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## ***Desmotheca* (Orthotrichaceae): Gondwanan fragmentation and the origin of a Southeast Asian genus**

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**Abstract.** *Desmotheca* Lindberg was proposed in 1872 as a replacement name for the illegitimate *Cryptocarpon* Dozy & Molk. (1844) and *Cryptocarpus* Dozy & Molk. (1846). Seven names have been placed in these genera, from which two species appear to be taxonomically valid. *Desmotheca apiculata* (Dozy & Molk.) Card. occurs from New Caledonia and New Guinea west to Indonesia and the Andaman Islands, north to Burma, Thailand, Vietnam and Mindanao in the Philippines, while *D. brachiata* (Hook. & Wils.) Vitt *comb. nova* is restricted to the island of Luzon in the Philippines. The evolution and dispersal of this genus can be related to the northward movement of Gondwanan island blocks during the Cretaceous.

The genus *Cryptocarpon* was described in 1844 by Dozy and Molkenboer from a specimen collected by P.W. Korthals in Borneo. They first used the herbarium name *Angiocarpon* for these plants, but published the name *Cryptocarpon*. In 1846, they revised their genus name to *Cryptocarpus*. In both these publications, and again in 1859 (Dozy & Molkenboer 1854-1861), they placed only one species, *C. apiculatus*, in their genus, although in the latter publication they placed Hooker & Wilson's *Macromitrium brachiatum*, described in 1845 from the Philippines, in the synonymy of *C. apiculatus*.

In 1872, Lindberg recognizing that both *Cryptocarpon* Dozy & Molk. and *Cryptocarpus* Dozy & Molk. were later homonyms (*Cryptocarpon* Dunal-1816 and *Cryptocarpus* Kunth-1817, both Phanerogams) and illegitimate, proposed the name *Desmotheca* as a replacement. Between 1873 and 1898, four species

were described in *Cryptocarpus*, including *C. cymosus* Mitt. from New Caledonia, *C. cuspidatus* C.M. from Burma, *C. manii* C.M. from the Andaman Islands, and *C. glaucus* C.M. from the Philippine Islands. In 1877, *Orthotrichum corolloides* Duby was described from the Philippines. All of these names were transferred to *Desmotheca* between 1897 and 1902 by Cardot, Paris, or Brotherus, except *M. brachiatum*. In 1902, Brotherus included five species in *Desmotheca*. He did not mention *D. manii* (originally collected from the Andaman Islands) but instead listed *D. cuspidatus* from this island group (originally collected from Burma) even though authentic material of both species is present in his herbarium. *Macromitrium brachiatum*, placed in the synonymy of *Cryptocarpus apiculatus* as early as 1859 by Dozy and Molkenboer, was never transferred to either that genus or to *Desmotheca*. In summary, Wijk et al (1962) listed six taxonomically valid names

under *Desmotheca* and considered *M. brachiatum* synonymous with *D. apiculatus*. Of these names, only *D. apiculatus* has been used in the modern literature.

During my revision of *Macromitrium* in New Guinea, I found specimens that were easily referred to the genus *Desmotheca*. Since the genus had not been previously recorded from New Guinea, I began a search for the correct name for these specimens. In due course, I have had the opportunity to study the type material of all names associated with *Desmotheca*.

***Desmotheca*** Lindb., Jour. Linn. Soc. Bot. 13: 184. 1872.

Holotype species: *Desmotheca apiculata* (Dozy & Molk.) Lindb. ex Card.

*Cryptocarpon* Dozy & Molk., Ann. Sci. Nat. Bot. ser. 3,2: 302. 1844. (*hom. illeg. orthogr. error*) - *hom. illeg. non Cryptocarpon* Dunal, Syn. Solan. 45. 1816 (Phanerogams).

*Cryptocarpus* Dozy & Molk., Musci Fr. Ined. Archip. India 2: 37. 1846. (*orthogr. corr. pro. Cryptocarpon* Dozy & Molk., 1844). - *hom. illeg. non Cryptocarpus* Kunth, Nov. Gen. Sp. 2: 187. 1817 (Phanerogams).

Plants small, 0.5-1.5 mm wide, up to 2 cm high, dull, olive-green to light-green above, brown to dark green below, stiff, stems and branches well-differentiated. Stems creeping, with numerous, erect, short (3-4 mm long), single branches, some of these terminating in a conspicuous perichaetium, others elongated and branched in upper portions, these mostly with terminal perichaetia. Stem leaves twisted-appressed when dry, squarrose-spreading when moist, lanceolate, gradually acuminate. Branch leaves of short branches irregularly and loosely twisted around branches, sometimes irregularly whorled-twisted when dry, loosely spreading to wide-spreading when moist, 1.0-1.6 mm long, ligulate-oblong to narrowly oblong-ovate,

obtuse to acute, apiculate, keeled; costa filling the apiculus, stout, abaxial surface with elongate costal cells exposed along entire length; margins plane to broadly reflexed, entire; leaves of elongate branches erect-twisted and indistinctly ranked when dry, stiffly reflexed-spreading and distinctly ranked when moist, 0.9-1.3 mm long, broadly ovate to ovate-elliptic, obtuse to acute, apiculate, costa and margins similar to those of leaves of short branches; upper cells 5-9  $\mu$ m wide, 6-9  $\mu$ m long, subquadrate to rounded-quadrate, densely to lowly pluri-papillose, obscure to clear, +/- flat to slightly bulging; medial cells 8-10  $\mu$ m wide, 6-12  $\mu$ m long, subquadrate to elliptic-quadrate, uni-papillose to +/- pluri-papillose, obscure to clear, somewhat bulging; basal cells 5-10  $\mu$ m wide, (10)15-40(50)  $\mu$ m long, short-rectangular, +/- elongate, straight, +/- mostly thin-walled, longer towards margins, smooth or a few cells with low tubercula, flat, clear. Perichaetial leaves 1.6-2.1 mm long, outer ones oblong, acute, apiculate to shortly cuspidate, erect, with elongate, clear, smooth cells extending to +/- 2/3 of leaf length, inner perichaetial leaves forming a pale, shiny, conspicuous sheathing, tubular perichaetium, each leaf lingulate-ovate to oblong-ovate, sheathing, truncate, often mucronate, retuse or rounded, minutely serrulate at apex, some leaves rugose above, lower margins entire to sparsely toothed, elongate, clear cells extending nearly to apex, with a few scattered papillae. Sexual condition phyllodioicous, male plants very small, bud-like on a short stalk, found among the leaves of elongate branches, sometimes in groups of 3-10. Setae very short, reduced to a junction between urn and foot; capsules 1.1-1.4 mm long, oblong to narrowly elliptic-oblong, immersed, smooth to wrinkled when old, light colored, abruptly contracted to seta, with a distinct reddish-black rim bordering a broad mouth; exothecial cells 16-28  $\mu$ m wide, 30-68  $\mu$ m long, irregularly quadrate to rectangular, very thin-walled, stomates infrequent at

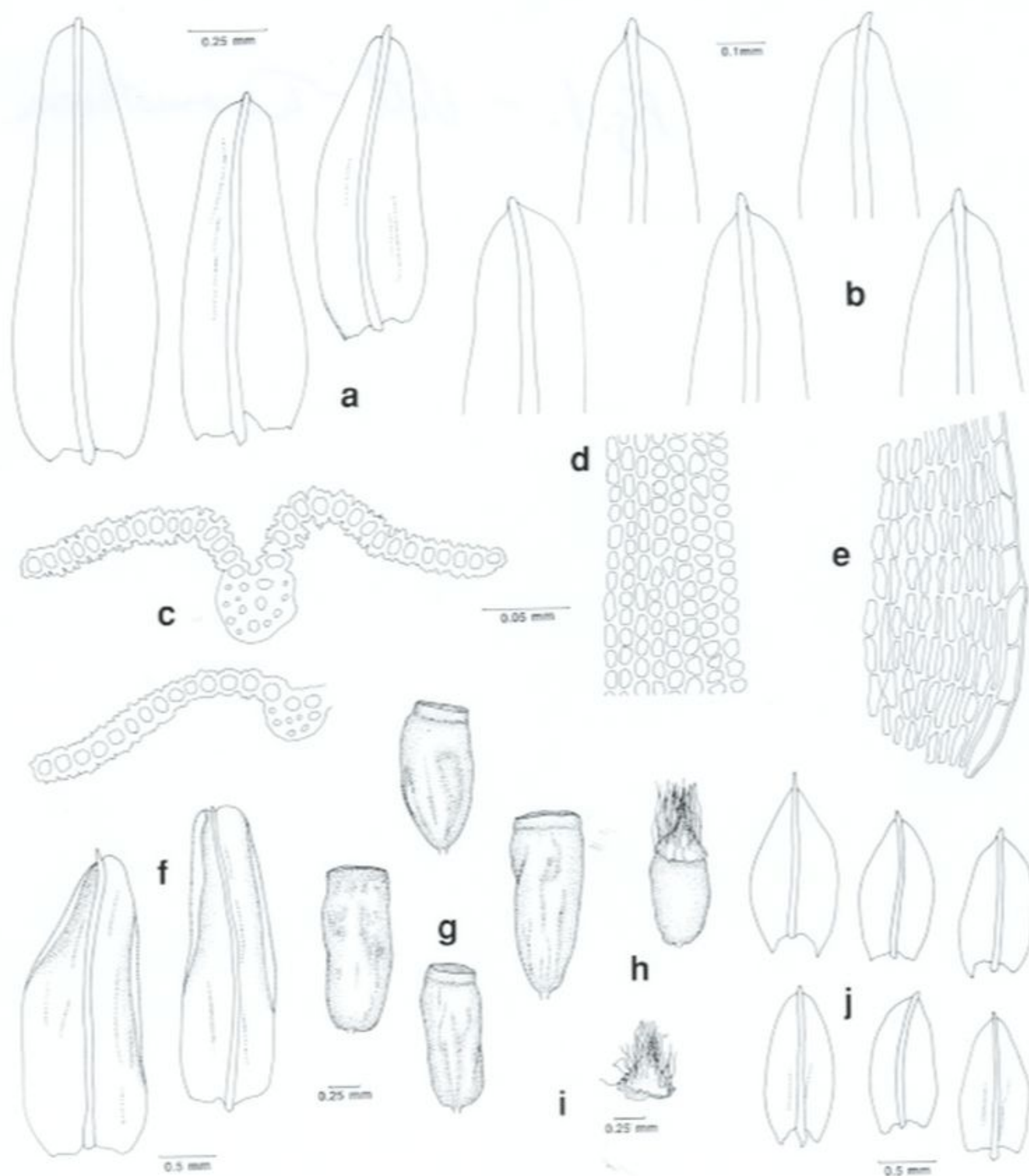
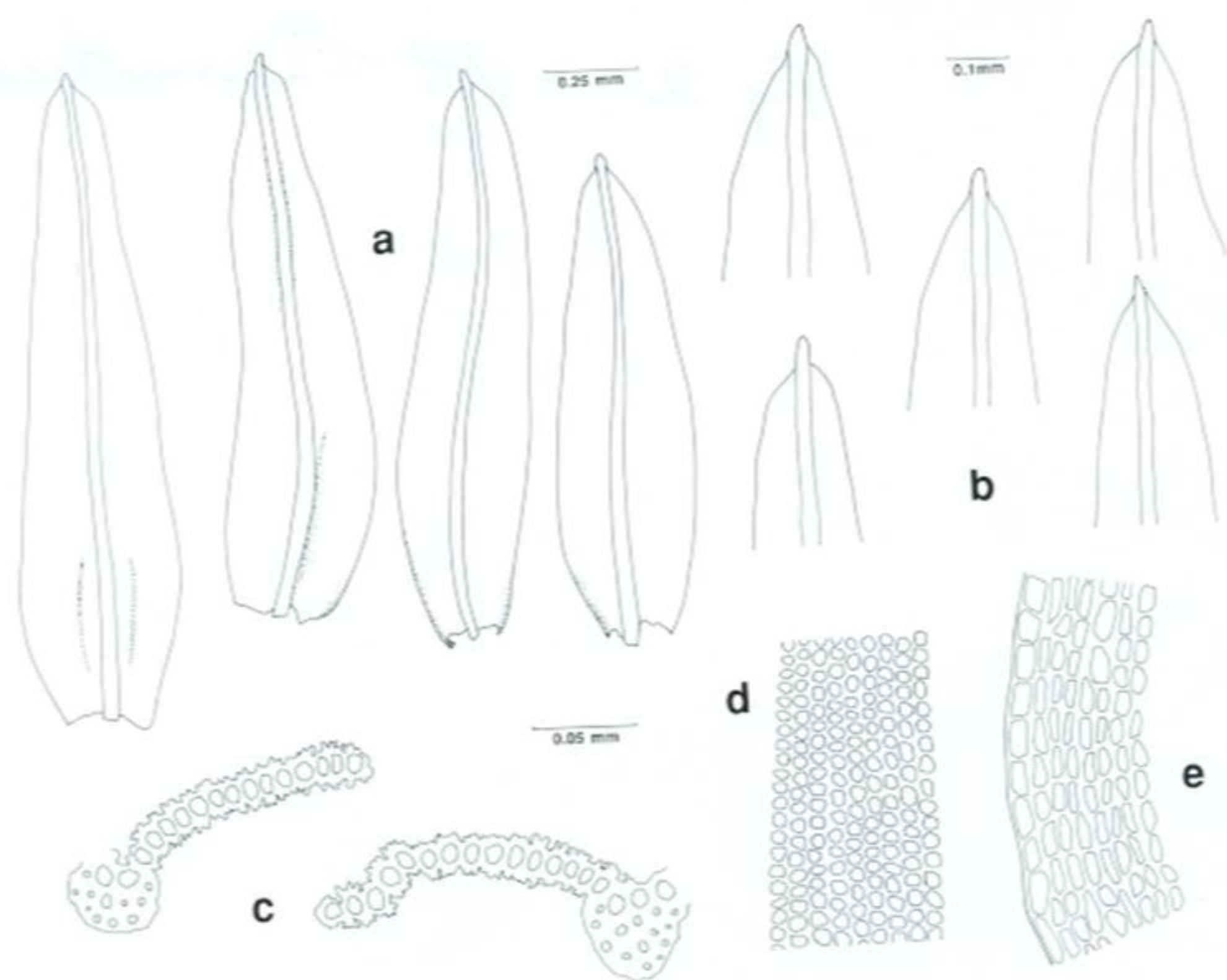


Fig. 1: *Desmotheca apiculata* (Dozy & Molk.) Card. a: Vegetative leaves (from type of *C. manii* [H], *C. apiculatus* [L], *C. cymosus* [NY]). b: Vegetative leaf apices (*Meijer 6923* [L]). c: Transverse sections of upper leaf cells (*Carr 12273* [NY], *Meijer 6923* [L]). d: Medial leaf cells (*Meijer 6923* [L]). e: Basal leaf cells (*Meijer 6923* [L]). f: Inner perichaetial leaves (*Streimann 14059* [ALTA]). g: Capsules (*Streimann 14059* [CBG], *17805* [CBG], *14081* [CBG], *14121* [CBG]). h: Capsule with calyptra (*Streimann 14059* [ALTA]). i: Calyptra (*Streimann 14121* [ALTA]). j: Leaves from elongate branches (*Streimann 14059* [ALTA])



**Fig. 2:** *Desmotheca brachiata* (Hook. & Wils.) Vitt. a: Vegetative leaves (*Williams 3140* [US], from type of *O. corolloides* [G], *C. glaucus* [H]). b: Vegetative leaf apices (*Ramos 7972* [H]). c: Transverse sections of upper leaf cells (*Ramos 7972* [H]). d: Medial leaf cells (*Ramos 7972* [H]). e: Basal leaf cells (*Ramos 7972* [H]).

base of capsule. Peristome none. Opercula erect-rostrate. Spores 15-45 µm, strongly anisomorphic. Calyptrae short, covering only operculum, non-plicate, conic, densely hairy, with irregularly lacerate, flaring base, mitrate.

Diagnostic Features. 1) Small plants with branches either short, or elongate and terminated by enlarged perichaetia, 2) leaves oblong and apiculate, 3) costa excurrent, conspicuous, 4) capsules delicate, immersed in lingulate-ovate perichaetial leaves, 5) setae reduced to a junction, 6) peristome none, and 7) calyptrae hairy, short and covering only the operculum.

The two species of this genus are differentiated from *Macromitrium* species by totally lacking a peristome; near absence of setae; and having enlarged, sheathing, lingulate perichaetial leaves. The oblong, apiculate branch leaves with nearly all cells short are also characteristic. The elongation of young branches with further terminal branching at once separates *Desmotheca* from all other Orthotrichaceae. The elongate branches have leaves differentiated from those of the short branches. The former are shorter, broader, stiffer and ranked along the branch, especially when moist.

#### Key to Species of *Desmotheca*

1. Vegetative branch leaves oblong to lanceolate-oblong, +/- obtuse; upper leaf cells +/- clear to obscure, lowly to densely pluri-papillose in upper 1/3, gradually becoming clear, tuberculate, and longer below, cells in middle 1/3 of leaves in distinct rows, quadrate, 9-10 µm wide, clear, lowly papillose to bulging; basal cells elongate, 20-50 µm long . . . . . 1. *Desmotheca apiculata*

1. Vegetative branch leaves

lanceolate-ligulate to narrowly oblong, +/- acute to obtuse; upper leaf cells very obscure, densely pluri-papillose in upper half, sharply differentiated from clear, +/- tuberculate cells in lower half, cells in middle 1/3 of leaves in indistinct rows, rounded, 8-9 µm wide, obscure, densely papillose; basal cells short-rectangular, 15-30 µm long. . . . . 2. *Desmotheca brachiata*

1. *Desmotheca apiculata* (Dozy & Molk.) Lindb. ex Card. (Fig. 1), Ann. Jard. Bot. Buitenzorg. Suppl. 1: 11. 1897. *Cryptocarpon apiculatum* Dozy & Molk., Ann. Sc. Nat. Bot. ser. 3, 2: 302. 1844. *Cryptocarpus apiculatus* Dozy & Molk. Musci Fr. Ined. Archip. Indici 2: 37. 1846. Based on *Cryptocarpon apiculatum* Dozy & Molk. Type: 'Borneo'. (Holotype L! Borneo: Maratapoera, P. W. Korthals).

*Cryptocarpus cymosus* Mitt. in Seem., Fl. Vit. 381. 1873. *Desmotheca cymosa* (Mitt.) Par., Ind. Bryol. Suppl. 114. 1900. Type: 'Ile of Pines on stones on the main peak (Milne!)'. (Lectotype NY-Mitt!; Isotypes NY-Mitt!, S!).

*Cryptocarpus marginatulus* C.M. in Jaeg., Ber. S. Gall. Naturw. Ges. 1874-75: 177. 1876. *nom. nud.*, authentic specimens described as *C. cuspidatus* C.M.

*Cryptocarpus cuspidatus* C.M., Hedwigia 37: 141. 1898. *Desmotheca cuspidata* (C.M.) Par., Ind. Bryol. Suppl. 114. 1900. Type: 'Birma, Pegu, Yomah: Sulpiz Kurz Coll. No. 3408, 1872 in Hb. Hmp., in cujus Hb. sub *C. marginata* C. Muell. occurs.' (Lectotype BM-Hampe!; Isotypes BM-Hampe!, H-Broth!).

*Cryptocarpus manii* C.M., Hedwigia 37: 141. 1898. *Desmotheca manii* (C.M.) Par., Ind. Bryol. Suppl. 114. 1900. Type: 'India orientalis, insula merid. Andaman, prope Port Blair: E. H. Man 1892 et 1895 in Hb. Levier.' (Lectotype H-Broth!; Isotypes BM!, G!, H-Broth!, S!).

Vegetative leaves oblong to lanceolate-oblong, obtuse, apiculate; upper cells 6-8  $\mu\text{m}$  wide, somewhat obscure to +/- clear, irregularly rounded, pluripapillose; medial cells 9-10  $\mu\text{m}$  wide, quadrate, in longitudinal rows; basal cells clear, some tuberculate, 20-50  $\mu\text{m}$  long, elongate-long rectangular, becoming long near margins.

Distribution (Fig. 3). Restricted to Southeast Asia. This species is known from New Caledonia westward in New Guinea, Java and Sumatra, northward to the Andaman Islands, southern Burma, Thailand, Vietnam, Borneo, Celebes and Mindanao, The Philippines. I have verified specimens from: Socialist Republic of the Union of Burma; Republic of India Andaman Islands; Republic of Indonesia Borneo, Celebes, Flores, Java, New Guinea, Sumatra; Malaysia Malaya, Sarawak; New Caledonia (France); Papua New Guinea; The Republic of the Philippines; Republic of Singapore; Kingdom of Thailand and the Socialist Republic of Vietnam.

Number of Specimens Seen. 168 ALTA-1; B-2; BM-10, C-2, CBG-15, E-2, F-3, FH-25, G-8, H-16, JE-5, L-28, M-7, MO-2, NY-10, PRC-1, S-24, US-8; including duplicate specimens.

Ecology. This species has been collected on the trunks and branches (including canopy branches) of trees and shrubs in rain forests, often in secondary forests. Seemingly a low- to mid-elevation species, collected from sea level up to 900 m elevation. In New Guinea it is known from the area surrounding the Forestry College at Bubolo on planted trees, in maintained gardens, and along roadsides. There it has been collected on tree trunks and branches of *Calliandra*, *Plumeria*, *Mangifera*, *Leucaena*, and *Araucaria*.

The relatively broad vegetative

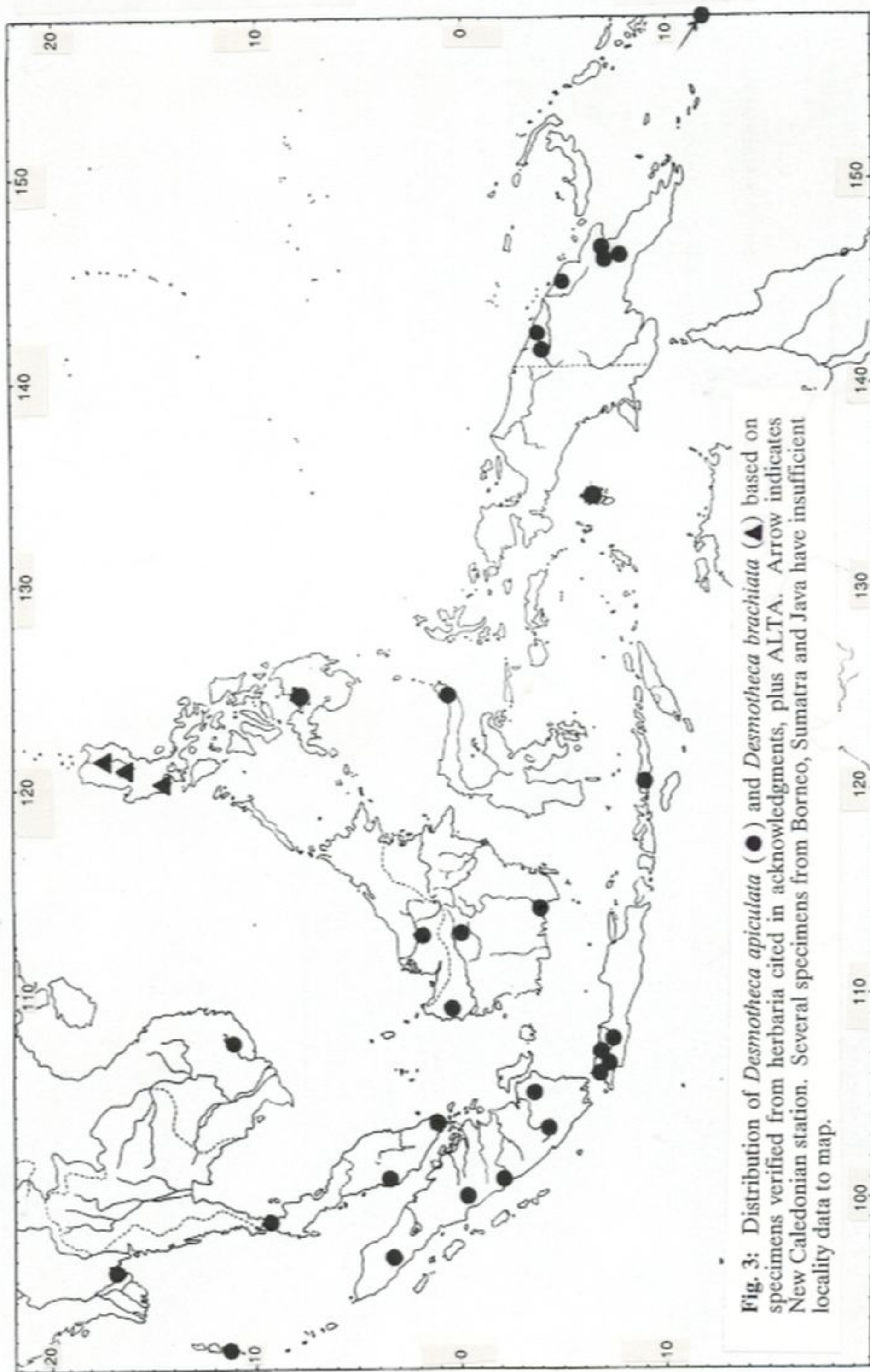
leaves and cell pattern (see key) are critical differentiating features of this species. There is some variability in the papillosity of the upper leaf cells. Populations from New Guinea and New Caledonia have less papillose upper cells with cell shapes clearly visible under the compound microscope, however Malaysian populations sometimes have more densely papillose, obscure upper cells. These latter plants can be confused with those of *D. brachiata* that is found only in the Philippines. These two species are best differentiated by leaf shape (see key), by the length of basal cells, and by the cell pattern of the medial leaf cells (Figs. 1-2). Plants of *D. apiculata* with obscure upper leaf cells have medial cells in longitudinal rows and relatively long basal cells, while those of *D. brachiata* have obscure medial cells that remain relatively short until the leaf base.

**2. *Desmotheca brachiata*** (Hook. & Wils.) Vitt *comb. nov.* (Fig. 2), *Macromitrium brachiatum* Hook. & Wils., *Icon. Pl. Rar.* 6: 746B. 1845. Type: 'Philippine Islands, Cuming 2195'. (Lectotype BM-Hook!; Isotypes BM-Hook!, BM-Wils!).

*Orthotrichum coralloides* Duby, *Flora* 60: 74. 1877. *Desmotheca coralloides* (Duby) Broth., *Nat. Pfl.* 1(3): 475. 1902. Type: 'Parasiticum ad arbores in oppido Aryat provinciae de Baluca Phillipinaru m detexit Padre Llanos.' (Lectotype G-Duby!; Isotypes G-Duby!).

*Cryptocarpus glaucus* C.M., *Hedwigia* 37: 142. 1898. *Desmotheca glauca* (C.M.) Par., *Ind. Bryol. Suppl.* 114. 1900. Type: 'Insulae Philippinae, Galumpit: Pater Llanos in Hb. J. Mueller Arg. 1876.'. (Lectotype H-Broth!; Isotype S!).

Vegetative leaves lanceolate-ligulate to narrowly oblong, acute to obtuse, apiculate; upper cells 5-7  $\mu\text{m}$  wide, very obscure, quadrate-rounded, densely pluripapillose; medial cells 8-9  $\mu\text{m}$  wide,



rounded, not in clear longitudinal rows, basal cells clear, some tuberculate, 16-30  $\mu\text{m}$  long, rectangular, becoming longer near margins.

Distribution (Fig. 3). This species is endemic to the Philippine Islands, where I have seen specimens only from the island of Luzon.

Number of specimens seen. 17 FH-3, G-2, H-3, M-1, NY-4, S-2, US-2, including duplicate specimens.

Ecology. Epiphytic, no further information available.

Identical to *D. apiculata* in sporophytic features, this species is differentiated by characters of the vegetative leaves. The upper leaf cells are so densely papillose that the individual cells are not discernible under the compound microscope. The dense papillosity continues until mid-leaf where it grades quickly to small, rounded medial cells that are not in obvious rows. The basal cells are longer, but remain short (about 2-3:1) near the costa and gradually are longer near the margin. Most basal cells are about 20  $\mu\text{m}$  long in mid-leaf.

## DISCUSSION

The genus *Desmotheca* (earlier as *Cryptocarpus*) has been generally accepted as a genus distinct from *Macromitrium* (Fleischer 1904, Brotherus 1925, Vitt 1972, Crum 1987). Both Brotherus (1925) and Crum (1987) placed the genus in its own subfamily, while Vitt (1972) considered it to belong in the relationship with *Macromitrium* and associated genera (e.g. *Schlotheimia*, *Groutiella*, and *Macrocoma*). Crum's (1987) arguments for placing *Desmotheca* in a monogeneric subfamily are persuasive. Indeed *Desmotheca* does possess several unique features among Orthotrichaceae. The strikingly dimorphic sterile and fertile

branches, sessile capsules without a hint of a peristome, and delicate, small, mitrate, hairy calyptrae serve to separate this genus from all others. However *Desmotheca* also possesses several basic features that characterize the Macromitrioideae. Of special importance are the following a) creeping stems with short erect branches terminated by perichaetia, b) the ability to produce tuberculate basal cells, c) upper leaf cells with papillae typical of those in *Macromitrium*, d) although small, the mitrate, hairy calyptrae are similar to those in *Macromitrium*, and e) anisomorphic spores and dwarf male plants. Within the Orthotrichaceae, items (b) and (e) are synapomorphic features of the Macromitrioideae, and when *Drummondia* is excluded from the family, then (a) is also a defining synapomorphy of this subfamily. If *Desmotheca* is excluded from the Macromitrioideae, then this latter taxon becomes paraphyletic. In summary, I agree with Crum that *Desmotheca* is patristically distinct from the assemblage of species around *Macromitrium*, however cladistic rationale indicates that the genus is best kept in the subfamily Macromitrioideae.

The Macromitrioideae are distributed largely in the southern hemisphere and tropical areas of the world. Vitt (1983) suggested that *Macromitrium* originated in Gondwanaland, after the split of Pangaea, but before the break up of the Gondwanaland continental areas. For *Macrocoma*, Vitt (1982) proposed that the species diversified in Late Jurassic and Cretaceous time, with origins on Gondwanaland, and subsequent migration onto Laurasia through contacts with either Africa or India. Expansion of these ideas suggests that the subfamily Macromitrioideae originated, and to a large extent, diversified on Gondwanaland. Migration into the modern Laurasian tropics is evident in Central America, the Caribbean and southern Mexico in the New World, and into China and Japan in the Old World.



Whereas the Indian subcontinent contains few species of the subfamily, Southeast Asia and New Guinea are rich in species. It seems illogical for such a rich flora on seemingly Laurasian land to be derived from a depauperate Indian group of species. Yet, what other explanation is there for the rich Gondwanan species assemblages (such as the Macromitrioideae) to be present in Southeast Asia? One potential answer is that diversification of these groups took place before the split of Pangaea. However, for me, this is not acceptable as it would mean the diversification of the Macromitrioideae as rainforest epiphytes before the presence of the dominant, present-day rainforest plants - the Angiosperms. Surely, the canopy epiphytes did not diversify in Gymnosperm canopies (where they do not occur today) and then move to Angiosperm phorophytes upon diversification of flowering plants. The second explanation is one involving a reinterpretation of plate tectonic happenings in the southwestern Pacific. Audley-Charles (1987) discussed the geological data indicating that Burma, western Thailand, the Malay Peninsula, and Sumatra comprise continental fragments that were rifted from northern Australia-New Guinea. These land masses contain fossil land plants and may have been above sea level in the late Jurassic and early Cretaceous. Only the eastern half of the Indochina Peninsula contains Mesozoic vertebrate fossils of Laurasian affinity. Audley-Charles (1987) also suggested that additional continental fragments may have rifted from Australia during the Jurassic, then become relatively isolated within the Tethys Ocean between Gondwanaland and the Laurasian mainland for as long as 60 million years. As these Gondwanaland fragments rafted northward, they provided an archipelago of islands that could have permitted dispersal in both directions, however these 'Noah's arks' may have possessed a Gondwanaland base flora that was transported northward. This northward

drift (that occurred between 44-100 million years ago) resulted in 1) collisions between Gondwanalandic fragments and the Laurasian mainland with the collision of western and eastern portions of Indochina taking place in early Cretaceous and 2) the collision of Australia-New Guinea with Southeast Asian volcanic island arcs (between 15 and 3 million years ago). These collisional events involving northern New Guinea and other Southeast Asian land masses, resulted in the uplift of new land areas in Malaysia. Geological data on movement of Laurasian terranes southward to Gondwanaland derived land is scarce. However McCabe et al (1985) discuss the evolution of the Philippine archipelago. Their analysis indicates that the Philippines are a composite terrane composed of at least five distinct terranes which were assembled prior to the late Miocene. Of these five, only one is suggested to be derived from Laurasian land (Hamilton 1979, Taylor & Hayes 1980, Holloway 1981). However this Laurasian terrane, composing mostly northern Palawan and western Mindoro, is comprised of late Paleozoic and Mesozoic continental derived strata overlain by Tertiary deep water and shallow-water sediments. The Pre-Cenozoic stratigraphy is similar to south China, whereas the Cenozoic stratigraphy is different. Thus, this terrane rafted southward in early and mid-Tertiary from Laurasian origins, however it was submerged during this time. So, there is at present little evidence for possibilities of Laurasian plants to be rafted southward, but numerous opportunities for Late Mesozoic and early Cenozoic migration northward by Gondwanan plants. Distribution patterns that reflect this scenario are numerous and nicely illustrated by *Hypnodendron* (Tow 1971).

One of the consequences of this interpretation of the Gondwanan origin of Southeast Asia is that another plausible route is available for the migration to Laurasian tropical areas of Gondwanan

plants (in late Jurassic and Cretaceous). At least in the Orthotrichaceae, much of the diversity of Southeast Asia can be explained by this scenario, rather than by Gondwanan plants rafting northward on the Indian plate and subsequently migrating eastward into Southeast Asia. This also explains the large Gondwanan affinities (especially in the Isobryales) of the mosses of Southeast Asia as opposed to the lack of large numbers of Laurasian derived Hypnobryales in the area.

*Desmotheca*, with certain relationships to *Macromitrium* is restricted to southeast Asia. Its present day range, as well as the large species richness of all Macromitrioideae in New Guinea and Southeast Asia can be well explained by the events discussed above. The dispersal of the Macromitrioideae into present-day Southeast Asia by means of late Mesozoic Gondwanan northward rafting (Audley-Charles, Figs. 2-4, 1987) and the subsequent habitat diversification due to island arc formation and mountain uplift are potentially the prime reasons for this Gondwanan group of mosses occurring in Southeast Asia.

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