

## A revision of the Splachnobryaceae (Musci)

Theo Arts (†)



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A revision of the Splachnobryaceae is presented. With the erection of *Koponobryum* to accommodate *Splachnobryum bengalense* Gangulee the family consists of two genera. World-wide only one species of *Koponobryum* and nine species of *Splachnobryum* are accepted, viz. *Koponobryum bengalense* (Gangulee) Arts comb. nov., *Splachnobryum aquaticum* Müll.Hal., *S. assamicum* Dixon, *S. crassinervium* Arts sp. nov., *S. gracile* Besch., *S. limbatum* D. H. Norris & R. H. Zander, *S. novae-guineae* Broth., *S. obtusum* (Brid.) Müll.Hal., *S. oorschotii* M. Fleisch. and *S. wiemansii* M. Fleisch. *S. valdiviae* is removed from the Splachnobryaceae and placed in *Bryum*. Sixteen other species are reduced to synonymy.

T. Arts, Kerklei 56, B-2960 St.-Job in 't Goor, Belgium.

The family Splachnobryaceae, erected by A. Koponen (1981), is a monogeneric family comprising rather small, laxly tufted, mosses of tropical or subtropical distribution. To date 56 species of *Splachnobryum* have been validly described world-wide [See Addendum I: *Splachnobryum* species index]. Many species are based on a single or a limited number of local records and they are often difficult to differentiate from similar species from other areas.

Many names have been put into synonymy, e.g. Mitten (1869) placed the four then known American specimens into a single species (*Weissia splachnifolia*). He was however heavily criticised for this by Müller (1872): “Dass Mitten ...sämtliche Arten Südamerikas als Eine Art hinstellt zeigt dass er dieselben keiner genaueren Untersuchung unterwarf;...”. But Mitten's opinion was confirmed by Breen and Pursell (1959) who considered 15 species from North America, Central America and the Caribbean synonymous with *S. obtusum* (Brid.) Müll.Hal., the only accepted species for that region.

Also several species were transferred to other gen-

era, such as *Bryum*, *Syrrhopodon* and *Distichophyllum*, which left 31 species accepted by Index Muscorum (Van der Wijk et al. 1959–1969). In the Index of Mosses (Crosby et al. 1992) one species is transferred to *Archidium* and four additional species are mentioned. In a recent revision of the African species of the genus, Arts (1996) transferred one species to *Bryum*, two others to *Gymnostomiella* and five species into synonymy. One new species was recently published (Banu-Fattah and Syed 1997). Thus 27 species remain in *Splachnobryum*, but relationships between many of these species are unclear.

This paper presents a world-wide revision of the Splachnobryaceae, which is still much needed to resolve limits of many problematic species from Asia, the Pacific and South America. The species concept applied here is a traditional phenetic one based on morphological resemblances and differences between the specimens studied.

### Materials and methods

The results presented here are based on the study of all available specimens of *Splachnobryum* from the

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following herbaria: ALTA, B, BISH, BM, BR, CANB, E, EGR, FH, H, HIRO, JE, K, KRAM, L, MELU, MICH, MO, NMW, OXF, U and US and the private herbaria of T. Arts, R. Düll, A. Schäfer-Verwimp, G. Schwab, and Ph. Sollman. In addition type material has been studied from BUF and PC. Line drawings and descriptions are based on material moistened in tap water and soaked in a 2% NaOH solution to rehydrate and stretch properly before mounting on slides. Lime encrusted plants were previously cleaned by soaking in a 2% HCl solution. For permanent slides the material was remounted in Hoyer's solution as formulated by Smith (1978). The bryological terms used in the descriptions follow the English Bryological Glossary (Magill and Stotler 1990).

### Splachnobryaceae

Splachnobryaceae A. K. Kop., Ann. Bot. Fennici 18: 123–132.

Holotype: *Splachnobryum* Müll.Hal., Verh. Zool.-Bot. Ges. Wien 19: 503. 1869.

#### Morphology

##### *The gametophyte*

Plants dioicous and rarely monoicous. Sterile and female plants essentially unbranched; male plants acrocarpous with a subapical sympodial branching pattern, often smaller with shorter, more distantly placed, leaves.

*Stem.* Erect, slender, about 5–50 mm long and 0.15–0.30 mm in diameter, green above, yellow or orange to reddish brown below; transverse section with large thin walled cells, 1 or 2(3) outer layers of smaller thick-walled cortical cells, central strand absent or weakly differentiated, consisting of smaller hyaline cells with very thin, readily disintegrating, walls. Paraphyllia absent.

*Leaves.* Rather distantly placed in lower part of stem, more or less crowded in the upper part; commonly contorted and laterally shrunk when dry; plane to conspicuously concave or carinate, erecto-patent to wide-spread, straight, slightly incurved or recurved when wet; pale to dark green, about 0.4–4.0 mm long and 0.3–1.5 mm wide, elliptic, ovate, lanceolate, spatulate or linear; apex usually broadly obtuse, rarely acute; leaf margins plane, or narrowly recurved on one or both sides in lower 1/3–2/3, entire below and minutely crenulate to distinctly crenate at apex; leaf base semi-amplexicaul, not or narrowly decurrent; costa very slender to rather strong, usually ending a few cells to

well below leaf apex, rarely percurrent, often branched at the apex, rarely with few very thin long branches, in transverse section usually uniform, with few smaller and slightly incrassate cells, rarely with central stereids.

*Laminal cells.* Median cell size and shape variable, hexagonal, rhomboidal or rectangular, length/width ratio between 1.2–1.5/1 to 6–9/1, gradually smaller towards leaf margins and larger towards costa; apical marginal cells often distinctly shorter than interior cells; basal cells usually rectangular, larger and longer than median cells; basal and mid-leaf marginal cells usually little differentiated from the interior cells, rarely with border of up to 6 rows of narrowly elongated cells. Laminal cells smooth, except in one species, which has upper laminal cells with single central papilla.

*Brood bodies.* Green filamentous brood bodies arise from more or less branched axillary and intercalary rhizoid stalks. About 120–250 µm long × 30–40 µm wide, consisting of 3–7 uniseriate inflated cells filled with small, light reflecting, starch grains. Although brood bodies may be abundantly present, they are sparse or absent in many specimens.

*Axillary hairs.* Arising in pairs above the leaf insertion from a wide bulging cortical base cell; either clavate, 70–100 µm long, consisting of one or two colourless to yellowish basal cells ca 15 µm long and 10 µm wide and a terminal slightly asymmetric clavate cell 50–70 µm long and 15–25 µm wide or linear, about 100–120 µm long and 4–8 µm wide, consisting of a uniseriate row of 3–5 cells, the upper cells distinctly longer than the lower.

*Rhizoids.* Arising along the lower part of the stem from non-clustered differentiated cortical initial cells, smooth, up to 40 µm in diameter, sparingly branched, colourless when young, turning pale yellowish to brownish with age.

*Rhizoidal tubers.* Arranged in strings and occurring lateral to the main rhizoid branches. Tubers irregular in shape and size, consisting of uniseriate inflated irregularly bent row of cells, little or not branched, or an irregular cell mass, 80–300 µm long and 40–150 µm wide, opaque, similar in colour to, or slightly darker than, the rhizoids; tuber cells isodiametric, 40–75 µm in diameter, with bulging, incrassate smooth walls, filled with light reflecting starch grains 2–5 µm in diameter; many cells accompanied by a laterally oriented lenticular initial cell 15–25 µm in diameter. The tubers are rather inconspicuous, but they may be absent to abundantly present.

**Gametangia.** *Antheridia* 200–350 µm long, usually with 2–8 clustered in terminal or pseudolateral perigonial buds. The original terminal perigonia become lateral on short branches after development of 1 (or 2) subapical innovations; paraphyses lacking; perigonial leaves usually shorter than cauline leaves with a broad, concave, often yellowish to orange coloured base, but otherwise similar. Rarely with conspicuously narrowed and reflexed upper part. Solitary lateral antheridia rarely present.

**Archegonia** 350–450 µm long, solitary, naked, often with a pedestal, axillary as well as intercalary among vegetative leaves, arising laterally, near the stem apex. Often more abundant towards the apex in what appear to be terminal buds, but interspersed with small leaves of the normal type, in such a way that with later prolongation of the apex they become single and naked along the stem. Perichaetial leaves and paraphyses lacking.

Distinction in archegonia placement, [i.e. terminal only, as opposed to both axillary and terminal (e.g. Miller et al. 1963)], obviously represents developmental stages of individual plants and is considered here taxonomically irrelevant.

#### *The sporophyte*

Usually single, lateral, or apparently apical but arising laterally near the stem apex of the gametophyte.

**Seta.** Straight, thin, smooth, about 4–15 mm long and 50–120 µm in diameter, pale green to orange or reddish brown; spirally twisted clockwise above.

**Theca.** Erect, ovoid to cylindrical, brown, about 0.7–1.5 mm long and 0.3–0.6 mm in diameter; exothecial cells thin-walled, irregularly rectangular; stomata few, phaneropore, restricted to the very short capsule neck; annulus persistent, consisting of 4–7 layers of transversely arranged, small but radially elongated, orange brown cells; peristome double, but apparently single, the exostome reduced to a layer of hyaline inflated cells, the endostome inserted below the mouth, consisting of 16 linear segments, about 100–120 µm long, irregularly papillose, reddish, often incomplete, rather brittle, bent inwards when moist thus closing the capsule mouth; operculum conical to apiculate or longly rostrate; columella persistent, reaching about 4/5 of the length of the theca; calyptra cucullate, smooth, very long and narrow, surrounding the whole capsule and the uppermost part of the seta.

**Spores.** Spherical, 12–15 to 23–28 µm in diameter, finely papillose to almost smooth.

#### *Discussion*

Sexual dimorphism, with male plants smaller, certainly is one reason for the rich synonymy in *Splachnobryum*.

A particular feature in *Splachnobryum* is the frequent occurrence of deformed leaves among "normal" leaves in many specimens. Frequently found deformities are widened leaves with broad bilobed apices and irregularly bifurcate or double costae or narrowed leaves with a reduced costa. (Fig. 1).

The presence of small starch grains in rhizoidal tubers, cauline brood bodies and to a lesser extent in some rhizoid, stem and leaf cells is easily proved by the blackish-blue colour reaction after soaking in an iodine/potassium iodide solution (I<sub>2</sub>/KI) in water.

Robinson (1964) described the synoicous *Splachnobryum synoicum* H. Robins. However careful examination of the holotype specimen by Gangulee (1974), Chopra and Sheel (1974) and myself revealed only sterile and female plants. Chopra and Sheel (1974) reported some monoicous plants of *S. obtusum* in which the archegonia and the antheridia were very closely aggregated near the stem apex, but always lateral and separated from one another by vegetative leaves.

Solitary lateral antheridia have been reported by Fleischer (1922) in *S. ovalifolium* M.Fleisch. and by Chopra and Sheel (1974) in *S. obtusum*. I observed a single solitary cauline antheridium in combination with perigonial buds in *S. novae-guineae*.

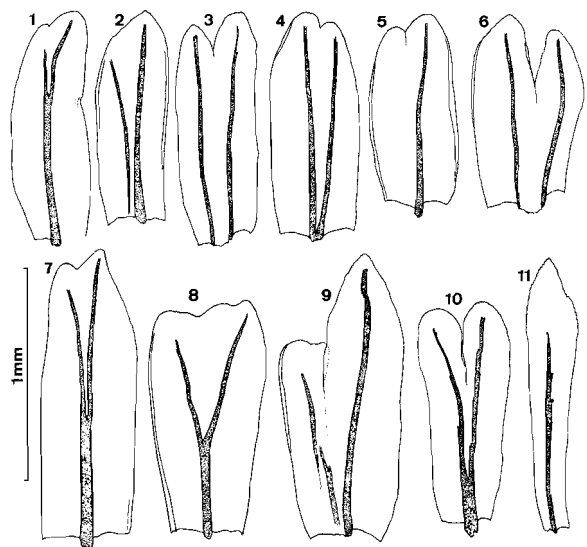


Fig. 1. Deformed leaves in *Splachnobryum*. 1–6: *S. obtusum* (Brid.) Müll.Hal.; 7–11: *S. oorschotii* (Sande Lac.) Müll.Hal. 1–4: from Java, leg. Dadi et Noesta 89 (L); 5–6: from Congo, leg. Overlaet 426 (BR); 7–9: from Java, leg. van Oorschot s.n., 1871 (L); 10–11: from Irian Jaya, leg. van Helleedoorn s.n., 26 Okt. 1949 (L).

The solitary lateral placement of the archegonia as already reported by Müller (1869) for one of his species, has been repeatedly confirmed for other species of the genus e.g. by Dixon (1907), Andrews (1949), Chopra et al. (1967), Chopra and Rashid (1969), Chopra and Sheel (1974), Dabhade (1974) and Koponen (1981). I could confirm these results for all *Splachnobryum* species as far as appropriate female plants were available for study.

Fleischer (1904) mentioned short filiform paraphyses in female plants of *S. geheebii* and long filiform paraphyses with fusiform enlarged apical cells in *S. indicum*. Undoubtedly his description applies to rhizoid stalks and cauline brood bodies such as mentioned above.

The description of the peristome structure and its interpretation accepted here, as a reduced diplolepidous peristome with the large teeth being the endostome, was originally formulated by Philibert (1890). See Koponen (1981) for a more detailed analysis, description and illustration of the peristome.

### Ecology

The plants grow on permanently or periodically moist or wet inorganic often calcareous substrates such as boulders, stone walls, tufa deposits and soil in regions of tropical and subtropical climate throughout the world, commonly at low altitudes, but exceptionally extending up to 1870 m. The species often behave as weedy adventive plants, found in man-made habitats such as road sides, water channels and gullies, or occasionally in greenhouses and hot wells in temperate climate.

### Taxonomy

The genus *Splachnobryum* was erected by Müller (1869) with four species. Mainly based on gametophytic resemblance it was originally placed in the diplolepidous Splachnaceae. Braithwaite (1872) however transferred it to the haplolepidous family Trichostomaceae (Pottiaceae) based on similarities of the peristome and calyptra. Later authors often placed it together with the superficially similar genus *Gymnostomiella* either in the Splachnaceae or in the Pottiaceae.

Andrews (1949) first used the term "Splachnobryaceae" but did not take the necessary steps to recognise it formally as a new family. The placement of *Splachnobryum* in a new family was also favoured by Corley et al. (1981). However according to Norris and Zander (1981) the "leaf flank grouping" pattern of rhizoid initials is typical of plants with endogenous branching, and confirms a placement in the Pottiaceae.

Koponen (1981) erected the monogeneric family Splachnobryaceae, which seems to have no obvious close affinities with other moss families. Based on the occurrence of solitary lateral gametangia it may be one of the most primitive moss families. She placed the Splachnobryaceae in the diplolepidous order of the Funariales. This placement is now generally accepted, e.g. Zander (1993).

After elimination of all species obviously belonging to other taxonomical categories, (see below: Excluded species), the Splachnobryaceae seems to be a homogeneous monophyletic group, except perhaps for one species: *S. bengalense* Gangulee. Based on similarities of the sporophyte I accept its placement in the Splachnobryaceae. The gametophyte however differs from all other species of *Splachnobryum* by the following characteristics: leaf apex truly acute, costa reaching apex in upper stem leaves, upper lamina cells regularly hexagonal with one central papilla and the occurrence of a differentiated leaf margin of narrow lanceolate smooth cells reaching the leaf apex.

This series of clear-cut differences is deemed sufficient to erect a new genus. Consequently the Splachnobryaceae is composed of two genera:

#### 1. *Koponobryum* Arts gen. nov.

*Splachnobryum* Müll.Hal. tangit, set foliis acutis cum nervo in apice desinenti; cellulae superiores laminae rhomboidales, papilla centrali munitae; lamina usque ad apicem cellulis angustis lanceolatis sine papillis marginata; plantae femineae, archegonia et sporophytæ *Splachnobryo* similis; plantae masculinae et antheridia ignotae.

Type of the genus: *Koponobryum bengalense* (Gangulee) Arts comb. nov. Basionym: *Splachnobryum bengalense* Gangulee, Mosses E. India 4: 865. f. 412. 1974; India. Konnagar prope Calcuttam, leg. Gangulee 6170, 24 Aug. 1969. Holotype: "herb. Gangulee".

The genus name refers to Aune Koponen in recognition of her contribution toward elucidating the taxonomical placement of *Splachnobryum*.

#### 2. *Splachnobryum* Müll.Hal., Verh. k.-k. Zool.-Bot. Ges. Wien 19: 503. 1869

Lectotype of the genus (sel. Braithwaite 1872): *Splachnobryum obtusum* Müll.Hal., Verh. k.-k. Zool.-Bot. Ges. Wien 19: 504. 1869. – *Weissia obtusa* Brid., Spec. Musc. 1, 118, 1806.

I accept only ten species of *Splachnobryaceae*: viz. *Koponobryum bengalense* (Gangulee) Arts, *Splachnobryum aquaticum* Müll.Hal., *S. assamicum* Dixon,

*S. crassinervium* Arts sp. nov., *S. gracile* Besch., *S. limbatum* D. H. Norris & R. H. Zander, *S. novae-guineae* Broth., *S. obtusum*, *S. oorschotii* M. Fleisch. and *S. wiemansii* M. Fleisch.

### Artificial key to the species

1. Leaf apex acute, costa reaching apex in upper stem leaves; upper lamina cells with one central papilla ..... (1) *Koponobryum bengalense*
1. Leaf apex obtuse, costa ending 1 or more cells below apex in upper stem leaves; all lamina cells smooth ..... 2
2. Costa ending far below apex in upper stem leaves ..... (2) *Splachnobryum aquaticum*
2. Costa ending within 1–5 cells below apex in upper stem leaves ..... 3
3. Mid-leaf marginal cells distinctly differentiated from the median cells, forming a border of 3–6 rows of narrow elongated cells ..... (3) *S. limbatum*
3. Mid-leaf marginal cells not or little differentiated from the median cells, or forming a border of less than 3 rows wide of narrow elongated cells ..... 4
4. Mid leaf cells 20–35  $\mu\text{m}$  wide; operculum long rostrate; axillary hairs linear ..... (4) *S. gracile*
4. Mid leaf cells smaller, (10)15–25  $\mu\text{m}$  wide; operculum conic or shortly rostrate; axillary hairs clavate or linear ..... 5
5. Costa rather strong, at the leaf base more than 50  $\mu\text{m}$  wide, in transverse section with central stereids; axillary hairs linear, 120–150  $\mu\text{m}$  long, consisting of 4 non-inflated cells ..... (5) *S. crassinervium*
5. Costa rather weak, at the leaf base less than 50  $\mu\text{m}$  wide, in transverse section with uniform cells; axillary hairs clavate, 60–100  $\mu\text{m}$  long, consisting of 1–2 short basal cells and one larger clavate terminal cell ..... 6
6. Leaves recurved, large, more than 0.5 mm wide, broadly ovate to spatulate with narrow insertion; basal leaf margin, up to mid-leaf, with (1)2–(3) rows of narrow elongated cells ..... (6) *S. wiemansii*
6. Leaves not recurved; basal marginal leaf cells not conspicuously narrow and elongated ..... 7
7. Leaves lingulate; basal leaf cells 70–170  $\mu\text{m}$  long; upper leaf cells arranged in divergent rows ..... 8
7. Leaves ovate, elliptic, lanceolate, spatulate or lingulate; basal leaf cells less than 70  $\mu\text{m}$  long ... 9
8. Leaf margins plane throughout, at most partially recurved in a few leaves, apical marginal cell-row not conspicuously smaller than interior cells ..... (7) *S. oorschotii*
8. Leaf margins distinctly recurved, at least at or below mid-leaf, on one or both sides in most leaves, apical marginal cell-row conspicuously smaller than

- interior cells ..... (8) *S. novae-guineae*
9. Leaves triangular-lanceolate, widest near insertion and narrowed from below mid-leaf, median lamina cells small, 25–50  $\mu\text{m}$  long and 10–15  $\mu\text{m}$  wide ... (9) *S. assamicum*
9. Leaves of variable shape, widest below or above mid-leaf, median lamina cells various in size ..... (10) *S. obtusum*

### 1) *Koponobryum bengalense* (Gangulee) Arts, comb. nov.

Basionym: *Splachnobryum bengalense* Gangulee, Mosses E. India 4: 865. f. 412. 1974. (Fig. 2)

Type: India. Konnagar prope Calcuttam, growing on rich clay soil near bamboo grove, leg. Gangulee 6170, 24 Aug. 1969. Holotype: "herb. Gangulee" (not seen).

Illustrations: Gangulee (1974).

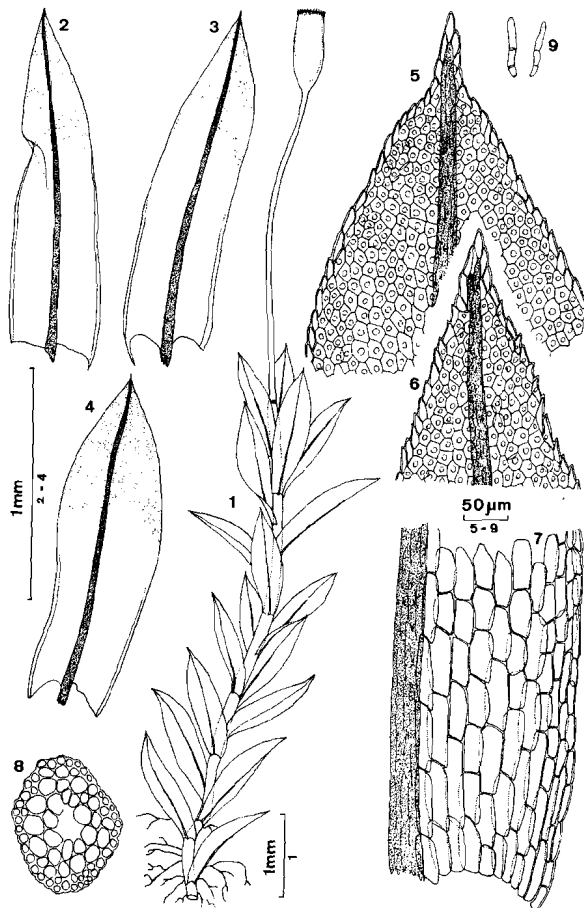


Fig. 2. *Koponobryum bengalense* (Gangulee) Arts, comb. nov. 1: plant with sporophyte; 2–4: leaves; 5–6: cells of leaf apex; 7: cells of leaf base; 8: transverse section of stem; 9: axillary hairs. From Sikkim, leg. Gammie 11384 (H-BR).

Plants small, growing in rather dense tufts, up to 5 mm tall, not or sparsely branched, dull green; stem about 0.2 mm wide, in transverse section with essentially uniform cells 20–30  $\mu\text{m}$  in diameter, most outer cortical cells somewhat smaller with slightly thicker and bulging walls; central strand consisting of smaller, thin-walled, hyaline, readily disintegrating, cells; leaves when dry shrunken, contorted and somewhat appressed to stem, when moist patent; lingulate-lanceolate, 1.3–1.5 mm long and 0.3–0.5 mm wide, rather flaccid, apex acute; costa 40–60  $\mu\text{m}$  wide at base, percurrent to shortly excurrent; leaf margins plane or narrowly recurved below, entire below and bluntly dentate above; upper lamina cells with a central papilla, nearly isodiametric, 10–20  $\mu\text{m}$  in diameter; upper marginal cell-row consisting of smooth, narrower, longer cells with projecting tips causing denticulation; median lamina cells smooth, oblong-hexagonal, 35–50  $\mu\text{m}$  long and 12–20  $\mu\text{m}$  wide, thin-walled; basal lamina cells smooth, elongate rectangular, 60–100  $\mu\text{m}$  long and 15–25  $\mu\text{m}$  wide, conspicuously narrower towards margin; median and lower juxtacostal cells conspicuously larger than adjacent cells; axillary hairs linear, about 70  $\mu\text{m}$  long, consisting of two short basal cells and one apical cell of about 35  $\mu\text{m}$  long; presumably dioicous; male plants not seen; female plants with a few subapical archegonia; sporophyte apparently apical; seta erect, twisted clockwise above when dry, ca 5 mm high; capsule erect, cylindrical; stomata restricted to the short capsule neck; urn 0.9–1.0 mm high and 0.35–0.40 mm in diameter; operculum conical, apiculate; peristome with 16 irregularly split, articulated papillose teeth, inserted far below mouth, ca 180  $\mu\text{m}$  high; spores spherical, brown, smooth, 10–15  $\mu\text{m}$  in diameter.

*Remarks.* The description above is based on the specimen from Sikkim because the type in the herbarium Gangulee at the Univ. of Calcutta was not available. The placement of the two specimens in a single species is based on comparison with the description and illustration of *S. bengalense* in Gangulee (1974); however, the occurrence of a central papilla on the upper lamina cells was not mentioned in this original description.

*Distribution.* Endemic to India, known from only two records.

*India:* West Bengal, Konnagar, prope Calcuttam (Type); Sikkim, alt. 300 ft, leg. G. A. Gammie 11384, 12 Jan. 1898 (H-BR)

2) *Splachnobryum aquaticum* Müll.Hal., *Linnaea* 40: 291. 1876. (Figs 3, 4)

Type: Somalia, prope Meid, reg. montosa 1200 m

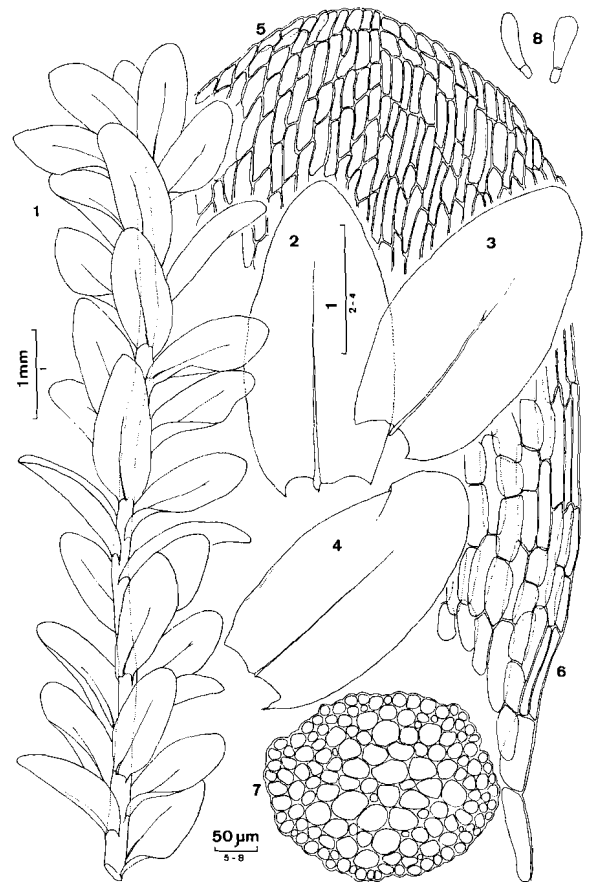


Fig. 3. *Splachnobryum aquaticum* Müll.Hal. 1: Sterile plant; 2–4: leaves; 5: cells of leaf apex; 6: cells of leaf base; 7: transverse section of stem; 8: axillary hairs. From China, leg. Handel-Mazzetti, type of *S. giganteum* (E).

elevationis, in fonte Daffer, April 1875, leg. J.M. Hildebrandt No. 1493 (isotypes: BM, PC, L).

Synonyms:

*S. arabicum* Dixon, *Ann. Bryol.* 7: 157. 1934. syn. nov.

*S. giganteum* Broth., *Symb. Sin.* 4: 49. 1929. syn. nov.

*S. procerrimum* Dixon et P.de la Varde, *Ann. Crypt. Exot.* 1: 38. 2 f. 2. 1928. syn. nov.

*S. vernicosum* Broth. in Bruehl, *Rec. Bot. Surv. India* 13(1): 128. 1931 nom. nud.

Illustrations: Arts (1996), Tewari and Pant (1989) as *S. procerrimum*.

Plants large, medium-sized to rather small, soft and flexuous, pale green or yellowish; stems simple or sparsely forked, up to 50 mm tall and about 0.25 mm in diameter, in transverse section with 1–2 outer layers of smaller thick-walled cells, central strand absent; leaves remotely placed, but more crowded to-

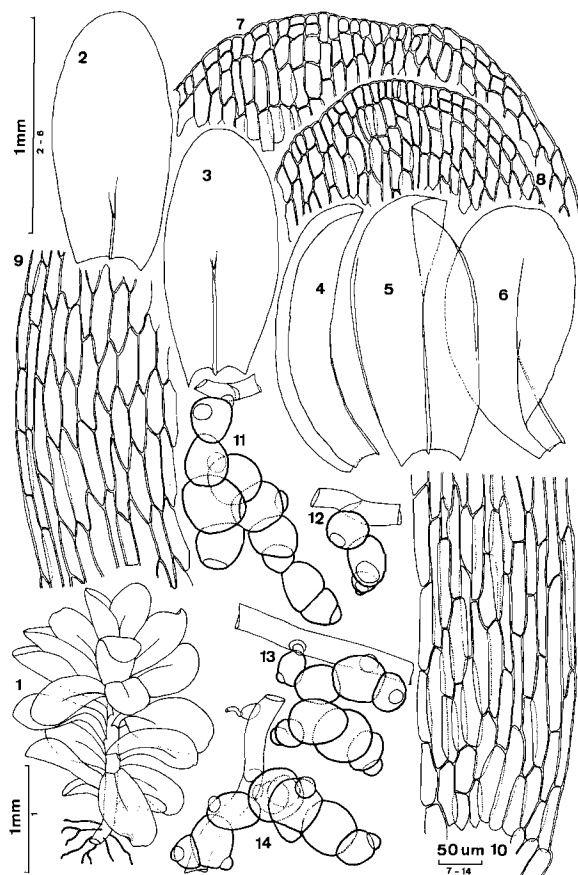


Fig. 4. *Splachnobryum aquaticum* Müll.Hal. 1: Sterile plant; 2-6: leaves; 7-8: cells of leaf apex; 9: mid-leaf marginal cells; 10: cells of leaf base; 11-14: rhizoidal tubers. From Oman, 1-10: leg. Fernandez s.n., type of *S. arabicum* (BM); 11-14: leg. Edmondson E 3275 (BM).

wards the stem apex, erect to spreading and more or less recurved, 1.0-2.5 mm long and 0.5-1.2 mm wide, upper leaves often distinctly longer than the lower, elliptic, with rounded obtuse apex; costa slender, ending far below apex, often with a few very thin branches or forked at the tip; leaf margin plane or narrowly recurved below on one or both sides, more or less crenulate at the apex; leaf base semi-amplexicaul, narrowly decurrent; leaf cells smooth, thin-walled, mid-leaf cells oblong-hexagonal 30-80 µm long and 14-30 µm wide, upper cells and those of 1-2(3) marginal rows much shorter, lower cells rectangular; axillary hairs usually arising in pairs, about 100 µm long, consisting of two colourless basal cells ca. 15 µm long and 10 µm wide and a terminal clavate cell ca 70 µm long and 15 µm wide; cauline brood bodies probably absent; rhizoidal tubers, similar to those described in *S. obtusum* (Arts 1996) occasionally present; dioicous; male plants with antheridia clustered in terminal

perigonia, paraphyses absent; female plants with solitary naked archegonia, arising laterally towards the stem apex; sporophyte typical of the genus, one or two lateral on the stem; spores 18-28 µm in diameter, finely papillose.

**Remarks.** *S. aquaticum* is distinguished from all other species of the genus by its short slender costa and narrowly decurrent leaf base. It is a variable species concerning leaf length, leaf width, the ratio leaf length to width and degree of recurvation of the basal leaf margin.

The synonymy of *S. giganteum* with *S. procerrimum* was already annotated by A. Koponen on the herbarium labels in H-BR. I found both types conspecific with the African *S. aquaticum*. Dixon (1934) distinguished *S. procerrimum* from *S. arabicum* as a much larger plant with much larger, suborbicular leaves. This differentiation is quite correct for the type specimens. All intermediate forms have, however, been collected, e.g. the specimen collected by Radcliffe-Smith Nr. OM21 mainly consists of large plants quite similar to *S. aquaticum* as well as intermediate forms and some small plants quite similar to *S. arabicum*. Leaf shape, cell shape and size as well as costa length are all identical. Hence the latter is reduced here into synonymy. The small specimens are most probably depauperate land forms of otherwise aquatic species.

**Distribution.** Somalia and Southern Asia.

**Africa: Somalia.** See type collection.

**Asia: Bhutan:** Phuntsholing District, Phuntsholing stream NE of town, dripping calcareous rocks in open valley, 26°52'N 89°24'E, leg. D. G. Long 7745, 5 May 1979 (E). **China:** province Yuennan, Manhao prope fines Tonkinensis, ad regionis tropicae fontem quendam calidum, alt. 200 m, leg. H. Handel-Mazzetti 2981 and 5811, 1 March 1915, type of *S. giganteum* (isotype B, BM, BR, H-BR, L, etc.). **India:** Kumaon Hills, Almora, over soapstone boulders, leg. Tewari A 20, 4 April 1982 (H); Siwalik Range, Mahand Pass, Dehra Dun, in running water on face of rocks, leg. W. Gollan 3870, 14 Oct. 1900, syntype of *S. vernicosum* (BM, H-BR); Ahmedabad Distr., banks of the Watrak river, leg. Sedgwick 1291, Dec. 1915, syntype of *S. procerrimum* (holotype BM, isotype H-BR, US). **Jordan:** province Al-Karak, Wadi el Hasa near Safi, on soil, leg. W. Frey & H. Kürschner 1-3463, 20 July 1980 (B). **Burma (Myanmar):** Maymyo, lime cave, alt. 3840 ft., leg. L.P. Khanna 14, 1928 (BM); Idem, Wetvin Hill, on rock near the bank of running stream, leg. R. Sarup s.n., 13 Dec. 1903, syntype of *S. vernicosum* (BM, H-BR); Near Station Thown Downg, on stone along the bank of a running stream leg. Ram Sarup s.n., 10 Dec. 1903 (H-BR). **Nepal:** Makawanpur

district, 2 km N of Hetauda, steep scrubby slope, on wet tuffa, leg. D.G. Long 21644, 29 Oct. 1991 (E). *Oman*: Nejd-el-Khubain, alt. 900 m, leg. J. Fernandez s.n., 17 Nov. 1925, type of *S. arabicum* (holotype BM); W. Hajar mts, Wadi Bani Ghafir, between Zawajah and Hawqayn, leg. J.R. Edmondson E. 3275, 6 March 1980 (E); Dhofar district, Ayn Arzat, under rock and in spring water flow, leg. J. R. Maconochie s.n., 21 Feb. 1982 (K); Dhofar district, Wadi Sarfait ca 12 km NW of Dalqut, on tufa on rocks in running wadi, leg. A. Radcliffe-Smith OM 20 (K); Dhofar district, Darbat, ca 13 km N of Taqah, on tufa in flowing wadi by waterfall, leg. A. Radcliffe-Smith OM 21 (K). *Pakistan*: Waziristan, Sarwekai, SW of camp, on decomposing limestone rocks, bank of stream, leg. J. Fernandez s.n., 7 June 1927, syntype of *S. procerrium* (BM); idem, Waziristan, Miran Shak, moist bank of Chesmai, tributary of the Jochi, leg. E. Blatter and J. Fernandez s.n., 24 March 1930 (BM). *Philippines*: Cebu Island, Cebu, camp 4, river bank, leg. F. Nemenzo s.n., 22 Feb. 1937 (MICH). *Thailand*: Payap, near Mae La Noi, deciduous forest, leg. A. Touw 10305, 27 Dec. 1965 (ALTA, BM, BR, L, MICH, MO). *United Arab Emirates*: between Dibba and Masafi in the Musadam mountains, leg. U. Deil 2180, 21 March 1987 (E). *Yemen*: Ta'izz, El Makhchab, near Wazahia, on wet rocks, alt. 700m, leg. M. Thulin, M. Ghebrehwet & A.N. Gifri 9353, 13 Nov. 1995 (K).

**3) *Splachnobryum limbatum* D. H. Norris & R. H. Zander, Bryologist 84: 404. f. 1-6. 1981. (Fig. 5)**

Type: Solomon Islands. San Christobal: in lowland forest along Puepue Creek above Kira-Kira, leg. Norris & Roberts 49140 (Isotype BUF).

Illustrations: Eddy (1996), Norris & Zander (1981).

*Plants* medium sized to rather large, to 30 mm high; *stems* not or sparsely branched, essentially uniform in transverse section with the cells 20–25 µm in diameter; with bulging outer cortical cell walls; *leaves* oblong-ovate, in male plants 1.8–2.4 mm long and 0.8–1.0 mm wide, 2.0–2.5 times as long as wide, in female plants up to 4.5 mm long and 1.5 mm wide; upper leaves crispate to irregularly twisted when dry; costa percurrent, ending within a few cells of the apex, somewhat broadened at its base, 2–3 cells wide; costa cells uniform in transverse section, 10–12 µm wide and slightly incrassate; *leaf margins* obscurely recurved in lower 1/2–2/3, entire below to minutely denticulate above; strongly differentiated by narrow elongate *marginal cells*, up to 15 times as long as wide, margin up to 6 cells wide below mid-leaf to 1 cell wide below apex, apical margin with nearly isodia-

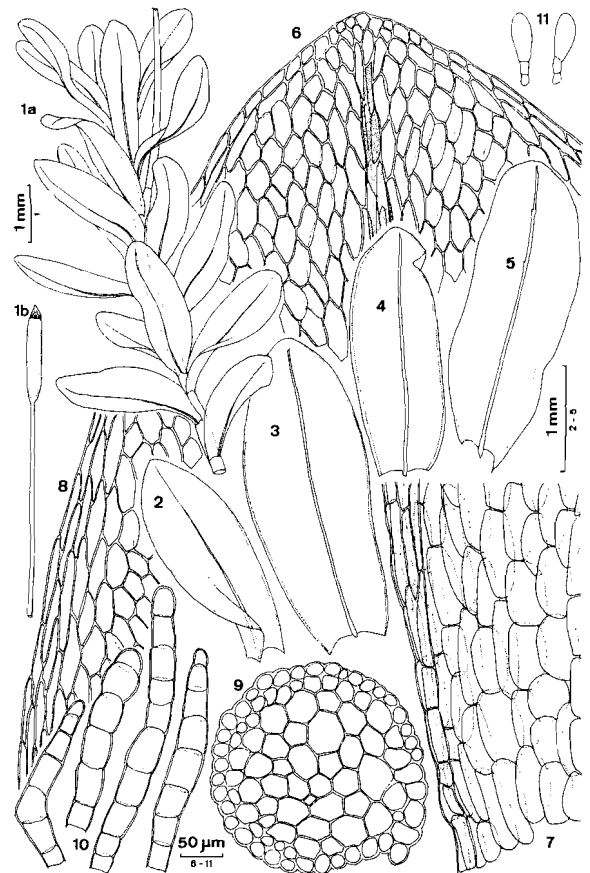


Fig. 5. *Splachnobryum limbatum* D.H.Norris & R.H.Zander. 1: Female plant with sporophyte; 2–5: leaves; 6: cells of leaf apex; 7: cells of leaf base; 8: cells of leaf margin; 9: transverse section of stem; 10: axillary gemmae; 11: axillary hairs. 1, 4–5 and 10–11: from New Ireland, leg. Eddy 6025 pp. (BM); 2–3, 6–9: from the type, leg. Norris & Roberts 49140 (BUF).

metric cells of 14–17 µm in diameter; median *leaf cells* irregularly rhomboidal, thin walled, 20–24 µm wide, 1.2–3.0 times as long as wide, with extreme variations in length; basal cells gradually enlarged but otherwise undifferentiated, up to 80 µm long and 30 µm wide; upper cells smaller and shorter than the median cells, 15 µm wide, 1.0–2.0 times as long as wide; juxtacostal cells nearly rectangular, longer than the adjacent median cells; *axillary hairs* usually arising in pairs, about 75 µm long, consisting of two colourless basal cells ca 15 µm long and ca 10 µm wide and a terminal clavate cell ca 50 µm long and 15 µm wide; *cauline brood bodies* sparse; *rhizoidal tubers* probably absent; *dioicous*; *male plants* with terminal perigonia, antheridia in a tight cluster without paraphyses; perigonial leaves undifferentiated from stem leaves; *female plants* with perichaetia lateral along the

stem; *sporophytes* also lateral; seta 9–11 mm long, capsule narrowly cylindrical, the urn about 1.5 mm long, operculum conical, peristome typical of the genus.

*Remarks.* Description of the male plants according to Norris and Zander (1981). The holotype said to be deposited in US is missing, the isotype in BUF is sterile.

*Distribution.* Endemic to the Pacific Islands East of Papua New Guinea. Known only from two records. *Papua New Guinea:* New Ireland, Danfu Valley, lowland primary forest, on calcareous wet rocks by stream, dense shade, alt. 240 m, leg. A. Eddy 6025 p.p., 26 Jan. 1970 (BM). *Solomon Islands:* type.

**4) *Splachnobryum gracile* Besch., Ann. Sc. Nat. Bot. sér. 7, 2: 89. 1885. (Fig. 6)**

Type: Mayotte (îles Comores), sur la terre, associé à *Philonotis comorensis* et *Microdus limosus*, à Magi M'Bini, leg. M. Marie 144, 21 July 1888 (holotype BM, isotypes E, JE, H, PC).

**Synonyms:**

- S. brotheri* Paris, Rev. Bryol. 31: 120. 1904.
- S. rostratum* Broth. et Paris, Rev. Bryol. 31: 45. 1904.
- S. subjulaceum* Cardot, Rev. Bryol. 36: 86. 1909.
- var. *laxifolium* P.de la Varde, Rev. Bryol. n. ser. 4: 67. 1931.
- var. *subspatulifolium* P.de la Varde, Rev. Bryol. Lich. 7: 234. 1935.

Illustrations: Arts (1996).

*Plants* small to medium sized, up to 20 mm tall, pale green; *stems* simple or sparsely forked, in transverse section with 1–2 outer layers of larger thick-walled cells, central strand absent; *leaves* imbricate, erect to spreading, 0.5–1.5(1.7) mm long and 0.3–0.7 mm wide, upper leaves often distinctly longer than the lower, elliptic to spatulate, with rounded-obtuse apex; leaf lamina more or less strongly incurved; costa slender, ending near the apex, often forked at the tip; leaf margin plane or narrowly revolute below, more or less crenulate at the apex; *leaf cells* smooth, with slightly incrassate walls, mid-leaf cells oblong-hexagonal to rectangular, 50–80 µm long and 20–35 µm wide; upper cells and those of 1–2(3) marginal rows much shorter, rectangular; basal cells larger, rectangular; *axillary hairs* linear, about 80–120 µm long and 5–6 µm wide, consisting of a uniseriate row of (3)4(5) cells; *cauline brood bodies* and *rhizoidal tubers* probably absent; *dioicous*; *male plants* with antheridia clustered in terminal perigonia, paraphyses absent,

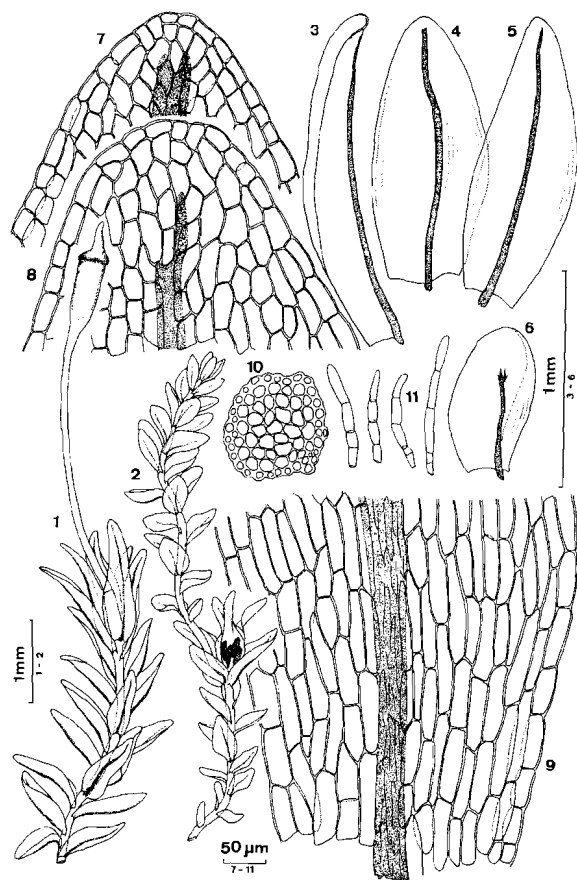


Fig. 6. *Splachnobryum gracile* Besch. 1: Female plant with sporophyte; 2: male plant with antheridia; 3–6: leaves; 7–8: cells of leaf apex; 9: cells of leaf base; 10: transverse section of stem; 11: axillary hairs. 1, 8: From Guinea, leg. Pobeguïn s.n., Sept. 1903 (L); 3, 9, 11: idcm, leg. Pobeguïn s.n., Aug. 1903, isotype of *S. brotheri* (H-BR); 2, 6: from Mayotte, isotype, leg. Marie s.n. (E); 4, 5, 7, 10: From Guinea, leg. Pobeguïn s.n., Sept. 1903, isotype of *S. rostratum* (H-BR).

perigonial leaves erect, broadly ovate and concave below, recurved lingulate above; *female plants* with archegonia solitary or clustered in or above the upper leaf axils; *sporophytes* apparently apical; setae slender, 2–7 mm long, yellowish-orange to reddish-brown smooth; capsules erect, symmetric, ovoid to cylindrical, smooth, operculum longly rostrate and oblique; spores 18–23 µm in diameter, finely papillose.

*Remarks.* Sterile and male plants are often smaller than female plants (Arts 1996). The long linear axillary hairs are shared only with *Splachnobryum crassinervium*.

*Distribution.* endemic to Africa.

Specimens examined from Cameroon, Central Afri-

can Republique, Comoros Islands, Congo (Zaire), Gabon, Guinea, Nigeria and Tanzania (Arts 1996); *Sierra Leone*: Jakala, alt. 175 ft., leg. Thomas 2352, 27 Sept. 1914 (BM).

**5) *Splachnobryum crassinervium* Arts sp. nov. (Fig. 7)**

*Splachnobryum assamico* Dixon affinis, sed caule dense folioso; laminae nervus crassior, basi 40–50  $\mu\text{m}$  latus, in sectione cum cellulis centralibus stereidiferis; laminae cellulae rectangulares; pili axillares lineares, 4-cellulosi; gametangia et sporophyta ignota.

Type: Norfolk Island, Philip Island, Red road valley, barren hillside of dry creek, alt. 60 m., leg. H. Streimann 32255, 04 Dec. 1984 (holotype CANB).

*Plants* small, up to 10 mm tall, not or sparsely branched, dull green above, brown below; *stems* 0.15–0.25 mm wide; in transverse section with 20–30  $\mu\text{m}$  wide medulla cells, 2–4 rows of outer cells distinctly smaller, 20–30  $\mu\text{m}$  in diameter with slightly thicker cell walls; central strand present, consisting of smaller, thin-walled cells; *leaves* closely placed; when dry little altered, loosely appressed towards stem; when moist erecto-patent, straight or slightly recurved; triangular-lingulate, widest near base, with rounded apex, 1.0–2.0 mm long and 0.3–0.4 mm wide, carinate, rather stiff; costa strong, 40–60  $\mu\text{m}$  wide at base, variable in length, ending 2–3 cells below apex, in transverse section with central stereids; leaf margins plane, entire below and more or less distinctly crenulate at apex; median and basal *lamina cells* essentially uniform in size and shape, rectangular, 25–65  $\mu\text{m}$  long and 10–15  $\mu\text{m}$  wide; 2–4 rows of marginal cells distinctly shorter but not narrower than the interior cells; basal juxtacostal cells up to 80  $\mu\text{m}$  long; upper lamina cells irregularly hexagonal, rectangular, or quadrate, 12–30  $\mu\text{m}$  long and 10–15  $\mu\text{m}$  wide; *axillary hairs* linear, about 100–120  $\mu\text{m}$  long and 5–6  $\mu\text{m}$  wide, consisting of a uniseriate row of 4 cells, the upper two cells distinctly longer than the lower; cauline *brood bodies* and *rhizoidal tubers* probably absent; archegonia, antheridia and sporophytes not seen.

*Remarks.* In general appearance this plant closely resembles a pottiaceous moss species. It is quite distinct from all hitherto described *Splachnobryum* species by its stiff appearance, its small cortical stem cells, its strong costa with central stereids in transverse section, its rather uniform leaf areolation with rows of essentially rectangular laminal cells which are evenly wide throughout from leaf base to apex. The long linear axillary hairs are shared only with *Splachnobryum gracile*.

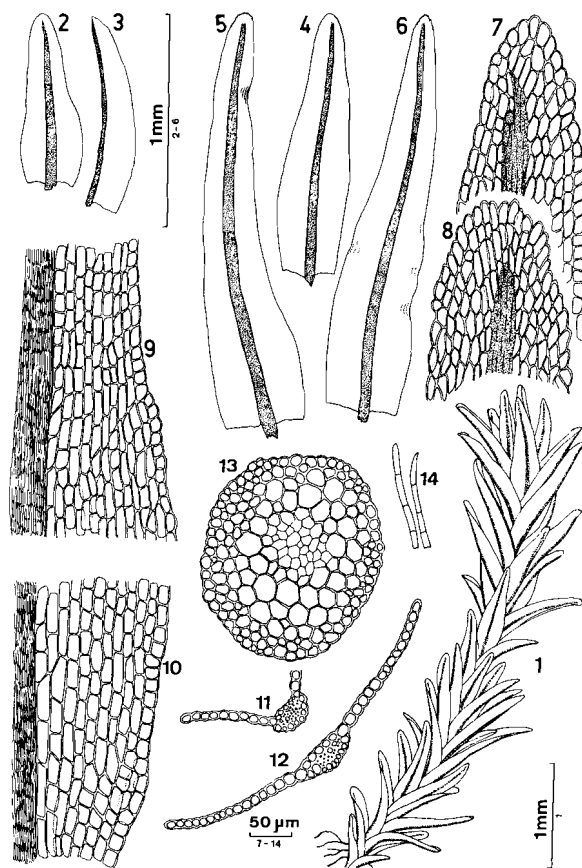


Fig. 7. *Splachnobryum crassinervium* Arts sp. nov. 1: sterile plant; 2–6: leaves; 7–8: cells of leaf apex; 9: mid-leaf cells; 10: cells of leaf base; 11–12: transverse section of leaves; 13: transverse section of stem; 14: axillary hairs. From the type, leg. H. Streimann 32255 (CANB).

*Distribution.* endemic to Norfolk Island.

*Norfolk Island:* type; idem, Philip Island, Red road valley, bare westerly slope, on shaded ground, alt. 90 m., leg. H. Streimann 53907, 19 April 1994 (CANB, H).

**6) *Splachnobryum wiemansii* M.Fleisch., Musci Fl. Buitenzorg 2: 474. 1904 (Fig. 8)**

Type: West Java, Flora Bogoriensis, Weltevreden, am Koningsplein an steinen in einer Wasserrinne, leg. F. Wiemans s.n. 1902. (isotype herb. L).

Synonyms:

*S. latifolium* Bartr., Philipp. J. c. 68: 126. 152. 1939.

*Plants* rather small, up to 15 mm tall, in dense soft tufts, dull green; *stems* unbranched to irregularly branched, about 0.2–0.3 mm in diameter, in transverse

section with essentially uniform cells of 20–30  $\mu\text{m}$  in diameter, most outer cortical cells somewhat smaller with slightly thicker and bulging walls; central strand consisting of smaller, thin walled, hyaline, readily disintegrating cells; *leaves* when dry shrunken and contorted, when moist patent to widely spreading and more or less recurved and concave, 1.5–2.0 mm long and (0.6) 0.8–1.2 mm wide, broadly ovate, much narrowed towards insertion, rounded to bluntly apiculate at apex; leaf margins plane, entire below and minutely crenulate in upper half; median *leaf cells* oval-hexagonal 40–60  $\mu\text{m}$  long and 15–20  $\mu\text{m}$  wide; basal cells larger, oblong-hexagonal; basal leaf margin differentiated by 1 to 2 rows of narrow elongated cells, apical margin with nearly isodiametric cells of 14–17  $\mu\text{m}$  in diameter; costa percurrent, ending within a few cells from the apex, somewhat broadened at its base, 2–3 cells wide; costal cells uniform in transverse section,

10–12  $\mu\text{m}$  wide and slightly incrassate; axillary hairs, about 60–85  $\mu\text{m}$  long, consisting of one or two colourless basal cells ca 15  $\mu\text{m}$  long and 10  $\mu\text{m}$  wide and a terminal clavate cell ca 50  $\mu\text{m}$  long and 20  $\mu\text{m}$  wide; cauline *brood bodies* sparsely present; *rhizoidal tubers* probably absent; dioicous; *male* plants with terminal perigonia, antheridia in a tight cluster without paraphyses; perigonial leaves undifferentiated from stem leaves; *female* plants with solitary axillary to extra-axillary archegonia; *sporophytes* unknown.

*Remarks.* Terricolous plants are smaller, with conspicuously narrower leaves than aquatic plants. According to Bartram (1939) *S. latifolium* has broader, often nearly suborbicular leaves and shows little or no evidence of the throatlike constriction at the apex which Fleischer attributes to *S. wiemansii*. The broader leaves of *S. latifolium* most probably result from the aquatic condition of the specimen. The throatlike constriction at the apex is formed through aplanation of the recurved leaf apex in microscopic slides. I observed this phenomenon in a few leaves of *S. latifolium* as well as in *S. wiemansii*. Based on the essentially identical leaf areolation and obvious similarities in other leaf characteristics the two species should not be taxonomically distinguished.

Large aquatic specimens of *S. obtusum* (e.g. Fig. 11) may closely resemble *S. wiemansii*. The latter can be distinguished by its recurved leaves and basal leaf margin differentiated by 1–3 rows of narrow elongated cells.

*Distribution.* Endemic to Malesia.

*Java:* West Java, Weltevreden (type); Im Lamongau-Gebiete bei Surabaya, Wasserfall über dem Ranu Bendali, auf Basalt Gestein im Sprühregen, leg. F. Ruttner s.n., 11 Nov. 1928 (B, BM, JE); idem, Bucht des Ranu Pakis, leg. F. Ruttner s.n., 30 Oct. 1928 (JE). *Malaya:* Selangor, Batu Caves, limestone hill, at the foothill, on soil in shade of undergrowth, leg. H. Mohamed 8989, 22 Aug. 1983 (B). *Philippines:* Luzon Isl., Rizal province, Hinulugan Taktak (waterfall) near Antipolo, leg. H.H. Bartlett 15281, 18 Aug. 1935, type of *S. latifolium* (isotype MICH); idem, Luzon Isl., Botanical Garden of the University of the Philippines, leg. C.L. Afabb No. 2 and 9, Aug. 1940 (MICH).

**7) *Splachnobryum oorschotii* (Sande Lac.) Müll.Hal., *Linnaea* 40: 293. 1876 (Fig. 9)**

*Basionym:* *Orthodontium oorschotii* Sande Lac., Nat. Verh. Ak. Wetensch. Amsterdam 13: 11. 1872.

*Type:* Java, Semarang, Grisfee, locis calcareis, leg. W. van Oorschot s.n., Jan. 1871 (isosyntype: BM, L);

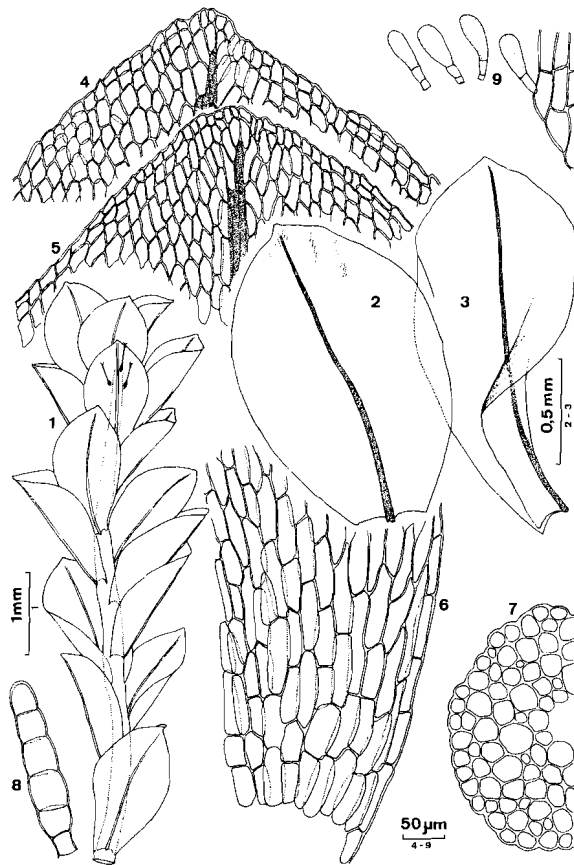


Fig. 8. *Splachnobryum wiemansii* M.Fleisch. 1: Female plant; 2–3: leaves; 4–5: cells of leaf apex; 6: cells of leaf base; 7: transverse section of stem; 8: axillary gemma; 9: axillary hairs. 1,3: from Java, leg. Ruttner s.n. (BM); 2, 4, 6, 8, 9: from Java, leg. Wiemans s.n., isotype of *S. wiemansii* (JE, L); 5, 6, 7: from the Philippines, leg. Bartlett 15281, isotype of *S. latifolium* (MICH).

prope Soerabaya, locis calcareis, leg. W. van Oorschot s.n., 1871 (isosyntype: BM, L).

Synonyms:

*S. siamense* Cardot et Thér., Bull. Ac. Geogr. Bot. 21: 269. 1911.

Illustrations: Eddy (1996).

*Plants* small, up to 15 mm tall, not or sparsely branched, dull green; *stems* about 0.2 mm wide, in transverse section with essentially uniform cells throughout, 20–30 µm in diameter, most outer cortical cells somewhat smaller with slightly thicker and bulging walls; central strand consisting of smaller, thin-walled, hyaline, readily disintegrating cells; *leaves* patent, lingulate to narrowly lingulate 1.3–2.0 mm long and 0.3–0.5 mm wide, rather flaccid, apex bluntly obtuse; costa 40–60 µm wide at base, variable in length, ending 1 to several cells below apex; leaf margins plane, rarely narrowly revolute on one or both sides in mid-

leaf, entire below and crenulate to bluntly dentate in upper half; median and upper *lamina cells* rectangular to rhomboidal or oblong-hexagonal, 35–75 µm long and 12–20 µm wide, thin-walled; basal and lower lamina cells elongate-rectangular, 100–150 µm long; upper marginal cells slightly shorter but not conspicuously smaller than the interior cells; *axillary hairs* usually arising in pairs, about 75 µm long, consisting of two colourless basal cells ca 15 µm long and ca 10 µm wide and a terminal clavate cell ca 50 µm long and 15 µm wide; cauline *brood bodies* sparsely present; *rhizoidal tubers* probably absent; *dioicous*; *male plants* not seen; *female plants* with solitary axillary to extra-axillary archegonia; *sporophytes* as in *S. obtusum*.

*Remarks.* *Splachnobryum siamense* was differentiated from *S. oorschotii* by, for example, its wider and longer leaves, reflexed lower leaf margins, and wider leaf cells with narrower cell walls (Thériot 1911). However these alleged differences fall within the range of variability observed in *S. oorschotii*.

I agree with Eddy (1996) that the type collection of *S. novae-guineae* is clearly separable from *S. oorschotii* on details of leaf apex (rounded instead of obtuse in *S. oorschotii*), revolute margins and abrupt transition from short apical (margin) to elongate interior cells. The two species are, however, closely related and rather variable in a way that determination should not be based on a single leaf, the possibility that *S. novae-guineae* is only a luxuriant form of *S. oorschotii* cannot be excluded.

*Distribution.* Endemic to South East Asia.

*Asia: Irian Jaya (West New Guinea):* Vogelkop Pen., Sorong, terrestrial, leg. V. Helledoorn 115A, 26 Oct. 1949. *Java:* Redong Djatie prope Semarang, leg. Van Oorschot s.n., Jan. 1871 (H-BR, L); Weltevreden an feuchten Mauern, leg. M. Fleischer s.n., March 1902 (H-BR, JE, L). *Singapore:* steril, auf feuchten Steinen am Wasser beim Reservoir, leg. M. Fleischer 135, March 1898 (M, E, H-BR, JE, L). *Thailand (Siam):* Bangkok, jardins de la légation de France, leg. Topend s.n., 1 Dec. 1909 holotype of *S. siamense* (PC).

**8) *Splachnobryum novae-guineae* Broth., Bot. Jahrb. 17: 477. 1893 (Fig. 10)**

Type: Nova Guinea, Morobe, Butaueng, leg. L. Kaernbach s.n. Dec. 1889 (holotype H-BR, isotype BM).

Illustrations: Eddy (1996).

*Plants* small, up to 10 mm tall, not or sparsely branch-

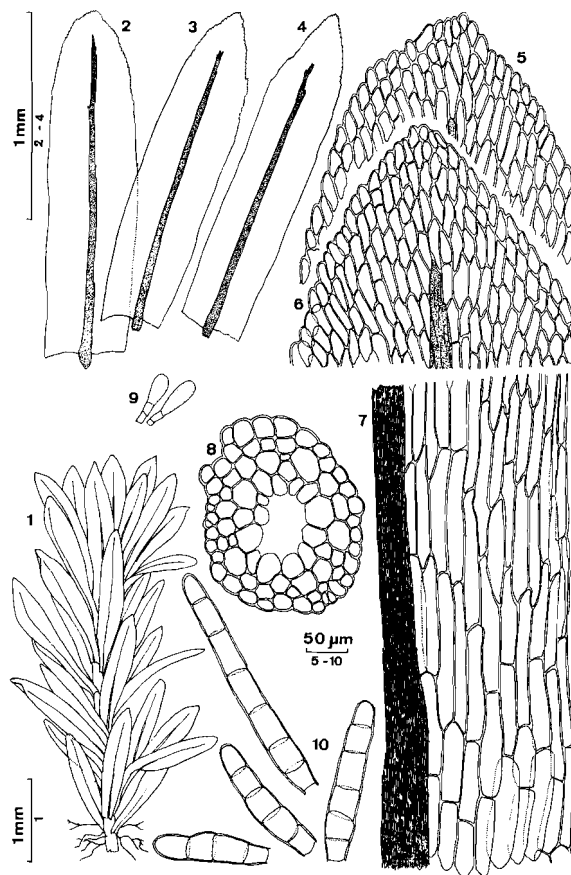


Fig. 9. *Splachnobryum oorschotii* (Sande Lac.) Müll.Hal. 1: sterile plant; 2–4: leaves; 5–6: cells of leaf apex; 7: cells of leaf base; 8: transverse section of stem; 9: axillary hairs; 10: axillary gemmae. From the isosyntype, prope Soerabaya, leg. van Oorschot s.n. (L).

ed, dull green; *stems* about 0.2 mm wide in transverse section with essentially uniform cells 20–30  $\mu\text{m}$  in diameter, most outer cortical cells somewhat smaller with slightly thicker and bulging walls; central strand consisting of smaller, thin-walled, hyaline, readily disintegrating cells; *leaves* when dry shrunken and contorted, when moist patent, lingulate to oblong, 1.3–2.0 mm long and 0.4–0.6 mm wide, rather flaccid, apex rounded, rarely bluntly obtuse; costa 40–60  $\mu\text{m}$  wide at base, ending 1 to 3 cells below apex; leaf margins often at base and/or in mid-leaf narrowly revolute, entire below and crenulate to bluntly dentate in upper half; median and upper *lamina cells* rectangular to rhomboidal to oblong-hexagonal, 35–75  $\mu\text{m}$  long and 12–20  $\mu\text{m}$  wide, thin-walled; basal and lower lamina cells elongate rectangular, 100–150  $\mu\text{m}$  long; one or two rows of upper marginal cells only, 15–30  $\mu\text{m}$  long, conspicuously smaller than the interior cells; *axillary hairs* clavate, 2–3 celled as in *S. obtusum*; cauline

*brood bodies* sparse; *rhizoidal tubers* probably absent; *dioicous*; *male plants* obviously smaller than female plants, with terminal perigonia, antheridia in a tight cluster without paraphyses; perigonial leaves, ca 1.0 mm long, slightly smaller but otherwise undifferentiated from stem leaves; *female plants* with solitary axillary to extra-axillary archegonia; *sporophytes* as in *S. obtusum*.

*Remarks.* *Splachnobryum novae-guineae* seems to be closely related to *S. oorschotii*, see that species.

*Distribution.* Endemic to Papua New Guinea, known only from three records.

*Papua New Guinea:* Morobe, Butaueng (type); Kairiru Isl., East Sepik province, 3°22' S / 143°33' E, on edge of cement floor of building, leg. J. Klei 24, 20 Juli 1979 (MO, herb. Sollman); idem, on tree trunk, leg. J. Klei 9, 18 Juli 1979 (herb. Sollman).

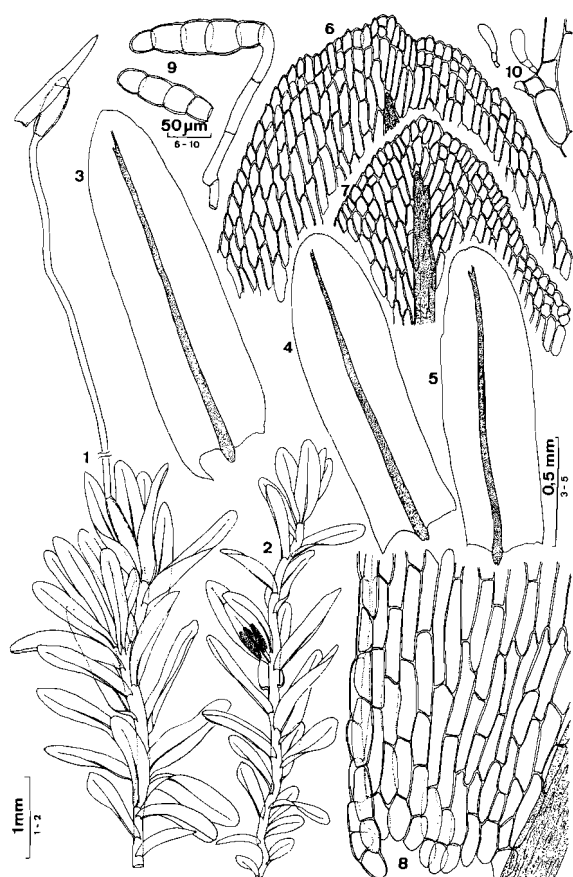


Fig. 10. *Splachnobryum novae-guineae* Broth. 1: Female plant with sporophyte; 2: male plant with antheridia; 3–5: leaves; 6–7: cells of leaf apex; 8: cells of leaf base; 9: axillary gemmae; 10: axillary hairs. 1,10: from Papua New Guinea, leg. Klei 24 (MO); 2, 7–9: idem, leg. Klei 9 (L); 3–6: idem, from the type, leg. Kaernbach s.n. (H-BR).

**9) *Splachnobryum assamicum* Dixon, J. Bombay Nat. Hist. Soc. 39(4): 778. 1937. (Fig. 11)**

Type: India, Assam, Charduar, on brickwork, leg. N.L. Bor s.n., 2 Aug. 1934 (holotype, BM in herb. Dixon No. 176).

Synonym:

*S. synoicum* H. Robinson, J. Hattori Bot. Lab. 27: 127. f. 8–9. 1964. syn. nov.

Illustrations: Gangulee (1974) as *S. synoicum*.

*Plants* small, up to 15 mm tall; *stems* not or sparsely branched, in transverse section with 1 to 2 outer layers of smaller, thick-walled cells, central strand absent; *leaves* erect to erecto-patent, triangular-lanceolate, widest near base and gradually tapering towards apex, concave, 1.2–1.5 mm long and 0.3–0.5 mm wide; leaf apex obtuse, more or less cucullate; leaf margin essentially plane throughout, entire below to more or less crenulate above; costa 30–50  $\mu\text{m}$  wide at base, ending a few cells below apex; median *leaf cells* irregularly hexagonal, about 30–50  $\mu\text{m}$  long and 12–18  $\mu\text{m}$  wide, becoming gradually smaller and more rectangular towards margin and towards the leaf apex; upper lamina cells small, irregularly rhomboidal, about 15–30  $\mu\text{m}$  long and 8–15  $\mu\text{m}$  wide; basal leaf cells irregularly rectangular, conspicuously larger towards costa; *dioicous*; *male plants* with antheridia clustered in terminal perigonia, paraphyses absent; *female plants* with solitary axillary to extra-axillary archegonia; *sporophytes* as in *S. obtusum*. spores 17–24  $\mu\text{m}$  in diameter.

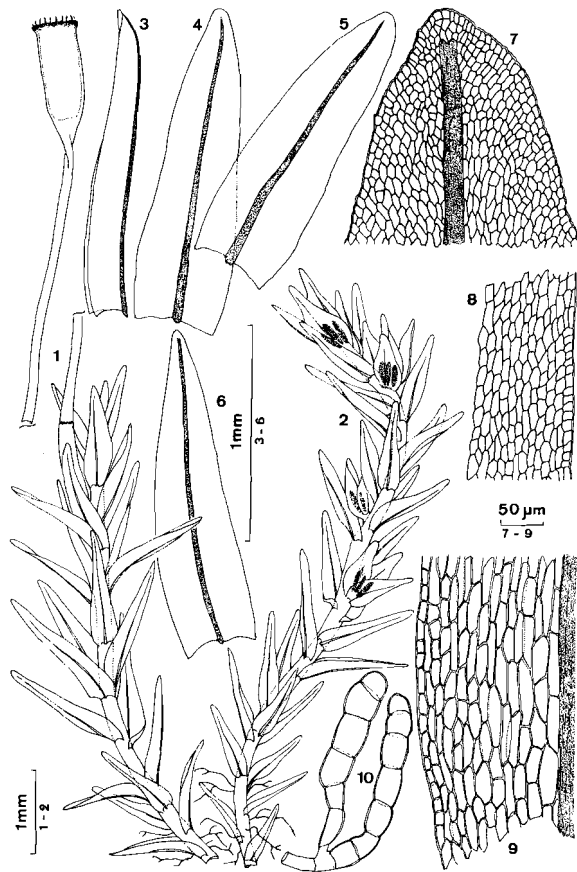


Fig. 11. *Splachnobryum assamicum* Dixon 1: Female plant with sporophyte; 2: male plant with antheridia; 3-6: leaves; 7: cells of leaf apex; 8: mid-leaf cells; 9: cells of leaf base; 10: axillary gemmae. From the type, leg. Bor s.n. (BM).

**Remarks.** The type of *S. assamicum* is distinguished from the variable *S. obtusum* by its long-lanceolate leaves combined with very small laminal cells. The two species are, however, linked as a series of specimens with intermediate leaf forms and cell areolation in a way that *S. assamicum* might as well be considered an extreme form of *S. obtusum*.

The illustration and description of *S. assamicum* in Gangulee (1974), with acuminate leaf apex and percurrent to shortly excurrent costa and quadrate upper and marginal cells, is an error. His specimen is obviously a misidentified sterile plant, that most likely belongs in the Pottiaceae, I found these plants intermingled with the type.

**Distribution.** Burma and India.

**Burma:** Kyauktaw, leg. Hj. Möller s.n., 29 Sept. 1897 (B, H-BR, MICH, MO).

**India:** Assam (type); Upper Assam, Chabua, on old stone post, leg. A.C. Cole 98, 15 July 1944, type of *S.*

*synoicum* (holotype: US); Uttar Pradesh, Kumaun region of NW Himalayas, Pithoragarh district, Askat, 1140 m, on copper tailing dumps, leg. S.D. Tewari s.n. 20 Sept. 1988 (US).

**10) *Splachnobryum obtusum* (Brid.) Müll.Hal., Verh. k.-k. zool.-bot. Ges. Wien 19: 503. 1869. (Figs 12-15)**

Type: Sto. Domingo, leg. Poiteau s.n., s.d. (isotype BM).

Basionym: *Weissia obtusa* Brid., Spec. Musc. I, 118, 1806.

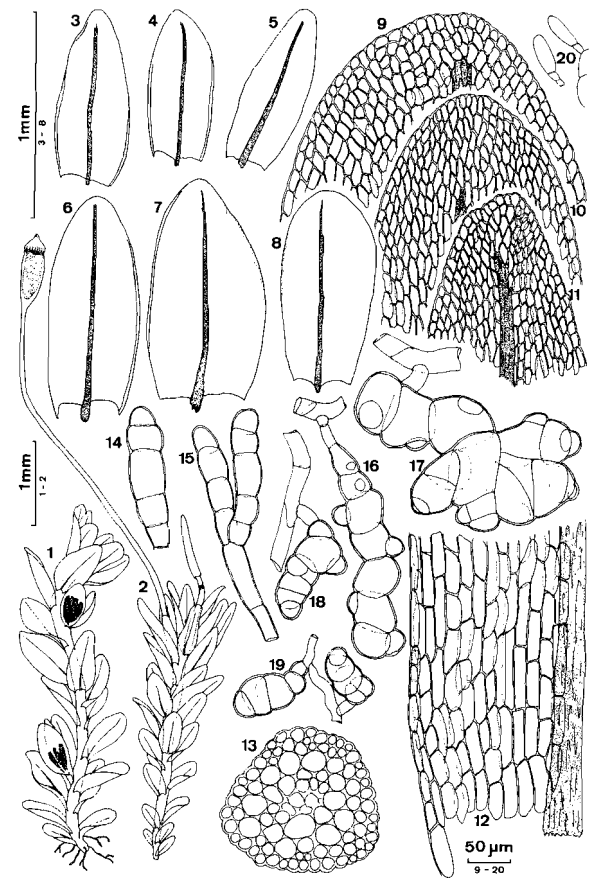


Fig. 12. *Splachnobryum obtusum* (Brid.) Müll.Hal. 1: Female plant with sporophyte; 2: male plant with antheridia; 3-8: leaves; 9-11: cells of leaf apex; 12: cells of leaf base; 13: transverse section of stem; 14-15: axillary gemmae; 16-19: rhizoidal tubers; 20: axillary hairs. 1, 6-9, 12: from Australia, leg. Bailey 297, type of *S. baileyi* (H-BR); 2-5, 10, 11: from India, leg. S. Kurz s.n., type of *S. indicum* (BM); 13-17, 20: from Java, leg. Fleischer 136, type of *S. geheebii* (L); 18-19: from Peru, leg. Spruce 209b, type of *S. spruceanum* (E).

Synonyms:

*Amblyphyllum hibernicum* Lindb. in A. Jaeger, Ber. S. Gall. Naturw. Ges. 1872-73: 190. 1874 (Ad. 1: 268) nom. nud.

*Amblyphyllum splachnifolium* Müll. Hal., Syn. 1: 140. 1848. nom. illeg.

*Didymodon splachnifolius* Hook., Musci Exot. 1: 76 f. 1-5. 1818. nom. superfl. illeg.

*Dissodon mariae* Besch., in Paris, Ind. Bryol. Suppl. 129. 1900. nom. nud.

*Dissodon rotundifolius* Müll. Hal., Syn. 1: 140. 1848. nom. nud.

*Splachnobryum atro-virens* Besch., Rev. Bryol. 18: 76. 1891.

*S. baileyi* Broth., Bot. Centralbl. 36: 85. 1888. syn. nov.

*S. bernoullii* Müll. Hal., Verh. Zool. Bot. Ges. Wien 19: 505. 1869.

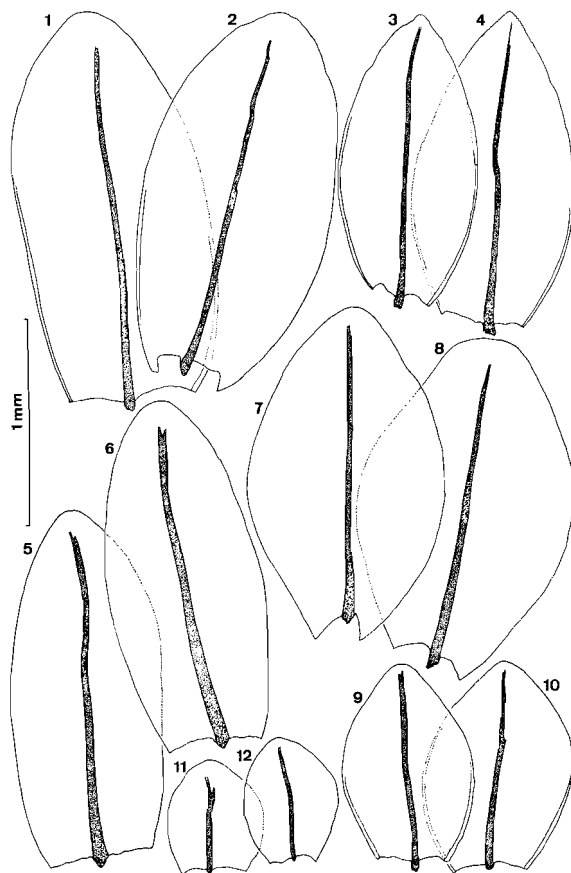


Fig. 13. Broad-leaved forms of *Splachnobryum obtusum* (Brid.) Müll. Hal. 1-2: From Peru, leg. Spruce 209b2, type of *S. spruceanum* (E); 3-4: from Papua New Guinea, leg. Eddy 6745 (BM); 5-6: from U.S.A., leg. Merrill 13363b (MICH); 7-8: from Cuba, leg. Benelde s.n. (BM); 9-10: from Guatemala, leg. Standley 73880 (MICH); 11-12: from Bali, leg. Schäfer-Verwimp 17014B (herb. Schäfer-Verwimp).

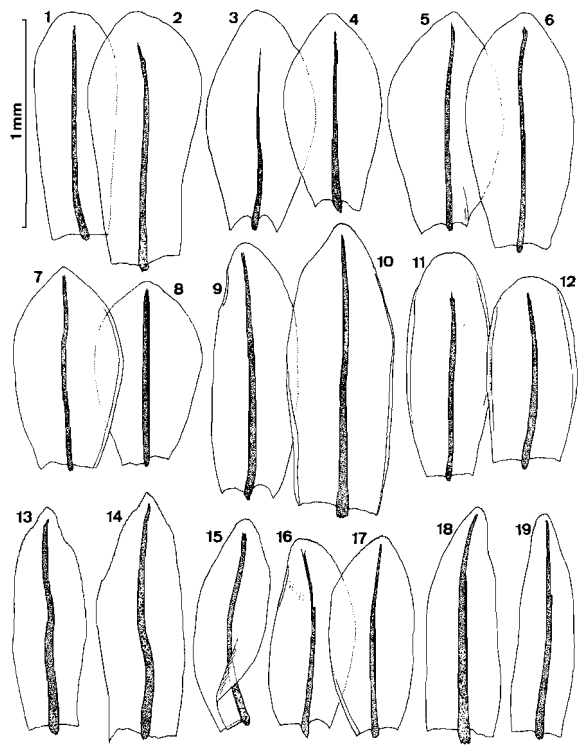


Fig. 14. Leaf forms of *Splachnobryum obtusum* (Brid.) Müll. Hal. 1-2: from Mexico, leg. Cárdenas 203 (MICH); 3-4: from Guadeloupe, leg. Marie 503, type of *S. atrovirens* (BM); 5-6: from Gilbert Islands, leg. Eastman s.n., type of *S. pacificum* (BM); 7-8: from Java, leg. Fleischer s.n., type of *S. ovalifolium* (JE); 9-10: from Java, leg. Fleischer 136, type of *S. geheebii* (L); 11-12: from Mexico, leg. Barnes & Lund 251, isosyntype of *S. crenulatulum* (JE); 13-14: from Guadeloupe, leg. Père Duss. 127 (H-BR); 15-17: from Madagascar, leg. Boivin s.n., type of *S. boivinii* (PC); 18-19: from Philippines, leg. Bartlett 16211, type of *S. luzonense* (H-BR).

*S. boivinii* Müll. Hal. in Besch., Ann. Sc. Nat. Bot. ser. 6, 9: 303. 1880.

*S. corbieri* Renaud & Cardot, Bull. Soc. R. Bot. Belg. 41(1): 61. 1905.

*S. crenulatulum* Cardot, Rev. Bryol. 36: 86. 1909.

*S. crenulatum* Cardot in Grand. Hist. Madag. 39: 263. 1915.

*S. delicatulum* Broth. in Dixon, J. Bot. 14: 81. 484A. 1907.

*S. elatum* Broth., in Urban, Symb. Antill. 3: 423. 1903.

*S. flaccidum* (Harv.) Braithw., Grevillea 1(2): 28. 1872. syn. nov.

*S. geheebii* M. Fleisch., Musci Fl. Buitenzorg 2: 472. 87. 1904. syn. nov.

*S. indicum* Hampe & Müll. Hal., Linnaea 37: 174. 1872. syn. nov.

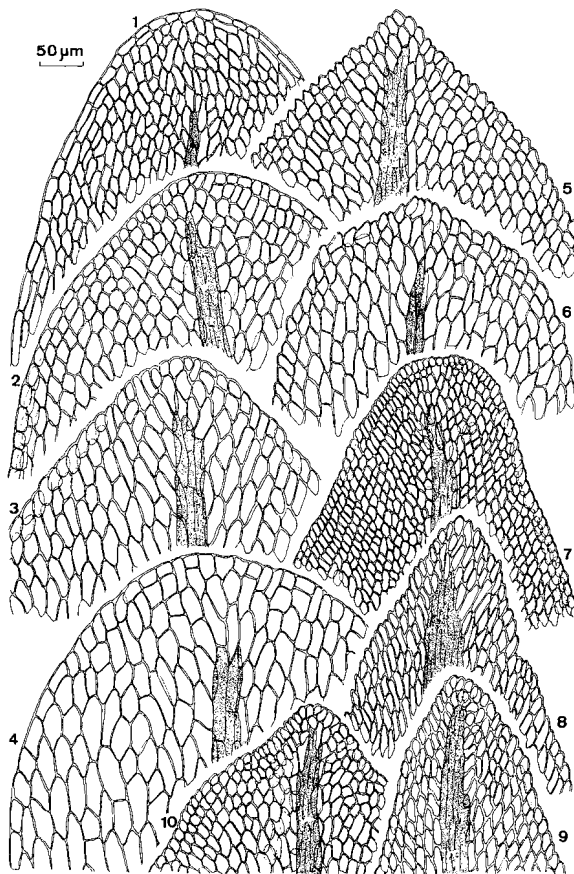


Fig. 15. Variation in leaf apex of *Splachnobryum obtusum* (Brid.) Müll.Hal. 1: from Guadeloupe, leg. Marie 503, type of *S. atrovirens* (BM); 2: from Antilles, leg. Poiteau s.n., type of *S. splachnifolium* (E); 3: from USA, leg. Merrill 13363b (MICH); 4: from Mexico, leg. Cárdenas 203 (MICH); 5: from Malaya, leg. Mohamed 8940 (B); 6: from the Gambia, leg. Arts Ga 10/03 (herb. Arts); 7: from Ghana, leg. Ameka 2 (K); 8: from Guadeloupe, leg. Père Duss. 127 (H-BR); 9: from Philippines, leg. Bartlett 16211, type of *S. luzonense* (H-BR); 10: from the Gambia, leg. Arts Ga 06/01 (herb. Arts).

- S. inundatum* Müll.Hal. in Besch., Ann. Sc. Nat. Bot. ser. 6, 9: 303. 1880.  
*S. julaceum* Besch., Rev. Bryol. 18: 76. 1891.  
*S. leoni* Thér., Mem. Soc. Cubana Hist. Nat. 13: 275. 34 f. 5. 1939.  
*S. ligulifolium* Cardot, Rev. Bryol. 36: 86. 1909.  
*S. luzonense* Broth., Philipp. J. Sc. C 8: 125. 70. 1913. syn. nov.  
*S. mariei* Besch., Rev. Bryol. 18: 75. 1891.  
*S. ovalifolium* M.Fleisch., Musci Fl. Buitenzorg 2: 471. 87. 1904. syn. nov.  
*S. pacificum* Dixon, Rev. Bryol. n. ser. 1: 12. 1928. syn. nov.  
*S. schofieldii* Banu-Fattah & Syed, Bangladesh J. Bot. 26: 61, f. 1. 1997. syn. nov.

- S. splachnifolium* (Hook.) Thér., Mem. Soc. Cubana Hist. Nat. 13: 275. 1939. nom. illeg.  
*S. spruceanum* Müll.Hal., Linnaea 37: 175. 1872. syn. nov.  
*S. sprucei* Müll.Hal. ex Kindb., Enum. Bryin. Exot. 76. 1888. nom. illeg.  
*S. suborbifolium* Paris & Broth., Rev. Bryol. 33: 39. 1906.  
*S. wrightii* Müll.Hal., Verh. Zool. Bot. Ges. Wien 19: 505. 1869.  
*S. wulschlaegelii* Müll.Hal., Verh. Zool. Bot. Ges. Wien 19: 504. 1869.  
*Syrhophodon obtusus* (Brid.) Schwaegr., Spec. Musc. Suppl. 2(2): 106. 182. 1827.  
*Weissia flaccida* Harv. in Hooker's Icon. Pl. 1: t. 18 f. 3. 1836; J. Bot. 2: 6. 1840.  
*Weissia obtusifolia* Rich. in Schwaegr., Spec. Musc. Suppl. 2(2): 106. 1827 nom. nud.  
*Weissia splachnifolia* (Hook.) Mitt., J. Linn. Soc. Bot. 12: 141. 1869.

Illustrations: e.g. Arts (1996), Breen and Pursell (1959), Brotherus (1924) as *Splachnobryum baileyi*, Eddy (1996) as *S. indicum* and *S. geheebii*, Fleischer (1904) as *S. geheebii*, Whittier (1976) as *S. indicum*, Koponen (1994) and others.

*Plants* small, up to 15 mm tall, pale green or yellowish; *stems* simple or sparsely forked, in section with 1 or 2 outer layers of larger thick-walled cells, central strand absent or weakly differentiated; *leaves* erect to spreading, 0.5–1.3(1,9) mm long and 0.3–0.5(0,9) mm wide, upper leaves often distinctly longer than the lower, ovate, lanceolate, spatulate to lingulate, with broadly rounded or obtuse apex; costa slender, ending near the apex, often forked at the tip; leaf margin plane to distinctly recurved on one or both sides, more or less crenulate at the apex; *leaf cells* smooth, thin-walled, mid-leaf cells oblong-hexagonal, 30–80 µm long and 15–20 µm wide, upper cells much shorter, nearly quadrate, lower cells larger, rectangular; *axillary hairs* usually arising in pairs, about 75 µm long, consisting of one or two colourless basal cells ca 15 µm long and 10 µm wide and a terminal clavate cell ca 50 µm long and 15–20 µm wide; cauline *brood bodies* and/or *rhizoidal tubers* present in many specimens; *dioicous*, *male plants* with antheridia clustered in terminal perigonia, paraphyses absent; *female plants* with naked solitary archegonia, scattered along the stem in or above the leaf axils; *sporophyte* apparently terminal or lateral; setae slender, 4–7 mm long, yellowish orange to reddish brown, smooth; capsules erect, symmetric, ovoid to cylindrical, smooth, annulus persistent, operculum conic to shortly rostrate, peristome double, the exostome reduced to a layer of hyaline inflated cells, the endostome inserted below

the mouth, consisting of 16 linear papillose segments, reddish, rather brittle; spores 12–25 µm in diameter, finely papillose; calyptra narrowly cucullate, smooth.

**Remarks.** The species obviously consists of a number of phenotypically polymorphic populations lacking, however, sufficient discriminatory characters for taxonomic recognition at specific or subspecific level. It often forms rather uniform colonies, which may represent single clones either male or female, of the same age and growth history. The species survives long seasonal drought by regenerating from old stem parts or rhizoidal tubers and locally spreads by dispersal of cauline gemmae.

The degree of variability and deviations from the typical plant is more pronounced in South East Asian specimens than in American and African specimens (Breen and Pursell 1959, Arts 1996). Some specimens from Malaya (e.g. H. Mohamed 8989) and from Papua New Guinea (e.g. A. Eddy 6745, mentioned in Eddy 1996) are difficult to place and are provisionally included in *S. obtusum*.

According to Eddy (1996) "*S. flaccidum* is one of the more easily recognised species because of its distinctive leaf shape, broadest at insertion". However, *S. flaccidum* has the same leaf areolation as *S. obtusum* and all intermediate leaf forms between the latter and the type of *S. flaccidum* can be observed.

*Splachnobryum geheebii* is a comparable large plant with rather long ligulate leaves, similar to the types of *S. elatum* from the Antilles, and *S. inundatum* from Madagascar. *Splachnobryum indicum* is a form with reflexed leaf margin and small leaf cells. *Splachnobryum luzonense* is a very small, narrow-leaved form similar to the type of *S. mariei* from Guadeloupe. *Splachnobryum pacificum* is a small broad-leaved juvenile plant similar to the type of *S. crenulatum* from Madagascar. *S. spruceanum* is an extremely large aquatic plant; similar large aquatic forms and all intermediates have, however, been collected from other localities. *Splachnobryum baileyi*, *S. ovalifolium* and *S. schofieldii* are typical forms of *S. obtusum*. The type of *S. schofieldii* was not available for study, but the description and the illustration of the species unequivocally places it in my concept of *S. obtusum*.

**Distribution.** *S. obtusum* is a subcosmopolitan species from the tropical and subtropical regions, spread by human agency. It has been collected from all continents except Antarctica. It has often been introduced in glasshouses in temperate regions of North America and Europe.

Specimens were examined from *Africa*: Botswana, Congo (Zaire), Equatorial Guinea (Bioko Isl. Malabo), Gambia, Gabon, Ghana, Guinea, Ivory Coast, Madagascar, Nigeria, Somalia and Chad, e.g. Arts (1996).

*Americas*: USA (Alabama, Arizona, Nevada, Florida, Georgia, Louisiana, Oklahoma, Texas), Mexico, Belize, Guatemala, El Salvador, Honduras, Panama, Colombia, Venezuela, Trinidad, Suriname, Brazil, Ecuador, Peru, Bolivia, Chile, and the West Indies: Cuba, Haiti, Jamaica, Puerto Rico, the Lesser Antilles (Barbados, Bonaire, Dominica, Guadeloupe, Martinique, Virgin Islands: Tobago). *Asia*: India, Burma (Myanmar), Thailand, Malaya, Indonesia (Bali, Irian Jaya, Java, Sumatra, Sumbawa), Philippines, Papua New Guinea. *Australia*: Northern Territory, Queensland. *Europe*: France, Germany, Hungaria, United Kingdom (England, Scotland). *Macaronesia*: Azores. *Pacific*: Gilbert Islands, Hawaii (Oahu), Marshall Islands, Tonga.

### Doubtful species

***S. lorentzii* Müll.Hal., Linnaea 43: 355. 1882.**

Type: Argentina temperata Cordobensis, Sierra de Cordoba, Las Peñas, leg. Lorentz Feb. 1871

This species is known only from the type, which could not be located and most probably was destroyed by the fire of 1943 in Berlin (comm. of H. Sipman litt.). According to Müller (1882) the plants closely resemble *S. mariei* (= *S. obtusum*). Hence there seems to be little doubt that it is only a small form of the subcosmopolitan *S. obtusum*.

***S. stuartii* H. Whittier, in H.A. Miller, H.O. Whittier & Bonner, Beih. Nova Hedwigia 11: 28. 1963.**

Type: Ifaluk, in Insulis Carolinis, leg. H.A. Miller & H.O. Whittier 7551, 10 Aug. 1960 (holotype ?).

Unfortunately the type specimen was not available for study. Despite the comments in various publications, e.g. in Miller et al. (1963), the herbarium BISH according to the curator does not possess any Whittier types. H. O. Whittier (in litt.) mentions that no specimen is available in FTU, nor in his personal herbarium. My letter to H.A. Miller remained unanswered. However, from the key, the description, and the illustration of the species, there seems to be little doubt that *S. stuartii* should be reduced to synonymy of *S. obtusum*.

***S. pulcherrimum* Dixon et P.de la Varde, J. Indian Bot. Soc. 10(2): 147. 1931 nom. nud., not seen.**

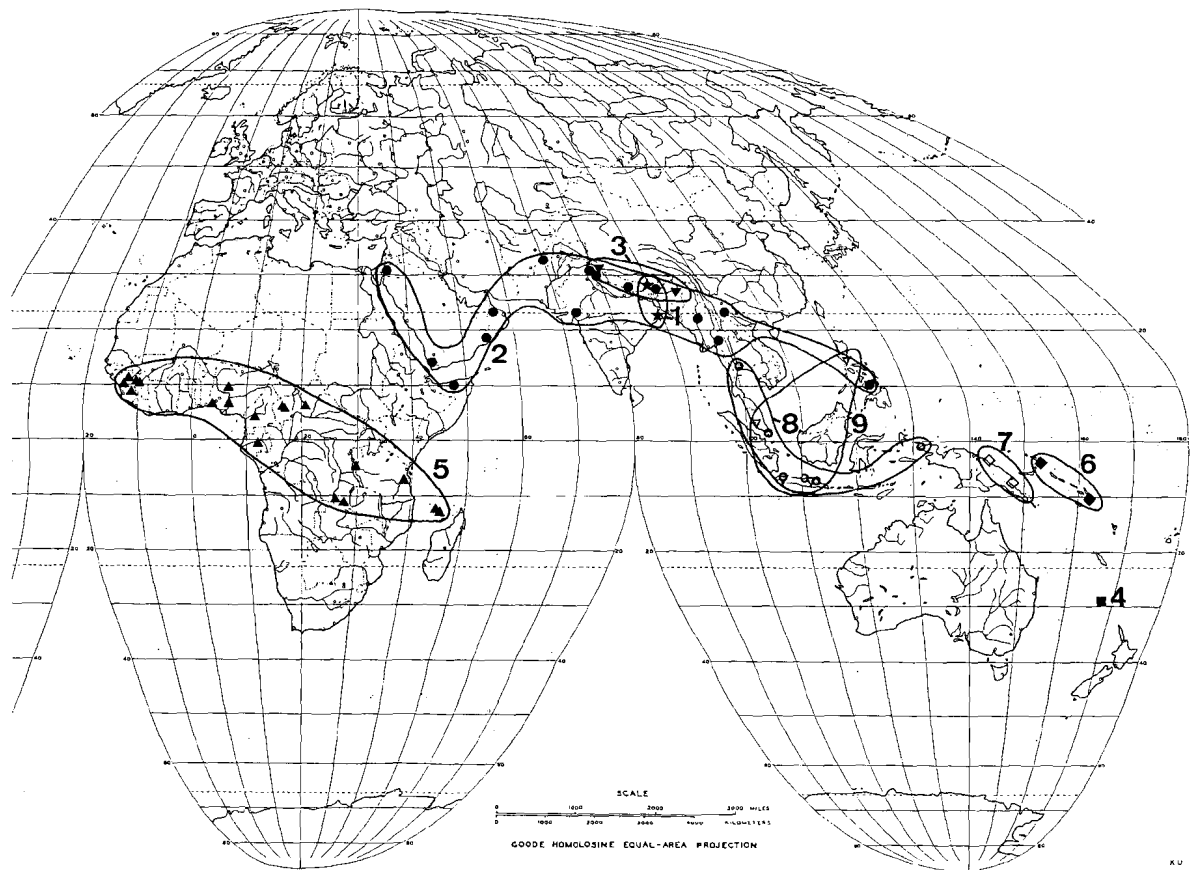


Fig. 16. Distribution ranges of Splachnobryaceae except *Splachnobryum obtusum*. 1: *Koponobryum bengalense*; 2: *Splachnobryum aquaticum*; 3: *S. assamicum*; 4: *S. crassinervium*; 5: *S. gracile*; 6: *S. limbatum*; 7: *S. novae-guineae*; 8: *S. oorschotii*; 9: *S. wiemansii*.

### Excluded species

- S. acutifolium* Thér., Rev. Bryol. n. ser. 3: 46. 12. 1930 = *Bryum acutifolium* (Thér) Arts (Arts 1996).  
*S. kieneri* Williams, Bryologist 38: 92. 1-8. 1936 = *Bryum turbinatum* (Hedw.) Turn. (Andrews 1949).  
*S. laevidorsum* (Besch.) Paris, Ind. Bryol. 1225. 1898 = *Syrrhopodon berterianus* (Brid.) Müll.Hal. (Williams 1920).  
*S. lixii* Broth., Oefv. Finsk. Vet. Soc. Foerh. 40: 175. 1898 = *Distichophyllum lixii* (Broth.) Thér.  
*S. pulvinatum* Müll.Hal., Linnaea 43: 336. 1882 nom. nud. = *Bryum* sp. (Fleischer 1904).  
*S. tenerum* Müll.Hal.ex Dusén, K. Svensk. Vet. Ak. Handl. 28(3): 39. a-c, f. 50. 1896 = *Gymnostomiella tenerum* (Müll.Hal.ex Dusén) Arts (Arts 1996).  
*S. valdiviae* Müll.Hal., Bull. Herb. Boiss. 5: 175. 1897 Type: Valdivia Chiles, leg. Dr. H. Hahn s.n. 1888 (isotype ex herb. Müll.Hal. in H-BR). This plant is a sterile *Bryum* sp. with obtuse leaf apex.  
*S. watsii* Broth., Oefv. Finsk. Vet. Soc. Foerh. 42: 99.

1900 = *Archidium watsii* (Broth.) I. G. Stone (Stone 1984).

Specimens of some species unrelated to *Splachnobryum*, such as *Bryum cyclophyllum*, *B. kieneri*, *B. turbinatum*, *Philonotis evanidinervis* and *Scopelophila ligulata* may have superficially similar gametophytes, and when sterile may be confused with *Splachnobryum* sp.

### Phytogeographical considerations

Most species of the *Splachnobryaceae* have a narrowly endemic distribution, e.g. *Koponobryum bengalense* from India, *Splachnobryum assamicum* from India and Burma, *Splachnobryum crassinervium* from Norfolk Island, *S. limbatum* from two Pacific Islands E of Papua New Guinea, *S. novae-guineae* from Papua New Guinea. A few species have a wider distribution, e.g.

*S. aquaticum*, *S. gracile*, *S. oorschotii* and *S. wiemanii*. Only one species, *S. obtusum*, has a subcosmopolitan distribution. The latter is most probably introduced to many localities of its actual range.

The distribution pattern of the *Splachnobryaceae*, except *S. obtusum* (Fig. 16), shows a basic range from Madagascar and western Africa over southern Arabia, India, Malesia to Norfolk Island, which points to the origin of the *Splachnobryaceae* in oceanic sectors of Gondwanaland, dating back from the late Palaeozoic to the early Mesozoic era, ca 100 million years BP, which is the period before the break-up of Gondwanaland. Except for the extensions into tropical Africa and the Arabian peninsula, this basic range is similar to the range of *Gottschelia* Grolle and other ancient bryophyte taxa such as the Treubiales (Schuster 1983).

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## References

- Andrews, A.L. 1949. Taxonomic Notes. IX. *Splachnobryum kieneri*. – *Bryologist* 52: 78–83.
- Arts, T. 1996. The genus *Splachnobryum* in Africa, with new combinations in *Bryum* and *Gymnostomiella*. – *J. Bryol.* 19: 65–77.
- Banu-Fattah, K. and Syed, H. 1997. A new species of *Splachnobryum* Müll.Hal. (Splachnaceae) from Bangladesh. – *Bangladesh J. Bot.* 26: 61–64.
- Bartram, E. B. 1939. Mosses of the Philippines. – *Philippine J. Sci.* 68: 1–425.
- Braithwaite, R. 1872. Recent additions to our moss flora. Part. V. – *J. Bot.* 10: 193–199. Table 123.
- Breen, R. S. and Pursell, R. A. 1959. The genus *Splachnobryum* in the United States, Mexico, Central America and the Caribbean. – *Rev. Bryol. Lichénol.* 28: 280–289.
- Brotherus, V. F. 1924. Musci. – In: Engler, A. and Prantl, K. (eds), *Die natürlichen Pflanzenfamilien*, Ed. 2. Band 10. Berlin.
- Chopra, R. N. and Rashid, A. 1969. The archegonia of *Splachnobryum*. – *Bryologist* 72: 525–527.
- and Sheel, 1974. Some new observations on the gametangia in *Splachnobryum*. – *Bryologist* 77: 623–628.
- , Lal, M. and Rashid, A. 1967. Unusual archegonial distribution in a moss: *Splachnobryum*. – *Naturwissenschaften* 54: 448.
- Corley, M. F. V., Crundwell, A. C., Düll, R., Hill, M. O. and Smith, A. J. E. 1981(1982). Mosses of Europe and the Azores; an annotated list of species, with synonyms from the recent literature. – *J. Bryol.* 11: 609–689.
- Crosby, M. R., Magill, R. E. and Bauer, C. R. 1992. Index of mosses 1963–1989. – *Monogr. Syst. Bot.* 42. Missouri Botanical Garden, St Louis. 646 p.
- Dabhade, G. T. 1974. Axillary archegonia in *Splachnobryum indicum* Hamp. et Müll.Hal. from Bombay. – *J. Bombay Nat. Hist. Soc.* 71: 342–343.
- Dixon, H. N. 1907. A new species of *Splachnobryum*, with notes on the peristome. – *J. Bot.* 45: 81–86. Tab. 484.
- 1934. *Bryophyta Nova* (18). – *Ann. Bryol.* VII: 157–158.
- Eddy, A. 1996. A handbook of Malesian mosses, Vol. 3. *Splachnobryaceae* to *Leptostomaceae*. – Natural History Museum, London.
- Fleischer, M. 1904. *Die Musci der Flora von Buitenzorg. Band 2.* – Leiden.
- 1922. *Die Musci der Flora von Buitenzorg. Band 4.* – Leiden.
- Gangulee, H. C. 1974. Mosses of eastern India and adjacent regions, Vol. II, fasc. 4–6. – Calcutta.
- Koponen, A. 1981. *Splachnobryaceae*, a new moss family. – *Ann. Bot. Fenn.* 18: 123–132.
- 1994. *Splachnobryaceae*. – In: Sharp, A. J., Crum, H. and Eckel, P. M. (eds). *The moss flora of Mexico*. *Mem. N.Y. Bot. Gard.* 69 (part one).
- Magill, R. E. and Stotler, R. E. 1990. English bryological glossary. – In: Magill, R. E. (ed.), *Glossarium Polyglotum Bryologiae*. Missouri Botanical Garden, St Louis.
- Miller, H. A., Whittier, H. O. and Bonner, C. E. B. 1963. *Bryoflora of the atolls of Micronesia.* – *Beih. Nova Hedwigia* 11.
- Mitten, G. 1869. *Musci Austro-Americani.* – *Linn. Soc. Bot.* 12.
- Müller, K. (C.) 1869. *Splachnobryum*, eine neue Gattung der *Splachnaceen.* – *Verh. Zool.-Bot. Ges. Wien* 19: 501–506.
- 1872. *Musci Indici novi, adjectis nonnullis aliis exoticis.* – *Linnaea* 37: 163–182.
- 1882. *Prodromus Bryologiae Argentinicae II, seu Musci Lorentziani Argentinici.* – *Linnaea* 43: 355–356.
- Norris, D.H. and Zander, R.H. 1981. *Splachnobryum limbatum* sp. nov. from San Christobal, Solomon Islands. – *Bryologist* 84: 404–407.
- Philibert, V. 1890. *Etudes sur le péristome. Huitième article. Différences entre les Némotodontées et les Arthrodonnées; transitions entre ces deux groupes.* – *Rev. Bryol.* 17: 8–12.
- Robinson, H. 1964. *Bryophytes from Upper Assam.* – *J. Hattori Bot. Lab.* 27: 127–128.
- Schuster, R. M. 1983. *Phytogeography of the Bryophyta.* – In: Schuster R. M. (ed.), *New manual of bryology*. Vol. I, chapter 10. Hattori Botanical Laboratory, Nichinan.
- Smith, A. J. E. 1978. *The moss flora of Britain and Ireland.* – Cambridge Univ. Press.
- Stone, I. G. 1984. *Archidium watsii* comb. nov. in Australia. – *J. Bryol.* 13: 153–157.
- Tewari, S. D. and Pant, G. 1989. *Splachnobryum procerrimum* Dixon & P. de la Varde, a little known species from Western Himalaya (India). – *J. Bryol.* 15: 555–557.
- Thériot, M. I. 1911. *Diagnoses d'espèces et de variétés nouvelles de mousses, 9e article.* – *Bull. Géogr. Bot.* 4e Série, 255: 265–272.

- Van der Wijk, R., Margadant, W.D. and Florschütz, P.A. 1959–1969. Index Muscorum. Vol. I–V. – Utrecht.  
 Whittier, H. O. 1976. Mosses of the Society Islands. – Gainesville.  
 Williams R.S. 1920. Calymperaceae of North America. – Bull. Torrey Bot. Club 47: 367–396.  
 Zander, R. H. 1993. Genera of the Pottiaceae: mosses of harsh environments. – Bull. Buffalo Soc. Nat. Sci. 32: 1–378.

**Addendum I: Splachnobryum species index**

- S. acutifolium* Thér. = *Bryum acutifolium* (Thér.) Arts  
***S. aquaticum* Müll.Hal.**  
*S. arabicum* Dixon = *S. aquaticum* Müll.Hal. **syn. nov.**  
***S. assamicum* Dixon**  
*S. atrovirens* Besch. = *S. obtusum* (Brid.) Müll.Hal.  
*S. baileyi* Broth. = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. bengalense* Gangulec = ***Koponobryum bengalense* (Gangulee) Arts. comb. nov.**  
*S. bernoullii* Müll.Hal. = *S. obtusum* (Brid.) Müll.Hal.  
*S. byssoides* Müll.Hal. = *Gymnostomiella vernicosa* (Hook.) M.Fleisch.  
*S. boivinii* Müll.Hal. = *S. obtusum* (Brid.) Müll.Hal.  
*S. brotheri* Paris = *S. gracile* Besch.  
*S. corbieri* Renaud & Cardot = *S. obtusum* (Brid.) Müll.Hal.  
***S. crassinervium* Arts sp. nov.**  
*S. crenulatulum* Cardot = *S. obtusum* (Brid.) Müll.Hal.  
*S. crenulatum* Cardot = *S. obtusum* (Brid.) Müll.Hal.  
*S. delicatulum* Broth. = *S. obtusum* (Brid.) Müll.Hal.  
*S. elatum* Cardot = *S. obtusum* (Brid.) Müll.Hal.  
*S. erosulum* Müll.Hal. ex Dusén = *Gymnostomiella erosulum* (Müll.Hal. ex Dusén) Arts  
*S. flaccidum* (Hook.) Müll.Hal. = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. geheebii* M.Fleisch. = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. giganteum* Broth. = *S. aquaticum* Müll.Hal. **syn. nov.**  
***S. gracile* Besch.**  
*S. indicum* Hamp. & Müll.Hal. = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. inundatum* Müll.Hal. = *S. obtusum* (Brid.) Müll.Hal.  
*S. julaceum* Besch. = *S. obtusum* (Brid.) Müll.Hal.  
*S. kieneri* R.S. Williams = *Bryum turbinatum* (Hedw.) Turn.  
*S. laevidorsum* (Besch.) Paris = *Syrrhopodon berterioanus* (Brid.) Müll.Hal.  
*S. latifolium* Bartr. = *S. wiemansii* M.Fleisch. **syn. nov.**  
*S. leoni* Thér. = *S. obtusum* (Brid.) Müll.Hal.  
*S. ligulifolium* Cardot = *S. obtusum* (Brid.) Müll.Hal.  
***S. limbatum* D.H.Norris & R.H.Zander**  
*S. lixii* Broth. = *Distichophyllum lixii* (Broth.) Thér.  
*S. lorentzii* Müll.Hal. = cf. *S. obtusum* (Brid.)

- Müll.Hal.  
*S. luzonense* Broth. = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. mariei* Besch. = *S. obtusum* (Brid.) Müll.Hal.  
***S. novae-guineae* Broth.**  
***S. obtusum* (Brid.) Müll.Hal.**  
***S. oorschotii* Sande Lac.) Müll.Hal.**  
*S. ovalifolium* M.Fleisch. = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. pacificum* Dixon = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. procerrimum* Dixon & P.de la Varde = *S. aquaticum* Müll.Hal. **syn. nov.**  
*S. pulcherrimum* Dixon & P.de la Varde nom. nud.  
*S. pulvinatum* Müll.Hal. nom. nud. = *Bryum* sp.  
*S. rostratum* Broth. & Paris = *S. gracile* Besch.  
*S. schofieldii* Banu-Fattah & Syed = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. siamense* Cardot & Thér. = *S. oorschotii* (Sande Lac.) Müll.Hal. **syn. nov.**  
*S. splachnifolium* (Hook.) Thér. = *S. obtusum* (Brid.) Müll.Hal.  
*S. spruceanum* Müll.Hal. = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. sprucei* Müll.Hal. ex Kindb. nom. illeg. = *S. spruceanum* Müll.Hal.  
*S. stuartii* H.O. Whittier = *S. obtusum* (Brid.) Müll.Hal. **syn. nov.**  
*S. subjulaceum* Cardot = *S. gracile* Besch.  
*S. subjulaceum* var. *laxifolium* P.de la Varde = *S. gracile* Besch.  
*S. subjulaceum* var. *subspatulifolium* P.de la Varde = *S. gracile* Besch.  
*S. suborbifolium* Paris & Broth. = *S. obtusum* (Brid.) Müll.Hal.  
*S. synoicum* H. Robinson = *S. assamicum* Dixon **syn. nov.**  
*S. tenerum* Müll.Hal. ex Dusén = *Gymnostomiella tenerum* (Müll.Hal. ex Dusén) Arts  
*S. valdiviae* Müll.Hal. = *Bryum* sp.  
*S. vernicosum* Broth. in Bruehl nom. nud. = *S. aquaticum* Müll.Hal.  
*S. watsii* Broth. = *Archidium watsii* (Broth.) I.G.Stone  
***S. wiemansii* M.Fleisch.**  
*S. wrightii* Müll.Hal. = *S. obtusum* (Brid.) Müll.Hal.  
*S. wulfschlaegelii* Müll.Hal. = *S. obtusum* (Brid.) Müll.Hal.