included in *Leucoloma*, *Dicnemoloma*, and *Dicranoloma* in the first edition of 'Die naturlichen Pflanzenfamilien', only commenting that some species that had been placed in *Dicranoloma* might be better classified in *Dicranum*.

Dicranoloma armitii and *D. fragile* are traditionally placed in *Dicranoloma*, but in the cladograms these species are never found among or even in the neighbourhood of the other species. The placement of these species was already questionable prior to the analysis. *Dicranoloma armitii* differs from the other species of *Dicranoloma* mainly by the immersed capsules and by peristome characters. The outer plates are thicker than the inner ones and the outer walls of the primary peristomial layer (PPL) as well as the walls of the outer peristomial layer (OPL) are incrassate as well. These form a properistome at the base of the teeth and similar fragments are attached to the upper part of the teeth. In these characters *D. armitii* agrees with *Leucoloma* which has outer plate of the peristome that are thicker than the inner ones. The species belonging to subg. *Leucoloma* have immersed capsules too. Some species of *Leucoloma* either have a properistome or the abruptly contracted leaves characteristic of *D. armitii*. However, *D. armitii* lacks the characters that separate *Leucoloma* from *Dicranoloma*. The lamina cells are uniform from the costa to the margin, the stem is densely covered with tomentum and the capsule bears stomata. For these reasons Bartram's (1938) transfer to his monotypic genus *Cryptodicranum* is accepted here.

Nevertheless, the position of *D. armitii* at the base of the cladogram is unexpected because one would expect a position somewhere intermediate between *Dicranoloma* and *Leucoloma*. The position of *D. armitii* at the base of the cladogram is fixed by the strong costa and especially the differentiated adaxial and abaxial epidermis.

Dicranoloma fragile, because of its small size and the lack of a limbidium is best placed in *Dicranum* among the species with single-layered alar patches. The costa, in which stereids are absent or very rare and all cells are approximately equally large, is more similar to that of some species belonging to subg. *Crassidicranum* than to that of any species of *Dicranoloma*. In the cladograms the position of *D. fragile* is among species of *Dicranum*, but never near any of the species of *Dicranum* with single-layered alar cells. In fact *D. fragile* seems to occupy a relatively isolated position within *Dicranum*. *Dicranoloma fragile* is transferred to *Dicranum* (under the name *D. psathyrum*).

Although *D. menziesii* is excluded from the *Dicranoloma* clade in some of the analyses after successive weighting, I see no reason to exclude this species from *Dicranoloma*. Renauld (1909), Brotherus (1928b), and subsequent authors assumed a close relation between this species and *Cryptodicranum armitii*, based on a similar habit and costal anatomy. This striking similarity was the reason for Renauld (1909) to assign *Dicranoloma armitii*, which has erect capsules, to a section that otherwise contains only species with arcuate capsules, including *D. menziesii*. Even before the peristome of *Cryptodicranum armitii* was studied, later authors (cf. Tan & Koponen 1983) discarded a close relation between the two species on account of the presence of a central strand, a much longer seta and arcuate capsules in *Dicranoloma menziesii*.

From a traditional taxonomic point of view rerecognition of *Megalostylium* and/or *Werneriobryum*, as suggested by Eddy (1988) and Norris & Koponen (1990) respectively, may be considered, as some odd elements would be removed from *Dicranoloma* and the latter genus would become less heterogenous. All species of *Dicranoloma* and *Dicranum* would then possess a central strand.

As suggested by Norris & Koponen (1990), *Werneriobryum* would at least include *Dicranoloma geluense* and *D. bartramianum*. In the context of the New Guinean or Malesian species of *Dicranoloma* these are more similar to each other than either of the two is to the other species. They share the absence of a central strand and very wide leaves with entire margins and a very narrow costa that is smooth abaxially. On the other hand the differences between the two species are also considerable. The leaves of *D. bartramianum* are longer than in *D. geluense*, have a long tapering acumen, and lack a differentiated border. Moreover, some non-Malesian species, e.g. the Tasmanian *D. eucamptodontoides* and *D. rugosum* from Tahiti, are superficially similar as well. Both have very wide leaves with entire margins and a smooth costa, but possess a central strand. In the cladogram *D. geluense*, *D. eucamptodontoides* and *D. rugosum* are placed in a polytomy that also includes a clade containing *Braunfelsia* and the Dicnemonaceae. Synapomorphies of this whole clade are entire leaf margins (11 : 1) and a smooth costa (18 : 3).

The group of species that would make up *Megalostylium* is represented in the analysis by *D. brevisetum* and is characterised with respect to other species of *Dicranoloma* by the absence of a central strand and short setae. In the cladogram these characters are synapomorphies of a clade in which *D. brevisetum* is the sister-group of the *Mesotus-Sclerodontium-Leucoloma* clade. A reversal to a longer seta occurs in the branch supporting *Sclerodontium* and *Leucoloma mittenii*. Links with other species of *Dicranoloma* are less obvious here than for the species that might be included in *Werneriobryum*. Still, I prefer not to revive either genus until all species of *Dicranoloma* have been revised.

A way to make *Dicranoloma* more homogeneous, and possibly obtain a fully nested classification would be to break up the large paraphyletic genus *Dicranoloma* into smaller monophyletic ones, but the present analysis does not yet allow this. An analysis including all species of *Dicranoloma* is needed, which means that the remainder of the species have to be revised first. Until then we are left with a heterogeneous genus consisting of a large element superficially similar to *Dicranum*, or rather the element of *Dicranum* including *D. scoparium*, and a few smaller, geographically limited, elements. The former element contains the majority of the species of *Dicranoloma* and occurs almost throughout the geographic range of the genus The latter elements include a mainly Malesian element containing species that lack a central strand and have short setae ($\leq$6 mm), a tropical northern Australian and New Caledonian element containing species with a very strong limbidium, an element containing species with very wide leaves with entire margins and a slender, smooth costa occurring in Papua New Guinea, Tasmania, and the Pacific, and an element containing *D. menziesii* and possibly related species. Additional small elements may be present among the unrevised species. Monophyly of all elements still has to be established.

The phytogeographic argument used by Renauld (1909) and Brotherus (1901) is still valid. *Dicranoloma* has a Gondwanan/Southern Hemisphere distribution, invading the Northern Hemisphere via Malesia to the Indian subcontinent, Sri Lanka, Japan and China. *Dicranum* on the other hand has a Northern Hemisphere distribution with one species reaching the Southern Hemisphere in East Africa and another one endemic to New Caledonia. Areas of overlap between the genera include East Africa, the Indian subcontinent, eastern China, Japan, Luzon and New Caledonia.

Most species can now be easily alotted to either *Dicranoloma* or *Dicranum*, using the presence or absence of a limbidium in combination with the number of cell layers in the alar patches, but some species in Brotherus' (1924) list may have to be transferred to other genera, e.g. *Dicranoloma trichopodum* (Mitt.) Broth. from New Zealand, which has been transferred from *Dicranum* to *Dicranoloma* and back (Brotherus 1901, 1924; Dixon 1913; Sainsbury 1955; Scott & Stone 1976), but belongs to neither genus. The leaves are intermediate between *Dicranoloma menziesii* and *Holomitrium*, the sporogone features are more similar to those of *Holomitrium* but the perichaetia are short. Many other species have already been transferred to other genera.

Dicranum and other genera

The data matrix was designed and characters were selected to study the relationship between the genera *Dicranum* and *Dicranoloma*. Clarification of the relationships within *Dicranum* was not the main aim of the analysis. The species of *Dicranum* included were selected to cover the variation within *Dicranum*, but as this variation was only studied in a limited number of species based on existing classifications that are either rather coarse or may be applied to species from a restricted area only, it is not certain that all relevant variation has indeed been covered. Therefore the results of the analysis may not give a complete picture of the relationships within *Dicranum*. Likewise, the other genera were included merely to test a possible relationship with *Dicranoloma*. Therefore, the following remarks are merely observations which are made in order to draw attention to questions which cannot be fully answered yet.

In the cladogram *Dicranum* is resolved as paraphyletic, basal to the *Dicranoloma* clade. The species belonging to sect. *Dicranum* are grouped together with the Asian species of subg. *Dicranum* and one of the two species included of subg. *Pseudochorisodontium*, in a clade that is the sister group of the *Dicranoloma* clade, the *D. kashmirense-D. scoparium* clade. Synapomorphies of this clade are upper lamina cells that are similar in length to the basal ones (13 : 1) and the absence of a differentiated annulus (30 : 3). Within this clade the *D. johnstonii-D. scoparium* clade is supported by multi-layered alar patches (9 : 2). In *D. kashmirense* the alar patches are either single-layered or two-layered.

The *D. gymnostomum-D. spurium* clade is always present, supported by multi-cellular alar patches (9 : 2) and persistent annulus cells (30 : 1; reversed to deciduous (2) in *D. spurium*). The placement of *D. gymnostomum* at the base of this clade is a bit odd as it is superficially more similar to species of the *D. kashmirense-D. scoparium* clade and moreover shares with those species upper lamina cells that are as long as the basal ones. The placement of *D. gymnostomum* outside the latter clade is caused by the differentiated annulus. Of the species of *Dicranum* with single-layered alar patches, *D. elongatum* is placed at the base of the *Dicranum* grade and *D. fulvum* and *D. montanum* are either placed at the base of the *Dicranum* grade or basal to the *D. gymnostomum-D. spurium* clade.

Of the subgenera in Brotherus' (1924) classification, subg. *Pseudochorisodontium* has been resolved as polyphyletic. Subg. *Dicranum* has been resolved as paraphyletic and is almost as heterogeneous as the genus as a whole. Nothing can be said about the monophyly of subg. *Crassidicranum* and *Orthodicranum* as they were each represented by one species only. Also, nothing can be said of Nyholm's (1986) infrageneric classification, all but one sections being represented by one species only. However, as the sections seem to be rather homogeneous, that classification seems promising if it can be extended to include also species occurring outside Europe and North America. Monophyly of the sections, however, still has to be demonstrated.

If, after the phylogeny of *Dicranum* is better known, the relationship between *Dicranum* and *Dicranoloma* remains the same and one wishes to keep *Dicranum* as a large genus divided in sections or subgenera, *Dicranoloma* must be placed as a subgenus or section within *Dicranum*. At this stage this would be premature. Alternatively, one could raise the infrageneric groups to genera and restrict *Dicranum* so as to include only *D. scoparium* and related species.

In accordance with the results of La Farge-England (1998) monophyly of a clade containing *Leucoloma* and *Sclerodontium* is supported by all most parsimonious trees. This is one of the few clades that is relatively well supported (3 character state changes in the accepted cladogram). In the tree shown (figs. 1, 2), *L. mittenii* is placed in a monophyletic group with *Sclerodontium*. In the trees obtained from some of the other analyses after successive weighting *L. molle* and *L. mittenii* are placed together in a clade. Therefore, the fact that *Leucoloma* is not monophyletic in the tree shown should not be construed as a refutation of La Farge-England's cladogram, which shows a basal split between *Sclerodontium* and *Dicranoloma*, as her monophyletic *Leucoloma* was supported by extra characters not included in the present analysis.

Mesotus is placed basal to the *Leucoloma-Sclerodontium* clade. The *Mesotus-Sclerodontium-Leucoloma* clade is supported by four character state changes. This is partly in agreement with Allen (1987b) who considered *Sclerodontium* to be the genus most closely related to *Mesotus*, but in disagreement with La Farge-England (1998) whose preliminary (not published) analyses indicated a closer relationship with *Holomitrium*. Synapomorphies of the *Mesotus-Sclerodontium-Leucoloma* clade are papillate upper lamina cells (16 : 2), smooth costa (18 : 3), capsules without stomata (29 : 2) and peristomes with the outer plates thicker than the inner ones (33 : 2). Characters that indicate a possible relationship with *Sclerodontium* are irregularly-shaped upper lamina cells that descend along the margins. In many species of *Holomtrium* upper lamina cells descend along the margins as well, but the split peristome teeth and the outer peristomial plates and trabeculae being thicker than the inner ones are contra-indicative of a close relationship with this genus. Short setae and mitrate calyptrae are shared with *Leucoloma* subg. *Leucoloma*. The uniqueness of *Mesotus* is emphasised by its cladocarpous condition.

In the cladogram, *Braunfelsia* is placed as sister group of the Dicnemonaceae, based on collenchymatous alar cells (10 : 3) and long sheathing perichaetial leaves (23 : 2). The *Braunfelsia*-Dicnemonaceae clade is placed in a polytomy with the broad-leaved species of *Dicranoloma*, *D. eucamptodontoides*, *D. geluense*, and *D. rugosum*. *Braunfelsia* was prior to the analysis assumed to be most closely related to *D. billardierei*, based on the long tapering leaves, the long upper lamina cells and the anatomy of the costa. Collenchymatous alar cells are also found in some collections of *D. billardierei* from New Caledonia and the Solomon Islands and in *D. blumei*, another assumed relative of *D. billardierei*.

Brotherobryum appears to be more closely related to *Holomitrium* than to *Dicranoloma*. In all analyses in which *Holomitrium* was included, *Brotherobryum* and *Holomitrium* are resolved as sister groups. *Holomitrium* and *Brotherobryum* share entire peristome teeth with a papillose ornamentation. Moreover, both genera have a strong nerve with well-developed stereid layers and a differentiated epidermis adaxially, as well as abaxially, long sheathing perichaetial leaves and a similarly shaped capsule with its largest width just above the base and narrowing towards the mouth.

A close relationship between *Braunfelsia* and *Brotherobryum*, suggested by Allen (1984) and Fleischer (1914, 1923), is not supported by the results of the analysis. Characters brought forward by Allen (1984) to support such a relationship include sporogones with long setae and smooth, cylindrical, slightly curved capsules having two to three rows of differentiated dark red, isodiametric cells below the mouth, a trend towards the eperistomate condition, perichaetial leaves that conspicuously sheath the seta, and entire, elimbate leaves. Of these, the long setae, slightly curved capsules and differentiated exthecial cell near the capsule mouth and the long sheathing perichaetial leaves occur in many species of *Dicranoloma* as well. In my opinion *Braunfelsia* does have a limbidium. A trend towards the eperistomate condition may be present in *Brotherobryum*, but reduction of the peristome appears to have occurred several times independently among the species included in the analysis.

A close relationship between *Parisia*, *Brotherobryum*, and *Braunfelsia* has been suggested by Allen (1986a) and Fleischer (1923). *Parisia* shares with *Brotherobryum* and *Parisia* an erect and densely foliate habit, a rudimentary peristome, strongly incrassate upper lamina cells, and a similar internal stem anatomy with a cortex consisting of thin-walled cells. The strongest link with *Braunfelsia* is that *Braunfelsia* also includes a species that lacks a costa. With both genera it shares long sheathing perichaetial leaves. The hyaline hair-point, which is not formed by the costa, is unique in *Parisia*. A hair-point is also found in *Sclerodontium*, but there it is the excurrent part of the costa. In the cladogram shown *Parisia* is placed as a sister group to *Brotherobryum*, but in the trees obtained by some of the other analyses it is placed in the *Dicranoloma* clade as a sister group to either *Braunfelsia* or the Dicnemonaceae. One of the reasons for the ambiguity of *Parisia* is that several characters could not be scored, because it lacks a costa. Another might be the coding of the characters concerning the costa used. When interpreted as the sister group of *Brotherobryum* it is placed in a clade containing species with a strong costa with well-developed stereid-layers and differentiated epidermis, which is lost along the branch leading to *Parisia*. When *Parisia* is placed as a sister group to either *Braunfelsia* or the Dicnemonaceae in the *Dicranoloma* clade, what is lost along the branch leading to *Parisia*, or a clade containing *Parisia*, is a very slender costa with not more than the minimal single layer of stereids cells. Although the cost for these losses is equal, the latter seems more likely. Therefore I have a slight preference for derivation of *Parisia* from *Dicranoloma* stock.

Allen (1987c) assumed that the Dicnemonaceae have been derived from the same element with a very slender costa in *Dicranoloma*. Again, the results of the various analyses are ambiguous with respect to the position of the Dicnemonaceae. In the cladogram shown the Dicnemonaceae are placed as sister group of *Braunfelsia* in a polytomy containing the broad-leaved species of *Dicranoloma* with slender leaf nerves, but in trees obtained in some of the other analyses it is placed as the sister group of *D. armitii*. The observations made concerning the coding of the characters of the costa for *Parisia* apply to the Dicnemonaceae as well. Moreover, the branch leading to the Dicnemonaceae is a very long one, which may obscure the relationships with other groups. Also in this case I find derivation from *Dicranoloma* likely.

Finally, *Chorisodontium* looks like a *Dicranoloma* with a strong nerve. In the cladogram, however, *Chorisodontium* is resolved as part of a clade otherwise containing *Brotherobryum*, *Parisia*, and *Symblepharis*, but when *Holomitrium* is included in the ingroup *Chorisodontium* is placed basal to the clade containing that genus and *Brotherobryum*. Its position in the cladogram is fixed by the strong nerve with well-developed stereid-layers and differentiated epidermis and its isodiametric upper lamina cells.

MORPHOLOGY

The following account of the morphology refers to the Malesian species of *Dicranoloma* and *Cryptodicranum armitii* and *Dicranum psathyrum*, species that were traditionally classified in *Dicranoloma*, but were transferred to other genera after the cladistic analysis.

Male plants

The species of which antheridia are known are all dioicous, mostly pseudoautoicous. All have dwarf males, which are up to 2.5 mm tall and grow on the stems of female plants. They have a persistent protonema with which they adhere to its tomentum.

Their stems are very short, single or subflorally branched, tomentose only at the base and bear only a few leaves, that are up to 1 mm long or slightly longer and ovate-lanceolate or ovate-linear. The margins are entire or minutely serrulate in the upper half; a narrow limbidium may be present. The costa is faint and mostly discernible only in the upper part of the leaf. The plants bear up to four globose perigonia. The perigonial leaves are slightly shorter than the longest stem leaves and much wider, being very broadly ovate with an acute or acuminate apex. The perigonia may contain 2-4 ellipsoid antheridia. Paraphyses are absent or scarce, filamentous and slightly longer than the antheridia.

Occasionally, somewhat dwarfed plants growing on female plants may reach lengths up to 2.5 cm and have slightly longer leaves and a better developed costa and limbidium. As perigonia or perichaetia have not been found, their sexual condition could not be established.

Males as large as females have been found once in *Dicranum psathyrum* and *Dicranoloma cutlackii*. These plants are indistinguishable from female plants. Their perigonia are similar to perichaetia, but shorter and contain up to 10 antheridia, which are several times longer than those in the dwarf males and are intermingled with many paraphyses. The perigonia are terminal, but soon laterally displaced by subfloral innovations. The perigonia are often situated close together, because the innovations bearing the second and subsequent perigonia can be very short.

Before, the only observations on male plants of *Dicranoloma* were published by Ramsay (1985). She studied the Australian species *D. billardierei*, *D. dicarpum*, *D. menziesii*, and *D. serratum*. In *D. dicarpum* and *D. menziesii* both tall males and dwarf males occur.

The tall males were distinct from the females. In mixed spore cultures male spores germinated and matured earlier than female ones, some of them yielding antheridia within 3–8 months. Plants morphologically similar to adult females were formed about one year later and did not produce archegonia within the two years the experiments lasted.

On these grounds Ramsay (1985) speculated that possibly the growth of female plants is inhibited by the male plants. At the same time she speculated that in the field the presence of the female plant, rather than inhibiting growth of male plants, resulting in the production of dwarf males, perhaps encourages growth of dwarf males at the expense of female spores. Single spore cultures of both male and female spores and spore cultures in the presence of female plant extract are needed to confirm these speculations.

Of the four species of *Dicranum* studied by Briggs (1964) *D. fuscescens* has males as large as the females, *D. majus* forms dwarf males only, the males of *D. scoparium* are either dwarfed or as large as the females, and *D. bonjeanii* has males of varying sizes.

Briggs considered male dwarfness to be genetically determined in *D. majus* because males as large as females were never found. He apparently did not manage to grow dwarf males from spores, but the dwarf males from one of his collections, when cultivated, continued to produce dwarf leaves for five months. On the other hand, dwarf males from a collection of *D. scoparium* which contained both dwarfed and tall males, grew into tall male plants under cultivation. Briggs postulated a great deal of phenotypic plasticity in the size of male *D. bonjeanii*.

The phenomenon of male dwarfness has been best studied in the genus *Macromitrium* (Orthotrichaceae) (Ernst-Schwarzenbach 1939, Une 1985). *Macromitrium* contains both monoicous and dioicous species, the dioicous species being dimorphic. Moreover, both isosporous and anisosporous species occur. Une (1985) proved that male dwarfness is genetically determined in anisosporous species, while in isosporous species it seems to be regulated by phytohormones. While the small spores from anisosporous species in culture consistently developed dwarf males, male spores of isosporous species only did so in mixed spore cultures or when the phytohormone auxin was added to the medium. Otherwise tall males were formed. In *Dicranoloma* all species are isosporous.

Life form

The life form, as defined by Mägdefrau (1982), is mostly a tall turf (classifications of Mägdefrau 1982, Richards 1984). Frequently pendulous stems are formed. These do not conform to pendants, i.e. with a creeping primary stem, hanging secondary stems and many short horizontal lateral branches. Initially in *Dicranoloma* always a turf is formed, but long stems may become pendent by lack of support, e.g. when the plants grow on tree branches or vertical surfaces. Very large masses may be formed in some species. In humid parts of tropical mountains of East Africa, *Dicranoloma billardierei* is known to form masses with a diameter of more than two meters (Frahm 1993). If much water is absorbed these may become so heavy that the branch on which they grow breaks and a terrestrial moss ball is formed, which may become so heavy that a single person cannot carry them (Frahm 1993). *Dicranoloma rugifolium*, and to a lesser extent also *D. reflexum* and *Cryptodicranum armitii*, form large cushions (definition of Richards 1984).

Growth form

Branching is sympodial, mostly by subperichaetial innovations. Frequently, two innovations arise below a perichaetium, making the plant forked. Occasionally innovations are formed near the stem base. In some species this occurs more frequently than in others.

In La Farge-England's (1996) scheme combining growth direction, branching pattern and perichaetial position, *Dicranoloma*, or rather *D. blumei*, is classified as plagiotropic, monopodial, and acrocarpous. The diagram exemplifying this combination (La Farge-England's fig. 2n) shows both sympodial and monopodial branching and I doubt whether monopodial branching does occur in *Dicranoloma* at all. It seems to me that all main axes potentially bear perichaetia and are of the same order. Moreover, although the stems are frequently pendent, growth direction is basically orthotropic. Also Meusel (1935) used the word monopodial in connection with the Dicranales, but he used it in the context of periodicity rather than branching pattern. Monopodial in this context seems to be synonymous with 'Fortwachsend' and means that the old stem may continue its growth during several growth seasons until terminal gametoecia are formed, while sympodial means that each new growth period an innovation is formed. In either case a heteroblastic series of leaves is formed.

Stem

Stem anatomy, especially the presence or absence of a central strand, is of systematic importance in *Dicranoloma* (Fig. 3). Of the six informal groups circumscribed in the previous section three possess a central strand, a narrow column of linear, very narrow, thin-walled cells in the centre of the stem. Among them, most species in the group around *D. assimile* and *Dicranum psathyrum* have thin-walled cortical cells and a relatively abrupt transition between the inner cortical cells, which make up the largest part of the stem, and the much narrower and more incrassate outer cortical cells which make up the outer 1–4 layers. Among the group consisting of *Dicranoloma billardierei* and *D. blumei*, the former has rather thick-walled cortical cells and the latter has very thick-walled ones. The transition between the inner cortical cells and the peripheral layers is gradual. All species lacking a central strand, except *Dicranoloma geluense*, have thick-walled cortical cells.

A trend towards increasing epiphytism in *Dicranoloma* is weakly correlated with loss of internal differentiation in the stem and a trade-off between internal water conduction and strength of the stem. The fact that such a relation is not clear at first inspection might be explained by assuming that the loss of the central strand and the change from thin-walled to thick-walled cortical cells have occurred several times independently as is suggested by the cladogram.

Epidermal cells of the costa are elongate to linear and rectangular in surface view.

Rhizoids

Rhizoids are present in all species. Their initials are found just below the insertion of the leaves, mostly 3–5 under each leaf. The rhizoids are uniseriate and strongly branched, brown at the base, colourless and transparent at the tips. The tips are often slightly papillose, but older cells have mostly lost this ornamentation. In *Dicranoloma bartramianum* and *D. geluense* the rhizoids may be pinkish or colourless throughout. Most species have

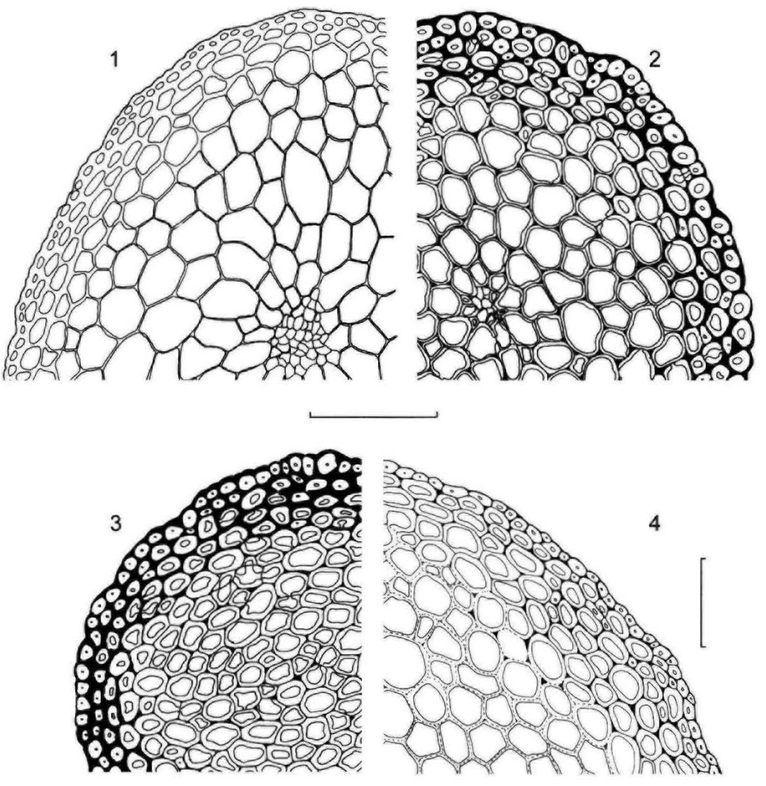

Fig. 3. Cross sections through the stem.—1. *Dicranoloma reflexum*, Agung, Kruijer & Kessler 941153 (L); 2. *D. billardierei*, Streimann 13579 (CBG); 3. *D. braunii*, Akiyama c-8795 (L); *D. geluense*, Norris 65752 (L)

densely tomentose stems, but in *Dicranoloma blumei* the stems are naked to laxly tomentose.

Gemmae

Two types of gemmae are found. Brown or colourless gemmae that arise at the tips of rhizoids are found in *Dicranoloma bartramianum*, *D. daymannianum*, *D. geluense* and, rarely, in *Dicranum psathyrum*. These gemmae are uniseriate and filamentous to club-shaped. The gemmae themselves are mostly unbranched, but the rhizoids on which they are borne are heavily branched. Thus, many gemmae may be borne on a single rhizoid. Newton & Mishler (1994) classified this type as "rhizoidal gemmae". In the species mentioned above they may be found in all parts of the stem but usually near the base.

A different type of gemmae is found in *Dicranoloma braunii* and *D. brevisetum*. These arise near the base of the rhizoids and often replace these. They are orange-brown or, occasionally, colourless, uniseriate, filamentous, mostly unbranched and are borne near the apex of the shoots. In *D. braunii* they may form very large clusters arising from initials in several subsequent metamers and completely replace the rhizoids. The number of initials per metamer is much higher than in the other parts of the stem. In *D. brevisetum* the gemmae are solitary or form small clusters.

Newton & Mishler (1994) classified these gemmae in *Dicranoloma* as "stem gemmae" that should be directly inserted on the stem or borne "on short branches apparently derived from cortical cells. The basal part of these gemmae, however, is typically rhizoidal with oblique cross walls. This is easily overlooked in large clusters of gemmae, but where the density of the gemmae is less high rhizoids can be found that partly develop into a gemma, the other part being more rhizoid-like. Therefore, the gemmae of *D. braunii* and *D. brevisetum* either should be classified as "rhizoidal gemmae", or the definition of the two categories should be adapted to the situation in *Dicranoloma*.

Newton & Mishler classified "rhizoidal gemmae" as diaspores formed on rhizoids and tomentum and "stem" gemmae as modified protonemata. These latter gemmae sensu stricto also include gemmae originating from leaf cells or costa cells. It may be noted that rhizoids can arise at the same places, sometimes in the same species that develop gemmae.

Axillary hairs

Axillary hairs were only found near the stem apex. They seem to have no systematic importance in *Dicranoloma* as they vary in length only. They are filamentous and uniseriate, up to 0.8 mm long and consist of up to 15 cells. Most cells are elongate to linear, colourless and smooth. The basal 1–3 cells are isodiametric to oblong and may be slightly brownly tinged. Mostly two axillary hairs are found at each side of the costa above leaf insertion.

Leaves

In species of *Dicranoloma* the leaves are similar in size to or slightly smaller than the leaves of the larger Dicranums (belonging to *Dicranum* sect. *Dicranum*) with the exception of *D. daymannianum* in which the leaves are much smaller. The leaves are mostly gradually tapering towards the apex, but in *Dicranoloma geluense* the apex is acute. In *Dicranoloma steenisii* the upper part of the leaf consists mainly of the costa.

In *Cryptodicranum* the leaves are abruptly contracted to a subula consisting mainly of the costa, like in *Dicranoloma steenisii*. In *Dicranum psathyrum* the leaves are much smaller than in most species of *Dicranoloma*.

Alar patches are very distinct in all species. They are single-layered, more or less triangular, colourless or yellowish to brown and mostly do not reach the costa, from which they are then separated by basal juxtacostal cells which are tainted yellowish or brownish. The alar cells are quadrate to rectangular. The thickness of the cell walls and the presence of inflated cells are of systematic importance.

The margin is rarely entire throughout. Mostly at least some minute teeth are present at leaf apex and often the upper half of the leaf is serrate. The size of the teeth and their cells and the shape of the marginal cells between the teeth are often diagnostic.

The limbidium reaches from the alar patches to the dentate part of the leaf. Its width varies from 1 to more than 10 cell rows. Narrow limbidia may be interrupted. Broad ones form a conspicuous colourless border. The limbidium cells are linear, narrow, and have incrassate walls lacking pits and a very narrow lumen. A limbidium is absent in *Dicranoloma* *braunii*, *D. bartramianum*, and *Dicranum psathyrum*. *Cryptodicranum armitii* rarely has an ill-developed limbidium.

The basal lamina cells are elongate to linear and have pitted walls. The wall lumen ratio constitutes an important difference between *Dicranoloma assimile* and *D. arfakianum*. In the species descriptions the lumen wall ratio is measured as the quotient between the width of the lumen the thickness of the wall. Tan & Koponen (1983) and Tan & Mohamed (1990) attached some significance to the arrangement of the basal lamina cells (see discussions under *Dicranoloma braunii* and *D. brevisetum*), but this is not corroborated by this study, and was already questioned by Eddy (1988). In general, wide leaves show a less regular cell pattern than narrower ones.

In some species the upper lamina cells are similar in size and shape to the basal ones, but in others they differ. Dixon (1913) considered the areolation of the upper lamina, among the most useful characters for separating *Dicranoloma* species from New Zealand, although "inconstancies" may occur in the thickness of the cell walls and the degree of porosity. Among the Malesian species the size and shape of the upper lamina cells is of great diagnostic value as well. *Dicranoloma assimile*, one of the most variable species, can almost always be recognised by its more or less vermicular upper lamina cells that are conspicuously shorter than the basal ones. *Dicranoloma cutlackii* can be distinguished from *D. brevisetum* by the presence of many oblong upper lamina cells among linear cells that are as long as the basal lamina cells.

A scheme indicating the position of the different cells in the leaf is given in Fig. 4.

Costa

The costa is well-marked in the largest part of the leaf, but is often ill-marked between the alar patches and mostly ends a few cells below the apex. Its width and thickness are extremely variable among the species, with the width varying from 20 to 160 μm and the thickness from 20 to 70 μm in the species studied for the present revision. The distal part of the abaxial costa surface may either be smooth or furnished with teeth or prorate cells, which are either scattered or arranged in rows. The arrangement of teeth is of systematic importance. The scattered prorate cells on the abaxial surface of the costa of *Dicranoloma billardierei* constitute the best character to distinguish this species from *D. assimile*.

The number of guide cells ranges from two (rarely one) to twelve. Adaxially of the guide cells lie one to four layers of stereids. Among these may be some cells with a distinct lumen, mostly adjacent to the guide cells. In some species this suggests the presence of two layers of guide cells. Abaxially the same number of cell layers is found. These layers consist entirely of stereids or they are mixed with cells with a distinct lumen. In extreme cases the latter cells form ribs and divide the stereids in three to five bundles. A differentiated epidermis, at one or both sides of the costa, is found in *Dicranoloma daymannianum*, *D. steenisii*, and *Cryptodicranum armitii*. In these species the epidermis consists of cells with a distinct lumen. In several other species some cells of the outermost layer have a distinct lumen. In *Dicranoloma cutlackii* the guide cell layer is mostly poorly developed and the costa consists of a mixture of stereids and cells with a distinct lumen. In *Dicranum*

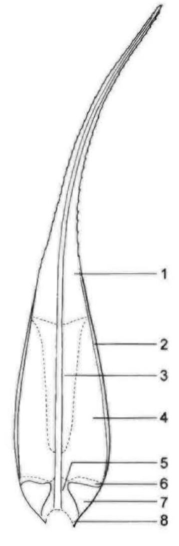

Fig. 4. Schematic drawing of leaf with position of cell types mentioned in the descriptions indicated. — 1. upper lamina cells; 2. limbidium: marginal cells; 3. juxtacostal cells; 4. basal lamina cells; 5. basal juxtacostal cells; 6. supra-alar cells; 7. alar patch: alar cells; 8. decurrency cells.

psathyrum guide cells are not differentiated at all. Its costa consists entirely of cells with a large lumen, sometimes mixed with some stereids abaxially at the sides.

Renauld (1909) recognised the systematic importance of the anatomy of the costa in *Dicranoloma* and described four types. The toxoneuron type was described as multi-layered, wide and in transverse section arch or crescent shaped. This type has 8–14 guide cells and several layers of stereids a both sides. A typical toxoneuron type costa is found e.g. in *Cryptodicranum armitii* (Fig. 37.8). The leptoneuron type costa is three-layered, consisting of a single layer of guide cells and a layer of stereids at both sides. This type of costa is narrow and in transverse section flat and scarcely thicker than the lamina. The number of guide cells is two. A costa of the leptoneuron type is found e.g. in *Dicranoloma blumei* (Fig. 15.8–9). According to Renauld (1909) this type is found in the largest number of species of *Dicranoloma*, but he also admitted species with four guide cells, which are better assigned to the next type. Most species he listed are now considered synonyms of *D. billardierei*. The heteroneuron type is intermediate between the former two, being three or more layered, intermediate in width and in transverse section flat or slightly convex at the abaxial side. *Dicranoloma assimile*, among others, has a costa of this type (Fig. 9.8–9). The cyrtoneuron type is intermediate in width, trapezoid in transverse section and ribbed on the abaxial side. The number of guide cells given by Renauld is four, but this is not in accordance with the species in his list. The layer of guide cells forms an arc. At the abaxial, convex side of the arc are 2–3 cells with a distinct lumen, dividing the stereid layers in bundles. Renauld considered these cells guide cells too and stated that the guide cells form an "X". A cyrtoneuron type costa is found e.g. in *Dicranoloma dicarpum* (Fig. 25.7).

Dixon (1913) also recognised the importance of the structure of the costa, but observed that Renauld's types should not "be looked upon as representing clearly defined and distinct groups of species, but rather as marked points in an intergrading series of types of structure". In this context he furthermore observed that the basal part of the costa could show another type than the upper part, giving as an example *Dicranum scoparium*, which, according to Dixon (1913), is "toxoneuron" in the basal part and "cyrtoneuron" in the upper part. Even if the system of Renauld (1909) is interpreted in this way it does not do justice to the variation present. Especially among the species that should be assigned to the toxoneuron and heteroneuron types there is a lot of variation not accounted for. For example, the "toxoneuron" costae of *Cryptodicranum armitii* and *Dicranoloma steenisii* are very different from the costa of the same type in e.g. *Dicranoloma platyloma*. The former two have 3–4 layers of stereids at both sides and are convex at both sides or convex abaxially and plane adaxially, while the latter has only two layers of stereids and is either plane at both sides or concave adaxially and convex abaxially, i.e. with the adaxial and abaxial surfaces parallel in either case.

Allen (1986b, 1987a) used the classification of Kawai (1968) in his publications concerning *Dicranoloma bartramianum* and *D. geluense*. I have not used this classification as the tissues are termed after their topology, rather than after the cell types present and layers with the same topography may contain very different cell types. If a typification is wanted, Renauld's system is preferred.

In the descriptions of the species I have described the costa in detail instead of indicating costa types.

Perichaetia

Perichaetia are terminal, but often laterally displaced. Sometimes this phenomenon is so inconspicuous that the perichaetial position might erroneously be interpreted as pleurocarpous, as has happened in the case of *Dicranoloma geluense* (Herzog 1909).

The perichaetial leaves are similar to the stem leaves, but have a clasping basal part in the outer perichaetial leaves and a sheathing one in the inner ones. Above the base the leaf is more or less abruptly contracted into a subula. This contraction is most pronounced in the inner perichaetial leaves. In *Dicranoloma brevisetum* the perichaetial leaves vary from abruptly contracted to gradually tapering, while in *D. cutlackii* the perichaetial leaves always are gradually tapering, like the stem leaves.

Proceeding from the outer perichaetial leaves to the inner ones the alar patches become increasingly less pronounced, the supra-alar transition area between the alar cells and basal lamina cells becomes increasingly wider, and the regions of basal and upper lamina cells move up a bit.

The characters of the perichaetial leaves are not diagnostic among the Malesian species of *Dicranoloma*. Outside Malesia, however, some species, e.g. *Dicranoloma platyloma*, from New Caledonia, and *D. fasciatum* Hedw., from New Zealand, have perichaetial leaves that are much longer than the stem leaves. In these species the perichaetium forms a long conspicuous sheath reaching to the theca or almost so. In Malesia a very long sheathing perichaetium is a diagnostic character of *Braunfelsia*, which is vegetatively very similar to some species of *Dicranoloma*.

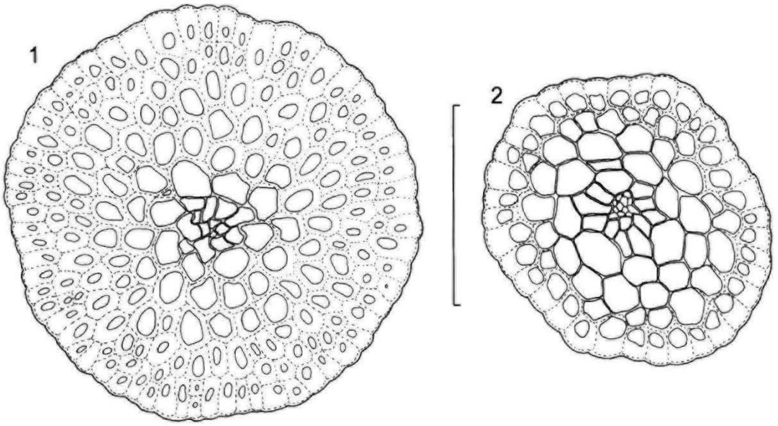

Fig. 5. Cross sections through the seta. — 1. *Dicranoloma assimile*, Hoogland 9451 (L); 2. *D. brevisetum*, Noerta & Soekar 2014 (L).

Sporogones

The sporogones are either solitary or aggregated, which, unlike in *Dicranum*, is of systematic importance above the species level in *Dicranoloma* (see previous section). Most species with aggregated sporogones have two to four sporogones per perichaetium, but there are often many more (up to eight) in *Dicranoloma arfakianum* and *D. dicarpum*.

Seta length is very variable and sometimes diagnostic, but never between otherwise very similar species. The shortest setae, with a length of less than 2 mm, are found in *Cryptodicranum armitii*. In the group containing *Dicranoloma braunii*, *D. brevisetum*, *D. cutlackii*, and *D. steenisii* seta length varies between 1.5 and 6 mm with slight differences in range between the species. In the group containing *Dicranoloma billardierei* and *D. blumei* and in the group around *D. assimile* much longer, up to 36 mm long, setae are found. In *Dicranoloma blumei* an especially wide range in seta length is found (see discussion under that species). The remaining species have setae which are intermediate in length. Seta length was measured from the tip of the vaginula to the base of the theca.

Two types of seta structure are encountered (Fig. 5). In one type the cortical cells become slightly smaller and more incrassate from the central strand outward. The walls of the outermost layer are not conspicuously thicker than those of adjacent layers. This type is encountered in the majority of the species of *Dicranoloma* and in all species of *Dicranum* studied for the cladistic analysis. In the other type the cortical cells are thin-walled, but the outermost layer forms an epidermis consisting of cells with strongly incrassate walls. *Cryptodicranum armitii* and the species in the group around *D. brevisetum* have this type of seta anatomy. The same anatomy is found in *Leucoloma* subg. *Leucoloma*.

The capsules are ovoid to cylindrical and vary in length from 1–5 mm. In general the shortest capsules are found in species with short setae and the longest ones in species with long setae. The capsules are straight or arcuate; species with short setae always have straight capsules. Cernuous or arcuate capsules may have a struma.

The exothecial cells vary from anywhere between isodiametric to linear and are irregular in shape to rectangular. They are mostly not arranged in longitudinal rows. In general, longer capsules have a more regular cell pattern. The exothecial cells may be arranged in rows at the convex side of long, arcuate capsules. In cross section they are rectangular to slightly keyhole-shaped and the anticlinal axis is longer than the periclinal one. The walls are more or less equally thickened. A few rows near the capsule mouth consist of more or less quadrate cells that are smaller than the other exothecial cells. Superficial stomata are always present at the base of the capsule.

A differentiated annulus is present in all species in which this character could be studied. According to Allen (1986b), *Dicranoloma geluense*, in which the character could not be studied, lacks a differentiated annulus. The annulus consists of two to three layers. In surface view the annular cells are quadrate to rounded. In longitudinal section they are rectangular with the longest axis anticlinal. The outer periclinal wall and especially the outer parts of the anticlinal walls are strongly incrassate. The annular cells are whitish whereas the adjacent cells are yellowish, brownish or reddish. The annulus initially remains attached to the capsule after the operculum is shed. In some species it is quickly lost and termed deciduous. In other cases it may remain attached to the capsule for a long time and can be observed in senile capsules; in that case they are termed persistent. These probably do not constitute distinct states but a more or less continuous series, which cannot be observed in herbarium material alone.

The peristome is inserted just below the orifice and consists of equally long deeply split teeth. Below the split they are often fenestrate. A difference between *Dicranoloma* and *Dicranum* on the one side and *Cryptodicranum* on the other is found in the relative thickness of the inner and outer plates. In the former genera the inner plates, formed by the inner peristomial layer (IPL), are much thicker than the outer ones, formed by the primary peristomial layer (PPL), while in the latter it is the other way around. Likewise, in *Dicranoloma* and *Dicranum* the inner trabeculae are the thicker and more strongly projecting ones, whereas in *Cryptodicranum* the outer ones are thicker.

The ornamentation of the peristomial plates is of some diagnostic value. In *Cryptodicranum armitii* the teeth are entirely smooth. In all other species at least the upper part of the teeth is papillose on both sides. In most species the inner plates are smooth in the basal half of the teeth. The ornamentation of the outer plates in the basal part of the teeth is variable between the species.

The operculum is obliquely rostrate above a conical base in all species of *Dicranoloma* and *Dicranum*. In *Cryptodicranum* the rostrum is shorter and often straight.

Calyptra

The calyptra is cucullate, with an entire to slightly lacerate lower margin. The upper part is often slightly rough because of prorate cell ends. In *Dicranoloma* and *Dicranum* the calyptra reaches to halfway the theca or farther down, whereas it just covers the operculum in *Cryptodicranum*.

Spores

The spores are unicellular, spherical and finely papillose. Spore size varies mostly between 15 and 40 μm, but many larger spores are found in *Dicranoloma reflexum*. In *Dicranum geluense* the spores are much larger and often ellipsoid rather than spherical. This observation might however be unreliable, as only a few spores could be measured from a single old capsule, the same one from which spores were measured by Herzog (1909), and spores which remain in the capsule after most spores have been shed often are larger.

Taxonomic Treatment

Key to the Malesian species of *Dicranoloma*, *Cryptodicranum* and *Dicranum*

1. Central strand absent 2
— Central strand present 8
2. Abaxial surface of costa smooth throughout; margin serrulate at extreme apex only; costa 20–60 μm; guide cells 2–3 3
— Abaxial surface of costa toothed distally; margin serrate in the upper half or farther down; costa at least 50 μm wide; guide cells 4–12 4
3. Limbidium present, leaves ovate, 4.5–7.5 mm long . . . . 11. *D. geluense*
— Limbidium absent, leaves ovate-lanceolate, (6.5–)10–13 mm long . . . . 3. *D. bartramianum*
4. Lamina cells of the acumen 10–25 μm long; leaves very abruptly contracted to a long setaceous acumen . . . . 16. *C. armitii*
— Lamina cells of the acumen 20–150 μm long, mostly much longer than 25 μm; leaves gradually tapering or more or less abruptly contracted, but then the acumen not setaceous and having a well-developed lamina 5
5. Costa almost entirely forming the upper half of the leaf; upper lamina consisting of a few cell rows only; guide cells 7–11 . . . . 15. *D. steenisii*
— Upper lamina at least as wide as the costa; guide cells 4–7(–8) 6
6. Leaf apices firm; costa with a well defined layer of guide cells; upper lamina cells all elongate to linear, (30–)40–150(–190) μm long 7
— Leaf apices brittle, mostly lacking in the lower part of the stem; costa consisting of a mixture of stereids and cells with a distinct lumen, layer of guide cells not differentiated; upper lamina with many oblong, (15–)30–50 μm long, cells among elongate to linear, (50–)60–110 μm long, ones . . . . 8. *D. cutlackii*
7. Limbidium absent; leaves plicate; filamentous gemmae often present, forming conspicuous orange to reddish brown clusters near stem apex . . . . 6. *D. braunii*
— Limbidium present, albeit often ill-defined; leaves smooth or slightly rugose; filamentous gemmae rarely present, forming only small clusters . . . . 7. *D. brevisetum*
8. Leaf apices brittle, lacking in many lower leaves 9
— Leaf apices firm, present in most lower leaves 11
9. Leaves 0.4–0.8 mm wide, smooth or slightly plicate, filamentous or clavate gemmae often present at the lower part of the stem 10
— Leaves 1–2 mm wide, smooth or rugose, gemmae absent . . . . 14. *D. rugifolium*
10. Stereids arranged in distinct layers at both sides of the guide cells; limbidium often present, consisting of 1–3 rows, reaching from just above the alar patches to a short distance below the serrate part of the margin; walls of the basal lamina incrassate . . . . 9. *D. daymannianum*
— Stereids absent or scattered; limbidium absent; walls of basal lamina cells thin . . . . 17. *Dicranum psathyrum*
11. Abaxial surface of the costa smooth throughout 12
— Abaxial surface of the costa bearing teeth in the distal part 13

12. Leaves widely patent, not falcate, apical part often subtubulous; upper lamina cells irregularly shaped, not vermicular; walls of the upper lamina cells incrassate, strongly pitted .... 12. *D. havilandii*
— Leaves erectopatent to falcate-secund, canaliculate throughout or basal part flat; upper lamina cells mostly vermicular; walls of the upper lamina cells rather thin, not or shallowly pitted..... .... 2. *D. assimile*
13. Abaxial teeth scattered; costa 20–50 µm wide, with (1–)2(–4) guide cells; sporogones almost always solitary 14
— Abaxial teeth in 2 or more rows on low ribs; costa 40–120 µm wide, with (3–)4–11 guide cells; sporogones mostly aggregated 15
14. Leaves falcate-secund; walls of the alar cells thin to firm, evenly thickened.... 4. *D. billardierei*
— Leaves erectopatent to widely patent; walls of the alar cells strongly collenchymatous......... .... 5. *D. blumei*
15. Leaves plicate, with 1–2 long, deep folds parallel to the costa 16
— Leaves smooth to slightly plicate at most, occasionally rugose; if plicate, then with short, shallow folds in the basal part of the leaf that are variously orientated with respect to the costa... 17
16. Capsules erect to slightly curved; seta 8–16(–19) mm long; 2–4 capsules per perichaetium; leaves with 2 folds at either side of the costa; guide cells 4–8; costa adaxially lacking cells with a large lumen.. 13. *D. reflexum*
— Capsules slightly curved to arcuate; seta (12–)17–23 mm long; 2–9 capsules per perichaetium; leaves with 1 fold at either side of the costa; guide cells 6–11; costa adaxially with some cells with a large lumen adjacent to the guide cells, thus giving the impression of 2 layers of guide cells .... 10. *D. dicarpum*
17. Juxtacostal cells at midleaf similar in size and shape to the median and intra-marginal cells .. 18
— Juxtacostal cells at midleaf forming a narrow band of quadrate to short-rectangular cells, similar to the upper lamina cells but conspicuously shorter than the median and intra-marginal cells ... . 10. *D. dicarpum*
18. Lumina of the basal lamina cells very wide, lumen wall ratio (2–)4–10; upper lamina cells only slightly shorter than the basal ones and similar in shape; lumina of the teeth at leaf margin distinctly larger than those of the adjacent cells; marginal cells between the teeth mostly quadrate to short rectangular or rhomboidal, distinctly shorter than the intra-marginal cells............ .... 1. *D. arfakianum*
— Lumina of the basal lamina cells mostly narrower, lumen wall ratio 1–3(–9); upper lamina cells mostly somewhat vermicular; if the basal lamina cells are wide then the upper lamina cells are either relatively thick-walled and distinctly vermicular or they are thin-walled, conspicuously shorter than the basal ones and rhomboidal; lumina of the teeth at leaf margin mostly not much larger than those of adjacent cells; marginal cells between the teeth similar in size and shape to the intra-marginal cells .... 2. *D. assimile*

Dicranoloma (Ren.) Ren. (1901: 85)[2]

Leucoloma Brid. subg. *Dicranoloma* Ren. (1898: 61). — *Leucoloma* subg. *Dicranoloma* sect. *Scoparioidea* Ren. (1898: 61). — *Leucoloma* sect. *Dicranoloma* (Ren.) Par.(1900: 120). — *Dicra-*

[2] Margadant & Geissler (1995) correctly pointed out that *Megalostylium* has priority over *Dicranoloma*. Their proposal to conserve *Dicranoloma* is supported here.

noloma sect. *Scoparioidea* (Ren.) Broth. (1909: 1183).[3] — *Dicranoloma* subg. *Scoparioidium* (Ren.) Ren. (1909: 21). Type: *Dicranum platyloma* Besch. Lectotype selected by Williams (1913).

Megalostylium Dozy & Molk. (1848: 145). Type: *M. brevisetum* Dozy & Molk.

Dicranum sect. *Hemicampylus* Mitt. (1869:62), *syn. nov.* Type: *D. billardierei* Brid. ex Anon. Lectotype selected here. Synonymised by Van der Wijk et al. (1962).

Leucoloma subg. *Dicranoloma* sect. *Oncophoroidea* Ren. (1898: 61), *syn. nov.* — *Dicranoloma* sect. *Oncophoroidea* (Ren.) Broth. (1909: 1183). — *Dicranoloma* subg. *Oncophoroidea* (Ren.) Ren. (1909: 21). Type: *Dicranum dichotomum* Brid. Lectotype selected here.

Dicranum [sect.] *Oncophoroloma* C. Müll. (1901: 285)[4]. — *Dicranum* [sect.] *Leucoloma* (Brid.) C. Müll. [subsect.] *Oncophoroloma* C. Müll. (1897b: 360), *nom. nud.* Synonymised with *Dicranoloma* by Van der Wijk et al. (1962).

Werneriobryum Herz. (1909: 122). Type: *W. geluense* Herz. Synonymised with *Dicranoloma* by Allen (1986b).

(description pertaining to Malesian species only)

Dioicous, nearly always pseudoautoicous, only in some species tall males very rarely found besides dwarf males; males unknown from some species. Dwarf males in tomentum on stem, 0.5–3 mm large. Leaves triangular-linear to ovate-linear, gradually tapering towards the apex, ecostate. Perigonia 1 or more per dwarfmale, terminal, laterally displaced. Perigonial leaves broadly ovate to suborbicular, mucronate. Antheridia 2–4 per perigonium, broadly ellipsoid. Paraphyses present or not. Female plants (0.5–)2–50 cm high, growing in cushions or turfs or pendent. Stem reddish to brown, unbranched, subflorally branched or forked, laxly to densely foliose, laxly to densely tomentose; central strand present or not, cortical cells thin-walled to thick-walled. Epidermal cells elongate to linear. Rhizoids arising from 4–6 elliptical initials just below leaf insertion. Paraphyllia absent. Pseudoparaphyllia absent. Axillary hairs mostly 4, 2 at both sides of the costa, 0.25–0.8 mm long, filamentous, consisting of up to 15 cells, the basal 1–3 cells isodiametric to oblong, often slightly brownly tinged, the upper ones oblong to elongate, colourless; walls smooth. Gem-

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[3] According to present nomenclatural rules the name of any subdivision of a genus that includes the type of the genus is to repeat the generic name unaltered as its epithet (Tokyo Code Art. 22.1). If the epithet does not repeat the generic name, the name is considered not to be validly published. There is no article in the code which says that the epithet of a section that includes the type of the subgenus it belongs to should repeat the epithet of that subgenus, but there is a recommendation to that effect (Rec. 22A.1). In the original publication of subgenus *Dicranoloma* (Renauld 1908), it was subdivided into two sections, *Scoparioidea* and *Oncophoroidea*. Brotherus (1901) placed all known species into the two sections. After *Dicranoloma* was given generic rank (Renauld 1901), both Brotherus (1909) and Renauld (1909) maintained the infrageneric taxa. Renauld (1909) gave the subdivisions subgeneric rank. Because the type of the genus must be in one of these subdivisions, the epithet of that subdivision should repeat the generic name. With the selection of *Dicranoloma platyloma* as the lectotype of *Dicranoloma* by Williams (1913), *Dicranoloma* sect. *Scoparioidea* and *Dicranoloma* subg. *Scoparioidium* must be considered as not validly published and should bear the autonym.

[4] Müller never indicated ranks for his infrageneric divisions. The ranks given here are the ones adopted in Index Muscorum (Van der Wijk et al. 1962).

mae present in some species, either as rhizoidal gemmae or arising near the stem.

Leaves 3–20 mm long, triangular-linear to ovate-linear or subulate to aristate above a broadly ovate to broadly elliptical basal part, smooth to variously plicate or rugose, flat to canaliculate below, canaliculate, subtubulous or folded above, decurrent, clasping at extreme base, falcate-secund or erectopatent to widely patent, frequently with falcate apices; apices brittle and often lacking in some species. Alar patches well-defined, triangular, separated from the costa by basal juxtacostal cells, single-layered. Margin serrate in the extreme upper part to as far down as the alar patches, entire below, plain throughout. Limbidium present in most species, ill-developed to well-developed, reaching from the alar patches to the serrate part of the margin, occasionally interrupted, consisting of one to several cell rows. Costa slender to relatively robust, well-defined in its entire length or from just above the alar patches, percurrent or ending some cells below leaf apex, abaxially smooth, rough because of prorate cell ends or with rows of teeth on low ribs in the upper part; guide cells 2–12; stereids rarely absent, adaxially in 1–4 layers, in some species frequently mixed with 1 or more cells with a lumen as large as that of the guide cells, adjacent to the guide cells; abaxially in 1–4 layers, frequently forming 3–5 bundles of stereids, separated by cells with a large lumen; epidermis mostly not differentiated, in some species differentiated at one or both sides, consisting of cells with a distinct lumen. Basal lamina cells elongate to linear; walls mostly incrassate, pitted. Alar cells quadrate to rectangular, inflated or not; walls colourless or yellowish to reddish brown, thin- to thick-walled, almost never pitted. Limbidium cells linear, with very thick, non-pitted walls and a very narrow, almost invisible lumen. Upper lamina cells similar to the basal ones or conspicuously different, variable in shape, pitted or not. Teeth at leaf margin minute to large, mostly consisting of one cell, the lumen of which may or may not be conspicuously larger than those of adjacent cells. Perichaetia terminal, laterally displaced. Perichaetial leaves either gradually tapering or abruptly contracted into a subula; basal part ovate to broadly elliptical, clasping to sheathing; subula often reflexed in the outer perichaetial leaves, in a few species brittle and often lacking. Archegonia up to 10 or more per perichaetium, up to 2 mm long, with a very long neck, intermingled with a few paraphyses.

Sporogones one to several per perichaetium. Seta very variable in length, yellowish to reddish brown, smooth; central strand present, cortical cells thin-walled, peripheral 1–4 layers with very thick walls. Capsule immersed or exserted, globose to cylindrical, erect, straight or arcuate. Theca wall consisting of one layer of thick-walled exothecial cells and 3–4 layers of thin-walled amphithecial cells. Exothecial cells irregular in shape, mostly not arranged in orderly longitudinal rows; in transverse section c. isodiametric or with the longer axis perpendicular to the theca wall, lumina quadrate to rectangular. Stomata present in the apophysis and the extreme base of the theca, phaneropore. Annulus mostly differentiated, consisting of 2–3 rows of large thick-walled cells. Peristome haplolepidous, consisting of 16 teeth. Peristome teeth narrowly triangular, tapering towards the apex, bifid in the upper 1/2 or deeper, often fenestrate below to base; outer face either smooth or vertically to obliquely striate throughout or in the basal part only and then papillose above, often with cross connections between the striae in the basal part; inner face smooth below, mostly papillose above; dorsal trabeculae thin, mostly smooth; ventral trabeculae thick, at least the upper ones often papillose; ventral plates thicker than the dorsal ones, except in D. armitii. Operculum rostrate above a conical base. Calyptra greenish, transparent, cucullate, reaching about halfway the theca. Spores spherical, finely papillose.

1. ***Dicranoloma arfakianum*** (C. Müll. ex Geh.) Ren. (1909: 11) Fig. 6

Dicranum arfakianum C. Müll. ex Geh. (1898: 3). — *Dicranum elimbatum* Broth. & Geh. in Geh. (1898: 3), nom. inval. in synon — *Leucoloma arfakianum* (C. Müll. ex Geh.) Broth. (1901: 322). Type: Indonesia. Irian Jaya, Mt. Arfak ad Hatam, 5000–7000', Beccari 167 (B-holo, destroyed, H-BR-lecto!, FH-FL!, L!, S!). Lectotype selected by Norris & Koponen (1990).

Pseudoautoicous. Dwarf males 0.6–2 mm tall. Leaves 0.3–1.2×0.08–0.12 mm, ovate-lanceolate, acuminate, ecostate, elimbate; margin entire throughout or with some minute teeth near apex. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 5–17 cm tall, growing in turfs, green to yellowish-green or yellowish-brown. Stem brown, simple or subflorally branched or forked, densely foliose, densely tomentose; diameter 0.5–0.6 mm, central strand present, cortical cells thin-walled. Gemmae absent.

Leaves 7–12×0.8–1.5 mm, ovate-linear, gradually attenuate, smooth to very slightly plicate, canaliculate, falcate-secund throughout or widely patent in the basal part of the stem, but always with falcate leaf apices. Alar patches distinct, 0.35–0.6×0.25–0.45 mm, triangular, not reaching the costa. Margin serrate in the upper 1/2–3/4, entire below. Limbidium consisting of 1–3(–5) rows of cells, reaching from the alar patches to the serrate part of the margin, often interrupted. Costa (40–)50–90 μm wide, (25–)30–45 μm thick, either well-marked in its entire length or from just above the alar patches, ending a few cells below leaf apex, abaxially bearing 2 rows of teeth on 2 ribs in the distal 1/2–3/4; guide cells (3–)4–5(–6); adaxially with 1–2 layers of stereids and, adjacent to the guide cells, often with 1–2 cells with a lumen as large as those of the guide cells, abaxially with 1–2 layers of stereids, occasionally intermingled with some cells with a distinct lumen; epidermis not differentiated adaxially as well as abaxially, but adaxially occasionally with some cells with a distinct lumen in the peripheral layer. Basal lamina cells 60–160(–190)× 12–25(–30) μm, elongate to linear; walls thin, shallowly pitted, lumen wall ratio (2–)4–10. Alar cells 30–120(–160)×20–50(–60) μm, quadrate to rectangular, often inflated; walls thin, 1–5 μm thick, not pitted, brown or colourless. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with yellowish-brown to brown walls. Limbidium cells 90–210×4–7 μm, linear, with very thick, non-pitted walls and very narrow, almost indiscernable lumina. Upper lamina cells 30–130(–160)×(6–)10–22 μm, elongate to short linear, straight, almost as long as the basal lamina cells or gradually shorter; walls thin, shallowly pitted, lumen wall ratio 2–10. Teeth at leaf margin 20–40 μm, consisting of a single cell; lumina mostly conspicuously larger than in the adjacent marginal cells. Perichaetial leaves 7–9×1.3–2.5 mm, abruptly contracted into a subula; basal part 1.5–7 mm long, broadly ovate to elliptical; subula reflexed in the outer perichaetial leaves.

Sporogones (1–)2–8 per perichaetium. Vaginula 2–3 mm long, brown. Seta 16–30 mm long, yellowish to yellowish-reddish, smooth; 0.16–0.2 mm in diameter, central strand pre-

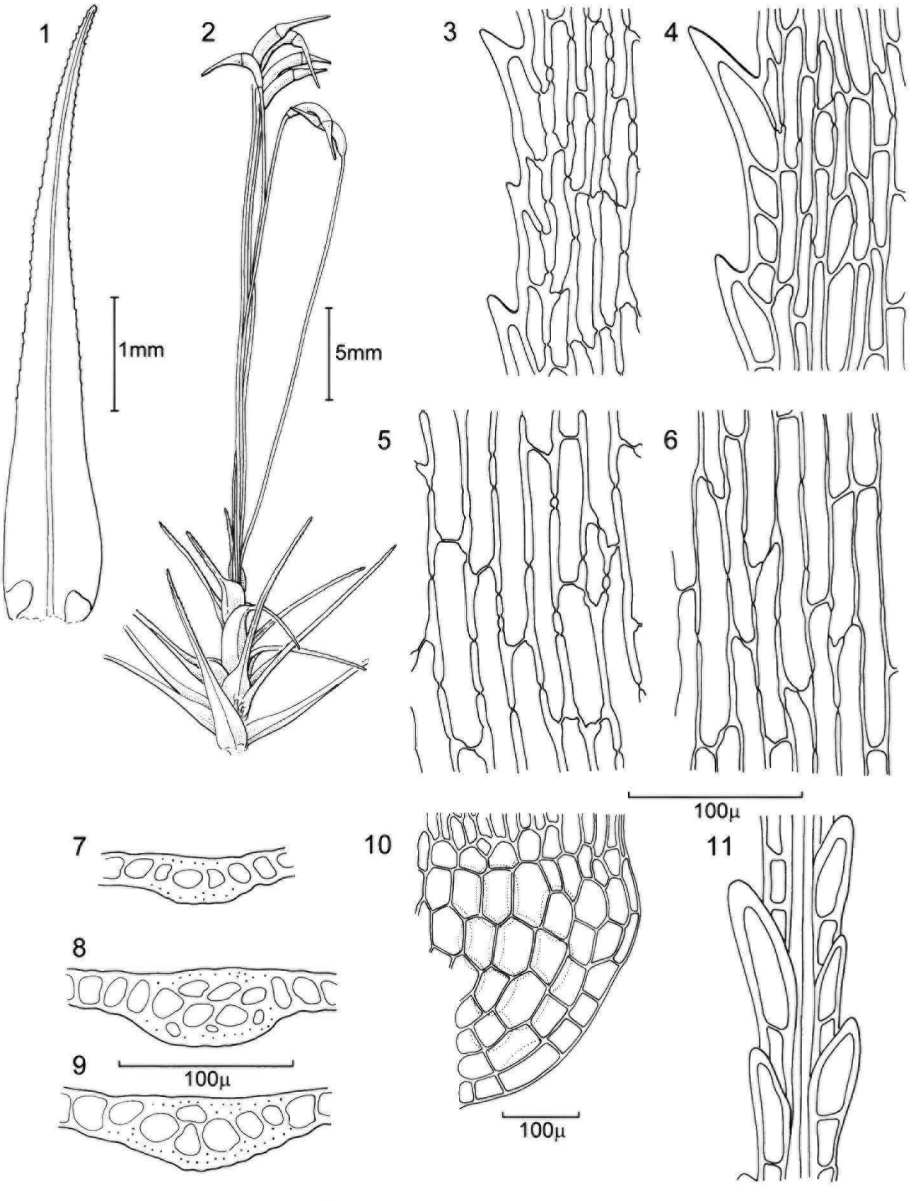

Fig. 6. *Dicranoloma arfakianum*— 1 . leaf; 2. perichaetium with sporogones; 3–4. upper lamina cells; 5–6. basal lamina cells; 7–9. cross section through the costa, just above the alar patches; 10. alar cells; 11. abaxial view of the costa, distal part.—1, 3, 5, 7, 10. Beccari 167 (H-BR, holotype; L); 2, 9, 11. Streimann 32479 (H); 4, 6, 8. Van Zanten 378 (L).

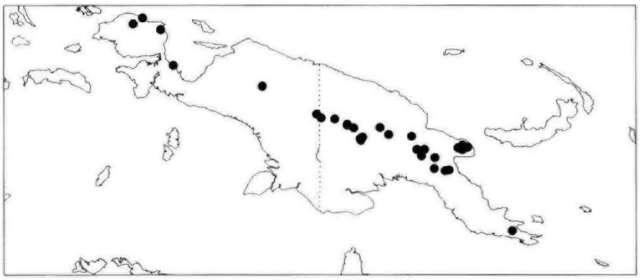

Fig. 7. Distribution of *Dicranoloma arfakianum*.

sent, cortical cells thin-walled, the peripheral 1–2 layers with very thick walls, central part often decayed at maturity. Capsule 2.5–3 mm long, yellowish-brown to brown, cylindrical, arcuate, often strumose. Exothecial cells 40–150×15–30 μm, oblong to linear, irregularly shaped to almost rectangular, mostly not in regular longitudinal rows. Annulus consisting of 2–3 rows of thick-walled cells, deciduous, often a few cells remaining attached at capsule mouth. Peristome teeth yellowish to reddish, 0.45–0.5 mm long, 80–100 μm wide at base, long-attenuate, asymmetrically bifid in the upper half, occasionally fenestrate below to base; outer face vertically to obliquely striate throughout, with cross-connections in the basal c. 2/3; inner face smooth in the basal c. 2/3, papillose above; outer trabeculae thin; inner trabeculae thick, the ones in the upper c. 1/2 papillose. Operculum 2–3 mm long, yellowish to reddish-brown, conical, obliquely rostrate above a conical base. Calyptra 4.5–5 mm long, green to brownish, more or less transparent, cucullate. Spores 18–20 μm, spherical, finely papillose.

Illustrations. Geheeb 1898: t. 1, f. 1–13; Tan & Koponen 1983: f. 39–40; Norris & Koponen 1990: f. 6 i–n.

Distribution. Endemic to New Guinea (Fig. 7).

Ecology. Growing in lower montane and upper montane forest, occasionally in subalpine grassland, from 1100 to 3550 m, mostly below 2700 m. Mostly terrestrial, but also frequently found on decaying wood and on tree stems and roots; occasionally on rocks.

Selected additional specimens examined. INDONESIA. IRIAN JAYA. Sorong, Sungai Aifat, Pegunungan Tohkiri (Tohkiri Mts.), Van Royen & Sleumer 7110 (CBG, H, L); Manokwari, Kebar Valley, Davis 830 IA (L), 830 IIA (L); Jayawijaya, Ilim (Swart Valley), Dagny Bergman M-43 (L); Jayapura, Pegunungan Sterren (Star Mts.), Mt. Antares, Van Zanten 378 (BM, L, NY). PAPUA NEW GUINEA. West Sepik, S of Oksapmin, Hoffmann 90–75 (BM, CBG, H, L, NY); Southern Highlands, Pribu Sawmill, Tari – Komo Road, Streimann 32479 (CBG, H, KLU, NY); Enga, Laiagam subdistrict, Lagaip Valley, Hoogland & Schodde 7411 (BM, CBG, FH, L); Eastern Highlands, Mt. Michael, Iserentant B-85 (H, NY); Morobe, Cromwell Mts., Koponen 31438 (FH, JE, NY); Central, Owen Stanley Range, Robbins 4264 (L).

Dicranoloma arfakianum is most likely to be confused with *D. assimile*. The two species can be distinguished from each other by the following combination of characters. The basal lamina cells are relatively wide, thin-walled and undeeply pitted in *D. arfakianum*, but mostly thick-walled and deeply pitted in *D. assimile*. The upper lamina cells are almost as long as or only slightly shorter than the basal lamina cells, similar in shape and mostly straight in *D. arfakianum*, but conspicuously shorter than the basal ones and differently shaped, mostly more or less vermicular, in *D. assimile*. *Dicranoloma arfakianum* has large marginal teeth with a lumen that is mostly conspicuously larger than those of adjacent cells. The marginal cells between the teeth are mostly short-rectangular to rhomboidal and conspicuously shorter than the adjacent intra-marginal cells. In *D. assimile* on the other hand the lumina of the teeth are mostly not conspicuously larger than those of adjacent cells, nor are the cells between the teeth conspicuously shorter than the intra-marginal cells. *Dicranoloma arfakianum* always has a narrow limbidium, while the limbidium in *D. assimile* is mostly wider. Finally, *D. arfakianum* has many, up to 8, sporogones per perichaetium, while *D. assimile* has at most 5 and mostly fewer. None of these characters alone are sufficient for a positive identification as *D. arfakianum*. The relatively wide thin-walled lamina cells form the most reliable single character. Within New Guinea, the only island where *D. arfakianum* has been found, this character is sufficient to distinguish between *D. arfakianum* and *D. assimile*. Outside New Guinea, plants belonging to *D. assimile* may be found with wide basal lamina cells similar to those of *D. arfakianum*. In these plants, however, the upper lamina cells are different from those in *D. arfakianum*, either narrower and then vermicular, or, if wide, rhomboidal and conspicuously shorter than the basal lamina cells. At least some teeth with a lumen larger than in the adjacent cells frequently occur in *D. assimile*. The marginal cells between these teeth, however, are never short-rectangular to short-rhomboidal and conspicuously shorter than the intra-marginal cells, like in *D. arfakianum*, but similar to and at most slightly shorter than the intra-marginal cells. On the other hand, also in *D. arfakianum* the short-rectangular to short rhomboidal intra-marginal cells are not always clearly developed in all plants or all leaves of a plant. This, for instance, is also the case in the lectotype, as was previously reported by Norris & Koponen (1990). The high number of sporogones in a single perichaetium is not more than an occasionally helpful additional character. Collections of *D. assimile* with relatively many sporogones, up to 5 per perichaetium, are found from northern Sumatra. Incidentally, these collections have also relatively wide basal lamina cells. All other characters, however, point towards *D. assimile*. On the other hand, occasional specimens of *D. arfakianum* with as few as 2, or even 1, sporogones have been found. The above-mentioned vegetative characters are, in combination, always sufficient to distinguish between *D. arfakianum* and *D. assimile* and sporogones are never needed for a positive identification.

Some shared character states suggest a relationship with *D. dicarpum*. These include large marginal teeth with lumina conspicuously larger than in the adjacent cells, short-rectangular to rhomboidal non-dentiform marginal cells and usually a high number of sporogones per perichaetium. New Guinean plants of *D. dicarpum* also frequently have relatively wide, thin-walled basal lamina cells. *D. dicarpum* can be distinguished from *D. arfakianum* by isodiametric to elongate, more or less rectangular upper lamina cells, conspicuously shorter than the basal ones, which descend along the costa in a narrow band. This juxtacostal band is sometimes ill-defined in some leaves in a collection of *D. dicarpum*, but is then more easily observed in other leaves from the same collection. *D. dicarpum*, moreover has a stronger costa than *D. arfakianum*, containing more guide cells, more layers of stereids and often a layer of cells with a large lumen adjacent to the guide cells, thus resembling a second layer of guide cells.

In the original description Geheeb (1898) compared *D. arfakianum* to small forms of *D. assimile*, differing by a looser leaf areolation and an almost lacking limbidium. Whereas the type specimen, described by Geheeb, is indeed smaller than typical *D. assimile*, most plants are of similar size. Geheeb considered *D. arfakianum* to be even more closely related to *D. polysetum* Hampe, now *D. dicarpum*, from which it could be separated again by its looser cell pattern and by its non-plicate leaf base. Although many New Guinea plants of *D. dicarpum* have a loose cell pattern, similar to *D. arfakianum*, and are not at all plicate both species are sufficiently distinguishable on the other characters mentioned above.

Bartram (1942), although recognising *D. arfakianum*, considered the differences between *D. arfakianum* and *D. assimile* "very slight" and had "little doubt" that both are forms of the same species. The only possible difference Bartram mentions is the limbidium, which, according to him, is usually indistinct in *D. arfakianum*, but occasionally just as apparent as in *D. assimile*. Van Zanten (1964) essentially followed Bartram, but mentioned an additional character, seta length, which was 2.5 cm in his collections identified as *D. arfakianum*, as opposed to 1.5 cm in *D. assimile*. Seta length is not considered a distinguishing character here as ranges are almost identical for both species. The fact that Bartram as well as Van Zanten failed to distinguish between the species may be explained, besides by the fact that the species are not easily distinguished, by the fact that all specimens cited by Bartram that I could examine, and half of the specimens cited by Van Zanten, belong to *D. assimile* rather than *D. arfakianum*. Interestingly, Van Zanten mentions the difference in the number of sporogones per perichaetium, his collection no. 378, which actually is *D. arfakianum*, having up to 8 sporogones (Van Zanten 1969 recorded 10) and no. 502, which belongs to *D. assimile*, having 1–3 only. Eddy (1988) concurred with Bartram and Van Zanten that *D. arfakianum* is doubtfully distinct from *D. assimile*, dismissing "peculiarities of lamina cell form" mentioned by Tan & Koponen (1983), leaving as the only, but "highly suspect", discriminatory character the weakly developed limbidium, the same as mentioned by Bartram.

Tan & Koponen (1983) and Norris & Koponen (1990) accepted *D. arfakianum* as a good species. Tan & Koponen emphasised the different leaf areolation, the lamina cells being broadly rectangular in outline and arranged regularly in straight rows, the lack of strong dentation of the leaf margin and the lack of a well-developed leaf border as features distinguishing *D. arfakianum* from *D. assimile*. However, if anything, the marginal teeth of *D. arfakianum* are stronger than those of *D. assimile*. Norris & Koponen emphasised the enlarged cells that form the marginal teeth and the sharply contrasting small quadrate non-dentiform marginal cells between the teeth as diagnostic characters separating *D. arfakianum* from *D. assimile*.

2. ***Dicranoloma assimile*** (Hampe) Ren. (1901: 69) Fig. 8–9

Dicranum assimile Hampe (1844: 24). — *Dicranum polysetum* Hampe, hom. illeg. var. [ß] *assimile* (Hampe) Dozy & Molk. (1847: 143). — *Leucoloma assimile* (Hampe) Broth. (1901: 322). Type: Indonesia. Java, Junghuhn s.n. (BM-holo!, L!).

Dicranum sumatranum Broth ex C. Müll. (1901: 285). — *Leucoloma sumatranum* Broth. ex Ren.

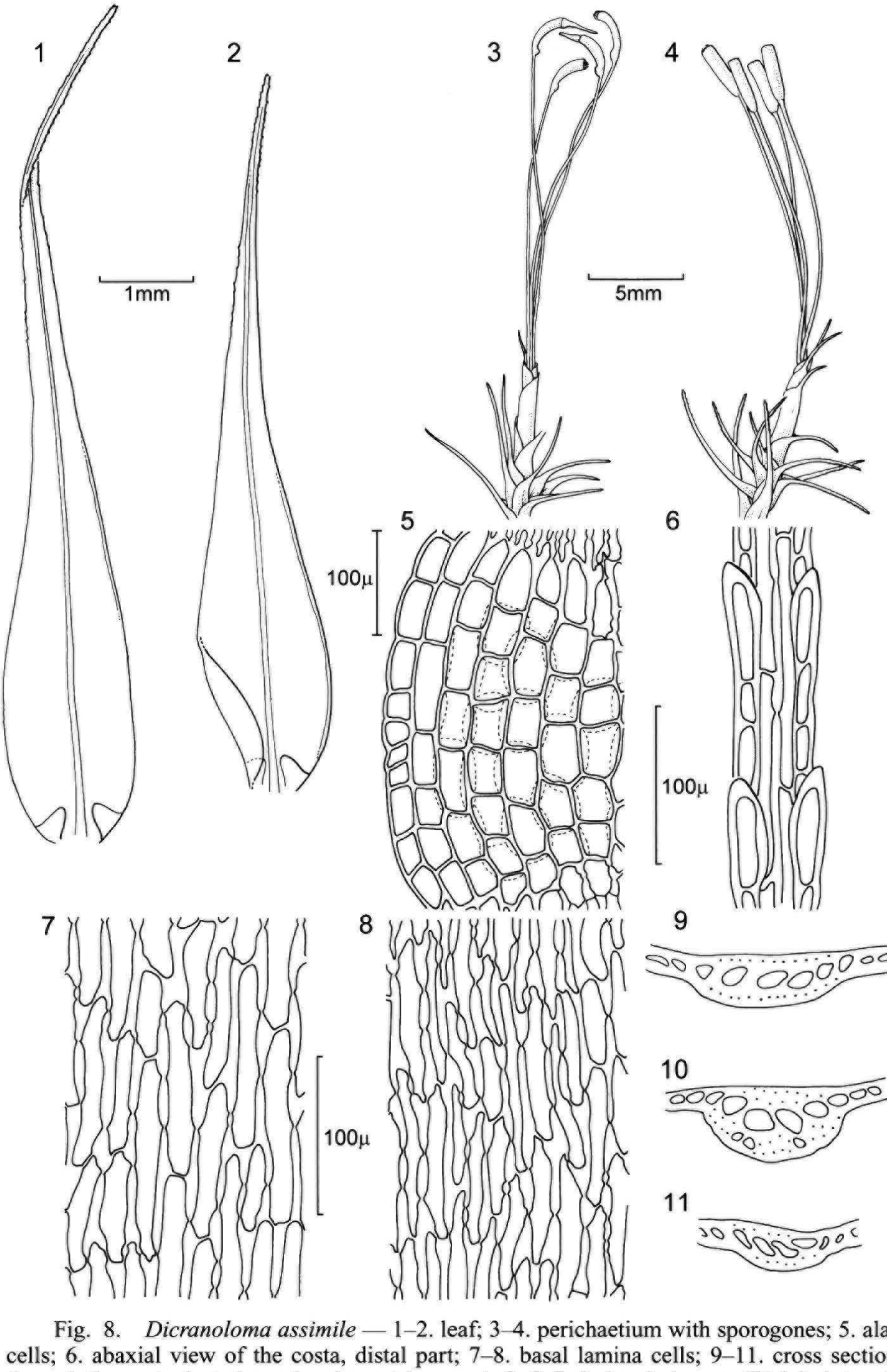

Fig. 8. *Dicranoloma assimile* — 1–2. leaf; 3–4. perichaetium with sporogones; 5. alar cells; 6. abaxial view of the costa, distal part; 7–8. basal lamina cells; 9–11. cross section through the costa, just above the alar patches. — 1, 3, 5–7, 9. Junghuhn s.n. (BM; holotype); 2, 4, 8, 10. Copeland 1126 (H-BR; holotype of *D. perarmatum*); 11. Van Zanten 677a (L; holotype of *D. havilandii* var. *latifolium*).

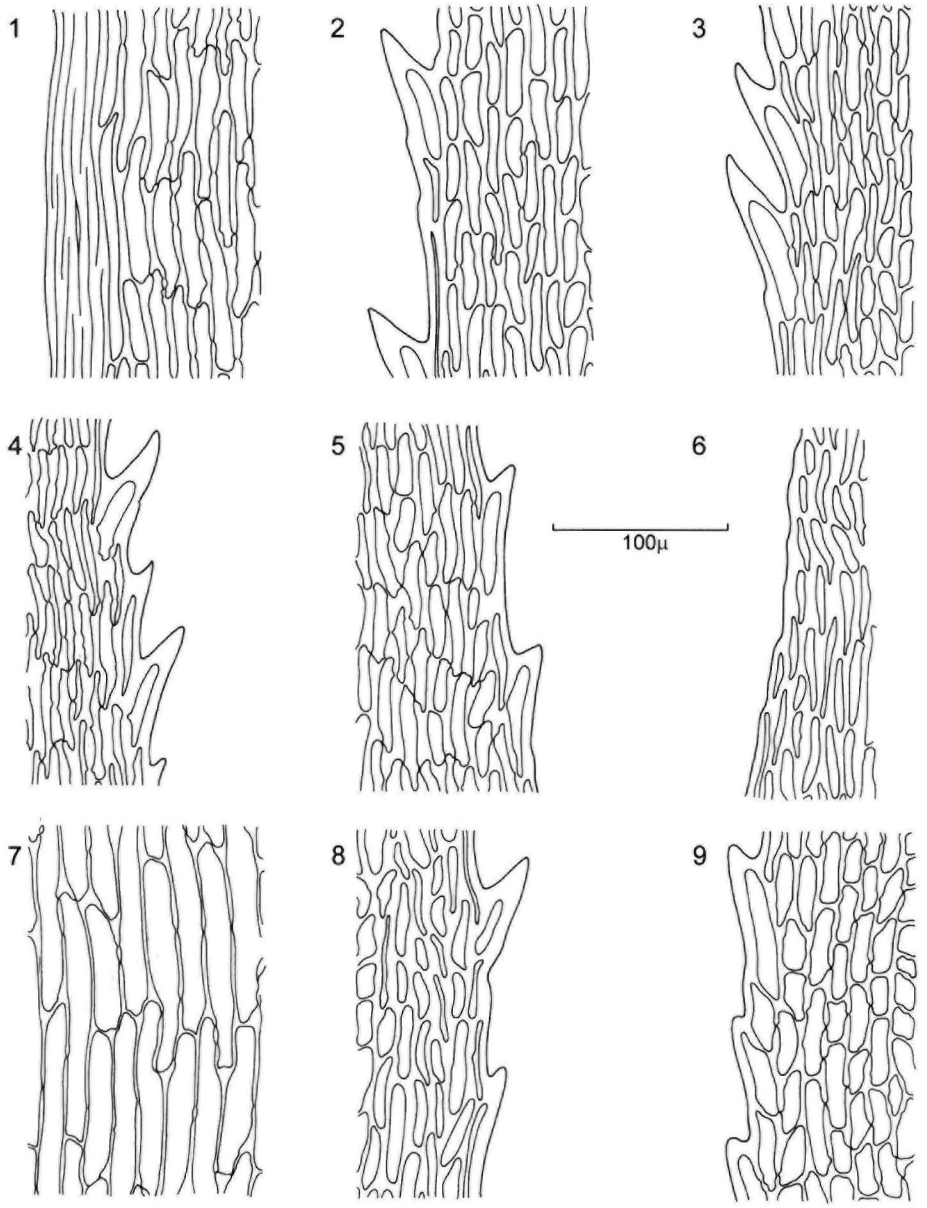

Fig. 9. *Dicranoloma assimile* — 1. marginal and intramarginal cells; 2–6, 8–9. upper lamina cells; 7. basal lamina cells. — 1–2. Junghuhn s.n. (BM; holotype); 3. Copeland 1126 (H-BR; holotype of *D. perarmatum*); 4. Mjöberg s.n. (BM; holotype of *D. euryloma* var. *rugifolium*); 5. Clemens 10245 (L; isotype of *D. brachyphyllum*); 6. Van Zanten 677a (L; holotype of *D. havilandii* var. *latifolium*); 7–8. De Wilde & De Wilde-Duyfjes 13150A (H); 9. Meijer B-12978 (L).

(1898: 61), *nom. nud.* — *Leucoloma sumatranum* (Broth. ex. C. Müll.) Broth. (1901: 322). — *Dicranoloma sumatranum* (Broth. ex C. Müll.) Ren. (1909: 14). Type: Indonesia. West Sumatra, W. Micholitz 48 (B-holo, destroyed; H-BR-lecto!, BM! FH-FL!, S!) Lectotype selected by Tan & Koponen (1983). Synonymised by Dixon (1932).

Dicranoloma gedeanum Ren. & Card. in Card. (1901: 117). Type: Indonesia. Java, Lefèbre s.n. (P-holo, not found; FH-FL-iso!). Synonymised by Renauld & Cardot (1905).

Dicranum assimile Hampe f. *major* Fleisch. (1904: 74), *syn. nov.* Type: Borneo. Korthals s.n. (FH-FL-holo!, L!).

Dicranoloma perarmatum Broth. (1905: 1). Type: Philippines. Mindanao, District of Davao, Mt. Apo, on trees, 1800 m, Copeland 1126 (H-BR-holo!, FH-Bartr.!, FH-FL!, NY!). Synonymised by Tan & Koponen (1983).

Dicranoloma monocarpum Broth. (1918: 202). Type: Philippines. Luzon, Camarines Prov., Mt. Isarog, Ramos BS 22114 (H-BR-holo!). Synonymised with *D. perarmatum* Broth. by Bartram (1939).

Dicranoloma euryloma Dix. (1935: 69). Type: Malaysia. Sabah, Tenompok, Lumu-Lumu, 1400–1600 m, Holttum 25633 (BM-holo!, FH-Bartr.). Paratype: Malaysia. Sarawak, Ulu Koyan, at base of tree in white sand forest, c. 1000 m, Oxford Expedition 1932 (P.W. Richards) 1853 (BM!). Synonymised by Eddy (1988).

Dicranoloma euryloma Dix. var. *rugifolium* Bartr. (1936: 237), *syn. nov.* Type: Malaysia. Sarawak, Mt. Tibang, 1600 m, Mjöberg s.n. (FH-Bartr.-holo!, BM, FH!).

Dicranoloma brachyphyllum Nog. (1953: 3), *syn. nov.* Type: Papua New Guinea. Morobe, Mt. Sarawaket, 11000–12000 ft., M.S. Clemens 10245 (NICH-holo, not seen; iso- in L!).

Dicranoloma havilandii Broth. var. *latifolium* Zant. (1964: 272), *syn. nov.* Type: Indonesia. Irian Jaya, Star Mts., Mt. Antares, below western summit, 3300 m, terrestrial and at base of shrubs in alpine peat, B.O. van Zanten 677a (L-holo!, BM!, NY!). Paratype: ibid., Van Zanten 680a (BM!, L!, NY!).

Leucoloma donaldii Broth. ex Dix. (1922: 497), nom. inval. in synon. of *Dicranoloma laevifolium* (Broth. & Geh.) Par. Authentic specimen: Papua New Guinea. Central Province, Mt.Owen Stanley Range, The Gap, J. McDonald s.n.(BM!, H-BR!). Synonymised by Norris & Koponen (1990).

Pseudoautoicous. Dwarf males 0.5–2.2(–8) mm tall. Leaves 0.15–1(–3)×0.05–0.3 mm, ovate-lanceolate, gradually tapering to slightly subulate, acuminate, ecostate or with a faint costa in the upper half, elimbate; margin serrulate in the upper half, entire below. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 2–16 cm tall, growing in turfs, pale green to yellowish-green or pale yellowish to reddish-brown. Stem brown, simple or subflorally branched, densely foliose, laxly to densely tomentose; diameter 0.3–0.55, central strand present, cortical cells mostly thin-walled. Gemmae absent.

Leaves (5–)6–12×(0.7–)0.8–2.5 mm, ovate-linear, gradually tapering, smooth to slightly plicate or rugose, canaliculate to almost flat, mostly falcate-secund throughout, occasionally patent in the lower part of the stem. Alar patches distinct, 0.2–0.6(–0.8)× 0.15–0.5(–0.6) mm, triangular, not reaching the costa. Margin serrulate in the apical part to serrate to as far down as 2/3 of leaf length, entire below, occasionally slightly undulate in leaf middle. Limbidium consisting of 1–11 rows of cells, reaching from the alar patches up to 1/3–1/2 of leaf length to well within the serrate part of the margin. Costa 40–80 μm wide, 25–50 μm thick, well-marked in its entire length, mostly ending a few cells below leaf apex, occasionally percurrent, abaxially bearing 2–4 rows of teeth on 2 ribs only at extreme apex to as far down as 3/4 of leaf length; guide cells (3–)4–5(–6); adaxially with 1–2 layers of stereids and, adjacent to the guide cells, occasionally with 1–2 cells with a lumen as large as those of the guide cells, abaxially with 1–2 layers of stereids, occasionally divided into (2–)3 small bundles, separated by cells with a distinct lumen or groups of such cells; epidermis not differentiated adaxially as well as abaxially, but adaxially occasionally with some cells with a distinct lumen in the peripheral layer. Basal lamina cells 30–160(–190)×8–20(–24) μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 1–3(–9). Alar cells 20–140×(10–)15–70(–95) μm, quadrate to rectangular, often inflated; walls thin, 1–5 μm thick, not pitted, yellowish-reddish to brown or colourless. Basal juxtacostal cells similar to the basal lamina cells, but with yellowish-brown or orangish walls. Limbidium cells (60–)80–250(–more than 400)×4–8 μm, linear, with very thick, non-pitted walls and very narrow, almost indiscernable lumina. Upper lamina cells 15–90(–130)×6–12(–16) μm, oblong to short-linear, vermicular to elongate-rhomboidal, occasionally elliptic, more or less rectangular or irregular, gradually becoming shorter than the basal lamina cells; walls rather thin, not or scarcely and shallowly pitted, lumen wall ratio 1–5(–6). Teeth at leaf margin 10–25(–40) μm, consisting of a single cell; lumina mostly not conspicuously larger than in the adjacent cells. Perichaetial leaves (3–)4–11×1–2.5 mm, abruptly contracted into a subula; basal part 1.5–10 mm long, broadly ovate to ellipsoid, sheathing; subula reflexed in the outer leaves.

Sporogones 1–5 per perichaetium. Vaginula 2.5–3(–4) mm long, reddish-brown to dark brown. Seta 15–26(–36) mm long, yellowish to reddish-brown throughout or from reddish or reddish-brown below to yellow above, smooth; 0.18–0.24 mm in diameter, central strand present, cortical cells thin-walled, the peripheral 2–4 layers with very thick walls, central part often decayed at maturity. Capsule 2.5–5 mm long, reddish-brown to dark brown, cylindrical, mostly slightly curved to arcuate, occasionally straight to slightly asymmetrical, strumose or not. Exothecial cells 20–140×15–40 μm, isodiametric to linear, irregularly shaped to rectangular to rhomboidal, mostly not in regular longitudinal rows, the longer cells at the convex side occasionally in regular rows. Annulus consisting of 2–3 rows of thick-walled cells, deciduous, often a few cells remaining attached at capsule mouth. Peristome teeth yellowish to reddish, 0.4–0.75 mm long, 75–130 μm wide at base, long-attenuate, asymmetrically bifid, occasionally trifid, in the upper 1/2–3/4, often fenestrate below to base; outer face vertically to obliquely striate with cross connections in the basal (1/8–)1/3 to throughout, papillose above; inner face smooth in the basal 1/3 to throughout, papillose above; outer trabeculae thin, the lower ones mostly smooth, the ones in the upper part of the teeth often papillose; inner trabeculae much thicker, smooth to coarsely papillose. Operculum 2.5–3.5 mm long, yellowish to brown, obliquely rostrate above a conical base. Calyptra 5.5–6 mm long, green to brownish, more or less transparent, cucullate. Spores 16–28(–40) μm, spherical, finely papillose.

Illustrations. Hampe 1844: t. 24, f. 1–6; Dozy & Molkenboer 1858: Vol. 1, t. 54, f. 1–16; Dixon 1935: t. 1, f. 4; Bartram 1939: f. 55, f. 57 (as *D. perarmatum*); Noguchi 1953: f. 1 1–6 (as *D.*

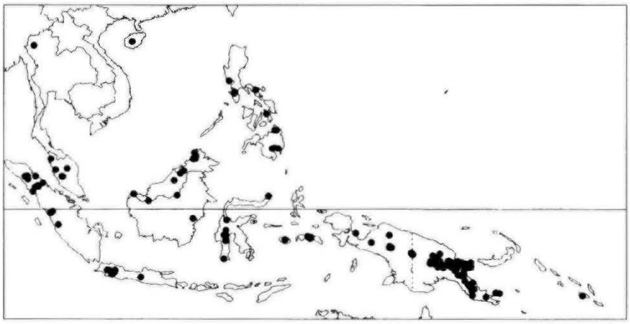

Fig. 10. Distribution of *Dicranoloma assimile*.

brachyphyllum); Van Zanten 1964: t. 23, f. 3 (as *D. havilandii* var. *latifolium*); Tan & Koponen 1983: f. 21–31, f. 34–36; Eddy 1988: f. 129 A–L, f. 134 A–D (as *D. perarmatum*); Norris & Koponen 1990: f. 7 g–l (as *Dicranum assimile*).

Distribution. China (Hainan), Thailand, Peninsular Malaysia, Sumatra, Java, Borneo, Philippines (Luzon, Mindoro, Leyte, Mindanao), Sulawesi, Maluku (Buru, Seram), New Guinea, d'Entrecasteaux Islands (Goodenough I., Fergusson I.), Solomon Islands (Guadalcanal) (Fig. 10).

Ecology. Growing in lower montane and upper montane forest from 800 to 4100 m Only in New Guinea, where it also grows in subalpine forest, heath and grassland, found above 3150 m. Occasionally found in secondary forest. Mostly epiphytic, on stems and bases of trees and shrubs, also frequently terrestrial, on rocks or on decaying wood; in New Guinea, at higher altitudes, often found on stems of tree ferns.

Selected additional specimens examined. THAILAND. Payap, Doi Inthanon, Touw 9947 (L), 10284 (BM, L, MO). CHINA. Guangdong, Hainan, Mt. Gianfengling, Chen et al. 366 (H). PENINSULAR MALAYSIA. Kedah, Gn. Jerai (Kedah Peak), Spare 2879 (BM); Perak, Gn. Hijau, Wray 648 (BM); Pahang, Sempang, Ridley 566 (H-BR); Gn. Tahan, Holttum 20882 (BM). INDONESIA. SUMATRA. Aceh, Gn. Leuser National Reserve, Gn. Bandahara, De Wilde & De Wilde Duijfjes 13150 A (CBG, H, MO, NY); Sumatera Utara, East Coast, Asahan, Bartlett & La Rue 508 (BM, H-BR, MO, NY); Sumatera Barat, Gn. Singgalang, Schiffner 3683 (BM, CBG, H-BR, MO, NY, S); Sumatera Selatan, Gn. Merapi, Alston 13730 a (BM). JAVA. Jawa Barat, Cibodas, Gn. Gede, Fleischer 11 (BM, FH, H-BR, JE, L, NY); Gn. Salak, Nyman 21 (BM, FH, H-BR, MO, NY, S); Gn. Pangerango, Möller 20 (H-BR); Gn. Kandangbadak, Yates 2712 (H, MO), 2713 (BM, KLU). BORNEO. SABAH. Gn. Kinabalu, Haviland 1428 (BM, SAR); Gn. Kinabalu, above Kemburongoh, Richards 5760 (L); Gn. Kinabalu, Pinosok Plateau, Meijer B-12978 (L); Gn. Tambuyukon, Meijer 11475 (L); 8 miles E of Tambunan, Wood 1505 (BM, FH, L). BRUNEI. Temburong, Amo, Bt. Tudal, Davis 489 (L). SARAWAK. Gn. Mulu, Touw 20908 (L); Ulu Koyan, Richards 1853 (BM, L); Pueh Range, S of Kampong Pueh, Bell 2058 (BM). KALIMANTAN. Kalimantan Barat, Gn. Keburau, Schmutz 7286/20A (L), 7286/31A (L); Kalimantan Timur, Gn. Beratus (Peak of Balikpapan), Meijer 1720 (L). PHILIPPINES. LUZON. Bataan Province, Lamas River, Williams 841 (FH, H, L, NY); Camarines Sur, Mt. Isarog, Edano BS 84233 (FH). VISAYAN ISLANDS. Mindoro Oriental, San Teodoro, Coode 5597 (L); Mt. Halcon, Tan 87–225 (NY); Leyte, Ormoc, Mt. Mamban, Edano PNH 12822 (L). MINDANAO. Agusan del Norte, Cabadbaran (Mt. Urdaneta), Elmer 14104 (BM, FH, H-BR, L, MO, NY); Davao del Sur, Mt. Apo, Williams 2656 (FH, H, L, NY); Davao, Mt. Mayo, Edano PNH 12903 (L). SULAWESI. Sulawesi Utara, Menado, De Vriese s.n. (L); Sulawesi Tengah, Gn. Nokilalaki, Meijer B 9900 b (MO); Sulawesi Selatan, Gn. Sesean, Touw & Snoek 24671 (L); Pegunungan Latimojong, Gn. Rantemario, Eddy 4611 (BM).

MALUKU. Buru, Gn. Kapalatmada, Deninger 6 (JE); Seram, Manusela National Park, Gn. Binaiya, Akiyama c-8894 (L, NY). NEW GUINEA. IRIAN JAYA. Manokwari, Wandammen, Pegunungan Wondiwoi, Schram BW 13316 (L); Paniai, Danau-danau Wissel, Eyma 5396 (L); Jayawijaya, Danau (Lake) Habbema, Brass 9384 (FH, L), 10945 (FH, BM); Jayapura, Pegunungan Sterren (Star Mts.), Mt. Antares, Van Zanten 379 (BM, L, NY). PAPUA NEW GUINEA. West Sepik, Star Mts., Mt. Capella, Touw 16961 (L); East Sepik, Burgers Mt., Veldkamp & Vinas 7490 C (L); Western, Mt. Karoma, Veldkamp & Wiakabu s.n. D (L); Southern Highlands, Mt. Giluwe, De Sloover 43173 (BM, CBG, H, L, MO, NY, S); Enga, Wabag area, Tsak Valley, Robbins 729 (BM, L); Western Highlands, near Wanki Village, c. 5 km SE of Mt. Hagen, Hoogland & Pullen 5873 (CBG, FH, L); Madang, 5 km NW of Teptep airstrip, Koponen 34567 (CBG, L); Simbu, Mt. Wilhelm, Lac Piunde, De Sloover 42765 (BM, CBG, L, MO, NY); Eastern Highlands, W of Daulo Pass, Iserentant B-41 (H, NY); Morobe, Huon Peninsula, Cromwell Mts., Mannasat, Hoogland 9451 (BM, FH, L); Central, Port Moresby, Owen Stanley Range, The Gap, Carr 13705 (BM, CBG, FH, H, L, MO, NY); Mt. Yule, Veldkamp & Kuduk 8553 A (L). D'ENTRECASTEAUX ISLANDS. Goodenough Island, Brass 24572 (CBG, H); Fergusson Island, Mt. Kilkerran, Croft et al. LAE 68971 (BM, L). SOLOMON ISLANDS. Guadalcanal, Mt. Popomanaseu, Robbins 4323 (L).

Among the Malesian species of *Dicranoloma D. assimile* is the most variable one and may be confused with several other species. From *D. billardierei* it is in most cases easily distinguished by the abaxial teeth at the upper part of the costa, which are arranged in two or more rows in *D. assimile*, but scattered in *D. billardierei*. Additional distinguishing characters are found in the shape of the upper lamina cells and the number of sporogones per perichaetium. In *D. assimile* the upper lamina cells are conspicuously shorter than the basal lamina cells, more or less vermicular and shallowly or not at all pitted, while they are almost as long as to slightly shorter than the basal lamina cells, straight and pitted in *D. billardierei*. Sporogones are mostly aggregate in *D. assimile* and almost always solitary in *D. billardierei*. Moreover, *D. billardierei* usually has longer and narrower leaves than *D. assimile* and has alar cells that are mostly not inflated and usually have slightly thicker walls than in *D. assimile*.

Species with which *D. assimile* shares the presence of a central strand and the abaxial teeth in the upper part of the costa being arranged in rows are *D. arfakianum*, *D. dicarpum* and *D. reflexum*. Differences between *D. assimile* and *D. arfakianum* have been discussed under *D. arfakianum*. Although plants of *D. assimile* with very wide, thin-walled basal lamina cells, like in *D. arfakianum*, are occasionally found, the upper lamina cells in these plants either have thicker walls and are vermicular or, if thin-walled, are conspicuously shorter than the basal ones and rhomboidal. The majority of plants belonging to *D. assimile* from northern Sumatra, as well as some specimens from Sabah and Mindanao, have such wide, thin-walled basal lamina cells.

D. dicarpum is easily separated from *D. assimile* by the rectangular to rhomboidal upper lamina cells that descend in a band along the costa. This juxtacostal band is sometimes ill-defined in some leaves, but never in all leaves in a collection. The costa of *D. dicarpum* is, with 6–11 guide cells, stronger than in *D. assimile*.

Most difficult to separate from *D. assimile* may be *D. reflexum*. In most cases the distinction is clear due to the strongly plicate leaves of *D. reflexum*, but some forms of *D. assimile* may have slightly plicate leaves as well. In such cases other distinguishing characters of *D. reflexum*, like the different shape of the upper lamina cells, differentiated juxtacostal cells, stronger marginal teeth, relatively short seta and straight to slightly asymmetrical capsule are of little help, because they are either not always present in *D. reflexum*, or present in some forms of *D. assimile* as well. There is, however, a difference in the nature of the folds between the two species. *D. reflexum* has 2 deep longitudinal folds at both sides of the costa, and the folds run parallel to the costa, the inner ones to well within the upper part of the leaf, whereas *D. assimile* may have one to several shallow, mostly oblique folds only near the leaf base.

Plants with relatively short and narrow leaves and large spiniform marginal and costal teeth are found particularly in the Philippines. The leaves of these plants may be slightly plicate, but never with the long and deep folds that are typical of *D. reflexum*. Seta length is at the lower end of the range given for *D. assimile* and the capsules are often only slightly asymmetrical. These plants were formerly included in *D. perarmatum* until Tan & Koponen (1983) reduced the latter to the synonymy of *D. assimile*. Eddy (1988) concurred with Tan & Koponen that *D. perarmatum* is an "unsatisfactory taxon" and does not deserve specific status, but tended towards inclusion in *D. reflexum*, of which he considered it to be a wet-ground expression, rather than in *D. assimile*. Eddy also mentions that he has seen collections that more clearly approach *D. assimile*. As indicated by Tan (1989) the information given on the labels of some of the collections, including the type collection of *D. perarmatum*, do not support their being wet-ground expressions. All collections of *D. assimile* from the Philippines from which the substrate is given are epiphytic. Tan thus thinks that *D. perarmatum* is better interpreted as a xeric form of *D. assimile*. In this revision Tan & Koponen and Tan are followed in including *D. perarmatum* in *D. assimile*. Most of the Philippine plants belonging to *D. assimile* belong to the above-described forms. Similar forms have been found from Borneo and Sulawesi as well.

Several plants collected from Hainan found in H have originally been identified as *D. perarmatum*. The upper lamina cells in these plants, however, are short-elliptical, a shape not found in any Malesian plant of *D. assimile*. Otherwise, the plants appear similar to small forms of *D. assimile*. The same form was found in Bartram's herbarium, under a never published herbarium name. This specimen, Tsang 24361, has 3 capsules per perichaetium, setae with a length at the lower end of the range given for *D. assimile* and straight capsules. Some plants from Guangdong, formerly identified as *D. kwangtungense*, are similar as well. I hesitate to include these forms in *D. assimile* until more specimens from Hainan and mainland China have been studied.

Some forms of *D. brevisetum* may also be similar to *D. assimile* in habit, but are easily distinguished by the lack of a central strand. Without making a cross section of the stem, *D. brevisetum* may also be distinguished from *D. assimile* by the thick-walled, never inflated alar cells and by the straight to slanted upper lamina cells that are similar in size to or only slightly shorter than the basal ones. If sporogones are present, the species will never be confused as *D. brevisetum* has a very short, up to 4 mm long seta, while in *D. assimile* the seta is at least 15 mm long.

High-altitude forms of *D. assimile*, found on Sulawesi and New Guinea may develop relatively wide, erect-spreading to spreading, often slightly rugose leaves with marginal dentation restricted to a few minute teeth at leaf apex. Abaxial teeth may be totally lacking or be restricted to a few minute teeth at leaf apex. These forms are easily confused with the Bornean *D. havilandii*, which can be separated by its widely patent, straight leaves which often are subtubulose in the upper half. The leaves in the high altitude forms of *D. assimile* described above are never widely patent and never subtubulose. Moreover, these forms of *D. assimile* always have more or less vermicular upper lamina cells, while those in *D. havilandii* are more irregularly shaped. The type specimens of *D. brachyphyllum* and *D. havilandii* var. *latifolium* are such high altitude forms of *D. assimile* and therefore these names are here synonymised with *D. assimile*.

Eddy (1988) joined forms with almost straight leaves which are either entire or bluntly dentate only at apex and have an almost smooth costa, i.e. both the Bornean plants and the high altitude forms of Sulawesi and New Guinea under *D. havilandii*. He wrote that it appears to be a high altitude, wet-ground variant of *D. assimile*. He did not, however, synonymise *D. havilandii*, because too few collections had been made to make a decision. From his drawings it appears that Eddy considered *D. havilandii* var. *latifolium* to belong to *D. havilandii*. Tan (1989) considered *D. havilandii* to be endemic to Borneo and wrote that *D. havilandii* var. *latifolium* probably does not belong to *D. havilandii* because the type specimen has leaves with a different type of leaf cell areolation, consisting mostly of elongate to vermicular cells with thick walls and narrow lumina. In his opinion the var. *latifolium* probably is a rugose variant of *D. brachyphyllum*, but not enough specimens had been studied to place it with certainty.

Norris & Koponen (1990) synonymised both *D. havilandii* var. *latifolium* and *D. brachyphyllum* with *D. rugifolium*. *D. rugifolium* differs from *D. assimile* by its erect-appressed to erect-spreading leaves with brittle leaf apices, by the elongate, rectangular or elliptical, upper lamina cells, minute teeth in the upper half of the margin and smooth peristome teeth. These features are not present in the type specimens of *D. havilandii* var. *rugifolium* and *D. brachyphyllum*. The inclusion of *D. havilandii* var. *latifolium* and *D. brachyphyllum* in *D. rugifolium* seems to imply that, according to them, plants that in the present revision are considered to be high altitude forms of *D. assimile*, should be included in *D. rugifolium*. However, Norris and Koponen also describe forms of *D. assimile* with inconspicuous marginal teeth and dorsal lamellae. The reason for Norris and Koponen's inclusion of the latter two names in *D. rugifolium* seems to be the rugose leaf apices. However, as in *D. assimile*, the leaves of *D. rugifolium* range from strongly rugose to completely smooth. Norris & Koponen did not mention *D. havilandii*.

From Mt. Fala and Mt. Yule, both in the Central Province of Papua New Guinea, several collections were seen which have wide, strongly rugose leaves and coarsely serrate leaf margins at the same time (cf. Veldkamp & Kuduk 8553 A). At the same locations plants with almost smooth leaf surfaces were found. These forms with strongly rugose leaves and strongly serrate margins might be transitional forms between the high altitude forms and more typical plants of *D. assimile*.

Apart from the above-mentioned high-altitude forms, the morphological variation in *D. assimile* seems not to be related to ecological factors, but some forms are geographically limited.

Tan's (1989) record of *D. platycaulon* from Borneo is based on the type specimen of *D. euryloma* var. *rugifolium*. The characters given by Tan for *D. platycaulon* do not apply to this specimen, nor do they apply to the other Bornean and the New Guinean plant which are cited. The upper lamina cells of *D. platycaulon* are irregularly isodiametric to short-elliptical, as can be seen in the drawings from Dixon (1913) and Tan, whereas the upper lamina cells in the Malesian plants are elongate and vermicular, albeit somewhat irregular. The rugose leaf surface is a normal feature in *D. assimile*. Therefore, in my view, the Bornean and New Guinean plants belong to *D. assimile* and the report of *D. platycaulon* from Borneo and New Guinea is erroneous.

3. ***Dicranoloma bartramianum*** (B.H. Allen) Klazenga, comb. nov. Fig. 11

Dicranum bartramianum B.H. Allen (1987a: 323). — *Dicnemon robustum* Bartr. (1945: 112). — *Eucamptodon robustus* (Bartr.) Bartr. (1959: 88). Type: Papua New Guinea. Rawlinson Range, 7000–12000 ft., Clemens 12493 (FH-holo!, FH, MICH).

Pseudoautoicous. Dwarf males 0.6–1.5 mm tall. Leaves 0.3–0.9×0.12–0.27 mm, ovate-lanceolate, acuminate, ecostate, elimbate; margin serrulate in the upper part, entire below. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 6–21 cm tall, growing in turfs, pale yellowish to yellowish-brown. Stem reddish to dark brown, simple or subflorally branched, densely foliose, laxly to densely tomentose; diameter 0.35–0.45 mm, central strand absent, cortical cells thick-walled. Gemmae often present, mostly in the lower part of the stem, at the tips of the rhizoids, narrowly club-shaped, uniseriate, up to 1.1 mm long, 40–60 μm wide, consisting of up to 35 quadrate cells; walls smooth, colourless to brown.

Leaves (6.5–)10–13×2–3.5 mm, ovate-lanceolate, gradually tapering, rugose when dry, slightly so to almost smooth when wet, canaliculate, erectopatent to widely patent. Alar patches distinct, 0.4–0.8×0.3–0.8 mm, triangular, not reaching the costa. Margin serrulate in the distal 1/10–1/2, entire below, undulate in the distal 1/3–1/2. Limbidium absent. Costa 20–40 μm wide, 20–30 μm thick, well-marked in its entire length, ending a short distance below leaf apex; abaxial surface smooth throughout; guide cells 2; adaxially as well as abaxially with a single layer of stereids, adaxially the stereids occasionally lacking; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells (40–)50–160(–190)×(8–)10–20 μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 0.75–1.5. Alar cells (20–)40–100(–120)×20–60 μm, the outer ones frequently inflated; walls rather thin, 26 μm thick, colourless to light yellowish. Basal juxtacostal and decurrency cells similar to the basal lamina cells, but the basal juxtacostal cells with yellowish or orangish-walls and the decurrency cells with brown walls. Upper lamina cells 30–100(–180)×12–20 μm, oblong to linear, irregularly shaped, straight or slightly slanted, gradually shorter than the basal lamina cells; walls incrassate, pitted, lumen wall ratio 1–2. Perichaetial leaves 5–9×1.5–3.5 mm, ovate-lanceolate, gradually tapering into a short acumen; basal part clasping to sheathing.

Sporogones (1–)2–3 per perichaetium. Vaginula 3–3.5 mm long, dark brown. Seta 7–10 mm long, yellowish, becoming red , smooth; ca. 0.25 mm in diameter, central strand

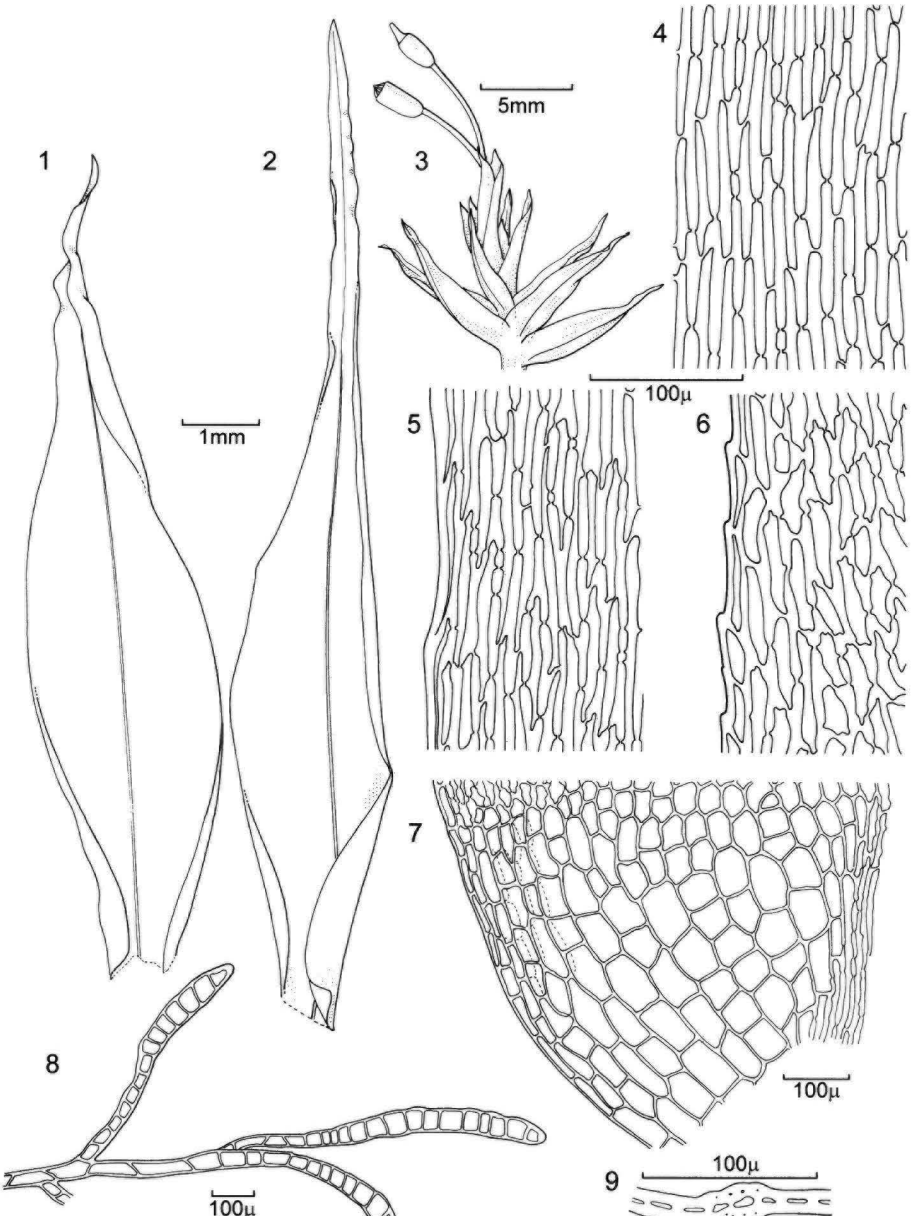

Fig. 11. *Dicranoloma bartramianum* — 1–2. leaf; 3. perichaetium with sporogones; 4. basal lamina cells; 5. marginal and intramarginal cells; 6. upper lamina cells; 7. alar cells; 8. rhizoidal gemmae; 9. cross section through the costa, just above the alar patches. — 1, 8. Weber & McVean B-31912 (MO); 2. Veldkamp & Vinas 7522 (L); 3, 7. Mundua 96 (CBG); 4–6, 9. Robbins 709 (L).

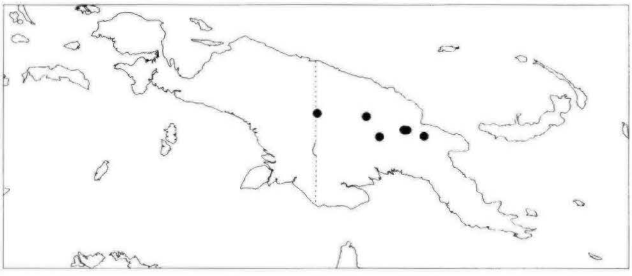

Fig. 12. Distribution of *Dicranoloma bartramianum*.

present, cortical cells thin-walled, the peripheral 1–2 layers with very thick walls, the central part decayed at maturity. Capsule 2–2.5 mm long, dark brown, yellowish when young, ovoid, straight, not strumose. Exothecial cells 30–85×15–50 μm, isodiametric to elongate, irregularly rectangular to polygonal or rounded, not in regular longitudinal rows. Annulus consisting of 2–3 rows of thick-walled cells, persistent. Peristome teeth yellowish to reddish, c. 1 mm long, 90–160 μm wide at base, long-attenuate, asymmetrically bifid in the upper half; outer face vertically striate with scattered papillae on the striae in the basal 1/2–2/3; inner face finely papillose below to densely so above, with fine striae in the basal 1/2–2/3; outer trabeculae thin, smooth; inner trabeculae slightly thicker, papillose. Operculum 2–2.5 mm long, yellowish-transparent to reddish-brown, obliquely rostrate above a conical base. Calyptra unknown. Spores 22–40 μm, spherical, finely papillose.

Illustrations. Allen, 1987a: t. 2–4; Norris & Koponen 1990: f. 9 a–f.

Distribution. Endemic to New Guinea (Fig. 12).

Ecology Growing in subalpine forest, shrubbery and grassland, from 3300 to 3700 m. Mostly on stems of tree ferns; also occasionally found on tree stems, on decaying wood or terrestrial.

Selected additional specimens examined. PAPUA NEW GUINEA. West Sepik, Star Mts., Mt. Capella, Touw 16280 (L, MO, NY), 16318 (L, NY); East Sepik, Burgers Mt., Veldkamp & Vinas 7522 (L, MO, NY); Southern Highlands, Mt. Giluwe, Streimann 24130 (BM, CBG, L, NY); Simbu, Bismarck Ranges, Mt. Wilhelm, Lake Aunde, Mundua 96 (CBG, NY); ibid., Robbins 709 (FH-Bartr., L), Weber & McVean B-31921 (MO); Morobe, Rawlinson Range, Clemens 12493 (FH-Bartr.).

Dicranum bartramianum appears to be closely related to *D. geluense* from which it may be separated by its longer, ovate-lanceolate, acuminate leaves, *D. geluense* having broadly ovate, acute to acuminate leaves, and by the absence of a limbidium. It may also be confused with some extremely broad-leaved forms of *D. assimile* from which it can be easily distinguished by the absence of a central strand and the absence of a limbidium.

The species was first described by Bartram (1945) as *Dicnemon robustus*. Sporogones were unknown then. Later, after finding entire peristome teeth on a collection which he did not cite, but probably is *Robbins 709*, Bartram (1959) transferred it to *Eucamptodon*. Bartram made no mention of its spores, a critical character in establishing a relationship to the Dicnemonaceae to which both the above mentioned genera belong, the Dicnemonaceae being characterised by multicellular spores. Allen (1987a), when revising the Dicnemonaceae, found typically dicranaceous peristome teeth in another collection of *Eucamptodon robustus*, Weber & McVean B-31921, the teeth being split in the upper half.

Moreover, the spores, also in Bartram's collections, are unicellular. Allen explained Bartram's mistake by the fact that the specimen studied by Bartram possesses only battered capsules with eroded peristome teeth. Allen placed *Eucamptodon robustus* in *Dicranum*. As the combination *Dicranum robustum* is blocked, a new name was necessary, *Dicranum bartramianum*. The name *Dicranoloma robustum* is also blocked. Although clearly closely related, Allen did not mention *Werneriobryum geluense*, which he removed from the Dicnemonaceae and placed in *Dicranoloma* a year earlier (Allen 1986b). By strictly applying the criterion that *Dicranoloma* should possess a limbidium he placed the one species in *Dicranoloma* and the other in *Dicranum*.

Allen (1987a) considered *D. bartramianum* to be exceedingly close to *D. peruvianum* Robinson. With the latter it shares robust size, aggregated sporogones, wide-spreading, concave leaves, lamina cells which are pitted throughout the leaf, weak costa, thick-walled cortical cells in the stem, dwarf males, long-necked archegonia, erect capsules and roughened rhizoids. In my opinion these two species are distantly related at most, the similarity being based on convergence and on characters which are common throughout *Dicranum* and *Dicranoloma*. The two species differ by the presence of a central strand and multi-layered alar patches in *D. peruvianum*, among others. Most of the shared features mentioned above are also shared by *Dicranoloma eucamptodontoides* Broth. & Geh. from Tasmania and *D. obesifolium* (R. Brown ter.) Broth. from New Zealand.

Allen (1987a) described a variant with erect to erect-spreading leaves giving the plants a swollen appearance very different from typical plants. Correlated with this tumid habit are broadly ovate, lanceolate leaves and shorter upper lamina cells. This form intergrades into typical *D. bartramianum* to such a degree that he finds a formal recognition of this variation not warranted. A more significant variation he found in the longer, up to 14 mm long, long-acuminate, smooth leaves found in some specimens from the Star Mountains (Veldkamp & Vinas 7522, Touw 16166, 16280, 16318). A variety was never effectively published, but the collections are all annotated as such, Veldkamp & Vinas 7522 (L) being marked as a holotype. Norris & Koponen (1990) also mention this variety, but do not recognise it because of their "normal pattern of non-recognition of varieties". The variety is also not recognised in the present revision, as the variation in the supposedly diagnostic characters was found to be continuous. Moreover, leaf length, relative length of the acumen and rugosity of the leaf surface appear not to be strictly correlated. Plants with relatively long, long-acuminate leaves that at the same time have a rugose leaf surface and plants with short and smooth leaves are frequently found.

4. ***Dicranoloma billardierei*** (Brid. ex Anon.) Par. (1904: 24 ["*Billardieri*"]). Fig. 13

Dicranum billardierei Brid. ex Anon. (1802: 214 ["*Billarderii*"]). — *Dicranum billardierei* Brid. (1798: 181 ["*Billarderi*"]), pre-Hedwigian name. — Oncophorus billardierei (Brid. ex Anon.) Brid. (1826: 401 ["*Billarderii*"]). — Leucoloma billardierei (Brid. ex Anon.) Broth. (1901: 323 ["*Billardierii*"]) Type: Australia [Nova Hollandia], De la Billardière s.n. (B (Bridel herbarium)-holo, not found).

Dicranum novoguineense Broth. & Geh. in Broth. (1895: 151 ["*novo-guinense*"]), syn. nov. — *Leucoloma novoguineense* (Broth. & Geh.) Broth. (1901: 323). — *Dicranoloma novoguineense* (Broth. & Geh.) Par. (1904: 28). Type: Papua New Guinea. Central, Owen Stanley Range, W.

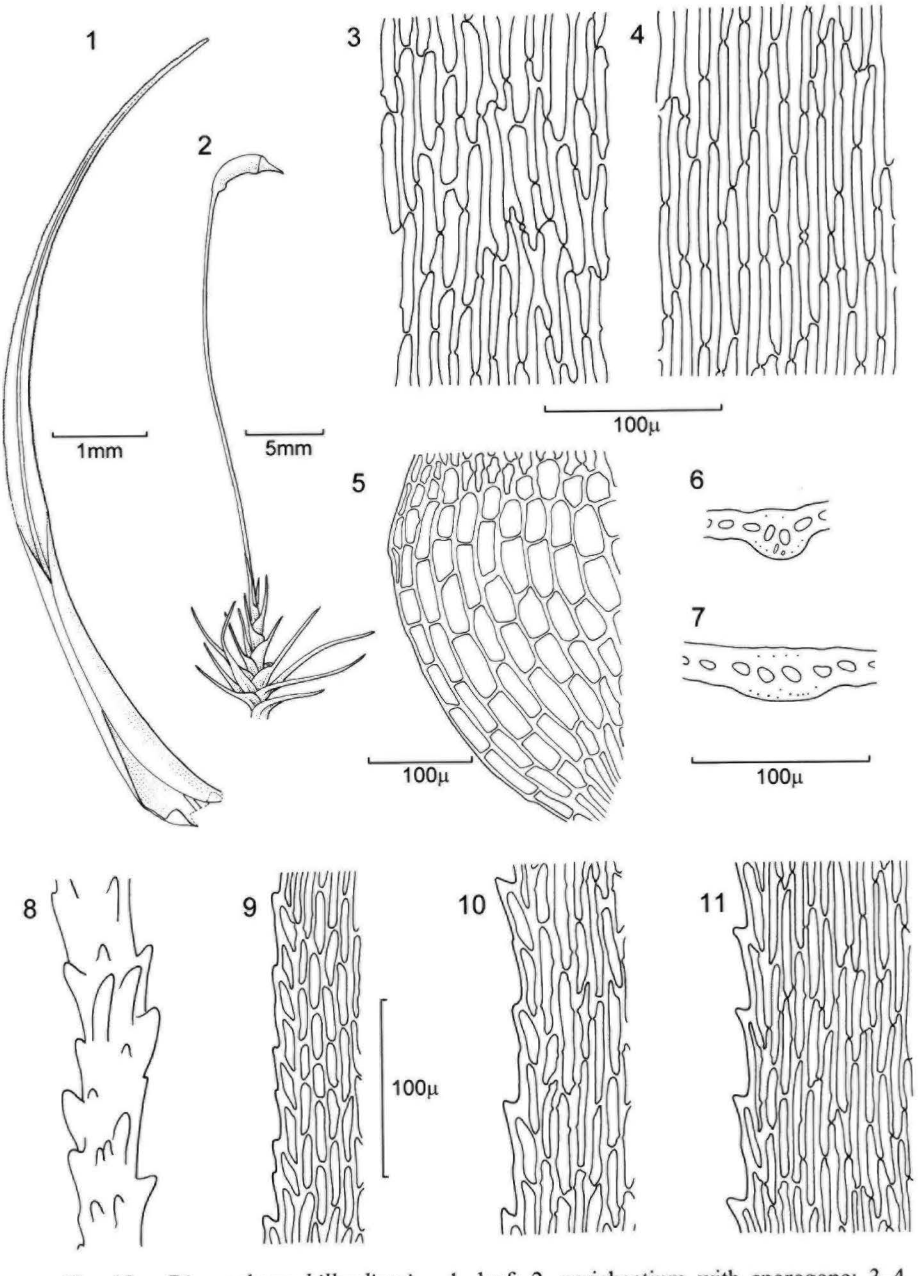

Fig. 13. *Dicranoloma billardierei* — 1. leaf; 2. perichaetium with sporogone; 3–4. basal lamina cells; 5. alar cells; 6–7. cross section through the costa, just above the alar patches; 8. abaxial view of the costa, distal part; 9–11. upper lamina cells. — 1–2, 4–5, 7–8, 11. Pullen 7981 (L); 3, 10. McGregor 6 (H-BR; holotype of *D. novoguineense*); 9. Brass 22755 (H).

MacGregor 6 (H-BR-holo!, BM!, other probable isotypes (unnumbered) in FH-FL!, S!).

Dicranoloma brevicapsulare Dix. (1924: 226). Type: Malaysia. Pahang, Gunong Tahan, 5500–7000 ft., Haniff & Nur 7915a (BM-holo!, KLU!, L!). Synonymised by Tan & Koponen (1983).

Dicranoloma subecostatum Dix. (1935: 69). — *Dicranoloma subenerve* Broth. (1928b: 117), hom. illeg., non *D. subenerve* Herz. (1925: 28). Syntypes: Malaysia. Sabah, Mt. Kinabalu, Kemberangah, Clemens BS 10552 (H-BR-lecto!, BM!, L!, NY!); Indonesia. Kalimantan, Bukit Raja, 1800 m, Winkler 3200 (BM!, H-BR!). Lectotype selected by Tan & Koponen (1983). Synonymised by Tan & Koponen (1983).

Dicranoloma phillipsiae Bartr. (1939: 53). Type: Philippines. Mindanao, Bukidnon, near Impalutao, Phillips 26 (FH-holo!, BM!). Synonymised by Tan & Koponen (1983).

Dicranoloma deningeri Herz. (1919: 289), *nom. nud.*, *syn. nov.* Authentic specimen: Indonesia. Maluku, NW Buru, Gunung Fogha, c. 2100 m, Stresemann 383 (JE!).

Pseudoautoicous. Dwarf males 0.3–1.4(–4) mm tall. Leaves 0.3–0.6(–1)×0.05–0.2 mm, ovate-linear to narrowly ovate, acuminate, ecostate, elimbate; margin serrulate in the upper half, entire below. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 2–15 cm tall, growing in turfs, green to yellowish-brown. Stem reddish brown to brown, simple or subflorally branched or forked, densely foliose, densely tomentose; diameter (0.25–)0.3–0.5 mm, central strand present, cortical cells rather thick-walled. Gemmae absent.

Leaves 6–14×0.6–1.5 mm, ovate-linear, gradually tapering, smooth, at insertion canaliculate, higher up canaliculate to subtubulose, mostly falcate-secund throughout, occasionally patent in the lower part of the stem. Alar patches distinct, 0.25–0.5×0.2–0.4 mm, triangular, not reaching the costa. Margin serrate in the distal 1/6–2/3, entire below. Limbidium consisting of 1–6 rows of cells, reaching from the alar patches to the serrate part of the margin or somewhat below, occasionally absent in some leaves. Costa (25–)30–50 μm wide, 20–40 μm thick, either well-marked in its entire length or from just above the alar patches, percurrent or ending a few cells below leaf apex, abaxially with scattered prorate cells in the extreme distal part to as far down as the upper 2/3 of leaf length; guide cells (1–)2(–3); adaxially with a single layer of stereids, abaxially with 1(–2) layers of stereids, occasionally with some cells with a distinct lumen among them; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells (35–)50–160(–180)×(8–)10–12(–16) μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 1–5. Alar cells 20–80(–100)×(10–)15–40(–45) μm, quadrate to rectangular, occasionally inflated; walls thin to firm, 1–5(–7) μm thick, not pitted, reddish-brown to brown or colourless. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells but with yellowish to orangish cell walls. Limbidium cells (60–)90–200×3–5(–10) μm, linear, with very thick, non-pitted walls and very narrow, almost indiscernable lumina. Upper lamina cells 20–120(–170)×6–10(–14) μm, oblong to linear, straight, as long as the basal lamina cells or gradually becoming shorter; walls rather thin to incrassate, pitted to scarcely and shallowly so, lumen wall ratio 1–6. Occasionally some cells in the apical part prorate. Teeth at leaf margin small, 5–15(–22) μm, consisting of a single cell; lumina never conspicuously larger than in the adjacent cells. Perichaetial leaves 4–9×0.8–2 mm, abruptly contracted into a subula; basal part broadly ovate to elliptical, clasping to sheathing; subula reflexed in the outer perichaetial leaves.

Sporogones 1 or very rarely 2 per perichaetium. Vaginula 2–3 mm long, dark reddish-brown to brown. Seta 17–33 mm long, light yellow to reddish throughout or reddish below and yellowish above, smooth; 0.18–0.26 mm in diameter, central strand present, cortical cells thin-walled, the peripheral 2–4 layers with very thick walls, the central part often decayed at maturity. Capsule 2–3 mm long, reddish-brown to dark brown, yellowish when immature, cylindrical, mostly arcuate, rarely straight, often strumose. Exothecial cells 20–90×10–35 μm, isodiametric to linear, irregularly shaped to rectangular, often with oblique end-walls, often in more or less regular longitudinal rows. Annulus consisting of 2 rows of thick-walled cells, persistent. Peristome teeth yellowish to reddish, 0.45–0.7 mm long, 100–120 μm wide at base, long-attenuate, asymmetrically bifid, occasionally trifid, in the upper 1/3–2/3, often fenestrate below to base; outer face vertically to obliquely striate throughout, with cross connections in the basal c. 2/3; inner face smooth throughout or papillate in the upper c. 1/3; outer trabeculae thin, smooth; inner trabeculae thick, smooth or the ones in the upper c. 1/3 of the tooth papillose. Operculum 2–3 mm long, yellowish-brown to reddish-brown or brown, obliquely rostrate above a conical base. Calyptra 4–6 mm long, green to brownish, more or less transparent, cucullate. Spores (14–)16–2 μm, spherical, finely papillose.

Illustrations. Tan 1989: f. 5–6 (as *D. novoguineense*); Tan & Koponen 1983: f. 38 (as *D. novoguineense*), f. 41–43; Del Rosario & Van Zanten 1980: t. 2a–c; Eddy 1988: f. 135 A–D (as *D. novoguineense*); f. 136 A–D (as *D. brevicapsulare*); Dixon 1924: t. 3, f. 2 (as *D. brevicapsulare*); Norris & Koponen 1990: f. 13 a–e (as *Dicranum novoguineense*). Norris & Koponen's (1990) f. 9 g–i is *Dicranoloma assimile*.

Distribution. In Malesia found in Peninsular Malaysia, Sumatra, Philippines (Mindanao), Borneo, Sulawesi, Maluku (Buru, Seram), New Guinea and the Solomon Islands (Guadalcanal). Also found in Vietnam. Further in Australia, New Caledonia, New Zealand, southern and eastern Africa, Antarctic Islands and southern South America (Fig. 14).

Ecology Growing in lower montane, upper montane and subalpine forest, from 900 to 3150 m, mostly between 1500 and 1600 m. Mostly terrestrial, but also often epiphytic or on decaying wood; rarely on rocks. Outside Malesia growing at far lower altitudes.

Selected additional specimens examined. VIETNAM. Phu Khanh, Nhatrang, Poilane 699 (PC, S). PENINSULAR MALAYSIA. Kedah, Gn. Jerai (Kedah Peak), Robbins 3694 (L); Pahang, Bt. Fraser, Herklots 168 (BM); Johor, Gn. Ledang (Mt. Ophir), Null 67 (GRO). INDONESIA. SUMATRA. Sumatera Barat, Gn. Kerinci, Meijer B 8747 (L); Bengkulu, Bt. Sago, Meijer 6082 (H, L, MO, NY, S). BORNEO. SABAH. Gn. Kinabalu, Tenompok, Clemens 28723 (BM); Gn. Kinabalu, Timpohon Gate, Tan 89-726 (CBG, NY); Bt. Hempuen, Meijer 12712 (L), 12716 (L, NY). SARAWAK. Gn. Mulu, Touw 20920 (L). SULAWESI. Sulawesi Tengah, Gn. Roroka Timbu, Hennipman 5405 A (L); Sulawesi Selatan, Pegunungan Latimojong, Gn. Rantemario massif, Gn. Batu Kapur, Eddy 5531 (BM). MALUKU. Seram, Manusela National Park, Gn. Roihelu, Akiyama c-9849 (L, NY). IRIAN JAYA. Sorong, Pegunungan Tamrau, Gn. Bagimana, Van der Zon s.n. (L); Manokwari, Pegunungan Arfak, Anggi Gigi, Sleumer & Vink 4476 (BM); Jayapura, Pegunungan Cycloop, Gn. Rara, Van Royen & Sleumer 6033a (CBG, H, L). PAPUA NEW GUINEA. Southern Highlands, Tari Gap, Streimann 24509 (CBG, H, NY); Enga, Wabag subdistrict, Yaki river Valley, Hoogland & Schodde 6972 (L); Simbu, Mt. Wilhelm, Eddy 2723 (BM); Eastern Highlands, Kratke Range, Robbins 4175 (L); Morobe, Huon Peninsula,

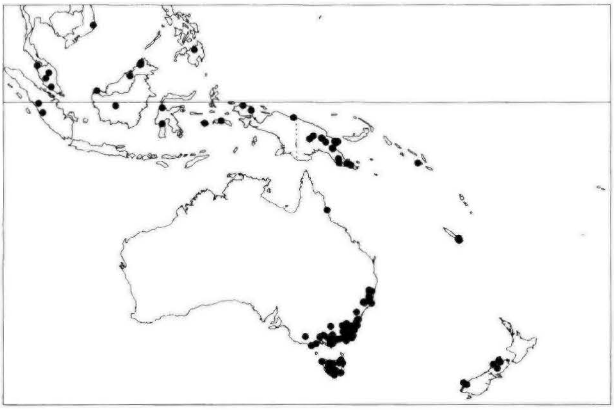

Fig. 14. Distribution of *Dicranoloma billardierei* in Malesia, Australasia and the Pacific. Data from outside Malesia are incomplete.

Sarawaket Range, Monarauwe, Hoogland 9765 (BM, FH, H, L); Central, Owen Stanley Range, Port Moresby, The Gap, Carr 15242 (BM, FH, H, L, MO, NY); Milne Bay, Maneau Range, Mt. Dayman, Brass 22755 (CBG, FH, H); Mt. Mon, Pullen 7981 (L). SOLOMON ISLANDS. Guadalcanal, Mt. Popomanaseu, Dennis BSI 20044 (GRO, L, S).

Dicranoloma billardierei shares with *D. blumei* elongate to linear, thick-walled and strongly pitted upper lamina cells that are similar to the basal ones, weakly serrate upper leaf margins and a costa with scattered abaxial teeth. *Dicranoloma blumei* can be separated from *D. billardierei* by its widely patent, straight leaves, collenchymatous alar cells and mostly erect capsules. From the Solomon Islands, specimens of *D. billardierei* are found which have alar cells with relatively thick, orange brown to brown walls, but never with angular thickenings. As some forms of *D. blumei* may develop long setae and slightly curved capsules, the only remaining character to separate these specimens from the Solomon Islands from *D. blumei* is the falcate leaves.

Differences from *D. assimile* are discussed under that species. Some forms of *D. brevisetum* may be confused with *D. billardierei*, but are easily separated by the absence of a central strand, a wider costa containing 4 or more guide cells, and often aggregate sporogones, with short, up to 4 mm long setae and straight capsules.

Dicranoloma brevicapsulare was synonymised under *D. billardierei* by Tan & Koponen (1983). The only slightly asymmetrical capsule without a trace of a struma, mentioned by Dixon (1924) in his protologue to be a distinctive feature of *D. brevicapsulare*, was considered by them to be well within the range of *D. billardierei*. Eddy (1988) doubted whether *D. billardierei* and *D. brevicapsulare* are indeed conspecific and preferred to call the Malesian specimens *D. brevicapsulare*, this taxon being, according to him, distributed southwards as far as Queensland. Tan (1989), when comparing Malesian material with herbarium specimens from Australia, New Zealand, Africa and South America, could see no differences between them. This comparison was repeated for this revision and Tan's conclusions were confirmed.

A problem here is that the holotype of *D. billardierei*, which should be in Bridel's herbarium, kept in B, could not been located. Moreover, *D. billardierei* is very variable, especially in the anatomy of the costa and the position of the leaves, i.e. whether they are falcate-secund or erectopatent to widely patent. In southern Australia and New Zealand extreme forms may occur which are difficult to separate from *D. robustum* (Hook.f. & Wils.) Par. The latter was even included in the synonymy of *D. billardierei* by Scott & Stone (1976). In Malesia and Queensland, however, *D. billardierei* is not that variable, all specimens having slender costae consisting of 2, rarely 3, guide cells and falcate-secund leaves. In the absence of a type specimen the species concepts of Dixon (1913) and Sainsbury (1955) are followed, as did Tan (1989). No neotype is selected here because this study mainly concerned Malesian plants, whereas the neotype should preferably be selected from Australian material.

When Brotherus and Geheeb (in Brotherus 1895) described *Dicranum novoguineense* they compared it with *D. dicarpum* from which it could easily be distinguished by the weak serrulation of the leaf margins and the abaxial side of the costa and by the linear cells throughout the leaf. *Dicranoloma novoguineense* has been maintained in all recent treatments of the genus. Tan & Koponen (1983) treated *Dicranoloma novoguineense* as a taxon related to *D. assimile* but also allied it with *D. billardierei*, *D. dicarpum* and *D. arfakianum* with which it shares the regular alignment of leaf cells. *D. novoguineense*, however, would differ from all the above-mentioned taxa by the dorsal teeth, which are distributed irregularly rather than on two ridges, as in the other species. It shares this feature with *Dicranoloma cylindrothecium* (Mitt.) Sak. from Japan. Eddy (1988) compared *D. novoguineense* with *D. brevicapsulare* from which he kept it separate by the thinner-walled upper lamina cells, a character, he admits, of which the constancy still had to be established. Tan (1989) and Norris and Koponen (1990) in their keys both use the irregular distribution of the teeth on the abaxial side of the costa to identify *D. novoguineense*. Study of all the available Malesian material and additional material from Australia and New Zealand revealed that *D. billardierei* and, for that matter, *D. blumei* also have their dorsal teeth scattered all over the distal end of the abaxial side of the costa. Also, the upper lamina cells in the holotype of *D. novoguineense* are relatively thick-walled and strongly pitted. Therefore all characters supposedly distinguishing *D. novoguineense* from *D. billardierei* are discarded here and *D. novoguineense* is treated as a synonym of the latter.

5. ***Dicranoloma blumei*** (Nees) Ren. (1901: 69). Fig. 15

Dicranum blumei Nees in Blume (1823: 131 ["*Blumii*"]). — *Leucoloma blumei* (Nees) Broth. (1901: 322 ["*Blumii*"]). Type: Indonesia. Java in montibus excelsis partim ignivomis Salak et Gédé, C. Blume s.n. (LE-holo?, not located; JE-lecto!; other probable isotypes in L!, NY!). Lectotype selected here.

Dicranum blumei Nees var. *laxifolium* Broth. et Geh. in Geh. (1898: 4 ["*Blumii* var. *laxifolium*"]). — *Dicranoloma blumei* (Nees) Par. var. *laxifolium* (Broth. & Geh.) Fleisch. (1914: 112 ["*Blumii* var. *laxifolium*"]). Type: Indonesia. Irian Jaya, Mt. Arfak ad Hatam, 5000–7000', O. Beccari 161 (H-BR-lecto!, FH-FL!, L!). Lectotype selected here. Synonymised by Tan & Koponen (1983).

Dicranoloma blumei (Nees) Par. var. *papillisetum* Fleisch. (1914: 112 ["*Blumii* var. *papillisetum*"]). Type: Indonesia. Irian Jaya, am Goliathgebirge an Baumasten, 1950–3000 m, A.C. de Kock 9 (FH-FL-holo!, L!). Synonymised by Norris & Koponen (1990).

Dicranoloma braunfelsioides Herz. (1919: 288), *syn. nov.* Type: Indonesia. Maluku, W. Seram, zwis-

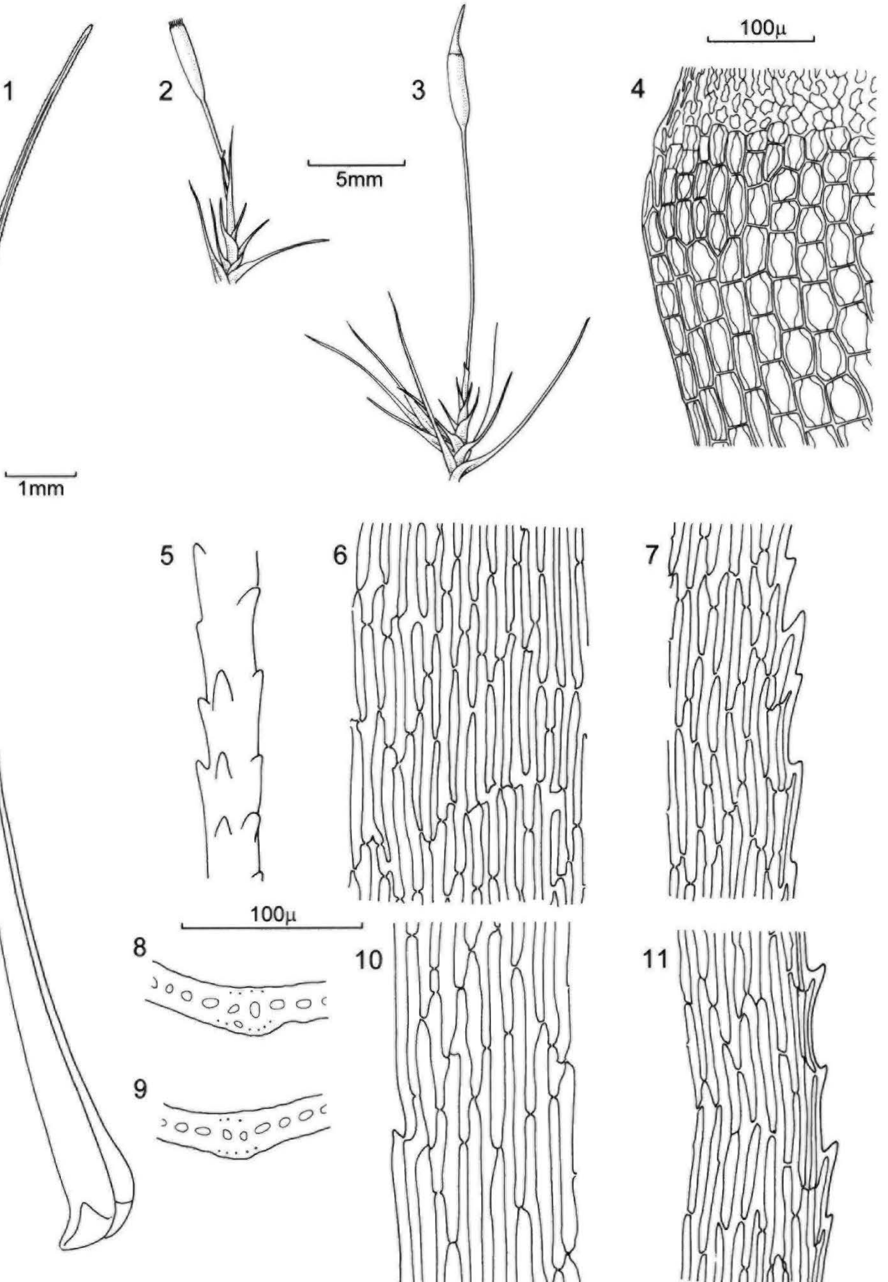

Fig. 15. *Dicranoloma blumei* — 1. leaf; 2–3. perichaetium with sporogone; 4. alar cells and supra-alar cells; 5. abaxial view of the costa, distal part; 6, 10. basal lamina cells; 7, 11. upper lamina cells; 8–9. cross section through the costa, just above the alar patches. — 1–2, 4–8. Van Royen, Sleumer & Schram 7808 (H); 3, 9. De Sloover 43164 (CBG); 10–11. Schiffner 3877 (MO).

chen Sepa und Sawai, Stresemann s.n. (JE-holo!, B!, S!).

Dicranoloma blumei (Nees) Par. f. *subintegra* Dix. (1942: 4 ["*Blumii* f. *subintegra*"). Type: Papua New Guinea. Alola, Owen Stanley Range above Port Moresby; on a tree in forest, c. 6200 ft., C.E. Carr 13651 (BM-holo!, H!, L! NY!). Synonymised by Norris & Koponen (1990).

Pseudoautoicous. Dwarf males c. 1 mm tall. Leaves 0.5–1.1 mm long, ovate-linear, acuminate, ecostate, elimbate; margin serrulate in the upper half, entire below. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 6–50 cm tall, growing in turfs or pendulous, light green to yellowish-brown. Stem reddish brown to brown, simple or subflorally branched, laxly to densely foliose, laxly tomentose; diameter 0.4–0.55 mm, central strand present, cortical cells thick-walled. Gemmae absent.

Leaves 8–20×(0.6–)0.8–1.5 mm, ovate-linear, gradually tapering, smooth, erecto-patent to widely patent, at insertion canaliculate, higher up subtubulose; leaf tips often thread-like and waved or curled, occasionally slightly falcate. Alar patches distinct, 0.35–0.95×0.25–0.65 mm, triangular, reaching the costa or not. Margin serrate in the upper 1/5–1/2(–2/3), entire below. Limbidium consisting of 1–6 rows of cells, reaching from just above the alar patches to the serrate part of the margin, occasionally interrupted. Costa 20–45 μm wide, 20–30(–45) μm thick, either well-marked in its entire length or from just above the alar patches, ending a few cells below leaf apex, abaxially with scattered prorate cells in the distal 1/6–1/2(–2/3); guide cells (1–)2(–4); adaxially with a single layer of stereids, abaxially with 1(–2) layers of stereids, occasionally with a single cell with a distinct lumen in the cavity between the guide cells; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells (30–)50–180×8–18 μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 1–2(–2.5). Alar cells 20–80×(10–)15–40(–50) μm, quadrate to rectangular, not inflated; walls, especially the lateral ones, incrassate, 4–16(–22) μm thick, strongly collenchymatous, the end walls often pitted, the lateral ones occasionally so, reddish-brown to brown. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with yellowish-brown to dark brown walls. Limbidium cells 70–200×3–4 μm, linear, with very thick, non-pitted walls and a very narrow, almost indiscernable lumen. Upper lamina cells (25–)30–120(–150)×6–12 μm, oblong to linear, straight, similar to the basal lamina cells or gradually becoming shorter; walls incrassate, pitted, lumen wall ratio 1–2(–3). Many cells of the apical part of the leaf prorate. Teeth at leaf margin small, 4–15(–20) μm, consisting of a single cell; lumina never conspicuously larger than in the adjacent cells. Perichaetial leaves 4–12×0.8–2 mm, abruptly contracted into a subula; basal part 1–7 mm long, broadly ovate to elliptical, clasping to sheathing; subula mostly reflexed in the outer perichaetial leaves.

Sporogones 1(–2) per perichaetium. Vaginula 1.2–3 mm long, reddish-brown to dark brown. Seta 5–30 mm long, yellowish or reddish brown throughout or from reddish-brown at base to yellowish near the capsule, mostly smooth, occasionally slightly papillose in the upper part; 0.2–0.27 mm in diameter, central strand present, cortical cells thin- to rather thick-walled, the peripheral 2(–3) layers with very thick walls, central part often decayed at maturity. Capsule 1.5–5 mm long, reddish-brown to dark brown, ellipsoid to cylindrical, straight, seldomly slightly curved. Exothecial cells 30–100(–150)×10–40 μm, elongate to

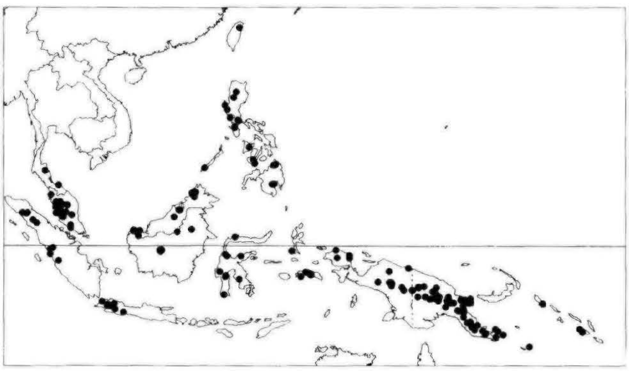

Fig. 16 Distribution of *Dicranoloma blumei*.

short-linear, irregularly shaped to more or less rectangular, not in regular longitudinal rows. Annulus consisting of 2 rows of quadrate, thick-walled cells, persistent. Peristome teeth yellowish to reddish, 0.45–0.75 mm long, (40–)60–100(–120) μm wide at base, long-attenuate, asymmetrically bifid and/or fenestrate almost to base, often the larger segment of some of the teeth also fenestrate; outer face vertically to obliquely striate, with cross connections, in the basal 1/3–1/2; papillose above, inner face smooth in the basal 1/3–1/2, papillose above; inner trabeculae much thicker than the outer ones, strongly projecting, smooth. Operculum 1.5–3 mm long, reddish-brown, obliquely rostrate above a conical base. Calyptra 3–5 mm long, greenish to light brown, more or less transparent, cucullate. Spores 12–20(–26) μm, spherical, finely papillose.

Illustrations. Blume 1823: t. 15, f. 1 a–c (as *Dicranum blumei*); Dozy & Molkenboer 1858: Vol. 1, t. 58, figs. 1–24 (as *Dicranum blumei*); Bartram 1939: f. 58; Lin 1981: f. 1–11; Eddy 1988: f. 137 A–F; Tan 1989: f. 1–4 (as *D. braunfelsioides*); Norris & Koponen 1990: f. 10 a–f (as *Dicranum blumei*).

Distribution. Taiwan, Thailand, Peninsular Malaysia, Sumatra, Java, Borneo, Philippines (Luzon, Mindoro, Negros, Mindanao, Palawan), Sulawesi, Maluku (Bacan, Seram), New Guinea, d'Entrecasteaux Islands (Goodenough I., Fergusson I., Normanby I.), Louisiade Archipelago (Rossell I.), Solomon Islands (Bougainville, Guadalcanal) (Fig. 16).

Ecology. Growing in the upper part of the lower montane forest, in the upper montane forest, and in subalpine forest and other vegetations, from 700 to 3900 m, mostly between 1500 and 3000 m. Very rarely found in secondary forest. Mostly epiphytic, on stems and branches of trees and shrubs, also frequently found terrestrial and on decaying wood, occasionally on rocks. In the lower montane forest and the lower part of the upper montane forest mostly growing on tree bases and stems, higher up also on branches forming very large pendulous masses, in the summit scrub and subalpine vegetations forming large masses together with other bryophytes growing over all available substrates.

Selected additional specimens examined. TAIWAN. Ilan, Taitung Hsiang, Yuangyang Lake, Lin in Lin, Bryophytes of Taiwan 271 (H, L, MO, NY). THAILAND. Pattani, Gn. Ina, Kerr 60 (BM); Nakhon Si Thammarat, Khao Luang, Touw 11733 (CBG, L, MO, NY). PENINSULAR MALAYSIA. Perak, Bt. Peninjau, Burkill 1167 (L); Pahang, Cameron Highlands, Gn. Brinchang, Inoue in Inoue, Bryophyta selecta exsiccata 130 (BM, H, JE, L, MO, NY); Genting Highlands, Khan 2 (KLU); Johor, Gn. Ledang (Mt. Ophir), Ridley 712 (BM). SUMATRA. Aceh, Gn. Leuser Nature Reserve, Gn. Ketambe, De Wilde & De Wilde-Duijfjes 14299 (L, NY); Sumatera Utara, Pulau Samosir, Missionar

Maibach s.n. (JE); Sumatera Barat, Gn. Singgalang, Beccari 90 (BM, L). JAVA. Jawa Barat, Gn. Pangrango, Meijer 859 (L); Gn. Salak, Zollinger 1728 (BM, H-BR, JE, L); Gn. Gede, De Vriese s.n. (L); Lebak Saat, Schiffner 3877 (BM, H-BR, L, MO, NY, S). BORNEO. SABAH. Gn. Kinabalu, Marai Parai Spur, Clemens 11120 (BM, H-BR, NY); Gn. Tambuyukon, Meijer B 11435 (L); Banjaran Crocker (Crocker Range), between Sunsuron and Pass, Menzel, Frahm, Frey & Kürschner 4595 (B). SARAWAK., Gn. Mulu, Jermy 14323 (BM, L); Gn. Mulu National Park, Gn. Api., Touw 19962 (L); Bt. Dulit, Richards 1066 (BM, FH, L); Gn. Tibang, Mjoberg s.n. (FH). KALIMANTAN. Kalimantan Timur, Kong Kemul, Endert 4516 (BM, L); Kalimantan Barat, Gn. Penerisan (Mt. Penrissen), Mjöberg s.n. (H-BR, NY); Kalimantan Tengah, Bt. Raja, Winkler 3178 (H-BR, L); Kalimantan Selatan, Gn. Besar, Barabai, Dransfield 2923 (L). PHILIPPINES. LUZON. Zambales, Mt. Tapolao, Ramos BS 5147 (BM, FH-Bartr., H-BR, NY); Bataan, Mt. Mariveles, Merrill 3557 (BM, H-BR, NY); Quezon, Mt. Banahao, Merrill 7529 (BM, H-BR, NY); Tayabas, Infanta, Robinson BS 9403 (FH-FL, H-BR, MO, NY). VISAYAN ISLANDS. Mindoro Oriental, Dilöydöy River, tributary of Subaan River inland from San Teodoro, Coode 5600 (L); Mt. Halcon, Edano PNH 9294 (L); Negros Oriental, near Dumaguete, Reyes 2973 (NY). MINDANAO. Agusan del Norte, Cabadbaran (Mt. Urdaneta), Elmer 14106 (BM, FH, H-BR, L, MO, NY); Davao del Sur, Todaya (Mt. Apo), Elmer 11669 (BM, FH, H-BR, JE, L, MO, NY); Davao, Mt. Batangan, Warburg s.n. (H-BR, NY). PALAWAN. Mt. Mantalingajan, Edano PNH 610 (L). SULAWESI. Sulawesi Utara, Bt. Poka Pindjang, Kjellberg 24 (BM, L, S); Sulewesia Tengah, Gn. Roroka Timbu, Van Balgooy 3336 (L); Sulawesi Selatan, Pegunungan Latimojong, Gn. Rantemario, Eddy 4175 (BM); Gn. Lompobattang (Bonthain Peak), Warburg s.n. (NY); Sulawesi Tenggara, Gn. Watuwila, Coode 6161 (L). MALUKU. Bacan, Gn. Sibella, Warburg s.n. (H-BR); Seram, Manusela National Park, Gn. Totaniwel, Tihulale, Akiyama c-15784 (L, MO, NY). IRIAN JAYA. Sorong, Pegunungan Tamrau, Gn. Kusemun, Van Royen, Sleumer & Schram 7808 (CBG, H, L, S); Manokwari, Gn. Arfak, Beccari 161 (FH-FL, H-BR, JE, L); Paniai, Puncak Jaya (Carstensz Mts.), Dayak Meadow, Hope CGE 82 (CBG, L); Jayawijaya, Puncak Trikora (Wilhelmina top), W of "Trikora Pass", Mangen P 55c (L); Sungai Taritatu (Idenburg River), Brass 12621 (FH, L); Jayapura, Pegunungan Sterren (Star Mts.), Mt. Antares, Van Zanten 480 (BM, CBG, L, NY). PAPUA NEW GUINEA. West Sepik, Table Mt., Koponen 35801 (FH, H, MO); Western, Mt. Karoma, Veldkamp & Wiakabu 7736 H (L); East Sepik, Burgers Mt., Veldkamp & Vinas 7491 D (L); Southern Highlands, Mt. Giluwe, De Sloover 43164 (BM, CBG, H, L, MO, NY); Enga, Wabag area, ranges W of Tabanaka, Middle Wage Valley, SW of Laiagam, Robbins 3311 (CBG, L); Western Highlands, Mt. Hagen, Van Zanten 68898 (GRO); Simbu, Mt. Wilhelm, between Keglsugl and Lake Piunde, De Sloover 42946 (BM, CBG, H, L, MO, NY); Eastern Highlands, Mt. Michael, Brass & Collins 31318 (L); Morobe, Sarawaket Range, above Hamelingan, Norris 66741 (L, MO); Northern, Hydrographers Range, Pullen 5949 (CBG); Central, Alola, Owen Stanley Range above Port Moresby, Carr 13651 (BM, CBG, H, L, NY); Milne Bay, Goropu Mts., Mt. Suckling, Veldkamp & Stevens 5897 (H, L, MO, NY). D'ENTRECASTEAUX ISLANDS. Goodenough Island, Brass 24565 (CBG, FH, NY); Fergusson Island, between Agamoia and Ailuluai, Brass 27002 (BM, FH, L); Normanby Island, Mt. Pabinama, Brass 25743 (BM, FH, L). LOUISIADE ARCHIPELAGO. Rossel Island, Mt. Rossel, Brass 28438 (BM, FH, L, S). SOLOMON ISLANDS. Bougainville, Lake Loloru, Ridsdale & Lavarack NGF 31513 (L); Guadalcanal, Mt. Popomanaseu, Dennis BSIP 20043 (GRO, S).

Dicranoloma blumei is easily distinguished from all other species of *Dicranum* by the combination of conspicuous reddish to dark brown alar patches, very loose tomentum and a narrow costa. Pendent forms stand out because of the widely spaced, very long and widely patent leaves. These forms can only be confused with pendent, narrow-leafed forms of *D. brevisetum* which can be distinguished by the absence of a central strand, the more robust costa and the densely tomentose stems and, when sporogones are present, by the shorter, up to 4 mm long, seta. Moreover, in *D. brevisetum* the alar cells are not collenchymatous and have colourless or yellowish brown walls. Other forms may be confused with *D. billardierei*. Differences between *D. blumei* and *D. billardierei* are discussed under the latter species.

Dicranoloma blumei shows considerable variation in seta length. Setae longer than 20 mm occur only in specimens with relatively short, erect stems, always shorter than 15 cm, mostly shorter than 10 cm, whereas shorter setae occur in specimens of any length. Other features correlated with a long seta are a denser foliation, erectopatent leaves and often a slightly curved capsule. In herbarium material seta lengths of 20 mm or longer have only been found in specimens from New Guinea and a single collection from Borneo. Among the New Guinean collections seta length is clearly correlated with altitude, plants with long setae only growing at high altitudes. During fieldwork in Sarawak specimens with setae longer than 20 mm were found in summit scrub on Gunung Mulu at an altitude of c. 2300 m. On Gunung Mulu *D. blumei* occurs from the higher part of the submontane forest to the summit of the mountain. Where the forest becomes more open and passes into summit scrub, *D. blumei*, which grows on tree stems and branches in the upper montane forest, descends to the bases of shrubs and to the ground. These plants have erect stems, are relatively densely foliose and have erectopatent to widely patent leaves and long setae. It therefore seems that the variation in seta length is correlated with habitat and growth form rather than with geography.

Fleischer (1914) described a var. *papillisetum* based on De Kock 9 from New Guinea, to accommodate plants with long setae. Although Fleischer wrote in his original description that the seta of this variety is up to 15 mm long, his type specimen possesses a 22 mm long seta. Other features mentioned by Fleischer include a papillose upper half of the seta, hence the name, and a longer operculum, equalling the capsule in length. I do not find the seta in the type specimen of the var. *papillisetum* any rougher than in other specimens of *D. blumei*. The ratio between operculum length and capsule length appears not to be higher in specimens with a long seta than in those with a shorter one. Fleischer contrasted his var. *papillisetum* to the earlier described var. *laxifolium*, which includes pendent plants with widely spaced, widely patent leaves and relatively short setae. The type of Dixon's (1942) f. *subintegra* has setae c. 13 mm long, and is in no way different from other plants with short setae. Because of the lack of a gap in the distribution of seta length and corroborating characters I prefer not to recognise any varietal segregation.

The distribution map of *D. blumei* given by Lin (1981) shows some dots which are outside the actual distribution area of this species. The record for East India is based on the type specimen of *Dicranum leptocaulon* C. Müll., which was made synonymous to *D. blumei* by Gangulee (1971), but which is, in my opinion, not conspecific and seems to belong to *Dicranum*. As the type specimen of *Dicranum leptocaulon* is in a rather bad state and no additional material has been found, the identity of *D. leptocaulon* remains obscure. Several authors, e.g. Brotherus (1924), Brühl (1931), and Abeywickrama (1960), mention the occurrence of *D. blumei* in Sri Lanka. All these publications seem to go back to Fleischer (1904), but he also did not cite a collection to corroborate this record. As no collections of *D. blumei* from Sri Lanka could be located, it seems probable that Fleischer made a mistake here, which was copied by the subsequent authors.

The collection on which Brotherus' (1906) record from New Caledonia was based, Bernier s.n. in H-BR, has been tentatively placed in *D. billardierei* although it resembles *D. blumei* in general appearance, because of the erectopatent to widely patent, filiform leaves. The specimen, however, lacks the conspicuously large alar patches, with the strong angular wall-thickenings of the alar cells. Tixier's (1974) record from Vanuatu could not been checked as the material on which it is based was not available for study. Bartram (1950) was the first to record *D. blumei* from Fiji. The specimen on which this record was based, however, has now been identified as *D. braunii*. *Dicranoloma blumei* was recorded from Samoa by Muller (1897a). The collection on which this record was based, Olosina 3, could not be located. Schultze-Motel (1974) gives two other collections, Christophersen 2402[a] and 2404[a] (BISH) which have been identified as *D. braunii* in the present revision (see under that species for further discussion).

Thériot (1931) cites a collection by Poilane from Vietnam as belonging to *D. blumei*. Although this collection was not available for study and no other collections from Vietnam were seen, occurrence of *D. blumei* in Vietnam does not seem unlikely.

In his original description of *Dicranoloma braunfelsioides* Herzog (1920) compared this species with *Braunfelsia scariosa* (Wils.) Par. and *Dicranoloma laevifolium* (Broth. & Geh.) Par. Tan (1989) accommodated three Bornean plants in *D. braunfelsioides* and considered it to be closer to *D. blumei*. He, however, maintains *D. braunfelsioides* next to *D. blumei*, although he admits that the distinction is difficult and the only distinguishing character mentioned is the relative length of the acumen, which in *D. blumei* should be more than five times as long as the expanded basal part and in *D. braunfelsioides* only twice as long. As this character is judged to be insufficient to distinguish species and many intermediates are found, as previously indicated by Tan, *D. braunfelsioides* is here considered to be a synonym of *D. blumei*.

6. ***Dicranoloma braunii*** (C. Müll. ex Bosch & Lac.) Par. (1904: 25). Fig. 17

Dicranum braunii C. Müll. ex Bosch & Lac. in Dozy & Molk. (1858: 69). — *Dicranum dicarpon* Dozy & Molk. (1848: 144), hom. illeg., non *Dicranum dicarpum* Nees. — *Leucoloma braunii* (C. Müll. ex Bosch & Lac.) Broth. (1901: 322). Syntypes: Indonesia. Sumatra, Teysmann s.n. (L-lecto!; H-BR!); Java, ad arbores vetustas secus paludes montis Gedé, Zippelius s.n. (not located, not in L); comm. Rochussen s.n. (L!); comm. Holle s.n. (not located, not in L). Lectotype selected here.

Dicranum brachypelma C. Müll. (1851b: 595), hom. illeg., non *Dicranum brachypelma* C. Müll. (1851a: 550). — *Leucoloma brachypelma* Broth. (1901: 322). — *Dicranum braunii* C. Müll. ex Bosch & Lac. ssp. *brachypelma* (Broth.) Fleisch. (1904: 82). — *Dicranoloma brachypelma* (Broth.) Par. (1904: 25). — *Dicranoloma braunii* (C. Müll. ex Bosch & Lac.) Par. ssp. *brachypelma* (Broth.) J. Baumg. ex Froehl. (1953: 72). Type: Indonesia. Java, C.L. Blume s.n. (B-holo, destroyed; L-lecto!). Lectotype selected here. Synonymised by Eddy (1988).

Dicranum graeffeanum C. Müll. (1874: 62). — *Leucoloma graeffeanum* (C. Müll.) Broth. (1901: 322). — *Dicranoloma graeffeanum* (C. Müll.) Par. (1904: 27). Type: Samoa. Savai'i, inter alios muscos, Graeffe (B-holo, destroyed; S-lecto!, H-BR!). Lectotype selected here. Synonymised by

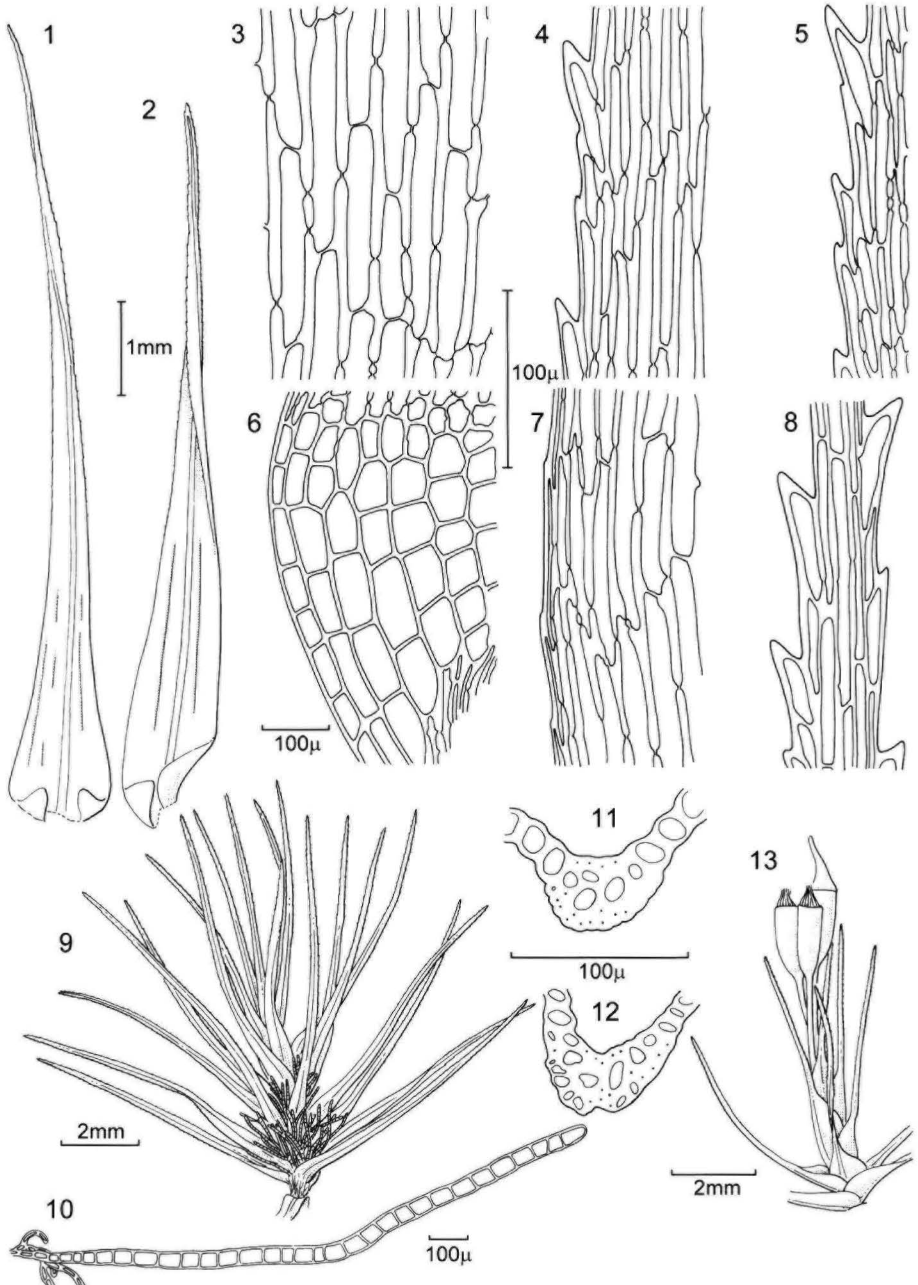

Fig. 17. *Dicranoloma braunii* — 1–2. leaf; 3. basal lamina cells; 4–5. upper lamina cells; 6. alar cells; 7. basal marginal and intramarginal cells; 8. abaxial view of the costa, distal part; 9. stem apex with clusters of gemmae; 10. gemma; 11–12. cross section through the costa, just above the alar patches; 13. perichaetium with sporogones. — 1, 5, 12. Fleischer s.n., Musci Frondosi Archipelagi Indici No. 84 (L); 2–4, 6-8, 11, 13. Iserentant 9512 (H); 9–10. Schiffner 10234 (L).

Bartram (1933).

Dicranum laevifolium Broth. & Geh. in Geh. (1898: 4), *syn. nov.* — *Leucoloma laevifolium* (Broth. & Geh.) Broth. (1901: 322). — *Dicranoloma laevifolium* (Broth. & Geh.) Par. (1904: 27). Type: Indonesia. Irian Jaya, Mt. Arfak ad Hatam, 5000–7000', Beccari 184 b (H-BR-holo!, FH-FL!, S!).

Dicranum nematosum Broth. & Geh. in Broth. (1898: 163). — *Leucoloma nematosum* (Broth. & Geh.) Broth. (1901: 323). — *Dicranoloma nematosum* (Broth. & Geh.) Par. (1904: 28). — *Dicranoloma brevisetum* (Dozy & Molk.) Par. var. *samoanum* (Broth.) Tan & T. Kop. f. *nematosum* (Broth. & Geh.) Tan & T. Kop. (1983: 326). Type: Papua New Guinea ["British New Guinea"]. In reg. inf., W. MacGregor 686 (H-BR-holo!, S!). Synonymised by Norris & Koponen (1990).

Dicranum braunii C. Müll. ex Bosch & Lac. f. *mindanense* Fleisch. (1904: 84). — *Dicranum mindanense* Broth. ex C. Müll. (1900: 288), *nom. nud.* — *Dicranoloma braunii* (C. Müll. ex Bosch & Lac.) Par. f. *mindanense* (Fleisch.) Sasaoka (1928: 184). — *Dicranoloma braunii* (C. Müll. ex Bosch & Lac.) Par. var. *mindanense* (Fleisch.) Ihsiba (1929: 4). — *Dicranoloma mindanense* (Fleisch.) Iwats. & Tan (1979: 188). Type: Philippines. South Mindanao, Mt. Batangan, O. Warburg s.n. (B-holo, destroyed; H-BR-lecto!). Lectotype selected by Tan & Koponen (1983). Synonymised with *Dicranoloma brevisetum* var. *samoanum* by Tan & Koponen (1983).

Dicranoloma braunii (C. Müll. ex Bosch & Lac.) Par. var. *samoana* Broth. in Rech. (1908: 387). — *Dicranoloma brevisetum* (Dozy & Molk.) Par. var. *samoanum* (Broth.) Tan & T. Kop. (1983: 326). Type: Samoa. Savai, Maungaafi, K. & L. Rechinger s.n. (H-BR-holo!); Urwald von Tiavi, K. & L. Rechinger s.n. (W!). Synonymised by Tan & Koponen (1983).

Dicranoloma braunii (C. Müll. ex Bosch & Lac.) Par. f. *brevifolia* Dix. (1922: 497). Type: Papua New Guinea. Central, near Boku, Port Moresby, J.B. Clark 4 (BM!). Synonymised with *Dicranoloma brevisetum* var. *samoanum* by Tan & Koponen (1983).

Dicranoloma hemineuron Dix. (1932: 22), *syn. nov.* Type: Indonesia. East Sumatra, Gn. Sibajak, Dg. Singkoet, in silvis primig., Sept. 1930, Fr. Verdoorn 74c (BM-holo!, JE!).

Dicranoloma angustifrondreum Dix. (1935: 70). Type: Malaysia. N. Borneo, Tenompok, on tree, 1220 m, Enriquez 18111 (BM-holo!; L-iso!). Synonymised by Eddy (1988).

Dicranoloma spiniforme Bartr. (1952: 237), *syn. nov.* Type: Australia. North Queensland, Mt. Finnegan, abundant on undergrowth in high mountain forest, 1100 m, Brass 20090 (FH-Bartr.!)

Bartramia pungentella C. Müll. ex Par. (1900: 35), *nom. nud.*, *syn. nov.* — *Breutelia pungentella* (C. Müll. ex Par.) Par. (1900: 53), nom. nud. Authentic specimen: Papua New Guinea "Nova Guinea austro-or." Distr. Moresby, in montosis Moroka, 1300 m, Loria 1585 (FH-FL!, H!).

Dicranum horridum Geh. ex C. Müll. (1901: 294), *nom. nud.*, *syn. nov.* Authentic specimen: Indonesia. West Sumatra, "Padangsche Bovenlanden", Mt. Singalang, O. Beccari 93a (BM!, JE!).

Pseudoautoicous. Dwarf males 1–3 mm tall. Leaves 0.8–2 mm long, ovate-lanceolate, acuminate, costate, elimbate; margin serrulate in the upper half, entire below. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants (0.5–)2–15(–18) cm tall, growing in turfs, occasionally pendulous, glossy yellowish green to yellowish-brown; large plants often with dull brown lower parts. Stem reddish brown to brown, subflorally branched, densely tomentose, densely foliose; diameter (0.2–)0.3–0.4 mm, central strand absent, cortical cells thick-walled. Gemmae often present in the apical part of the stem, frequently in large clusters, at the base of the rhizoids and replacing them, reddish, filamentous, uniseriate, up to 5 mm long; walls smooth to slightly rough.

Leaves 3–13×0.5–1.3 mm, either triangular-linear to ovate-linear, gradually tapering or above a broadly ovate basal part rather abruptly contracted into a subula, flat to canaliculate, plicate, widely patent throughout, occasionally falcate-secund or circinate. Alar patches distinct, 0.2–0.6×0.2–0.5 mm, triangular, reaching the costa or not. Margin just above the alar patch entire or serrulate, upwards becoming more strongly serrate; upper 2/3–3/4 coarsely serrate. Limbidium almost always absent. Costa 50–100 μm wide, 20–50(–60) μm thick, either well-marked in its entire length or from just above the alar patches, percurrent or ending a few cells below leaf apex, abaxially bearing 2(–4) rows of teeth in the distal 1/2–3/4; guide cells 4–6(–8); adaxially with 1–2(–3) layers of stereids and, adjacent to the guide cells, very rarely with 1–2 cells with a lumen as large as those of the guide cells, abaxially with 1–2 layers of stereids, mostly divided into (2–)3(–5) small bundles, separated by cells with a distinct lumen or groups of such cells; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells (30–)50–180×8–18 μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 1–3. Alar cells 20–100×15–50 μm, quadrate to rectangular, not inflated; walls firm, 2–7 μm thick, mostly not pitted, colourless or yellowish to brown. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with orange-brown to brown walls. Upper lamina cells (30–)40–150(–190) μm, elongate to linear, straight, similar to the basal lamina cells; walls incrassate, pitted, lumen wall ratio 1–3. Cells at extreme apex occasionally distinctly shorter. Teeth at leaf margin 10–30 μm, consisting of 1(–2) cells; lumina not conspicuously larger than in the adjacent cells. Perichaetial leaves (2.5–)4–8×0.6–1.5 mm, abruptly contracted into a subula; basal part 1–3 mm long, broadly ovate, clasping to sheathing; the outer perichaetial leaves resembling stem leaves.

Sporogones (1–)2(–5) per perichaetium. Vaginula 1–1.5 mm long, reddish-brown to dark brown. Seta 1.5–2.5 mm long, light yellow to reddish-yellow, smooth; 0.14–0.2 mm in diameter, central strand present, cortical cells thin-walled, peripheral layer with very thick walls, central part decayed at maturity. Capsule (0.8–)1–2 mm long, reddish-brown to dark brown, ellipsoid to cylindrical, straight. Exothecial cells 30–110×10–50 μm, elongate, irregularly shaped, mostly not in regular longitudinal rows. Annulus consisting of 2–3 rows of quadrate, thick-walled cells, persistent. Peristome teeth yellowish to reddish, 0.4–0.7 mm long, 50–90(–140) μm wide at base, long-attenuate, asymmetrically bifid in the upper 2/3–7/8, often fenestrate below almost to the base; outer face papillose above; basal half either irregularly vertically to obliquely striate or striate and papillose; inner face either papillose throughout or smooth in the basal half; distal trabeculae densely papillose, the inner ones much thicker and more strongly ornamented than the outer ones. Operculum 0.8–1 mm, reddish-brown, obliquely rostrate above a conical base. Calyptra 2–3 mm long, greenish brown, more or less transparent, cucullate. Spores 18–30 μm, spherical, finely papillose.

Illustrations. Dozy & Molkenboer 1858: Vol. 1, t. 56, f. 1-21 (as *Dicranum brachypelma*); t. 57, f. 1–21 (as *Dicranum braunii*); Dixon 1935: t. 1, f. 3 (as *Dicranoloma angustifondreum*); Bartram 1939: f. 62; Tan & Koponen 1983: f. 55–58 (as *Dicranoloma brevisetum* var. *samoanum*); Eddy 1988: f. 140 A–H; Akiyama 1990: f. 26, f. 41; Norris & Koponen 1990: f. 10 g–m (as *Dicranum braunii*).

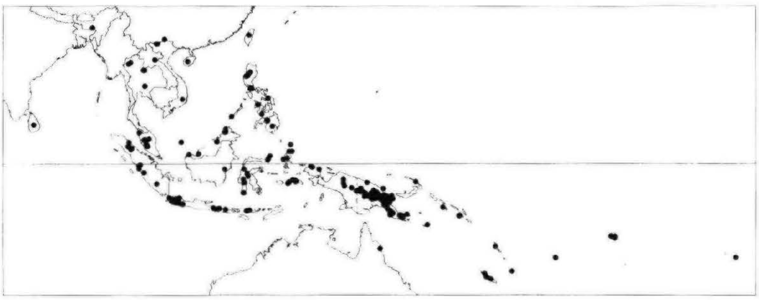

Fig. 18. Distribution of *Dicranoloma braunii*.

Distribution. Sri Lanka, India (Khasi Hills), China (Hainan), Taiwan, Thailand, Laos, Vietnam, Peninsular Malaysia, Sumatra, Java, Natuna Islands (Natuna Besar), Borneo, Philippines (Luzon, Negros, Samar, Mindanao), Sulawesi, Nusa Tenggara (Bali, Lombok, Flores), Maluku (Morotai, Ternate, Halmahera, Seram, Ambon, Saparua), New Guinea, Bismarck Archipelago (New Ireland), d'Entrecasteaux Islands (Goodenough I.), Louisiade Archipelago (Rossel I.) Solomon Islands (Kolombangara, Guadalcanal), Vanuatu (Espiritu Santo, Anotom), New Caledonia, Fiji (Viti Levu), Samoa (Savai'i, Upolu), Society Islands (Tahiti) (Fig. 18).

Ecology. Growing in lower montane and upper montane forest and in New Guinea also in subalpine forest and grassland, from 100 to 3800 m, mostly above 600 m and only on New Guinea above 3000 m. Often found in disturbed and secondary forest, in garden sites and in swampy, grassy areas in the montane forest zone. In Java occasionally found in *Pinus* plantations. Also occurring in areas with a monsoon climate. Mostly epiphytic, on stems and branches, mostly in turfs, but along forest edges and along streams also pendulous; also often found on logs and stumps, occasionally terrestrial or on rocks; occasionally epiphyllous.

Selected additional specimens examined. SRI LANKA. Hunasgirias Peak, Fleischer 255 (L). INDIA. Meghalaya, Khasi Hills, Mawphlang, Griffith 71 (NY). THAILAND. Payap, Doi Suthep, granitic massive W of Chiengmai, Doi Buak Ha, Touw 8817 (BM, FH, L, MO, NY); Udawn, Phu Luang, Touw 10579 (BM, FH, L, MO, NY); Prachinburi, Khao Yai National Park, Khao Khieo, Touw 12038 (BM, L, MO, NY). LAOS. Xiangkhoang, Pu Muteng, Kerr 511h (BM). VIETNAM. Eberhardt 491 (H-BR), 492 (H-BR); Hoang-Lien Son, Mts. Hoang-Lien Son, Bartke 195 (EGR); Sapa, Petelot 97 (PC); Lam Dong, Mt. Lang Bian, Tixier s.n. (EGR). CHINA. Hainan Island. Bawanglin Forestry Station, Reese 17661 (H, MO, NY). TAIWAN. Pingtung, Arika, Matsuda 1288 (H-BR). PENINSULAR MALAYSIA. Kedah, Gn. Jerai (Kedah Peak), Holttum (BM, KLU, L); Selangor, Gn. Nuang, Meijer B 12330 (L); Pahang, Sri Genting, Gn. Ulu Kali, Haji Mohamed 4753 (KLU); Cameron Highlands, Haji Mohamed 8971 (KLU); Bt. Fraser, Wood 1332 (BM, L). INDONESIA. SUMATRA. Sumatera Utara, Gn. Sinabung, Touw & Snoek 25382 (L); Sumatera Barat, Gn. Singgalang, Schiffner 10251 (L, S); Gn. Kerinci, Meijer B 8923 (L). JAVA. Jawa Barat, Gn. Gede, Gn. Kandangbadak, Fleischer s.n., Musci Frondosi Archipelagi Indici, No. 84 (BM, H-BR, JE, L, NY); Gn. Pangrango, Nyman 25 (BM, FH, H-BR, NY); Gegerbentang, Noerta & Soekar 1277 (L); Gn. Megamendong, Schiffner 10234 (L, S); Jawa Timur, Dataran-tinggi Ijen (Idjen Plateau), Herb. Fleischer 82 (FH-FL). NATUNA BESAR. Gn. Ranai, Van Steenis 1449a (BM, L). BORNEO. SABAH. Gn. Kinabalu, Kilembun River, J. & M.S. Clemens s.n. (FH-Bartr.); Gn. Kinabalu, Kemburongoh, Meijer B 11762 (L); Banjaran Crocker (Crocker Range), Gn. Alab, Menzel, Frahm, Frey & Kurschner 4729 (FH). SARAWAK. Gn. Mulu, Touw 20545 (L); Pueh Range, Kampong Pueh, Bell 1957 (BM); KALIMANTAN. Kalimantan Timur, Gn. Beratus (Peak of Balikpapan), Meijer B 2378 (L). PHILIPPINES. LUZON. Abra, Lepanto, Mt. Lamunan, Micholitz s.n. (JE, L); Mountain [Bontoc Subprovince], Vanoverbergh BS 524 (BM, FH-Bartr., H-BR, MO, NY); Benguet, Baguio, Elmer 8542 (BM, FH, H-BR, L, MO, NY); Pauai, Santos BS 32062 (BM, H-BR, NY); Ifugao, Mt. Polis, McGregor BS 20313 (BM, FH-Bartr., H-BR, NY); Laguna, Mt. Makiling, near Los Banos, Baker 2751 (BM, H-BR, L, MO, NY); Quezon, Mt. Santo Tomas, McGregor BS 47445 (FH-Bartr.); La Union, Mt. Santo Tomas, Williams 3134 (FH, H-BR, NY). VISAYAN ISLANDS. Samar, Mt. Sinogbungan, Tan & Price 75-1 (MO); Negros Oriental, Dumaguete, Chapman 44 (FH-Bartr.). MINDANAO. Lanao del Sur, Palao Amopo, Iligan River, Bartlett 15946 (FH, FH-Bartr., NY); Davao del Sur, Mt. Apo, Williams 2655 (FH, H-BR, NY); Davao, Mt. Batangan, Warburg s.n. (H-BR). PALAWAN. Mt. Mantalingajan, Edano PNH 594 (L). SULAWESI. Sulawesi Utara, Gn. Ambang Nature Res., Gn. Muajat, De Vogel & Vermeulen 7261 O (L); Minahassa, Manado, De Vriese s.n. (H-BR, L, S); Sulawesi Tengah, Gn. Roroka Timbu, Hennipman 5247 (L); between Pendolo and Mangkatana, Touw & Snoek 24411 (L); Sulawesi Selatan, Pegunungan Latimojong, Gn. Rantemario, Eddy 4820 (BM); Gn. Lompobattang (Bonthain Peak), Prince Leopold 2 (BM), 14 (BM). NUSA TENGGARA. Bali, Bt. Tapui, Meijer 10509a (MO, NY); Gn. Batur, Touw 22392 (L); Lombok, Rinjani, Gn. Pussuk, Elbert 1717 (H-BR, L); Flores, Ruteng, Poco Tador Walok, Schmutz 6844 (L); Gn. Pontanao, Touw & Snoek 22465 (L). MALUKU. Morotai, Gn. Sangowo, Main s.n. (L); Ternate, De Vriese (L); Halmahera, Gn. Sembilan, Pleyte 331d (L); Seram, Gn. Totaniwel, Akiyama c-15918 (L, NY); Ambon, Toena, Boerlage s.n. (FH-FL); Saparua, De Vriese s.n. (L). IRIAN JAYA. Sorong, Pegunungan Tamrau, Gn. Kusemun, Van Royen, Sleumer & Schram 7811 (CBG, H, L); Jayawijaya, Puncak Trikora (Mt. Wilhelmina), Brass & Meijer-Drees 9768 (FH-Bartr.); Jayawijaya, "Bele River", 18 km NE of Danau (Lake) Habbema, Brass 11518 (FH); Jayapura, Pegunungan Sterren (Star Mts.), Mt. Antares, Van Zanten 630 (BM, L, NY). PAPUA NEW GUINEA. West Sepik, Sepik River, downstream from Telefomin, O'Hara 18 (H, L); Star Mts., Folongonom, Touw 17909 (L); East Sepik, Prince Alexander Range, Robbins 1382 (L); Madang, Herzog Mts., Wago, Eddy 1636 (BM); Southern Highlands, Onim Forestry Station, Ialibu, Streimann 24545 (CBG, H, MO, NY); Enga, Sugarloaf Mts, Tsak Valley, Robbins 2837 (L); Western Highlands, Mur Mur Pass, Streimann 21178 (CBG, H, NY); Simbu, Mt. Wilhelm, Van Zanten 683604 (BM, JE, L, NY); Eastern Highlands, Mt. Zapaliga, Iserentant 9512 (BM, CBG, H, L, MO, NY); Morobe, Mt. Missim, Bellamy 231 (CBG, H, MO, NY); Central, Owen Stanley Range, The Gap, Carr 15079 (BM, CBG, H, L, NY); Mt. Yule, Veldkamp & Kuduk 8553 (L); Milne Bay, Maneau Range, Mt. Dayman, Brass 22326 (CBG). BISMARCK ARCHIPELAGO. Karkar Island, E of Mom, Hoffmann 89-732 (BM, CBG, L, MO); New Ireland, Lelet Plateau, Koie (Danish Noona Dan Expedition) 2117 (L, NY). D'ENTRECASTEAUX ISLANDS. Goodenough Island, Brass 24478 (FH). LOUISIADE ARCHIPELAGO. Rossel Island, Mt. Rossel, Brass 28405 (BM, FH, L) SOLOMON ISLANDS. Kolombangarah, Braithwaite 4426 (L); Guadalcanal, Mt. Popomanaseu, Robbins 4321 (L). VANUATU. Espiritu Santo, Lairiri (Santo Peak), Robbins 3842 (L); Anatom, Gunn 276 (H-BR). NEW CALEDONIA. Plateau de Dogny, Franc in Theriot, Musci et Hep. Nov. Cal. 153 (FH-FL, JE, L); Mt. Boulinda, Moore 10080a (MO), 10085 (MO, NY). FIJI. Viti Levu, Tomanivi (Mt. Victoria), Gillespy 414 (BM, FH-Bartr.); ridge between Mt. Nanggaranambuluta and Mt. Namama, E of Nandarivatu, Smith 5682 (BM, L, NY). SAMOA. Savaii, Mt. Mafane, Bartlett 32438 (B); above Matavanu, Christophersen 2402 a (BISH, FH-Bartr.), 2404a (BISH, FH-Bartr.); W of Mauga Silisili, Whistler 2550 (B). SOCIETY ISLANDS. Tahiti, Mt. Aorai, Whittier 2708 (BISH, BM, MO, NY, PC).

Dicranoloma braunii is easily distinguished from all other species of *Dicranoloma* by the combination of the following features: absence of a central strand, leaves which are triangular-linear or abruptly contracted above a broadly ovate basal part and mostly plicate, absence of a limbidium, and often present large clusters of vegetative propagulae.

Bryologists have had much trouble distinguishing *Dicranoloma braunii* from *D. brevisetum* and *D. leucophyllum* (Hampe) Par. Fleischer (1904) used the presence of a limbidium to distinguish *Dicranum leucophyllum* from *D. brevisetum* and *D. braunii* and the length of the leaves and the serration of the leaf margin to discriminate between *D. brevisetum* and *D. braunii*. Bartram (1939), in his "Mosses of the Philippines", used the presence of vegetative propagulae and the golden brown colour of the plants to distinguish *Dicranoloma braunii* from *D. leucophyllum*.

In their treatment of the Philippine Dicranolomas, Tan & Koponen (1983) discovered that Bartram's primary distinguishing character did not work, because the isosyntype of *Dicranum leucophyllum* they studied (*Teysman s.n.*, the Sumatran plant) also bears vegetative propagulae. After comparing the type specimens of *D. braunii*, *D. brevisetum*, and *D. leucophyllum* they decided that "the morphological differences appear to be rather subtle and often tenuous or, at times, even lie in trivial and minute details" and that it was wise to merge the three species into one and separate two taxa at the varietal level. Their var. *brevisetum* corresponds with *D. brevisetum* in this revision, their var. *samoanum* with *D. braunii*. Their distinction between the varieties is based on falcate-secund leaves, lamina cells that are arranged in straight rows and only occasional presence of filiform propagulae in var. *brevisetum* and erect-spreading to spreading leaves, lamina cells that are not arranged in straight rows and frequent presence of filiform propagulae in var. *samoanum*. Besides, as strongly falcate- and even circinate-leaved forms of var. *samoanum* do occasionally occur, they established a f. *nematosum* to accommodate such forms. Tan (1989), when treating *Dicranoloma* in Sabah, did not mention varieties.

In his "Malesian Mosses", Eddy (1988) maintained three species, *Dicranoloma braunii*, *D. brevisetum* and *D. leucophyllum*. His main characters to distinguish *D. braunii* from *D. brevisetum* and *D. leucophyllum* were the plicate leaves and the contraction of the leaf above the alar patches in *D. braunii*.

In their treatment of Dicranaceae of the Huon Peninsula, Papua New Guinea, Norris and Koponen (1990) maintained only one species, *Dicranum braunii*, which is actually the same as Tan and Koponen's interpretation of *Dicranoloma brevisetum*, the older name *Dicranum brevisetum* being illegal. As to segregation at the varietal level they stated that while some of their specimens were easily keyed out to one of the varieties many showed intermediate characteristics. However, all the plants they studied probably belonged to *D. braunii*, as in the present revision only one collection of *D. brevisetum* from New Guinea was found.

Akiyama (1990), dealing with mosses from Seram, distinguished two species, *Dicranoloma braunii* and *D. leucophyllum*, using the presence of gemmae and the plication of the leaves as the main characters to distinguish *D. braunii* from *D. leucophyllum*.

In this treatment two species are distinguished, *Dicranoloma braunii* and *D. brevisetum*. *Dicranoloma braunii* may be distinguished from *D. brevisetum* by the plicate leaves and the absence of a limbidium, *D. brevisetum* having smooth to slightly rugose, but never plicate, leaves and a limbidium, which, however, may be ill-developed. All the other characters mentioned above, except Fleischer's characters and the arrangement of the cells, do apply in most cases, but not in all.

There is a difference in distribution between *D. brevisetum* and *D. braunii*, *D. braunii* reaching farther than *D. brevisetum* at all sides of its range, except for southern India. From Fiji and Samoa specimens are found with long filiform, mostly smooth leaves like in some forms of *D. brevisetum*. These forms, however, lack a limbidium, the most reliable distinguishing character, and therefore are placed in *D. braunii*. Most of these specimens have earlier been identified and reported as *D. blumei*.

In the original publication of *Dicranum laevifolium*, Geheeb (1898), compared his new species with *D. reflexum* and *D. reflexifolium*, from which it should differ by smooth leaves. Eddy (1988) wrote that "nothing in the description rules out conspecifity with *Dicranoloma assimile*". According to Tan, in an annotation of the holotype, made in 1987, *Dicranoloma laevifolium* is "probably conspecific with [the] *Dicranoloma robustum* group because of the thick costa at leaf base". Norris and Koponen (1990), finally, synonymised *Dicranum laevifolium* with *D. billardierei*. However, the absence of a central strand and a limbidium in the type specimen of *Dicranum laevifolium* rules out conspecifity with any of the above-mentioned species. Although not readily recognised as such because of the gradually attenuate leaves and the absence of propagulae, the type of *D. laevifolium* resembles *D. braunii* in every aspect and is treated here as a synonym of that species. Contrary to what Geheeb (1898) writes in his protologue, the leaves of the type of *D. laevifolium* are plicate, as was observed previously by Norris and Koponen (1990).

Dicranum hemineuron Dix. was synonymised with *D. brevisetum* var. *brevisetum* by Tan & Koponen (1983). The slightly plicate leaves and the absence of a limbidium in the type, however, point to conspecifity with *D. braunii*. Epiphyllic plants, like the type of *D. hemineuron*, have been frequently found of *D. braunii* but not of *D. brevisetum*.

Bartram (1952) described *D. spiniforme*, based on a collection made by Brass on Mt. Finnigan in northern Queensland. Bartram compared his new species with *D. blumei* from which it could be distinguished by the shorter leaves and sharply spinose-serrate leaf margins, with the teeth reaching downwards as far as leaf base. Although in some leaves of the type specimen a rudimentary limbidium could be discerned, consisting of a few cells only, it is identical to *D. braunii* in all other respects and therefore treated as a synonym. *Dicranoloma braunii* was not earlier reported from Australia and is known only from the type locality of *D. spiniforme*.

Another significant range extension was found at the western end of the distribution area, where *Dicranum braunii* was formerly not known to occur west of Thailand. During the present revision collections were seen from Sri Lanka and East India. The specimen from Sri Lanka was found in Fleischer's exsiccatae series Musci Frond. Archipelagi Indici no. 255 which was distributed as *Leucoloma molle* (C. Müll.) Mitt. var. *longipilum* Fl. The larger part of the packet in L consists of *D. braunii* but a few shoots of *Leucoloma insigne* (C. Müll.) Jaeg. (det. C. La Farge-England) are mixed with it, so other duplicates may consist completely of that species. The collection from East India is *Griffith 71* (NY) from Mawphlang [Moflong] in the Khasi Hills. It was found in Mitten's herbarium under a herbarium name. This name is absent from Mitten's Musci Indiae Orientalis (1859).

7. ***Dicranoloma brevisetum*** (Dozy & Molk.) Par. (1904: 25). Fig. 19

Megalostylium brevisetum Dozy & Molk. (1848: 146). — *Dicranum brevisetum* Dozy & Molk. (1844: 302), hom. illeg., non *Dicranum brevisetum* Brid. (1819: 56). — *Didymodon brachypus* Hampe ex C. Müll. (1848: 376), nom. inval. in synon. — *Leucoloma brevisetum* (Dozy & Molk.) Broth. (1901: 322). Syntypes: Indonesia. Java, rarissime in summo monte Gedé, Zippelius s.n. (L-lecto!); Java, in monte Pangerango, Kuhl & Van Hasselt s.n. (H-BR!, L!, S!). Lectotype selected here.

Dicranum brevisetum Dozy & Molk, hom. illeg. var. *angustum* Lac. (1870: 225), *syn. nov.*. — *Dicranum brevisetum* Dozy & Molk, hom. illeg. var. *argenteum* Par. (1895: 346), nom. illeg. err. pro *D. brevisetum* Dozy & Molk. var. *angustum* Lac. Syntypes: Indonesia. Java, in monte Pangerango, 7000–9000', De Vriese s.n. (L-lecto!); Zippelius s.n. (not located, not in L). Lectotype selected here.

Dicranum leucophyllum Hampe ex Lac. (1872: 10). — *Leucoloma leucophyllum* (Hampe ex Lac.) Broth. (1901: 322). — *Dicranoloma leucophyllum* (Hampe ex Lac.) Par. (1904: 27). Syntypes: Indonesia. Sumatra, Teysmann s.n. (L-lecto!, H-BR!, S!); Java, Teysmann s.n. (not located, not in L). Lectotype selected here. Synonymised by Tan & Koponen (1983).

Dicranum leucophyllum Hampe ex Lac. var. *kurzii* Fleisch. (1904: 85). — *Dicranum leucophyllum* Hampe ex Lac. var. *kurzii* Fleisch., Musci Archip. Indici, ser. 2, no. 85. 1899, *nom. nud.*. — *Dicranoloma leucophyllum* (Hampe ex Lac.) Par. var. *kurzii* (Fleisch.) Par. (1904: 27). Type: Indonesia. Java, Kandang-Badak bis Gipfel des Pangerango, Juli 1898, Fleischer s.n. (FH-FL-holo?, not found; BM!, FH-Bartr.!, H-BR!, JE!, L!, NY!, S!). Synonymised by Dixon (1919).

Dicranoloma defoliatum Froehl. (1962: 91), *syn. nov.* Type: Malaysia. Sabah ["North Borneo"]. Kinabalu, North of Ranau, Bukit Ampuan, summit region, 4000–4200 ft., Meijer s.n. (S-holo?, not found; iso in L! under No 12717).

Dicranoloma damanhurii Tan & Mohamed (1990: 359), *syn. nov.* Type: Malaysia: Malay Peninsula, Pahang, Gunung Jasar Trail no 11, near peak, Damanhuri 2028 (KLU-holo, not available; FH!, H!, NICH, NY, UKMB). Paratypes: Malaysia. Malay Peninsula, Pahang, Gunung Jasar, Damanhuri 1983 (KLU, UKMB, US); Cameron Highlands, Gunung Beremban, Damanhuri 1625 (H, KLU, L!, UKMB), 1641 (H, KLU, UKMB).

Dicranoloma leucophyllum (Hampe ex Lac.) Par. f. *rufescens* Fleisch., Musci Archip. Indici ser. 10, No. 453. 1908 *nom. nud.*, *syn. nov.* Original specimen: Sri Lanka. Hortonplains am Berg Totopolayagalla an Baumen, 2600 m, Fleischer s.n. (BM!, FH-Bartr.!, JE!, L!, NY!).

Pseudoautoicous. Dwarf males 0.5–2 mm tall. Leaves 0.5–1 mm long, ovate-lanceolate, acuminate, ecostate, elimbate; margin serrulate in the upper half, entire below. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 4–16 cm tall, growing in turfs or pendulous, pale green or brown to glossy yellowish or reddish-brown. Stem reddish brown to brown, subflorally branched, laxly to densely foliose, densely tomentose; diameter 0.25–0.6 mm, central strand absent, cortical cells thick-walled. Gemmae occasionally present near stem apex, never in large clusters, at the base of the rhizoids, reddish, filamentous, uniseriate, up to 5 mm long; walls smooth to slightly rough.

Leaves 6–20×0.5–2.5 mm, ovate-lanceolate to ovate-linear, gradually tapering, mostly smooth throughout, occasionally slightly rugose in the basal c. 1/2, either canaliculate throughout or canaliculate at base and subtubulose higher up, either falcate-secund throughout or erectopatent to widely patent. Alar patches distinct, (0.2–)0.25–0.5(–0.6)×

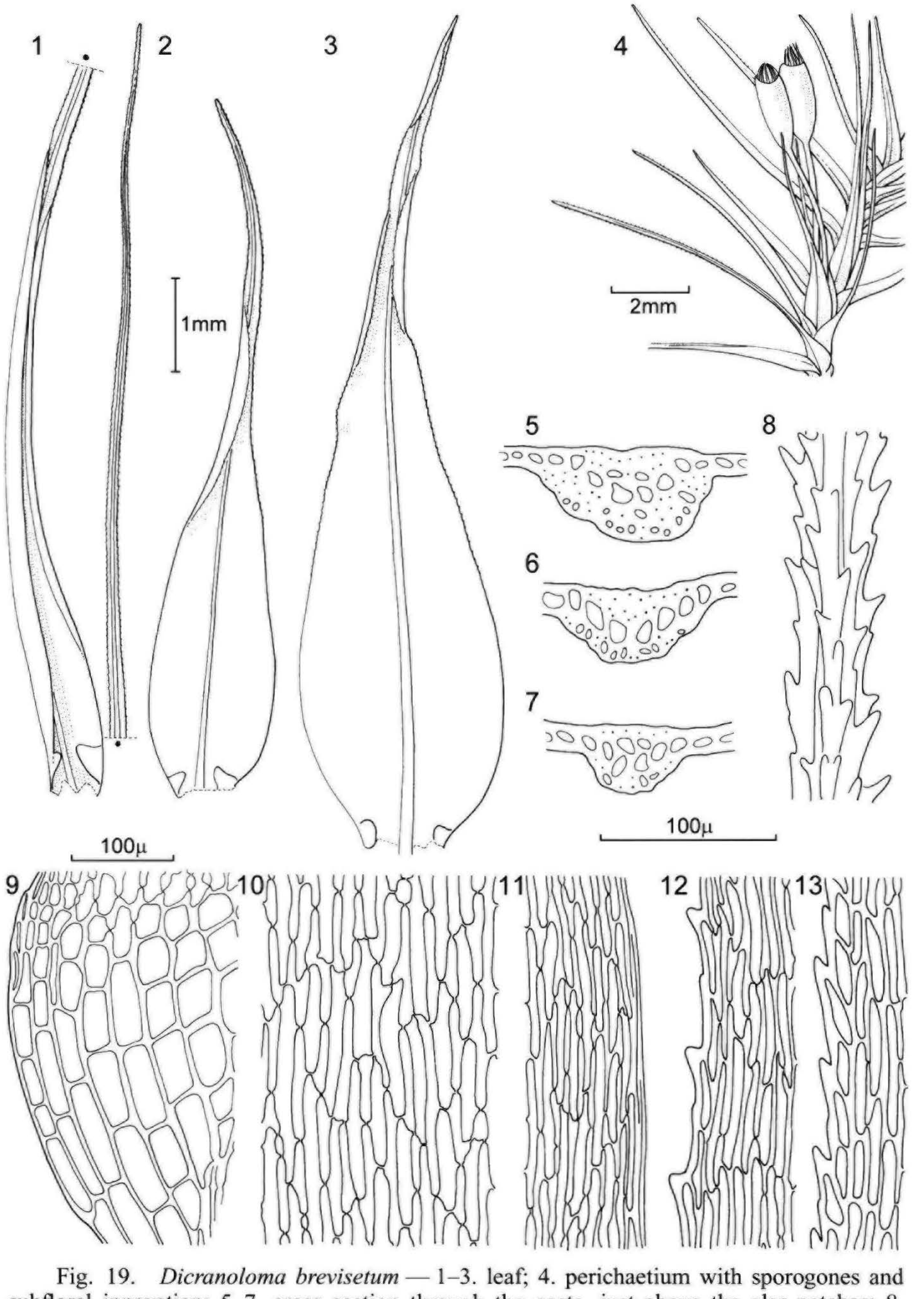

Fig. 19. *Dicranoloma brevisetum* — 1–3. leaf; 4. perichaetium with sporogones and subfloral innovation; 5–7. cross section through the costa, just above the alar patches; 8. abaxial view of the costa, distal part; 9. alar cells; 10. basal lamina cells; 11. marginal and intramarginal cells; 12–13. upper lamina cells. — 1. Noerta & Soekar 2014 (L); 2, 6, 13. Fleischer s.n., Musci Frondosi Archipelagi Indici No. 85 (H-BR, L; isotype of *D. leucophyllum* var. *kurzii*); 3, 5, 8. Schiffner 10286 (L); 4, 7, 9–12. De Wilde & De Wilde-Duyfjes 14260 A (L).

(0.2–)0.25–0.4 mm, triangular, not reaching the costa. Margin serrate in the upper 1/2–3/4, entire below, mostly straight, occasionally slightly undulate in the basal c. 1/2 of the leaf. Limbidium consisting of 1–5 rows of cells, reaching from just above the alar patches to the dentate part of the margin. Costa (45–)60–100(–120) μm wide, 30–55 μm thick, either well-marked in its entire length or from just above the alar patches, percurrent or ending a few cells below leaf apex, abaxially bearing 2–4 rows of teeth in the distal 1/2–3/4; guide cells 4–7; adaxially with 1–2(–3) layers of stereids and, adjacent to the guide cells, often with 1–3 cells with a distinct lumen, which may be as large as those of the guide cells, abaxially with 1–2(–3) layers of stereids, mostly divided into (2–)3(–4) small bundles, separated by cells with a distinct lumen or groups of such cells; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells 30–160(–180)×8–16(–20) μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 1–3.5. Alar cells 20–100(–140)×(15–)20–50 μm, quadrate to rectangular, not inflated; walls firm, 2–8(–10) μm thick, equally thickened to slightly collenchymatous, mostly not pitted, colourless or yellowish to brown. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with orange-brown to brown walls. Limbidium cells 70–180×3–4 μm, linear, with very thick, non-pitted walls and very narrow, almost indiscernable lumina. Upper lamina cells 30–140×6–12(–14) μm, elongate to linear, mostly straight, often with some cells slightly slanting or bent, similar to the basal lamina cells or gradually shorter; walls incrassate, pitted, lumen wall ratio 1–3(–4). Cells at extreme apex occasionally distinctly shorter. Teeth at leaf margin 10–20(–30) μm, consisting of a single cell; lumina not conspicuously larger than in the adjacent cells. Perichaetial leaves 5–13×1–1.3 mm, either gradually tapering or abruptly contracted into a subula; basal part 1–4 mm long, broadly ovate to elliptical, clasping to sheathing; subula, if present, often reflexed in the outer perichaetial leaves.

Sporogones 1–2(–4) per perichaetium. Vaginula 1.4–2 mm long, reddish-brown to dark brown. Seta 2.5–4 mm long, yellowish to reddish-brown, smooth; 0.2–0.22 mm in diameter, central strand present, cortical cells thin-walled, peripheral layer with very thick walls, central part decayed at maturity. Capsule 1.5–2 mm, reddish-brown to dark brown, ellipsoid to cylindrical, straight. Exothecial cells 30–100(–130)×15–40(–50) μm, elongate, irregularly shaped, mostly not in regular longitudinal rows. Annulus consisting of 2(–3) rows of quadrate, thick-walled cells, persistent. Peristome teeth yellowish to reddish, 0.3–0.8 mm long, 65–100 μm wide at base, long-attenuate, asymmetrically bifid in the upper 3/4–7/8, often fenestrate below almost to the base, the wider segment occasionally bifid and/or fenestrate as well; outer face mostly vertically to obliquely striate, occasionally almost smooth, in the basal c. 1/2, papillose above; inner face either papillose throughout or smooth in the basal half; trabeculae papillose, the inner ones thicker than the outer ones. Operculum 1.2–1.7 mm, reddish-brown, obliquely rostrate above a conical base. Calyptra 1.8–3 mm long, greenish to brownish, more or less transparent, cucullate. Spores 20–35 μm, spherical, finely papillose.

Illustrations. Dozy & Molkenboer 1848: t. 64, f. 1–21 (as *Megalostylium brevisetum*); Van der Sande Lacoste 1872: t. 4C, f. 1–7 (as *Dicranum leucophyllum*); Fleischer 1904: f. 8 a–b (as *Dicranum brevisetum*); Bartram 1939: f. 63 (as *Dicranoloma leucophyllum*); Tan & Koponen 1983: f. 46–53; Eddy 1988: f. 138 A–E, f. 141 A–H (as *Dicranoloma leucophyllum*); Akiyama 1990: f. 27; f. 42 (as

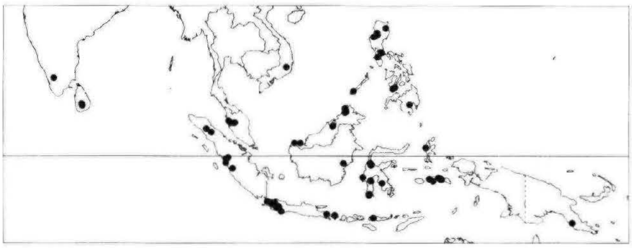

Fig. 20. Distribution of *Dicranoloma brevisetum*.

Dicranoloma leucophyllum); Tan & Mohamed 1990: f. 3 a–j (as *Dicranoloma damanhurii*).

Distribution. India, Sri Lanka, Vietnam, Peninsular Malaysia, Sumatra, Java, Borneo, Philippines (Luzon, Negros, Mindanao, Palawan), Lesser Sunda Islands (Bali, Flores), Sulawesi, Maluku (Halmahera, Seram) (Fig. 20).

Ecology. Growing in lower montane and upper montane forest, from 600 to 3000 m, mostly above 1000 m. Rarely found in disturbed forest. Also occurring in areas with a monsoon climate. Mostly epiphytic, on stems and occasionally branches of trees, often pendent; occasionally terrestrial or on logs and stumps.

Selected additional specimens examined. SRI LANKA. Hunasgirias Peak, Fleischer 255 (L); Pidurutalaga, Beccari 9 (BM, L); Rhamboda Pass, Nuwara Eliya, Herzog s.n. (BM, S). INDIA. Kerala/Tamil Nadu, Anaimalai Hills, Beddome 533 (BM, NY); "South India, High Wavy Mts.", Blatter & Hallberg 319 (BM). VIETNAM. Lam Dong, Lang Bian, Tixier 9119 (PC). PENINSULAR MALAYSIA. Perak, Gn. Hijau, Burkill 12636 (BM); Maxwell Hill, trail to Gn. Hijau, Haji Mohamed et al. 8084 (KLU); Pahang, Cameron Highlands, Gn. Beremban, Spare 3473 (BM). SUMATRA. Aceh, Gn. Leuser Nature Reserve, Gn. Ketambe, De Wilde & De Wilde-Duijfjes 14260 (NY), 14260A (L); Sumatera Utara, Gn. Sinabung, Touw & Snoek 25349 (L); Sumatera Barat, Gn. Singgalang, Beccari 92 (BM, FH-FL, JE); Sumatera Selatan, Gn. Merapi, Van der Wijk 1479 (L). JAVA. Jawa Barat, Schiffner 10286 (L, S); Cibodas, Fleischer 83 (BM, H-BR, JE, L, NY); Gn. Pangrango, Schiffner 3880 (BM, H, L, NY); Gn. Megamendong, Motley s.n. (NY); Gn. Malabar, Wichura 2487 (BM, H-BR); Gegerbentang, Noerta & Soekar 2014 (L); Jawa Timur, Dataran-tinggi Ijen (Idjen Plateau), Gandrup 484 (H-BR). BORNEO. SABAH. Gn. Kinabalu, Sungai Mesilau, Menzel, Frahm, Frey & Kürschner 4165 (B, FH); Gn. Kinabalu, Silau-Silau trail, Tan 89-853 (FH, NY); Gn. Tambuyukon, Meijer B 11042 (L). SARAWAK. Gn. Mulu, Touw 20912 (L); Gn. Pueh, Everett 56 (H-BR, NY). KALIMANTAN. Kalimantan Timur, Gn. Beratus (Balikpapan), Meijer 2630 (L). PHILIPPINES. LUZON. Cagayan, Mt. Dos Cuernos, Ramos 84365 (FH-Bartr.); Mountain, Mt. Data National Park, Hale & Banaag 26742 (L, NY); La Union, Mt. Santo Tomas, Williams 1853 (FH, H-BR, L, NY); Benguet, Suyoc to Pauai, Merrill 4942 (BM, H-BR, NY); Laguna, Mt. Bana, Robinson 6604 exp (H-BR); Quezon, Mt. Banahao, Alvarez Jr. O-77346 (MO, NY). VISAYAN ISLANDS. Mindoro Oriental, Mt. Malaimbo, Puerto Galera, Bartlett 13867 (FH-Bartr,); Negros Oriental, Dumaguete, Elmer 10056 (BM, FH, H-BR, L, MO, NY). MINDANAO. Davao del Sur, Mt. Apo, Williams 1954 (FH, NY); Davao, Mt. Batangan, Herb. Fleischer s.n. (FH-FL). PALAWAN. Mt. Mantalingajan, Tan 91–228 (FH). SULAWESI. Sulawesi Tengah, Gn. Roroka Timbu, Van Balgooy 3344 C (L); Gn. Nokilalaki, Meijer 9776a (NY); Sulawesi Selatan, Pegunungan Latimojong, Buntu Pese, Eddy 5332 (BM); Gn. Lompobattang (Bonthain Peak), Everett s.n. (NY); Sulawesi Tenggara, Bt. Watuwila, Kjellberg 8 (BM, L). NUSA TENGGARA. Bali, Bedugul, Gn. Catur, Touw & Snoek 24844 (L); Flores, Poco Gurung above Ruteng, Schmutz 5275 (L). MALUKU. Halmahera, Gn. Jailolo, Alston 16859b (BM); Seram, Manusela National Park, Wae Ili, Akiyama c-9739 (L, MO). PAPUA NEW GUINEA. "In montosis Moroka", Loria s.n. (S).

Dicranoloma brevisetum may be confused with the other species of *Dicranoloma* that lack a central strand, *D. braunii*, *D. cutlackii*, and *D. steenisii* and with some species with a central strand, *D. assimile*, *D. billardierei*, and *D. blumei*. Differences between *D. brevisetum* and those species have been discussed under the other species.

Dicranoloma brevisetum is very variable, particularly in leaf shape. Leaves grade from very narrow and widely spreading to somewhat wider and slightly falcate-secund (i.e. in the type specimen of *Megalostylium brevisetum*), still wider and strongly falcate-secund (type specimen of *Dicranum leucophyllum* var. *kurzii*), to very wide and erect-spreading to widely spreading (type specimen of *Dicranum leucophyllum*).

There appears to be some difference in the geographical distribution of the above mentioned forms. Plants with very wide spreading leaves occur only on Sumatra and Java, plants with somewhat narrower, falcate leaves occur throughout the range of the species, and very narrow-leafed plants occur from Sumatra eastwards, becoming more abundant towards the east.

Occasionally specimens were encountered with lamina cells much shorter than the mean but there appears to be no correlation with the variation in leaf shape described above. Specimens with vegetative propagulae have been collected in Java, Sumatra, and the Malay Peninsula only. Only specimens with relatively wide leaves bear these propagulae.

Eddy (1988) maintained *D. leucophyllum*, along with *D. brevisetum*. In his opinion *D. brevisetum* has less than 1.1 mm wide, very long and filiform leaves and alar cells with some orange pigmentation and with markedly thickened and pitted longitudinal walls, whereas *D. leucophyllum* has more than 1.4 mm wide, non-filiform leaves and alar cells with thin or slightly thickened, usually colourless, longitudinal walls. I agree with Tan & Koponen (1983) that there is no distinct gap between these two taxa and that they should be merged into a single species.

Akiyama (1990), in his treatment of *Dicranoloma* from Seram and Ambon, although aware of the publication of Tan & Koponen, preferred to call his specimens *D. leucophyllum*. He wrote: "Since Seram plants have much longer leaves with long-setaceous and filiform apices, they cannot be assumed to be *D. brevisetum* var. *brevisetum*." His decision, however, must be based on a misunderstanding about the circumscription of *D. brevisetum* and *D. leucophyllum*. Even if one would prefer to distinguish two species his specimens would belong to *D. brevisetum*, *D. brevisetum* being the one with the filiform leaf apices.

Tan (1989) synonymised *Dicranoloma defoliatum* Froehl. with *D. blumei*. However, the type collection of *D. defoliatum* lacks a central strand and has a rather thick costa. Moreover it lacks the conspicuous brown alar patches typical of *D. blumei* and possesses a dense tomentum. Therefore, *D. defoliatum* is conspecific with *Dicranoloma brevisetum* and not with *D. blumei*. The type specimen of *Dicranoloma defoliatum* has fugacious leaves, most being broken off just above the alar patches. This phenomenon has been encountered frequently among the narrow-leafed collections of *D. brevisetum*, albeit not so extremely as in the type collection of *D. defoliatum*, in which most of the leaves were found at the bottom of the packet and only a few leaves at the tip of the shoots were still attached.

According to Tan & Mohamed (1990) their new species *Dicranoloma damanhurii* was formerly confused with *Dicranoloma brevisetum*, but differs from it in the leaf areolation pattern. *Dicranoloma brevisetum*, however, as mentioned earlier, is a very variable species and shows considerable variation in leaf areolation, ranging from lamina cells arranged in orderly longitudinal rows to a more irregular pattern. The pattern tends to be more irregular in wide leaves, especially in the widest part of the leaf and the part just above the alar patches. The areolation found in the type and paratypes of *D. damanhurii* may be at the extreme end of the range, but certainly not outside it. Hence I prefer to keep *D. damanhurii* within *D. brevisetum*. Tan & Mohamed indicated that they did not observe propagulae in *D. damanhurii*. However, these are present in at least one of the paratypes (Damanhuri 1625 in L).

8. ***Dicranoloma cutlackii*** (Norris & T. Kop.) Klazenga, *comb. nov.* Fig. 21

Dicranum cutlackii Norris & T. Kop. (1990: 38). Type: Papua New Guinea: Morobe Province, Mt. Sarawaket Southern Range, 3 km SSE of Lake Gwam. In elfin forest, on moist, diffusely lit bark of tree, 3350 m, Norris 62827 (H-holo!, BM!, HSC, LAE). Paratypes: Papua New Guinea: Western Highlands, Nebilyer River, 28 km WNW of Mt. Hagen, 2760 m, Streimann 20541 (H!); Simbu, Kombugomambuno, Mundua 64 (H!); 4 km N of Tep-tep, 2950–3100 m, Norris 65024 (H!), 65040 (H!), 65173 (H!); Morobe, Mt. Sarawaket Southern Range, 4 km E of Lake Gwam, 3200–3300 m, Koponen 32780 (FH!, H!), 32825 (H!, L!); Mt. Sarawaket Southern Range, 3 km SSE of Lake Gwam, 3350 m, Norris 62709 (H!), 63044 (H!), 63051 (H!); 2.5 km S of Lake Gwam, 3550 m, Norris 63260 (H!, JE!), 63348 (H!); 3 km SW of Lake Wamba, 2800 m, Norris 63995 (H!); 3 km SW of Lake Wamba (Mt. Finisterre), 3000 m, Norris 64304 (H!, NY!).

Pseudoautoicous or, rarely, dioicous. Dwarf males 0.8–2 mm tall. Leaves 0.2–0.7×0.12–0.18 mm, ovate, acuminate, ecostate, elimbate; margin serrulate at apex, entire below. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 5–15 cm tall, growing in turfs, glossy yellowish-brown to dark reddish-brown. Stem reddish brown to brown, subflorally branched, densely foliose, densely tomentose; diameter 0.3–0.5 mm, central strand absent, cortical cells thick-walled. Gemmae absent.

Leaves 10–17×(1–)1.5–2 mm, ovate-linear, gradually tapering, either erect-spreading to spreading throughout the stem, homomallous, or falcate-secund in the apical part of the stem, basal 1/3–1/2 canaliculate, subtubulose above, smooth to slightly rugose; subula straight or flexuose, brittle, mostly missing in older leaves. Alar patches distinct, 0.5–0.8×0.35–0.7 mm, triangular, not reaching the costa. Margin serrate in the upper 1/2–3/4, entire below. Limbidium absent or ill-defined, consisting, if present, of scattered linear hyaline cells between the alar patches and the dentate part of the leaf margin. Costa 50–120 μm wide, 30–50 μm thick, either well-marked in its entire length or from just above the alar patches, percurrent or ending a few cells below leaf apex, abaxially bearing 2(–4) rows of teeth in the distal 1/2–3/4; layer of guide cells mostly ill-defined, consisting of (2–)4–6 cells; adaxially as well as abaxially with a single layer of stereids or 1–2 layers of a mixture of stereids and cells with a distinct lumen; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells 40–170×10–16(–20) μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 1–1.5. Alar cells 20–90×20–50 μm, quadrate to rectangular, not inflated; walls firm to thick, 2–10(–14) μm thick, frequently strongly collenchymatous, mostly not pitted, colourless or brown. Basal juxtacostal cells and decurrency cells similar to the

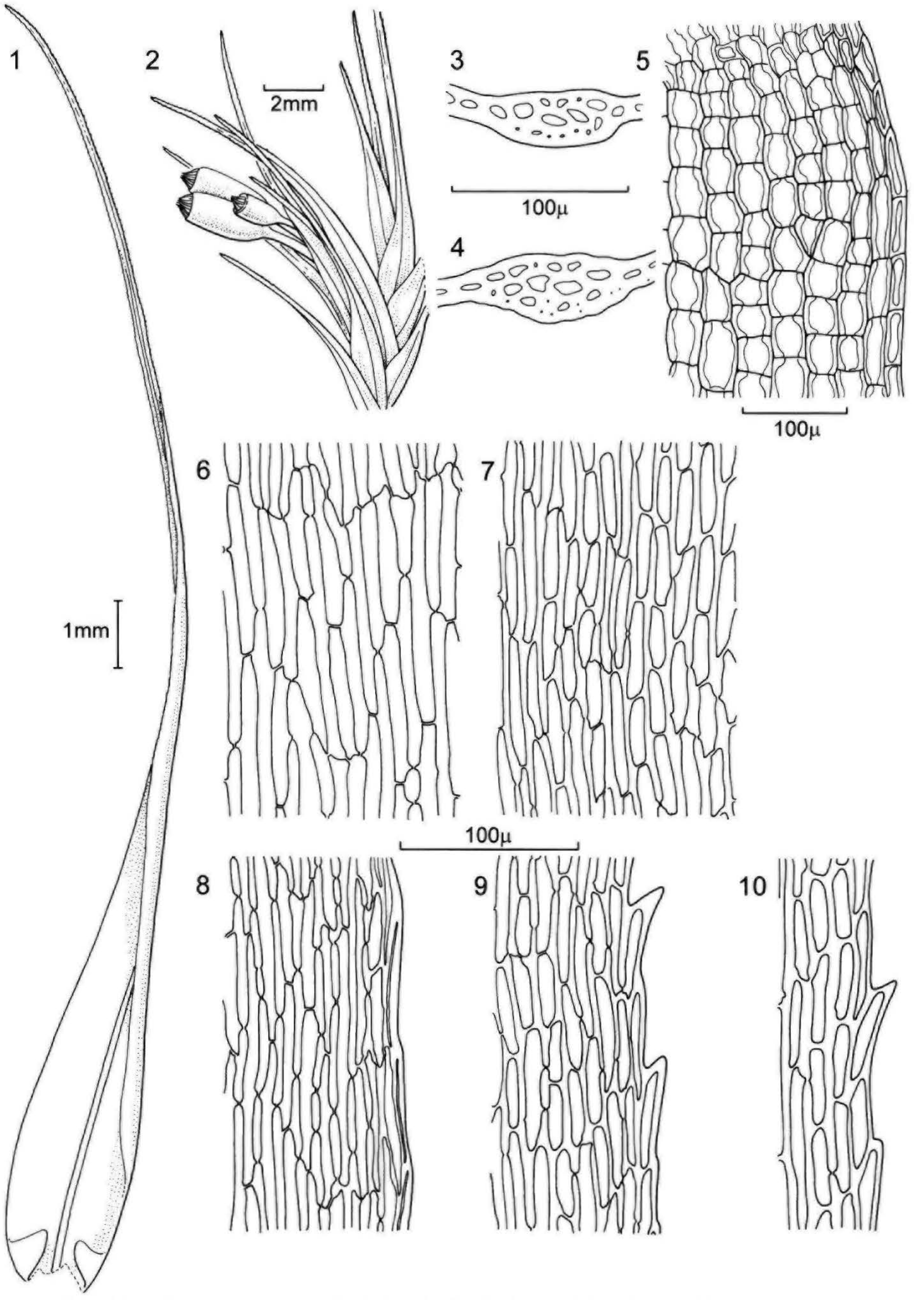

Fig. 21. *Dicranoloma cutlackii* — 1. leaf; 2. perichaetium with sporogones; 3–4. cross section through the costa, just above the alar patches; 5. alar cells; 6. basal lamina cells; 7. lamina cells c. halfway the leaf length; 8. basal marginal and intramarginal cells; 9–10. upper lamina cells. — 1–3, 5–9. Norris 62827 (H; holotype); 2, 4, 10. Koponen 32825 (H).

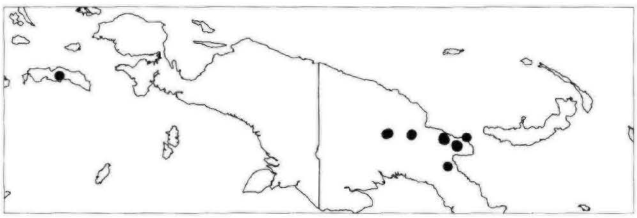

Fig. 22. Distribution of *Dicranoloma cutlackii*.

basal lamina cells but with brown walls. Upper lamina cells (15–)30–110×8–12(–20) μm, oblong to linear, with short-oblong cells among elongate to linear cells, mostly straight, often some cells slightly bent, similar to the basal lamina cells or gradually shorter; walls incrassate, pitted, lumen wall ratio 1–1.5(–3). Teeth at leaf margin 6–20(–35) μm, consisting of a single cell; lumina not conspicuously larger than in the adjacent cells. Perichaetial leaves 12–16×1–2 mm, ovate-lanceolate, gradually tapering towards the apex; basal part clasping to sheathing.

Sporogones 1–2 per perichaetium. Vaginula 2–2.5 mm long, reddish-brown to dark brown. Seta 5–6 mm long, yellowish to reddish-brown, smooth; 0.20–0.22 mm in diameter, central strand present, cortical cells thin-walled, peripheral layer with very thick walls, central part often decayed at maturity. Capsule reddish 2.5–2.8 mm, brown to dark brown, cylindrical, straight. Exothecial cells 25–90×15–50 μm, elongate, irregularly shaped, mostly not in regular longitudinal rows. Annulus consisting of 2–3 rows of thick-walled cells, persistent. Peristome teeth yellowish to reddish, 0.5–0.95 mm long, (80–)110–160 μ m wide at base, long-attenuate, asymmetrically bifid in the upper 3/4–7/8, often fenestrate below almost to the base; outer face vertically to obliquely striate in the basal half, papillose above; inner face either papillose throughout or smooth in the basal half; trabeculae papillose, the inner ones thicker than the outer ones. Operculum 1.8–2.5 mm, orange to reddish-brown, obliquely rostrate above a conical base. Calyptra unknown. Spores c. 24 μm, spherical, finely papillose.

Illustrations. Norris & Koponen 1990: f. 11 a–h; Akiyama 1990: f. 28; f. 29–39 (misinterpreted as *Dicranoloma daymannianum*).

Distribution. Maluku (Seram), New Guinea (Fig. 22).

Ecology. Mostly growing in the upper montane forest or in subalpine vegetations, from 2750 to 3600 m; once found in lower montane forest at 1300 m (Bellamy 1531). Mostly epiphytic, on stems of trees and occasionally tree ferns, only rarely in the canopy; also frequently on logs and stumps and occasionally terrestrial.

Selected additional specimens examined. INDONESIA. MALUKU. Seram, Manusela National Park, between O'wae Puku and Gn. Binaiya, Akiyama c-9015 (L, NY). PAPUA NEW GUINEA. Madang, 5 km NW of Teptep airstrip, Koponen 34535 (H); Western Highlands, Mt. Hagen, Van Zanten 683044 a (GRO); Simbu, Mt. Wilhelm, between Keglsugl and Lake Piunde, De Sloover 42956 (CBG, NY); Morobe, near Mt. Missim, Bellamy 1531 (CBG, NY).

Dicranoloma cutlackii appears to be closely related with and difficult to separate from *D. brevisetum*. In *D. cutlackii* the layer of guide cells is poorly differentiated; in *D. brevisetum*, it is well differentiated from the stereid layer. In *D. brevisetum* all upper lamina cells are almost as long as to slightly shorter than the basal ones, whereas in *D. cutlackii*, among linear cells which are as long as or only slightly shorter than the basal ones, also appreciable numbers of far shorter, oblong cells occur in a large part of the acumen. The combination of long and relatively wide, erectopatent, rather stiff leaves, which are often fragile, is typical of *D. cutlackii* is not found in *D. brevisetum*. Finally, seta length is slightly, but consistently, longer in *D. cutlackii*, 5–6 mm vs. 2.5–4 mm in *D. brevisetum*.

Dicranoloma cutlackii might further be confused with *D. blumei*, because the two species often have a similar habit and share a sheathing basal part of the lamina and because *D. cutlackii*, like *D. blumei*, possesses conspicuous alar patches. *Dicranoloma cutlackii* is easily distinguished from *D. blumei* by the absence of a central strand. Norris & Koponen (1990) furthermore compared *D. cutlackii* with *D. armitii*, but those species are so distinct from each other that confusion does not seem likely.

A collection from Seram, Akiyama c-9015, identified by Akiyama (1990) as *D. daymannianum* ["*dymannianum*"] belongs to *D. cutlackii*. Thus, the geographic range of *D. cutlackii* extends as far west as Maluku. The gap in the Indonesian part of New Guinea may probably be explained by the fact that collecting in this area has been much less intensive then for instance in Papua New Guinea.

9. ***Dicranoloma daymannianum*** Bartr. (1957: 35). Fig. 23

Dicranum daymannianum (Bartr.) Norris & T. Kop. (1990: 40). Type: Papua New Guinea. Milne Bay, Maneau Range, north slope of Mt. Dayman, 2000 m, Brass 22560a (FH-Bartr.-holo!, FH!, H!).

Males not found. Female plants 2.5–7 cm tall, growing in loose cushions or turfs, yellowish-green to yellowish-brown. Stem reddish brown to brown, simple or subflorally branched or forked, densely foliose, densely tomentose; diameter 0.2–0.3 mm, central strand present, cortical cells thick-walled. Gemmae mostly present in the lower part of the stem, at the apices of the rhizoids, colourless, filamentous to club-shaped, uniseriate, up to 0.6 mm long, 20–35 μm wide, consisting of up to 30 quadrate cells; walls smooth.

Leaves 4.5–8.5×0.5–0.8 mm, ovate-linear, gradually tapering, with a faint fold at both sides of the costa in the lower c. 1/2, at base canaliculate, higher up V-shaped, erectopatent, those at stem apex often with a falcate tip; leaf tips brittle, often fallen off, except near stem apex. Alar patches distinct, 0.15–0.3×0.12–0.2 mm, triangular, not reaching the costa. Margin serrate in the upper 1/2–3/4, entire below. Limbidium consisting of 1–3 rows of cells, reaching from just above the alar patches to a short distance below the dentate part of the margin, often interrupted, occasionally absent. Costa 30–80 μm wide, 30–55(–60) μm thick, well-marked in its entire length, percurrent or shortly excurrent, abaxially with several rows of low teeth (or rather prorate cells) in the distal c. 1/2; guide cells 4–7; adaxially with 1–3 layers of stereids, occasionally with 1–2 cells with a distinct lumen among them, abaxially with 2–3 layers of stereids; adaxial epidermis not differentiated proximally, consisting of cells with a distinct lumen distally; abaxial epidermis mostly consisting of cells with a distinct lumen, proximally often not differentiated. Basal lamina cells (25–)30–110×8–12 μm, elongate to linear; walls incrassate, pitted to shallowly so, lumen wall ratio 1–3. Alar cells 12–50×12–30 μm, quadrate to rectangular or rounded, the outer ones very rarely inflated; walls thin to firm, 2–5 μm thick, not pitted, colourless to orange-brown. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but

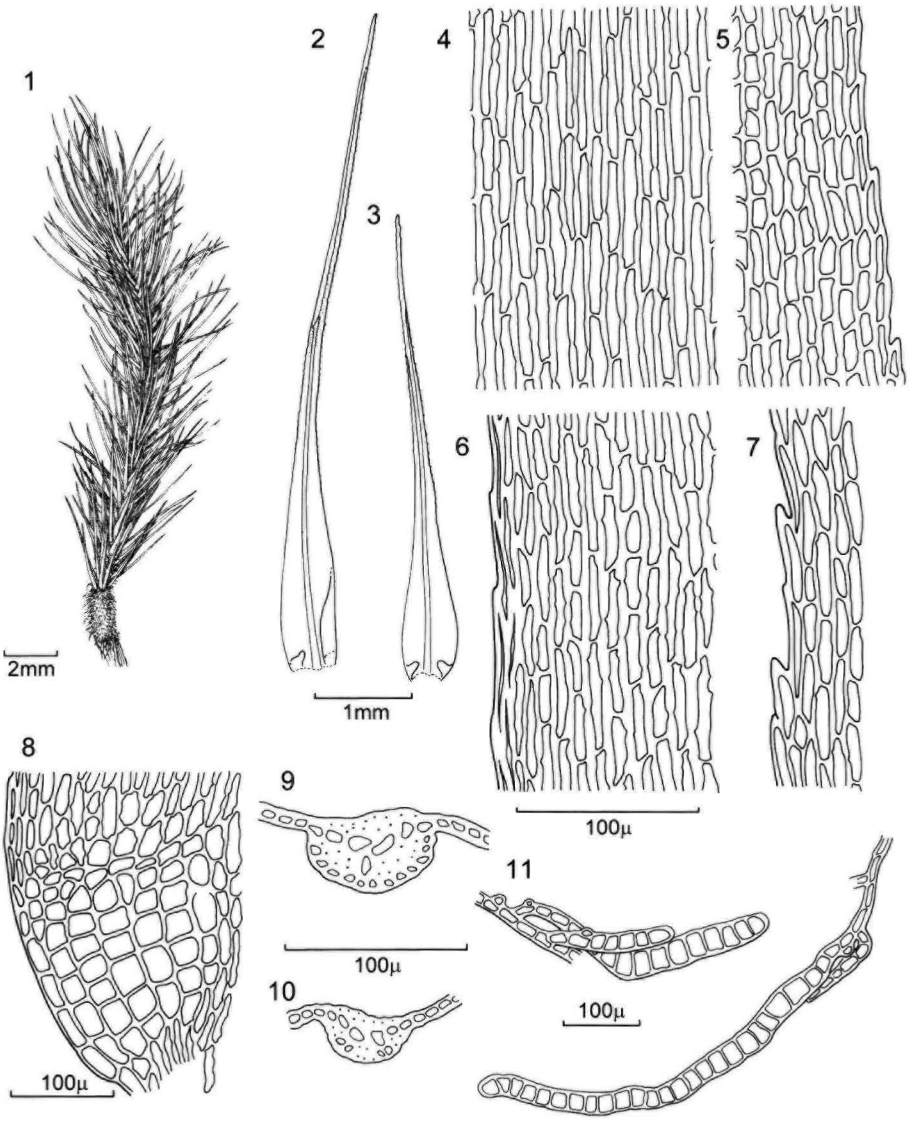

Fig. 23. *Dicranoloma daymannianum* — 1. habitus; 2–3. leaf; 4. basal lamina cells; 5, 7. upper lamina cells; 6. marginal and intramarginal cells; 8. alar cells; 9–10. cross section through the costa, just above the alar patches; 11. rhizoidal gemmae. — 1. Streimann 19150 (CBG); 2, 4–6. Streimann 32306 (H); 3. Brass 22560a (FH; holotype); 7, 10. Touw & Snoek 22256 (L); 8–9, 11. Streimann 33978 (H).

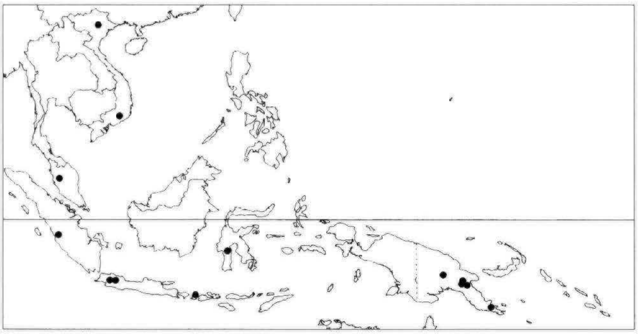

Fig. 24. Distribution of *Dicranoloma daymannianum*.

with orange-brown to brown walls. Limbidium cells 60–120×4–6 μm, linear, hyaline, with very thick, non-pitted walls and very narrow, almost indiscernable lumina. Upper lamina cells 10–50(–60)×8–12 μm, isodiametric to elongate, more or less rectangular to rhomboidal or elliptical, mostly irregularly so, conspicuously shorter than the basal lamina cells; walls scarcely or not pitted, lumen wall ratio 1–3. Teeth at leaf margin 5–15 μm, consisting of a single cell; lumina not conspicuously larger than in the adjacent cells. Cells at upper leaf margin occasionally prorate. Perichaetial leaves 3–5×0.5–0.6 mm, more or less abruptly contracted into a subula; basal part ovate, clasping to sheathing; subula mostly reflexed in the outer perichaetial leaves.

Sporogones unknown.

Illustrations. Tan & Koponen 1983: f. 59; Norris & Koponen 1990: f. 11 i–l (as *Dicranum daymannianum*). Eddy's (1988) f. 139 A–F, as *Dicranoloma fragile*, are probably also *D. daymannianum*.

Distribution. Vietnam, Peninsular Malaysia, Sumatra, Java, Sulawesi, Lesser Sunda Islands (Lombok), Papua New Guinea (Fig. 24).

Ecology. Growing in lower montane and upper montane forest, mostly from 1500 to 2000 m, only the collection from Sulawesi made at a higher altitude, at 2700 m. Frequently found in disturbed forest. Also occurring in areas with a monsoon climate. Epiphytic on stems and, occasionally, on branches of trees.

Selected additional specimens examined. VIETNAM. Hoang-Lien Son, near Sapa, Pócs 2584/h & j (EGR); Bac Thai/Vinh Phu, Tam Dao, Pócs 2563/o (EGR); Lam Dong, Dalat, Da Pampéi, Tixier s.n. (1959) (PC). PEMIMSULAR MALAYSIA. Pahang, Cameron Highlands, Gn. Brinchang, Haji Mohamed & Zamzuri (KLU). SUMATRA, Sumatera Barat, Gn. Kerinci, Meijer 7711 (L). JAVA. Jawa Barat, Gn. Tangkubanperahu (Praoa), Herb. Fleischer s.n. (FH-FL); Gegerbentang, Noerta & Soekar 1092 (L). NUSA TENGGARA. Lombok, Gn. Rinjani, ascent from Senaro, Touw & Snoek 22256 (L). SULAWESI. Sulawesi Selatan, Pegunungan Latimojong, Buntu Pese (Gn. Rantemario), Eddy 5322 pp. (BM). PAPUA NEW GUINEA. Southern Highlands, Paunde logging area, 15 km NNW of Ialibu, Streimann 32306 (CBG, H); Morobe, Herzog Mts., Wago, Eddy 1937 (BM); Yinimba, 9 km N of Menyanya, Streimann 19150 (CBG, H); Upper Nawata Banda, 10 km S of Bulolo, Streimann 33978 (CBG, H, NY).

Dicranoloma daymannianum is superficially similar to *Dicranum psathyrum* Klazenga (≡*Dicranoloma fragile* Broth.). Eddy (1988) even went as far as sinking *D. daymannianum* into *Dicranoloma fragile* without any comment. Accordingly, most of the character states in his description of *D. fragile* relate to *D. daymannianum* while some others are based on a combination of the two species. As Tan & Koponen (1983) already pointed out plant size is not a reliable diagnostic character by itself. The species can, however, be separated by their costal anatomy and the wall thickness of the lamina cells. Most importantly, *D. daymannianum* has distinct stereid layers in the costa while stereids are absent or scattered in the costa of *D. psathyrum*. The basal lamina cells are relatively narrow and mostly have relatively thick, distinctly pitted walls in *D. daymannianum*, while in *D. psathyrum* they are relatively wide and mostly have thin, shallowly pitted walls. Alar cells have firm walls and are not inflated in *D. daymannianum*, but have thin walls and are often enlarged in *D. psathyrum*. Finally, marginal teeth in *D. daymannianum* are smaller than those in *D. psathyrum* and frequently double. Rhizoidal gemmae are mostly present in *D. daymannianum*, whereas they are very rare in *D. psathyrum*.

Although the two species are superficially similar, *D. daymannianum* is maintained in *Dicranoloma* while *D. psathyrum* has been transferred to *Dicranum*. *D. daymannianum* lacks the features that make the transfer of *D. psathyrum* to *Dicranum* necessary, specifically the lack of a limbidium, the small size and the lack of stereid layers in the costa. However, *D. daymannianum* is incompletely known, less then 20 collections being available scattered over a large distribution area and sporogones being competely unknown, and therefore the inclusion in *Dicranoloma* remains provisional at this stage. Within *Dicranoloma*, *D. daymannianum* is most similar to *D. rugifolium* with which it shares the brittle leaf apices and rectangular to elliptical upper lamina cells. *Dicranoloma rugifolium* is easily distinguished from *D. daymannianum* by its more compact habit and wider, smooth or rugose leaves.

Because of its erectopatent, often slightly plicate leaves, *D. daymannianum* may be confused with *D. braunii*. However, it can be easily distinguished from the latter by the presence of a central strand and short upper lamina cells.

With the discovery of collections of *D. daymannianum* from Sulawesi, Lombok, Java, Sumatra, Peninsular Malaysia and Vietnam, the species is shown to be widespread, albeit scattered, in the region. Norris & Koponen (1990), although discarding Eddy's (1988) synonymy, did not check Eddy's report of *D. fragile* from Sulawesi which actually concerns *D. daymannianum* and cite the species as being endemic to Papua New Guinea. Akiyama's (1990) report from Seram is incorrect, the collection on which it is based, Akiyama c-9015 (L, NY), actually belonging to *D. cutlackii*.

Three collections from Vietnam (Pocs 2563/o and 2584/h & j in EGR) have hesitantly been identified as *D. daymannianum*. All microscopic characters fit well in *D. daymannianum* but the leaf apices are not brittle and in habit these collections are quite different from typical *D. daymannianum* and resemble small forms of *D. braunii* or *D. reflexum*. From the former these plants are separated by the presence of a central strand and short upper lamina cells, from the latter by the presence of gemmae and the leaf margin being only slightly serrulate. Some shoots bear rather large and conspicuous clusters of colourless gemmae.

10. ***Dicranoloma dicarpum*** (Nees) Par. (1904: 26). Fig. 25

Dicranum dicarpum Nees in Spreng. (1827: 322) — *Leucoloma dicarpum* (Nees) Broth. (1901: 322).

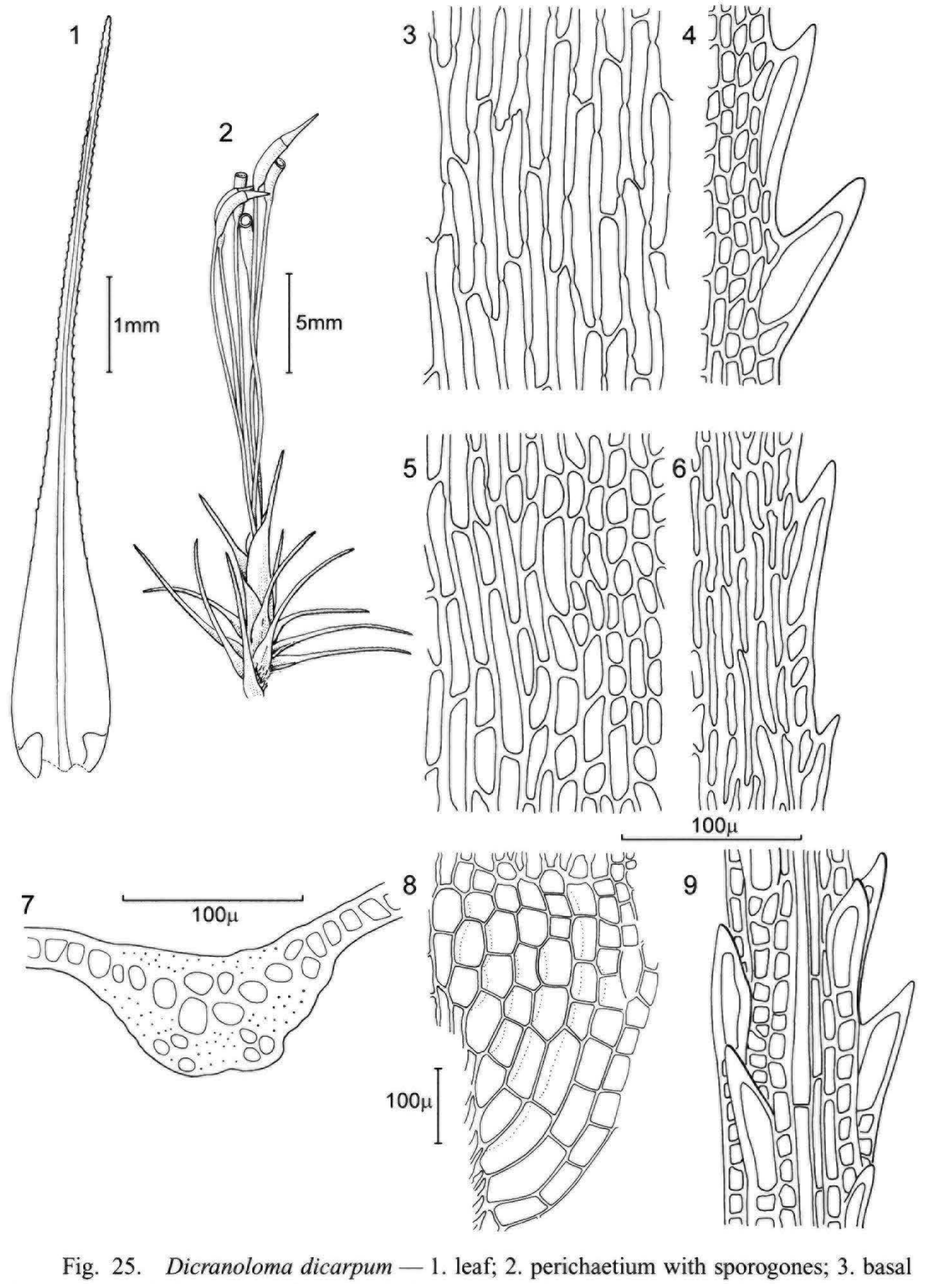

Fig. 25. *Dicranoloma dicarpum* — 1. leaf; 2. perichaetium with sporogones; 3. basal lamina cells; 4, 6. upper lamina cells; 5. juxtacostal cells (costa to the right); 7. cross section through the costa, just above the alar patches; 8. alar cells; 9. abaxial view of the costa, distal part. — 1–5, 7–9. Brass 22854 (H; isotype of *D. brassii*); 6. Brass 29526 (L).

Type: Australia ["Nova Hollandia"]. Sieber 10 (LE (Hb. Nees)-holo, not seen; JE!, L!, MO!, NY!).

Dicranoloma formosanum Broth. (1928a: 17), syn. nov. Syntypes: Taiwan. Taichu, Mt. Tankitake, Shimada 2468 (H-BR-lecto!); Mt. Hassen, Sasaki 2412 (H-BR!). Lectotype selected by Tan & Koponen (1983).

Dicranoloma brassii Bartr. (1957: 34). Type: Papua New Guinea. Milne Bay Province, Mt. Dayman, north slopes, mossy forest, 2250 m, on ground, Brass 22854 (FH-Bartr.-holo!, CBG!, FH!, H!). Paratypes: ibid., 2230 m, lower tree trunks in mossy forest, Brass 22390 (FH, not seen); ibid., dryish forest of slopes, tufted on logs and lower tree trunks, 2000 m, Brass 22558 (FH, not seen; CBG!). Synonymised by Norris & Koponen (1990).

Pseudoautoicous. Dwarf males 0.4–1.6 mm tall. Leaves 0.3–1.5×0.08–0.16 mm, narrowly ovate to ovate-linear, acuminate, ecostate, elimbate; margin with some minute teeth at apex or, occasionally, with teeth descending as far as halfway leaf length. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 4–12 cm tall, growing in turfs or cushions, glossy yellowish-green to yellowish-brown throughout or dull brown in the lower parts. Stem reddish brown to brown, subflorally branched, densely foliose, densely tomentose; diameter 0.45–0.7 mm, central strand present, cortical cells thin-walled. Gemmae absent.

Leaves 6–12×0.7–1.3 mm, ovate-linear, gradually tapering, smooth or plicate, canaliculate, falcate-secund or widely patent with falcate tips. Alar patches distinct, 0.3–0.55×0.25–0.4 mm, triangular, not reaching the costa. Margin serrate in the upper 1/2–3/4, entire below. Limbidium consisting of 1–3 cell rows, reaching from the alar patches to the dentate part of the margin or just below. Costa 80–120 μm wide, 30–70 μm thick, well-marked in its entire length, mostly percurrent, occasionally ending a few cells below leaf apex, abaxially with teeth in the upper 1/2–3/4, situated on 2 ribs in the distal part and up to 4 ribs at the proximal end; guide cells 6–11; adaxially with 2–3(–4) layers of stereids, mostly with cells with a distinct lumen among them, and, adjacent to the guide cells, mostly some cells with a lumen as large as those of the guide cells, abaxially with 2–3(–4) layers of stereids, divided into (2–)4–5(–7) small bundles, separated by groups of cells with a distinct lumen; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells 40–160×(6–)10–20 μm, elongate to linear; walls thin to incrassate, pitted, lumen wall ratio 1–4. Alar cells 20–140×15–80 μm, quadrate to rectangular, inflated; walls thin, 1–3 μm thick, not pitted, yellowish-brown to brown. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with yellowish to orangish walls. Limbidium cells 90–230×5–8 μm, linear, hyaline, with very thick, non-pitted walls and a very narrow, almost indiscernible, lumen. Upper lamina cells 10–100×6–16 μm, oblong to short-linear, irregularly rectangular, rhomboidal or more or less elliptical to straight, gradually shorter than the basal lamina cells; walls scarcely and shallowly pitted, lumen wall ratio 1–4. Along the costa with an up to 8 cell rows wide band of cells similar to the upper lamina cells, which may reach as far down as the basal 1/4 of leaf length, at the bottom and at the sides gradually passing into the basal lamina cells, at the sides often bordered by a fold. Also higher up the juxtacostal cells often distinctly shorter than the intra-marginal cells.

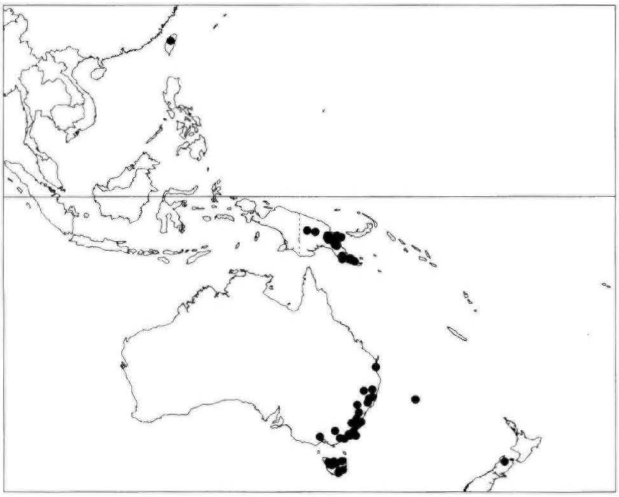

Fig. 26. Distribution of *Dicranoloma dicarpum*. Data from Australia and New Zealand are incomplete.

Teeth at leaf margin 10–40(–50) μm; lumina conspicuously larger than in the adjacent cells. Perichaetial leaves 5–12×1.2–3 mm, abruptly contracted into a subula; basal part 1–8 mm long, broadly ovate to broadly elliptical, clasping to sheathing; subula reflexed in the outer perichaetial leaves.

Sporogones (1–)2–9 per perichaetium. Vaginula 2–2.5 mm long, reddish-brown to dark brown. Seta (12–)17–23 mm long, yellowish to reddish throughout, or reddish at base and yellowish above, smooth; 0.18–0.22 mm in diameter, central strand present, cortical cells thin-walled, the peripheral 2–3 layers with very thick walls, central part often decayed at maturity. Capsule 2.5–4 mm long, yellowish-brown to dark brown, cylindrical, slightly curved to arcuate, not strumose. Exothecial cells 35–120×15–40 μm, oblong to linear, irregularly shaped, not in regular longitudinal rows. Annulus consisting of 2–3 rows of thick-walled cells, deciduous, often a few cells remaining attached at capsule mouth. Peristome teeth yellowish to reddish, up to 0.72 mm long, 70–120 μm wide at base, long-attenuate, asymmetrically bifid in the upper 1/2–2/3; outer face vertically to obliquely striate throughout, with cross-connections in the basal c. 2/3; inner face smooth in the basal half to almost to apex, papillose above; outer trabeculae thin, smooth; inner trabeculae thick, papillose. Operculum 2–3 mm long, yellowish-brown, obliquely rostrate above a conical base. Calyptra 4–5 mm long, greenish-transparent, cucullate. Spores 16–22 μm, spherical, finely papillose.

Illustrations. Tan & Koponen 1983: f. 32–33 (as *Dicranoloma formosanum*); f. 37, f. 44–45 (as *D. brassii*); Norris & Koponen 1990: f. 12 a–d.

Distribution. Within Malesia restricted to New Guinea. Furthermore in Australasia and Taiwan (Fig. 26).

Ecology. In Malesia growing in lower montane and upper montane forest, between 750 and 2900 m. Mostly terrestrial, but also often on logs and stumps and on tree roots and stems. In Australia and New Zealand found at far lower altitudes. No ecological information was given for the type collections of *D. formosanum* from Taiwan.

Selected additional specimens examined. PAPUA NEW GUINEA. West Sepik, SW of Oksapmin, Hoffmann 90–284 (H, NY); Enga, Lagaip Valley, Hoogland & Schodde 7411 (BM, CBG, FH, FH-Bartr., L); Eastern Highlands, Wopeia, Aiyura-Omara Road, Streimann 18342 (CBG, H, NY); Morobe, Mt. Amungwina, Moi 5 (CBG, H, L, MO, NY); Mt. Kaindi, Brass 29526 (FH-Bartr., L); Central, Mt. Kenive, Croft et al. LAE 65016 (BM, L); Milne Bay, Milne Bay, Goropu Mts. (Mt. Suckling), Pumpunipon, Veldkamp & Stevens 5610A (H, L, MO, NY).

Dicranoloma dicarpum can easily be distinguished from all other Malesian species but *D. reflexum* by its bands of short-rectangular cells along the costa. Specimens of *D. reflexum* may also possess such bands of juxtacostal cells. When sporogones are present these two species are readily distinguished, *D. reflexum* having erect capsules and relatively short, 8–16(–19) mm long, setae and *D. dicarpum*, at least the New Guinean specimens, having arcuate capsules and longer, (12–)17–23 mm long, setae. Moreover, *D. dicarpum* mostly has more sporogones per perichaetium, (1–)2–9 vs. (1–)2–4(–5) in *D. reflexum*. On gametophytic characters the two species are separable as well, the juxtacostal cells in *D. reflexum* being less well-marked than in *D. dicarpum* or not differentiated at all and the leaves of *D. dicarpum* being less strongly plicate than in *D. reflexum*, if plicate at all, and having one fold at both sides of the costa, *D. reflexum* having two. The costa in *D. dicarpum* is mostly wider than in *D. reflexum*, containing 6–11 guide cells vs. 4–8 in *D. reflexum*, and mostly has an adaxial layer of cells with a large lumen which is always lacking in *D. reflexum*.

Dicranoloma brassii was described by Bartram (1957) as related to *D. dicarpum*, but differing by the cells of the upper lamina being uniformly narrowly rectangular. Norris & Koponen (1990), after finding the characteristic juxtacostal cells in most leaves of the isotype of *D. brassii*, concluded that the latter is conspecific with *D. dicarpum*. They noted that the leaves of the New Guinean specimens lack significant plication, but they found similar specimens among Australian material of *D. dicarpum*. Norris & Koponen are followed in treating *D. brassii* as a synonym of *D. dicarpum*.

When Brotherus (1928a) described *D. formosanum* he compared it with *D. dicarpum* from which it could, according to him, easily be distinguished by a laxer leaf areolation and linear lamina cells throughout the leaf. Chuang (1973), without further discussion, considered *D. formosanum* to be very close to and possibly conspecific with *D. perarmatum* Broth. Tan & Koponen (1983) synonymised *D. perarmatum* and *D. formosanum* with *D. assimile*. However, the presence of a band of short rectangular cells along the costa, conspicuously different from the intra-marginal cells, points towards *D. dicarpum* or *D. reflexum*. The arcuate capsules and the strong costa with adaxially a few cells with a large lumen adjacent to the costa, settle the case in favour of *D. dicarpum*. Tan & Koponen found differentiated juxtacostal cells in a few leaves only. This would explain why Brotherus, in his original description, did not mention this feature and even distinguished *D. formosanum* from *D. dicarpum* by the lack of these cells. In this study however, I found bands of differentiated juxtacostal cells in all leaves that were studied. Besides, also among New Guinean material of *D. dicarpum* a few collections were found in which differentiated cells could not be discerned in all shoots or in all leaves on a shoot. These shoots were sometimes difficult to distinguish from *D. arfakianum* as New Guinean specimens of *D. dicarpum* often have relatively wide and thin-walled cells similar to those in *D. arfakianum*. Tan & Koponen furthermore mentioned that they observed a few Bornean and Philippine specimens of *D. assimile* that possess juxtacostal cells. They did not cite these specimens and I could find only one collection from Mindanao (Robbins 4302 in L) in which groups of juxtacostal cells about halfway leaf length could be discerned. Even if this feature could be found more often in *D. assimile*, as suggested by Tan & Koponen, the strong costa with an abaxial layer of cells with a large lumen directly above the guide cell layer rules out conspecifity with *D. assimile* and strongly points in the direction of *D. dicarpum*.

Gao (1994) compared the type of *D. kwangtungense* Chen with the type of *D. dicarpum* and found them to be identical, apart from the capsule which was straight in the type of *D. kwangtungense*, while slightly curved in the type of *D. dicarpum*. The holotype could not been located in PE, but an isotype from S was studied for the present revision. Although the type of *D. kwangtungense* shows a rather close similarity with *D. dicarpum* the leaf cell areolation was found to be different. The upper lamina cells are isodiametric and oblong and more or less rounded and, although they descend in a band along the costa in some leaves, they only do so for a very short distance. As only the type specimen could be studied no conclusion on the correct placement of *D. kwangtungense* could be reached. Other specimens from the same area, formerly identified as *D. kwangtungense*, were found to be different from the type and show a closer similarity to either *D. assimile* or *D. reflexum*.

The type of *D. dicarpum*, from Australia, differs from the New Guinean collections in having erect capsules and short, 7-8 mm long, setae. A quick scan through Australian and New Zealand material revealed that most collections by far of *D. dicarpum* have arcuate capsules. Shorter setae occur quite often. Also from New Guinea a collection with rather short, 12–15 mm long, setae was found (Streimann 17037). According to Sainsbury (1955) capsules of *D. dicarpum* are curved to arcuate; Scott & Stone (1976), on the other hand, write that they are erect. Dixon (1913) restricted *D. dicarpum* to contain only plants with long setae and arcuate capsules and recognised *Dicranum argutum* Hampe in which plants with shorter setae and erect capsules were placed. The two species are identical in the vegetative characters. I studied the type specimens of the two species and found them to be identical. A more thorough study of New Zealand and Australian material, however, may reveal that more species exist within what I now consider to be a single species. If two species can be separated along the lines proposed by Dixon (1913), *D. dicarpum* has to include plants with short setae and erect capsules and another species has to be reinstated to contain plants with longer setae and arcuate capsules, including the New Guinean plants.

11. ***Dicranoloma geluense*** (Herz.) B.H. Allen (1986b: 278). Fig. 27

Werneriobryum geluense Herz. (1909: 122). — *Dicranum geluense* (Herz.) Norris & T. Kop. (1990: 43). Type: Papua New Guinea. Auf dem Gipfel des Gelu (Finisterregebirge), c. 1700 m, Werner s.n. (JE-holo!)

Pseudoautoicous. Dwarf males 0.8–1.9 mm tall. Leaves 0.3–1.0×0.2–0.35 mm, ovate-lanceolate, acute, ecostate, elimbate; margin entire or, frequently, with some minute teeth at apex. Perigonial leaves slightly shorter and broader than the largest stem leaves,

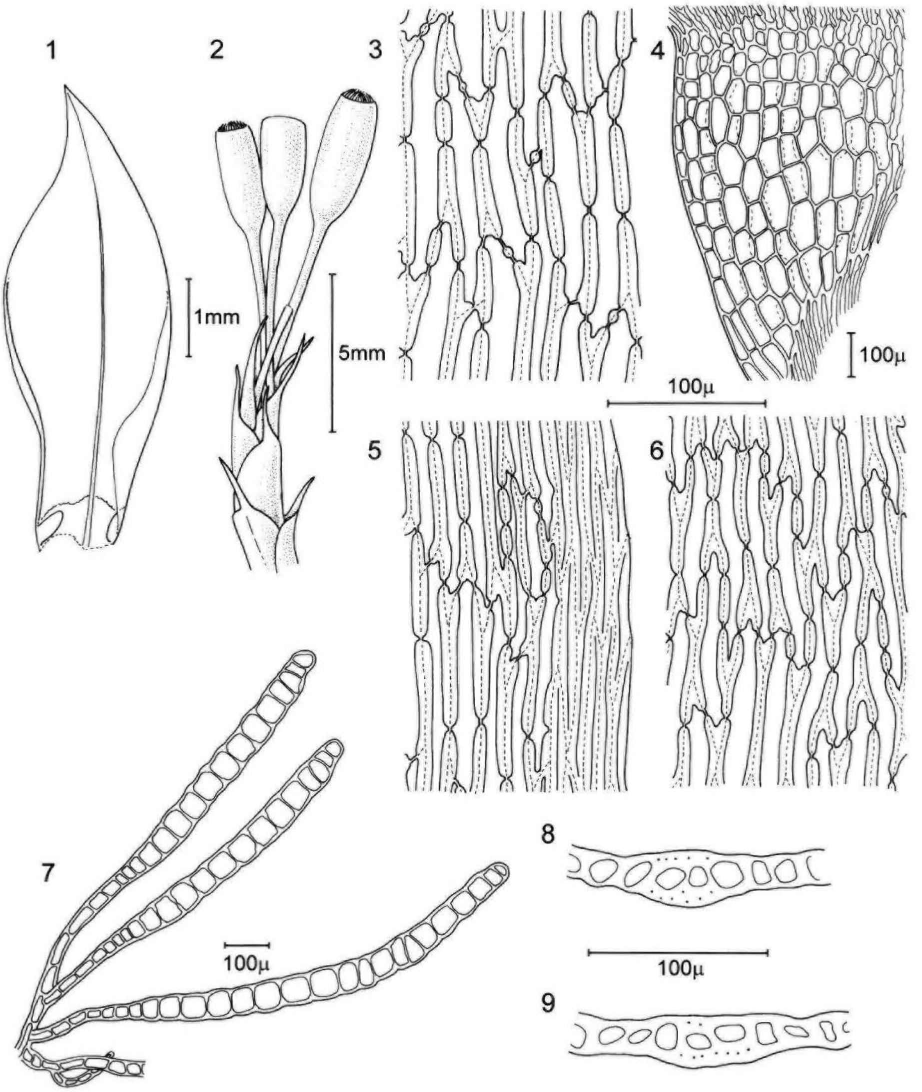

Fig. 27. *Dicranoloma geluense* — 1. leaf; 2. perichaetium with sporogones; 3. basal lamina cells; 4. alar cells; 5. marginal and intramarginal cells; 6. upper lamina cells; 7. rhizoidal gemma; 8–9. cross section through the costa, just above the alar patches. — 1, 9. Eddy 211 (BM); 2–8. Werner s.n. (JE; holotype).

broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 5–15 cm tall, growing in turfs, pale yellowish-brown. Stem reddish to dark brown, simple or subflorally branched, densely foliose, densely tomentose; diameter (0.3–)0.55–1 mm, central strand absent, central cortical cells thin-walled, becoming more thick-walled towards the perifery. Gemmae often present in the lower parts of the stem, at the apices of the rhizoids, brown, narrowly club-shaped, uniseriate, up to 1 mm long, 45–65 μm wide, consisting of up to 10–21 quadrate cells; walls smooth.

Leaves 4.5–7.5×1.8–3 mm, ovate, rugose and plicate when dry, slightly plicate to almost smooth when wet, concave, erectopatent to widely patent. Alar patches distinct, (0.35–)0.5–0.7×0.35–0.5 mm, triangular, not reaching the costa. Margin mostly entire throughout, occasionally with some minute teeth at extreme apex. Limbidium consisting of 4–6 rows of cells, reaching from the alar patches to leaf apex or a short distance below. Costa 30–60 μm wide, 25–35 μm thick, well-marked in its entire length, percurrent or ending a few cells below leaf apex; abaxial surface smooth throughout; guide cells 2; adaxially as well as abaxially with a single layer of stereids, adaxially the stereids occasionally lacking; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells (70–)90–200(–220)×(10–)12–20(–25) μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 0.8–2. Alar cells 20–140(–170)×20–65 μm, quadrate to rectangular, often inflated; walls rather thin, 1–4(–6) μm thick, not pitted, colourless to brown. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but the juxtacostal cells with yellowish or orangish walls and the decurrency cells with brown walls. Limbidium cells 130–220×6–10 μm, linear, hyaline, with very thick, non-pitted walls and very narrow, almost indiscernable lumina. Upper lamina cells 40–150×12–20(–25) μm, oblong to linear, straight or very slightly vermicular, almost similar to the basal lamina cells; walls incrassate, pitted, lumen wall ratio 0.75–1.5. Perichaetial leaves 4–8×1.5–3.5 mm, abruptly contracted into a subula; basal part ovate to broadly ovate, clasping to sheathing; subula often slightly reflexed in the outer perichaetial leaves.

Sporogones 1–4 per perichaetium. Vaginula 2.5–3 mm long, dark brown. Seta 7–8 mm long, reddish, smooth; Capsule 3–3.5 mm long, yellowish to dark brown, ellipsoid to cylindrical, straight, not strumose. Exothecial cells thick-walled, irregularly incrassate. Annulus absent. Peristome teeth yellowish to reddish, c. 0.3 mm long, long-attenuate, asymmetrically bifid in the upper c. 1/2; outer face striate throughout, with cross connections between the striae in the basal part; inner face smooth; outer trabeculae thin; inner trabeculae thick. Operculum conical, obliquely rostrate above a conical base. Calyptra unknown. Spores 40–120×40–65 μm, the smaller ones spherical, the larger ones ellipsoid, finely papillose (see note).

Note: Some spores could be obtained from a single specimen only. As these were spores from an old capsule from which most spores had been shed the size of the remaining spores may be to some extend abnormal, probably larger than normal spores. Spore sizes given here do, however, agree with Herzog (1909) and Allen (1986b). As capsules were so rare that I did not venture to section one, characters of the capsule are after Allen (1986b).

Illustrations. Eddy 1988: f. 142; Norris & Koponen 1990: f. 12 e–i.

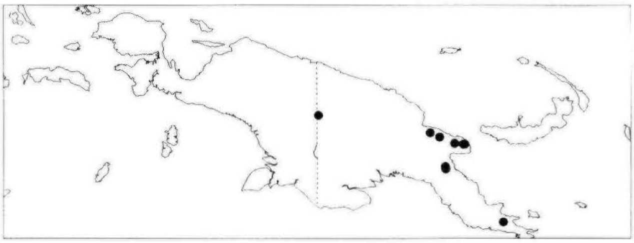

Fig. 28. Distribution of *Dicranoloma geluense*.

Distribution. Endemic to New Guinea (Fig. 28).

Ecology. Growing in upper montane forest and subalpine scrub, from 1800 to 3300 m. Mostly epiphytic or on logs and stumps; also frequently terrestrial.

Selected additional specimens examined. PAPUA NEW GUINEA. West Sepik, Star Mts., ascent from Tamanagabip to Mt. Capella Base Camp, Touw 16159 (L); Madang, Finisterre Range, Eddy 1311 pp. (BM); Western Highlands, Mt. Hagen, Van Zanten 68894 (GRO); Morobe, Mt. Kaindi, Eddy 211 (BM); Finisterre Range, Mt. Abilala, Lake Naho area, Eddy 1370 pp. (BM); Milne Bay, Mt. Mon, Pullen 8038 (BM, L).

Dicranoloma geluense may only be confused with *D. bartramianum*. Differences between the two species are discussed under *D. bartramianum*.

Eddy (1988) considers *D. geluense* to be related to *D. leucophyllum* (Hampe ex Lac.) Par. and its allies in a manner analogous to the relationship of *Campylopus exasperatus* (Nees & Blum.) Brid. var. *exasperatus* to *C. exasperatus* var. *archboldii* (Bartr.) Eddy, the var. *archboldii* representing alpine forms with exceedingly broad, imbricate leaves. However, *D. geluense* is only distantly related to *D. brevisetum*, which is here considered to include *D. leucophyllum*, and is certainly not conspecific with it. Besides the leaf shape characters, which are indeed very variable in *D. brevisetum*, *D. geluense* also differs by a longer seta, larger spores and relatively thin-walled cortical cells of the stem.

Allen (1986b) considers *D. geluense* to belong to an atypical element of *Dicranoloma*, consisting of *D. geluense*, and *D. rugosum* (Hook.) B.H. Allen from Tahiti, *D. obesifolium* (R. Brown ter.) Broth. from New Zealand, *D. eucamptodontoides* (Broth. & Geh.) Par. from Tasmania, and *D. undulatifolium* (Dix.) Bartr. from New Guinea. These species share a similar habit, wide leaves and long sheathing perichaetia. In my opinion, however, this element consists of a mixture of relatively distantly related species. *Dicranoloma geluense* differs from all the other species by the absence of a central strand. *Dicranoloma undulatifolium* is here considered to be a synonym of *Brotherobryum undulatifolium* Van Zanten.

The present species was first described by Herzog (1909) as *Werneriobryum geluense* and initially placed in a family of its own, the *Werneriobryaceae*. Brotherus (1909), without any comment, moved the genus to the Dicnemonaceae. It was Allen (1986b) who, when revising the Dicnemonaceae, gave *W. geluense* its present position in *Dicranoloma*.

12. ***Dicranoloma havilandii*** Broth. (1928b: 117). Fig. 29

Syntypes: Malaysia. Sabah, Mt. Kinabalu, Paka Cave to Lobang, Clemens 10747 (H-BR-lecto!, BM!, FH!, JE, L!, NY!); Mt. Kinabalu, c. 3500 m, Haviland 1424 (BM!, H-BR!). Lectotype selected by Tan (1989).

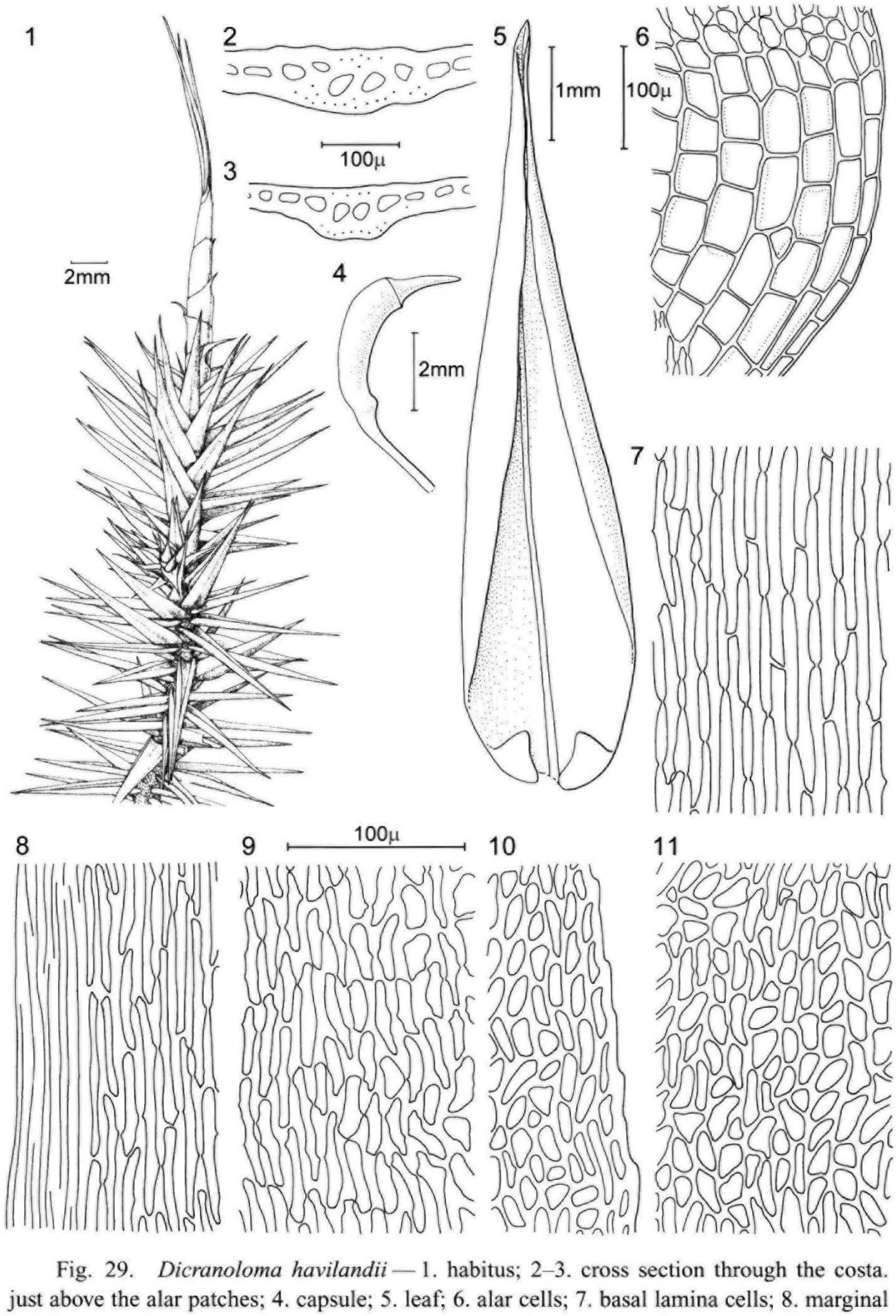

Fig. 29. *Dicranoloma havilandii* — 1. habitus; 2–3. cross section through the costa. just above the alar patches; 4. capsule; 5. leaf; 6. alar cells; 7. basal lamina cells; 8. marginal and intramarginal cells; 9–11. upper lamina cells. — 1, 3, 5–10. Klazenga 631 (L); 2, 11. Haviland 1424 (H-BR; syntype); 4. Klazenga 632 (fieldno.; L).

Pseudoautoicous. Dwarf males 0.4–0.9 mm tall. Leaves 0.25–0.6×0.08–0.12 mm, ovate to ovate-linear, acuminate, ecostate, elimbate; margin entire. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 3–7 cm tall, growing in turfs, pale green to glossy yellowish-green or yellowish-brown. Stem brown, subflorally branched or forked, densely foliose, densely tomentose; diameter 0.4–0.5 mm, central strand present, cortical cells thin-walled. Gemmae absent.

Leaves 6–9×1.2–2 mm, ovate-linear, gradually tapering, smooth to rugulose, canaliculate below, often becoming subtubulose towards the apex, widely patent throughout. Alar patches distinct, 0.3–0.55×0.25–0.4 mm, triangular, not reaching the costa. Margin serrulate in the extreme apical part only, entire below. Limbidium consisting of 4–15 rows of cells, reaching from the alar patches to the serrulate part of the margin. Costa 50–80 μm wide, 30–40 μm thick, either well-marked in its entire length or from just above the alar patches, percurrent or ending a few cells below leaf apex; abaxial surface smooth throughout; guide cells (3–)4; adaxially as well as abaxially with 1(–2) layers of stereids, rarely with some cells with a distinct lumen among them; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells (40–)60–160×10–20 μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 1–2(–3). Alar cells (15–)25–70×25–50(–60) μm, quadrate to rectangular, occasionally some of them inflated; walls thin, 1–4 μm thick, not pitted, yellowish to orange-brown, colourless in young leaves. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with yellowish to orange-brown walls. Limbidium cells 60–300×4–6 μm, linear, with very thick, non-pitted walls and a very narrow, almost indiscernable lumen. Upper lamina cells 20–80(–100)×8–18(–25) μm, isodiametric to elongate, irregularly shaped to almost straight, gradually shorter than the basal lamina cells; walls rather thin to thick, pitted or scarcely and shallowly so, lumen wall ratio 1–3. Teeth at leaf margin small, 6–20 μm, consisting of a single cell; lumina not conspicuously larger than in the adjacent cells. Perichaetial leaves 3–13×1.2–3 mm, abruptly contracted into a subula; basal part 2–11 mm long, broadly ovate to elliptical, clasping to sheathing; subula reflexed in the outer perichaetial leaves.

Sporogones 1–3 per perichaetium. Vaginula 2.5–3 mm long, reddish to dark brown. Seta 13–21 mm long, yellow to reddish-brown, smooth; 0.26–0.30 mm in diameter, central strand present, cortical cells thin-walled, the peripheral 3–4 layers with very thick walls, central part often decayed at maturity. Capsule 3–4 mm long, reddish to dark brown, green when young, cylindrical, slightly curved to arcuate, strumose. Exothecial cells 35–80×15–40 μm, isodiametric to elongate, irregularly shaped, not in regular longitudinal rows. Annulus consisting of 2–3 rows of thick-walled cells, deciduous, often a few cells remaining attached at capsule mouth. Peristome teeth yellowish to reddish, up to 0.8 mm long, 80–120 μm wide at base, long-attenuate, asymmetrically bifid in the upper 1/2–2/3, fenestrate below to somewhat above the base; outer face vertically to obliquely striate throughout, irregularly so in the basal few plates, with cross connections between the striae in the lower c. 2/3 of the teeth; inner face papillose throughout, densely so in the upper c.1/2; outer trabeculae thin, smooth; inner trabeculae thick, papillose. Operculum c. 2 mm long, yellowish to reddish-brown, obliquely rostrate above a conical base. Calyptra 8–8.5 mm

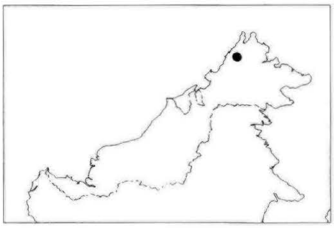

Fig. 30. Distribution of *Dicranoloma havilandii.*

long, yellowish-greenish, more or less transparent, cucullate. Spores 22–24 μm, spherical, very finely papillose to almost smooth.

Illustrations. Tan 1989: f. 7–12. Eddy' s (1988) f. 131 is *D. assimile.*

Distribution. Endemic to Gn. Kinabalu on Borneo (Fig. 30).

Ecology. Growing in subalpine forest, from 2400 to 3500 m. Terrestrial, on humus-covered boulders, on logs and stumps and on bases of trees and shrubs.

Selected additional specimens examined. BORNEO. SABAH. Gn. Kinabalu, South Ridge Route between Layang-Layang staff quarters and Laban Rata hut, Klazenga 631, 632 (L); Gn. Kinabalu, Kemburongoh, Richards 5757 (L); Gn. Kinabalu, Shea 2635 (SAN), 2723 (SAN), 3074 (SAN); Gn. Kinabalu, between Laban Rata and Carson Camp, Tan s.n. (NY); Gn. Kinabalu, Kemburongoh to Paka Cave, Wood 1528 (BM, FH, L).

Dicranoloma havilandii is very close to *D. assimile*. Differences between the two species are discussed under *D. assimile*.

Although Eddy (1988) maintains *Dicranoloma havilandii* as a species, he writes that "it appears to be a high altitude, wet-ground variant of *D. assimile*, but has been collected too infrequently to make dogmatic pronouncements upon." Tan (1989), on the other hand, considered *D. havilandii* to be only remotely related to *D. assimile*.

This difference of opinion is caused by too broad a concept of *D. havilandii* by Eddy (1988), which also includes high altitude forms of *D. assimile* from New Guinea and Sulawesi. According to Tan's (1989) and my view only the Bornean specimens differ specifically from *D. assimile*. *Dicranoloma havilandii* thus appears to consist of an isolated population, occurring in the higher regions of Gn. Kinabalu. High altitude forms of *D. assimile*, like those found on Sulawesi and New Guinea (and described under *D. assimile*), seem not to occur on Borneo. *Dicranoloma assimile* has almost never been found above 2500 m on Borneo, and thus the two species show very little overlap in altitudinal range.

Eddy (1988) also compared *D. havilandii* with *D. rugifolium*. *Dicranoloma havilandii* is easily distinguished from *D. rugifolium* by the widely patent, not brittle leaves, *D. rugifolium* having erect-appressed to erectopatent leaves with brittle apices that are mostly lacking from a large part of the leaves. Tan (1989) laid strong emphasis on the rugosity of the leaf surface and therefore also compared *D. havilandii* with *D. rugosum* (Hook.) B.H. Allen from the Society Islands, which can easily be separated by a more compact habit, erectopatent leaves, a stronger costa and long sheathing perichaetial leaves, of which the sheathing part often reaches the capsule.

13. ***Dicranoloma reflexum*** (C. Müll.) Ren. (1909: 14). Fig. 31

Dicranum reflexum C. Müll. (1848: 373). — *Dicranum reduncum* Duby ex C. Müll. (1848: 374), nom. inval. in synon. — *Dicranum polymorphum* Duby ex Bosch & Lac. (1858: 67), nom. inval. in synon. Type: Indonesia. Java, Zollinger 2101 (B-holo, destroyed; BM!, H-BR!, JE!, L-lecto!, NY!, S!).

Dicranum reflexifolium C. Müll. (1848: 382). — *Leucoloma reflexifolium* (C. Müll.) Broth. (1901: 322). 1901. — *Dicranoloma reflexifolium* (C. Müll.) Broth. in Par. (1904: 29). Type: Indonesia. Java, Hb. Miquelianum (B-holo, destroyed; S-lecto!). Synonymised by Tan & Koponen (1983).

?*Dicranum dives* C. Müll. ex Bosch & Lac. (1858: 72). — *Leucoloma dives* (Bosch & Lac.) Broth. (1901: 322). — *Dicranoloma dives* (C. Müll. ex Bosch & Lac.) Par. (1904: 26). Type: Indonesia. Java, Herb. Al. Braun (not in L, not located). Synonymised by Eddy (1988).

Dicranum limprichtii Fleisch. (1904: 78); Musci Frond. Archipelagi Indici, ser. 2, No. 87, 1899, *nom. nud.* — *Dicranoloma limprichtii* (Fleisch.) Par. (1904: 27). Type: Indonesia. Java, auf dem Gipfel des Pangerango bei Kandang Badak am Gedeh, an Baumen und auf Waldboden, Fleischer s.n. (holotype in FH-FL could not be pin-pointed; L-lecto!, BM!, FH-Bartr.!, H-BR!, JE!, NY!, S!). Synonymised by Tan & Koponen (1983).

Dicranoloma ramosii Broth. (1910: 138). — *Dicranoloma ramosum* Broth. (1924: 209), nom. ill. err. pro D. ramosii. Type: Philippines. Luzon, Benguet, Mount Ugo, Ramos, Bur. Sci. 5867 (H-BR-holo, not found; BM!, NY!). Synonymised with *D. reflexifolium* by Bartram (1939).

Dicranoloma tenuirete Broth. (1918: 202). Type: Philippines. Luzon, Abra, Mount Posuey, Ramos, Bur. Sci. 27090 (H-BR-holo!, BM!, L!, NY!). Synonymised by Bartram (1939).

Pseudoautoicous. Dwarf males 0.4–0.8 mm tall. Leaves 0.45–0.8×0.1–0.13 mm, ovate-lanceolate to ovate-linear, acuminate, ecostate or with a faint costa in the upper half, elimbate; margin serrulate in the upper half, entire below. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 1.5–10 cm tall, growing in turfs or cushions, glossy yellowish-green to yellowish-brown. Stem brown, subflorally branched, densely foliose, laxly to densely tomentose; diameter 0.3–0.55 mm, central strand present, cortical cells thin-walled. Gemmae absent.

Leaves (4–)5–10×0.7–1.3 mm, triangular-linear to ovate-linear, gradually tapering, strongly plicate, flat to canaliculate, mostly falcate-secund to circinate, occasionally patent. Alar patches distinct, 0.2–0.55×0.15–0.4 mm, triangular, not reaching the costa. Margin serrate in the upper (1/3–)1/2 to almost as far down as the alar patches, entire below, occasionally slightly undulate in leaf middle. Limbidium consisting of 1–4(–6) rows, reaching from the alar patches to c. 1/4 of leaf length to well within the dentate part of the margin, occasionally interrupted or even absent in some leaves. Costa 40–100(–120) μm wide, 25–70 μm thick, well-marked in its entire length, percurrent or ending a few cells below leaf apex, abaxially bearing teeth in the upper 2/5–5/6; teeth in rows situated on 2 ribs in the distal part and on up to 4 ribs at the proximal end; guide cells 4–8; adaxially with (1–)2(–3) layers of stereids, occasionally intermingled with some cells with a distinct lumen, and, adjacent to the guide cells, occasionally with 1–2 cells with a lumen as large those of the guide cells, abaxially with (1–)2–3 layers of stereids, divided into (2–)3–4(–5) small bundles, separated by groups of cells with a distinct lumen; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells (20–)40–120(–180)×(6–)8–12(–18)

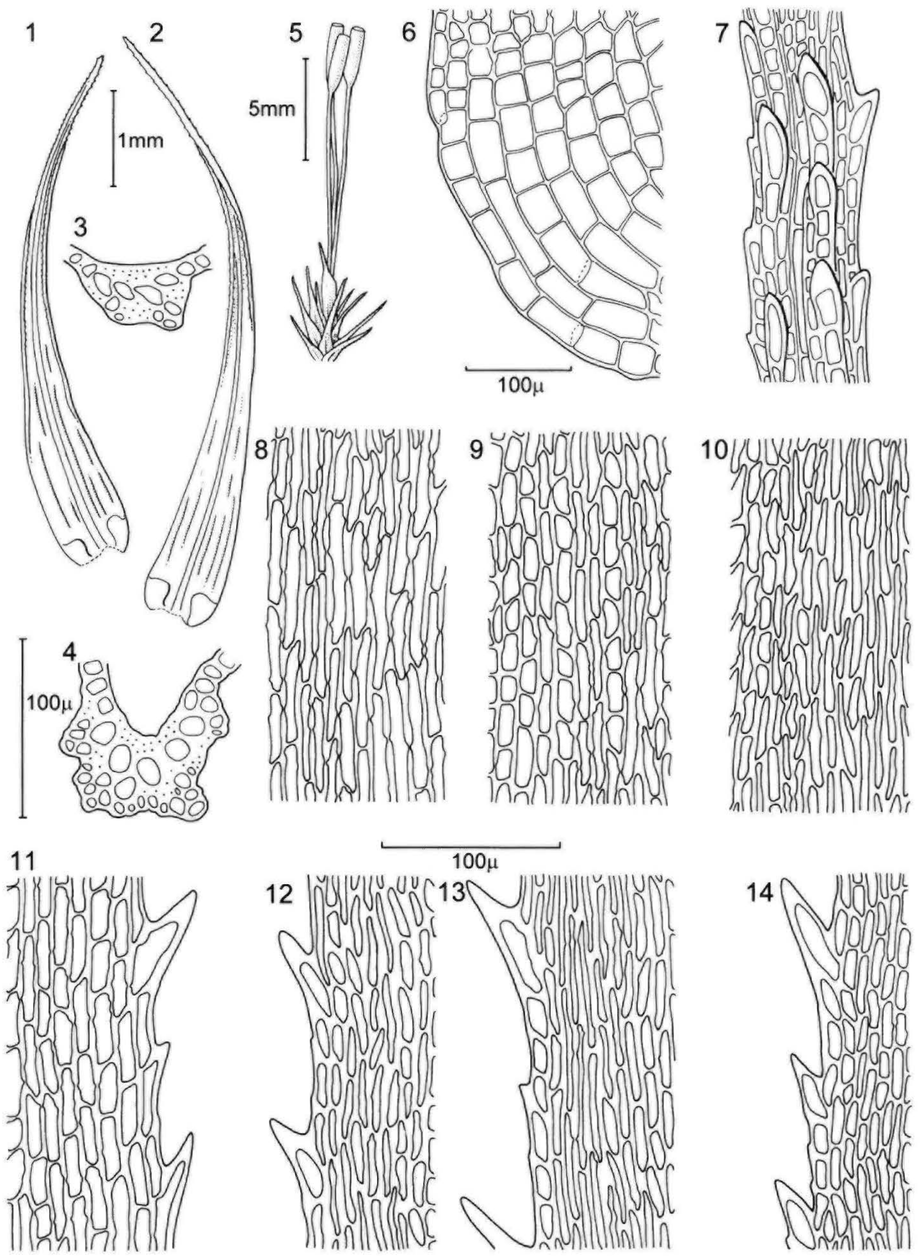

Fig. 31. *Dicranoloma reflexum* — 1–2. leaf; 3–4. cross section through the costa, just above the alar patches; 5. perichaetium with sporogones; 6. alar cells; 7. abaxial view of the costa, distal part; 8. basal lamina cells; 9–10. juxtacostal cells; 11–14. upper lamina cells. — 1. Zollinger 2101 (L; lectotype); 2, 13. Ridley 565 (H-BR); 3. Fleischer s.n., Musci Archipelagi Indici, No. 87 (L; lectotype of *D. limprichtii*); 4, 7–9, 11. Mohamed, Reese & Mohamed 9201 (L); 5–6. Agung, Kruijer & Kessler 941153 (L); 10, 12. Meijer B-3310 (L); 14. Noerta & Soekar 2238 (L).

μm, elongate to linear; walls thin to incrassate, pitted, lumen wall ratio 1–4(–8). Alar cells 15–120×15–60(–70) μm, quadrate to rectangular, often inflated; walls thin, 1–4 μm thick, not pitted, yellowish-orange-brown to brown or colourless. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with yellowish-brown or orangish walls. Limbidium cells 70–300×4–8 μm, linear, with very thick, non-pitted walls and very narrow, almost indiscernable lumina. Upper lamina cells 10–80(–100)×6–12(–14) μm, isodiametric to short-linear, more or less rhomboidal to straight or slightly curved, gradually becoming shorter than the basal lamina cells; walls thin to incrassate, pitted, often scarcely and shallowly so, lumen wall ratio 1–4. Along the costa frequently with an up to 5 rows wide band of cells similar to the upper lamina cells, which may reach as far down as the basal 1/4 of leaf length, at the sides and at the bottom gradually passing into the basal lamina cells. Teeth at leaf margin 10–50(–60) μm, consisting of a single cell; lumina mostly conspicuously larger than in the adjacent cells. Perichaetial leaves 3–9.5×0.8–2.5 mm, abruptly contracted into a subula; basal part 1–6.5 mm long, broadly ovate to elliptical, clasping to sheathing; subula reflexed in the outer leaves.

Sporogones (1–)2–4(–5) per perichaetium. Vaginula 1.5–3 mm long, orange-brown to dark brown. Seta 8–16(–19) mm long, yellowish to reddish-brown throughout or from reddish or reddish-brown below to yellow above, smooth; 0.15–0.22 mm in diameter, central strand present, cortical cells thin-walled, the peripheral 2–3 layers with very thick walls, central part often decayed at maturity. Capsule (1.5–)2–3.5 mm long, yellowish to brown, ellipsoid to cylindrical, straight to slightly curved, rarely strumose. Exothecial cells 20–120×10–45 μm, isodiametric to short-linear, irregularly shaped to rectangular, not in regular longitudinal rows. Annulus consisting of two rows of thick-walled cells, deciduous, often a few cells remaining attached at capsule mouth. Peristome teeth yellowish to reddish, 0.3–0.45 mm long, 60–110 μm wide at base, long-attenuate, asymmetrically bifid in the upper 1/3-3/4, occasionally fenestrate below to base; outer face vertically to obliquely striate, with cross-connections between the striae, in the basal 2/3 to throughout, papillose above; inner face smooth or with scattered papillae in the lower 2/3 to throughout, papillose above; outer trabeculae thin, smooth, inner trabeculae thick, smooth or papillose. Operculum c. 2 mm long, yellowish to yellowish-brown, obliquely rostrate above a conical base. Calyptra 4–6 mm long, green to brownish, more or less transparent, cucullate. Spores (16–)25–55(–64) μm, spherical, finely papillose.

Illustrations. Dozy & Molkenboer 1858: Vol 1, t. 55, f. 1–21 (as *Dicranum reflexum*); t. 59, f. 1–19 (as *Dicranum dives*); t. 60, f. 1–23 (as *Dicranum reflexifolium*); Bartram 1939: f. 60 (as *D. reflexifolium*); f. 61; Tan & Koponen 1983: f. 1–17, f. 18–20 (as *D. dives*), f. 39–40 (as *D. formosanum*); Eddy 1988: f. 133.

Distribution. Vietnam, Peninsular Malaysia, Sumatra, Java, Lesser Sunda Islands (Bali, Lombok, Flores, Timor), Philippines (Luzon, Negros, Mindanao, Palawan), Borneo, Sulawesi, Maluku (Ternate, Seram), New Guinea (Fig. 32).

Ecology. Growing in submontane and montane forest, from 600 to 3000 m. Only on Java found above 2250 m. Often found in disturbed forest. Also occurring in areas with a monsoon climate. Mostly epiphytic on stems and branches, but also often on logs and stumps or terrestrial. On Java frequently found on stems of *Pinus merkusii* Jungh. & De Vriese.

Selected additional specimens examined. VIETNAM. Vallée de Fongman, Krempf 1624 pp.

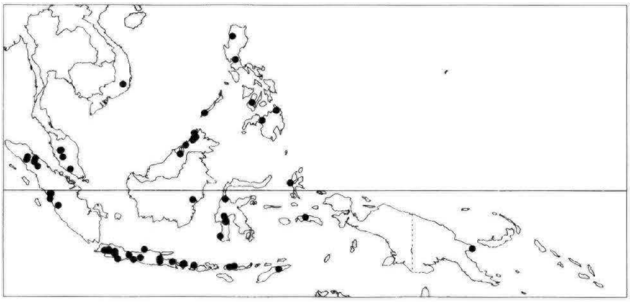

Fig. 32. Distribution of *Dicranoloma reflexum*.

(PC). PENINSULAR MALAYSIA. Pahang, Cameron Highlands, trail from Tanah Rata to Robinson's Fall, Haji Mohamed, Reese & Mohamed 9201 (BM, CBG, H, KLU, L, MO, NY); Sempang (Fraser Hill), Ridley 565 (H-BR); Sungai Bertam, Spare 3347 (BM); Johor, Mt. Ophir, Anonymus 971 (NY). SUMATRA. Sumatera Utara, Tongkoh, Touw & Snoek 25399 (L); Sumatera Barat, Gn. Singgalang, Beccari 95 (BM, JE); Gn. Kerinci, Meijer 7674 (H, L, S); Sumatera Selatan, Gn. Merapi, Schiffner 11453 (W). JAVA. Jawa Barat, above Cibodas, Fleischer s.n., Musci Frondosi Archipelagi Indici, No. 86 (BM, H-BR, JE, L, NY); Gn. Mas, Meijer B-3310 (L); Cibodas, Noerta & Soekar 2238 (L, S); Gn. Pangrango, above Cibeurreum, Schiffner 3878 (BM, H, L, MO, NY); Gn. Halimun area, Nimala Tea Estate, Van Balgooy & Wiriadi 2871 (L); Jawa Tengah, Gn. Slamet, Van der Gaag 6 (L); Gn. Merapi, Junghuhn s.n. (L); Jawa Timur, Cangar Forest Arboretum, Agung, Kruijer & Kessler 941153 (L); near Malang, Wiemans 1393 (BM, H-BR, JE, L, NY). BORNEO. SABAH. Gn. Kinabalu, above Poring, Meijer 10966 (L); Gn. Kinabalu, Mempening trail, Menzel, Frahm, Frey & Kürschner 3426 (FH); along road to Mammut Copper Mine, Shea 1020 (SAN); Banjaran Crocker (Crocker Range), between Sunsuron and pass, Menzel, Frahm, Frey & Kürschner 4658 (FH); Sipitang, Ulu Majoh, 10 m. SSE of Malaman, Wood 1688 (BM, L). SARAWAK. Trusan, Haviland s.n. (BM); Gn. Mulu National Park, Gn. Api, Touw 20535 (L). KALIMANTAN. Kalimantan Timur, Gn. Beratus (Peak of Balikpapan), Meijer 2176 (L). PHILIPPINES. LUZON. Rizal, Montalban, Loher 229459 (BM). VISAYAN ISLANDS. Negros Occidental, Kinabkaban River, Edano PNH 20212 (L). MINDANAO. Lanao, Ulango Mt., Ebalo 1183 (NY); Bukidnon, near Silipon (Silipau); Agusan del Norte, Cabadbaran, Mt. Hilong-Hilong, Mendoza & Convocar PNH 10947 (L). PALAWAN. Mt. Mantalingajan, Sitio Tabud near Brooke's Point, Tan 91-226 (FH). SULAWESI. Sulawesi Tengah, Gn. Roroka Timbu, Hennipman 5247 J (L); Sulawesi Selatan, Tana Toraja, Gn, Sesean, Touw & Snoek 24549 (L). NUSA TENGGARA. Bali, near Penulisan, Hegewald 10087 (NY); Lombok, Gn. Rinjani, S of Gn. Pussuk, Elbert 1810 (FH, L); Flores, Ruteng, Poco Tador Walok, Schmutz 6903 (FH, L); Gn. Pontanao, Perang village near Alo Lahu, Touw & Snoek 22502 (FH, L); Timor, Floris Mt. Stemodon, Teysmann 10627 (FH-FL, H-BR). MALUKU. Ternate, De Vriese s.n. (L); Seram, De Vriese s.n. (L). PAPUA NEW GUINEA. Morobe, Sattelberg, Zahn s.n. (S).

Dicranoloma reflexum is mostly easily distinguished from other species of *Dicranoloma* by its strongly plicate leaves. Some forms of *D. assimile*, however, may approach *D. reflexum*. Differences between these two species have been discussed under *D. assimile*. Differences between *D. reflexum* and *D. dicarpum*, which may share plicate leaves and differentiated juxtacostal cells, are discussed under *D. dicarpum*.

On account of its plicate leaves *D. reflexum* may also be compared with the relatively distantly related *D. braunii* and with *Braunfelsia plicata*. From the former it can be distinguished by the presence of a central strand in the stem and by the upper lamina cells which are conspicuously shorter than the basal ones. *Braunfelsia plicata* may be distinguished from *D. reflexum* by almost entire leaf margins, a very narrow costa devoid of abaxial teeth, and upper lamina cells that are similar to the basal ones.

Within what is here considered to be *D. reflexum*, Fleischer (1904) recognised four species, *D. reflexum*, *D. reflexifolium*, *D. dives* and *D. limprichtii*. In Fleischer's concept *D. reflexum* differs from the other species by shorter, thin-walled basal lamina cells. In his key *D. dives* is separated by its almost smooth leaves. *D. limprichtii* and *D. reflexifolium* are distinguished from each other by the limbidium, which is wide in *D. limprichtii* and narrow in *D. reflexifolium*, and by the annulus, which is revoluble in *D. reflexifolium* and absent in *D. limprichtii*.

Bartram (1939) recognised two species, *D. reflexum* and *D. reflexifolium*, differing by the thickness of the walls of the lamina cells. Two other Philippine taxa, *D. ramosii* and *D. tenuirete*, were placed in the synonymy of *D. reflexifolium* and *D. reflexum*, respectively.

As many intermediates between incrassate, pitted lamina cells and thin-walled lamina cells are found the two taxa cannot be separated. Therefore, in all more recent treatments (Tan & Koponen 1983, Eddy 1988, Tan 1989), only one species, *D. reflexum*, is recognised. The previous authors did not locate a type specimen of *D. reflexifolium*, the holotype in B being destroyed, but during this revision an isotype was found in S and this is here selected as the lectotype. Examination of this isotype confirmed the inclusion of *D. reflexifolium* in *D. reflexum*. Tan & Koponen and Eddy also agreed on the inclusion of *D. limprichtii* in *D. reflexum*. According to Tan & Koponen the limbidium is variably developed in *D. reflexum* and they also found remnants of annular cells at the capsule mouth in the type specimen of *D. limprichtii*. Eddy considered *D. limprichtii* to be just a robust state of *D. reflexum*. Also in this case, I agree with the previous authors.

Dicranoloma dives was synonymised with *D. reflexum* by Eddy (1988), who considered it to be a compact variant. Although no type specimen could be located, the original description and the accompanying drawings seem to justify this reduction. It should be noted that Fleischer's (1904) long description of *D. dives* did not describe the type specimen, but rather a collection from Borneo made by Korthals. The original description mentioned that *D. dives* has leaves which are plicate, especially in the upper part of the leaves, which is in contrast with Fleischer's observation that the leaves of *D. dives* are almost smooth. Of the collections made by Korthals found in Fleischer's herbarium and identified as *D. dives*, half were re-identified as *D. assimile* and the other half as *D. reflexum*.

Eddy's (1988) concept of *D. reflexum* appears to be slightly wider than in this revision, as he synonymised *D. perarmatum* with *D. reflexum* rather than with *D. assimile* as was done by Tan & Koponen (1983) and Tan (1989) and in this revision. Thus, Eddy included in *D. reflexum* forms of *D. assimile* resembling it.

I have compared *Dicranoloma reflexum* with the continental Southeast Asian *D. subreflexifolium* (C. Müll.) Par. as the names suggest that these species might be similar and because Mitten (1859) placed the type of *D. subreflexifolium* in *D. reflexifolium*. *Dicranoloma subreflexifolium* is indeed very similar to *D. reflexum* but also shows some similarity to *D. assimile*. The relatively short setae and straight to slightly curved capsules point towards

D. reflexum while the smooth or only slightly plicate leaves point towards *D. assimile*. The shape of the upper lamina cells points either way. As *D. subreflexifolium* does not really fit in either *D. assimile* or *D. reflexum* and only very few collections of *D. subreflexifolium* have been made, no conclusion on its placement could be reached and I have chosen to maintain *D. subreflexifolium* for the moment.

14. ***Dicranoloma rugifolium*** Bartr. (1942: 251). Fig. 33

Dicranum rugifolium (Bartr.) Norris & T. Kop. (1990: 44). Type: Indonesia. Irian Jaya, Lake Habbema, 3225 m, Brass 9252 (FH-holo!, BM!, L!, NY!)

Pseudoautoicous. Dwarf males 1.2–1.4 mm tall. Leaves 1.2–1.4×0.1–0.17 mm, ovate-lanceolate, acuminate, ecostate, elimbate; margin entire, sometimes involute in the upper 1/2-2/3 of the leaf, entire. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 2–8 cm tall, growing in dense cushions, yellowish-brown or greenish. Stem brown, subflorally branched or forked, densely foliose, densely tomentose; diameter 0.25–0.4, central strand present, cortical cells thin-walled. Gemmae absent.

Leaves 6–11.5×1–2 mm, ovate-lanceolate, gradually tapering, smooth to rugose, especially along the costa, canaliculate below, often subtubulose in the apical part, erectopatent throughout; leaf tips brittle, often fallen off. Alar patches distinct, 0.24–0.5×0.2–0.4 mm, triangular, not reaching the costa. Margin serrulate in the upper 1/3–2/3, entire below. Limbidium consisting of 1–3 rows of cells, reaching from the alar patches to just below the dentate part of the margin, occasionally interrupted. Costa 40–70 μm wide, 20–40 μm thick, either well-marked in its entire length or from just above the alar patches, percurrent or ending a few cells below leaf apex, abaxially with 2 rows of low teeth in the distal 1/3–1/2; guide cells 3–5; adaxially with 1–2(–3) layers of stereids, occasionally with 1–2 cells with a lumen as large as those of the guide cells adjacent to the guide cells, abaxially with 1–2 layers of stereids, often intermingled with cells with a distinct lumen, which very rarely divide the stereids into ill-defined bundles; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells (30–)40–150(–160)×8–16 μm, elongate to linear; walls incrassate, pitted, lumen wall ratio 1–1.5(–2.5). Alar cells 20–70×15–50 μm, quadrate to rectangular, occasionally some of them inflated; walls thin, 1–6 μm thick, occasionally pitted, yellowish to orangish-brown, colourless in young leaves. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with orangish to brown walls. Limbidium cells (75–)100–200(–440)×5–10 μm, linear, with very thick, non-pitted walls and very narrow, almost indiscernable lumina. Upper lamina cells (10–)20–75×8–15 μm, isodiametric to elongate, more or less rectangular or elliptical to straight or slightly bent; walls rather thin, scarcely and shallowly pitted, lumen wall ratio 2–6. Teeth at leaf margin 6–20 μm, consisting of a single cell; lumina not conspicuously larger than in the adjacent cells. Perichaetial leaves 4.5–10×1.2–2 mm, abruptly contracted into a subula; basal part broadly ovate to elliptical, clasping to sheathing; subula brittle, mostly fallen off, often reflexed in the outer perichaetial leaves.

Sporogones 1–3 per perichaetium. Vaginula c. 2.5 mm long, orange-brown to brown. Seta 11–18 mm long, yellowish to reddish-brown, smooth; 0.24–0.27 mm in diameter, cen-

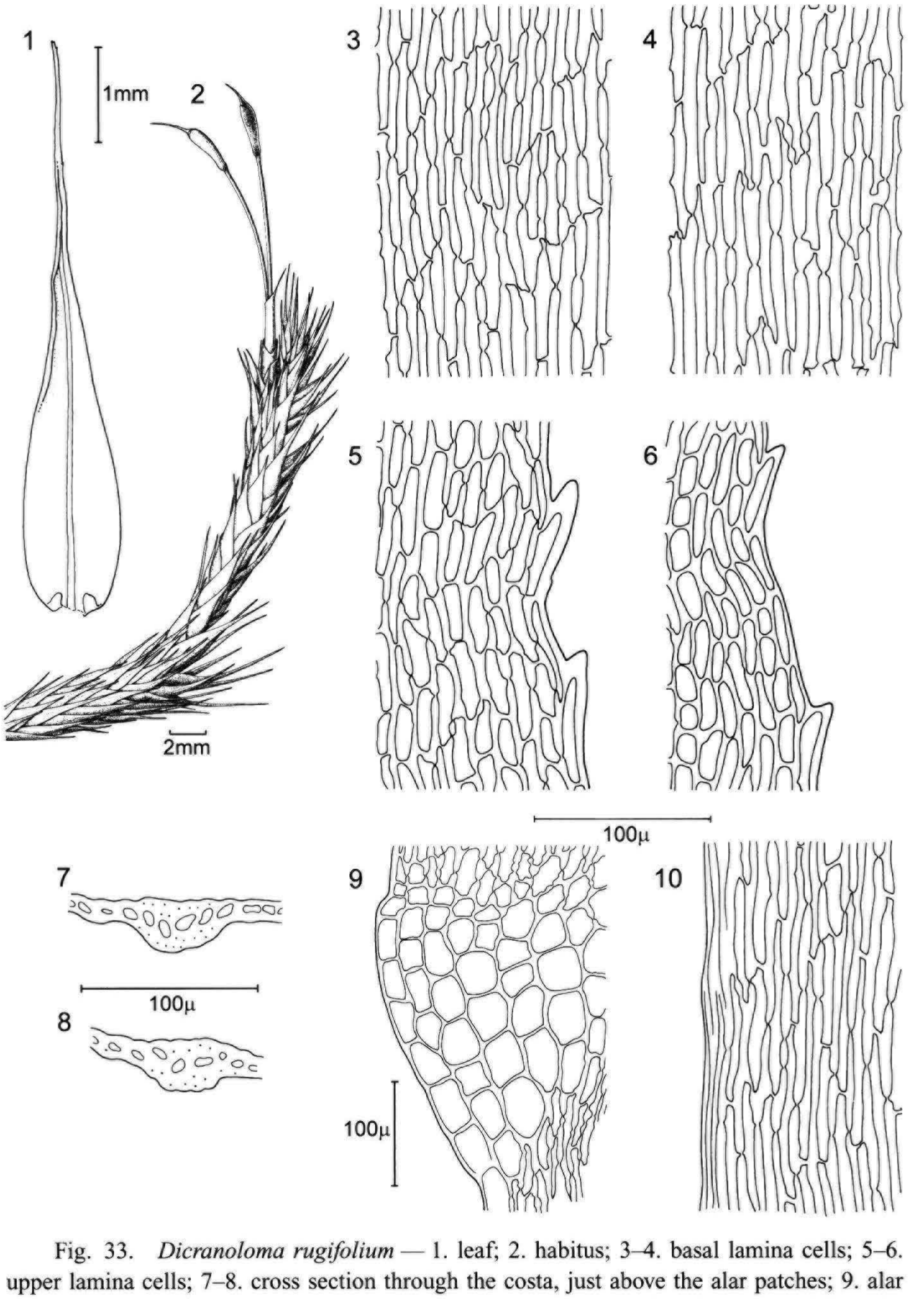

Fig. 33. *Dicranoloma rugifolium* — 1. leaf; 2. habitus; 3–4. basal lamina cells; 5–6. upper lamina cells; 7–8. cross section through the costa, just above the alar patches; 9. alar cells; 10. marginal and intramarginal cells. — 1, 4, 6, 8. Brass 9252 (FH; holotype); 2. Robbins 2840 (L); 3, 5, 7, 9–10. Robbins 4235 (L).

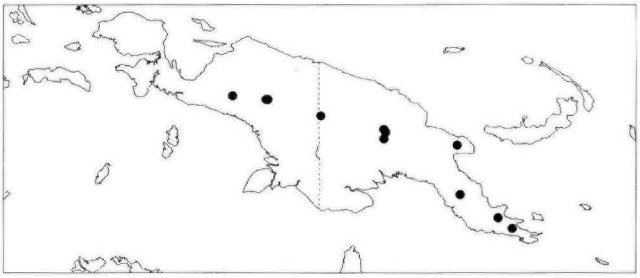

Fig. 34. Distribution of *Dicranoloma rugifolium*.

tral strand present, the peripheral 1–4 layers with very thick walls, central part often decayed at maturity. Capsule 2.5–3 mm long, yellowish to light brown, cylindrical, straight to slightly curved, not or slightly strumose. Exothecial cells 25–80(–130)×15–40 μm, isodiametric to elongate, irregularly shaped, not in regular longitudinal rows. Annulus consisting of 2–3 rows of thick-walled cells, persistent. Peristome teeth yellowish to reddish, 0.3–0.48 mm long, 50–100 μm wide at base, long-attenuate, asymmetrically bifid in the upper 1/2–2/3, fenestrate below to base; outer face papillose throughout or smooth in the basal 1/2–2/3 and papillose above, inner face smooth in the basal 1/2–2/3, papillose above; outer trabeculae thin, the ones in the upper c. 1/2 mostly papillose, inner trabeculae thick, all or only the ones in the upper c. 2/3 of the teeth papillose. Operculum 1.5–2 mm long, yellowish to yellowish-brown, rostrate or obliquely so above a conical base. Calyptra 6–7 mm long, greenish below to brown above, cucullate. Spores 19–27 μm, spherical, very finely papillose to almost smooth.

Illustrations. Bartram 1941: f. 5; Eddy 1988: f. 132 A–F; Norris & Koponen 1990: f. 13 f–k.

Distribution. Endemic to New Guinea (Fig. 34).

Ecology. Growing in the upper part of the lower montane forest (*Nothofagus* forest), in upper montane forest, and in subalpine forest, scrub and grassland, from 2550 to 3550 m. Mostly epiphytic, on stems of trees, shrubs, and tree ferns; occasionally terrestrial or on stumps and logs.

Specimens examined. INDONESIA. IRIAN JAYA. Paniai, Puncak Jaya (Carstensz Mts.), Zebra Flat, Hope CGE 93 (CBG); Jayawijaya, Puncak Trikora (Mt. Wilhelmina), Brass & Meijer-Drees 9745 (L). PAPUA NEW GUINEA. West Sepik, Star Mts., Mt. Capella, Touw 16299 (L); Southern Highlands, Mt. Giluwe, De Sloover 43041 (CBG); Enga, Sugarloaf Mountains, S of Wapenamanda, Robbins 2793 (CBG, L); Tsak Valley, near Wapenamanda, Robbins 2840 (L); Morobe, Mt. Sarawaket Southern Range, Norris 63013 (L), 63265 (H); Central, Guilala, NNE of Waitape, Croft LAE 61537 (BM); Wharton Range, track to Mt. Albert Edward area, near Woitape Patrol Post, Robbins 4235 (L); Milne Bay, (Mt. Suckling), Goë, Veldkamp & Stevens 5836 (L).

In its typical form, *Dicranoloma rugifolium* is easily distinguished from other Malesian Dicranolomas by its dense cushions and stiff, appressed leaves with brittle apices. Frequently, however, plants are found that have erectopatent leaves and form looser cushions, but possess all other characters of *D. rugifolium*. These plants may be confused with *D. assimile*. Differences between these two species are discussed under *D. assimile*. Differences between *D. rugifolium* and *D. havilandii* are discussed under *D. havilandii*.

The rugosity of the leaf surface in *D. rugifolium* is variable. Contrary to what its name seems to imply, *Dicranum rugifolium* needs not have rugose leaves. Plants with strongly rugose and completely smooth leaves on the same shoot have been found, as well as plants with only smooth leaves.

Norris & Koponen (1990) placed *Dicranoloma brachyphyllum* Nog. and *D. havilandii* var. *latifolium* Van Zanten in the synonymy of *D. rugifolium*. As argued already under *D. assimile*, the types of these names are high-altitude forms of *D. assimile*. They share with *D. rugifolium* the erectopatent, rugulose leaves, but lack the other distinguishing characters, i.e. the stiff leaves, the brittle leaf apices, the rectangular to elliptical upper lamina cells, and the smooth to papillose outer face of the peristome teeth.

Norris & Koponen (1990) compared *D. rugifolium* with *D. billardierei* with which, according to them, it shares a very similar pattern of leaf areolation, especially in the upper part of the leaf. *Dicranoloma rugifolium*, however, differs from *D. billardierei* in its leaf orientation, erect-appressed to erectopatent rather than falcate, convolute leaf apices, very lightly dentate to almost entire apices, and in usually having more or less symmetrical capsules. To the distinguishing features may be added the mostly aggregated sporogones and the wider costa.

15. ***Dicranoloma steenisii*** Klazenga (1996: 11). Fig. 35

Type: Papua New Guinea. Eastern Highlands, Watabung terr., between Goroka and Kundiawa, 2620 m, Iserentant B-48A (H-holo!, NY!). Paratypes: Papua New Guinea. Enga, Wabag area, Sugarloaf area south of Wapenamanda, 3000 m, Robbins 2813 (FH-Bartr.!, L!); Western Highlands, Nebilyer River, 28 km WNW of Mt. Hagen, 2760 m, Streimann 20602 (CBG!, H!); Eastern Highlands, Doulo Pass (25 km W of Goroka), north of Highlands Highway, 2550 m, Hoffmann 89–352 (CBG!, NY!); Madang, Finisterre Range, Lake Naho region, 2500 m, Eddy 1172 (BM!); Morobe, 5 km SE of Lake Wamba (5 km S of Tep-Tep Airstrip, on saddle of ridge leading to top of Mt. Finisterre, 3000 m, Norris 64304 pp. (H!, among paratype of *D. cutlackii*).

Pseudoautoicous. Dwarf males 0.5–2 mm tall. Leaves 0.25–1.1 mm long, ovate-acuminate to ovate-linear, ecostate or with a costa in the upper 2/3 or less, elimbate; margin entire throughout or with some minute teeth near apex. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants up to 13 cm tall, growing in turfs, green to yellowish-brown. Stem subflorally branched, densely tomentose, loosely foliose; diameter 0.25–0.35 mm, central strand absent, cortical cells thick-walled. Gemmae absent.

Leaves (6–)11–16×0.5–0.8 mm, ovate-linear, gradually tapering, smooth, spreading or falcate-secund throughout the stem; basal part canaliculate to subtubulose; subula almost entirely formed by the costa, cross-section V-shaped, occasionally brittle. Alar patches distinct, 0.4–0.5×0.35–0.4 mm, triangular, reaching the costa or not. Margin serrate in the upper 2/3–7/8, entire below. Limbidium absent. Costa 100–160 μm wide, 40–60 μm thick, well-marked in its entire length, percurrrent, abaxially bearing scattered teeth in the distal half; guide cells 7–11, often separated from the lamina at one or both sides by stereids; adaxially as well as abaxially with a 2–3 layers thick band of stereids; epidermis consisting of cells with a distinct lumen adaxially as well as abaxially. Basal lamina cells (20–)40–120×6–16 μm, elongate to short-linear; walls incrassate, porose, lumen wall ratio

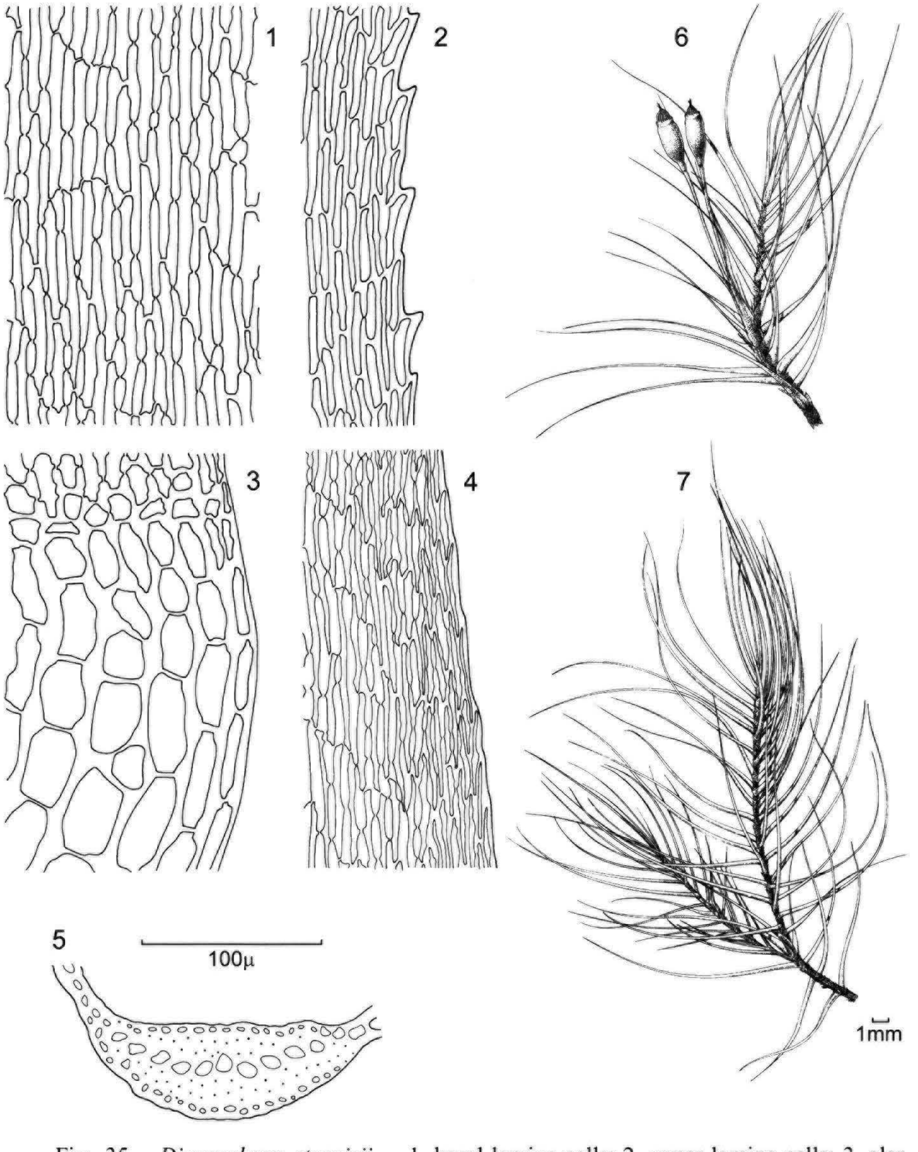

Fig. 35. *Dicranoloma steenisii* — 1. basal lamina cells; 2. upper lamina cells; 3. alar cells; 4. basal marginal and intramarginal cells; 5. cross section through the costa, just above the alar patches; 6–7. habit. — 1–5. Iserentant B-48 A (H; holotype); 6. Hoffmann 89-352 (CBG); 7. Eddy 1172 (BM).

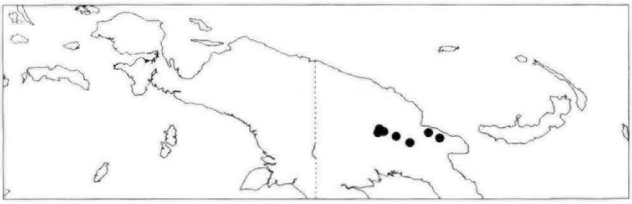

Fig. 36. Distribution of *Dicranoloma steenisii*.

1–2. Alar cells 15–80×15–40 μm, quadrate to rectangular, not inflated; walls incrassate, the lateral walls 4–12 μm thick, much thicker than the end walls, often with angular thickenings, occasionally pitted, colourless, or yellowish to brown. Decurrency cells and juxtacostal cells similar to the lamina cells, but with yellowish to brown walls. Upper lamina cells 20–90×6–10 μm, oblong to short-linear, straight, gradually shorter than the basal lamina cells; walls incrassate, pitted or not, lumen wall ratio 1–2. Cells at extreme apex 20–30 μm long, oblong, not pitted. Teeth at leaf margin small, 4–20 μm, consisting of 1(–2) cells; lumina not larger than in the adjacent cells. Perichaetial leaves 7–11×0.8–1 mm, abruptly contracted into a long subula; basal part ovate to broadly ovate, clasping to sheathing; subula almost entirely consisting of the costa.

Sporogones 1–2 per perichaetium. Vaginula 1.7–2 mm long, dark brown. Seta 4.5–5 mm long, yellowish to reddish-brown, smooth; 0.16–0.18 mm in diameter, central strand present, cortical cells rather thick-walled, peripheral layer with very thick walls, central part often decayed at maturity. Capsule 1.5–2 mm long, reddish-brown, cylindrical, straight. Exothecial cells 30–75×(10–)15–40 μm, isodiametric to elongate, irregularly shaped, not in regular longitudinal rows. Annulus consisting of 2–3 rows of thick-walled cells, persistent. Peristome teeth yellowish to reddish, up to 0.6 mm long, 50–70 μm wide at base, long-attenuate, asymmetrically bifid in the upper 3/4–7/8, sometimes fenestrate below almost to the base; outer face vertically striate in the basal 2/3, papillose above; inner face smooth in the basal half, papillose above; upper trabeculae papillose. Operculum c. 2 mm long, yellowish to yellowish-brown, obliquely rostrate above a conical base. Calyptra unknown. Spores 20–28 μm, spherical, finely papillose.

Illustrations. Klazenga 1996: 12, f. a–b; 13, f. a–e.

Distribution. Endemic to New Guinea (Fig. 36).

Ecology. Growing in upper montane and subalpine forest, from 2500 to 3550 m. Mostly epiphytic, on stems and, occasionally, branches of trees; rarely terrestrial.

Selected additional specimens examined. PAPUA NEW GUINEA. Southern Highlands, Mt. Giluwe, Van Zanten 68 3288 b (GRO); Western Highlands, Mt. Hagen, Van Zanten 682964 (GRO); Eastern Highlands, Mt. Otto, Veldkamp & Obedi 8706 B (L).

Dicranoloma steenisii has been confused with *D. brevisetum* and *D. blumei*. From both species it can be separated by hand-lens already by the strong costa which almost entirely fills the upper half of the leaf. Moreover, it can be distinguished easily from both these species by the absence of a limbidium. In addition, *D. steenisii* can be distinguished from *D. blumei* by the dense tomentum on the stem and by the absence of a central strand.

In a previous publication (Klazenga 1996) I considered *D. steenisii* to be closely related to *Cryptodicranum armitii*, with which it shares a strong costa and similar costal anatomy. A more thorough study of the peristome of both species, however, revealed that the peristome characters in *C. armitii* are so different from *D. steenisii*, or any other *Dicranoloma*, that I now think the affinities of *D. steenisii* rather lie with *D. braunii* and *D. brevisetum*. With these species *D. steenisii* shares, besides a similar peristome design and ornamentation, the absence of a central strand, a short seta, and an erect capsule.

Cryptodicranum Bartr. (1938: 127)

Type: *C. setosum* Bartr.

Cryptodicranum is a monotypic genus separated from *Dicranoloma* and *Dicranum* by its immersed capsule, smooth peristome teeth and the outer plates of the peristome being thicker than the inner ones.

The immersed capsules and smooth peristome teeth were reason for Bartram (1938) to create a separate genus, *Cryptodicranum*, in which initially *C. setosum* was placed. In a later publication Bartram (1942) synonymised *C. setosum* with *Dicranoloma armitii*, but considered the generic characters distinguishing *Cryptodicranum* still "perfectly valid". The genus *Cryptodicranum* was also recognised by Van Zanten (1964), Eddy (1988) and Akiyama (1990). Tan & Koponen (1983) found that the peculiar characters of *C. armitii* also occur in species of *Dicranoloma*. Short seta, erect capsule, lack of a central strand and, according to Tan & Koponen, smooth peristome teeth, are features shared with *D. brevisetum* and *D. braunii*. They therefore preferred to keep *D. armitii* in *Dicranoloma* "until more convincing evidence has accumulated". Tan (1989) and Norris & Koponen (1990) take a similar position.

This evidence can be found in the design of the peristome teeth. The peristome is rather deeply inserted. Extremely thickened walls of the outer peristomial layer (OPL) form a preperistome at the base. In older capsules this preperistome may become detached from the peristome thus forming extra, rudimentary teeth which, however, are not visible from the outside. Higher up, fragments of the locally thickened inner walls of the OPL may remain attached to the peristome. The inner walls of the primary peristomial layer (PPL) are extremely thickened, resulting in outer plates that are thicker than in species of *Dicranoloma* and also thicker than the inner ones. The inner plates are ill-developed and even lacking at the base of the peristome.

Peristomes with the outer plates thicker than the inner ones are never found in *Dicranoloma*. Moreover, peristome teeth are never completely smooth in *Dicranoloma* and the setae of *D. brevisetum* and *D. braunii*, although relatively short, are still longer than those of *C. armitii*. Therefore, and because of the position of *C. armitii* in the cladograms, *Cryptodicranum* is accepted here.

Peristomes with thicker outer plates than inner plates are also found in all species of *Leucoloma* and in *Sclerodontium*. *Leucoloma* subg. *Leucoloma* also has immersed capsules, although the setae are slightly longer than in *Cryptodicranum*. Thickened OPL walls are also found in some species of section *Caespitulosa* Besch. of *Leucoloma* (cf. La Farge-England 1998). Leaves with a broadly elliptic base and long setaceous apex, like in *C. armitii*, also occur in *Leucoloma*, in the *fuscifolium* species group (cf. La Farge-England 1998). However, the robust size of the plants, the homogeneous smooth lamina cells, the tomentose stem, the presence of dwarf males on the tomentum and the wide costa with abaxial teeth, exclude *C. armitii* from *Leucoloma*.

16. ***Cryptodicranum armitii*** (C. Müll.) Bartr. (1942: 252 ["*Armiti*"]). Fig. 37

Dicranum armitii C. Müll. (1897b: 358 ["*Armiti*"]). — *Dicranum cryptopodium* Broth. & Geh. in Geh. (1898: 3), nom. inval. in synon. — *Leucoloma armitii* (C. Müll.) Broth. (1901: 322). —

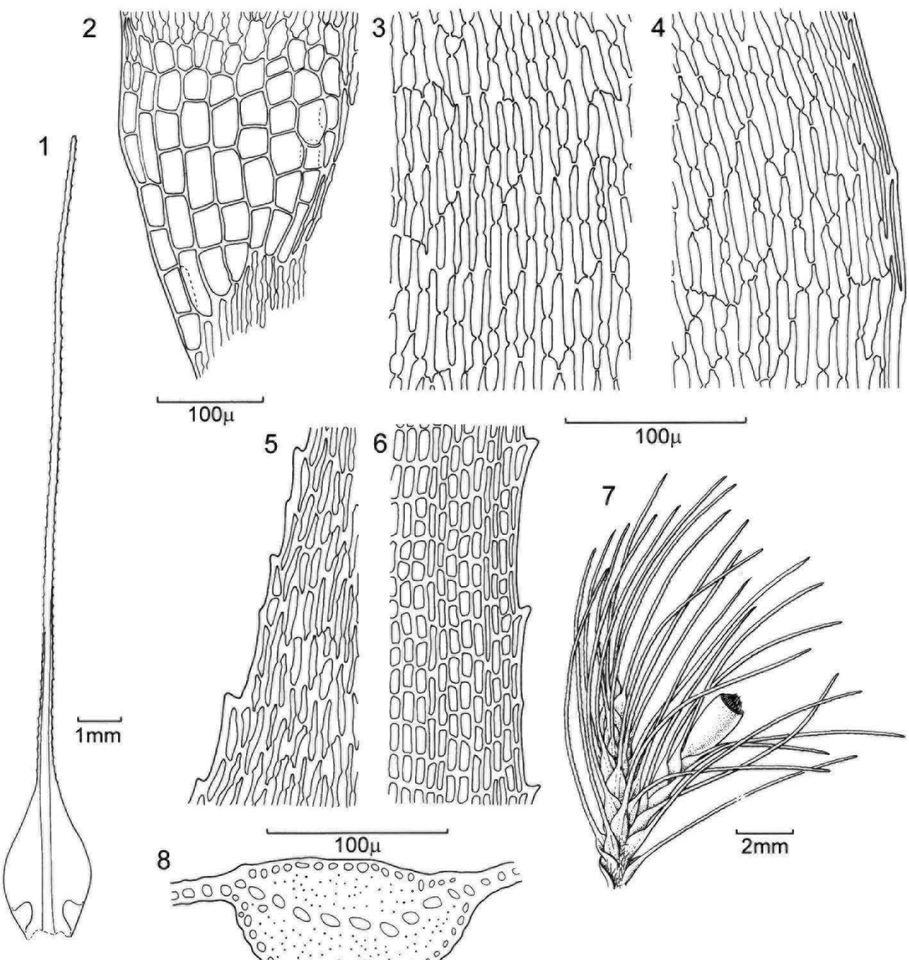

Fig. 37. *Cryptodicranum armitii* — 1. leaf; 2. alar cells; 3. basal lamina cells; 4. basal marginal and intramarginal cells; 5. cells at leaf shoulder; 6. abaxial side of subula, epidermal costa cells and a single row of lamina cell (at extreme left); 7. perichaetium with sporogone and subfloral innovation; 8. cross section through the costa, just above the alar patches. — 1–8. Eddy 1937 p.p. (BM).

Dicranoloma armitii (C. Müll.) Par. (1904: 24). Syntypes: Indonesia: Irian Jaya, Mt. Arfak ad Hatam ["Halam"], 5000–7000 ft., O. Beccari 173 (B, destroyed; H-BR-lecto!, FH-Bartr. !, FH-FL!, L!); Papua New Guinea: Cape Armit, Dedouri, J-a-la-River, "Hb. Melbourne 1885 misit", s. coll., s.n. (B, destroyed; not in MEL). Lectotype selected here.

Dicranoloma buruense Broth. & Herz. in Herz. (1926: 343). Type: Indonesia: Maluku, Mittelburu, W. Elen, c. 1600 m, K. Deninger s.n. (JE-holo!, BM!, S!). Synonymised by Tan (1989).

Dicranoloma johannis-winkleri Broth. (1928b: 116 ["*Johannis Winkleri*"]). Type: Indonesia. Kalimantan, West Borneo, Bukit Raja, c. 1300 m, H. Winkler 3181 (H-BR-holo!). Synonymised by Tan & Koponen (1983).

Cryptodicranum setosum Bartr. (1938: 128). Type: Solomon Islands. Bougainville, near Lake Luralu, S.F. Kajewski no. (D.) (FH-Bartr.-holo!, FH!). Synonymised by Bartram (1945).

Cryptodicranum armitii (C. Müll.) Bartr. var. *fragilifolium* Bartr. (1945: 111). Type: Papua New Guinea: Morobe, A-mieng (A-mien), on Yaneng (Yamen) River, a tributary of the Buso River, above mouth of Tosapik Creek, 5000–6000 ft., M.S. Clemens 12229.12 (FH-holo!). Synonymised by Eddy (1988).

Pseudoautoicous. Dwarf males 0.5–2 mm tall. Leaves 0.5–0.7 mm long, ovate, acuminate, elimbate; costa absent or present in the upper up to 2/3; margin entire throughout or serrulate in the upper part. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants in dense 2–8 cm high turfs or up to 15(–20) cm long pendulous stems, yellowish-green to yellowish-brown. Stem subflorally branched, densely foliose, densely tomentose; diameter 0.3–0.4 mm, central strand absent, cortical cells thick-walled. Gemmae absent.

Leaves 6–12×0.8–1.5 mm, falcate-secund in the upper part of the stem, erectopatent to patent below, occasionally erectopatent to patent throughout; basal part 1–3 mm long, broadly ovate, plicate when dry, with a short fold at leaf shoulder when wet, abruptly contracted into a long subula; subula setaceous, almost entirely formed by the costa, V-shaped in cross-section, often flexuose, sometimes brittle. Alar patches distinct, 0.2–0.5×0.2–0.35 mm, triangular, not reaching the costa. Margin entire or minutely serrulate near the insertion of the leaf, upwards the teeth becoming more pronounced and in the greater part of the subula irregularly coarsely serrate. Limbidium mostly absent, rarely present, consisting of 1–2 rows of cells, reaching from just above the alar patches to just below leaf shoulder, often interrupted. Costa 100–150 μm wide, 40–60 μm thick, well-marked in its entire length, percurrent, abaxially with 2 rows of low teeth in the distal 1/2–2/3 of the subula; guide cells 7–12, occasionally separated from the lamina at one or both sides by stereids; adaxially as well as abaxially with a 4–5 layers thick band of stereids; adaxial and abaxial epidermis consisting of cells with a distinct lumen. Lamina cells of the basal part 25–90×8–12(–15) μm, elongate to short-linear; walls incrassate, pitted, lumen wall ratio 0.7–1.5(–2). Alar cells (25–)30–80×20–40 μm, quadrate to rectangular, mostly some inflated; walls rather thin, 2–3 μm thick, not pitted, colourless or brown. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with yellowish-brown to brown walls. Limbidium cells, if present, linear, thick-walled, with very thick, non-pitted walls and very narrow, almost indiscernable lumina. Cells at leaf shoulder 15–60(–80)× 5–10 μm, oblong-elliptic to rhomboid to short-linear; walls incrassate, mostly scarcely and

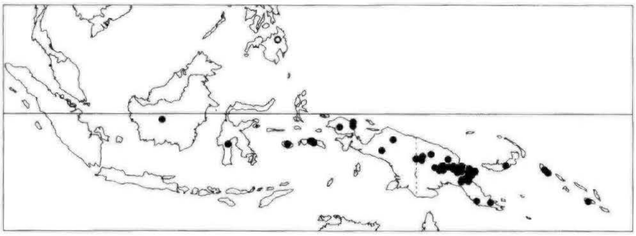

Fig. 38. Distribution of *Cryptodicranum armitii*. Dots: based on verified herbarium specimens; circle: based on literature report.

shallowly pitted, lumen wall ratio 1–2. Lamina in the subula consisting of 1–3 rows of cells; cells 10–25×6–10 μm, oblong to elongate-rectangular; walls incrassate, not pitted, lumen wall ratio 1–2. Teeth at leaf margin irregular, mostly widely spaced, 8–25 μm, consisting of 1–2 cells; lumina mostly not conspicuously larger than in the adjacent cells. Perichaetial leaves 8–12 mm long, similar to stem leaves, but with a somewhat longer, clasping to sheathing basal part and less distinct alar patches, which may reach the costa.

Sporogones 1–2 per perichaetium. Vaginula c. 1 mm long, dark brown. Seta 1–2 mm long, yellowish to reddish, smooth; 0.25–0.30 mm in diameter, central strand present, cortical cells thin-walled, peripheral layer with very thick walls. Capsule 1.5–2 mm long, reddish-brown to dark brown, ellipsoid to cylindrical, straight, not strumose. Exothecial cells 20–55×(10–)20–30 μm, irregularly elongate, not in regular longitudinal rows. Annulus consisting of 2–3 rows of flattened, thin-walled cells, deciduous, often the thick outer walls remaining attached at capsule mouth. Peristome teeth yellowish to reddish, 0.35–0.5 mm long, 100–140 μm wide at base, long-attenuate, asymmetrically bifid in the upper 1/2–3/2, fenestrate almost to base, the wider segment of each tooth sometimes bifid at apex; outer as well as inner face mostly smooth, outer face rarely with a fine obliquely striate ornamentation in the basal 1/2–2/3; outer plates thicker than the inner ones, occasionally with fragments of thickened OPL walls attached; trabeculae smooth. Operculum c. 1 mm long, reddish-brown, rostrate above a conical base. Calyptra c. 1.5 mm long, brown, cucullate. Spores 20–45 μm, spherical, finely papillose; occasionally with a slightly bimodal size distribution within a single capsule.

Illustrations. Geheeb 1898: t. 2, f. 1–11 (as *Dicranum armitii*); Bartram 1938: f. 1–8 (as *Cryptodicranum setosum*); Tan & Koponen 1983: f. 67–77 (as *Dicranoloma armitii*); Eddy 1988: f. 143 A–H; Norris & Koponen 1990: f. 7 a–f (as *Dicranum armitii*).

Distribution. Borneo (Kalimantan), Philippines (Mindanao), Sulawesi, Maluku (Buru, Seram), New Guinea, Bismarck archipelago (New Britain), Solomon Islands (Bougainville, Guadalcanal) (Fig. 38). The record from Mindanao (Tan 1987) has not been checked, but is considered to be reliable.

Ecology. Growing in lower montane and upper montane forest, rarely in subalpine grassland, from 900 to 3500 m, mostly below 3000 m. No altitude is given for the only record from alpine grassland, Mundua 43 (H). Mainly in primary forest, but also frequently collected from disturbed and secondary forest. Mostly epiphytic on stems and branches of trees, often high up in the canopy, also frequently on dead wood and occasionally terrestrial or on rocks.

Selected additional specimens examined. INDONESIA. SULAWESI. Sulawesi Selatan, Pegunungan Latimojong, lower slopes of Gn. Rantelemo, Eddy 5176 (BM). MALUKU. Seram, Manusela National Park, Akiyama c-9729 (L). IRIAN JAYA. Sorong, Nettoti Range, Van Royen & Sleumer 7919 (L); Paniai, Puncak Jaya (Mt. Carstensz), Boden Kloss 27 (BM); Jayawijaya, Sungai Taritatu (Idenburg River), Brass 12687 (FH); Jayapura, Pegunungan Sterren (Star Mts.), Van Zanten 606 (BM, L). PAPUA NEW GUINEA. West Sepik, Frieda River, Mt. Ekvaidebom, Koponen 35517 (H, L); Star Mountains, above Fologonom, Touw 18202 (L); East Sepik, Sumset (Mt. Hunstein), Hoogland & Craven 10977 (CBG, L); Southern Highlands, Paunde logging area, Streimann 26995 (H); Madang, Finisterre Range, Moro, Eddy 1035 (BM); Western Highlands, Mt. Hagen, Van Zanten 683128 (BM, FH, L); Simbu, Kombugomambuno, near Mt. Wilhelm, Mundua 43 (H); Eastern Highlands, Arau, Brass 31961 (L); Morobe, Herzog Mts., Wago, Eddy 1937 pp. (BM); Central, Mt. Durigolo, Clark 5 (BM); Milne Bay, Mt. Dayman, Brass 22371 (FH-Bartr.). BISMARCK ARCHIPELAGO. New Britain, Mt. Lululua, Stevens et al. LAE 58443 (L). SOLOMON ISLANDS. Bougainville, Lake Loloru Crater, Craven & Schodde 344 (L); Guadalcanal, Mt. Popomanaseu, Van Zanten 682777 (L).

Cryptodicranum armitii is a very distinctive species unlikely to be confused with any Malesian species of *Dicranoloma* due to its stiff, patent leaves with broadly ovate, abruptly contracted basal parts and long setaceous subulae, which are almost completely filled by the costa. *Dicranoloma braunii* often has somewhat contracted leaves but never as much as in *C. armitii*, and in *D. braunii* the subula has a well-developed lamina which is wider than the costa. *D. steenisii* shares with *C. armitii* a similar costal anatomy and upper part of the lamina almost completely filled by the costa, but in *D. steenisii* the leaf is gradually tapering.

Cryptodicranum armitii has been allied with *Dicranoloma menziesii* (Tayl.) Par. (Müller 1897b, Geheeb 1898, Brotherus 1928 (under its synonym *Dicranoloma johannis-winkleri*)), which it resembles in habit and in its long excurrent costa and with which it shares a similar costal anatomy. *Dicranoloma menziesii* differs from *C. armitii* by the presence of a central strand, a gradually tapering leaf blade, polygonal to isodiametric upper lamina cells, a longer (1 cm or more) seta and an arcuate capsule. Tan & Koponen (1983) assumed that *C. armitii* and *D. menziesii* are anisosporous. Norris & Koponen (1990), however, did not find a bimodal distribution of spore sizes in all their material of *C. armitii*. Also in this revision a bimodal distribution was not always found, although a large difference between the smallest and the largest spores was found in many capsules.

Dicranoloma rufifolium Besch. from the Marquesas Islands resembles *C. armitii* in its abruptly contracted leaves but differs in the presence of a central strand and the costa, albeit strong and almost completely filling the upper part of the leaf, being considerably narrower. Sporogones of *D. rufifolium* are unknown.

Cryptodicranum armitii is not a very variable species, the main source of variation being the length of the setaceous leaf apex. Also the fragility of leaf apices is variable. Leaves with the tips broken off are found in most plants and in some plants only a few leaves at shoot apex are left intact. Bartram (1945) described a variety, var. *fragilifolium*, to accommodate these extreme cases but, as intermediates are numerous, this variety is not maintained here.

Dicranum Hedw. (1801: 126)

Type: *D. scoparium* Hedw. Lectotype selected by Williams (1913).

Dicranum differs from *Dicranoloma* by the absence of a differentiated leaf border. Moreover, most species of *Dicranum* have multi-layered alar patches. Species with single-layered alar patches always form small plants and will therefore not be confused with *Dicranoloma*. The only Malesian representative is such a small-statured species.

17. ***Dicranum psathyrum*** Klazenga, *nom. nov.* Fig. 39

Dicranoloma fragile Broth. (1924: 209). — *Dicranum fragile* Hook. (1819: 134), hom. illeg., non *Dicranum fragile* Brid. (1800: 296). Type: Nepal. In Nepaul legit Hon. D. Gardner, et ad J. Banks Baronetum communicavit Gul. Wallich, (BM!).

Holomitrium fragillimum Dix. in Verdoorn, Musci Selecti et Critici Series V., no. 219, 1938, *nom. nud.* Authentic specimen: Burma. Sin Lum, Khanna s.n. (L!). Synonymised by Horikawa & Ando (1964)

Nomenclatural note. The new name is necessary because the epithet *Dicranum fragile* is occupied by *D. fragile* Brid. (≡*Campylopus fragilis* (Brid.) Bruch & Schimp.). "Psathyros" in Greek means the same as "fragile" in Latin, or in English.

Pseudoautoicous or, rarely, dioicous. Dwarf males 0.7–1.6 mm tall. Leaves 0.4–1.1×0.1–0.3 mm, ovate-lanceolate, acuminate, ecostate, elimbate; margin entire throughout or with some minute teeth at leaf apex. Perigonial leaves slightly shorter and broader than the largest stem leaves, broadly ovate, acute to acuminate, clasping, ecostate, elimbate; margin entire throughout. Female plants 0.5–4 cm tall, growing in loose cushions or turfs, glossy yellowish-green to yellowish-brown. Stem reddish brown to brown, simple or subflorally branched, densely foliose, densely tomentose; diameter 0.2–0.4 mm, central strand present, cortical cells thin-walled. Gemmae rarely present in the lower parts of the stem, at the tips of the rhizoids, 0.1–0.3 mm long, 20–30 μm, filamentous to club-shaped, colourless, consisting of up to 20 cells; walls smooth.

Leaves (2.5–)3–5(–7.5)×0.4–0.8 mm, ovate-linear to triangular-linear, plicate when dry, slightly so to almost smooth when wet, canaliculate, widely patent to erectopatent, often with falcate tips, to falcate-secund; leaf tips brittle, mostly fallen off, except at stem apex. Alar patches distinct, (0.15–)0.2–0.35×0.12–0.25 mm, triangular to almost quadrate, not reaching the costa. Margin serrate in the upper 1/2–3/4(–5/6), entire below. Limbidium absent. Costa (40–)50–100(–130) μm wide, 30–55 μm thick, either well-marked in its entire length or from just above the alar patches, percurrent, abaxially with 2 rows of teeth in the distal (1/3–)1/2–3/4; guide cells 4–8(–10); adaxially with a single layer of cells with a lumen as large as or almost as large as those of the guide cells, often intermingled with some stereids, abaxially with 1(–2) layers of cells with a large lumen, mostly with some scattered stereids among them; epidermis not differentiated adaxially as well as abaxially. Basal lamina cells (20–)30–90(–120)×(8–)10–20 μm, oblong to linear; walls mostly thin, pitted or shallowly so, lumen wall ratio (1.5–)2–5(–6). Alar cells (15–)20–90×(15–)20–45 μm, quadrate to rectangular, often slightly enlarged to inflated; walls thin, 1–3(–4) μm thick, not pitted, yellowish to yellowish-brown or colourless. Basal juxtacostal cells and decurrency cells similar to the basal lamina cells, but with slightly more yellowish walls. Upper lamina cells (7–)10–70(–80)×8–16 μm, isodiametric to elongate (– short-linear), irregularly rectangular; walls not pitted or scarcely and shallowly so, lumen wall ratio 3–6. Teeth at leaf margin 5–45 μm large, consisting of a single cell; lumina mostly conspicuously larger than in the adjacent cells. Perichaetial leaves 3–7×0.7–1.8 mm, abruptly contacted

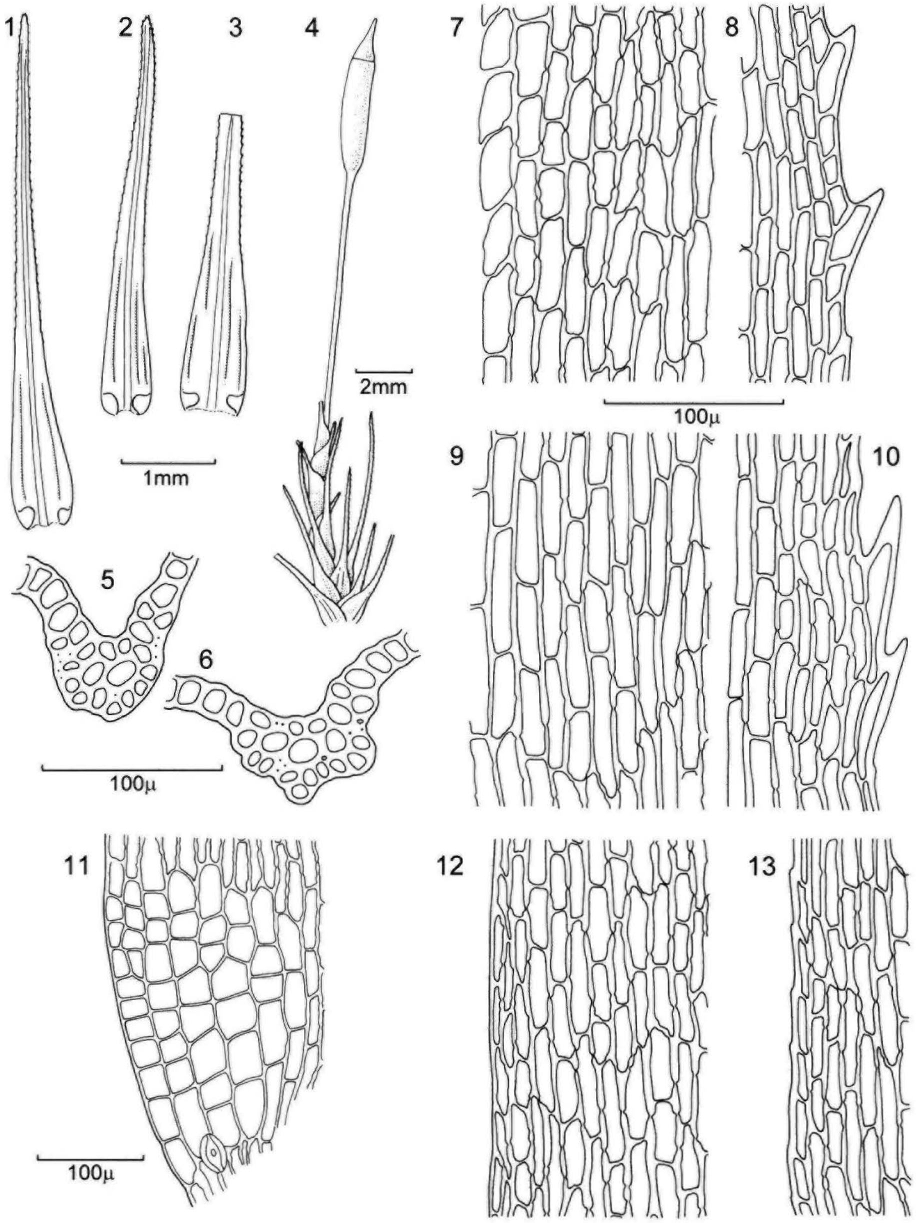

Fig. 39. *Dicranum psathyrum* — 1–3. leaf; 4. perichaetium with sporogone; 5–6 cross section through the costa, just above the alar patches; 7, 9. basal lamina cells; 8, 10. upper lamina cells; 11. alar cells, with rhizoid initial at centre bottom; 12–13. basal marginal and intramarginal cells. — 1, 4, 6, 9–10, 13. Williams 1852 (H-BR); 2–3, 5, 7–8, 11–12. Micholitz 308 (H-BR).

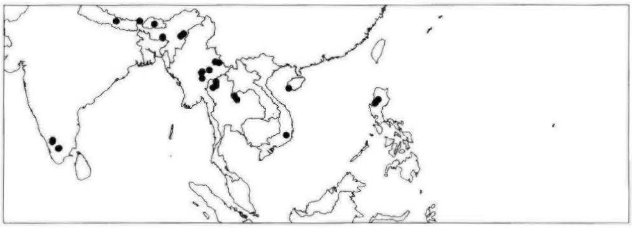

Fig. 40. Distribution of *Dicranum psathyrum*.

into a subula; basal part 0.7–4 mm long, ovate to broady ovate, clasping to sheathing; subula brittle, mostly fallen off, often reflexed in the outer perichaetial leaves.

Sporogones 1–3 per perichaetium. Vaginula 1–2.5 mm long, reddish-brown to dark brown. Seta (6.5–)9–12 mm long, yellowish to orange-brown throughout or orange brown below and yellowish above, smooth; 0.18–0.2 mm in diameter, central strand present, cortical cells thin-walled, the peripheral 2–4 layers with very thick walls, central part often decayed at maturity. Capsule 2–3 mm long, yellowish-brown to brown, cylindrical, striaght, not strumose, often slightly sulcate. Exothecial cells 35–160×12–35 μm, oblong to linear, irregularly shaped, not in regular longitudinal rows. Annulus consisting of large thick-walled cells, persistent or deciduous. Peristome teeth yellowish to reddish, 0.25–0.4 mm long, 50–75 μm wide at base, long-attenuate, asymmetrically bifid in the upper 1/2–3/4, mostly fenestrate below to base; outer face either vertically to obliquely striate throughout, occasionally with cross connections between the striae in the basal half, or smooth in the basal ca. 2/3 and papillose above; inner face smooth in the basal c. 2/3, papillose above; outer trabeculae thin, smooth; inner trabeculae thick, papillose, the most basal ones often almost smooth. Operculum 1.5–2 mm long, yellowish to yellowish-brown, obliquely rostrate above a conical base. Calyptra not seen. Spores 20–32 μm, spherical, finely papillose, rarely smooth.

Illustrations. Hooker 1819: t. 134, f. 1–7 (as *Dicranum fragile*); Bartram 1939: f. 59 (as *Dicranoloma fragile*); Gangulee 1971: f. 189 (as *Dicranoloma fragile*); Tan & Koponen 1983: f. 60–66 (as *Dicranoloma fragile*). Eddy's (1988) f. 139 A–F probably are *Dicranoloma daymannianum*.

Distribution. Within Malesia only found on Luzon. Further occurring in India, Nepal, Bhutan, Birma, Thailand, and Vietnam (Fig. 40).

Ecology. In Luzon found from 1500 to 2500 m on tree stems, mostly *Pinus*; once found on a rock face. Outside Malesia found on stems and branches in evergreen forest, between 600 and 2400 m, mostly above 1200 m.

Selected additional specimens examined. INDIA. Tamil Nadu, Nilgiri Hills, Ootacamund, Weir 30 (BM, NY); Palni Hills, Kodaikanal, Foreau 1923 (H, L, NY); Meghalaya, Khasi Hills, Nongkhlaw, Hooker & Thomson 54 (BM, H-BR, H-SOL); Nagaland, Kohima, Micholitz s.n. (FH, JE). NEPAL. Hooker 41 (BM), s.n. (NY). BHUTAN. Griffith 25 (BM), 332 (BM). BURMA. Shan State, Micholitz 260 (BM, H, JE); Pang Yang, Dickason 9675 (FH); Mong Pawk, Dickason 9825 (FH, FH-Bartr.); Taunggyi, Egerod (FH-Bartr., MO). THAILAND. Payap, Doi Suthep, Chiengmai, Doi Pui, 8733 (BM, L, MO, NY); Udawn, Phu Luang, Touw 10568 (BM, FH, L, MO, NY). VIETNAM. Lam Dong, Lang Bian, Micholitz 308 (BM, H-BR, JE); Dalat, Col de Prenn, Tixier s.n. (PC). PHILIPPINES. LUZON. Ifugao, Mt. Polis, Pancho 10850 (MO); Mountain, Mt. Data, Hadden 107 (FH-Bartr.); Benguet, Micholitz 154 (BM, H-BR); Baguio, Bartlett 13340 (FH), 13342 (NY); ibid., Sanchez 5 (BM); ibid., Williams 1852

(FH, H-BR); Loakan near Baguio, Williams 2069 (NY).

Dicranum psathyrum is a Southeast Asian species, which, in Malesia, is found on Luzon only. Because of its small stature and its fragile leaf apices, which are mostly lacking except at the extreme apex of the shoot, it is easily differentiated from most species of *Dicranoloma*. It may only be confused with *D. daymannianum*, differences have been discussed under that species.

The lack of a limbidium and the costal anatomy which is different from all species of *Dicranoloma* and similar to some species of *Dicranum* fix the position of *D. psathyrum* in the cladograms among species of *Dicranum* and together with its small size necessitate its transfer to *Dicranum*.

EXCLUDED AND DOUBTFUL SPECIES

Dicranoloma braunfelsiopsis Dix. (1942: 4).

Type: Papua New Guinea. Central, main range above Port Moresby, NW of the Gap, 2600 m, Carr 15244 (BM-holo!, FH-Bartr.!, H!, L!, NY!).

As already pointed out by Allen (1985), this is a synonym of *Brotherobryum macgregorii* (Broth. & Geh.) Fleisch.

Braunfelsia involuta Fleisch. (1904: 96).

Dicranum involutum Lac. (1872: 9), hom. illeg. — *Dicranoloma involutum* (Fleisch.) Par. (1904: 27). Type: Borneo, Mt. Sakoenbang, Korthals s.n. (L-holo!).

From Van der Sande Lacoste's figure 6A it can be easily seen that Fleischer (1904) was right in placing the species in *Braunfelsia*. Dixon (1935) considered *Braunfelsia involutum* to be synonymous with *B. scariosa* Par. As pointed out by Van der Wijk & Margadant (1962), *B. scariosa* is an illegal name, as it includes in its synonymy an older basionym, *Dicranum edentulum* Mitt., *D. scariosum* Wils., the supposed basionym of *Braunfelsia scariosa*, being a nomen nudum. Thus, the legitimate name is *Braunfelsia edentula* (Mitt.) Wijk & Marg.

Dicranoloma perintegrum Dix. (1924: 226).

Type: Malaysia, Malacca, Mt. Ophir, Dec. 1898, Ridley 780 (BM-holo!).

I concur with Eddy (1988) and Tan (1989) that this is a synonym of *Braunfelsia plicata* (Lac.) Broth.

Dicranoloma singalangense Dix. ex Froehl. (1953: 72).

Type: M.-Sumatra. Nord-Hang des Singalang, 1720 m, Schiffner 11457 (not located).

The type of *D. singalangense* could not been located, so its identity remains unclear. From the latin diagnosis it appears that the author considered the new species to be close to *D. subenerve* Broth., which is now considered to be a synonym of *D. billardierei*.

Dicranoloma subassimile Ren. (1909: 31).

No specimens were cited so it is impossible to judge about the status of this name. In the original description of this species only a description of the costal anatomy is given, accompanied by a drawing of a cross section through the costa. The costal anatomy is identical to that of *D. assimile*. Although Renauld's publication did not say where the species occurs, Index Muscorum (Van der Wijk et al. 1962) gives As. 4 as its distribution area. The name has not turned up in more recent literature.

Dicnemos undulatifolius Dix. (1943: 28).

Dicranoloma undulatifolium (Dix.) Bartr. (1957: 35). Type: Papua New Guinea. Central, above Port Moresby, 1600–2000 m, Carr 13787b (BM-holo!, FH-Bartr.!, L).

Dicranoloma undulatifolium is conspecific with *Brotherobryum undulatifolium* Van Zanten, as was earlier concluded by Tan (1989).

Campylopus validinervis (Dix.) Tan (1989: 510).

Dicranoloma validinerve Dix. (1941: 58). Type: Malaysia. Sarawak, Miri Division, Baram District, Hose 738 (BM-holo!).

I agree with Tan (1989) that this is a species of *Campylopus*.

Dicranoloma platycaulon Dix. (1913: 15).

Dicranoloma platycaulon, known only from New Zealand and Tasmania, was reported from Malesia by Tan (1989), who considered *Dicranoloma euryloma* var. *rugifolium* to be a synonym. As pointed out under *D. assimile*, the type of *D. euryloma* var. *rugifolium* and all other Malesian material identified by Tan (1989) as *D. platycaulon* belong to *D. assimile*.

Dicranum species reported from Malesia that have not been moved to other genera before:

Dicranum ophirense Hampe ex C. Müll. (1901: 290), *nom. nud.*

Authentic specimen: Malaysia. Peninsular Malaysia ["Malakka"], Mt. Ophir, Capt. Nixon s.n. (BM!).

The specimen cited here was found in Hampe's herbarium labelled as *Dicranum ophirense* n. sp. It is identical with *Braunfelsia plicata* (Lac.) Broth.

Dicranum semperi Hampe ex C. Müll. (1901: 297).

Type: Philippines. Luzon, Bataan Province, Mariveles, Semper s.n. (BM-holo!, FH-FL!, L!).

This is a *Leucoloma*, probably *L. perviride* Broth. If so, a new combination will be necessary, as *D. semperi* is the older name.

Dicranum thraustophyllum C. Müll. (1901: 297).

A type of this species is not given in the original description and no candidates were located. As this species should occur in Java and the name implies fragile leaves, it could be *D. daymannianum*, the only species of *Dicranoloma* with fragile leaves occurring on Java. On the other hand, Müller included many genera other than *Dicranum* and *Dicranoloma in Dicranum*, so we cannot be sure that he was writing about a *Dicranoloma*. Therefore, the identity of this species will remain unknown.

Dicranum cf. *bonjeanii* De Not.

Mitten & Wright's (1894) report of this species from Sabah is based on Haviland 1424, a syntype of *Dicranoloma havilandii*, as was already noted by Tan (1989).

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REFERENCES

Abeywickrama, B. A., 1960. The genera of mosses of Ceylon. Ceylon J. Sci., Biol. Sci. 3: 41–123.

Akiyama, H., 1990. Taxonomic studies of mosses of Seram and Ambon (Moluccas; East Indonesia) collected by Indonesian-Japanese botanical expeditions II. J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 14: 385–413.

Allen, B. H., 1984. A review of the genus *Brotherobryum* Fleisch. (Bryopsida: Dicranaceae). Lindbergia 10: 111–120.

Allen, B. H., 1985. A note on the genus *Brotherobryum*. Bryologist 88: 268.

Allen, B. H., 1986a. A review of the genus *Parisia* (Musci: Dicranaceae). Bryologist 89: 206–212.

Allen, B. H., 1986b. Notes on the Dicnemonaceae (Musci): II. The status of *Dicnemon rugosum* and *Werneriobryum geluense*. J. Hattori Bot. Lab. 61: 273–280.

Allen, B. H., 1987a. Notes on the Dicnemonaceae (Musci): I. A systematic account of *Dicranum bartramianum* nom. nov. Cryptog. Bryol. Lichénol. 8: 321–329.

Allen, B. H., 1987b. A revision of the genus *Mesotus* (Musci: Dicranaceae). J. Bryol. 441–452.

Allen, B. H., 1987c. A revision of the Dicnemonaceae. J. Hattori Bot. Lab. 62: 1–100.

Allen, B. H., 1990. A preliminary treatment of the *Holomitrium* complex (Musci: Dicranaceae) in Central America. Trop. Bryol. 3: 59–71.

Allen, B. H., 1994. Moss flora of Central America. Part 1. Sphagnaceae – Calymperaceae. Monogr. Syst. Bot. Missouri Bot. Gard. 49: 1–242.

Allen, B. H., 1998. The genus *Orthodicranum* (Musci: Dicranaceae) in Maine. Evansia 15: 9–20.

Anonymus, 1802. Recensionen. Muscologia recentiorum. Bot. Zeitung (Regensburg) 1: 209–218, 225–235.

Bartram, E. B., 1936. Bornean mosses, principally from Mount Kinabalu. Philipp. J. Sci. 61: 235–251.

Bartram, E. B., 1938. Mosses of the Solomon Islands. Bryologist 41: 127–132.

Bartram, E. B., 1939. Mosses of the Philippines. Philipp. J. Sci. 68: 1–422.

Bartram, E. B., 1942. Third Archbold Expedition mosses from the Snow Mountains, Netherlands New Guinea. Lloydia 5: 245–292.

Bartram, E. B., 1945. Mosses of Morobe District, northeast New Guinea. Bryologist 48: 110–126.

Bartram, E. B., 1950. Additional Fijian mosses II. Occas. Pap. Bernice Pauahi Bishop Mus. 20(2): 27–33.

Bartram, E. B., 1952. North Queensland mosses collected by L.J. Brass. Farlowia 4: 235–237.

Bartram, E. B., 1957. Mosses of eastern Papua, New Guinea. Brittonia 9: 32–56.

Bartram, E. B., 1959. Contributions to the mosses of the highlands of eastern New Guinea. Brittonia 11: 86–98.

Bellolio-Trucco, G. and R. R. Ireland, 1990. A taxonomic study of the moss genus *Dicranum* (Dicranaceae) in Ontario and Quebec. Can. J. Bot. 68: 867–909.

Blume, C., 1823. Pugillus plantarum iavanicarum, e cryptogamicarum variis ordinibus selectus. Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11: 119–140.

Bremer, K., 1988. The limits of amino acid sequence data in Angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

Bridel-Brideri, S. E., 1798. Muscologia recentiorum. Vol. 2. Gotha.

Bridel-Brideri, S. E., 1800. Animadversiones in Muscologiae recentiorum tomum secundum. J. Bot. (Schrader) 1800 (2): 268–299.

Bridel-Brideri, S. E., 1819. Muscologia recentiorum. Suppl. 4. Gotha.

Bridel-Brideri, S. E., 1826. Bryologia universa. Vol. 1. Leipzig.

Briggs, D., 1965. Experimental taxonomy of some British species of the genus *Dicranum*. New Phytologist 64: 366–386.

Brotherus, V. F., 1895. Some new species of Australian mosses described. III. Öfv. Förh. Finsk. Vet. Soc. 37: 149–172.

Brotherus, V. F., 1898. Some new species of Australian mosses described. IV. Öfv. Förh. Finsk. Vet. Soc. 40: 159–193.

Brotherus, V. F.,, 1901. Dicranaceae. In: A. Engler & K. Prantl (ed.), Die natürlichen Pflanzenfamilien. T. I, Abt. 3, H. I, pp. 289–342. Leipzig.

Brotherus, V. F., 1905. Contributions to the bryological flora of the Philippines. I. Öfv. Förh. Finsk. Vet. Soc. 47 (14): 1–12.

Brotherus, V. F.,, 1906. Contribution a la flore bryologique de la Nouvelle Caledonie. Öfv. Förh. Finsk. Vet. Soc. 48(15): 1–28.

Brotherus, V. F., 1908. Musci. In: Rechinger, K., Botanische und zoologische Ergebnisse einer wissenschaftlichen Forschungsreise nach den Samoainseln. Denksch. Kaiserl. Akad. der Wiss., Wien Math.-Naturwiss. Kl. 84: 3–16.

Brotherus, V. F., 1909. Nachträge und Verbesserungen. In: A. Engler & K. Prantl (ed.), Die natürlichen Pflanzenfamilien. T. I, Abt. 3, H. II, pp. 1173–1239. Leipzig.

Brotherus, V. F., 1910. Contributions to the bryological flora of the Philippines, III. Philipp. J. Sci., C. 5: 137–162.

Brotherus, V. F., 1918. Contributions to the bryological flora of the Philippines, V. Philipp. J. Sci., C. 13: 201–222.

Brotherus, V. F., 1924. Bryales. In: A. Engler & K. Prantl. (ed.), Die natürlichen Pflanzenfamilien. Ed 2, Bd. 10: 143–478. Leipzig.

Brotherus, V. F., 1928a. Musci novi japonici. Ann. Bryol. 1: 17–27.

Brotherus, V. F., 1928b. Musci. In: E. Irmscher, Beiträge zur Kenntnis der Flora von Borneo. Mitt. Inst. Allg. Bot. Hamburg 7: 115–140.

Brühl, P., 1931. A census of Indian mosses. Rec. Bot. Surv. India 12 (1,2): 1-135, 1–152.

Cardot, J., 1901. Note sur deux collections de mousses de l'archipel indien. Rev. Bryol. 28: 112–118.

Carpenter, J. M., 1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291–296.

Carpenter, J. M., 1994. Successive weighting, reliability and evidence. Cladistics 10: 215–220.

Chappill, J. A., 1991. Quantitative characters in phylogenetic analysis. Cladistics 5: 217–234.

Chuang, C.-C., 1973. A moss flora of Taiwan exclusive of essentially pleurocarpous families. J. Hattori Bot. Lab. 37: 419–509.

Crum, H., 1986. A survey of the moss genus *Sclerodontium*. Hikobia 9: 289–295.

Dixon, H. N., 1913. A revision of the New Zealand species of *Dicranoloma*. In: Studies in the bryology of New Zealand with special reference to the herbarium of Robert Brown, of Cristchurch, New Zealand. New Zealand Inst. Bull. 3: 7–29.

Dixon, H. N., 1916. Miscellanea Bryologica — V. J. Bot. 54: 352–359.

Dixon, H. N., 1922. The mosses of the Wollaston expedition to Dutch New Guinea, 1912–1913; with some additional mosses from British New Guinea. J. Linn. Soc., Bot. 45: 477–510.

Dixon, H. N., 1924. New species of mosses from the Malay Peninsula. J. Torrey Bot. Cl. 51: 225–259.

Dixon, H. N., 1932. Contributions to the moss flora of Sumatra. Ann. Bryol. 5: 17–50.

Dixon, H. N., 1935. A contribution to the moss flora of Borneo. J. Linn. Soc., Bot. 50: 57–140.

Dixon, H. N., 1941. New and rare Bornean mosses. J. Bot. 79: 57–62.

Dixon, H. N., 1942. Papuan Mosses. J. Bot. 80: 1–11, 25–38.

Dixon, H. N., 1943. Alpine mosses from New Guinea. Farlowia 1: 25–40.

Dozy, F. & J.-H. Molkenboer, 1844. Musci frondosi ex archipelago indico et Japonia. Ann. Sc. Nat., Bot. sér.3, 2: 297–316.

Dozy, F. & J.-H. Molkenboer, 1845–1854. Musci frondosi inediti archipelagi indici. Leiden.

Dozy, F. & J.-H. Molkenboer, 1854–1870. Bryologia Javanica. 2 vols. Leiden.

Eddy, A., 1988. A handbook of Malesian mosses. Vol. I. Sphagnales to Dicranales. British Museum (Natural History), London.

Ernst-Schwarzenbach, M., 1939. Zur Kenntnis des sexuellen Dimorphismus der tropischen Laubmoos Gattung *Macromitrium*. Arch. Julius Klaus-Stift. Vererb.-Fosch. 17: 458–461.

Farris, J., 1969. A successive approximation approach to character weighting. Syst. Zool. 19: 83–92.

Farris, J., 1989. The retention index and the rescaled consistency index. Cladistics 5: 417–419.

Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791.

Fleischer, M., 1901–1902 [1904]. Die Musci der Flora von Buitenzorg. Vol. 1. Leiden.

Fleischer, M., 1914. Musci. In: Uitkomsten der Nederlandsche Nieuw-Guinea-expeditie in 1912 en 1913 onder leiding van A. Franssen Herderschee. Nova Guinea 12: 109–128.

Fleischer, M., 1915–1923 [1922]. Die Musci der Flora von Buitenzorg. Vol. 4. Leiden.

Frahm, J.-P., 1981. Bestimmungsschlüssel und Illustrationen zu Gattung *Chorisodontium* Broth. Herzogia 5: 499–516.

Frahm, J.-P., 1989. The genus *Chorisodontium* (Dicranaceae, Musci) in the Neotropics. Trop. Bryol. 11–24.

Frahm, J.-P., 1991. A phenetic and cladistic study of the Campylopodioideae. J. Hattori Bot. Lab. 69: 65–78.

Frahm, J.-P., 1993. Taxonomic results of the BRYOTROP Expedition to Zaire and Rwanda, 17. Andreaeaceae, Bruchiaceae, Dicranaceae, Rhizogoniaceae, Bartramiaceae, Rhacocarpaceae, Hed-

wigiaceae, Cryphaeaceae, Leucodontaceae. Trop. Bryol. 8: 153–169.
Frahm, J.-P., 1997. A taxonomic revision of *Dicranodontium* (Musci). Ann. Bot. Fenn. 34: 179–204.
Frey, W., J.-P. Frahm, E. Fischer & W. Lobin, 1995. Die Moos- und Farnpflanze Europas. Kleine Kryptogamenflora. Bd. 4. Gustav Fischer Verlag, Stuttgart, Jena, New York.
Froehlich, J., 1953. Die von Prof. Dr. Viktor Schiffner in den Jahren 1893/94 in Ceylon, Penang, Singapore, Sumatra und Java gesammelten Laub- und Torfmoose. Ann. Naturhist. Mus. Wien 59: 66–116.
Froehlich, J., 1962. Musci novi malesiani collecti a Dre. Guil. Meijer. Rev. Bryol. Lichénol. 31: 91–94.
Gangulee, H. C., 1971. Mosses of Eastern India and adjacent regions. Fasc. 2. Archidiales, Dicranales & Fissidentales. Calcutta.
Gao, C., 1994. Flora bryophytarum sinicorum. Vol. 1. Beijing. [in Chinese]
Gao, C. & Cao, T., 1992. A synopsis of Chinese *Dicranum* (Dicranaceae, Musci). Bryobrothera 1: 215–220.
Geheeb, A., 1898. Weitere Beiträge zur Moosflora von Neu-Guinea. I. Über die Laubmoose, welche Dr. O. Beccari in den Jahren 1872–1873 und 1875 auf Neu-Guinea, besonders dem Arfak-Gebirge, sammelte. Biblioth. Bot. 44: 1–25.
Goloboff, P. A., 1991. Homoplasy and the choice among cladograms. Cladistics 7: 215–232.
Goloboff, P. A., 1993. Estimating character weights during tree search. Cladistics 9: 83–91.
Goloboff, P. A., 1995. Parsimony and weighting: a reply to Turner and Zandee. Cladistics 11: 91–104.
Hampe, E., 1844. Icones Muscorum. Bonn.
Hedenäs, L., 1997. A cladistic overview of the "Hookeriales". Lindbergia 21: 107–143.
Hedenäs, L., 1998. Cladistic studies on pleurocarpous mosses: research needs, and use of results. In: Bates, J. W., N. W. Ashton & J. G. Duckett (eds.), Bryology for the twenty-first century, pp. 125–141. Leeds.
Hedwig, J, 1801. Species muscorum frondosorum.
Hegewald, E., 1978. Critical notes on *Holomitrium* (Dicranaceae) from the Antilles. Bryologist 81: 524–531.
Herzog, Th., 1909. Laubmoose aus Deutsch-Neu-Guinea und Buru. Hedwigia 49: 119–127.
Herzog, Th., 1919. Die Laubmoose der II. Freiburger Molukkenexpedition. Hedwigia 286–299.
Herzog, Th., 1925. Neue Bryophyten aus Brasilien. Repert. Spec. Nov. Regni Veg. 21: 22–33.
Herzog, Th., 1926. Bryophyten der weiteren Indomalaya (Ceylon, Sumatra, Borneo, Celebes, Molukken, Neuguinea). Hedwigia 66: 337–358.
Hooker, W. J., 1818–1820. Musci Exotici. 2 vols. London.
Horikawa, Y. & H. Ando, 1964. Contributions to the moss flora of Thailand. In: T. Kira & T. Umesao, Nature and life in Southeast Asia. Vol. 3. Flora and Fauna Research Society, Kyoto.
Hovenkamp, P., 1999. Unambiguous data or unambiguous results? Cladistics 15: 99–102.
Hyvönen, J., 1991. *Chorisodontium* (Dicranaceae, Musci) in southern South America. Ann. Bot. Fenn. 28: 247–258.
Ihsiba, E., 1929. Nihonsan Senrui Sosetsu. Tokyo
Iwatsuki, Z. & B. C. Tan, 1979. Checklist of Philippine mosses. Kalikasan 8: 179–210.
Kallersjö, M., J. S. Farris, A. G. Kluge & C. Bult, 1992. Skewness and permutation. Cladistics 8: 275–287.
Kawai, I., 1968. Taxonomic studies on the midrib in Musci (1). Significance of the midrib in systematic botany. Sci. Rep. Kanazawa Univ., Biol. 13: 127–157.

Kenrick, P. & P.R. Crane, 1997. The origin and early evolution of land plants, a cladistic study. Smithsonian University Press, Washington.

Klazenga, N., 1996. *Dicranoloma steenisii* (Musci: Dicranaceae), a new species from Papua New Guinea. Blumea 41: 11–15.

Kluge, A. G., 1997. Testability and the refutation and corroboration of cladistic hypotheses. Cladistics 13: 81–96.

La Farge-England, C., 1996. Growth form, branching pattern, and perichaetial position in mosses: cladocarpy and pleurocarpy redefined. Bryologist 99: 170–186.

La Farge-England, C., 1998. The infrageneric phylogeny, classification, and phytogeography of *Leucoloma* (Dicranaceae, Bryopsida). Bryologist 101: 181–220.

Lewinsky-Haapasaari, J. & L. Hedenäs, 1998. A cladistic analysis of the moss genus *Orthotrichum*. Bryologist 101: 519–555.

Lin, S.-H., 1981. *Dicranoloma blumii*, a new record for the moss flora of Taiwan. Misc. Bryol. Lichenol. 9: 11.

Margadant, W. D. & P. Geissler, P., 1995. Seventeen proposals concerning nomina conservanda for genera of Musci. Taxon 44: 613–624.

Meusel, H., 1935. Wuchsformen und Wuchstypen der europaischen Laubmoose. Nova Acta Leop. 3: 123–277.

Mishler, B. D., 1994. Cladistic analysis of molecular and morphological data. Am. J. Phys. Anthropol. 94: 143–156.

Mitten, W. J., 1859. Musci indiaea orientalis; an enumeration of the mosses of the East Indies. J. Proc. Linn. Soc., Bot. Suppl. 1: 1–171.

Mitten, W. J., 1869. Musci austro-americani. J. Linn. Soc., Bot. 12: 1–659.

Mitten, W. J. & C.H. Wright, 1894. Muscinae. In: O. Stapf, On the flora of Mount Kinabalu, in North Borneo. Trans. Linn. Soc. London ser. 2, 4: 255–260.

Müller, C., 1848. Synopsis Muscorum omnium hucusque cognitorum. Part. 1. Berlin.

Müller, C., 1851a. Die von Samuel Mossman im Jahre 1850 in Van Diemen's Land, Neuseeland und Neuholland gemachte Laubmoossammlung. Bot. Zeitung (Berlin) 9: 545–552.

Müller, C., 1851b. Synopsis muscorum omnium hucusque cognitorum. Part. 2. Berlin.

Müller, C., 1874. Musci polynesiaci praesertim Vitiani et Samoani Graeffeani. J. Mus. Godeffroy, 1873/1874, heft 6: 11–40.

Müller, C., 1897a. Musci. In: F. Reinecke, Die Flora der Samoa-Inseln. Bot. Jahrb. Syst. 23: 317–332.

Müller, C., 1897b. Symbolae ad bryologiam Australiae I. Hedwigia 36: 331–365.

Müller, C., 1901. Genera muscorum frondosorum. Leipzig.

Newton, A. E. & B. D. Mishler, 1994. The evolutionary significance of asexual reproduction in mosses. J. Hattori Bot. Lab. 76: 127–145.

Noguchi, A., 1953. Mosses of Mt. Sarawaket, New Guinea. J. Hattori Bot. Lab. 10: 1–23.

Norris, D. H. & T. Koponen, 1989. Typification of *Dicranoloma* Ren., a small genus of mosses from northern Australia and New Caledonia. Acta Bryolich. Asiatica 1: 1–4.

Norris, D. H. & T. Koponen, 1990. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXXV. Dicranaceae and Dicnemonaceae (Musci). Acta Bot Fenn. 139: 1–64.

Nyholm, E., 1986. Illustrated flora of Nordic mosses. Fasc. 1. Fissidentaceae – Seligeriaceae. Odense.

Paris, E. G., 1894–1898. Index bryologicus. Paris.

Paris, E. G. 1900. Index bryologicus. Suppl. 1. Lyon.

Paris, E. G. 1904. Index bryologicus. Ed. 2., vol. 2. Paris.

Poitier de la Varde, R., 1943. Récoltes bryologiques de M. H. Humbert en Afrique Équatoriale. Bull. Mus. Hist. Nat. Paris ser. 2, 14: 363. 1943.
Ramsay, H. P., 1985. Cytological and sexual characteristics of the moss *Dicranoloma* Ren. Monogr. Syst. Bot. Missouri Bot. Gard. 11: 93–110.
Ramsay, H. P., 1986. Studies on *Holomitrium perichaetiale* (Hook.) Brid. (Dicranaceae: Bryopsida). Hikobia 9: 307–314.
Renauld, F., 1898 [1897]. Prodrome de la flore bryologique de Madagascar. Monaco.
Renauld, F., 1901. Nouvelle classification des Leucoloma. Rev. Bryol. 28: 66–70, 85–87.
Renauld, F., 1909. Essai sur les Leucoloma. Monaco.
Renauld, F. & J. Cardot, 1905 [1904]. Musci exotici vel minus cogniti. Bull. Soc. Roy. Bot. Belgique. 41: 7–122.
Richards, P.W., 1984. The ecology of tropical forest bryophytes. In: R.M. Schuster (ed.) New manual of bryology, Vol. 2: 1233–1270. The Hattori Botanical Laboratory, Nichinan.
Robinson, H., 1967. Six new bryophytes from South America. Bryologist 70: 317–322.
Rosario, R.M. del & B.O. van Zanten, 1980 [1979]. Mosses new to the Philippines. Philipp. J. Sci. 108: 199–211.
Sainsbury, G.O.K., 1955. A handbook of the New Zealand mosses. Roy. Soc. New Zealand Bull. 5: 1–490.
Salmon, E. S., 1898. A revision of the genus *Symblepharis* Montagne. J. Linn. Soc. Bot. 33: 486–501.
Sande Lacoste, C. M. van der, 1872. Species novae vel ineditae muscorum archipelagi indici. Verh. Kon. Akad. Wetensch., afd. Natuurk. 13: 1–12.
Sanderson, M. J. & Donoghue, 1989. Patterns of variation in levels of homoplasy. Evolution 43: 1781–1795.
Schultze-Motel, W., 1974. Die Moose der Samoa-Inseln. Willdenowia 7: 333–408.
Scott, G. A. M. & I. G. Stone, 1976. The mosses of Southern Australia. Academic Press, London.
Sprengel, K., 1827. Caroli Linnaei, . . . Systema Vegetabilum. Ed 16, vol. 4, part. 2. Göttingen.
Swofford, D. L., 1993. Phylogenetic Analysis Using Parsimony, ver. 3.1.1. Computer program distributed by the Illinois Natural History Survey, Champaign, IL.
Takaki, N., 1966. A revision of Japanese *Dicranoloma*. J. Hattori Bot. Lab. 29: 214–222.
Tan, B. C., 1987. New records of Philippine mosses. Mem. New York Bot. Gard. 45: 446–454.
Tan, B. C., 1989. The bryophytes of Sabah (North Borneo) with special reference to the BRYOTROP transect of Mount Kinabalu. II. *Dicranoloma* and *Brotherobryum* (Dicranaceae, Bryopsida). Willdenowia 18: 497–512.
Tan, B. C. & T. Koponen, 1983. *Dicranoloma* (Musci, Dicranaceae) in Southeast Asia, with special reference to the Philippine taxa. Ann. Bot. Fenn. 20: 317–334.
Tan, B. C. & H. Mohamed, 1990. Novelties for Peninsular Malayan moss flora. Cryptog., Bryol. Lichénol. 11: 353–362.
Thériot, I., 1931. Mousses de l'Annam, 4^e contribution. Rev. Bryol., n.s. 4: 135–137.
Tixier, P., 1974. Contribution to the bryological knowledge of Malaysia. Nat. Hist. Bull. Siam Soc. 25: 15–28.
Turner, H. & R. Zandee, 1995. The behaviour of Goloboff's tree fitness measure F. Cladistics 11: 57–72.
Une, K., 1985. Sexual dimorphism in the Japanese species of *Macromitrium* Brid. (Musci: Orthotrichaceae). J. Hattori Bot. Lab. 59: 487–513.
Wijk, R. van der & W. D. Margadant, 1958. New combinations in mosses I. Taxon 7: 287–290.

Wijk, R. van der, W. D. Margadant & P .A. Florschutz, 1959–1969. Index muscorum. Regnum Veg. 17 (A–C), 26 (D–Hypno), 33 (Hypnum–O), 48 (P–S), 65 (T–Z, Appendix). IAPT, Utrecht.

Williams, R. S., 1913. (Bryales) Dicranaceae, Leucobryaceae. North American Flora 15 (2): 77–166. New York.

Zander, R. H., 1993. Genera of the Pottiaceae: mosses of harsh environments. Bull. Buffalo Soc. Nat. Sci. 32: i–vi, 1–378.

Zanten, B. O. van, 1964. Mosses of the Star Mountains expedition. Nova Guinea, Bot. 10: 263–368.

Zomlefer, W. B., 1993. A revision of *Rigodium* (Musci: Rigodiaceae). Bryologist 96: 1–72.

APPENDIX: SELECTED SPECIMENS STUDIED TO ASSIGN CHARACTER STATES

The Malesian species of *Dicranoloma* were completely revised. Representative specimens are cited in the taxonomic part of this paper. Representative specimens studied of the remaining species are listed below:

Braunfelsia dicranoides (Dozy & Molk.) Broth. Papua New Guinea. Minj-Nona Divide, Kubor Range, Pullen 5271 (L); Enga, Wabag area, Middle Wage Valley, Robbins 3309 (L).

Brotherobryum macgregorii (Broth. & Geh.) Par. Papua New Guinea. Enga, Wabag area, Marimuni track, Robbins 3027 (L); West Sepik, Star Mts., Touw 16676 (L).

Chorisodontium aciphyllum (Hook. f. & Wils.) Broth. Chile. Hermit Island, Cape Horn,1847, J.D. Hooker s.n. (L); South Georgia, Cumberland Bay, Skottsberg 13 (L);

Dicnemon novae-guineae (Dix.) B. H. Allen. Papua New Guinea. West Sepik, Star Mts., Tel Basin, Touw 15765 (L); Enga, Wabag area, track to Marimuni from upper Ambun Valley, Robbins 3023 (L); Morobe, Sarawaket Southern Range, Koponen 32797 (L).

Dicranoloma austroscoparium (C. Müll. ex Broth.) Par. Australia. Queensland, Bellender Ker Range, Bailey 609 (BM); Queensland, Talbunjie, Flecker 6085 (BM).

D. eucamptodontoides (Broth. & Geh.) Par. Australia. Tasmania, Jones Track, south of Sprent River, Moore 60 (H-BR); Tasmania, Huon River, Scotts Peak Rd., Norris 30810 (CBG).

D. menziesii (Tayl.) Par. Australia. Norfolk Island, Cunningham s.n. (L); Victoria, Cement Creek National Reserve, Streimann 50787 (CBG). New Zealand. North Island, Rimutaka Forest, Streimann 58098 (L).

D. platyloma (Besch.) Ren. ex Par. New Caledonia. Mandjélia, W. of Pouebo, Lowry II 3888 (MO); Mt. Me Maoya, ab. Mime Emma, McPherson 2943 (MO); in parte meridionale, Pancher 759 (BM).

D. rugosum (Hook.) B. H. Allen. Society Island. Tahiti, Mt. Aorai, Van Balgooy 1795 A (L); Tahiti, Fare Rau Ape-Mt., Aorai Trail, Whittier 2774 (B)

D. serratum (Broth.) Ren. Australia. New South Wales, Brogers Creek, Bexton 66 (L); New South Wales, Cambawarra, Forsyth 1079 (JE); New South Wales, Gibberrgunyah Range, Streimann 309 (CBG).

Dicranum elongatum Schleich. ex Schwaegr. Norway. Finnmark, Karasjok, During 7107201 (L); Finland. NW-Le, Konkamaeno, Peerakoski, Puolikko, 18.07.1934, Roivainen s.n. (L); Canada. Alberta, moraine Lake, Banff National Park, Crum & Schofield 3942 (L); U.S.A. Colorado, Indian Peaks Region of Front Range, Silver Lake Valley, Touw 14038 (L).

D. fulvum Hook. Luxembourg. Hallerbachtal SE of Bourscheid, Touw 13623 (L); U.S.A. North Carolina, Macon County, along Buck Creek, W of Highlands, Anderson 15140 (L); North Carolina, Pisgah National Forest, Millers & Myers 5351 (L); North Carolina, Great Smoky Mountain National Park, Schofield 10347 (L)

D. fuscescens Turn. United Kingdom. Scotland, Stirling, Lower Clyde, Loch Katrina, Sollman 71061

(L). Canada. Quebec, Parc de la Vérendrye, Crum & Williams 10196 (L); Alberta, Jasper National Park, trail to Mt. Edith Cavell, Redfearn 36790 (L).

D. gymnostomum Mitt. India. Sikkim, Kambachen, J.D. Hooker 67b (BM); Sikkim, Phalloot, Kurz 2099 (BM).

D. johnstonii Mitt. Tanzania. Kilimanjaro, Johnston 52 (BM); ibid., Pócs & Kundaeli 6718/AR (L). Kenya. Mt. Kenya, Van der Hammen 3494 (BM).

D. kashmirense Broth. Kashmir, Liddar Valley, Duthie 14210 (BM); Kashmir, N of Tragbal Pan, Duthie 14429 (BM).

D. lorifolium Mitt. India. Assam, Cherrapungi, Khasia Hills, Bor 399 (BM); Kashmir, Kemaon, Thomson 52 (BM).

D. montanum Hedw. Netherlands. Utrecht, Dirkse 2768 (L). Poland. Bialowies, Chwoinek, 06.1918, Fleischer s.n. (L). Canada. Quebec, Parc de la Montagne Tremblante, Crum & Williams 10353 (L).

D. muehlenbeckii Bruch & Schimp. Austria. Pottenstein, 15.08.1867, Juratzka s.n. (L); U.S.A. Colorado, Rocky Mountains National Park, Vitt 15447 (L).

D. polysetum Sw. France. Haute-Saône, between Faucogney and Esmoulières, Frahm 161 (L). Canada. Ontario, Thunder Bay District, Dorion Township, Ouimet Canyon, Allen 9520 (L).

D. scoparium Hedw. Netherland. Terschelling, Groene Strand, Jalink 7464 (L). Czech Republic. Bohemian Forest, 1996, Van Dort s.n. (L).

D. spurium Hedw. Austria. Near Rossatz am Donau, Baumgärtner 290 (L); Steiermark, Mühlfeldberg, Glowacki 93 (L). U.S.A., Pennsylvania, Bear Cap, Allen 4850 (L).

Eucamptodon muelleri Hampe & C. Müll. Australia. Queensland, Mt. Bellender Ker, S. Peak, Van Balgooy 1466 A (L); New South Wales. S of Monge, Touw 18796 (L).

Leucoloma molle C. Müll. Indonesia. Flores, Manggarai Prov., Ngando Napu, S of Ruteng, Touw & Snoek 23160 (L); Seram, Manusela National Park, Akiyama 14789 (L).

L. mittenii Fleisch. Thailand. Payap, Mai Hoi River, Sop Aep, Touw 9457 (L); Prachinburi, Khao Yai National Park, Kong Keo, Larsen, Smitinand & Warncke 182 (L).

Mesotus celatus Mitt. New Zealand. South Island, Lake Waikareiti, Sainsbury s.n. in Verdoorn, Musci Selecti et Critici ser. IV (1937), no. 188; South Island, West Nelson Forest Reserve, S of Motueka, Streimann 51030 (L).

Parisia neocaledonica Broth. New Caledonia. Massif du Boulinda, Crosby 14019 (L); Montagne des Sources reserve, McPherson 1798 (L).

Sclerodontium pallidum (Hook.) Schwägr. Australia. Australian Capital Territory, Tidbinbilla National Reserve, Touw 18660 (L); Tasmania, East Coast, Derby, Weymouth 2702 (L). Indonesia. Lombok, Elbert 1128 (L); Lombok, Gn. Rinjani, Touw 22327 (L).

Holomitrium perichaetiale (Hook.) Brid. Australia. Queensland, Poverty Creek, 41 km WSW of Ingham, Streimann 5755 (H); Lord Howe Island, Mt. Lidgbird, Van Balgooy 1078A (L). New Zealand. Stewart Island, Port Pegasus, Vitt 10284 (L).

Symblepharis vaginata (Wils.) Wijk & Marg. Mexico. Michoacan. Cerro del Aguila, Cárdenas 5500 (H). Peru. Junin Dept., Huancayo-Parihuanca, Hegewald 9250 (H, L);

Dicranodontium uncinatum (Harv.) Jaeg. Philippines. Northern Luzon, Mt. Pulog, Robbins 4089 (L). Papua New Guinea. Western Highlands, Mt. Hagen, Van Zanten 683050 (L). Canada. British Columbia, Queen Charlotte Islands, Moresby Island, Schofield 30477 (L).