
Original article

Taxonomic revision of the genus *Trismegistia* (Pylaisiadelphaceae, Musci)

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Abstract

The genus *Trismegistia* is a member of the Pylaisiadelphaceae (or Sematophyllaceae *sensu lato*) and can be distinguished from allied genera (*Brotherella*, *Mastopoma*, *Pseudotrismegistia* and *Wijkia*) by upright or obliquely ascending secondary stems with more or less developed stipes arising from prostrate primary stems; an often sharp differentiation in shape among stipe-, stem-, and branch leaves; distinctly bordered and mostly strongly serrate, dentate, or spinose leaf margins; strongly inflated, reddish brown alar cells of which the outer ones are segmented in several rows; setae up to 6 cm long, smooth; capsules mostly ovoid or short cylindrical, straight to weakly curved with superficial stomata; hypnoid peristome; and small spores. The genus is distributed in tropical Southeast Asia and some Western Pacific island groups. Nine species are recognized; *T. brachyphylla* M. Fleisch., *T. calderensis* (Sull.) Broth., *T. complanatula* (Müll. Hal.) Müll. Hal., *T. lancifolia* (Harv.) Broth., *T. malayana* H. Akiyama, **sp. nov.**, *T. maliauensis* H. Akiyama & Suleiman, *T. panduriformis* (C.H. Wright) Broth., *T. plicata* H. Akiyama, **sp. nov.**, and *T. spinosodontata* (Zanten) H. Akiyama, **stat. nov.** Species with wide distribution ranges were divided into morphologically and geographically distinct infraspecific entities: two types of *T. brachyphylla* (Western- and Eastern-type), five varieties of *T. lancifolia* (var. *lancifolia*, var. *austlariana* **var. nov.**, var. *everettii* **var. nov.**, var. *pseudoplicata* **var. nov.**, and var. *valetonii* **comb. nov.**), three varieties of *T. calderensis* (var. *calderensis*, var. *rigida* **comb. nov.**, and var. *subintegriifolia* **comb. nov.**), and two varieties of *T. panduriformis* (var. *panduriformis* and var. *prionodontella* **comb. nov.**). The interrelationship among *Mastopoma*, *Pseudotrismegistia*, *Trismegistia*, and *Wijkia* is briefly discussed.

Key Words: *Brotherella*, *Mastopoma*, Malesia, moss taxonomy, *Pseudotrismegistia*, Pylaisiadelphaceae, Sematophyllaceae, *Wijkia*.

Introduction

The genus *Trismegistia* is one of the dominant moss groups growing on the floors of lowland and montane forests in tropical Southeast Asia and the Western Pacific islands and a huge number of specimens have been accumulated in herbaria all over the world. The identification of specimens is extremely difficult since each species shows a wide range of variation in morphological features, such as in branching patterns, differentiation into creeping stems and ascending

branch systems, presence/absence of stipes and fronds, and size and shape of leaves. In addition, none of the species in the genus have been critically revised, including common species such as *T. lancifolia*, *T. rigida*, *T. korthalsii*, and *T. panduriformis*. As a consequence, numerous specimens in herbaria remain either misdetermined or unidentified.

The history of classification of the genus began when Müller (1874, p. 90) established a new section *Trismegistia* of the genus *Hypnum*. He defined the

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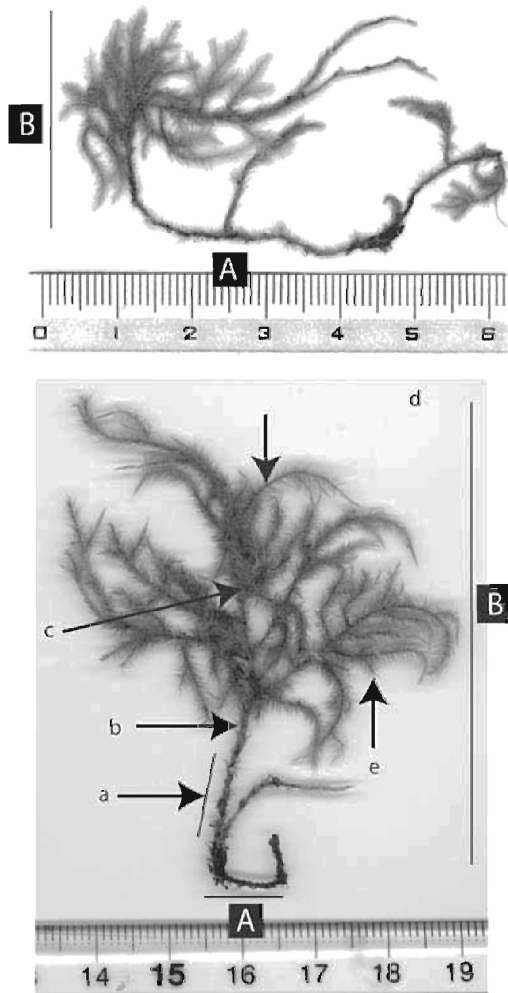


Figure 1. Features used in the descriptions 1. A; primary stem. B; secondary stem. a; stipe. b; lower stem. c; upper stem. d; branch. e; branchlet. Note that branching patterns, differentiation into creeping primary stems and ascending secondary stems, and presence/absence of stipes and fronds are not stable even in a single species.

section as follows: ‘Caulis repens decumbens vel assurgens longe prostratus, ramis primariis fasciculatis subdendroideis, foliis involuto-concavis grosse serratis, binervatis, cellulis alaribus magnis vesiculosus aureis instructis, ramulos cuspidatos pungentes sistentibus’ and included five species in it: *Hypnum (Trismegistia) complanatum* Müll. Hal. [≡ *T. complanata* (Müll. Hal.) Broth. in this paper], *Hypnum rigidum* Mitt. [≡ *Acanthodium rigidum* Mitt. ≡ *Trismegistia rigida* (Mitt.) Broth.], *H. lancifolium* (Harv.) Müll. Hal. [≡ *T. lancifolia* (Harv.) Broth.], *H. calderense* Sull. [≡ *T. calderensis* (Sull.) Broth.], and *H. platyacron* Müll. Hal. (*nom. nud.*). Since then, more than fifty taxa have been added to the genus, mostly from tropical Asia and the Western Pacific islands (Wijk et al. 1969). All species reported from Africa, America, and temperate East Asia are now

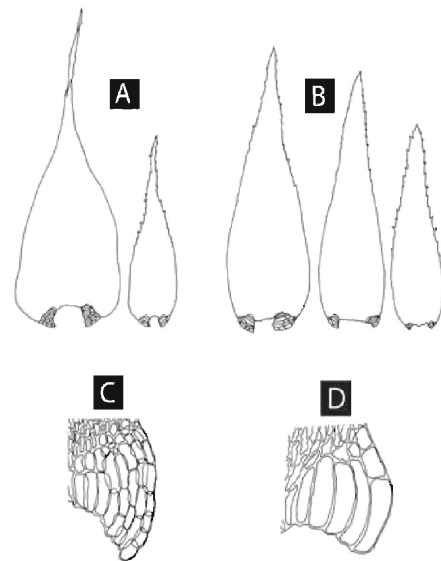


Figure 2. Features used in the descriptions 2. Rounded leaf insertion (A) and scarcely rounded or almost straight leaf insertion (B). Highly multitiered alar regions in a stem leaf of *Trismegistia calderensis* var. *rigida* (C) and partially multitiered alar region in a stem leaf of *T. lancifolia* var. *lancifolia* (D).

classified in different genera (Akiyama & Tsubota 2001, Akiyama 2006a).

Trismegistia has long been classified in the Sematophyllaceae. Among the members of the Sematophyllaceae *sensu lato*, *Brotherella*, *Mastopoma*, *Trismegistia*, *Pseudotrismegistia*, and *Wijkia* share long setae and distinct teeth at the leaf margins (Brotherus 1925, Fleischer 1915–1923, and many others). Fleischer (1913, 1915–1923) placed these genera in the subfamily Heterophyllieae M. Fleisch. along with *Gammiella* Broth. and *Aptychopsis* (Broth.) M. Fleisch., and Brotherus (1925) followed his treatment. Tan & Buck (1989) transferred *Brotherella*, *Mastopoma* and *Trismegistia* to the Sematophylloideae (“Group 2”). Hedenäs & Buck (1999) proposed a new classification of the Sematophyllaceae on the basis of cladistic analyses of morphological features and established Wijkioideae to accommodate only three genera, *Acanthorrhynchium*, *Trismegistia*, and *Wijkia*, leaving *Mastopoma* in the Sematophylloideae and transferring *Brotherella* to the Hypnaceae. In recent work based on *rbcL* sequence data (Tsubota et al. 2000, 2001a, 2002), *Trismegistia* was shown to be remotely related to both *Wijkia* and *Mastopoma*. Akiyama & Tsubota (2001) established a new genus *Pseudotrismegistia* to accommodate *Trismegistia undulata* Broth. & Yasuda and *T. perundulata* Dixon, which were shown to be closely related not to *Trismegistia* but to *Mastopoma*

subfiliferum Horik. & Ando or *Heterophyllum affine* (Hook.) M. Fleisch. Recently, Goffinet *et al.* (2009) proposed a new classification of the mosses and placed *Trismegistia* in the family Pylaisiadelphaceae along with *Brotherella*, *Mastopoma*, *Heterophyllum*, *Pseudotrismegistia*, *Wijkia* (all these genera having long setae), and several other genera. Among the former five genera, however, *Mastopoma* possesses the feature of a single row of alar cells, and thus the

genus should be included not in the Pylaisiadelphaceae but in the Sematophyllaceae *sensu stricto* and provisional analyses based on *rbcL* gene sequences support this alliance (Tsubota *et al* 2000, 2001b, Akiyama & Tsubota 2001). Morphological differences between these genera are summarized in the following key [partially revised from Akiyama (2006a)]:

Keys to the *Trismegistia* and allied genera

1. Alar cells of stipe-, stem-, and branch leaves always arranged in a single row except outermost column (usually with subquadrate to quadrate cells above alar cells in *Wijkia* and *Brotherella*). 2
1. Alar cells of stipe- and stem leaves more or less segmented at least the innermost several columns, and thus arranged in multitiars (those of branch and branchlet are often arranged in a single row). 4
2. Plants larger, usually growing on soils, rotten logs, and the base of tree trunks (rarely on shrub trunks) on forest floors. Leaves weakly curled (especially leaf tip curled downwards), often abruptly narrowed at shoulders; margins more or less serrate but never geminate; alar cells arranged in a single row but outermost column usually segmented. 3
2. Plants smaller, growing on branches of shrubs and small trees especially at river and stream sides. Leaves straight to strongly curled, gradually narrowed into acuminate tips; margins often with geminate serration; alar cells arranged in a single row (except for *M. subfiliferum*, with scalariform alars). *Mastopoma**
3. Plants bi- or tripinnately (rarely pinnately) branched, sometimes with flagelliform branches (secondary stems creeping on substrata, except *Wijkia tanytricha*). Stem- and branch leaves differing in size and shape; stem (and usually branch) leaves narrowed into subulate or narrow-ligulate apices above shoulder; outermost alar cells often thin-walled. Annuli present. *Wijkia*
3. Plants almost always pinnately branched, without flagelliform branches. Stem- and branch leaves \pm equal in size and shape, gradually narrowed to apices; outermost alar cells thick-walled. Annuli absent. *Brotherella*
4. Secondary stems usually ascending or upright; stipes more or less developed. Stipe-, stem-, and branch leaves differing in size and shape; leaf margins more or less serrate; borders at margins well differentiated with somewhat elongate laminal cells; costa absent or faintly developed; alar regions composed with cells different in size and shape. *Trismegistia*
4. Secondary stems creeping on substrata or procumbent; stipes not developed. Stem- and branch leaves almost similar in size and shape; leaf margins entire, crenulate or serrate, not bordered; costa short, double; alar regions composed with cells almost equal in size. 5
5. Leaves of secondary stems and branches spreading all around stem, narrowed into ligulate upper portion from an oblong base, distinctly undulate; upper margin serrate, often spinose. *Pseudotrismegistia*
5. Leaves of secondary stems and branches more or less complanately arranged, gradually narrowed to the apices, never undulate; margins serrulate or serrate above, entire or minutely serrulate below. *Heterophyllum*

*In spite of some recent studies (e.g., Akiyama 2006a, b, Akiyama & Tsubota 2001, Tan & Chang 2004), *Mastopoma* still remains as paraphyletic; for example, *Mastopoma subfiliferum* has alar regions with numerous cells arranged in scalariform manner and thus should be classified under *Heterophyllum* (Akiyama & Tsubota 2001).

In the course of the taxonomical revision of *Trismegistia*, specimens kept in the following herbaria (BM, BO, BORH, E, FH, H, HIRO, HYO, JE, KLU, KYO, L, MEL, MO, NICH, NSW, NY, PC, SING, SINU, TCD, and TNS) were examined as well as

the types of taxa so far described. In addition, field observations were conducted at the localities where typical variants of each species were recognized. As for the taxa removed from *Trismegistia* to other genera, see Akiyama (2006a).

Taxonomic Treatments

Trismegistia (Müll. Hal.) Broth. in Engler & Prantl.

Die Natürlichen Pflanzenfamilien I (3): 1077 (1908).

Basionym: *Hypnum* sect. *Trismegistia* Müll. Hal., Journal des Museums Godeffroy 3 (6): 89 (1874) ≡ *Sematophyllum* subgen. *Trismegistia* (Müll. Hal.) Renauld, Prodrome de la Flore Bryologique de Madagascar des Mascareignes et des Comores: 234 (1898).

Type species: *Trismegistia lancifolia* (Harv.) Broth., **newly designated here**, non *T. subauriculata* Müll. Hal. (1896), *vide* Wijk et al. (1969). See note 2 below.

Plants medium to robust in size, rarely smaller when growing on shrub branches, dull- to fresh-green to yellowish-green, easily turning yellow in herbarium specimens, glossy or dull, forming extensive wefts or turfs on various substrata on forest floor, rarely ascending on shrub trunks. Paraphyllia absent. Pseudoparaphyllia narrowly lanceolate, surrounding dormant buds. Rhizoids confined to lower surfaces of prostrate primary stems, in fascicules, pale brown to reddish brown, smooth. Asexual reproductive organs absent.

Primary stems prostrate on substrata, elongating monopodially, reddish brown in color, with scaly leaves smaller than those of secondary stems; irregularly or pinnately branched; central strand absent. Secondary stems, if present, obliquely ascending or upright, often differentiated into stipes, stems and branches or scarcely differentiated (*T. malayana* and *T. plicata*), reddish brown in color; sometimes stem tips merging into secondary flagelliform shoots which become prostrate on substrata; in transverse section cortical cells evenly thick-walled, epidermal cells scarcely differentiated, central strand absent. Leaves on stipes, stems, and branches more or less differentiated in shape, size, and alar formation. Stipes densely covered by leaves. Stipe leaves oval, ovate or widely ovate at base, narrowed at shoulder into long, more or less cuspidate apices; laminal cells varying from oval, short rhomboid to linear, usually pitted, becoming much longer towards the base, smooth, plane; margins plane, entire below, serrate, often spinose above, usually bordered with longer laminal cells above, well contrasting to inner shorter cells; costa absent or rarely short and forked at base (*T. spinosodentata*). Stems irregularly or regularly, pinnately or bipinnately branched, often forming more or less flat fronds in one plane, sometimes becoming palmate (*T. calderensis* var. *rigida*, var. *subintegrifolia*, and *T. lancifolia* var. *korthalsii*), densely covered with leaves. Lower stem leaves similar to stipe leaves in

shape and size. Upper stem leaves more gradually narrowed at shoulder; alars and laminal cells similar to stipe leaves. Branch leaves often much smaller than stipe and stem leaves, often involute or concave at base; laminal cells similar to stipe leaves; alar cells mostly arranged in a single row except for outermost columns. If branchlet present, leaves similar in shape but smaller in size than branch leaves. Axillary hairs smooth, with two to five upper, colorless, elongate cells and two, lightly colored quadrate basal cells.

Dioicous? Male plants not seen and no male organ apparently present on mature female plants [according to Fleischer (1915–23), either normal or dwarf; perigonia on secondary shoots, bud-like in shape; perigonial leaves concave, shortly ovate, ecostate]. Perichaetia on primary stems and at the base of stipes of secondary stems; paraphyses abundant. Perichaetial leaves linear lanceolate, paler in color, becoming longer after fertilization; more or less plicate, ecostate; entire to denticulate below, sharply serrate or spinose above, borders indistinct or well differentiated; alars not differentiated as in vegetative leaves, but having larger, thinner, and lightly colored cells at both angles forming indistinct regions. Calyptrae cucullate, smooth, naked, reaching 5.5mm long. Vaginula short cylindrical.

Setae long, ca. 40mm in length or longer, smooth, pale brown to reddish brown. Capsules ovoid to short-cylindrical, smooth, reddish brown, inclined or horizontal; exothecial cells smooth, collenchymatous, quadrate to rectangular above, becoming longer towards the base, much smaller suborally; annulus absent; stomata absent or present, if present, small, confined on neck, superficial; columella present, thick. Opercula conical or rostrate with short to long beaks, reaching 1.5mm long. Peristome double, *Hypnum*-type in structure. Exostome teeth 16, linear-lanceolate, pale yellow to yellowish brown, densely striated, finely papillose above, with shallow dorsal median furrows. Endostome whitish, segments lanceolate, keeled, coarsely papillose; cilia linear to

linear-lanceolate, appendiculate, 0–3 in number; with high basal membrane. Spores isosporic, spherical, thin-walled, finely papillose, less than 20 µm (mostly 12–15 µm) in diameter.

Distinguishing features. (1) Larger plant size, (2) differentiation of leaves in size and shape according to their position on a single shoot (Fig.1), (3) leaf margins often bordered with more or less differentiated laminal cells, (4) distinct serration at upper leaf margins, (5) smooth laminal cells, (6) well differentiated alar regions with more or less inflated, colored cells arranged more or less in scalariform manner, at least the outer one or two columns, (7) smooth setae, longer than 40 µm in length, (8) linear to linear-lanceolate peristome teeth densely striated with shallow dorsal furrows, (9) high basal membranes and appendiculate cilia of endostome, and (10) isosporic, small spores. (Sporophytes are generally not very different in size and shape among species except for *T. malayana* which has shorter, ovoid capsules.)

Habitat. Often forming large, always pure wefts or turfs on soil, boulders, base of tree trunks, fallen logs, stumps, sometimes ascending shrub trunks (especially *T. brachyphylla*) and pendent (especially *T. calderensis* var. *calderensis*), rarely on bare boulders in rheophytic zones along streams in lower to upper montane forests, rarely found in coastal lowland forests. It is noteworthy that all the members of *Trismegistia* are strictly confined to more or less shaded forest floors or are found at the edge of natural forests and never in open habitats. Especially in Southeast Asia, *Trismegistia* is one of the dominant mosses of forest floors.

Distribution. Thailand, Vietnam, Cambodia, Philippines, Malaysia, Indonesia, Papua New Guinea, Australia (Queensland), Solomon Islands, Vanuatu, New Caledonia, Fiji, Samoa. All previous reports outside these countries are based on misidentification (Akiyama 2006a, Akiyama & Tsubota 2001).

Note 1. (Authority for *Trismegistia*). The authority for the genus is given as *Trismegistia* (Müll. Hal.) Müll. Hal. in Engler & Prantl (Wijk et al. 1969 and others), but the treatment of the Bryales in 'Die natürlichen Pflanzenfamilien I (3)' was written by Brotherus (Koponen 2005, Stafleu 1972), not by Müller.

Note 2. (Typification of *Trismegistia*). Wijk et al.

(1969) listed *T. subauriculata* Müll. Hal. (1896) as a type species of *Trismegistia*. However, the type species should have been selected from one of the five species Müller (1874) listed when he established *Hypnum* sect. *Trismegistia*. They are: *Hypnum rigidum* Hornsch. & Reinw. (*hom. illeg.*, treated here as a synonym of *Trismegistia calderensis*), *H. lancifolium* (Harv.) Müll. Hal. [= *Neckera lancifolia* Harv.], *H. calderensis* Sull., *H. platyacron* Müll. Hal. (*nom. nud.*), and *H. complanatum* Müll. Hal. *Trismegistia lancifolia* is designated here as type species of *Trismegistia*.

Note 3. (Sexuality). Fleischer (1915–1923) reported and illustrated dwarf males found in *Trismegistia brauniana*. However, because Akiyama (2006a) transferred the species to a different genus *Mastopoma*, no dwarf male is known for *Trismegistia*. I have not seen normal or dwarf male plants among herbarium specimens so far examined or in field observations of fruiting populations, and thus the real status of the sexuality of *Trismegistia* remains ambiguous. The reason of this apparent rareness of male plants is a subject for future studies.

Note 4. (Variation and flexibility in gametophyte morphology). One of the characteristic features of *Trismegistia* is the extensive variation found in morphological characteristics such as plant size and color, branching pattern, and leaf shape and size even in the same population. It is most obvious when plants grow on trunks and branches of shrubs: they are pendent and show much elongate prostrate primary stems and sparse branching patterns. Such morphological variability is most pronounced in *T. lancifolia* and *T. calderensis* (= *T. rigida*), and a number of infraspecific taxa (varieties and forms) have been reported (e.g., see Fleischer 1915–1923). None of these variants is treated as an infraspecific category in this revision except for *T. lancifolia* var. *valetonii*, which has characteristic small plants and a unique distribution.

Note 5. (Plication in leaves). *Trismegistia plicata*, *T. panduriformis*, and *T. spinosodontata* have deeply plicate leaves. In *Trismegistia lancifolia* var. *pseudoplicata*, only stipe and stem leaves show shallow plication and branch leaves are somewhat concave or inrolled but not at all plicate. Plication found in leaves can be a good characteristic to distinguish these species from the rest.

Keys to the species of *Trismegistia*

1. Leaves deeply plicate or rugose. 2
1. Leaves plane, neither plicate nor rugose. 5
2. Stem- and branch leaves usually patent, rarely appressed. Upper median laminal cells short rhomboid to linear, never quadrate. 3
2. Stem- and branch leaves widely spreading even in dry conditions. Upper median laminal cells small and quadrate or short rectangular, clearly distinct from elongate marginal cells. (Widely distributed in southeast Asia). (7) *T. panduriformis*
3. All leaves plicate or rugose. Stipe leaves more than 3.5 mm in length. 4
3. Only stem- and stipe leaves plicate, others plane. Stipe leaves less than 3 mm in length. (Distributed in Southern part of Malay Peninsula and North Sumatra). (4-4) *T. lancifolia* var. *pseudoplicata*
4. Leaves gradually narrowed; apex acute or weakly acuminate; acumen narrowly triangular; costa of stem leaves absent or indistinct; margin distinctly bordered by 2-3 rows of linear cells. [Bornean (Sarawak and West Kalimantan) lowland species]. (8) *T. plicata*
4. Leaves acuminate, acumen narrowly lingulate; costa of stem leaves often distinct; margin weakly bordered. (New Guinean mountainous species). (9) *T. spinosodentata*
5. Apex of stipe- and lower stem leaves straight (sometimes twisted in *T. complanatula*), shape various. Alar region multitiered at outer several columns (Figure 2D), inner ones arranged in a single row. Branch leaves serrate to spinose at upper margin; basal insertion lines straight or shallowly curved in upwards (Figure 2B). 6
5. Apex of stipe- and lower stem leaves twisted, long acuminate. Alar regions multitiered except for inner several columns (Figure 2C). Branch leaves mostly low serrate at upper margin; basal insertion lines rounded (Figure 2A). (2) *T. calderensis*
6. Stem- and branch leaves widely ovate, apex acute. 7
6. Stem- and branch leaves variable in shape, apex acuminate. 8
7. Plants green, ascending stems forming fronds, more or less complanately foliate. Growing on various substrata, often on shrub branches, in rather dry habitats in montane forests. (Widely distributed from Malay Peninsular to Western Pacific). (1) *T. brachyphylla*
7. Plants blackish green, never forming fronds on ascending stems. Confined to rheophytic zones at streambeds in primeval lower montane forests. [Endemic to North Borneo (Sabah)]. (6) *T. maliauensis*
8. Plants usually with ascending secondary stems with more or less developed stipes. Stem- and branch leaves variable in shape, never ligulate above. Capsules ovoid to short ovoid. (Widely distributed in Malesia and Western Pacific). 9
8. Plants prostrate on substrata, forming flat mats. Stem- and branch leaves narrowly ligulate above. Capsules globose to subglobose. (Restricted to southern part of the Malay Peninsula). (5) *T. malayana*
9. Stipe- and stem leaves 2.5-3.7 mm long. Branch leaves gradually narrowed into long, slender apices; laminal cells just below apex fusiform to linear. (Distributed from eastern part of New Guinea to Samoa). (3) *T. complanatula*
9. Stipe- and stem leaves usually less than 2.5 mm long, rarely reaching 3.2 mm long (often reaching 3.7 mm long in var. *australiana*). Branch leaves acute to widely acute; laminal cells just below apex quadrate, rectangular, or fusiform (linear in var. *australiana*). (Widely distributed in Malesia region and the Western Pacific). (4) *T. lancifolia* (excluding var. *pseudoplicata*)

1. *Trismegistia brachyphylla* M. Fleisch. [Plates 1–3]

Die Musci der Flora von Buitenzorg 4:1218 (1923). Type: Sumatra, Bataklanden, im Urwald, Barisangebirge, c. 900 m, Sept. 1912, *Fleischer s.n.* (holotype FH!).

Trismegistia ovifolia Herzog in sched. (HBG!).

Plants more or less glossy even in old herbarium specimens, rarely dull colored; irregularly pinnately branched. Primary stems prostrate, sparsely branched. Secondary stems, 3–6 (–8) cm long, obliquely

ascending, densely or sparsely branched, forming more or less flat fronds. Stipes often developed. Stipe- and stem leaves ovate to shortly lanceolate, 2.5–3.7 mm long, acute or long acuminate, leaf base insertion nearly straight, ecostate; laminal cells just below apex elliptic to fusiform, 18–35 µm in length, smooth; upper laminal cells short rhomboid to linear, 25–50 µm in length, sinuate or pitted, smooth; margins plane, entire below, serrate above, bordered with longer cells above; alar regions multitiered at least outer several columns, sometimes becoming auriculate; cells inflated, colored. Branch leaves similar in shape to stem leaves, but smaller in size.

Dioicous? Perigonia not observed. Perichaetia on prostrate stems or at the base of stipes of ascending secondary stems; paraphyses abundant. Perichaetial leaves pale yellowish green, 3–4 mm long after fertilization, narrowly triangular, gradually narrowed into long acumen, plicate, ecostate; margins entire to denticulate below, serrate to spinose above; laminal cells linear, distinctly pitted, becoming long rectangular and thin-walled below; alars not differentiated. Seta 40–60 mm long, reddish brown, smooth. Capsules 2–3 mm long, ovoid, inclined to curved when mature, often narrowed just below the mouth; exothecial cells quadrate to rectangular, collenchymatous, becoming smaller suborally; stomata superficial, small, restricted to neck. Opercula short, not observed [conic according to Fleischer (1915–1923)]. Peristome double. Exostome teeth 16, 400–600 µm in length, linear lanceolate, pale yellow, with shallow median dorsal furrows, densely striated below, finely papillose above. Endostome segments as long as exostome teeth, deeply keeled, finely papillose with high basal membrane; cilia 2–3, linear, appendiculate. Spores spherical, finely papillose, 12–17 µm in diameter.

Distinguishing features: (1) More or less complanate foliation of the fronds of secondary stems, (2) stipe-, stem-, and branch leaves weakly differentiated in size and shape, ovoid, widest above the middle, not abruptly narrowed at shoulder, (3) well multitiered alar regions, and (4) weak serration at leaf margins (often serrate in Eastern-type).

Two types (Western-type and Eastern-type) are recognized in this widely distributed species by their distribution and faint morphological differences as detailed in note 1 below.

Habitat. On dead wood, stumps, tree trunk bases in montane forests, often growing on shrub branches in drier habitats for the genus, such as montane slopes;

occurring from (350–) 900–1400 (–1600) m alt.

Distribution. Malaysia, Indonesia, Papua New Guinea, Solomon Islands, Vanuatu. It is notable that this species is apparently absent from the Wallacea region (see note 1 below). Judging from specimens so far examined, *Trismegistia brachyphylla* (Western-type) is most abundant in Sumatra, around Lake Toba.

Other specimens examined. WESTERN-TYPE: MALAYSIA. Pahang: Bukit Fraser resort area, Jeriau waterfalls vicinity, *Tan 89-1336* (NY!); *ibid.*, around water fall, *Inoue 10372* (TNS!). **Perak:** Maxwell's Hill, *Ridley 815* (BM!, SING!). **Selangor:** Bukit Hitan, *Ridley 387* (NY!, SING!). **Penang:** 1896, *Curtis s.n.* (BM!, NY!). **Sabah:** Tawau, NNW of Kalabakan, Maliau Basin, *Akin & Awang MB56* (HYO!, BORH!); *ibid.*, *Akin & Awang MB 83* (HYO!, BORH!); Papar, Crocker Range Park, *Akiyama Crocker-101, 102, 105, 110 & 223* (all HYO!). **Sarawak:** Dulit Range, *Richards 1810-bis* (MO!). **INDONESIA. Sumatra:** Atjeh, Gunung Leuser Nature Reserve, Gunung Mamas, SW from the mouth of Lau Ketambe, ca. 30 km NW of Kutatjane, *de Wilde & de Wilde-Duyffes 14800B* (L!), *14813C* (L!) & *16950B* (L!); Sumatra Utara, N of Lake Toba, along Brastagi road, *Otto-Surbeck 166A* (L!); Brastagi (between Lake Toba and Medan), path to Petani waterfall, *van der Wijk 1720* (L!); *ibid.*, *Verdoorn 72a* (BM!); surrounding of Petani waterfall, east of Lake Toba, *Staal 207* (L!); West Sumatra, Mt. Tandikat, *Meijer 6403 & B8069* (both L!); Sibolangit, Bukit Kluang, *Mohd Nur 7424* (BM!, L!, SING!); Ostküste, Sibajak, *Arnes 532 & 595* (both L!); *ibid.*, 1949, *Cobben s.n.* (L!); Nordabhang, Dolok Baros, 1920, *Heusser s.n.* (BM!, HBG!; as *Trismegistia ovifolia* Herzog in herb.). **Java:** *collector unknown s.n.* (BM!; ex herb. Bescherelle); *collector unknown s.n.* (BM!; ex herb. Montague); West Java Prov., north side of G. Salak, 5 Aug., 1893, *Schiffner s.n.* [MO!, L!, NICH!, TNS!; Cryptogamae exsiccatae editae a Museo Hist. Natur. Vindobonensi, no. 4096 as *Trismegistia lancifolia*; Gunung Salak, *Akiyama Salak-2* (HYO!); Gunung Gede, 1400 m alt., 15/12 1901, *Fleischer s.n.* (H-BR!). **Kalimantan (Borneo):** East Kalimantan, Long Bawan, in the vicinity of Gunung Paris, *Akiyama 24030* (HYO!); Paraye, 04°01' N, 115°45' E, *Suleiman 1127 & 1132* (BORH!, HYO!).

EASTERN-TYPE: INDONESIA. Irian Jaya: Yapen Isl., Eiori Mt., *Cheesman 119* (BM!). **PAPUA NEW GUINEA. Prov. unknown:** Cloudy Mountains, *Micholitz 114* (H-BR!). **Western Highlands:** Baiyer River-Ruti Road, Jimi valley, 42 km N of Mount Hagen, 5°28' S, 144°16' E, *Streimann 22248* (CBG, MO!). **Gulf:** Hepataewa, 6 km S of Kaintiba, 7°33' S, 146°01' E, *Streimann 33861* (CBG, H, LAE, NHW, NY!). **Milne Bay:** Raba Raba Subdist., Junction Ugat and Mayu Rivers, near Mayu I, 9°37' S, 149°10' E, *Streimann & Katik NGF-28909 & NGF-34063* (both CBG, LAE, L!); *ibid.*, *Streimann & Katik NGF-28676* (BM!, L!, LAE). **Isl. Bougainville:** Lower south slope of Lake Laloru ciader, ca. 15 miles north of Buin, *Craven & Schodde 297* (BM!, BO!, FRI, L!, NSW!). **SOLOMON ISLANDS. Isl. Guadalcanal:** Mt. Gallego, 16/9/1966, *Dennis s.n.* [BSIP no. 20.029a (L!, NY!) & BSIP 20.020a (L!)]]; above Malakuna village on track to Mt. Popamanasiu, *Robbins 4301* (L!); near Mt. Papamansia, *Wimmer*

270 (L!); locality unknown, *Braithwaite* 4107 & 4458 (both L!). **San Cristobal:** top of south of Manighai, *Norris & Roberts* 49005 (MO!, NY!). **VANUATU (NEW HEBRIDES).** **Espiritu Santo:** south slopes of Santo Peak, track from Tasmaloun, *Robbins* 3862 & 3863 (both L!); *ibid.*, Mt. Vutimele (40 km north of Mt. Tabwemasana), 15°00' S, 166° 40' E, *Higuchi* 32156 (TNS!); *ibid.*, *Higuchi* 32287 & 32303 (HYO!, TNS!); 1909, *Bowie s.n.* (H-BR ex herb. *Watts* 32!); 1914, *Bowie s.n.* (herb. *Watts* 505 & 528; both in H-BR!). **Tongoa:** *Bowie* 542 (BM!).

Note 1. Though widely distributed in Malesia and the Western Pacific islands, *Trismegistia brachyphylla* has not been found from the Wallace region (between Wallace's line and Weber's line in Malesia). Thus its distribution area can be divided into two subareas, one from the Malay Peninsula to Borneo and the other from western New Guinea to Vanuatu. In this paper, *T. brachyphylla* specimens occurring in the former area are referred to as the Western-type [Plates 1 (4–6) & 2] and those from the latter area as Eastern-type [Plates 1 (1–3) & 3]. There are slight differences in morphology between these two types. The Eastern-type is characterized by larger and coarser plants (ascending secondary stems to 6 cm in length), longer stipe leaves with narrowly acuminate apices, and longer (30–50 µm) upper median laminal cells. While, the Western-type is characterised by smaller and more delicate plants (ascending secondary stems often less than 3 cm in length), shorter stipe leaves with more or less acute apices, and shorter (25–40 µm) upper median laminal cells. Since there are exceptions in these differences, however, each of the

two types is temporarily not recognized as representing a variety as in the case of *T. lancifolia*, *T. calderensis*, and *T. panduriformis*. Further studies using molecular markers are needed to make a final decision.

Note 2. Within the genus *Trismegistia*, one of the most striking features of *T. brachyphylla* (especially the Western-type) is its preference for rather drier habitats (for example, mountain ridges in forests. Fleischer (1915–1923) wrote of the species as a “Mesophyte”. From field observations in north Borneo (Maliau Basin and Crocker Range) and Java (Mt. Salak) as well as information written on specimen labels, its mesophytic status is confirmed. For the Eastern-type, information on its habitat is scarce.

Note 3. Broadly ovate, acute leaves of *Trismegistia brachyphylla*, as well as stipe leaves without elongated apices in the Western-type, show much resemblance to those of *T. maliauensis*. The latter, however, is a typical rheophytic moss (Akiyama & Suleiman 2003) and never found outside streambeds. In addition, *T. maliauensis* has a sparse branching pattern and teretely foliated stems. For further details, refer to the description and notes under the species.

Ovate and acute leaves had been reported in *T. lancifolia* var. *lancifolia* occurring at the base of branches on secondary stems (Fleischer 1915–1923, Figure 200a: e). They are also constantly present in the condensed type of *T. calderensis* var. *rigida* [Cameron Highland (Plate 8)].

2. *Trismegistia calderensis* (Sull.) Broth. [Plates 4–11]

Die Natürlichen Pflanzenfamilien I (3): 1078 (1908).

Basionym: *Hypnum calderense* Sull., Proceedings of the American Academy of Arts and Science 3: 184 (1855). Type: Philippines, Mindanao, Caldera, 1842, *Wright s.n.* (holotype FH-Sull!).

Plants very variable in size, branching pattern, and growth form, glossy or dull, complanately foliated (var. *calderensis*) or roundly foliated (var. *rigida* and var. *subintegrifolia*) on secondary stems. Primary stems short or long, pinnately branched, forming long, sparsely branched pendulous secondary stems without stipes, or upright secondary stems with distinct, long stipes. Stipe leaves, if present, round to short rectangular at base, more or less abruptly narrowed at shoulders into long, slender apices, markedly rounded at insertion at base, ecostate; apices almost always twisted one to two times; margins entire below, weakly toothed above, borders scarcely differentiated

(var. *calderensis*) or well differentiated with linear, thick-walled cells (var. *rigida* and var. *subintegrifolia*); laminal cell quadrate to linear above, becoming longer below, smooth, usually well pitted; alar regions well developed and often auriculate, multitiered except for several innermost columns; alar cells colored reddish brown, bulging. Stem leaves similar to stipe leaves in size and shape, rarely broadly ovate. Branch leaves linear lanceolate, twisted at apices, rounded at basal insertion, ecostate; upper margins serrate and well bordered; laminal cells quadrate to fusiform above, becoming longer below, smooth; alar regions multitiered except for inner columns.

Dioicous? Male plants or perigonia not observed. Perichaetia on primary stems and the base of stipes of secondary stems; paraphyses abundant. Perichaetial leaves becoming elongate after fertilization, reaching 5.5 mm in length, rectangular below, with long and narrow, twisted apices, more or less plicate, ecostate; margins entire below, sharply spinose above; alar regions with larger and thinner cells at both angles. Sporophytes rarely produced (especially in var. *calderensis*). Setae 40–75 mm long, reddish brown, smooth. Capsule ovoid to short cylindrical, straight to slightly curved, inclined to horizontal, narrowed below the mouth, reddish brown to yellowish brown in color; exothecial cells hexagonal to rectangular, more or less collenchymatous; stomata superficial, at neck. Opercula with short to long, straight or oblique beaks. Peristome as for the genus. Spores spherical, 12–15 µm in diameter, finely papillose.

Distinguishing features: (1) Larger, more or less glossy (often small and dull green in var. *subintegrifolia*) plants with distinct stipes (stipes often absent in var. *calderensis*), usually growing at higher elevations, (2) leaf apices distinctly twisted especially of the stipe- and stem leaves, (3) leaf margins weakly serrate, (4) leaf bases cordate and rounded at insertion even of branch- and branchlet leaves, and (5) well developed, multitiered alar regions. Fleischer (1915–1923: 1222) recognized the twisted leaf apices to be a good feature of *T. calderensis* and wrote ‘Letztere sind bei *T. rigida* immer sehr schmal zugespitzt und in der Spitze gedreht.’

Habitat. Growing on tree trunks, base of tree trunks, branches, rotten logs, damp rocks, soil banks of mountain paths in montane forests, occurring from (200–) 800–2000 (–3000) m alt., usually more than

1000m. [rarely found at lower altitudes; for example, at 600 m alt. in the vicinity of Kuala Lumpur (*Meijer B12196*), and 200m alt. on Sulawesi Isl. (*de Vogel 5031C*)]. Often pendulous from shrub trunks and branches in mossy forests.

Distribution. Thailand, Vietnam, Cambodia, Malaysia, Philippines, Indonesia, Papua New Guinea, Solomon Islands.

Note 1. Ramsay et al. (2002) reported *Trismegistia rigida* (= *T. calderensis* var. *rigida*) from Queensland, Australia. It is treated as a new variety, *T. lancifolia* var. *australiana* in this revision. For more details, see Note 1 there.

Note 2. *Trismegistia calderensis* is one of the most variable species among congeneric members in plant size, branching pattern, and leaf shape. A number of species and infraspecific taxa have been proposed to accommodate such variants, most of which are here treated as synonyms of three varieties under the species.

Plants hanging from shrub trunks and branches show an irregular and sparse branching pattern and lack distinct stipes. Plants with long, upright stipes and dendroid fronds on secondary stems are common on the floor of montane forests. The former corresponds to var. *calderensis*. The latter is here divided into two varieties; var. *rigida* with larger plants and var. *subintegrifolia* with small plants. Intermediate forms are often difficult to distinguish, even if they look very different when compared to typical plants of these varieties. These varieties also overlap in their distribution areas. Three varieties are here recognised under *T. calderensis*, each of which is distinguished as follows:

Keys to the varieties of *Trismegistia calderensis*

1. Plants more or less glossy, often pendulous from substrata; irregularly branched or sometimes densely branched in upper portions. Stipe usually indistinct, rarely developed. Leaves usually loosely attached to stem or patent when dry; borders scarcely developed at margins. Stem leaves (and stipe leaves, if present) gradually narrowed from an ovate-rectangular base. Branch- and branchlet leaves usually similar in size and shape to stem leaves. var. *calderensis*
1. Plants usually not glossy, forming dense turfs, rarely hanging from shrub stems and branches; secondary stems with stipes, forming dendroid or pinnately branched fronds. Leaves widely spreading to patent, especially on stipes; markedly bordered with elongate cells at margins. Stipe- and stem leaves round below and abruptly narrowed into long acuminate apices. Branch and branchlet leaves densely serrate, much smaller than stem leaves. 2
2. Plants larger. Stipe and stem leaves 2.8–3.8 mm long, base oblong, more or less gradually narrowed into a long, narrower upper portion. Widely distributed from continental part of Thailand to eastern part of Papua New Guinea. var. *rigida*
2. Plant smaller. Stipe and stem leaves 1.5–2.8 mm long, base rounded, abruptly narrowed at shoulder, more or

less ligulate above. Restricted to southern part of Malay Peninsula, Sumatra, Borneo, Luzon, Negros, Mindanao. var. *subintegrifolia*

2-1. var. *calderensis* [Plates 4–5]

Trismegistia rigida (Reinw. & Hornsch.) Broth. f. *pendula* M. Fleisch, Die Musci der Flora von Buitenzorg 4: 1218 (1923), hom. illeg. Type: West-Java, Gedeh, am Poentjak, 1350 m alt., 3 April, 1902, *Fleischer s.n.* (holotype FH!, Isotype H-BR!). **Syn. nov.**

Plants more or less glossy, yellowish green in color, mostly pendulous from branches and stems of shrubs, sometime forming turfs stretching downward on soil banks. Leaves usually loosely attached to stem or patent even when dry. Primary stems prostrate on substrata, pinnately branched, roundly or more or less complanately foliate. Secondary stems, more or less complanately foliate, sparsely branched, pendulous or prostrate, often without stipes and fronds; central strand absent. Stem leaves (and stipe leaves, if present) 2.7–3.6 mm long, abruptly narrowed from an ovate-rectangular base into a long, slender, twisted apex, rounded at leaf insertion, ecostate; margins entire below, serrulate to serrate above, border scarcely developed; laminal cells just below apex fusiform to linear, 35–50 µm in length, smooth; upper median laminal cells linear, 60–100 µm in length, strongly pitted, smooth; alar regions well developed, usually auriculate, segmented except for innermost columns; alar cells reddish brown, bulging. Branch and branchlet leaves shorter than stipe and stem leaves, oblong below, acute to acuminate, rounded at leaf insertion, ecostate; margins entire to denticulate below, serrulate to serrate above, scarcely bordered; alar cells segmented except for innermost columns.

Dioicous? Male plants not observed. Perichaetia on primary stems. Sporophytes rare. Setae 50 mm long, reddish brown, smooth. Other features not observed.

Distinguishing features: (1) Plants more or less glossy, irregularly pinnately branched, (2) stipe- and stem leaves indistinctly narrowed at shoulder, (3) branch leaves acute to acuminate, not much differentiated from stem leaves, (4) leaf apices twisted, (5) alar regions multitiered except for innermost columns, (6) leaf margins weak serrate and borders scarcely developed, and (6) leaf insertion deeply rounded.

Habitat. Growing at the base of tree trunks, stumps, rotten logs, often pendulous from shrub trunks and branches, rarely on soil banks in humid montane forests, occurring from (600–) 1000–2000 (–2800) m alt. (reported from 2800 m alt. in western Sumatra, and 600 m alt. in eastern New Guinea).

Distribution. Thailand, Philippines, Malaysia, Indonesia, Papua New Guinea, Solomon Islands. Apparently absent from the Wallacea region.

Other specimens examined. **THAILAND.** Nakohn Si Thammarat: Khao (Mt.) Luang, 08°30' N, 99°45' E, *Touw 11658* (MO!, L!), *11674* (MO!, L!, NY!), *11678*, *11741* (both L!), *11844* (BM!, L!, MO!) & *11851* (L!, MO!); *ibid.*, *van Beusekom B22*, *B42* & *950* (all L!). **PHILIPPINES.** **Luzon:** Laguna Prov., *Calvin 331* (H-BR!), MO!, NY!, PH); *ibid.*, Mt. Maquiling (Makiling), *Elmer 18426* (BM!, BO!, FH!), *18428a* (FH!); *ibid.*, *June-Juli 1917*, *Elmer s.n.* (NY!); *ibid.*, *Robinson s.n.*, *Feb. 1909* (Bureau of Science no. 6623; BM!, FH! & NY!); *ibid.*, *Pancho 202* (NICH!); *ibid.*, Mt. Banahao, *Baker 6364* (MO!); Mt. Banajao, *Ocampo 28015* (BO, L!), *Ocampo s.n.* [Bureau of Science no. 28017; BO!, FH!, H-BR!, L!, MO!, NY!; quoted as *T. calderensis* in Bartram (1939)]; Mt. Province, Baynian, Banaue, Ifugao, *Conklin & Buwaya PNH-79637* (L!). **Negros:** Mt. Marapara, *Currion & Foxworthy*, *Sept. 1909* (BM!, NY!; Forestry Bureau no. 13647); Mt. Kanlaen, *Salgado 729* (NICH!); Dumaguete, *Elmer 9995* (BO!). **Sibuyan:** Romblon, Mt. Guiting-Guiting, on ridge to Mays Peak, *Strain 28* (L!). **Mindoro:** Halcon foothills, above Pa'itan, *Coode 5772* (L!). **Palawan:** *Motley s.n.* (NY-Mitt!). **MALAYSIA.** **Perak:** locality unknown, *Curtis s.n.*, 1896 (SING!; as *Acanthocladium ochroloma* Mitt. ms.); Maxwell Hill, *Tixier 5780* & *5785* (both SING!). **Pahang:** Cameron Highlands, from summit G. Brinchang downwards, *Gunaseelan & Ponniah 370* (KLU!, HYO!); Gunong Berenbun (Brinchang), *Holtum 23411* (BM!, SING!), *Inoue 10073*, *10073*, *10789* and *11051* (TNS!); *ibid.*, *Henderson 11756*, *11765* & *11770* (SING!); Gunong Jasar, near Tanah Rata, *Inoue 10444*, *10445* & *10566* (TNS!); Tanah Rata, *Inoue 10065* & *16298* (both TNS!); Cameron Highland, 04°30' N, 101°20' E, *Akiyama 884* & *887* (both HYO!); *ibid.*, around the Robinson's Water Fall, *Inoue 16469* (TNS!); *ibid.*, Wireless Quarts, Tanah Rata, *Inoue 16293* (TNS!); *ibid.*, track from Robinson Falls to peak of G. Beremban, 4°30' N, 101°25' E, *Hedenäs MY92-172* & *MY92-173* (both SINU!); *ibid.*, around water fall, *Inoue 10392* (TNS!); *ibid.*, *Holtum 11374* (SING!); Gunong Brumbau (Beremban), *Henderson s.n.* (BM!); Gunong Jasar, *Spare 3537-b* (BM!). **Perak:** G. Hijau, *Burkill 12639* (SING!). **Kedah:** Kedah peak, *Tixier 5704* (SING!). **Kelantan:** G. Sitong, *Mohd Nur 1233B* (SING!). **Selangor:** Gunung Nuang, E. of Kuala Lumpur, *Meijer B12230*, *B12234*, *B12254*, *B12264*, *B12265*, *B12299* & *B12335* (all L!); Huluh Selangor, G. Semangka, *Ridley 281b* (SING!). **Malacca:** Mt. Ophir, *Ridley 708* (BM!, NY!, SING!) & *725* (BM!, NY!). **Sabah:** Lahad Datu, Tawau Reserve, Mt. Silam, *Meijer B10600*, *B10607* & *B10613* (all L!); *ibid.*, *Iwatsuki 5454* (NICH!);

Kinabalu National Park, Liwagu Trail, *Akiyama et al.*, 319 (Herbarium of Kinabalu National Park!, HYO!, UMS!); *ibid.*, *Akiyama et al.* 419 (HYO!, UMS!); Mt. Kinabalu, between Tenompock Pass and Kamaranga Radio Station, *Iwatsuki* 348 (NICH!); West Coast Res., Mt. Tambuyokon, ca. 15 miles NE of Kinabalu Peak, *Meijer B11217 & B11484* (both L!); Mt. Kinabalu, around Headquarters, *Akiyama Kinabalu-1009* (HYO!, UMS!); locality unknown, *Meijer B12670* (L!). **Sarawak:** Gunong Mulu, 04°05' N, 114°55' E, *Touw 20817 & 20843* (both L!); Mount Dulit (Ulu Tinjar), Dulit trail, *Richards 1516* (BM!). **INDONESIA. Sumatra:** Atjeh, Gunung Leuser Nature Reserve, Gunung Bandahara, *de Wilde & de Wilde-Duyffes 15085C & 15136B* (both L!); Atjeh, Gunung Leuser Nature Reserve, Gunung Ketambe and vicinity, *de Wilde & de Wilde-Duyffes 13804C* (L!); *ibid.*, upper Mamas River valley, W. of Kutacane, *de Wilde 18268A & 19189A* (both L!); North Sumatra, Brastigi-Tonkkeh, summit of Delangsikut, *van der Wijk 1640* (L!); West Sumatra, Pajakumbuh, northern slope of Mt. Sago, *Meijer 6057, 6092, 6095, 6103, 6112, 6121, B9525* (all L!) & *6064* (L!, NICH!); *ibid.*, Air kesimbukan, *Meijer B6963a* (L!); West Sumatra, in cacumine montis Singalang, regio alpina, *Schiffner 11875* (L!); Tapanuli, Lae Pondon, *Alston 149206* (BM!, BO!); East Coast, Karoland, summit of Deleng Baroes, *Bartlett 8485* (BM!, NY!); East Coast, Asahan, *Bartlett & La Rue 247* (MO!, PC!). **Java:** without exact locality, *Blume s.n.* (BM!; ex herb. Hampe); montis Gedogan Jaya, *unknown collector s.n.* (L!; L0109829); Mt. Salak, *Blume s.n.* [L!; L0109834, noted as one of the syntypes of *Hypnum korthalsii* Dozy & Molck. on the label by mistake]; *ibid.*, 1893, *Möllerr s.n.* (NY!); Tidodas, *Noerta 174 & 180* (both L!); Geger Bentang (Mandalawangi), *Noerta 1449* (BO!, L!), 1477 & 2004 (all L!); Natural reserve, Tjibeureum, *Noerta 292* (L!); Mt. Gede, *Noerta 1445, 1510 & 1515* (all L!); Mt. Pangerango, above Tjibodas, *Schiffner 11868* (L!, NY!); Mt. Pangerango, oberhalb Tjibodas, *Schiffner s.n.*, 24 IV, 1894 (MO!, NY!); Cryptogamae exsiccatae editae a Museo Hist. Natur. Vindobonensi, no. 4097 as *Trismegistia rigida*; Vicinity of Tjibodas, west end of Gajonggong between Tjibodas & Tjibeureum, *Alston 12734b* (BM!, BO!); National Reserve, Tjibeureum, *Noerta B50/293* (BO!). **Kalimantan (Borneo):** West Kalimantan, Sambas, west slope of Gunung Niut, *Akiyama B-30746* (HYO); Kalimantan Selatan, Barabai, G.

Besar, *Dransfield 2902* (L!). **Morotai:** Gt. Sabatai, *Smiet M4 & M99* (both L!). **PAPUA NEW GUINEA. West Sepik:** Frieda River Prospecting Area, 04°40' N, 141°43' E, *Koponen 34947* (H, MO!); Copper Co., Mt. Ekvaidebom, 8 km W of Frieda Base Camp, 4°43' S, 141°43' E, *Koponen 35520* (H, HSC, NY!). **Morobe:** Table Mts., 12km WNW of Frieda Base Camp, 4°38' S, 141°41' E, *Koponen 35911* (BM!, H, HSC); Wagau-Malolo Track, 26km NE of Mumeng, 06°53' S, 146°50' E, *Streimann 19651* (CBG, H, FLAS, LAE, NICH!, NY!, S, W), 19555 (CBG, H, LAE, NICH!, NY!), 19582 (CBG, H, LAE, NICH!, NY!), 19651 (LAE, H, NICH!, NY, S, FLAS, W) & 19680 (CBG, H, NICH, NY!, S, W). **Central:** Port Moresby, near Boku, Mt. Durigolo, *Clark 40* (BM!). **Milne Bay:** Mt. Dayman, *Arwit s.n.*, 1874 (H-BR! ex herb. Melbourne no. 643). **SOLOMON ISLANDS. Kolonganbara (Kilim-Bangara):** at top of Mt. Veve in center of island, 7°57' S, 157°05' E, *Norris & Roberts 49616* (MO!, NY!).

Note 1. *Trismegistia rigida* f. *pendula* represents more or less glossy plants pendulous from shrub or tree trunks and lacking distinct stipes of secondary stems. The indistinct shoulder of the stem leaves, scarcely developed borders at leaf margins, and long linear branch leaves, segmented alars and the deeply rounded leaf insertion, even in branch leaves, suggest its affinity to *T. calderensis* var. *calderensis*.

Note 2. The holotype specimen of *Hypnum calderensis*, collected in the Philippines, contains only portions of branches and thus features of plant size, appearance, and stipe leaves are unknown. Stems are more or less complanately foliate, and stem- and branch leaves are glossy with scarcely differentiated borders and weak serration at margins.

Note 3. Among the specimens examined by the author, only two, collected in Luzon (*Robinson s.n. Mar. 5-7, 1920*, NY!) and the Malay Peninsula (*Akiyama 887*, HYO!), bear sporophytes with setae and fragments of capsules.

2-2. var. *rigida* (Reinw. & Hornsch.) H. Akiyama, **comb. nov.** [Figure 3, Plates 6–9]

Basionym: *Hypnum rigidum* Reinw. & Hornsch., Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia Ephemerides sive Observationes Historias et Experimenta **14** (Suppl.): 731 (1829), *hom. illeg.*, non Schwägr. (1816) ≡ *Acanthodium rigidum* Mitt., Journal of the Linnean Society, Botany **10**: 182 (1868) ≡ *Acanthocladium rigidum* (Mitt.) Broth., Monsunia, Beiträge zur Kenntniss der Vegetation des Süd- und Ostasiatischen Monsungebietes **1**: 51 (1899) ≡ *Trismegistia rigida* (Mitt.) Broth., Die Natürlichen Pflanzenfamilien **I** (3): 1078 (1908). Type: Java, collector unknown (lectotype L!; L0109843). [For information about the collections of Reinwardt in L, see Touw (2006)].

Hypnum rigidum Reinw. & Hornsch. var. *β convolutum* Bosch & Sande Lac., Bryologia Javanica **2**: 140 (1866) ≡ *Trismegistia rigida* (Reinw. & Hornsch.) Broth. var. *convoluta* (Bosch & Sande Lac.) M. Fleisch. Type: Java, *Junghuhn s.n.* (holotype L-Sande Lac., L0194416). [Fleischer (1915–1923) treated this name as a synonym of *Trismegistia korthalsii*.]

Trismegistia rigida (Reinw. & Hornsch.) Broth. f. *corticola* M. Fleisch., Die Musci der Flora von Buitenzorg **4**: 1217 (1923). Type: Gedeh, Telaga bei Sindanglaya, 25 May, 1913, *Fleischer s.n.* (lectotype FH!), **lectotype**

selected here. Syn. nov.

Trismegistia rigida (Reinw. & Hornsh.) Broth. f. *viridis* M. Fleisch., Die Musci der Flora von Buitenzorg 4:1218 (1923). Type: Nord-Sumatra, Battaklanden am Vulkan Sibayak auf schattigem Urwald-Boden, 1450 m alt., 30 Aug. 1913, *Fleischer s.n.* (lectotype FH!; distributed as Musci Frond. Archipelagi Indici et Polynesiaci, Ser. XI, no. 531; see note 2), **lectotype selected here. Syn. nov.**

Hypnum trismegistum Mont., London Journal of Botany 3: 633 (1844) ≡ *Acanthodium trismegistum* (Mont.) Mitt., Trans. Linnean Soc. London, Botany 4: 260 (1894). Type: Java Prov., Buitenzorg, 1843, *Miquel s.n.* [holotype BM-Shuttleworth! (BM000660264), isotypes L! (L0194412 & L0194414), H-BR! (4327-013)]. (See note 9).

Plants green, not glossy, forming dense turfs on substrata, often pendulous from stems and branches of shrubs. Primary stems prostrate, pinnately branched; without a central strand. Secondary stems with stipes (if not pendulous from substrata), roundly foliate, with more or less dendroid or palmate fronds above. Stipe- and stem leaves 2.8–3.8 mm long, oblong at base, more or less gradually narrowed into long, acuminate, twisted apices, more or less rounded at leaf insertion, ecostate; margins entire below, serrulate above, with distinct borders with linear cells; laminal cells just below apex elliptic to short rhomboid, 8–40 μm in length (rarely reaching 50 μm in length for Seram plants); upper median laminal cells elliptic to fusiform, 20–50 μm in length, smooth; alar regions multitiered except for innermost columns, forming an auriculate base; alar cells reddish brown, more or less bulging. Branch leaves lanceolate or similar to stem leaves, smaller, ecostate, deeply rounded at leaf insertion; entire below, serrulate to low serrate above, with a distinct border; laminal cells short rectangular to fusiform above, becoming longer below, smooth; alar regions multitiered at outer two to four columns.

Dioicous? Perigonia not observed. Perichaetia on primary stems and at the base of stipes. Perichaetial leaves rectangular at base, narrowed into long, twisted apices, plicate, ecostate; entire below, spinose above; laminal cells linear; alar regions with longer and wider cells at basal angles. Calyptrae not observed. Setae 60–75 mm long, reddish brown, smooth. Capsules ovoid, narrowed below mouth, smooth, reddish brown to yellowish brown; exothecial cells hexagonal to rectangular, collenchymatous, becoming smaller near the mouth and longer below; stomata small, at neck, superficial. Opercula straight, shortly beaked. Peristome and spores as in the genus.

Distinguishing features. (1) Larger, not glossy plants with upright, well developed stipes, (2) widely spreading leaves, especially on stipes, (3) stipe and stem leaves short rectangular below and rather abruptly narrowed at shoulder, with well developed

borders at margins, (4) twisted leaf apices, (5) alar regions multitiered, and (6) branch leaves deeply rounded at insertion.

Habitat. Growing on soil, rotten logs, tree trunk bases, boulders on forest floors, sometimes hanging from shrub trunks and branches, occurring from (200–) 800–2300 m alt.

Distribution. Vietnam, Cambodia, Thailand, Philippines, Malaysia, Indonesia, Papua New Guinea. This variety has been found at the most northerly locality (Phu Luang, Northern Thailand) within the distribution area for the genus *Trismegistia*.

Other specimens examined. VIETNAM. Vallée du Aong Man, *Krempt 1620 pp.* (PC-Th!); *ibid.*, *Krempt 1624 pp.* (H-BR! ex Herb. Theriot); Massif du Honba, 1919, *Vincens s.n.* (PC-Th!); Lam Dong, piste de la B'Su Dalao, Nov. 11, 1960, *Tixier s.n.* (PC-Th!). **CAMBODIA.** Bokor, piste de Kam Chay, Nov. 17, 1967, *Tixier 2832* (PC-Th, MO!). **THAILAND. Udawn:** Phu (Mt.) Luang, 17°25' N, 101°25' E, *Touw 10643* (L!, MO!) & *10688* (L!, MO!, NY!). **Nakohn Si Thammarat:** Khao (Mt.) Luang, 08°30' N, 99°45' E, *Touw 11706, 11731 & 11788* (all L!, MO!); *ibid.*, *Smitinand 1292* (N!). **PHILIPPINES. Luzon:** Laguna Prov., Mt. Maquiling, *Villamil s.n.* (H-BR!; Bureau of Science no. 20854); *ibid.*, Mt. Banajao (Banahao), *Robinson Mar. 5-7 1910* (NY!; Bureau of Science no. 9794); *ibid.*, Mt. Banahao, *Baker 2326* (NY!); Sorsogon Prov., Irosin, Mt. Bulawan, *Elmer 17137* (BO!, NY!). **Mindanao:** Cotabato, Kidapawan side, Mt. Apo National Park, in mossy forest above Lake Venade, *Tan 82-357* (FH, L!, NICH!); Davao area, Apo from Toril, *Robbins 3966* (L!); Mt. Apo, *Williams 2667* (H-BR!, NY!); *ibid.*, *Schumm & Schwarz 4433, 4434 & 4665* (all SINU!); Mt. Apo, *Pancho 2598 & 2601* (both MO!, PH); Mt. Talumo, *Reynoso 2108* (MO!, SINU!) & *2141* (MO!); Davao Prov., Mt. McKinley, *Edaño 71/311* (L!); Davao Prov., Mt. Kampalili, *Edaño 71/322* (L!); Davao, Mt. Mayo, *Edaño 12893* (MO!); Mt. Malindang, *Reyes 609* (*Patterson 2942*; NY!); Mt. Malindang, *Mohagan 857 & 894* (both SINU!); Bukidnon Prov., Mt. Kitanglad, 08° 09' N, 124°55' E, *Schumm & Schwarz 4272* (SINU!); Camaguin de Mindanao, *Ramos s.n.*, March-April 1912 [Bureau of Science no. 14900; H-BR!, NY! reported as *Trismegistia rigida* in Bartram (1939: 319)]; Bukidnon Subprov., Mt. Candoon, June-July 1920 *Ramos & Edaño s.n.* (FH!; Bureau of Science no. 37182); Mt Malambo, Datu Salumay, Marilog Dist, *Lubos D39* (SINU!). **Negros:** Oriental

Prov., near Dumaguete, *Patterson 1305* (collected by M.P. Mack, April 20 1951, NY!), Dumaguete, In Mts., east of city, *Patterson 2893* (collected by M.P. Mack, Jan. 1959, NY!); Oriental Prov., mountain in southern part of province, *Brown 2864* (NY!). **MALAYSIA. Selangor:** 3 miles mark on old Genting Highland road, *Manuel 2799* (KLU, MO!, NY!); environs of Kuala Lumpur, Batu Gombak, *Meijer B12196* (L!); Ginting Bidai, *Ridley 423* (SING !); Bukit Etam, *Kelsall 209* (SING!). **Pahang:** Fraser Hill, *Henderson 11068* (BM!, SING!); *ibid.*, trail to Pine Tree Hill, *Manuel 2769* (MO!); Gunong Jasar, near Tanah Rata, Cameron Highlands, *Inoue 10567* (TNS!); Gunung Brinchang, along road between 1850–2031 m alt., *Hedenäs MY92-150* (SINU!), *MY92-284* (SINU!); Wireless Quarts, Tanah Rata, Cameron Highlands, *Inoue 16203* (TNS!); Cameron Highland, *Henderson 17833 & 17834* (both SING!); *ibid.*, *Tsubota 20000919-0019* (HIRO!, HYO!); *ibid.*, G. Berembun, *Ridley 130* (SING!); Fraser Hill, 1 miles along the peak to Pine Tree Hill, *Wood 1331* (BM!); Taman Negara, foot of Gunung Tahan, *Akiyama 784* (HYO!); *ibid.*, G. Tahan, *Ridley 31* (BM!); *ibid.*, *Holtum 20852* (SING!); on old Genting Highland road near intersection with the new road, *Manuel 2900* (KLU, MO!). **Perak:** Maxwell's Hill, *Spare 2062* (BM!). **Sabah:** SE slope of Mt. Kinabalu, Ulu Liwagu, *Iwatsuki 1191* (NICH!); Mt. Kinabalu, en route from Power Station to Laban Rata, 06°00' N, 116°32' E, *Akiyama et al. 131* (HYO!, UMS!, herbarium of Kinabalu National Park!). **INDONESIA. Sumatra:** Sumatra Utara, Batak-landen, Lae Pandom, Dairi road km 124, *Otto-Surbeck 235* (L!); Atjeh, Gunung Leuser Nature Reserve, Gunung Ketambe and vicinity, *de Wilde & de Wilde-Duyffes 14031B* (L!, NICH!, NY!, TNS!); Atjeh, Gunung Leuser Nature Reserve, upper Mamas River Valley, *de Wilde 19183C* (L!); North Sumatra, Batak-landen, Dairi, km 115, *Otto-Surbeck 270* (L!); Sibajak, 1949, *Cobben s.n.* (BO!, L!; L0276930, L0276972 & L0277053); Sibajak, *Heusser 1678* (HBG!); North Sumatra, Sibajak (SE of Lake Toba), 1994, *Cobben s.n.* (L!); North Sumatra, auf dem Dolok Baros bei Brastagi, *Arens 373* (BO!, L!); North Sumatra, Brastagi–Tonkkeh, summit of Delangsikut, *van der Wijk 1685A* (L!); North Sumatra, Prapat (east coast of Lake Toba), Simarbelatuk, *van der Wijk 1837A* (L!); Central Sumatra, Pajakumbuh, northern slope of Mt. Sago, *Meijer 6079, 6877 & 6117A* (all L!); *ibid.*, Mt. Sago, Air Kesimbukan, *Meijer 6103* (L!); West Sumatra, Gunung Tahan, *Meijer 15968* (MO!); East Coast, Asahan, *Bartlett & La Rue 247* (NY!); East Coast, Karoland, summit of Deleng Baroes, *Bartlett 8485* (DPU, NY!). **Java:** without exact locality, *Reinwardt s.n.* (L!; L0194413); m. Gedokan, *Kuhl & van Hasselt s.n.* (L!; L0194400, one of syntypes of *Hypnum rigidum* var. *braunianum*); G. Tjjsalak, Bakhuizen, *van den Brink 5886* (BM, BO!, L!); Salak, *Möller 373 & 455* (both H-BR!); Salak, 7-8 July 1897, *Möller s.n.* (NY!); Salak, *Nyman 455* (MO!, NY!); *ibid.*, *Nyman 608* (H-BR!); Gunung Salak, *Akiyama Salak-5* (HYO!); Mt. Gede, *Meijer B4140* (BO!, L!); *ibid.*, *Fleischer s.n.* (H-BR!); *ibid.*, *Akiyama Gede-66* (HYO!); West Java, Urwälder am Südhang des Pangerango, oberhalb Tjibodas, 24 IV 1894, *Schiffner s.n.* (L!, NY!, S, TNS!; Cryptogamae exsiccatae editae a Museo Hist. Nat. Vindobonensi no. 4097); West Java, Preanger Prov., Kawah Manuk, *Schiffner 11870* (L!); West Java, Megamendong

Gebirge am Telaga, *Fleischer s.n.*, 25 May 1913 (BO!, L!, TNS!; Musci Frond. Archipelagi Indici et Polynesiaci Ser. XI, no. 530); Naturemonument, *Noerta 50/180B* (BO!). **Kalimantan (Borneo):** East Kalimantan, upper region of the Mahakam river, en route from Muara Teple to Gunung Babi, 00°38' N, 116°00' E, *Akiyama K-22477* (HYO!); East Kalimantan, Kab. Bulungan, Long Bawan, around Gunung Batu Linanit, 04°20' N, 115°50' E, *Akiyama K-24336* (HYO!); *ibid.*, en route from Tadur Bangar to Gunung Batu Harun, 04° 15' N, 115°50' E, *Akiyama K-24278* (HYO!); West Kalimantan, Sambas, Singkawang, Gungun Poteng, *Akiyama B-31456* (HYO); South Kalimantan, Mt. Gunung Batu Besar, en route from Sungai Mentohoi to the top, 02°20' S, 115°30' E, *Akiyama K-24738 & K-24770* (both HYO!). **Sulawesi:** North Sulawesi, Bolaang Mongandow, Dumoga Bone National Park, Gunung Mogogonipa, ca. 00°27' N, 123°57' E, *de Vogel & Vermeulen 7089A & 7092A* (both L!); Central Sulawesi, surroundings of Karumba, ca. 8 km E of Tawaeli on road to Parigi, 00°43' S, 119°56' E, *de Vogel 5031C* (BO, L!); Central Sulawesi, Roroka Timbu, 00°30'–01° 30' S, 119°30'–120°30' E, *Hennipman 5246D, 5247, 5395E, 5403 & 5356a* (all L!); *ibid.*, *van Balgooy 3228C* (L!); Central Sulawesi, Danu Tambing, 00° 30'–01°30' S, 119°30'–120°30' E, *van Balgooy 3476B & 3477* (both L!); Central Sulawesi, Lore Kalimata National Park, Bukit Habantu, *Meijer 9511j* (MO!); South Sulawesi, Tana Toraja, Gunung Sesean (N of Rantepao), ascent from Batutumonga, *Touw & Snoek 24640* (L!). **Morotai:** *Tangkilisan s.n.*, 1949 (BO!). **Ambon:** Gunon Salhutu, *Beccari 113* (L!). **Seram:** Kecamatan Tehoru, en route from Wae Nua to Gunung Mahahue, 3°15' S, 129°29' E, *Akiyama C-14802* (HYO!, L, NY!); Piliiana–Gunung Watane, *Akiyama C-14946* (BO!, HYO!, L!, MO!); Central Seram, Wae Puo–Wae Ili, *Akiyama C-9685* (BO!, HYO!, L!, NY!); Central Seram, Wae Nua–Gunung Mapahue, 770 m alt., *Akiyama C-14723* (BO!, HYO!, MO!), *C-14802* (BO!, HYO!, L!); Central Seram, Maneuratu–Gunung Musamutua, *Akiyama C-16391* (BO!, HYO!, L!); West Seram, Gunung Tiang Bendera, *Akiyama C-15575* (HYO!, NY!); West Seram, Gunung Totaniwel, *Akiyama C-15819* (BO!, HYO!, NY!). **Irian Jaya:** Vogelkop Peninsula, Tamrau Range, Gunung Bagimana, 00°40' S, 132° 40' E, 1-1-1978, *van der Zon s.n.* (L!); Vogelkop Peninsula, Manokwari Dist., Kebar Valley, trail from Andjai to Gunung Nettoti, *Davis 735A & 830-IG* (both L!); Jayawijaya, Star Mts., Mt. Antares, bivouac 39a, *van Zanten 332a, 347b, 390a, 392a* (all L!) & *344* (L!, NY!); Jayapura, Cyclop Mountains, along path Iffar–Ormoe, *van Royen 3610B* (L!); 4 km SW of Bernhard Camp, Idenburg River, *Brass 13306* (A, BO!). **PAPUA NEW GUINEA. Without exact locality:** Finisterregebirge, *Eiffert 24* (BM! ex Hb-Herzog, two specimens). **West Sepik:** Frieda Copper Co., Frieda River prospecting area, 04°40' S, 141°43' E, *Koponen 34948* (H, HST, L!, NICH!); Wewak–Angoram area, slopes of Mt. Toru, near Yangoru, *Robbins 2353* (L!); Lumi subdis., Torricelli Mts., peaks ca. 4 miles N of Wigotei village, *Darbyshire 470* (CANB, L!); Star Mts., Busilmin, ca. 05°S, 141°05' E, *Touw 15003* (L!). **Central:** east of Port Moresby, Astrolabe Range, *Clark 97* (BM!). **Morobe:** Wagau–Malolo Track, 26 km NE of Mumeng, 06°53' S, 146°50' E, *Streimann 19577A* (ASU, CBG, MO!, NY!, TBA), *19602* (CBG, H, LAE, MO!, NAM, NICH!,

NY!), 19556 (CBG, H, LAE, NICH!) & 19582 (CBG, H, LAE, NICH!, NY!); Huon Peninsula, east slope of Mt. Rawlinson, ridge between Gang Creek and bulum river, *Hoogland 9136* (CANB, K, L!, LAE, US). **Milne Bay:** Daga Area, Mt. Garatun, *Cruetwell 24 p.p. & 26* (both L!); Fergusson Island, mountain between Agamoia and Ailuluai, *Brass27017 & 27036A* (both L!). **New Ireland:** Island New Ireland, Lelet, *Koie 2125 & 2137* (both L!).

Note 1. *Trismegistia calderensis* var. *rigida* is the most common of the three varieties. Typical plants with upright, long stipes and palmate to dendroid fronds have been collected at Mt. Salak and Mt. Gedeh (West Java). Though the exact place of the type locality of *Hypnum rigidum* in Java Island is unknown, it could be from either of the two places.

Note 2. *Trismegistia rigida* var. *corticola* is a form found hanging from trunks of shrubs or trees and lacking distinct stipes. In spite of its resemblance to var. *calderensis* in habitat preference, the stem leaves abruptly narrowed at the shoulder with distinct marginal borders and the smaller branch leaves suggest an affinity with var. *rigida*.

Thought the author was not able to locate another syntype of *Trismegistia rigida* f. *viridis* (“im Barisan-gebirge bei Bandar borea! 11–1200 m, coll. *Fleischer*”), an alternative syntype (*30 Aug. 1913, Fleischer s.n., FH*) is here selected as lectotype because its duplicates have been widely distributed as a part of the “Musci Frond. Archipelagi Indici et Polynesiaci”.

Note 3. A total of four specimens are known from Indochina (Vietnam and Cambodia). They are much smaller in size comparing to those collected from other parts of the distribution range. In addition, they show scarce differentiation of stipes, irregular branching pattern of ascending stems, and leaves with weak marginal borders compared to the typical plants of var. *rigida*. Though they are tentatively classified under var. *rigida*, additional collections might suggest recognition as a separate variety.

Note 4. When he treated *Trismegistia calderensis* and *T. rigida* as separate species, Tan (1991) wrote that “The secondary branching system can become dendroid or remain bipinnate. The leaf apices vary from obtuse, acute to short acuminate. The leaf borders and marginal serration are either markedly or weakly differentiated” (p.104). Judging from these sentences and the synonyms listed there, it becomes apparent that he regarded *T. rigida* as including both *T. lancifolia* var. *lancifolia* and *T. calderensis* var. *rigida*, in the sense of the present revision. It then becomes clear why Australian plants were identified

as *T. rigida* (Ramsay et al. 2002).

Note 5. Mitten (1868, p. 182) reported *T. calderensis* var. *rigida* from Mt. Tutuila (Samoa) under the name of *Acanthodium rigidum* (= *Hypnum calderense* Sull., namely *T. calderense*) based on a single specimen (*Powell 5*). Later, Müller (1874) cited the specimen as one of the syntypes of *Hypnum complanatum* Müll. Hal. [= *Trismegistia complanata* (Müll. Hal.) Müll. Hal.]. Müller probably did not check the specimen himself because he did not refer to the presence of sporophytes on the specimen. I have examined the specimen and designate it as a lectotype of *T. complanata*. Therefore, Samoa is omitted from the distribution range of *T. calderensis* var. *rigida*.

Note 6 [Plate 8]. Plants smaller in size than typical types of var. *rigida* and bearing smaller leaves have been collected at several localities, from Thailand to Borneo Island. They are tentatively designated as the “condensed type” in this revision. According to my field observations at the altitude of ca. 1400 m alt. in the Cameron Highlands (Malaysia), especially around the path to Robinson Falls and the foot of Gunung Jasar, almost all plants belong to this type. Shorter, acute leaves often with short, double costa that are found on the upper part of short stipes and at the base of branches of secondary stems are distinctive for this type.

Specimens examined. MALAYSIA. Pahang: Cameron Highland, *Akiyama 887* (HYO!); *ibid.*, en route from Tanah Rata to Gunung Jasar, *Akiyama 15614* and many others (all HYO!; total 30 specimens); *ibid.*, around Robinson's Waterfall, *Inoue 16293 & 16489* (both TNS!); *ibid.*, Tanah Rata, Robinson Falls, *Akiyama 15595* and many others (all HYO!; total 10 specimens); Fraser Hill, *Holtum 11370 & 11374* (both SING!). All specimens were collected at 1200–1400 m alt.

Note 7 [Plate 9]. Plants with (1) leaves having serrate to spinose upper margins and (2) larger alar regions with a number of quadrate cells arranged in an almost scalariform manner even in branch leaves, are known from Mindanao and Palawan Islands (Philippines). Since other features agree with typical plants of var. *rigida*, they are tentatively included there.

Specimens examined: PHILIPPINES. Mindanao: Gumate, on slopes of Mt. Talomo, *Robbins 3965* (L!, FH); Bukidnon, forest near Silipan, *Phillips 22* [MICH, NY!; quoted as *Trismegistia rigida* by Bartram (1939)]; Davao area, upper slopes Mt. Talomo above Gumate, *Robbins 4037* (L!). **Palawan:** Penigisan, *Olsen 2161a* (L!).

Note 8. The specimen used for the illustrations of *Hypnum rigidum* presented in the *Bryologia Javanica* (Tabs. CCXXXVII) is deposited at L (Java, collector

unknown s.n.; L0194410, Herb. Lugd. Bat. No. 909.188-28 ex Herb. Dozy & Molkenboer, annotated by Dr. Touw in 2003). It is referable to *Trismegistia calderensis* var. *rigida*.

Note 9. Wijk et al. (1969) synonymized *Hypnum trismegistum* under *Trismegistia lancifolia*, which is not adopted here. The confusion must have been

caused by Mitten & Wright (1894: 260), who listed *Neckera lancifolia* Harv. [= *Acanthodium lancifolium* (Harv.) Mitt.] as a synonym of *Acanthodium trismegistum* (Mont.) Mitt., but considered the former to be a different species because of its 'complanate panduriform foliage'.

2-3. var. *subintegrifolia* (Broth.) H. Akiyama, **comb. nov.** [Figure 3, Plates 10–11]

Basionym: *Trismegistia subintegrifolia* Broth., Mitteilungen aus dem Institut für allgemeine Botanik in Hamburg 7: 131 (1928). Type: West-Borneo, Bukit Raya, ca. 1400 m, *H. Winkler 3187* (holotype H!).

Trismegistia gracilicaulis Dixon & Herzog in Dixon, Journal of the Linnean Society, Botany 50: 115 (1935). Type: East Borneo, *Balneti 1925* (holotype BM!; isotype JE!). **Syn. nov.**

Trismegistia squarrosa Dixon, Annales Bryologici 5: 40 (1932). Type: Sumatra, Tapanoeli, Habinsaran, *H. H. Bartlett 7993b* (holotype BM!). **Syn. nov.**

Plants small to medium, not glossy, forming dense, low turfs on substrata, sometimes pendulous from shrub branches and stems. Primary stems pinnately branched with upright secondary stems with distinct stipes (stipes absent in pendulous forms). Secondary stems bipinnately branched and forming compact fronds, roundly foliate; central strand absent. Stipe leaves (if present) and stem leaves 1.5–2.8 mm long, round at base, abruptly narrowed at shoulders into long acuminate, twisted apices, well rounded at leaf insertion, ecostate; margins entire below, denticulate to serrulate above, borders well differentiated; laminal cells just below apex elliptic to fusiform, 8–20 µm in length, smooth; upper median laminal cells elliptic to rhomboidal, 12–25 µm in length, smooth; alar regions multitiered except for innermost columns, more or less auriculate; alar cells reddish brown, bulging. Branch leaves narrowly lanceolate or similar to stem leaves, round at leaf insertion, ecostate; margins entire below, serrulate to lowly serrate above, distinctly bordered; laminal cells quadrate to fusiform above, becoming longer below, ecostate; alar regions multitiered at several outer columns.

Dioicous? Male plants or organs not observed. Perichaetia on prostrate stems or at the base of stipes, with ca. 30 archegonia; paraphyses numerous. Inner perichaetial leaves to 5 mm long, more or less plicate, apex twisted several times when dry, ecostate; alar regions not differentiated. Setae ca. 40 µm long, reddish brown, smooth. Capsules short ovoid, 1.5–2.5 mm long, narrower below mouth, reddish brown or yellowish brown, horizontal to inclined, smooth; exothecial cells hexagonal to rectangular, smooth, thick-walled, weakly collenchymatous, much smaller below capsule mouth and longer below; stomata at

neck, small, superficial, ca. 15 in number. Opercula obliquely beaked, ca. 1.3 mm long. Peristome and spores as in the species.

Distinguishing features. (1) Smaller, not glossy plants forming dense and compact tuft on substrata, (2) upright stipes distinct with widely spreading leaves, (3) stipe- and stem leaves round below and abruptly narrowed at shoulder into long acuminate apices, (4) leaf margins serrulate to lowly serrate above with highly differentiated borders, (4) twisted leaf apices, (5) multitiered alar regions, and (6) rounded leaf insertions even in branch leaves.

Habitat. Growing on soil, rotten logs, tree trunk bases, boulders on forest floor, sometimes hanging from shrub trunks and branches, occurring from (500–) 1000–2100 m alt.

Distribution. Philippines, Malaysia, Indonesia.

Other specimens examined. **PHILIPPINES.** **Luzon:** Laguna Prov., Mt. Maquiling, *Tan 74-099* (FH, MO!, NICH!); *ibid.*, Paete, *July 1900, Ramos s.n.* (NY!, Bureau of Science no. 10061). **Negros:** Oriental Prov., Mountains in the southern part of the province, *Patterson 2858* (collected by W. Brown, May 1, 1958; MO!, NY!). **Mindanao:** Davao, Mt. Batangan, *IV 1888, Warburg s.n.* [H-BR!, NY!: reported as *Trismegistia rigida* in Bartram (1939: 319)]; Bukidnon subprov., Mt. Candon, *1920, Ramos & Edaño s.n.* (BM!, Bureau of Science no. 38381). **MALAYSIA.** **Pahang:** Sempang (Fraser Hill), *Ridley 290* (BM!, SING!). **Johor:** Gunong Blumut, *Holtum 10761* (BM!, SING!). **Sabah:** Papar, Ulu Kimanis, Crocker Range, *Akiyama Crocker-1, 5, 46, 47, 66, 67, 70, 103, 106, 107, 109, 194, 213, 214, 229, 230, 322, 324 390, 392 & 393* (all HYO!); Alab Pass, Crocker Range, *Akiyama Crocker-436 & 437* (both HYO!); *ibid.*, near Sungai Nukakatan between G. Alab and Bundu Tuhan, camping site, *Meijer 10195* (L!); *ibid.*, Bundum (Bundong?), *Butter 229 & 230* (both BM!); Lahad Datu, Tawau Res., Mt. Silam, *Meijer B10560, B10576 & B10613* (all L!); Tawau River Forest Reserve, *Meijer B10832 & B10871* (both L!); West Coast Reserve, Mt. Kinabalu,

Kambaranga, *Meijer B11004 & B11780* (both L!); *ibid.*, Batu Hampuan, *Meijer B12642* (L!); *ibid.*, Mt. Templer, N of Mt. Kinabalu, *Meijer B10178* (L!); Mt. Kinabalu, Carson's Waterfall, 1989, *Clifton s.n.* (MO!); Mt. Kinabalu, Tenempok, *Clemens & Clemens 16, 17 & 18* (all SING, NY!); Mt. Kinabalu, Colombon basin, Numeruk ridge, *Clemens 40081* (BO!, FH, NY!); Mt. Kinabalu National Park, around Headquarters, *Akiyama et al. 63 & 118* (HIRO!, HYO!, UMS!, Herbarium of Kinabalu National Park!); *ibid.*, *Akiyama & Yamaguchi 533* (HYO!); *ibid.*, Liwagu trail, *Akiyama & Yamaguchi 413* (HYO!, UMS!); *ibid.*, between Tenempok Pass and Kamaranga Radio Station, *Iwatsuki 336* (L!, NICH!); *ibid.*, Tenempok-Lumut-Lumut, *Holtum 25694* (NY!, SING!); Mt. Kinabalu, Park Headquater, Silau-Silau trail, *Little 893* (L!); *ibid.*, *Tan 89-826 & 89-851* (both NY!); West Coast Res., Mt. Kinabalu, Ranau, *Meijer B12403* (L!); *ibid.*, Mt. Tambuyokon, 15 miles NE of Kinabalu Park, *Meijer B11107* (L!). **Sarawak:** without exact locality, *Dec. 1906, Merres et al. s.n.* (NY-Mitt.); Poeh Mts., *Everett 45* [NY-Mitt!, isotype of *Acanthodium brevifolium* Dixon. The holotype deposited in BM was revealed to be *Mastopoma pulchellum* (Herzog) H. Akiyama (see Akiyama 2006a). The name of *A. brevifolium* itself is superfluous for *Trismegistia delicatula* Broth., because the former was established based on the same type specimen of the latter.]; Mt. Mulu, *Shackleton M2689* (BM!); Gunong Mulu National Park, Gunung Mulu, near Camp 4, 04°05' N, 114° 5' E, *Touw 21103* (L!); *ibid.*, *Jermy 13262 p.p.* (L!); *ibid.*, around Camp 3, *Jermy 13263* (L!, BM!); *ibid.*, Camp 2, along west ridge, *Jermy 13071* (BM!); 4th Division, Gunong Mulu National Park, 04°05' N, 114°55' E, *Touw 20721, 20807, 20816, 20865, 20926, 20946, 21049 & 21057* (all L!); auf dem bukit Mulu, *Winkler 3081* (HBG!). **INDONESIA. Sumatra:** west slope of Mt. Sibajak, 12 km Brastagi, *Meijer 15658b* (BO, MO!); East Coast, Asahan, *Bartlett & La Rue 53* (BO!, MO!, NY!) & *247* (H-BR!); Atjeh, Gunung Leuser Nature Reserve, Gunung Bandahara, ca. 6 km NE of Kampung Seldok, *de Wilde & de Wilde-Duyffes 14908C* (L!); West Sumatra, Sibajak, 1949, *Cobben s.n.* (L!; L0276963 & L0276964). **East Kalimantan (Borneo):** Long Bawang, 04°20' N , 115°50' E, *Akiyama K-24336* (HYO!).

Note 1. Plants showing intermediate features between var. *subintegrifolia* and var. *rigida* are not uncommon and thus it is sometimes difficult to distinguish these two varieties. However, if comparing typical plants of both varieties growing at the same

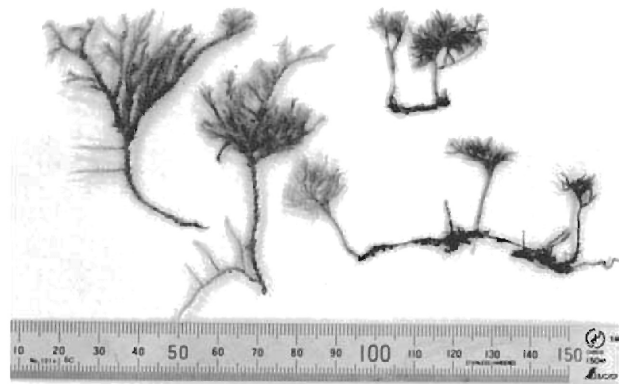


Figure 3. Typical plants of *Trismegistia calderensis* var. *rigida* (left two; *Akiyama Kinabalu-131*) and var. *subintegrifolia* (right two; *Akiyama Kinabalu-533*) from Mt. Kinabalu.

locality, they have quite different appearances. For example, plants growing at a middle elevation of Mt. Kinabalu (Figure 3) illustrate why var. *subintegrifolia* is recognized in this revision.

Note 2. One of the most distinctive features of var. *subintegrifolia* is its narrower distribution, compared with var. *calderensis* and var. *rigida*. It is apparently confined to areas around the Riau pocket (see the note under *T. lancifolia* var. *valetonii*).

Note 3. Tan (1991, p. 103) proposed to synonymize *T. subintegrifolia* under *T. calderensis*. In the present revision, I have partly followed his opinion, but treat the former as a separate variety.

Note 4. According to my field observations, this variety is abundant and constitutes most of the populations of *Trismegistia* at middle elevations on Mt. Kinabalu (1500–1700 m alt.) and also at the Crocker Range [(600–) 1000–1650 m alt.]. They represent a form of *Trismegistia gracilicaulis* originally described from East Borneo. It is also notable that most populations of var. *subintegrifolia* so far known lack sporophytes, but they are abundant in the Kinabalu populations.

3. *Trismegistia complanatulula* (Müll. Hal.) Broth. [Plates 12–13]

Die Natürlichen Pflanzenfamilien I (3): 1078 (1908).

Basionym: *Hypnum complanatum* Müll. Hal., Journal des Museums Godeffroy 3: 89 (1874). Type: (American) Samoa, Tutuila Isl., 14°S, 170°W, in a gully about 1200 ft above sea level, *Powell 55* [lectotype NY-Mitt. (NY0038214)!; isolectotypes BM!, FH, HBG!, NY-Mitt. (NY0038205, NY00388211 & NY00388215)!], quoted as *Acanthodium rigidum* Nees & Reinw. in Mitten (1868)], **lectotype selected here.**

Trismegistia complanata Müll. Hal., Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 23: 331 (1896a). (This is an orthographic variant for *complanatulula*).

Acanthocladium pedunculatum Mitt., Proceedings of the Linnean Society of New South Wales 7 (1): 102

(1882). ≡ *Trismegistia pedunculata* (Mitt.) Broth., *Die Natürlichen Pflanzenfamilien I* (3): 1078 (1908). Type: Aneityum, *Milne 364* (lectotype NY-Mitt.!, isolectotype BM!), **lectotype selected here. Syn. nov.** (see note 4).

Acanthocladium strangei Mitt. & F. Müll., *Proceedings of the Linnean Society of New South Wales* 7 (1): 102. 1882. ≡ *Trismegistia strangei* (Mitt. & F. Müll.) Broth., *Die Natürlichen Pflanzenfamilien I* (3): 1078 (1908). Type: New Caledonia, Isle of Pines, 1906, *Strange s.n.* [holotype NY-Mitt! (NY00012463), isotypes BM!, NY-Mitt! (NY00012460)]. **Syn. nov.** (see note 5).

Plants medium to large, variable in branching patterns, forming sparse turfs on substrata. Primary stems prostrate, pinnately branched. Secondary stems 2–4 cm long, obliquely ascending, sparsely branched or densely branched to form more or less flat fronds, with stipes; central strand absent. Stipe leaves patent to obliquely spreading, to 3.8 mm long, ovate below, gradually narrowed into long, slender apices; costa mostly absent, rarely present, short and double; apices straight or weakly twisted; margins entire below, serrulate above, scarcely bordered; alar regions multitiered only at outer two to three columns, supra-alar cells quadrate. Lower stem leaves similar to stipe leaves. Upper stem leaves 2.2–3.2 mm long, lanceolate, acute, ecostate; margins entire or denticulate below, serrate above, scarcely or weakly bordered with linear cells; upper and median laminal cells linear, 35–75 µm in length, smooth, pitted, becoming longer below; cells of alar regions similar to those of stipe and lower stem leaves. Branch leaves linear lanceolate, weakly curved or straight at leaf insertion, ecostate; margins entire to denticulate below, serrate to spinose above, weakly bordered; laminal cells similar to those of stem leaves; alar cells mostly arranged in a single row except for the outermost column.

Dioicous? Perigonia not observed. Perichaetia on primary stems and base of stipes. Perichaetial leaves linear lanceolate, to 4.0 mm long, plicate. Setae to 5–6 cm long, reddish brown throughout or becoming blackish at base, smooth. Capsules ovoid to short ovoid, 2.0–2.5 mm long, yellowish brown to reddish brown in color, smooth above, plicate below; necks distinct, to 0.8 mm long; exothecial cells quadrate, hexagonal to short rectangular, strongly collenchymatous, becoming much larger towards the base; stomata apparently lacking. Opercula not observed. Spores not observed. Other features as for the genus.

Habitat. On rotten logs and base of tree trunks along streams in lowland and lower montane forests, occurring at 300–800 m alt.

Distribution. Papua New Guinea, New Caledonia (Isl. Pine), Vanuatu (Anatom), Fiji, Samoa.

Distinguishing features. (1) Ascending stems

sparsely branched, lacking distinctive stipes and branchlets, with complanate foliation, (2) stipe- and stem leaves with long, narrowly elongate apices often slightly twisted, (3) acute apices of branch leaves, (4) leaf margins scarcely or weakly bordered, (4) weakly curved or straight leaf insertion of branch leaves, and (5) longer uppermost laminal cells just below apex in branch leaves.

Trismegistia complanatulata resembles *T. calderensis* in having stipe leaves with long, slender, and often twisted apices. However, leaves of *T. calderensis* are deeply rounded at leaf insertion, suddenly narrowed at the shoulders, and have highly multitiered alar regions composing auriculate leaf angles.

Other specimens examined. PAPUA NEW GUINEA.

Morobe: Lae Subdist., Buso, Mt. Kawea, 7°25' S, 147°10' E, *Foreman & Streimann LAE-52027A* (L!, LAE). **Milne Bay:** Sudest Island, Mt. Riu, north slope, *Brass 27891* (L!); Rossel Island, Abaleti, *Brass 28331* (L!); *ibid.*, Mt. Rossel, south slope, *Brass 28416* (L!). **Central:** 30 km E from Prot Moresby, Kokada trail, just below Owen Corner, S 09°22' 12", E 147°29' 23", *Akiyama 16802 & 16804* (both HYO!); Varirata National Park, *Akiyama 16841* (HYO!). **NEW CALEDONIA. Isle de Pine:** Tao, *Jan. 1910, Franc s.n.* (PC-Th!; Musci et Hep. Novae-Caledoniae exsiccati, no. 115, distributed as *T. rigida* var. *brauniana*); Mt. Panié, ca. 20 km NW of Hienghene, *McPherson 3745* (MO!). **VANUATU (NEW HEBRIDES). Anatom (Aneityum):** *Milne 371* (BM!, NY-Mitt.); *Schmid 175* (PC!); *1851-1855, Remy s.n.* (PC-Th!); *ibid.*, *G. B. 8* (BM!, NY-Mitt!); *Aug. 1911, Gunn s.n.* (H-BR ex herb. *Watts 284!*); *Aug. 1912, Gunn s.n.*, (BM!, H-BR ex herb-*Watts 283!*); *Feb. 1913, native collector* (H-BR ex herb-*Watts 362!*); *June 1914, Gunn s.n.* (H-BR ex herb-*Watts 589!*); *July 1914, Gunn s.n.* (H-BR ex herb-*Watts 602!*), *Mar. 1911, Gunn s.n.* (PC-Th!, BM! both ex herb. *Watts 222*). **FIJI: Viti Levu:** Rewa Prov., near Colo-i-Suva, east of city of Suva, *Norris 44295* (MO!, NY!). **SAMOA.** Exact locality unknown, *Powell 204* (BM!, NY-Mitt!). **Savaii:** *Graeffe s.n.* (NY; syntype of *Hypnum complanatum*).

Note 1. Müller (1874) does not seem to have checked the specimen *Powell 55*, which Mitten (1868) cited when he reported *Acanthodium rigidum*. Although citing the specimen in parenthesis, Müller (1874) wrote that no sporophyte had been found. In fact, the specimen bears good sporophytes (Plate 12-4). Judging from the original description, the *Powell 55* specimen should be designated as the lectotype of

Trismegistia complanatula. According to Mitten (1868), the lectotype was collected at 1200–1500 feet in altitude growing on trees and rocks in gullies on the sides of the mountains of Tutuila Island.

Note 2. When Dixon & Greenwood (1930: 298) reported *Trismegistia complanatula* from Fiji on the basis of a specimen [Ovalau reg. montosa, Graeffe s.n. (H-BR!, NY-Jaeger!)], they gave the following short comment, “doubtfully distinct from *T. rigida*”. Later, compiling the moss flora of Samoa, Schultze-Motel (1974) quoted the comment and doubted its distinctness as a species. Examination of the specimen reveals that it is *Trismegistia lancifolia* var. *lancifolia*.

Note 3. A specimen collected in Samoa [Upolu: am Lanutoo, 25/5/1903, Fleischer s.n. (BM!, H-BR!, L!, NY!; Musci Frond. Archipelagi Indici et Polynesiaci, ser. X, no. 494)] has much shorter leaves with short rhomboid laminal cells at the leaf apex and it is

Trismegistia lancifolia var. *lancifolia*.

Note 4. There are two syntype specimens of *Acanthocladium pedunculatum* Mitt. collected by Milne at Aneityum (*Milne 364* and *Milne 371*). As the original description refers to sporophytic features and only the former specimen bears sporophytes, *Milne 364* is here designated as the lectotype.

Note 5. There are two packets of *Acanthocladium strangei* (numbered as NY 00012463 & NY00012460, both NY-Mitt.!) pasted on a single herbarium sheet. Both were collected by Strange from New Caledonia, Isle of Pines, in 1906. One of them (NY 00012463) bears sporophytes while (NY00012460) is sterile. Examining plants in both packets, they are revealed to be the same species. Since the original description refers to sporophyte features, the former should be a holotype.

4. *Trismegistia lancifolia* (Harv.) Broth. [Plates 14–25]

Die Natürlichen Pflanzenfamilien I (3): 1078 (1908).

Basionym: *Neckera lancifolia* Harv., Hooker's Icones Plantarum 2 (4): tab. XXI, fig. 5 (1836); Harvey & Hooker, J. Bot. 2: 14 (1840). Type: Nepal (or East India or Singapore), *Wallich* s.n. (holotype; TCD-Harv.!, isotypes: BM-Hook.!, E!, NY-Mitt.!). [For the original locality of the type specimen, see Long (1995) and note 1].

Plants variable in size and branching patterns, mostly not glossy, more or less complanately foliated, especially in the fronds of ascending stems. Primary stems long, prostrate, pinnately branched. Secondary stems 1–4 cm long, sparsely or tripinnately branched, often forming more or less flat fronds. Stipes of secondary stems more or less developed, absent when growing on wet boulders or on trunks and branches of shrubs. Stipe leaves, if present, ovate below, narrowed into long, slender apices, rarely oblong-ovate at base and acute, plane or plicate (only var. *pseudoplicata*), ecostate; margins entire below, minutely serrulate above, bordered; alar regions well developed, outer 2–4 columns multitiered, inner ones in a single row; alar cells colored and bulging; quadrate to rectangular supra-alar cells present. Stem leaves ovate to ovate-lanceolate, rarely ligulate, acute, usually less than 2.5 mm long, rarely to 3.2 mm long (reaching 3.7 mm long in var. *australiana*), shallowly rounded or almost straight at leaf insertion, plane or plicate (only var. *pseudoplicata*), ecostate; margins entire to denticulate below, serrate to spinose above, bordered; alar regions well developed, similar to those of stipe leaves. Branch leaves similar to stem leaves in shape but smaller, plane, often concave below; alar regions

small in size with cells arranged in a single row except for the outermost column. Branchlet leaves, if present, much smaller in size than branch leaves. Branch and branchlet leaves taken from lateral side of stems with alars bilaterally asymmetric in size and number of cells. Laminal cells subquadrate, short rectangular or fusiform above, becoming linear and much longer below, smooth, sinuate or pitted, well differentiated at margins forming distinct borders.

Dioicous? Perigonia not observed. Perichaetia on primary stems and at the base of stipes of secondary stems. For other features, see descriptions of varieties.

Distinguishing features. (1) Narrowly elongate, almost always straight apices of stipe leaves, (2) upper stem and branch leaves with lanceolate acute apices, (3) well differentiated borders at upper leaf margins, and (4) almost straight or scarcely curved leaf insertions of stem-, branch- and branchlet leaves with smaller alar regions.

Distribution. Thailand, Malaysia, Philippines, Indonesia, Papua New Guinea, Solomon Islands, New Caledonia, Vanuatu, Fiji, and Samoa. As detailed in note 1 below, Nepal and East India are excluded from the distribution areas of *Trismegistia lancifolia*.

Habitat. On soil, rotten logs, base of tree trunks,

often climbing to lower part of tree trunks, hanging from shrub trunks and branches, sometimes on rocks of streambeds in lowland forests and lower to upper montane forests, occurring from sea level to 1000 m alt. [Two specimens were exceptionally known from higher places at 1700 m alt. from Atjeh (North Sumatra) and Selangor (Malay Peninsula)].

Note 1 [Plates 16–17]. Long (1995) pointed out that the original materials of *Neckera lancifolia* (*Wallich s.n.*; holotype in TCD-Harv.!, isotypes BM-Hook.!, E! & NY!) was possibly not collected in Nepal. According to Long (1995, p. 12), “A significant proportion of the localities given in Harvey & Hooker (1840) are almost certainly erroneous. These errors probably resulted from inaccurate labeling of specimens.” He also stated that “the Wallich collection is only record [of *T. lancifolia*] for the Himalaya and almost certainly an error; the species should be deleted from the Nepal checklist. Singapore is much more likely to be the country of origin.” (p. 29).

Examining all the original materials (including that labeled as from East India; *Wallich H-2132*, BM!) deposited in the three herbaria, as well as that collected in Singapore (*Wallich s.n.*, 1824, E!), it became apparent that (1) all the original materials show almost the same appearance and leaf morphology and thus seem to come from the same collection, and (2) the specimen from Singapore shows many similarities and coincides well with these original materials. Therefore, I agree with Long (1995) to designate the locality of the original materials of *Neckera lancifolia* as Singapore and delete Nepal (and East India) from the distribution areas of *Trismegistia lancifolia*.

Note 2. Gangulee (1980) reported *Trismegistia lancifolia* from Eastern India but did not cite any additional specimens. His illustration (Fig. 951) of the species is based on typical plants of *T. plicata*, judging from the large size of the plants and leaves and the deep plication of the leaves. For more details, see note 2 under the species.

Note 3. Previous reports often confuse ‘*Trismegistia korthalsii*’ (= *T. lancifolia* var. *lancifolia* in this revision) with ‘*T. rigida*’ (= *T. calderensis* var. *rigida*) and this is possibly the main reason why so many specimens had been misidentified in local floras (for

example, Bartram 1939, Brotherus 1925, Gangulee 1980, Ramsay et al. 2002) and deposited under incorrect names in herbaria. Both species can be distinguished by the following morphological features:

1. Leaves more or less gradually narrowed into apices. Apices of stipe- and stem leaves long acuminate but rarely twisted. Margins densely serrate, often spinose with more than a single cell in each tooth at upper margins of stem and branch leaves. Leaf insertions of branch- and branchlet leaves nearly straight or weakly curved with narrow alar regions; alar cells mostly arranged in a single row except for outermost one to two columns

..... *T. lancifolia* var. *lancifolia*

1. Leaves more or less abruptly narrowed at shoulder. Apices of stipe- and stem leaves long acuminate, always twisted. Upper leaf margins with weak serration, never spinose with more than a single cell in each tooth. Leaf insertions of branch- and branchlet leaves markedly rounded with wide alar regions; alar regions multitiered even in branch leaves, except for several innermost columns

..... *T. calderensis* var. *rigida*

Note 4. Some specimens from Mindanao Isl., Seram Isl., and New Guinea have extraordinarily large teeth at upper leaf margins (Plate 20–2). It is notable that most of the plants from Seram Isl. uniformly show this feature. However, they are not treated as representing an infraspecific taxon here, because serration itself shows much variation even among leaves taken from a single stem.

Note 5. There is much variation in the size and shape of laminal cells from just below leaf apices, ranging from isodiametric, subquadrate, short rhomboid to linear, even in the leaves taken from a single population. Therefore, such variation is not given any taxonomic status in this revision, although it is sometimes highly impressive when viewed under a microscope because the small inner cells contrast markedly with the long rectangular, thick-walled, and distinctly pitted cells at the margins.

Trismegistia lancifolia grows on various kinds of substrata and is distributed widely from the Malay Peninsula to the Western Pacific islands. There are a number of populations showing distinctive features that appear to be confined to local geographical regions and share ecological features such as habitat preference and epiphytic nature. Five varieties of *T. lancifolia* are recognized in this revision and they can be distinguished as follows:

Key to the five varieties of *Trismegistia lancifolia*

1. Leaves plane or slightly concave, sometimes more or less involute below, but never plicate. 2
1. Leaves of stipes and stems distinctly plicate (Southern part of Malay Peninsula and North Sumatra).
..... var. *pseudoplicata* (4-4)
2. Plants small to large (fronds of ascending stems more than 2 cm long with stipes). Leaves 1.2–3.8 mm (excluding those at branch tips). Laminal cells just below apex quadrate to fusiform, usually 9–25 µm in length. 3
2. Plants small (fronds of ascending stems less than 1 cm long including stipes). Leaves 0.9–2.0 mm long. Laminal cells just below apex quadrate, 4.5–9.0 µm in length. (Endemic to North Borneo).
..... var. *everettii* (4-3)
3. Plants growing on soils, rotten logs, stumps, and the base of tree trunks, becoming pendulous when climbing to shrub trunks and branches. Stem leaves often more than 2.3 mm long. 4
3. Plant growing on shrub trunks, branches and the base of tree trunks, not becoming pendulous. Stem leaves less than 2.3 mm long. (Philippines and Borneo).
..... var. *valetonii* (4-5)
4. Plant small to large. Stem leaves rarely reaching 2.8 mm long. Upper laminal cells varying in shape, subquadrate to short rhomboid, usually less than 50 µm in length. (Widely distributed from southern part of Malay Peninsula to the Western Pacific).
..... var. *lancifolia* (4-1)
4. Plants robust in size. Stem leaves reaching 3.8 mm long. Upper laminal cells constantly linear, longer than 60 µm in length. (Endemic to Queensland, Australia).
..... var. *australiana* (4-2)

4-1. var. *lancifolia* [Plates 14–20]

Acanthocladium merrillii Broth., Philippine Journal of Science 3: 29 (1908) ≡ *Trismegistia merrillii* (Broth.) Broth., Die Natürlichen Pflanzenfamilien I (3): 1078 (1908). Type: Philippines, Luzon, Atimonan, Tayabas Prov., 700 ft., on wet, prostrate, rotten logs in forest, *E. D. Merrill 3985* (holotype H-BR!; isotypes NY!).

Hypnum korthalsii Dozy & Molk., Annales des Sciences Naturelles, Botanique, sér. 3, 2: 307 (1844) ≡ *Trismegistia korthalsii* (Dozy & Molk.) Broth., Philippine Journal of Science 5: 159 (1910). Type: Insulis Java, *Korthals s.n.* (lectotype L!; HDM sheet no. 3, L0109833), **lectotype selected here.**

Trismegistia densiretis Broth., Philippine Journal of Science 31: 295 (1926). Type: Luzon, Apayao subprov., Mt. Sulu, *May 1917, Fenix s.n.* (Bureau of Science no. 28453) (holotype H-BR!, isotype H-BR!, TNS!).

Plants variable in size and branching patterns, not glossy, more or less complanately foliate especially in the fronds of ascending stems. Primary stems prostrate, pinnately branched. Secondary stems to 2–4 cm long, obliquely ascending or upright, rarely horizontal on substrata, branching sparse to tripinnate, usually forming more or less flat fronds. Stipes of ascending stems more or less developed, absent when growing on wet boulders or shrub trunks and branches. Stipe leaves ovate below, narrowed into a long, slender acumen (rarely acute and ovate-lanceolate), plane, ecostate; margins entire below, serrulate above, bordered; alar regions multitiered at outer 2–4 columns, in a single row at inner columns; supra-alar cells quadrate to rectangular. Stem leaves rarely reaching 2.5 mm long, ovate-lanceolate to lanceolate, rarely lingulate, acute, weakly curved or almost straight at leaf insertion, plane, ecostate; margins entire to denticulate below, serrate to spinose above, bordered at upper margins; laminal cells just below apex quadrate to fusiform, 10–25 µm in length,

smooth; upper median laminal cells short rectangular to fusiform (rarely linear), 12–40 µm in length, smooth, becoming longer below; alar regions well developed, similar to those of stipe leaves. Branch leaves narrowly lanceolate, acute to broadly acute, often shallowly concave below, straight or weakly curved at leaf insertion, ecostate; margins entire to denticulate below, serrate to spinose above, well bordered; alar regions narrow; alar cells arranged in a single row except for the outer one to two columns. Branchlet leaves, if present, much smaller in size than branch leaves. Branch- and branchlet leaves taken from lateral side of stems with alars bilaterally asymmetric in size and numbers of cells, often concave below. Laminal cells subquadrate, short rectangular or fusiform above, becoming linear and much longer below, smooth, sinuate or pitted, well differentiated at margins and forming distinct borders. Calyptrae cucullate, naked, smooth, reaching 5.5 mm long.

Male plants not observed. Perichaetia on primary stems and the base of stipes of secondary stems.

Perichaetial leaves to 5.5 mm long, rectangular below, narrowed into long, slender, apices, ecostate; margins entire below, sharply spinose above; alar cells not differentiated. Setae 45–60 mm long, reddish brown, smooth. Capsules ovoid, horizontal to inclined, ca. 2 mm long, narrowed just below mouth after deoperculation, yellowish brown to reddish brown in color, with neck. Opercula with oblique, long beak, ca. 1.5 mm long. Other features as for the genus.

Distinguishing features. (1) stem leaves ovate-lanceolate to lanceolate, acute and plane, (2) complanate fronds developed on more or less clearly developed stipes, (3) upper leaf margins of stem- and branch leaves serrate to spinose, (4) borders well developed at leaf margins, with long rectangular to linear, pitted cells sharply contrasting to shorter inner laminal cells, (5) branch- and branchlet leaves weakly curved or almost straight at leaf insertions, (6) alar regions narrow, with a single row of alar cells.

Distribution. Widely distributed from southern part of Thailand to Samoa. This is one of the most common mosses in the Malesia region.

Habitat. On soil, boulders, rotten logs, stumps, base and lower part of tree trunks, sometimes climbing shrub trunks and branches, in lowland and lower montane forests, occurring from 50–1000 (–1700) m alt., mostly abundant beside streams, never found outside forest floors.

Other specimens examined. **THAILAND.** **Nakohn Si Thammarat:** Khao (Mt.) Luang, 8S°30' N, 99°45' E, *Touw 11978* (BM!, L!, MO!). **Narathiwat:** Chatvarin Falls at Sungai Padi, 6°04' N, 101°52' E, *Charoenphol et al. 4018* (MO!) & *4055* (BM!, MO!, NY!). **Chanthaburi:** Khao Soi Dao, *Kerr m534* (BM!). **Phuket:** Panon Bencha (= Phuket Isl.), *Kerr m510* (BM!). **PHILIPPINES.** **Basilan:** Land Grant of the University of the Philippines, *Aug.-Sept. 1912, Reillo s.n.* (NY!: Bureau of Science no. 16266); Land Grant of the University of the Philippines, *Liborio Ela Eballo 971* (NY!); *ibid.*, *Santos 4139* (MO!, PH). **Luzon:** Laguna Prov., San Antonio, *Aug. 1910, Ramos s.n.* (BM!, BO!, NY!: Bureau of Science no. 12095); *ibid.*, *Aug. 1910, Ramos s.n.* (BO!, H-BR!, MO!, NY!: Bureau of Science no. 12096); Laguna Prov., San Antonio, *Sept-Oct. 1912, Ramos s.n.* (BO!, NY!: Bureau of Science No. 16669); Laguna Prov., *June-Aug. 1915, McGregor s.n.* (NY!: Bureau of Science no. 23271); Laguna Prov., Siniloan, Pulang Lupa, University Philippines Forest Reserve, *Alvarez O-257* (MO!); Quezon Prov., Real, National Botanical Garden, *Alvarez et al. O-771081* [BM!, L!, MO!, NICH!, TNS!; distributed as *Musci Philippinensis Exsiccati Fasc. 1, no. 24* (as *Trismegistia rigida*)]; *ibid.*, *Alvarez O-213* (MO!); *ibid.*, Rizal, *Feb. 1911, Ramos s.n.* (BO!, L!, NY!: Bureau of Science no. 13442); *ibid.*, Llavac, UP Land Grant, *Reyes 60 & 102* (both NY!); *ibid.*, *Reyes 104* (CAHP, MO!, NY!); Mountain Prov., RECORP logging area 30 km south of Luna, *Hale &*

Banaag 25923 (L!, NY!, TNS!) & *25936* (L!, NY!, NICH!); Apayao Subprov., Mt. Sulu, *May 1917, Fenix s.n.* (Forestry Bureau no. 28453; MO!, TNS!); Tayabas Prov., *Whitford 793* (NY!); Tayabas Prov., valley of Tignaon, *Leiberg 1225* (MO!, H-BR!, NY!); Camarines Prov., Magnas, *Aug. 27-18, 1908, Robinson s.n.* (BO!, NY!: Bureau of Science No. 6356 & No. 6325); Mount Banahao, *Pancho 3409* (PC!). **Negros:** near Dumaguete, *Patterson 1346* (collected by M.P. Mack, April 20 1951, NY!); Cadiz, *Celestino 7360* (BM!, BO!, L!, MO!). **Mindoro:** without locality, Apr.-May 1908, *Merritt 12141* (BO!, H-BR!, L!, NY!); N. coast, Headwaters of Subaan River inland from San Teodoro, *Coode 5647* (L!); Canlapan, Mt. Halcon, *Reynoso 2002, 2003, 2011 & 2015* (all MO!, PH); Binabay River, *Merrill 5602 & 5637* (both H-BR!). **Mindanao:** Prov. Misamis, *Jan.-Feb., 1913, Miranda 17950* (BO!, L!, NY!, TNS!). **Sibuyan:** Mt. Guiting-Guiting, *Strain 7* (L!). **Palillo:** *Oct.-Nov. 1909, McGregor s.n.* (BM!, BO!, H-BR!, MO!, NY!: Bureau of Science no. 10517 & 10519). **MALAYSIA.** **Pahang:** without exact locality, *Curtis s.n., 1890* (BM!); National Park of Gunung Tahan, en route from Kuala Melantai to Sungai Puteh, *Akiyama 657* (HYO!); Jeriau waterfall vicinity, upper margins of lowland rainforest, Bukit Fraser resort area, *Tan 89-1337* (NY!); around Water Fall, Fraser's Hill, *Inoue 10222* (TNS!); Penang Island, Western Hill, *Holtum 19311* (BM!, SING!); Taman Negara, Lata Berkoh area on Sungai Thaha, *Manuel 2567* (KLU, NY!) & *2573* (KLU, MO!); *ibid.*, Sungai Teku, *Holtum 20836* (BM!, SING!); Tahan river, *Ridley s.n., 1891* (SING!); Penang Island, hollow north of the Crag, *Burkill 756* (BM!, SING!). **Perak:** Lumut Dinding, *Ridley 842* (SING!); Maxwell's Hill, 3250 ft., *Spare 2122* (BM!); Taiping Hill, *Burkill 13179* (SING!). **Selangor:** KL-Karak Highway, 16th mile mark, *Haji Mohamad 7754* (NICH!; *Musci Malaysian Exsiccati Fasc. 1, 1983*); 15th miles Pahang track, Selangor, *Ridley 483* (NY-Mitt!, SING!); Ulu Gombak Forest Reserve, Genting Sepah Road 25 miles, *Inoue 10251, 10252, 10253, 10271 & 10272* (all TNS!). **Johor:** Gunung Pulai, *Mohd Nur & Kiah 7772* (BO!, L!, SING!); a duplicate deposited at BM is *T. lancifolia* var. *pseudoplicata*; G. Panti Timur, *Haji Mohamed 9351* (KLU, MO!); Kota Tinggi, *Johnson 431a* (SINU!); G. Muntahak, *Holtum 19959* (SING!). **Kedah:** Lankawi Isl., Gunung Raya, *Haniff & Nur 7053* (BM!) & *7083* (SING!). **Malacca:** Bujong, *Ridley 738* (BM!, NY!); Mt. Ophir, *Ridley 227 & 706* (both SING!). **Sarawak:** Gunung Mulu National Park, western entrance of Gua Payau (Deer Cave), *Touw 19399* (L!); Gunung Serapi, 15 km north of Kuching, *Haji Mohamed & Bakar 3008, 3071, 3116, 3117, 3148, 3138 & 3120* (all KLU, MO!); Gunung Gading National Park, 90 km east of Kuching, Lundu, *Mohamed & Bakar 3047* (KLU, MO!); Kuching, near Matang village, Kubah National Park, *Akiyama Sarawak-74* (HYO!). **Sabah:** Telupid, Bukit Tawai waterfall, *Ali & Kiew AI-589 & AI-595* (both SING!); Tawau, 50km W of Lahad Datu, Danum Valley Conservation Area, *Akiyama et al. 7* (HYO!, UMS!); Tawau, NNW of Kalabakan, foot of Maliau Basin, 04°40' N, 117°00' E, *Akiyama Maliau-5, 90, 108, 175, 502 & 572* (all HYO!); Sandakan Res., Sungai Kapur, near mouth of Segama River, *Meijer B12651* (L!); Tawau River Forest Reserve, *Meijer B10699* (L!). **SINGAPORE.** *Wallich s.n.* (type of *Neckera lancifolia*; TCD-Harv., E!, BM-Hook!; written as

collected in Nepal on the labels); *Wallich H-2132* (BM-Hook.!; written as collected in 'East India' on the labels); *Wallich 1824* (E!); Bukit Timah, *Ridley 315* (H-BR!, NY-Mitt!, SING!), *331*, (NY-Mitt!, SING!), *351* (NY-Mitt!), *217*, *595* & *687* (all SING!); Bukit Timah Nature Reserve, *Tan 98-302* (SINU!).

BRUNEI DARUSSALAM. Temburong Dist.: Batu Api Forest Reserve, Kuala Belalong Forest Research Station, riverine forest at mouth of Sungai Sitam draining into Sungai Belalong, *Tan 95-1094* (MO!); Bryophyte Exiccata Brunei Darussalam, no. 24, distributed as *Trismegistia brauniana*).

INDONESIA. Sumatra: without exact locality, *Korthals s.n.* (H-BR!, L!; L0109837, L0194405, L0194406 & L0194407, isosyntypes of *Hypnum korthalsii*); Atjeh Prov., Gunung Leuser Nature Reserves, ca. 15 km W. of Kutatjane, 3°25' N, 97°40' E, *de Wilde 19174B* & *18322B* (both L!); Atjeh Prov., Gunung Ketambe and vicinity, 8-15 km SW from the mouth of Lau Ketambe, ca. 40 km NW of Kutatjane, *de Wilde & de Wilde-Duyffjes 13704C* (L!); *ibid.*, ca. 30 km NW of Kutatjane, *de Wilde & de Wilde-Duyffjes 14634* (L!); North Sumatra Prov., Sibajak, *Arens 530* (L!); West Sumatra Prov., East of Lubuksikaping, west side of Mt. Gadang, *van Borssum Waalkes 1921* & *2021* (both L!); West Sumatra Prov., 10 km east of Padang, Reserve forest of University Andalas, *Akiyama S-144* (HYO!); West Sumatra, Padangsche Bovenlanden, Ajer Pantau, collector unknown *s.n.* (BO!); West Sumatra, Pajakumbuh, Harau-canyon, *Meijer 6033* (L!); Riau Prov., Tigapulu Mts., 5 km W of Talanglakat on Rengat—Jambi road, Bt. Karampal area, 00°46' N, 102°46' S, *Burley et al.*, *1799* (L!); Bengkulu Prov., R. Lembong, Tambang Sawah, *Windadri 335* & *312* (both BO!); *ibid.*, Lebong Utara, Rejang Lebong, *Windadri 428* (BO!); Bengkulu Selatan, V. Talo, *Windadri 364* & *377* (both BO!); Jambi Prov., Pladju, *Meruo Senami, Breedveld 1* & *3* (both BO, L!); Lampung Prov., Mt. Tanggamus, 5°26' S, 104°41' E, *Jacobs B821* & *B849* (both L!); Siberut Island, *Boden-Kloss 14463-b* (SING!).

Engano: without exact locality, *1894, Modigliani s.n.* (NY ex herb. Levier!).

Java: exact locality unknown, *Apr. 1860, unknown collector s.n.* [L!; L0109839 & L0109838: Though written on the label that this specimen was collected by Molkenbor, Touw (2006) pointed out that actual collector was not unknown.]; Gunung Salak, *Akiyama Salak-3* & *Salak-7* (both HYO!); Salak, *Möller 390* (H-BR!, HBG!); West Java Prov., Monte Pangrango, unknown collector *s.n.* [L!; L0109830: Though written on the label that this specimen was collected by Molkenbor, Touw (2006) pointed out that actual collector was not unknown.]; West Java Prov., *Megamendonggebirge am Lemoe* (near Bogor), *1899, Fleischer s.n.* (Musci Frond. Archipelagi Indici et Polynesiaci, Serie XI, no. 532 as *Trismegistia lancifolia* var. *korthalsii*, BM!, BO!, L!); Salak, *Möller 340* & *389* (both H-BR!); Salak, *1-6-1893, Möller s.n.* (NY!); vicinity of Pelabuan Ratu, forest above Pasir Telaga Estate, *Alston 12978a* (BM!, BO).

Banka: G. Paling, *Sept. 1949, Anta & Kostermans s.n.* (BO!).

Kalimantan (Borneo): without exact locality, *de Viries s.n.* (L!; L0109832); Mt. Sakoembang, *Korthals s.n.* (L!; L0109835 & L0194411, isosyntypes of *Hypnum korthalsii*); East Kalimantan, Bulungan, Long Bawan, en route from Long Riman to Sungai Pa Muruk, 03°56' N, 115°35' E, *Akiyama K-24601* (HYO!); East Kalimantan, Kab. Bulungan, Long Bawan, in the vicinity

of Gunung Paris, 220 km W of Tarakan, *Akiyama K-24011* (HYO!); East Kalimantan, en route from Pa Raya to Pa Ru Sudang, *Akiyama K-24115* & *24167* (HYO!); East Kalimantan, in the vicinity of Bulu Kinuab, 04°05' N, 115°50' E, *Akiyama K-24198* (HYO!); East Kalimantan, in the vicinity of Tador Bangar, 04°15' N, 115° 50' E, *Akiyama K-24303* (HYO!); East Kalimantan, en route from Long Riman to Gunung Tapa Sia, 03°56' N, 115°35' E, *Akiyama K-24509* (HYO!); East Kalimantan, Nunukan Island, *Kostermans 9333d* (L!); *ibid.*, Bukit Banglirai, 58 km NW of Balikpapan, *Yamaguchi et al. 21742* (HIRO!, HYO!); West Kalimantan, Kapuas Hulu, Putusibau, Gunung Mahaba, 350 m alt., *Akiyama B-32187* (HYO!); West Kalimantan, Pontianak, Gunung Raya, *Akiyama B-30623* (HYO!); West Kalimantan, Sambas, west slope of Gunung Niut, 750 m alt., *Akiyama B-30723* (HYO!); West Kalimantan, Gunung Pallung Nature Reserve, on Air Putih River, 20 km SE of Telukmelano, 1°15' S, 110°05' E, *Mori et al. 17828* (NY!); South Kalimantan, Hinas Kiri, at the foot of Gunung Batu Besar, en route from Datar Alei to Sungai Menntohoi, 02°20' N, 115°30' E, *Akiyama K-24690* & *K-24709* (both HYO!); East Kutei Dist., Seman R., *Meijer 1517d* & *1528b* (BO!); *ibid.*, terr. Beul, *Meijer 1540c* (BO!); Kutei Nature Reserve, 40m alt., *Dransfield 1613* (BO!).

Sulawesi: South Sulawesi, Soroako, Powerstation, Larona, 24 km from Malili, *Hennipman 5916A*, *5917D*, *5919A* & *5924A* (all L!); South Sulawesi, Soroako-Wasuponda road, *van Balgooy 3635* (L!); *ibid.*, *Hennipman 5751A* (L!); Southeast Sulawesi, Kolaka area, Gunung Watoewila foothills, above Sanggona on Konaweha R., slope of Gunung Sopura, *Coode 6127* (L!); Southeast Sulawesi, Bukit Watoewila, *Kjellberg 7M* (BO!, L!); Kendari, *Kjellberg 62* (BM!, BO!, L!).

Obi: Anggai, Gunung Batu Putih, *de Vogel 4062* (L!).

Ambon: *Robinson 2280* (BO!, H-BR!, NY!).

Seram: Manusela National Park, Kanikeh, *Akiyama C-8576* (BO!, HYO!, L!); *ibid.*, Maraina—Hatuolo, *Akiyama C-9179* (BO!, HYO!, L!); Sawai, Wae Niniyoa—Wae Puo, *Akiyama C-9605* (BO!, HYO!, L!, NY!); Wolu, upper part of Wae Waya, *Akiyama C-10319* (BO!, HYO!, L!); Kairatu, Gunung Okale, *Akiyama C-16817* (HYO!, MO!); Tehoru, en route from Wae Pasola Hatu to Gunung Meseleinan, *Akiyama C-16193* (HYO!, MO!); *ibid.*, en route from Wae Heka Heka to Wae Pasola Hatu, *Akiyama C-16033* (HYO!, MO!); *ibid.*, en route from Wae Selane to Wae Nua, *Akiyama C-14593* (BO!, HYO!, NY!); West Seram, G. Totaniwel, *Akiyama C-15873* (BO!, HYO!, L!); *ibid.*, en route from Tanahgoyang to Gunung Sia Putti, *Akiyama C-15598* (HYO!).

Buru: NW of Buru, *van Balgooy 246* (L!); Air Buaya, Wae Ha, *Mogea & Ismail 5344B* (L!).

Halmahera: Peak of Dguilolo, *Alston 1860a* (BM!).

Batjan: N. slope of Mt. Sibeloe, *Alston 17012a* (BM!, BO); NW slope of Mt. Sibeloe, *Alston 16949a* (BM!, BO).

Morotai: Kali Songowo, *Main & Aden 1654* (BO!); Sangowo, *Main s.n.*, *1949* (BO!).

West Papua (Irian Jaya): Waigeo Dist., Waigeo Isl., Mt. Nok, *Cheesman 104*, *117*, *132*, *141* & *143* (all BM!); Sorong Dist., *Hellendoorn 82C* & *96A* (both L!); Jappen-Biak, Wasaberi near Seroei, *Aet & Idjan 375* (BO!); Sorong, *Hellendoorn 582* (BO!); *ibid.*, 6 Nov. 1949, *Hellendoorn s.n.* (BO!).

Papua: Jayapura Dist., Cyclop Mountains, southern slope of Makanoi Range, W of Kujabu River, *van Royen & Sleumer 6560a* & *6563b* (both L!); Sarmi Dist., Siduars Mts., *Vink 2017* (L!); van Rees Mts., between Kasonoweja and

Banau Bira, 02°26' S, 137°55' E, 3-12-1977, *van der Zon s.n.* (L!); Merauke, Tanahmerah, *van Zanten 101c & 104a* (both L!); *ibid.*, 8 km from Tanahmerah along the road to Mindiptana, *van Zanten 100* (L!, NY!), *107d & 109b* (both L!); 12km from Tanahmerah along the road to Mindiptana, *van Zanten 111a* (BM!, L!), *110* (L!, NY!) & *114a* (L!); *ibid.*, Ajerok, *van Zanten 143* (L!, NY!), *147a* (L!) & *151* (L!, NY!); *ibid.*, Koekoekoem, *van Zanten 234a* (L!) & *265* (L!, NY!); Sg. Bianogga, Aergoemi village, *Aet 626* (BO!). **PAPUA NEW GUINEA. Prov. unknown:** Kaiser–Wilhelmsland, Bismarck Hochland, *Lauterbach 3159* (H-BR!); St. Joseph Valley, *MacGregor s.n.* (H-BR!). **West Sepik:** Utavin village, May River in the Sokamin area of Telefomin, *Bellamy 1515* (CBG, KRAH, MO!, NY!, TBA); Frieda River prospecting area of Frieda Copper Co., Nena River, 5 km NNW of Frieda Base Camp, 04°40' S, 141°45' E, *Koponen 35602* (H, HSC, L!, NICH!, NY!); *ibid.*, Peache Creek, 4°42' S, 141°47' E, *Koponen 35202* (H, HSC, L!); *ibid.*, 04°42' S, 141°47' E, *Koponen 36090* (BO!, H, HSC); Frieda Copper Co., 9 km NW of Frieda Base Camp, 04°40' S, 141°43' E, *Koponen 34938* (H, HSC, NICH!, NY!) & *34912* (H, MO!). **East Sepik:** Wewak–Angoram area, southern slopes of Mt. Toru (Prince Alexander Ranges) near Yangoru, *Robbins 2339* (CAMB, FH, L!) & *2343* (L!); *ibid.*, Maprik–But track, *Robbins 2024* (L!); Kairuru Island, 03°22' S, 143°33' E, *Borrell 6* (CBG, L!); *ibid.*, 1934, *Winzenhoerlein s.n.* (L!); Frieda River, Frieda Air Strip, 04°36' S, 141°58' E, *Koponen 36189* (BO!, H, HSC). **Madang:** Lower Ramu–Atitau area, Adelbert Ranges, near Dogodogo village, *Robbins 1688* (L!); *ibid.*, Asai Valley, Schrader Range, vicinity of Mt. Aiome, *Robbins 1376 & 1423* (both L!). **Western Highlands:** Baiyer River–Ruti Road, Jimi Valley, 42 km N of Mount Hagen, 05°28' S, 144°16' E, *Streimann 22054* (CBG, NICH!, NY!), *22065* (CBG, H, L!, LAE, MO!, NICH!, NY!), *22245* (CBG, H, LAE, NICH!, NY!), *22000* (CBG, H, LAE, NY!) & *22054* (CBG, H, LAE, NHW, NY!). **Morobe:** Owen Stanley Range, in silvis prope Koitaki, *Carr 12509* (BM!, HBG!, BO!, MO!, NY!, SING!; Musci Select et Critici ser. VII, no. 347 as *T. lancifolia*); Buso village, *Bellamy 1614* (CBG, LAE, NICH!, NY!); Huon Peninsula, between Masba Creek and Pependango, ca. 2 km miles S of Pindiu, *Hoogland 8990* (CAMB, FH, K, L!, LAE, US). **Central:** locality unknown, *Nov. 1892, Loria s.n.* (BM!, H-BR!); Sogeri, Subatano, near Port Moresby (foothills Owen Stanley Range), *Robbins 2633* (CANB, FH, L!, LAE); Sogeri Plateau, some 25 miles from Port Moresby, inland slopes of Astrolabe Range near Lake Surinum, *Robbins 4109* (L!); K. B. Sawmill, Ehu Creek, 13 km SW of Sogeri, 09°29' S, 147°31' E, *Streimann & Naoni 16509* (CBG, H, LAE, MO!, NICH!, NY), *16575* (CBG, H, LAE, MO!, NICH!, NY!) & *16657* (CGB, NY!); Mt. Durigolo, near Boku, Port Moresby, *Clark 45* (BM!); Kuriva Logging area, 52 km N of Port Moresby, 09°00' S, 147°10' E, *Streimann & Vinas 14371* (CBG, H, L!, NICH!, NY!) & *14378* (CBG, H, LAE, NICH!, NY!); Road to Musgrave River, just past Itikinumu Plantation, 16 km E of Sogeri, 9°25' S, 147°21' E, *Streimann & Naoni 15267* (CBG, LAE, H, NY!, S, FLAS, W); *ibid.*, *Streimann & Naoni 15268* (L!, MO!, TNS!; distributed as Musci Australasiae Exsiccati no. 139 as *T. rigida*); Bereina–Angabanga River Road, 37km ENE of Bereina, *Streimann & Naoni 16296* (H, KRAM, LAE, MHA, NICH!, NY!), *16322* (CBG, H, NY!,

TAL) & *16356* (CBG, H, LAE, NICH!, NY!). **New Britain:** West New Britain Dist., Kandrian Subdist., Mt. Klalang, 25miles NNE of Gasmata, *Croft & Katik NGF-15561* (L!, LAE); Kandrian subdist., Pirilongi village, 06°06' S, 150°45' E, *Sayers NGF-21966* (BO!, L!, LAE); Kakanai Mountains, 48 km SE of Hoskins, 05°45' S, 150°46' E, *Streimann 40509* (B, CBG, LAE, NICH!). **West New Britain:** Nakanai Mountains, 48km SE of Hoskins, 5°45' S, 150°46' E, *Streimann 40412, 40497 & 40500* (all CBG, LAE, NY!, TAL). **Milne Bay:** North slope of Mt. Dayman, Maneau Range, *Brass 23625* (NICH!, FH); locality unknown, *Micholitz 113* (BM!, H-BR!, NY!); Louisiade Archipelago, Sudest Island, Mt. Riu, west slope, *Brass 27945* (L!); Woodlark Island, mountain behind Luluai, *Brass 28801* (BM!, L!); d'Entrecasteaux Archipelago, Normanby Island, Waikauima, *Brass 25628* (CBG, L!; see note 6); *ibid.*, Fergusson Island, mountain between Agamoia and Ailuluai, *Brass 27034* (CBG, L!; see note 6). **SOLOMON ISLANDS. Bougainville:** lower south slopes of Lake Lololu, c. 16 miles north of Buin, *Craven 162* (L!, LAE) & *297* (L!). **FIJI. Naviti:** *Milne s.n.* (BM!, NY-Mitt!); Colo-i-Suva Forest Reserve, ca. 3 miles N of Suva, *Buck 7170* (NY!); *ibid.*, *Akiyama Fiji-1, 2, 3, 4, 5, 6, 78, 93 & 94* (all in HYO!); Waterfall near Tamavuna, Suva vicinity, *Whitehouse 29904a* (MO!). **Ovalau:** locality unknown, *Graeffe s.n.* (H-BR!, NY-Jaeger!); *Milne, s.n.* (BM!, NY-Mitt!). **SAMOA. Upolu:** am Lanutoo, *25/5/1903, Fleischer s.n.* (BM!, H-BR!, L!, NY!; distributed as Musci Frondosi Archipelagi Indici et Polynesiaci, ser. X, no. 494).

Note 1. *Trismegistia lancifolia* var. *lancifolia* corresponds to *Trismegistia korthalsii* (or *T. lancifolia* var. *korthalsii*) frequently reported in the literature. Features of the lectotype specimen of *Hypnum korthalsii* (Plate 18: 1) agree well with those of the holotype of *Neckera lancifolia* (Plates 16–17).

Note 2. This variety occurs at lower elevations throughout its distributional range than *T. calderensis* or *T. panduriformis*. For example, at Crocker Range (north Borneo) where I have undertaken extensive field observations, var. *lancifolia* occurred below 800 m alt., (rarely reaching 1000 m alt.), while *T. calderensis* and *T. panduriformis* were found at altitudes higher than 1000 m alt.

Note 3. Where found on wet boulders or rocks of streambeds in Western Malesia, this variety tends to grow prostrate on the substratum with only short, lateral branches on both sides and lacking ascending stems. The plants then take on a rather different appearance to the typical plants with ascending stems and upper fronds (Plate 14: 4). Such plants do not bear branchlets and thus there is little difference in the size and shape of stem- and branch leaves. In addition, the leaf borders are usually scarcely differentiated in such plants. Most of the specimens previously collected in Singapore belong to this type.

Note 4. When Bartram (1939) reduced *Trismegistia densiretis* to synonymy of *T. rigida* (= *T. calderensis* var. *rigida* in this revision), he wrote “*T. densiretis* Broth. is usually one of the forms of this variable species”, a conclusion with which I do not concur. The stipe- and stem leaves scarcely narrowed at the shoulder, acute and lanceolate branch leaves, the coarsely serrate leaf margins, and the alar cells arranged in a single row in branch- and branchlet leaves (Plate 18: 2) suggest a close affinity of *T. densiretis* to *T. lancifolia* var. *lancifolia*, not to *T. calderensis*.

Note 5. Plants of var. *lancifolia* always show more or less complanate foliation of ascending stems and fronds. A single specimen cited below showed exceptional terete foliation (other features do not differ from those of typical plants). In addition, plants collected from Seram Island and New Guinea often show strong differentiation of stipes and their stipe are roundly foliate (fronds of ascending stems are more or less complanately foliate).

Specimen examined: MALAYSIA. Sarawak: Kuching, near Matang village, Kubah National Park, 600m alt., *Akiyama Sarawak-73* (HYO!).

Note 6. Two specimens collected at d'Entrecasteaux Archipelago, Papua New Guinea [*Brass 25628* from Normanby Island (Plate 20: 5) and *Brass 27034* from

4-2. var. *australiana* H. Akiyama, var. nov. [Plate 21]

A typo differt foliis majoribus ad 3.8 mm longis, margine dilute limbatis, stipitibus, caulibus et foliis caulinis in formis vix diversis.

Type: Australia, Queensland: Cook Dist., Noah's Creek., Cape Tribulation, 16 07 S, 145 25 E, *Stone 18054* (holotype MELU!).

Plants large, forming a dense turf. Primary stems long, prostrate, curved, pinnately branched; without central strand. Secondary stems more or less ascending, sparsely branched, not forming fronds; stipes weakly or scarcely differentiated. Stipe leaves, if present, ovate below, more or less narrowed at shoulder into long, straight apices; ecostate; margins entire below, denticulate to lowly serrate above, scarcely bordered; alar region well developed, auriculate, segmented except for inner several columns, with one to two rows of quadrate cells above. Stem leaves ovate-lanceolate, to 3.7 mm long, more or less gradually narrowed, acute; ecostate; margins entire below, denticulate to serrate above, scarcely bordered; laminal cells just below apex elliptic to linear, 20–38 μm in length, smooth; upper median laminal cells fusiform to linear, 30–40 μm in

Fergusson Island] have an extraordinary feature for var. *lancifolia*, that is, leaves almost lacking marginal borders. They are tentatively included in var. *lancifolia* because of their lanceolate, acute leaves and weak alar development.

Note 7. Some plants from the Fiji Islands (Plates 14: 9, 17: 5–6, and 20: 4) show a sparse branching pattern in ascending stems and there is only a weak differentiation in size and shape between stem- and branch leaves. From field observations I have made, such plants grow on wet to moist boulders and rocks covered with thin soil along streams in lowland forests. It is notable that they are never found growing directly on soils nearby.

Note 8. The illustrations of *Hypnum lancifolia* presented in the Bryologia Javanica (Tab. CCXXXIX) are not *T. lancifolia* var. *lancifolia*. The specimen used for the illustrations is deposited at L (L0194402, Herb. Lugd. Bat. No. 910.104-964, annotated by Dr. Touw in 2005) is *T. calderensis* var. *rigida*, judging from the shape of the stipe- and stem leaves being rather abruptly narrowed at the shoulders into long and distinctly twisted apices, and also from the shape of the branch leaves which are gradually narrowed into acuminate apices and markedly rounded at leaf insertion.

length, smooth, becoming longer below; alar cells large or small, outer two or three columns segmented. Branch leaves ovate lanceolate to ligulate, acute, often concave near insertion, slightly curved or almost straight at base; ecostate; margins denticulate below, densely serrate to spinose above; marginal cells scarcely differentiated; alar cells arranged in a single row. Sexual organs and sporophytes not observed.

Distinguishing features. (1) Larger size and weak differentiation between stipe-, stem-, and branch leaves, both in size and shape (except for much smaller leaves at branch tips), (2) stipe leaves more or less gradually narrowed into straight apices, (3) leaf margins with weak borders, (3) branch leaves ligulate to linear lanceolate, with acute apices, (4) leaf margins serrate to spinose, (5) linear laminal cells (longer than 60 μm) just below apex, (6) slightly or weakly curved

leaf insertion of branch leaves, and (7) alar regions of branch leaves arranged in a single row except for the outermost 2–3, multitiered columns.

Habitat. Growing in tropical rain forests. No other information is available.

Distribution. Australia (Queensland).

Other specimens examined. AUSTRALIA. Queensland: Cook Dist., Noah's Creek., Cape Tribulation, 16°07'S, 145°25'E, *Stone 18055, 18056, 19329* (all MEL!); *ibid.*, Mt. Mistake, *Stone 20919* (MEL).

Note 1. Though Ramsay et al. (2002) cited the specimens collected in Queensland as *Trismegistia rigida*, it should be noted that they synonymized *T. lancifolia*, treated as a different species in this revision, under *T. rigida*. Features listed above, especially those of (2), (3), (4), (6), and (7), clearly suggest its close affinity to *T. lancifolia* not to *T. rigida*. One of the specimens Ramsay et al. (2002) cited, *Stone 20919* (Mt. Mistake N. P., MEL) was not available for study by the author.

Note 2. Full descriptions and good illustrations of gametophytes were given by Ramsay et al. (2002).

4-3. var. *everettii* H. Akiyama, var. nov. [Plate 22]

A typo differt plantis multo minoribus, foliis caulinis cordiformibus vel breviter rectangularibus vel late ovatis cum apicibus tenuibus, cellulis laminaribus superis stabiliter quadratis.

Type: Malaysia. Borneo, Sarawak, *Everett s.n.* (holotype NY-Mitt.!, isotype BM!).

Plants small. Primary stems short, prostrate, wiry, with scaly leaves, sparsely branched. Secondary stems upright, densely branched and forming dendroid fronds, 1.5–2.0 cm long. Branches rarely reaching 5 mm long. Stipe leaves short triangular with round base narrowed to a short, acute apex or abruptly narrowed at shoulder into a long, slender apex, 1.4–2.0 mm long, straight at leaf insertion, ecostate; margins entire below, serrate above; markedly bordered with two to three rows of short rectangular, pitted cells; laminal cells quadrate to short rhomboid above, becoming longer below; alar regions well developed, multitiered at outer two to three columns. Stem leaves cordate or wide ovate with slender apices, slightly or scarcely rounded at leaf insertion, ecostate, ca. 1.5 mm long; margins entire to denticulate below, densely serrate or spinose above; markedly bordered with two to three rows of short rectangular, pitted cells; laminal cells quadrate to short rhomboid, 8–20 µm in length above, becoming longer below, smooth; alar regions well developed, mostly multitiered, except inner ones. Branch leaves short lanceolate, broadly acute, 0.9–1.2 mm long, straight at leaf

Their figure 12 showing sporophytic features, however, is based on a New Guinea specimen (*Streimann 19860*, CANB), which was also unavailable for study.

Note 3. Considering the disjunct distribution from the other populations of *Trismegistia* and the unique features of its leaves (larger size, scarcely differentiated borders, etc.), it might be better to treat Australian plants as a separate species in future after enough samples are accumulated to evaluate such differences.

Note 4. There is a specimen from West Sumatra, which bears large leaves like those of var. *australiana*. It differs from the Australian plants, however, in having leaf margins well bordered and short, rectangular upper laminal cells just below apex, precluding its inclusion in the same taxon. Its identity is left for future studies.

Specimen examined: INDONESIA. West Sumatra. Mt. Sago (Bukit Nantigo) near Pajakumbuh, natural forest, 900–1000 m alt., *Meijer 7169* (L! ex Herarium Agricultural Faculty, Universitas Andalas).

insertion, ecostate; margins densely serrate to spinose in upper 2/3 of leaf; markedly bordered with two to three rows of short rectangular, pitted cells; laminal cells quadrate to short rectangular just below apex, becoming longer below; alar cells arranged in a single row.

Dioicous? Male plants not seen. Perichaetia on prostrate stems. Perichaetial leaves with long, slender apices, ecostate; margins entire below, serrate above. Seta ca. 3–4 cm long, smooth, reddish brown. Capsule ovoid, 1.5 mm long. Other features not observed.

Distinguishing features. (1) Small plant size with ascending stems to 2 cm long, (2) well developed stipes, (3) branch leaves short lanceolate with broadly acute apices, (4) almost straight leaf insertion, (5) shorter laminal cells, quadrate to short rectangular in branch leaves, (6) leaf margins serrate to spinose upper with markedly differentiated borders, and (7) small size of capsules.

Habitat. No information is available.

Distribution. Borneo (Sarawak, Sabah).

Other specimen examined. MALAYSIA. Sabah: Mt.

Trus Madi, Tambunan Road, 1800 m alt., *Marabini 37* (L!).

Note 1. The broadly acute branch leaves with almost straight leaf insertion lines at base, and alar cells arranged in a single row of *Trismegistia lancifolia* var. *everettii* suggest its close affinity to *T. lancifolia* var. *lancifolia*, although plant size is much smaller than var. *lancifolia*.

Note 2. Only two specimens from Borneo Island

4-4. var. *pseudoplicata* H. Akiyama, var. nov. [Figure 4, Plates 23 (1–4) & 24]

A typo stipitibus et foliis caulinis distincte plicatis differt.

Type: Malaysia, Pahang, Genting Highland, nearby Gohtong Raya, 1000 m alt., *Akiyama 15688* (holotype in HYO!; isotypes BM!, L! & NY!).

Plants mostly similar to var. *lancifolia*, but differs in having gradually narrowed, lanceolate, and distinctly plicate stipe- and stem leaves. Stems leaves tightly appressed throughout. Branch leaves are smaller than stem leaves, not plicate, often concave below, and lingulate with acute to broadly acute apices. Other features as in the type variety.

Distinguishing features. (1) Secondary stems upright or obliquely ascending, usually with distinct stipes, (2) fronds of ascending stems more or less complanately foliated, (3) stipe- and stem leaves gradually narrowed at shoulder, acute, distinctly plicate, (4) each stem leaf, from the base to apex, tightly appressed to stem, (5) branch leaves smaller than stem leaves in size, lingulate, broadly acute, almost straight at leaf insertion, margins serrate to spinose above and well bordered with linear cells, (6) upper laminal cells quadrate to short rhomboid, and (7) alar cells of branch leaves arranged in a single row.

have been collected. They are different in leaf shape; stipe leaves of the holotype are acute, while those of the other are long acuminate with more or less twisted apices. As the other features coincide well, such differences are treated as variation within this variety.

Note 3. There is no record of *Trismegistia* species in the recent report on the moss flora of Mt. Trus Madi (Suleiman & Edwards 2002).

Distribution. Southern part of Malay Peninsula and North Sumatra.

Habitat. Growing on rotten logs, boulders, base of tree trunks on floors of lowland and lower montane forests, occurring from 100–1000 m alt.

Other specimens examined. MALAYSIA. **Kelantan:** Taman Negara, Kualah Koh, vicinity of ATM, *Kien Thai 1850* (HYO!, KLU!). **Pahang:** Taman Negara, Lata Berkoh area on Sungai Thaha, *Manuel 2553* and *2575* (both KLU, MO!, NY!); *ibid.*, along Sungai Tahan, *Akiyama 610* (HYO!); *ibid.*, en route from Kuala Melantai to Sungai Puteh, *Akiyama 657* (HYO!); Gunung Tahan, *Haniff & Nur 8075* (BO!, L!, SING!); Genting Highland, nearby Gohton Raya, *Akiyama 15689, 15690, 15692 & 15693* (all HYO!); Pulau Penang, *Binstead 756* (BM!). **Negri Sembilan:** Gunung Angsi, *Herklots 214* (BM!). **Perak:** Penang? *1896, Curtis s.n.* (BM!, SING!). **Selangor:** Ulu Gombak Forest Reserve, Genting Sempah Road 25 miles, *Inoue 10250* (TNS!); Genting Sempah, *Stone 5534* (L!); Ginting Simpak (Genting Sempah?), *Holtum 28129* (BM!, SING!). **Johor:** Gunung P'ulai, *Nees & Kiah 7772* [BM!; duplicates deposited at BO, L, and SING (collectors are designated as *Mohd Nur & Kiah* or *Md Nur*) are *T. lancifolia*

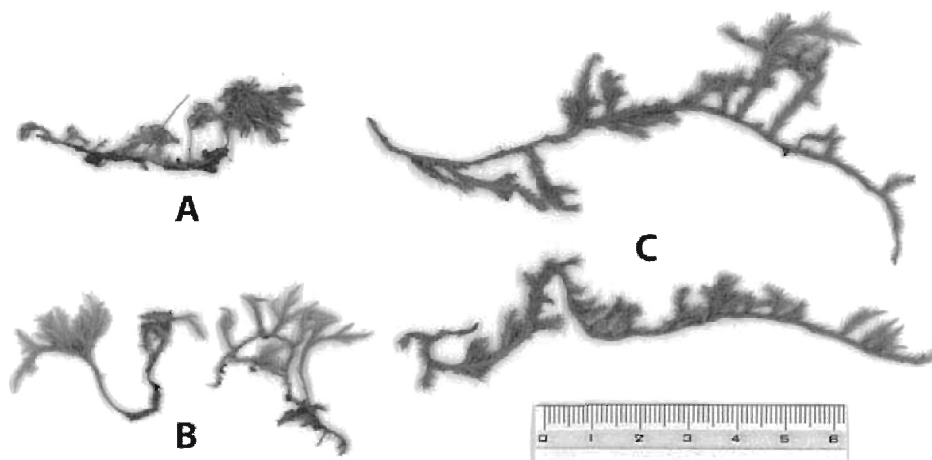


Figure 4. Plants of *Trismegistia lancifolia* var. *pseudoplicata* (A & B) and *T. plicata* (C). A ; holotype, *Akiyama 15688*. B; *Akiyama 610*. C; holotype, *Akiyama Sarawak-68*.

var. *lancifolia*]; Kota Tinggi, *Johnson 431* (KLU, SING!); Gunung Pantii, *Ridley 265* (H-BR!, SING!), Gunung Pantii, near Kota Jingg, *Manuel 3485* (MO!). **SINGAPORE.** Fern Valley, Bukit Timah Forest Reserve, *Sinclair 7210* (A, BM!, C, CANB, E, L!, PNH, SING!, UC); Fern Valley, *26 Jan. 1953, Sinclair s.n.* (Singapore Field No. 39470; BM!, BO!, L!, SING!); Bukit Timah, *Ridley 12549B* (BM!, SING!); Botanic Gardens, *Ridley 606* (BM!, NY!, SING!). **INDONESIA.** **Sumatra:** Atjeh, Gunung Leuser Nature Reserves, Sikunder Forest Reserve, ca. 75 km WNW of Medan, Besitang River, 3° 55' N, 98° 05' E, *de Wilde 19453B* (L!). **Riau:** North Natunas (Bunguran Isl.), *Everett 62 & 72* (SING!).

Note 1. *Trismegistia lancifolia* var. *pseudoplicata* has affinity to var. *lancifolia* in (1) wider upper lamina of stipe- and stem leaves, (2) ligulate, broadly acute branch leaves that are smaller than stem leaves, and (3) branch leaf alar cells arranged in a single row. Its restricted geographical distribution also suggest its distinctness from the other varieties of *T. lancifolia*.

Note 2. Distinct plication of stipe- and stem leaves is well marked but sometimes difficult to recognize by

eye in the field. In addition, stipe- and stem leaves that are not plicate or only shallowly plicate are sometimes intermingled with distinctly plicate leaves on the same plant. Careful examination of such features is necessary to recognize this variety.

Note 3. Plication in stipe- and stem leaves of var. *pseudoplicata* might suggest its relationship to *Trismegistia plicata*. The latter species, however, has much coarser plants (Figure 4) and larger leaves. Sparse and irregular branching pattern (not forming complanate fronds), often lacking stipes in secondary stems in *T. plicata* also suggest their remote inter-relationships. It is interesting that *T. lancifolia* var. *pseudoplicata* and *T. plicata* show so-called complementary distribution patterns, that is, var. *pseudoplicata* is distributed in the southern part of the Malay Peninsula and northern most part in Sumatra Island, while *T. plicata* is restricted to western coasts of Borneo. More extensive examination is needed to reveal their true inter-relationships.

4-5. var. *valetonii* (M. Fleisch. ex Dixon) H. Akiyama, **comb. nov.** [Plates 23 (5–6) & 25]

Basionym: *Trismegistia valetonii* M. Fleisch. ex Dixon, *Journal of the Linnean Society, Botany* **50**: 116 (1935). Type: Borneo, Liang Gagang, *1893-94 Hallier B2657* (holotype FH!; isotype BM!, BO!, L!).

Plants small to medium, forming a dense, short turf. Primary stems long, prostrate, pinnately branched; without central strands. Secondary stems upright or obliquely ascending, densely branched and thus forming more or less dendroid fronds; stipes more or less differentiated. Stipe leaves, 2.0–2.3 mm long, round to rectangular at base, more or less abruptly narrowed at shoulder into long and slender apices, ecostate; margins entire below, serrate and well bordered above; alar regions narrow to wide, sometime auriculate, multitiered only in outermost one to three columns, supra-alar cells quadrate, in one to two layers. Stem leaves 1.8–2.3 mm long, rectangular to round at base, not or weakly narrowed at shoulder into broad acute apices, ecostate; margins entire to denticulate below, serrate to spinose above, well bordered with longer cells; laminal cells just below apex short rectangular, 8–20 µm in length, smooth; upper median laminal cells fusiform (rarely linear), 12–30 (–50 µm) in length, smooth, becoming longer below; alar regions multitiered in outer two to four columns. Branch leaves ca. 1.3 mm long, ligulate, broadly acute to obtuse, almost straight at leaf insertion, ecostate; margins densely serrate to spinose in upper 2/3 of leaf, well bordered; alar regions narrow and alar cells arranged in a single row.

Branchlet leaves, if present, similar to branch leaves in shape, but smaller.

Dioicous? Perigonia not observed. Perichaetia on prostrate stems or base of stipe. Perichaetial leaves reaching 4.3 mm long, linear triangular with long, slender apices, smooth, ecostate; margins entire below, serrate above; alar cells not differentiated. Seta to 30–40 mm long, reddish brown, smooth. Capsules oblong ovoid, ca. 2 mm long; exothecial cells hexagonal, thin-walled, slightly collenchymatous; stomata on neck, ca. 30 in number. Peristome double. Exostome teeth whitish, ca. 70 µm high, lanceolate, densely striated throughout. Segment with high basal membrane, sparsely papillose; cilia 3 in number. Spores spherical, green in color, thin-walled, with low sparse papillae, 9–12 µm in diameter.

Distinguishing features. (1) Small to medium size of plants, (2) secondary stems upright or obliquely ascending, usually with distinct stipes, (3) more or less complanately foliated fronds of ascending stems, (4) stipe- and stem leaves gradually narrowed at shoulder, acute, distinctly plicate, (5) branch leaves smaller than stem leaves, ligulate, broadly acute to obtuse, almost straight at leaf insertion, margins serrate to spinose above, well bordered, (6) upper laminal cells short rectangular to fusiform, (7) alar

cells of branch leaves arranged in a single row, and (8) epiphyte habitat preference.

Habitat. Growing on shrub branches and the base of tree trunks, rarely on limestone (Gunung Serapi, Sarawak), in lowland and lower montane forests, occurring from 150–1260 m alt.

Distribution. Philippines, Borneo.

Other specimens examined. **PHILIPPINES.** **Basilan:** Zamboanga Prov., Lamitan Dist., 5–6 km south of University Philippines Landgrant, upper slope of Mt. Quibang, *Santos 4551* (MO!, PH). **Luzon:** Rizal Prov., *Ramos 13447* (BO!, L!, NY!); Tayabas Prov., valley of Tignaon, *Leiberg 1225* (NY!); Quezon, Atimonan, *Tan 74-310* (CAHP, MO!); Quezon, Llavac, University Philippines Landgrant, *Reyes VR-69* (CAHP, MO!); Tawas, near Yawas River, *Santos 4135* (MO!, PH). **Negros:** Cadiz, *Celestino s.n., 1909* (BM!, MO!, NY!; Bureau of Science no. 7360). **Polillo:** *Robinson Aug. 1909* (BM!, NY!; Bureau of Science no. 9107). **Mindanao:** Butuan subprov., *Weber 1293* (NY!). **Catanduanes:** *Nov. 14–Dec. 11, 1917, Ramos 30612.* (BO!, L!, MO!, NY!). **MALAYSIA.** **Sabah:** Papar, Crocker Range, *Akiyama Crocker-212* and many others (HYO!); Ulu Tongod, Rara Camp, *Meijer 10-92* (MO!); Nabawau, Batu Saap, *Chia cc98-21* (SING!); Tawau, NNW of Kalabakan, foot of Maliau Basin, 04°40' N, 117°00' E, *Akiyama Maliau-90, 175 & 518* (HYO!). **Sarawak:** Ulu Tinjar, Mt. Dulit, near Long Kapa, Dulit trail, *Richards 1503* (BM!, SING!); G. Mulu National Park, W. of Sungai Berar Camp, *Jermy 13646:2* (BM!, L!), *13664:1* (L!), *13664:5 p.p.* (L!), *13664: 7* (L!, BM!), *13664: 8* (BM!), *13664: 18 p.p.* (L!), *13777:7* (L!); *ibid.*, trail to Hedden Valley between Camp 1 and Halfway Camp, *Touw 21172* (L!); *ibid.*, Wooded bed of Snake River near Camp 1, *Touw 20699* (L!), *20666* (L!); *ibid.*, near Camp 1, *Touw 20607* (L!); *ibid.*, on slope at Camp 2, *Touw 20707* (L!); Marudi Forest Reserve, 3 miles south east of Marudi town, *Jermy 13365* (BM!); Ulu Tongod, Rara Camp, *Meijer 11-92, 38-92 & 77-92* (all MO!); Gunung Serapi, 15 km north of Kuching, *Haji Mohamed & Bakar 3133 & 3136* (both KLU, MO!); *ibid.*, at the peak around the telecommunication complex, *Haji Mohamed 3108A* (KLU, MO!); Mt. Poah, *Aug. 1892, Everett s.n.* (H-BR!). **BRUNEI DARUSSALAM.** **Temburong:** Batu Apoi Forest Reserve, Kuala Belalong Forest Research Station, *Tan 95-1433* (FH, L!). **INDONESIA.** **Kalimantan (Borneo):** East Kalimantan, Wanariset, 2.5 hours walk SE of Long Sungai Barang, 1°40' N, 115° E, *van Valkenburg 1215* (L!); Nunukan Dist., Krayan Subdist., Paraye, *Suleiman 1037 & 1075* (BORH!, HYO!); West Kalimantan, G. Kenepai, *Hallier B1956 p.p.* (BO!, L!; original specimen of *Trismegistia microides* M. Fleisch. in sched.); West Kalimantan, Kapuas Hulu, Putussibau, Talai River (branch of Kerinau River), Mt. Mahaba, near Salim village 00°48' N,

113°15' E, *Akiyama B-32186 & B-32191* (HYO!); *ibid.*, Sambas, Gunung Niut, *Akiyama B-30767* (HYO!); Central Kalimantan, Riam Batang, Sampit, *Windaderi 718* (BO!).

Note 1. The holotype of *Trismegistia valetonii* and most of the specimens listed above are consistently smaller in size than plants of *T. lancifolia* var. *lancifolia*. However, there are intermediates in size between the two varieties and their distribution areas overlap. The var. *valetonii* is thus included under *T. lancifolia*.

Note 2. There are three paratypes of *Trismegistia valetonii* deposited in BM. Among them, “Ref. 1503b, G. Dulit., *Oxford Exp., 27, Aug. 1932*” and “Ref. 1516, Dulit trail, *Oxford Exp., 26, Aug. 1932*” are *T. lancifolia* var. *lancifolia*, and the third, “Ref. 2703, Mt. Mulu, *Oxford Exp., Nov. 1932*” is referable to *T. calderensis* var. *subintegrifolia*.

Note 3. Three specimens collected from limestone at Gunung Serapi, Sarawak (*Haji Mohamed & Bakar 3133 & 3136, Haji Mohamed 3108A*) tend to have shorter stipe leaves.

Note 4. It is notable that this variety have been found at localities surrounding the “Riau Pocket”, which is regarded as a refugee during historical dry periods (Ashton 1992, Corner 1960, Wong 1998).

Note 5. (Plate 25: 7–8) Plants showing similarities to var. *valetonii* in having small plant size and similar leaf shapes, but differing in the branchlet leaves being more or less deeply inrolled at the base and in the terrestrial habitat preference, are known from the southeastern and northwestern part of Borneo Island. They are listed below and tentatively excluded from var. *valetonii* for future studies.

Specimens examined. **MALAYSIA.** Sarawak: Mt. Dulit, *Richards s.n., 1932* (BM!, K, NICH!, SING!). **INDONESIA.** **Kalimantan (Borneo):** East Kalimantan, East Kutai, Dist. Muara Muntai, Peak of Balikpapan (= Gunung Beratus or Beratoes), terr. Bewai, *Meijer B1302C* (BO!, L!, NICH!), *B1419* (BO!), *1422* (BO!, L!, NICH!) & *1470b* (BO!); *ibid.*, terr. Beul, *Meijer B1914* (L!); *ibid.*, terr. Sulau Mandau, *Meijer B1706c* (L!, NICH!), *B1733a, B1740, B1762a, B2620a, B2624a, B2797a* (all L!) & *B2552* (BO!).

Habitat. On moist sandstone rocks and decaying wood in lowland or montane forests, occurring from 150–1200 m alt.

5. *Trismegistia malayana* H. Akiyama, sp. nov. [Plates 26 (1–3) & 27]

Trismegistiae lancifoliae similis, sed differt ascendentibus caulibus secundariis absentibus, foliis apice plus minusve transeverse undulatis, margine leniter serratis et vix limbatis, et capsulis globosis vel subglobosis.

Type: Malaysia, Pahang, Cameron Highlands, en route from Tanah Rata to Gunung Jasar, 1470 m alt., Oct. 8, 2003, *Akiyama 15622* (holotype HYO!).

Plants slender, medium in size, green in color, dull or slightly glossy, forming low, more or less flat lawns. Primary stems long, prostrate, wiry, pinnately branched, not forming ascending stems. Lateral stems to 1.5 cm long, pinnately branched. Leaves of lateral stems oblong below, rather abruptly narrowed at shoulder into narrowly ligulate apices, often with shallow transverse undulation above when wet, weakly rounded or almost straight at leaf insertion; costa often developed, short, forked or double; margins entire below, serrulate above, scarcely bordered; laminal cells just below apex fusiform to linear, 20–40 μm in length, smooth; upper median laminal cells linear, 30–50 μm in length, smooth, becoming longer below; alar regions multitiered except for innermost two to three columns, supra-alar cells hexagonal. Branch leaves similar to stem leaves, with wider upper portion; often with short, double costa; margins entire below, serrulate above, scarcely bordered; alar cells arranged in a single row except for outer one to three multitiered columns.

Dioicous? Perigonia not observed. Perichaetia mostly on prostrate shoots. Inner perichaetial leaves to 4 mm long, plicate; alar cells scarcely differentiated. Vaginula pale yellow. Calyptrae not observed. Seta reddish brown, smooth, to 5–6 cm long. Capsules 1.6–2 mm long, globose to subglobose, somewhat pendent, curved when dry; exothecial cells collenchymatous; stomata few, at neck. Annulus cells in 2–3 rows. Urn with short beak, 0.6 mm long. Exostome teeth yellowish, densely striated below, roughly papillose above. Endostome with high basal membranes; segments transparent, whitish, minutely papillose, almost equal in length to teeth; cilia short and filamentous, 0–1. Spores pale brown, finely papillose, (8–) 10–12 μm in diameter.

Habitat. On decaying logs and base of tree trunks in evergreen montane forests, usually forming flat lawns on substrata, locally very abundant, occurring from (1000–) 1200–1600 m alt.

Distribution. Thailand (Peninsular), Malaysia (Peninsular states)

Distinguishing features. (1) Plants totally prostrate on substrata and lacking ascending secondary stems, (2) upper portions of leaves more or less transversely undulate when wet, (3) stem leaves narrowly ligulate with long apices, scarcely rounded or almost straight at leaf insertion, (4) leaf margins with weak serration and scarcely bordered, and (5) capsules globose to subglobose with long setae.

Other specimens examined. THAILAND. Nakhon Si

Thammarat: Khao Luang, 23.5.1968, van Beusekom s.n. (L!; L0277206) & B41 (L!); *ibid.*, 8°30' N, 99°45' E, Touw 11695 (BM!, L!, MO!, NY!). **MALAYSIA. Pahang:** Telom, Ridley 123 (SING!); Cameron Highlands, Robinson Fall, Akiyama 15599 (HYO!); *ibid.*, Henderson 11718 (SING!); Gunung Jasar, Akiyama 15615, 15622, 15652, 15653, 15654 & 15655 (all HYO!); *ibid.*, Gunung Jasar, Chin 308 (NICH!); *ibid.*, trail above Brinchang village, Stone 5704 (L!); *ibid.*, Tanah Rata, Henderson 17823, 17834 (both BM!, SING!), 17830 & 18011 (both SING!); *ibid.*, Spare 3415 (BM!); *ibid.*, Gunung Berembun, Henderson 11754 (BM!, SING!); *ibid.*, track from peak of G. Berembun to golf course near Tanah Rata, 4°30' N, 101°25' E, Hedenäs MY-92-199 (SING!); Fraser Hill, upon the Selangor border, Burkill & Holttum 8399 (BM!, BO!, SING!), 8820 (SING!); *ibid.*, Spare 1693 (BM!, SING!); Gunung Ulu Kali, Akiyama 15675 & 15677 (both HYO!); *ibid.*, Stone 12286-A (KLU, L!, MO!), 13386-A (KLU, L!, MO!); *ibid.*, off road to water strain below Sri Genting, Manuel 3439, 3441 & 3468 (all KLU, MO!); *ibid.*, Stone 13377bis (MO!); on the way to Genting Resort, Akiyama 1569, 15701, 15702, 15703 & 15704 (all HYO!); Ulu Gombak Forest Reserve, Genting Sempah Road 25 miles, Inoue 10273 (TNS!); Maxwell's Hill, Tixier 6187 (PC!). **Kedah:** Kedah Peak, Tixier 5604 & 6086 (both PC!); *ibid.*, Nov. 1915, Mohd Haniff s.n. (SING!). **Perak:** Taiping, Maxwell's Hill, Spare 1517 (BM!); Buyong Malacca, Ridley 720 (BM!, NICH!, SING!); Gunung Hijau, Burkill 12764 (SING!). **Selangor:** Halbinsel, Malakka, Batang, Padangtal, 1910, Stresemann s.n. (JE!; paratype of *Trismegistia deningeri* Herz.).

Note 1. Although the narrowly ligulate upper lamina, weakly serrate and scarcely bordered leaf margins, as well as long setae and globose to subglobose capsules might suggest its affinity to *Wikia*, the species is placed in *Trismegistia* because of its weak but distinct differentiation in size and shape between stem- and branch leaves, more or less multitiered alar regions, complete peristome, and smaller size of the spores, ranging from (8–) 10–12 μm in diameter [According to Fleischer (1915–1923), *Wikia* species in Southeast Asia have larger spores, ranging from 15–30 μm in diameter]. The presence of short, double or forked costae, absence of ascending secondary stems, stem leaves with narrowly ligulate upper portions, and transverse undulation, often found in *Trismegistia malayana*, also suggest its affinity to *Pseudotrismegistia*. However, *Pseudotrismegistia* differs from *T. malayana* in its strongly rugose, undulate upper lamina, multitiered alar regions with quadrate to short rectangular, scarcely bulging alar cells, and leaf margins with dense and strong serration. These discussions are based on morphological features alone and thus further studies using molecular markers are needed to determine its final taxonomical position.

Note 2. The paratype of *Trismegistia deningeri* Herz. (*Stresemann s.n.* JE!) is *T. malayana* as noted above in “Other specimens examined”. The holotype of *T. deningeri* was revealed to represent a separate

species and a new combination, *Mastopoma deningeri* (Herzog) H. Akiyama, had been proposed (Akiyama 2006a).

6. *Trismegistia maliauensis* H. Akiyama & Suleiman [Plates 28–29]

Bryological Research 8 (6): 134 (2003). Type: Malaysia, Sabah; around the Agathis Camp site, foot of Maliau Basin, NNW of Kalabakan, Tawau, 500–600 m alt., 4° 40' N, 117° 00' E, *Akiyama Maliau-141* (holotype HYO!, isotype BORH!)

Plants shiny green, blackish brown in older portions. Primary stems densely branched, prostrate on the substrata. Secondary stems ascending, usually less than 2 cm high (rarely to 3 cm); sparsely and irregularly branched, never forming complanate fronds, roundly foliate even in wet conditions. Stipe leaves appressed, ovate, broadly acute to obtuse, straight at leaf insertion, ecostate; margins entire below, serrulate above, bordered by linear, pitted cells; laminal cells just below apex short rectangular, 8–12 µm in length, smooth; upper median laminal cells fusiform, 12–25 µm in length, smooth; alar regions well developed and becoming auriculate, multitiered in outer several columns, cells reddish brown, inflated. Stem leaves not appressed to stems even in dry conditions, ovate below, more or less gradually narrowed into a wide, short acumen, broadly acute or more or less acuminate, slightly rounded or almost straight at leaf insertion, ecostate; margins entire below, serrate above, well bordered; laminal cells similar to those of stipe leaves; alar regions multitiered in outer two to three columns. Branch leaves widely lanceolate, broadly acute, slightly rounded or almost straight at leaf insertion, ecostate; margins entire below, serrate to spinose above, well bordered; alar cells well developed, often arranged in a single row. Sexual organs and sporophytes unknown.

Distinguishing features. (1) Sparse and irregular branching in ascending secondary stems with round foliation, (2) wider leaves often broadly acute with differentiated marginal borders, (4) well developed alar regions even in branch leaves, (5) serrate to spinose branch leaves with slightly rounded or almost straight leaf insertion, and (6) habitat preference to the

rheophytic zone along streams.

Habitat. Forming sparse turf on wet boulders in riverbeds in moist, primeval lower montane forests, occurring at around 600 m alt.

Distribution. Only found at the type locality (North Borneo, Maliau Basin).

Other specimens examined. MALAYSIA. Sabah: the same locality of the type, *Akiyama 82, 141 and 192* (all HYO!, BORH!); *ibid.*, *Akiyama Maliau-506, 507, 511 and 537* (all HYO!, BORH!).

Notes 1. *Trismegistia maliauensis* always grows in the rheophytic zone along streams and is often found at the base of tall turfs of *Dipteris lobbiana* (Hook.) Moore, a typical rheophytic fern species (Plate 28-2). Morphological features of *T. maliauensis*, such as low ascending secondary stems with round foliation and leaves usually with broadly acute apices, suggest morphological adaptation of this species to the rheophytic habitat (Akiyama 1992a, b, 1995).

At the type locality, *Trismegistia lancifolia* var. *lancifolia* is also found on forest floors nearby and sometimes it grows on boulders together with *T. maliauensis*. Even in such cases, *T. maliauensis* occupies the places nearest to the streams.

Note 2. As Akiyama & Suleiman (2003) already pointed out, *T. brachyphylla*, another species with widely ovate and acute stem- and branch leaves, differs in plant color, branching pattern of ascending stems, and narrowly acute to acuminate apices in stipe leaves. In addition, *T. brachyphylla* has never been found in streambeds: My own field observations indicate that on Borneo Island it often grows on shrub branches and rotten logs in rather drier habitats, such as on the ridges of mountain slopes.

7. *Trismegistia panduriformis* (C.H. Wright) Broth. [Plates 30–32]

Die Natürlichen Pflanzenfamilien I (3): 1237 (1909).

Basionym: *Sematophyllum panduriformis* Wright, Trans. Linn. Soc. London, Bot. ser. 2, 4: 258 (1894). Type:

Malaysia, Kinabalu, 6500 ft., *G. D. Haviland 1426* (holotype BM!).

Plants robust in size, forming thick wefts. Primary stems long, prostrate, irregularly branched. Secondary stems irregularly and sparsely branched; not clearly differentiating into stipe, stem and branches. Stipe-, stem- and branch leaves scarcely or weakly differentiated in size and shape, 2.0–4.5 mm long, widely lanceolate or somewhat ligulate, oblong to ovate below, acute, spreading even when dry, strongly plicate, sometimes rugose, weakly rounded or almost straight at leaf insertion, ecostate; upper and median laminal cells quadrate to short rhomboid, 8–20 µm in length, smooth, becoming longer below; margins plane or undulate, densely serrate almost to the base, well bordered with long-rectangular cells; alar regions of the *lancifolia*-type (Fig. 2-D), outer columns multi-tiered and inner two to three ones with single large cells; alar cells of branch leaves arranged in a single row.

Perigonia not observed. Perichaetia on prostrate shoots; paraphyses few. Inner perichaetial leaves ecostate, linear lanceolate, narrowing into long slender apex, deeply plicate, reaching 5 mm long; margins spinose. Vaginula pale yellow; foot of seta deeply penetrating into vaginula. Setae 4–7 cm long, often sinuose, reddish brown, smooth. Capsules ovoid to short cylindrical, reddish brown, smooth. Other features of sporophytes as for the genus.

Habitat. See under the varieties.

Distribution. Malaysia, Philippines, Indonesia, and Papua New Guinea.

Distinguishing features. (1) Robust, rigid plants, forming thick wefts, (2) stipe-, stem- and branch leaves scarcely or weakly differentiated in size and shape, with deep plication and weakly rounded or almost straight leaf insertion, (3) borders and serration of leaf margins almost reaching 4/5 of leaf length, (4) upper and median laminal cells uniformly small and quadrate above and showing clear contrast to linear cells at leaf margins, and (5) alar regions of branch leaves narrow and cells arranged in a single row as in the case of *T. lancifolia* var. *lancifolia*.

Note. *Trismegistia panduriformis*, together with *T. spinosodontata* known from higher places in New Guinea, is one of the largest species not only for the genus but also for mosses in the Malesian region. It often forms dense wefts at the bases of tree trunks, on rotten logs, and rocks in moist montane forests. Rigid plants, strong serration of the leaf margins, and distinct plication of the leaf lamina are key distinguishing features for the species, even in the field.

There are two varieties recognized here mainly separated from each other by plant size and leaf length. In addition, var. *panduriformis* is restricted in its distribution to upper elevations of Mt. Kinabalu (Borneo Island), while var. *prionodontella* is widely distributed in the Malesian region.

Key to the varieties

1. Plants robust in size, secondary ascending stems 8–12 cm in length; leaves 3–4.5 mm long. Endemic to upper elevations (higher than 1500 m alt.) of Mt. Kinabalu. var. *panduriformis*
1. Plants smaller, secondary ascending stems 4–8 cm in length; leaves 2–3.5 mm long. Widely distributed in Malesia, including Mt. Kinabalu. var. *prionodontella*

7-1. var. *panduriformis* [Plates 30–31]

Habitat. Forming dense and large tufts on soil, on the base of tree trunks, and on rotting logs on the floor of mossy montane forests, occurring at 1500–2100 m alt.

Distribution. Only known from the upper elevations on Mt. Kinabalu, North Borneo.

Distinguishing features. See those of the species and the above key to the varieties.

Other specimen examined. MALAYSIA. Sabah: Kinabalu, *Richards R5733* (L!); Kinabalu National Park, around the Headquarter, *Akiyama et al. 64* (HIRO!, HYO!, UMS!, Herbarium Kinabalu Park!); *ibid.*, along a Liwagu trail,

Akiyama et al. 314 & 416 (all HIRO!, HYO!, UMS!, Herbarium Kinabalu Park!); Mt. Kinabalu, *Akiyama Kinabalu-1140* (HYO!, UMS!); Mt. Kinabalu, Kamborangah, *Holtum 25653* (BM!, SING!); Mt. Kinabalu, Tenompok - Lumu Lumu, *Holtum 25636* (BM!, NY!, SING!); near Kambaranga, *Meijer B11980* (L!).

Note. *Trismegistia panduriformis* was originally described on the basis of the specimen collected from the upper elevations of Mt. Kinabalu, north Borneo. On examining a number of specimens from all over its distribution area, however, it became clear that the type specimen represented the local endemic

population of upper elevations of Mt. Kinabalu and the population was able to be segregated by plant size and leaf length, from those of other places. Thus, two varieties are recognized in this revision, one as a local montane endemic and the other with a wide

distribution.

All specimens previously reported as *Trismegistia panduriformis* from Mt. Kinabalu by Akiyama *et al.* (2001) belong to var. *panduriformis*.

7-2. var. *prionodontella* (Broth.) H. Akiyama, **comb. nov.** [Plates 30 & 32]

Basionym: *Acanthocladium prionodontella* Broth., *Monsunia* **1**: 177 (1900) \equiv *Trismegistia prionodontella* (Broth.) Broth., *Die Natürlichen Pflanzenfamilien I* (3): 1078 (1908). Type: Philippines, Mindanao, Davao, Mt. Dagatpan, 2–6000 ft., 1888 *vi*, *Warburg s.n.* (holotype H-BR!).

Prionodontella warburgii Müll. Hal., *nom. inval. in synonym.*, *Monsunia*, *Beiträge zur Kenntniss der Vegetation des Süd- und Ostasiatischen Monsungebietes I*: 177 (1900)

Trismegistia dendroides Herz., *Hedwigia* **57**: 240 (1916). Type: Mittel Ceram, Passhöhe zwischen Manusela und Wolu, 1750 m alt., *Stresemann I* (holotype JE!, isotype BM). **Syn. nov.**

Differs from the type variety in having smaller plants and leaves.

Habitat. On boulder, rotten logs, tree trunk bases, rarely shrub branches, in rather moist, montane forests, occurring mostly from 960–2000 m alt. However, var. *prionodontella* occurs at higher places, 1800–2250 m alt., in New Guinea.

Distribution. Philippines, Malaysia, Indonesia, and Papua New Guinea. One of the most typical species of the Malesian elements in bryophytes.

Distinguishing features. See those of the species and the above key to the varieties.

Other specimens examined. **PHILIPPINES. Mindanao:** Davao Prov., Mt. Kampalili, *Edaño 71/349* (L!); Bukidnon subprov., Tangulan and vicinity, *June-July 1920, Ramos & Edaño s.n.* (BM!, BO!, NY!, PC!; Bureau of Science no. 37177); Mt. Malindang, *Tan 2001-955* (SINU!). **Mindoro:** Mt. Halcon, *Merrill 5499* (BM!, NY!). **Negros:** Mt. Malbug, *Edaño 71/183*. (L!); near Dumaguete, *Patterson 1341 & 1413* (both NY!); Dumaguete City, in mountain near town, *Patterson 2896* (NY!). **MALAYSIA. Sabah:** Gunung Alab, *Nooteboom 1009A* (L!); Crocker Range, *Meijer B12466* (L!); West Coast Res., Mt. Tambuyokon, c 15 miles NE of Kinabalu peak, *Meijer B11140, B11255, B11400 & B11417* (all L!); Mt. Kinabalu, path from Tenompok to Lumu Lumu, *Wood 1546* (BM!); Mt. Kinabalu, *Akiyama Kinabalu-1001 & Kinabalu-1002* (both HYO!); Mt. Kinabalu, Tenompok–Lamalama (Lumu Lumu?), *Holtum 25635 & 25333* (both BM!, SING!); Mt. Kinabalu, Columbon river basin, *Clemens 34066* (BO!, NY!); Mt. Kinabalu, Ulu Langanani, 6°04' N, 116°40'–44' E, Mamut River, Chew, *Corner & Stainton 2160* (BM!); Mt. Kinabalu, Park Headquarter, Silau-Silau trail, *Little 874, 894 & 900* (all L!); Mt. Kinabalu, below Kamborangah, *Richards R5788* (L!). **Sarawak:** 4th Division, G. Mulu National Park, below camp 4, *Touw 21078* (L!, MO!, NY!); Division 1, Lundu, *Brooke 8467* (L!). **INDONESIA. Sumatra:** exact locality unknown, *Meijer 15903* (MO!). **Kalimantan (Borneo):** East Kalimantan, Bulungan, Long Bawan, en route from Long Riman to Gunung Muruk, 03°56' N, 115°35' E, *Akiyama B-24525, B-24577, B-24298 & B-24221* (all HYO!); West Kalimantan, Bukit Raya,

0° 30' S, 112°50' E, *Mogea & de Wilde 3994A* (L!, MO!, NICH!, NY!); West Kalimantan, Bentuang Karimun National Park, Bukit Condong, *Heri Sujadmiko 170* (BO!); West Kalimantan, Sambas, west slope of Gunung Niut, *Akiyama B-30754* (HYO!); West Kalimantan, Bukit Raya, *Winkler 3148* (L!). **Sulawesi:** Roroka Timbu, 0°30'–1°30' S, 119°30'–120°30' E, *Hennipman 5507A* (L!, MO!, NY!). **Seram:** Central Searm, trail between Wae Puo and Wae Ili, *Akiyama C-9684* (HYO!, BO!, L!); Central Seram, Losa–Nihehata, *Akiyama C-16587* (BO!, HYO!, L!); Central Seram, Kanikeh–Wae Angsela, *Akiyama C-8667* (BO!, HYO!, L!, NY!); Central Seram, Piliiana–Gunung Watane, *Akiyama C-14945* (BO!, HYO!, L!); Central Seram, Wae Pasola Hatu–G. Meseleinan, *Akiyama C-16150* (BO!, HYO!, MO!); Central Seram, Tehoru, Losa–Nihehata, *Akiyama C-16587* (BO!, HYO!, NY!). **Papua:** Star Mts., Mt. Antares, bivouac 39a, *van Zanten 337* (BM!, L!, NY!); Orion Mountains, Tenmasigin, *Vervoort 310a* (L!) & *308* (BM!, NY!); Manokwari Subdist., *Kostermans 2210* (BO!). **PAPUA NEW GUINEA. West Sepik:** Star Mts., Fologonom, between Ok Din river and Papuan hunting camp, 05°S, 141° 05' E, *Touw 18241* (L!, LAE). **Western Highlands:** Wabag area, near Tibinini village, Porgera Valley 25 miles W of Laiagam Patrol Post, *Robbins 3407* (FH, L!). **Eastern Highlands:** Aiyura, ca. *van Royen 4438* (L!); Purosa, Okapa area, *Brass 31666* (L!). **Southern Highlands:** Lama Sawmill logging area, 5 km SE of Ialibu, 6°20' S, 144°02' E, *Streimann 24681* (MO!; Musci Australasiae Exiccati no. 201 as *Trismegistia lancifolia*); Onim Forestry Station, 14 km NNW of Ialibu, 6°09' S, 143°59' E, *Streimann 24745* (CBG, H, MO!, NICH!, NY!, TBA; chromosome count voucher, identified as *Trismegistia lancifolia*); Yasare, 6°27' S, 144°05' E, *Kolema 69* (BRNH, CBG, H, LAE, MO!, NAH, NICH!, NY!, TBA); Andawe River, Lama Sawmill logging Area (Rongo), 6 km SE of Ialibu, 6°27' S, 145°40' E, *Streimann 26472* (CBG, KKAH, H, MO!, NICH!, NY!, TBA). **Morobe:** Sreader Divide, Aseki-Menyamya road, 6 km NW of Aseki, 7° 19' S, 146° 09' E, *Streimann 26054* (CBG, H, NICH!, NY!, TBA).

Note 1. All the specimens formerly reported as *Trismegistia panduriformis* outside Mt. Kinabalu correspond to var. *prionodontella*. This variety,

although distributed widely in the Malesian region as *T. lancifolia* and *T. calderensis*, is rather stenotypic and shows little variation in morphology among local populations.

Note 2. As shown in “Other specimens examined”, both var. *panduriformis* and var. *prionodontella* occur at Mt. Kinabalu. They can be distinguished from each other as shown in the key above. In addition, on Mt.

Kinabalu var. *panduriformis* often occurs at higher elevations than var. *prionodontella*. A similar situation is also known for the two varieties of the moss *Racopilum spectabile* Reinw. & Hornsch. var. *spectabile* and var. *subisophyllum* Herzog (= *R. johannis-winkleri* Broth.) on Mt. Kinabalu (Akiyama & van Zanten 1999, van Zanten 2006).

8. *Trismegistia plicata* H. Akiyama, **sp. nov.** [Figure 4 & Plates 33–34]

Trismegistiae lancifoliae similis, sed differt plantis robustioribus, caulibus secundariis sparse et irregulariter ramosis, stipitibus vix evolutis, foliis totis profunde plicatis.

Type: Malaysia, Sarawak: Kubah National Park, near Matang village, west of Kuching, 540 m alt., *Akiyama Sarawak-68* (holotype HYO!; isotypes distributed as exsiccata).

Trismegistia lancifolia (Harv.) Broth. var. *obtusata* Herzog, *nom. nud. in synonym.*, *Annales Bryologi* **5**: 40 (1932).

Plants large, often more than 15 cm long, dull yellowish green, forming wefts on substrata, roundly or more or less complanately foliated; leaves usually patent below, slightly spreading above, rarely attached to stems. Primary stems prostrate, pinnately branched; central strand absent. Secondary stems sparsely and irregularly branched, not forming fronds; stipes scarcely developed. Stem leaves 3.2–4.3 mm long, deeply plicate, ovate below, long acuminate or acute, acumen narrowly triangular, slightly rounded at leaf insertion; costa absent or indistinct; entire below, margins serrate above, well bordered with linear, pitted cells; laminal cell just below apex fusiform, 12–20 µm in length, smooth; upper median laminal cells fusiform to linear, 25–38 µm in length, becoming longer below, smooth; alar regions well developed, large, multitiered except for innermost columns, supra-alar cells in several rows, quadrate; alar cells large, bulging, reddish brown. Branch leaves variable in shape and size, 2.3–4.2 mm long, deeply plicate (rarely indistinct), ovate to ligulate, acute to broadly acute or obtuse, acumen narrowly triangular, slightly rounded at leaf insertion; ecostate; laminal cells similar to those of stem leaves; margins entire below, serrate to spinose above, well bordered with linear, pitted cells; alar regions with large, bulging cells arranged in a single row except for outermost multitiered columns. Calyptrae not observed.

Dioicous? Perigonia not observed. Perichaetia on primary stems. Perichaetial leaves, to 4.0 mm long, linear triangular, narrowed into long, more or less ligulate apices, plicate, ecostate; laminal cells linear, thick-walled, smooth, becoming larger, rectangular,

and thin-walled at both angles. Setae 5–6 cm long, reddish brown, smooth. Capsules short cylindrical, ca. 2 mm long, slightly curved, yellowish brown in color; exothecial cells quadrate to short rectangular, collenchymatous; stomata at neck, superficial, ca. 20 in number. Opercula obliquely rostrate with short beaks. Peristome double. Exostome teeth lanceolate, pale yellow, finely striated throughout, with shallow dorsal median furrows. Endostome segments as long as exostome teeth, with high basal membranes, coarsely papillose; cilia linear, 2–3 in number. Spores not observed.

Distinguishing features. (1) Large plants with long, sparsely and irregularly branching primary stems, (2) secondary stems not forming fronds, (3) distinct plication of stem- and branch leaves with fewer alar cells than other species of *Trismegistia*, (4) upper margins of branch leaves well bordered and serrate to spinose, (5) stem- and branch leaves slightly rounded at leaf insertion, (6) alar cells of branch leaves arranged in a single row, (7) long setae reaching 6 cm in length, and (8) habitat preference to lower altitudes.

Habitat. On boulders, base of tree trunks, often beside small streams, in lowland forests, lowland heath forests, and swamp forests occurring from sea level to 700 m alt., mostly between 10–150 m alt. *Trismegistia plicata* is often found beside small streams, but it is not a rheophyte and seems to prefer wetter environmental conditions.

Distribution. Known only from the southwestern, coastal regions of Borneo Island (Sarawak and West Kalimantan).

Other specimens examined. MALAYSIA. Sarawak: without exact locality, *Beccari 40* (BM!); *ibid.*, *Native collector 1205* (BO!, NY!); *ibid.*, *1911, Native collector s.n.* (H-BR, L!); Matang, *Ridley 12241* (BM!, SING!); Mt. Kalulong, *Hose 9* (BM!); Baram, *Hose 107* (from inside a monkey skin) & *109* (both BM!); Baram, Marudi (Claudetown), *Richards (Oxford Expedition) 1021* (BM!, SING!); Mt. Loe, *Everett 651* (BM!, SING!); Mts. Matang, *Everett s.n.* (BM!); Marudi Forest Reserve (4th Division), near sea level, *Richards R5641* (L!); Gunong Mulu National Park, West of Sungei Berar Camp, *Jermy 13664: 11* (BM!), *13664: 13* (BM!), *13664: 18 p.p.* (BM!, L!); *ibid.*, Alluvial forest plot 1A, SE of Base Camp, 4°05' N, 114°55' E, *Touw 19539* (L!); *ibid.*, FEG Kerangas plot, NW of Camp 5 (Melinau Gorge), *Touw 19666* (L!); Division 3, Kelapaan, *Brooke 8873* (L!); Bako National Park, N of Kuching, *Akiyama Sarawak-91* (HYO!); Gunung Serapi, 15 km north of Kuching, *Haji Mohamed & Bakar 3156* (KLU, MO!); *ibid.*, *Mohamed 3185* (KLU, MO!); Mt. Mattang, *Beccari 29* (BM!, NY-Jaeger!); auf dem Bukit Mehhipit, *Winkler 3102* (L!, HBG); Mt. Gading, *Beccari 4* (BM!, L!); Sibuloba, Loba Kabang Protected Forest, 8 miles NNW of Sibuloba, *Wood 1413* (BM!); Mt. Dulit, *Chittenden s.n.* (BM!). **INDONESIA. West Kalimantan (Borneo):** ad ripas fluminis Kapoeas, *1923, Wegner s.n.* (BM!, BO!, MO!, NY!, SING!); Musci Selecti et Critici, ser. 1, no. 50; original specimen of *T. lancifolia* var. *obtusata* Herz., nom. nud.); Gunung Palung Nature Reserve, on Air Putih River, 20 km SE of Elukmelano, 1°15' S, 110°05' E, *Mori et al. 17885 & 17886* (both NY!); Tumbang Riang, 0°47' S, 112°47' E, *Veldkamp 7871* (L!); Batu Badinding, Katingan

Timber Company, 1°15' S, 112°50' E, *Veldkamp 8472C & 8472G* (both L!); Kapuas Hulu, Putussibau, around Kuala Nuo, *Akiyama B-32103 & B-32026* (both HYO!); Pontianak, Serimbu, *Akiyama B-31470* (HYO!); Sambas, west slope of Mt. Niut, *Akiyama B-30715* (HYO!).

Note 1. *Trismegistia plicata* is similar to *T. lancifolia* var. *pseudoplicata* in having distinctly plicate leaves. However, the latter is much smaller in plant size (Figure 4) and the plication restricted to the stipe- and stem leaves. It is notable that both species are separately distributed on each side of the southern part of South China Sea.

Note 2. The illustration of *Trismegistia lancifolia* [Fig. 951, based on *Richards 1021* (BM!) collected at Sarawak, Baram, Marudi] given by Gangulee (1980) is apparently of *T. plicata*. It represent a more or less complanately foliate form of the species, not the roundly foliated form.

Note 3. According to information written on the label of a specimen (*Hose 107*, BM: Plate 33-3), *Trismegistia plicata* was found from amongst monkey furs exported from Sarawak. Since *T. plicata* is one of the most robust mosses around Sarawak and forms large populations at lower altitudes, it may have been used as a natural packing material at that time.

9. *Trismegistia spinosodentata* (Zanten) H. Akiyama, **stat. nov.** [Plates 26 (4–5) & 35]

Basionym: *Trismegistia rigida* (Hornsch. & Reinw.) Broth. var. *spinoso-dentata* Zanten, Nova Guinea, Botany 10: 327 (1964). Type: Indonesia, Irian Jaya, Orion Mts., Tenmasigin, 1800 m, *Vervoort 308e* (holotype L!, isotype NY!).

Plants robust to large, irregularly branched, mostly lacking stipes. Primary stems long, prostrate, pinnately branched. Secondary stems sparsely branched, obliquely ascending. Stipe leaves, if present, and stem leaves spreading or patent when dry, narrowly oblong to ovate below, rather gradually narrowed into a more or less ligulate upper portion, deeply plicate or rugose, 3.0–4.5 mm long, scarcely rounded or almost straight at leaf insertion; margins denticulate to almost entire below, coarsely serrate above (teeth rarely composed of more than two cells), borders scarcely differentiated above; laminal cells just below apex linear, 35–100 µm in length, smooth; upper median laminal cells linear, 50–75 µm in length, smooth; alar regions multitiered, cells colored, inflated; costa often present, short and double or bifid. Branch leaves similar in shape but smaller in size than stem leaves, scarcely rounded or almost straight at leaf insertion, ecostate; alar cells except for the outer-

most one to three columns arranged in a single row.

Dioicous? Perigonia not observed. Perichaetia on prostrate stems. Perichaetial leaves much longer than vegetative leaves after fertilization, to 5 mm long; deeply plicate, paler in color, ecostate; colored, bulging cells absent at alar regions. Seta to 5.5 cm long, reddish brown, smooth. Capsule short-cylindric, slightly arcuate when dry, to 3.0 mm long. Operculum, to 0.7 mm long, shortly rostrate. Other features as in the genus.

Distinguishing features. (1) robust or large plants with irregular branching, (2) deeply plicate leaves sometimes with short, double costae, (3) leaf margins with scarcely differentiated borders, (4) slightly rounded or almost straight leaf insertion of stem- and branch leaves, (5) alar cells arranged in a single row in branch leaves, and (6) narrowly fusiform laminal cells even below leaf apices.

Habitat. Growing on tree trunk bases, fallen trunks,

rotten logs, humus rich ground, sometimes on tree trunks, in the *Nothofagus*, Podocarpaceae, Lauraceae, Fagaceae dominated forests, usually occurring from 1200 m to 2500 m alt., exceptionally known from 580 m alt. (*Streimann & Naomi 14934*) and 700 m alt. (*Streimann 15268*).

Distribution. Endemic to higher altitudes of New Guinea.

Other specimens examined. INDONESIA. West Irian: Vogelkop Peninsula, Arfak Mts., Mt. Saru-mot near Iray, Anggi Gigi Lake, *Sleumer & Vink 4474a* (L!). Central Mountains, Swart Valley, Kadubaka, *Bergman M60* (L!, MO!, NICH!, TNS!), *M85* (L!) & *M113* (L!, MO!, TNS!). Star Mts., Sibil-valley, basis camp, *van Zanten 865 & 888a* (both L!, NY!); Mt. Antares, bivouac 39a, *van Zanten 344* (NY!), *347c* (L!), *383 & 391* (both L!, NY!); Mt. Antares, above bivouac 39a, *van Zanten 544b* (L!). **PAPUA NEW GUINEA. Without exact locality:** Boridi, *Carr 13359* (BM!, NY!) & *13566* (BM!); the Gap, *Carr 15254* (BM!, NY!). **West Sepik:** Amtingin, Eliptamin, 10 km NNE of Telefomin, 5°03' S, 141°41' E, *Macrosimmok 46* (CBG, LAE, H, MO!, NICH!, NY!); Star Mts., between Folongonom and Artis' Camp, 5°S, 141°05' E, *Touw 17960, 18157 & 18127* (all L!). **Southern Highland:** Onim Forestry Station, Iaro River, 14 km NNW of Ialibu, 6°09' S, 143°57' E, *Streimann 32967* (CBG, NY!, H); Nagoti, Tagari River, Tari–Komo Road, 20 km SW of Tari, 5°57' S, 142°47' E, *Streimann 32593* (MO!, TNS!; Musci Australasiae Exsiccati no. 336 as *Trismegistia rigida*); Mendi Subdist., south slope Mt. Giluwe, half mile west of Taro bridge, 6°10' S, 143°59' E, *Groft et al. 61024* (L!, LAE); Kengaput, 6 km SSE of Mendi, 6°13' S, 143°41' E, *Streimann 26934* (CBG, LAE, MO!, NICH!, NY!, H, MO!); Lama Sawmill, 6 km SE of Ialibu, 6°20' S, 144°01' E, *Streimann 26619* (CBG, LAE, H, MO!, NICH!, NY!). **Western Highlands:** Minj Subdist., Kubor Ranges between Kuli and Minj, *Robbins 540* (L!); Wabag Area, Sugarloaf Mt., S. of Wapenamanda, *Robbins 2811* (L!); Wabag Area, Lai Valley, *Robbins 2853* (L!); Wabag Area, Tumandan–Tibini track, Porgera Valley, 20 miles NW of Laiagam, *Robbins 3412* (L!). **Chimbu (Simbu):** Dirima Mission, 2 km NW of Gumine, 6°11' S, 144°55' E, *Tola 202* (CBG, LAE, MO!, NICH!, NY!) & *223* (CBG, KRAM, LAE, MO!, NICH!, NY!). **Eastern Highlands:** Entabindi-Pusarasa Area, 2 km NNW of Okapa, 6°31' S, 145°36' E, *Streimann 26367* (CBG, NICH!, H, NY!); Near Hogabi village, 6 km SW of Lufa, 6°21' S, 145°16' E, *Streimann & Bellamy 18680* (CBG, LAE, H, NICH!, NY!); Track to Mt. Michael, 4 km SW of Lufa, 6°21' S, 145°16' E, *18776* (CBG, LAE, H, NICH!, NY!); Gahavisuka Provincial Park, above Nagamiza village, 5 km N of Goroka, 6°01' S, 145°25' E, *Streimann 18243* (CBG, LAE, H, NICH!, NY!, TBA); Goroka Subdist., Upper Asaro Valley, forest above Kwong village, *Robbins 1284* (L!); Daulo Pass, between Goroka and Chuave, track from summit village to high point of north ridge, *Weber & McVean B-34114* (NY!); Kratke Range, Baruya clan area, Kuku country, near Woneara Patrol Post, *Robbins 4191* (L!); Arau, *Brass 32196* (L!). **Central:** road to Musgrave River, just past Itikinumu Plantation, 16 km E of Sogeri, 9°25' S, 147°27' E, *Streimann 15268* (MO!; Musci Australasiae Exsiccati, no. 139 as *Trismegistia rigida*); Owen

Stanley Ranges, near Myola grassland, along Kokoda track, *Robbins 4262* (L!); *ibid.*, on track to Menari just S. of Efogi village, *Robbins 4153* (L!); near Dabamura on Ower's Corner Road, 40 km NE of Port Moresby, 9°23' S, 147°27' E, *Streimann & Naomi 14934* (CBG, LAE, H, MO!, UPNG). **Morobe:** Spreader Divide, 12 km NW of Aseki, 7°16' S, 146°06' E, *Streimann & Tamba 12013* (L!, MO!, TNS!; Musci Australasiae Exsiccati, no. 39 as *Trismegistia rigida*); Slate Creek and Gumi Creek Divide, 17 km W of Bulolo, 7°10' S, 146°28' E, *Streimann 13799* (CBG, H, L!, MO!, NICH!); *ibid.*, 25 km W of Bulolo, 7°13' S, 146°25' E, *Streimann, 25297* (CBG, H, NICH!); *ibid.*, on Gumi Creek side, 19 km W of Bulolo, 7°13' S, 146°28' E, *Streimann 22715* (CBG, H, NY!); Mt. Kaisinik, SE of Wau, *Touw 14799* (L!); Salamaua Track, 14 km NE of Wau, 7°18' S, 146°49' E, *31 Aug. 1982, Kumei s.n.* (L!, LAE, NICH, NY, H); Mt. Kaindi Road, 5 km W of Wau, 7°21' S, 146°41' E, *Streimann 19799* (CBG, LAE, H, NICH, NY!); Spreader Divide, 12 km NW of Aseki, 7°16' S, 146°06' E, *Streimann & Tamba 11938* (CBG, LAE, H, NICH!); Spreader Divide, Aseki–Menyamy Road, 9 km NW of Aseki, 7°18' S, 146°08' E, *Streimann 25965* (CBG, H, NICH!, NY!); 1 km NW of Aseki, *Streimann 26081* (CBG, H, MHA, MO!, NICH!, NY!); Wau–Salamaua Track, head of Black Cat Creek, 14 km NE of Wau, 7°18' S, 146°49' E, *Streimann 22829* (CBG, H, NICH!), *25408* (CBG, H, LAE, MO!, NICH!, NY!), *25629* (CBG, H, MO!, NICH!, NY!, TBA) & *25665* (CBG, LAE, H, NICH!, NY!); Ekuti Divide, Aseki–Bulolo Road, 33 km WSW of Bulolo, 7°19' S, 146°23' E, *Streimann 20101* (CBG, LAE, H, NICH!, NY!, TBA); Aseki–Bulolo Road, 1 km NW of Aseki, 7°21' S, 146°11' E, *Streimann 26081* (CBG, H, NICH!, NY!, MHA, MO!); Araulu Logging Area, 26 km SE of Wau, 7°28' S, 146°48' E, *Streimann 13721* (CBG, LAE, H, NICH!, NY!), *13709* (CBG, H, LAE, NY!, S), *13908* (CBG, H, LAE, NAH, NY!, S) & *13532* (CBG, FLAS, H, LAE, NY!, S).

Note 1. Judging from information written on labels of examined specimens, *Trismegistia spinosodontata* is one of the dominant moss species at the higher altitudes in New Guinea.

Note 2. Bartram (1959, p. 95) wrote that two specimens (*Robbins 549* and *Robbins 1284*), both collected at the elevation higher than 1800 m., represented a “robust form [of *Trismegistia lancifolia*] with the branch leaves to 3.5 mm long and strongly spinose-serrate”. Later van Zanten (1964) described a new variety, *Trismegistia rigida* var. *spinosodontata*. Though van Zanten (1964) placed the variety under *T. rigida* (= *T. calderensis* var. *rigida* in this revision), the large plant size and irregular branching pattern, deeply plicate leaves more or less ligulate above, scarcely differentiated leaf borders, slightly rounded or almost straight leaf insertion found in the var. *spinosodontata* suggest their remote relationship. Since *T. spinosodontata* is so far known only from higher places of New Guinea, in addition to the above morphological features, I treat it here as representing

a distinct species.

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Index of scientific names: Species and infraspecific taxa accepted are
in **bold type**, synonyms in *italics*.

<i>Acanthocladium brevifolium</i> = <i>Mastopoma pulchella</i> (fide Akiyama 2006a)	<i>T. densiretis</i> = <i>T. lancifolia</i> var. <i>lancifolia</i>
<i>A. merrillii</i> = <i>Trismegistia lancifolia</i> var. <i>lancifolia</i>	<i>T. gracilicaulis</i> = <i>T. calderensis</i> var. <i>subintegrifolia</i>
<i>A. pedunculatum</i> = <i>Trismegistia complanatulata</i>	<i>T. korthalsii</i> = <i>T. lancifolia</i> var. <i>lancifolia</i>
<i>A. prionodontella</i> ≡ <i>Trismegistia panduriformis</i> var. <i>prionodontella</i>	T. lancifolia 17
<i>A. rigidum</i> Mitt. ≡ <i>Trismegistia calderensis</i> var. <i>rigida</i>	T. lancifolia var. <i>australiana</i> var. <i>nov.</i> 24
<i>A. strangei</i> = <i>T. complanatulata</i>	T. lancifolia var. <i>everettii</i> var. <i>nov.</i> 25
<i>A. trismegistum</i> = <i>T. calderensis</i> var. <i>rigida</i>	<i>T. lancifolia</i> var. <i>korthalsii</i> = <i>T. lancifolia</i> var. <i>lancifolia</i>
<i>Acanthodium brevifolium</i> = <i>Mastopoma pulchellum</i>	T. lancifolia var. <i>lancifolia</i> 20
<i>A. rigidum</i> ≡ <i>Trismegistia calderensis</i> var. <i>rigida</i>	<i>T. lancifolia</i> var. <i>obtusata</i> , <i>nom. nud.</i> = <i>T. plicata</i>
<i>A. trismegistum</i> = <i>Trismegistia calderensis</i> var. <i>rigida</i>	T. lancifolia var. <i>pseudoplicata</i> var. <i>nov.</i> 26
<i>Hypnum calderense</i> ≡ <i>Trismegistia calderensis</i>	T. lancifolia var. <i>valetonii</i> <i>comb. nov.</i> 27
<i>H. complanatulatum</i> ≡ <i>Trismegistia complanatulata</i>	T. malayana <i>sp. nov.</i> 28
<i>H. korthalsii</i> = <i>T. lancifolia</i> var. <i>lancifolia</i>	T. maliauensis 30
<i>H. rigidum</i> ≡ <i>Trismegistia calderensis</i> var. <i>rigida</i>	<i>T. merrillii</i> = <i>T. lancifolia</i> var. <i>lancifolia</i>
<i>H. rigidum</i> var. <i>convolutum</i> = <i>T. calderensis</i> var. <i>rigida</i>	T. panduriformis 30
<i>H. sect. Trismegistia</i> ≡ <i>Trismegistia</i>	T. panduriformis var. <i>panduriformis</i> 31
<i>H. trismegistum</i> = <i>Trismegistia calderensis</i> var. <i>rigida</i>	T. panduriformis var. <i>prionodontella</i> <i>comb. nov.</i> 32
<i>Neckera lancifolia</i> = <i>Trismegistia lancifolia</i>	<i>T. pedunculata</i> (Mitt.) Broth. = <i>T. complanatulata</i>
<i>Sematophyllum</i> subgen. <i>Trismegistia</i> ≡ <i>Trismegistia</i>	T. plicata <i>sp. nov.</i> 33
<i>S. panduriformis</i> ≡ <i>Trismegistia panduriformis</i>	<i>T. pulchella</i> = <i>Mastopoma pulchella</i> (see Akiyama 2006a)
Trismegistia 4	<i>T. prionodontella</i> ≡ <i>T. panduriformis</i> var. <i>prionodontella</i>
Trismegistia brachyphylla 6	<i>T. rigida</i> ≡ <i>T. calderensis</i> var. <i>rigida</i>
<i>T. brauniana</i> ≡ <i>Mastopoma brauniana</i> (see Akiyama 2006a)	<i>T. rigida</i> var. <i>convoluta</i> = <i>T. calderensis</i> var. <i>rigida</i>
T. calderensis 8	<i>T. rigida</i> var. <i>spinoso-dentata</i> ≡ <i>Trismegistia spinosdentata</i>
T. calderensis var. <i>calderensis</i> 10	<i>T. rigida</i> f. <i>corticola</i> = <i>T. calderensis</i> var. <i>rigida</i>
T. calderensis var. <i>rigida</i> <i>comb. nov.</i> 11	<i>T. rigida</i> f. <i>pendula</i> = <i>T. calderensis</i> var. <i>calderensis</i>
T. calderensis var. <i>subintegrifolia</i> <i>comb. nov.</i> 15	<i>T. rigida</i> f. <i>viridis</i> = <i>T. calderensis</i> var. <i>rigida</i>
<i>T. complanata</i> = <i>T. complanatulata</i>	T. spinosdentata <i>stat. nov.</i> 34
T. complanatulata 16	<i>T. strangei</i> = <i>T. complanatulata</i>
<i>T. delicatula</i> = <i>Mastopoma pulchellum</i> (see Akiyama 2006a)	<i>T. squarrosa</i> = <i>T. calderensis</i> var. <i>subintegrifolia</i>
<i>T. dendroides</i> = <i>T. panduriformis</i> var. <i>prionodontella</i>	<i>T. subauriculata</i> = <i>Heterophyllum subauriculatum</i> (see Wijk et al. 1969)
<i>T. deningeri</i> = <i>Mastopoma deningeri</i> (see Akiyama 2006a)	<i>T. subintegrifolia</i> ≡ <i>T. calderensis</i> var. <i>subintegrifolia</i>
	<i>T. valetonii</i> ≡ <i>T. lancifolia</i> var. <i>valetonii</i>

Explanation of Plates (1–35).

Plate 1. *Trismegistia brachyphylla* (1–3; Eastern-type. 4–6; Western-type).

1; Vanuatu, *Higuchi 32287*. 2; New Caledonia (*Franc 1*). 3; Papua New Guinea (Morobe, *Streimann & Katik 28676*). 4; Borneo (Sabah, *Akiyama Crocker 101*). 5; Malaysia (Fraser Hill, *Tan 89-1337*). 6; Malaysia (Pahang, *Tan 89-1336*).

Plate 2. *Trismegistia brachyphylla* (Western-type).

1; holotype of *Trismegistia brachyphylla* (Sumatra, *Fleischer s.n.*). 2; Borneo (Sabah, *Akin & Awang MB56*). 3; Malaysia (Pahang, *Tan 89-1336*). 4; Java (*Abumgatner s.n.*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; apex of branch leaf. f; upper margin of branch leaf. g; alar cells of upper stem leaf.

Plate 3. *Trismegistia brachyphylla* (Eastern-type).

1; Guadalcanal (*Robbins 4301*). 2; Vanuatu (Espiritu Santo, *Higuchi 32287*). 3; Vanuatu (Tongoa, *Bowie 542*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; apex of branch leaf. f; upper margin of branch leaf.

Plate 4. *Trismegistia calderensis* var. *calderensis* (plants and habitat).

1 & 7; Borneo (Kinabalu, *Akiyama-Kinabalu 1009*). 2; Luzon (Mt. Makilin). 3; Malaysia (Genting Highland). 4; Java (G. Salak). 5; Malaysia (Cameron Highland). 6; PNG (Morobe Dist., *Streimann 19651*). 8; Luzon (Laguna Prov., *Calvin 331*). 9; Malaysia (Cameron Highland, *Hedenäs MY92-172*).

Plate 5. *Trismegistia calderensis* var. *calderensis* (variation).

1; holotype of *Hypnum calderense* (*Wright s.n.*). 2; holotype of *T. rigida* f. *pendula* (*Fleischer s.n.*). 3; Malaysia (G. Jasar, *Spare 35376*). 4; Borneo (Kinabalu, *Akiyama Kinabalu-1009*). 5. Thailand (*Touw 11658*). 6; syntype of *Hypnum korthalsii* (*Blume s.n.*).

a; lower stem leaf. b; upper stem leaf. c; branch leaf. d; upper margin of stem leaf. e; upper margins of branch leaf. f; apex of branch leaf. g; alar cells of stem leaf. h; plant.

Plate 6. *Trismegistia calderensis* var. *rigida* (plants and habitat).

1; Java, Mt. Salak. 2; Java, Mt. Salak, pendulous type. 3; Java, Mt. Gede. 4; Cameron Highland. 5; Java, Mt. Gede (*Akiyama Gede-66*). 6; Kuala Lumpur (*Meijer B12196*). 7; Cambodia (*Tixier 2832*). 8; Vietnam (*Tixier s.n.*).

Plate 7. *Trismegistia calderensis* var. *rigida* (variation).

1; lectotype of *Hypnum rigidum*. 2; holotype of *Trismegistia rigidum* var. *corticola*. 3. Borneo (Kinabalu, *Akiyama et al. 131*). 4; Sumatra (*de Wilde 19183C*). 5; Papua New Guinea (*Koponen 34948*). 6; Negros (*Paterson 2858*). 7; Cambodia (*Tixier 2832*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; branchlet leaf. f; apex of branch leaf. g; upper margin of branch leaf.

Plate 8. *Trismegistia calderensis* var. *rigida* (condensed type). Note that at the base of each branch, there are leaves with differentiated shape with shortly acute apices. 1; Cameron Highland (Robinson Fall, *Akiyama 15600*). 2; *ibid.* (Gunung Jasar, *Akiyama 15628*). 3; *ibid.* (*Akiyama 15621*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; leaf at the base of a branch. e; branch leaf. f; upper margin of branch leaf.

Plate 9. *Trismegistia calderensis* var. *rigida* (plant with developed alar cells.).

1; Palawan (*Olsen 2161a*). 2; Mindanao (*Robbins 3965*). 3; Mindanao (*Robbins 4037*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; upper margin of branch leaf. f; alar cells of stem leaf. g; apex of branch leaf.

Plate 10. *Trismegistia calderensis* var. *subintegrifolia* (plants and habitat).

1, 2 & 7; Crocker Range. 3 & 4; Kinabalu Park. 5; holotype of *Trismegistia gracilicaulis*. 6; East Kalimantan (*Akiyama 24336*).

Plate 11. *Trismegistia calderensis* var. *subintegrifolia* (variation).

1; holotype of *Trismegistia subintegrifolia*. 2; holotype of *T. gracilicaulis*. 3; holotype of *T. squarrosa*. 4; isotype of *Acanthocladium brevifolium*.

a; stipe leaf. b; stem leaf. c; branch leaf. d; branchlet leaf. e; upper margin of branch leaf. f; margin of stem leaf at shoulder. g; apex of branch leaf.

Plate 12. *Trismegistia complanatulata* (plants).

1; holotype of *T. pedunculata* (Vanuatu, *Milne 364*). 2; Vanuatu (*Schmid 175*). 3; holotype of *T. strangei* (New Caledonia, *Strange s.n.*). 4; lectotype of *Hypnum complanatum* (Samoa, *Powell 55*).

Plate 13. *Trismegistia complanatulata* (variation).

1; lectotype of *Hypnum complanatum* (Samoa, *Powell 55*). 2; holotype of *Trismegistia strangei* (New Caledonia, *Strange s.n.*). 3; holotype of *Trismegistia pedunculata* (Vanuatu, *Milne 364*). 4; Vanuatu (*Schmid 175*). 5; Papua New Guinea (*Forman & Streimann 52027A*). 6; Fiji (*Milne s.n.*).

a; stipe leaf. b; stem leaf. c; branch leaf. d; branchlet leaf. e; apex of branch leaf. f; upper margin of branch leaf.

Plate 14. *Trismegistia lancifolia* var. *lancifolia* (variation of plants).

1; Thailand (*Kerr M510*). 2; Singapore (*Ridley 351*). 3; East Kalimantan (*Yamaguchi et al. 21742*). 4; Sabah (*Ibrahim & Kiew A1589*). 5; Sumatra (*de Wilde & de Wilde-Duyffes 13704C*). 6; Sulawesi (*van Balgooy 3635*). 7; Papua New Guinea (Morobe, *Akiyama 16802*). 8; Papua New Guinea (New Britain, *Streimann 40500*). 9; Fiji (*Akiyama Fiji-93*).

Plate 15. *Trismegistia lancifolia* var. *lancifolia* (plants and habitat).

1; Sarawak (Kubah). 2; Sabah (Maliau Basin). 3; Java (Salak). 4; Papua New Guinea (Port Moresby). 5 & 6; Fiji (Suva).

Plate 16. *Trismegistia lancifolia* var. *lancifolia* (Type materials of *Neckera lancifolia*).

1; portion of holotype (Nepal, *Wallich s.n.*, TCD). 2; portion of possible type material (E. India, *Wallich 109*, TCD). 3; isotype (*Wallich 108*, BM). 4; possible isotypes (E. India, *Wallich s.n.*, H2132, BM). 5; isotype (Nepal, *Wallich s.n.*, E). 6; possible isotype (Singapore, 1824, *Wallich s.n.*, E).

Plate 17. *Trismegistia lancifolia* var. *lancifolia* (type materials of *Neckera lancifolia*).

1; holotype (Nepal, *Wallich s.n.*, TCD). 2; isotype (Nepal, *Wallich s.n.*, BM). 3; possible isotype (Singapore, 1824 *Wallich s.n.*, E). a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; leaf at branch tip. f; branchlet leaf. g; apex of branch leaf. h; upper margin of branch leaf.

Plate 18. *Trismegistia lancifolia* var. *lancifolia* (comparison of types).

1; lectotype of *Hypnum korthalsii* (Java, *Korthals s.n.*, L0109833). 2; holotype of *T. densiretis* (Luzon, *Fenix s.n.*). 3; isotype of *Acanthocladium merrillii* (Luzon, *Merrill 3985*).

a; leaf of prostrate shoot. b; stipe leaf. c; stem leaf. d; branch leaf. e; branchlet leaf. f; upper margin of branch leaf. g; apex of branch leaf. h; plant.

Plate 19. *Trismegistia lancifolia* var. *lancifolia* (variation: Thailand–Philippines)

1; Thailand (*Kerr M510*). 2; Singapore (*Ridley 351*). 3; Malaysia (Pahang, *Tan 89-1337*). 4; Negros (*Paterson 1346*). 5; Sabah (*Akiyama Maliau-56*). 6; Luzon (*Hale 25936*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; branchlet leaf. f; upper margin of stem leaf. g; upper margin of branch leaf. h; apex of branch leaf.

Plate 20. *Trismegistia lancifolia* var. *lancifolia* (variation: Sulawesi–Samoa).

1; Sulawesi (*van Balgooy 3635*). 2; Seram (*Akiyama C-8576*). 3; Papua New Guinea (*Streimann 33861*). 4; Fiji (*Akiyama Fiji-6*). 5; Papua New Guinea (Normanby Island, *Brass 25628*). 6; Samoa, (*Fleischer s.n.*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; apex of upper stem leaf. f; apex of branch leaf. g; upper margin of branch leaf.

Plate 21. *Trismegistia lancifolia* var. *australiana*.

1 & 3; *Stone & Richards 18055*. 2 & 4; *Stone 18054* (holotype).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; leaf at branch tip. f; branchlet leaf. g; apex of branch leaf. h; upper margin of branch leaf.

Plate 22. *Trismegistia lancifolia* var. *everettii*.

1; holotype (Sarawak, *Everett s.n.*). 2; Sabah (Trus Madi, *Marabini 37*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; apex of branch leaf. f; upper margin of branch leaf. g; apex of stem leaf. h; upper margin of stem leaf. i; alar cells of branch leaf. j; alar cells of stem leaf. k; plant.

Plate 23. *Trismegistia lancifolia* var. *pseudoplicata* (1–4) and var. *valetonii* (5–8).

1; Pahang (Taman Negara, *Akiyama 610*). 2–4; holotype, Pahang (Genting Highland, *Akiyama 15688*). 5; holotype (*Hallier B2657*). 6; Crocker Range (*Akiyama Crocker-305*). 7 & 8; Crocker Range (*Akiyama Crocker 212*).

Plate 24. *Trismegistia lancifolia* var. *pseudoplicata*.

1; holotype (Pahang, Genting Highland, *Akiyama 15688*). 2; Sumatra (*de Wilde 19453B*). 3; Singapore (*Sinclair 7210*). 4; Genting Highland (*Stone 5534*).

a; leaf of prostrate stem. b; stipe leaf. c; stem leaf. d; branch leaf. e; apex of branch leaf. f; upper margin of branch leaf. g; apex of stem leaf.

Plate 25. *Trismegistia lancifolia* var. *valetonii*.

1; holotype. 2; Brunei Darussalam (*Tan 95-1433*). 3; Mindanao (*Weber 1293*). 4; Sulawesi (*Hennipman 5751A*). 5; Sarawak (*Mohamed & Bakar 3133*). 6; Luzon (*Leiberg 1225*). 7; East Kalimantan (*Meijer 1733a*). 8; East Kalimantan (*Meijer B1422*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; branchlet leaf. f; upper margins of branch leaf. g; apex of branch leaf. h; alar cells of branch leaf. i; alar cells of stem leaf. j; plant.

Plate 26. Plants of *Trismegistia malayana* (1–3) & *T. spinosodentata* (4–5).

1; plants forming a flat mat on soil (Cameron Highland). 2; *ibid.* close up. 3; holotype of *T. malayana*. 4; holotype of *T. rigida* var. *spinosodentata*. 5; Papua New Guinea (*Touw 18127*).

Plate 27. *Trismegistia malayana*.

1; paratype of *T. deningeri* Herz (*Stresemann s.n., 1910.*). 2; Thailand (*van Beusekom s.n., 23 May 1968*). 3; holotype of *T. malayana* (*Akiyama 15622*). 4; Thailand (*Touw 11695*). 5; Malaysia (Kedah, *Stone 5704*).

a; plant. b; stem leaf. c; branch leaf. d; upper margin of branch leaf. e; apex of branch leaf. f; alar cells of branch leaf.

Plate 28. *Trismegistia maliauensis* (plants and habitat).

1 & 2; habitat of the type locality of *T. maliauensis*. 3; holotype. 4; close up of living plants.

Plate 29. *Trismegistia maliauensis* (holotype).

a; stipe leaf. b; lower stem leaf. c; upper stem leaves. d; branch leaves. e; alar cells of branch leaf. f; upper margin of branch leaf. g; upper laminal cells. h; apex of branch leaf.

Plate 30. *Trismegistia panduriformis* var. *panduriformis* & var. *prionodontella*.

1, 3 & 5; var. *panduriformis* (Mt. Kinabalu, *Akiyama Kinabalu-1140*). 2 & 4; var. *prionodontella* (Mt. Kinabalu). 6; holotype of *Acanthocladium prionodontella* (Mindanao, *Warburg s.n.*).

Plate 31. *Trismegistia panduriformis* var. *panduriformis*.

1; holotype (*Haviland 1426*). 2; Mt. Kinabalu (*Holtum 23636*). 3; Mt. Kinabalu (*Akiyama Kinabalu-64*).

a; stipe leaf. b; lower stem leaf. c; upper stem leaf. d; branch leaf. e; upper margin of branch leaf. f; apex of branch leaf.

Plate 32. *Trismegistia panduriformis* var. *prionodontella*.

1; holotype of *Acanthocladium prionodontella* (Mindanao, *Warburg s.n.*). 2; Mt. Kinabalu (*Akiyama Kinabalu-1001*). 3; East Kalimantan (*Akiyama B-24298*). 4; Sulawesi (*Hennipman 5507A*). 5; Seram (*Akiyama C-9637*). 6; Papua New Guinea (*van Royen 4438*).

a; stem leaf. b; branch leaf. c; apex of branch leaf. d; upper margin of branch leaf.

Plate 33. *Trismegistia plicata* (plants and habitat).

1; showing the habitat at Bako National Park, Sarawak. 2 & 4; holotype (*Akiyama Sarawak-68*). 3; Plants (*Hose 107*).

Plate 34. *Trismegistia plicata* (variation).

1; holotype (*Akiyama Sarawak-68*). 2; Sarawak (*Richards R5641*). 3; Sarawak (*Brooke 8873*).

a; prostrating stem leaf. b; branch leaf. c; upper margin of branch leaf. d; apex of branch leaf. e; alar cells of branch leaf.

Plate 35. *Trismegistia spinosodentata*.

1; holotype of *T. rigida* var. *spinosodentata* (*Vervoort 308e*). 2; *Streimann 18243*. 3; *Touw 18127*.

a; lower stem leaf. b; stem leaf. c; branch leaf. d; alar cells of branch leaf. e; alar cells of stem leaf. f; upper margin of branch leaf. g; apex of branch leaf. h; upper margin stem leaf. i; apex of stem leaf. j; median laminal cells of branch leaf.

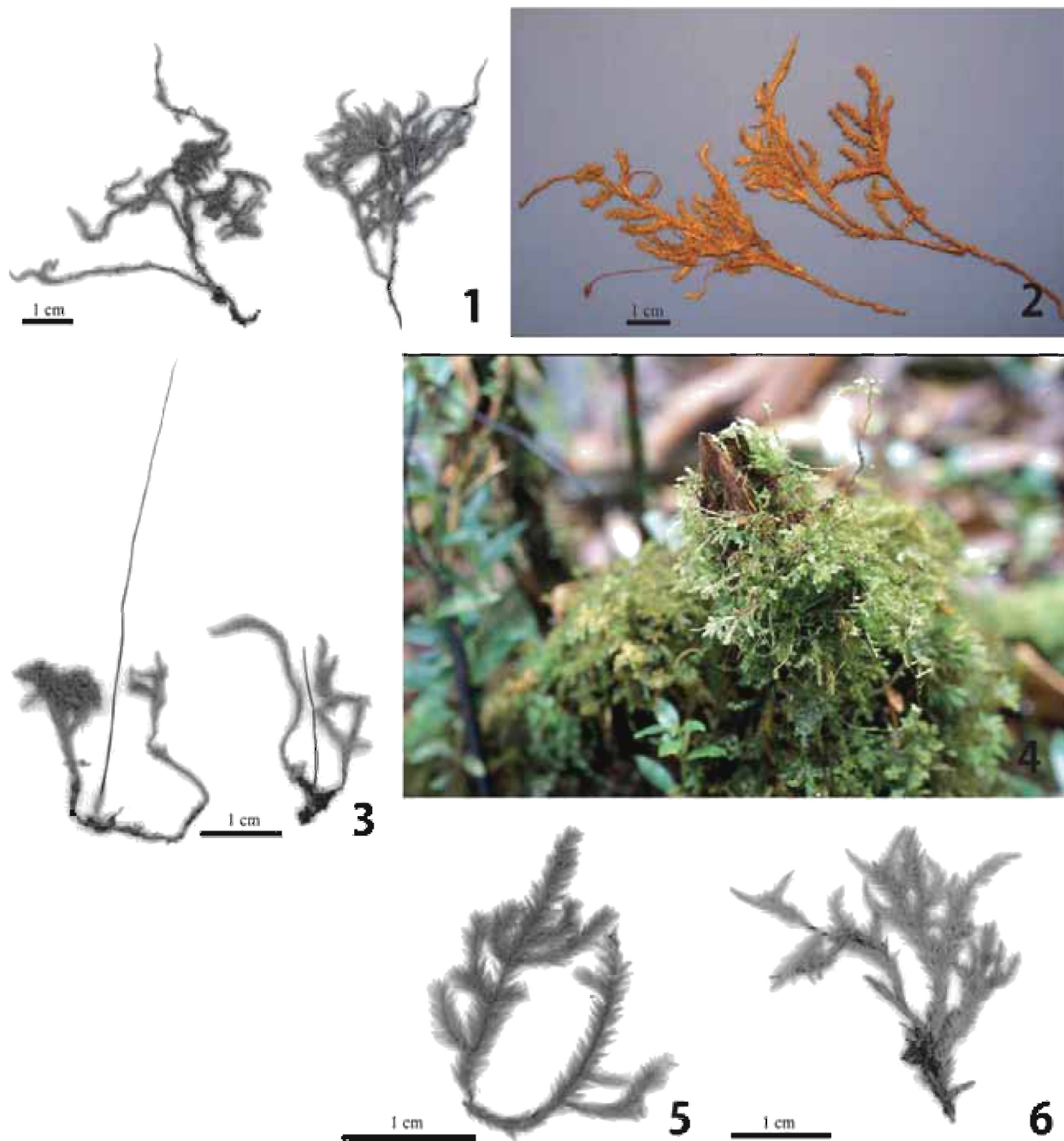


Plate 1 *Trismegistia brachyphylla*

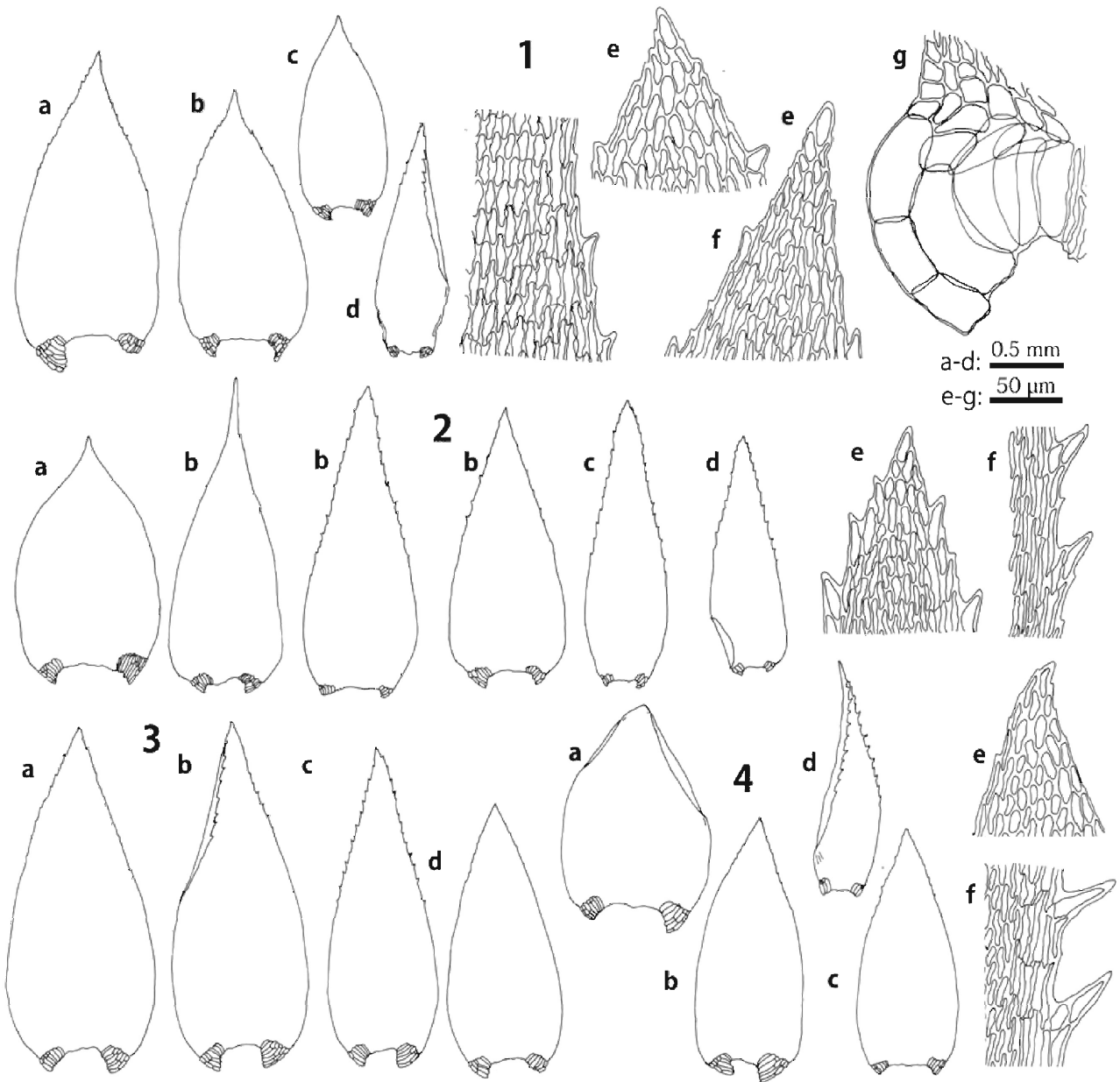


Plate 2 *Trismegistia brachyphylla* (Western-type)

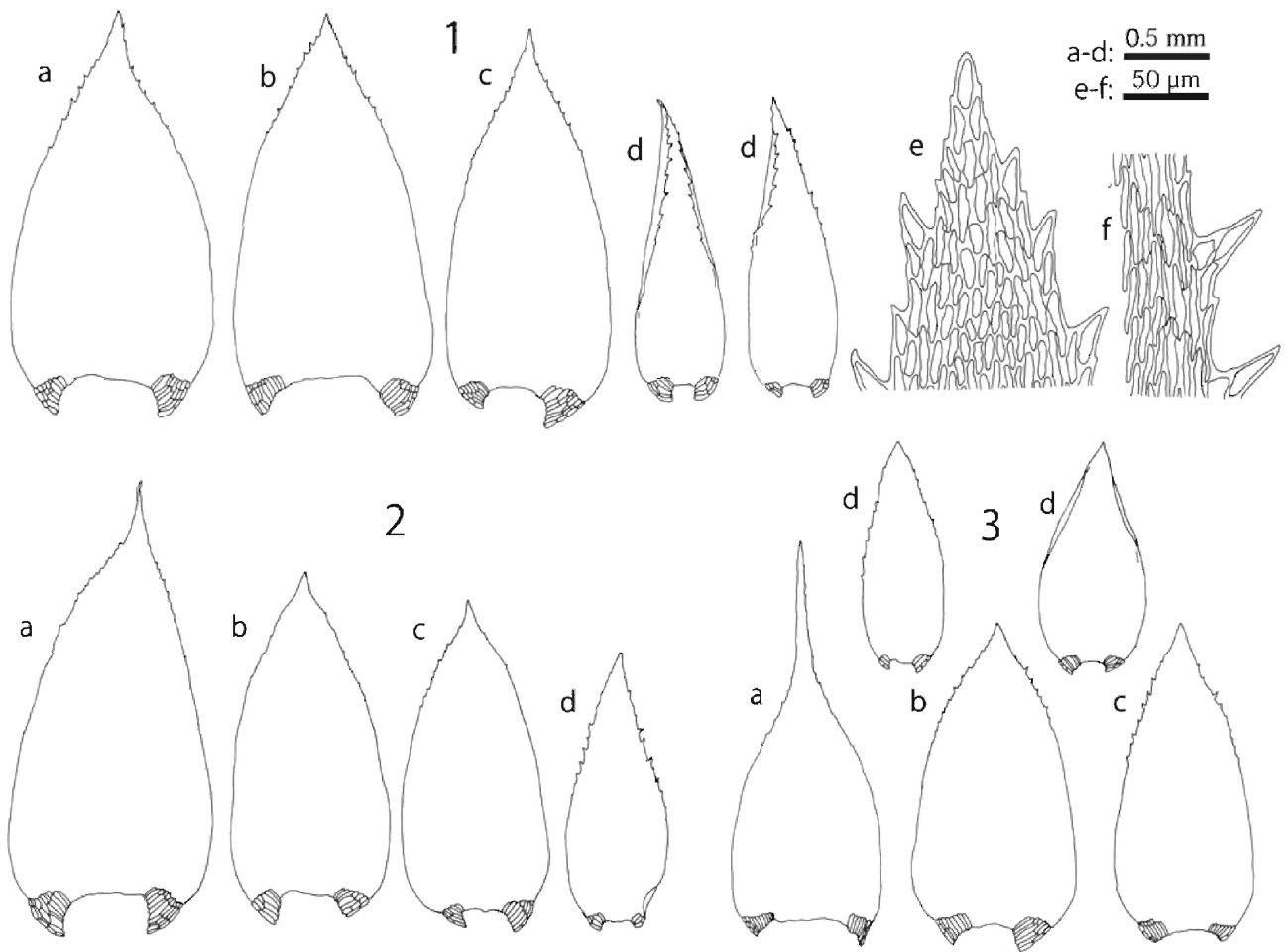


Plate 3 *Trismegistia brachyphylla* (Eastern-type)

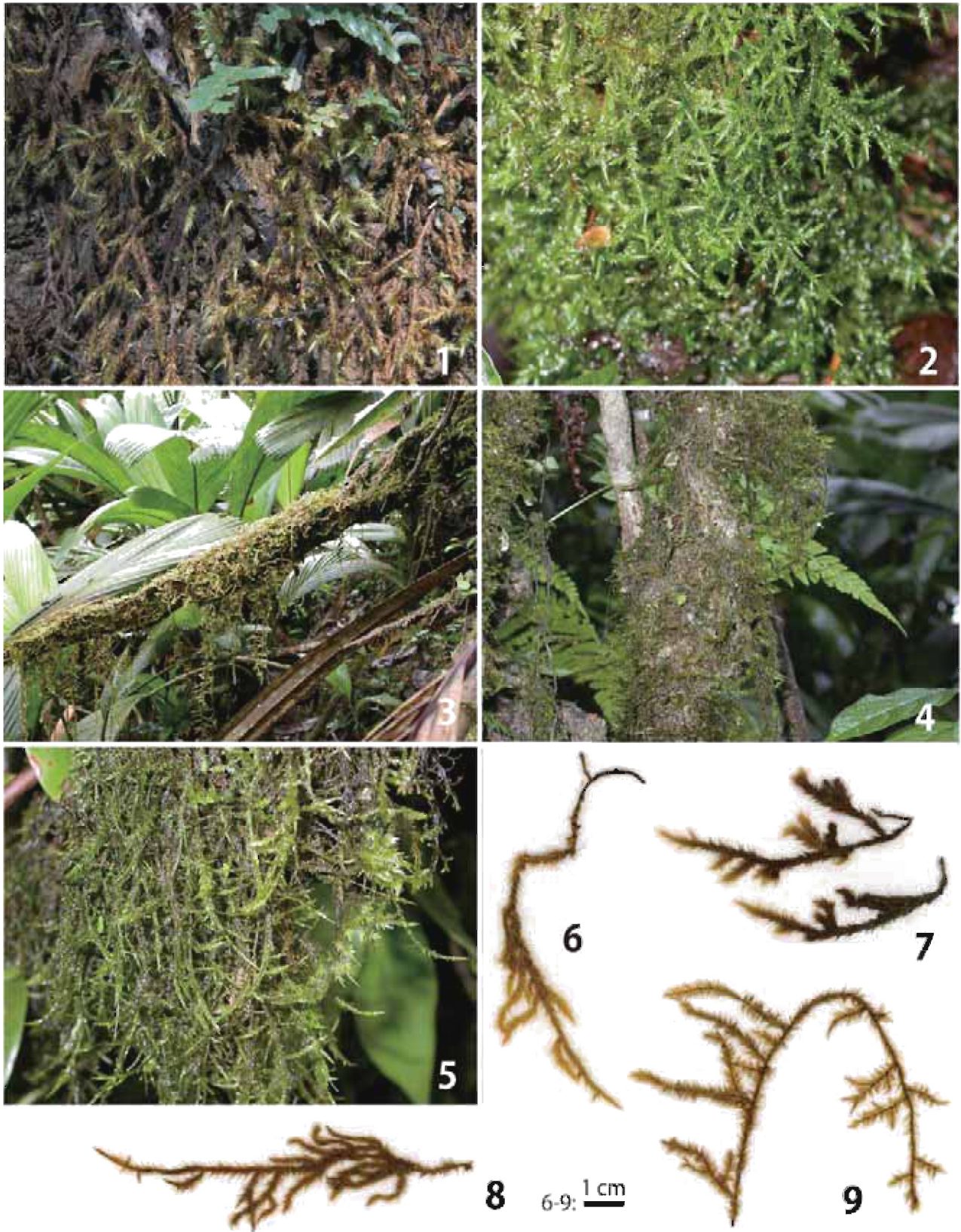


Plate 4 *Trismegistia calderensis* var. *calderensis* (plant and habitat)

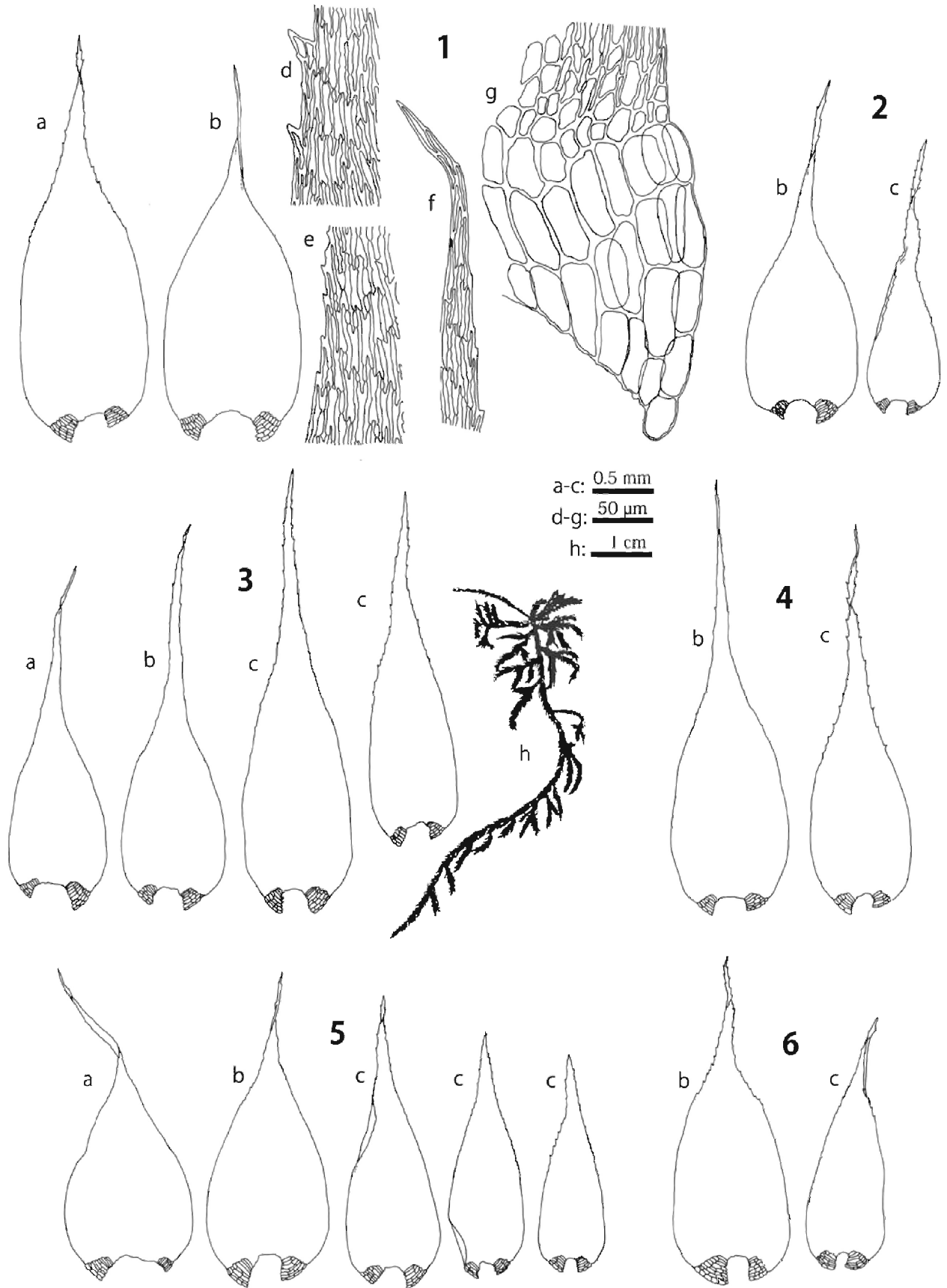


Plate 5 *Trismegistia calderensis* var. *calderensis* (variation)

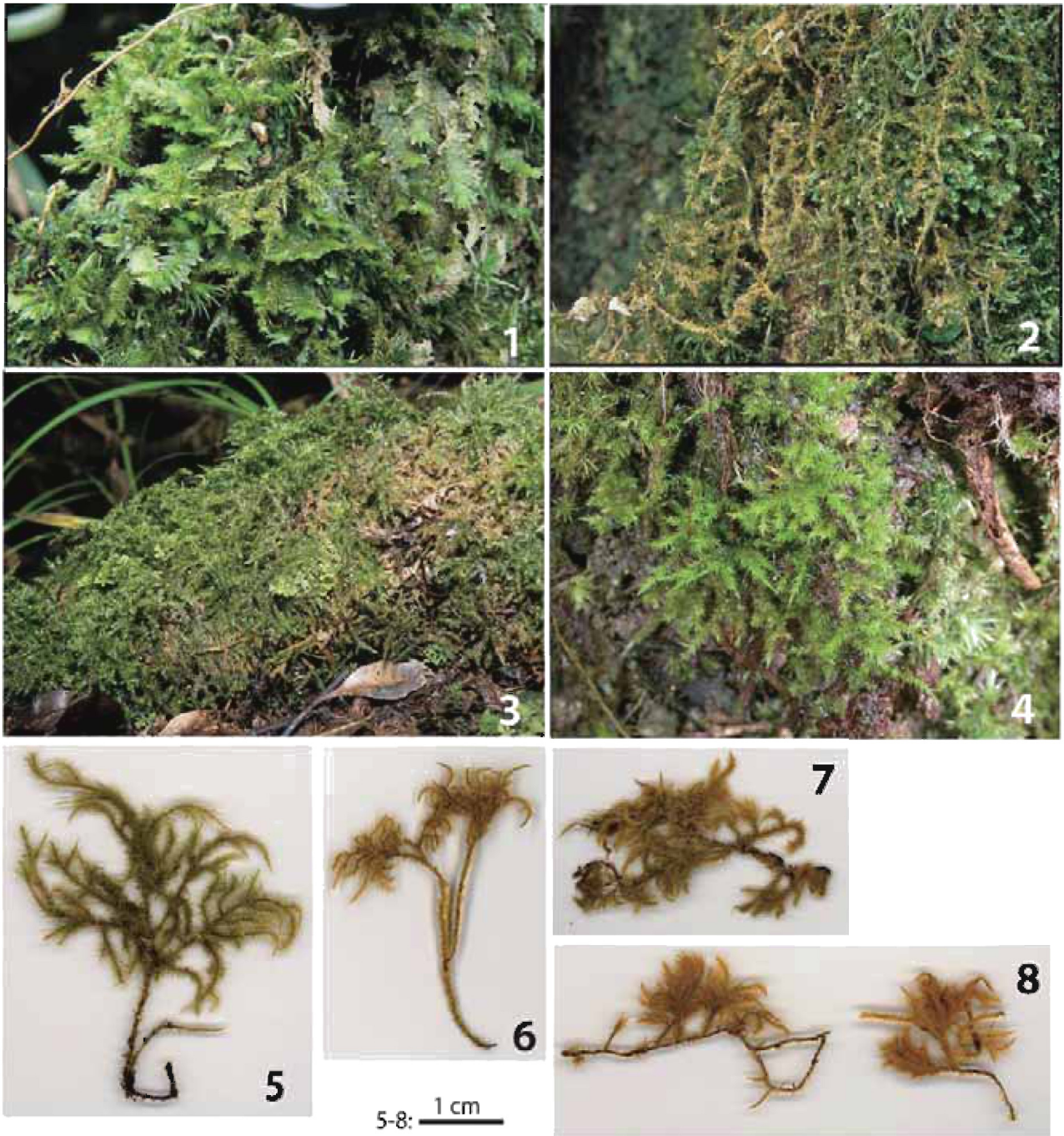


Plate 6 *Trismegistia calderensis* var. *rigida* (plants and habitat)

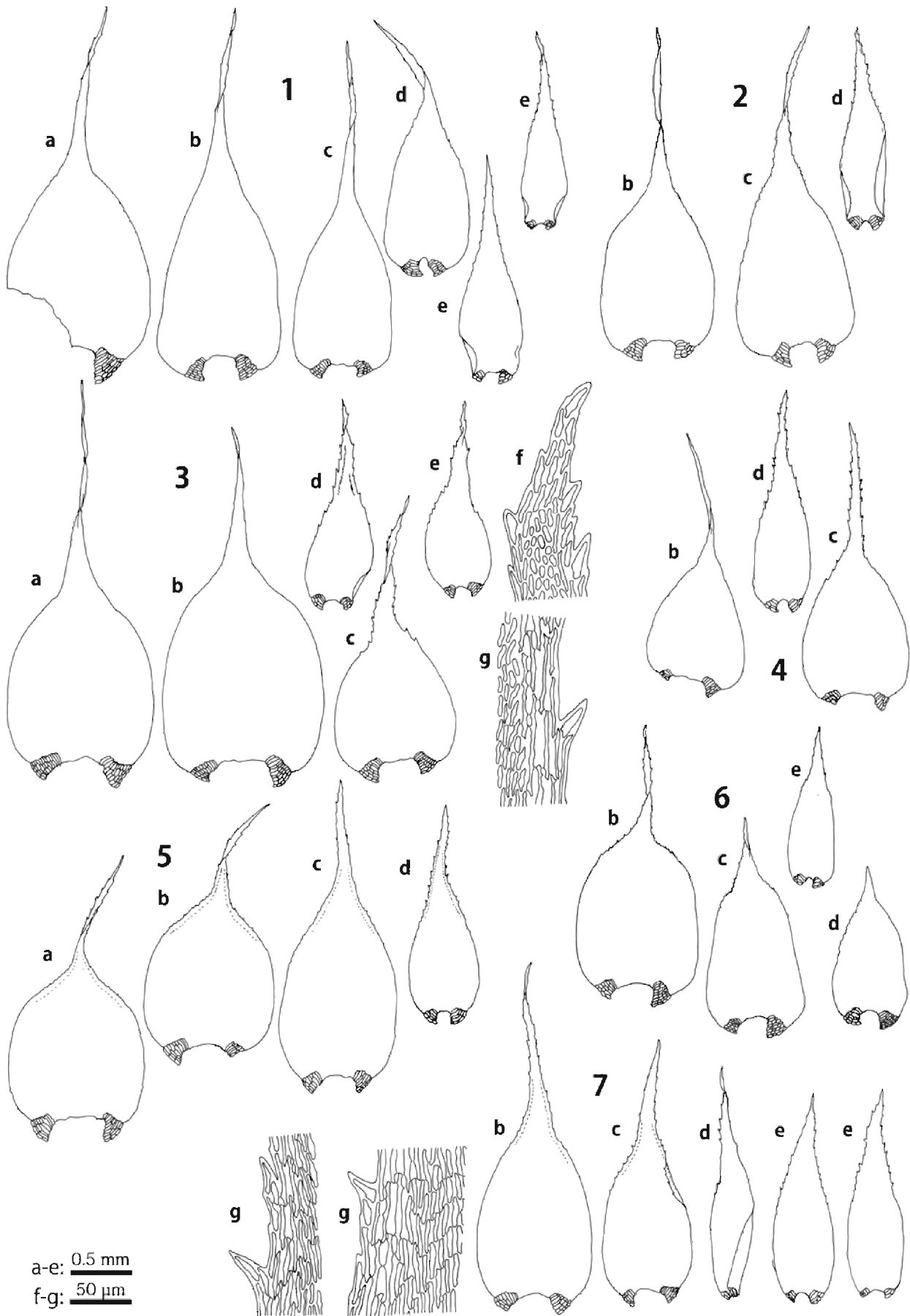


Plate 7 *Trismegistia calderensis* var. *rigida* (variation)

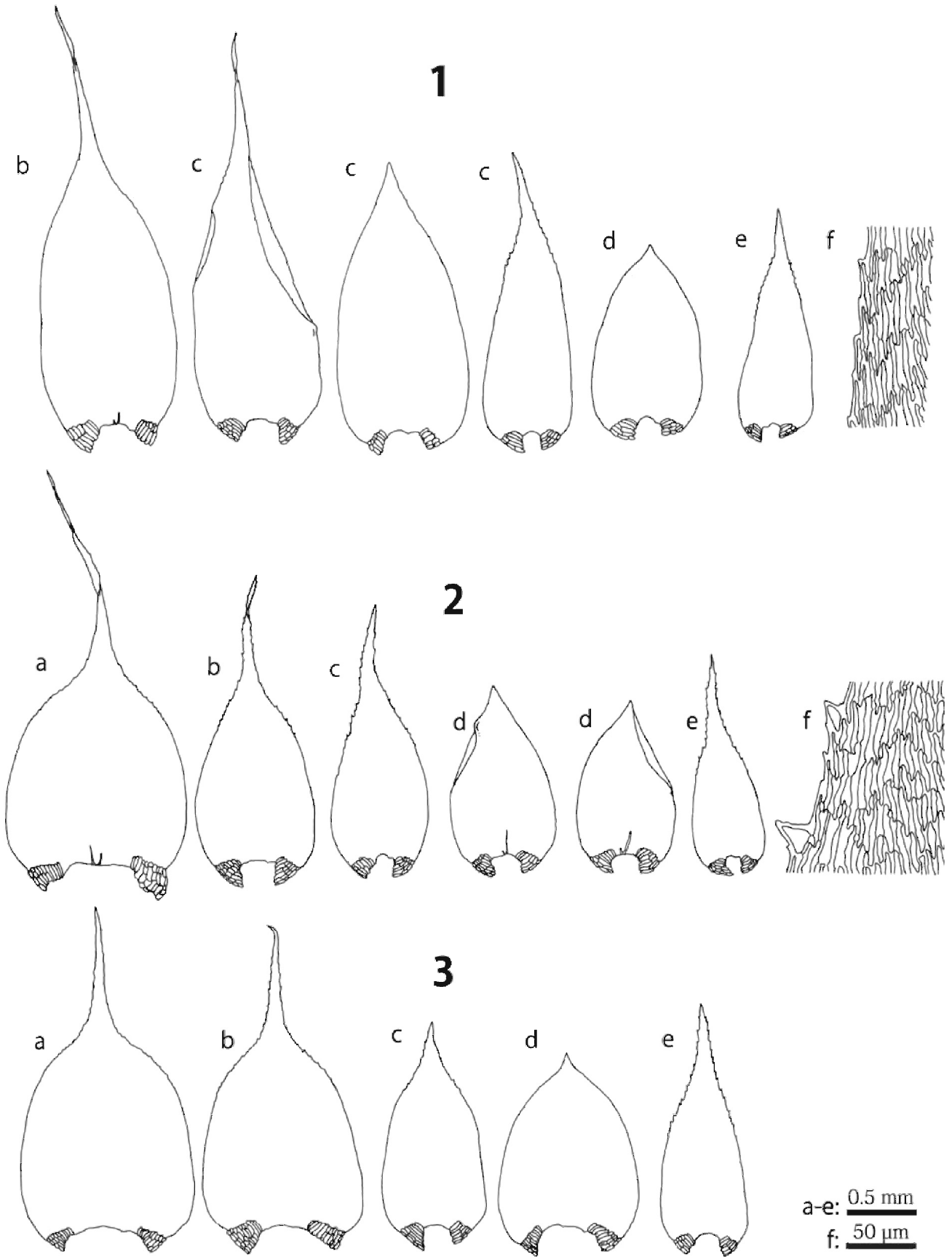


Plate 8 *Trismegistia calderensis* var. *rigida* (condensed type)

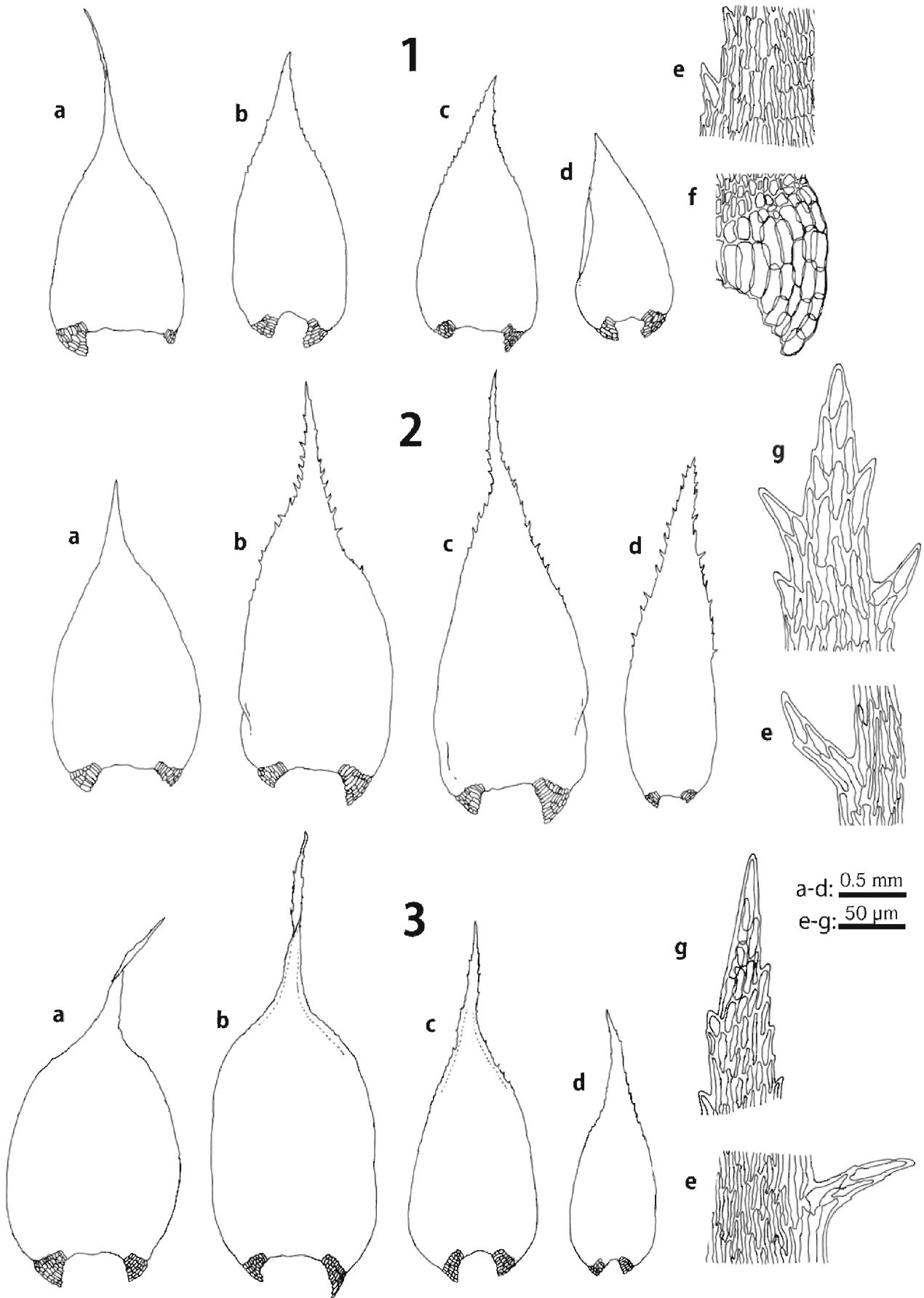


Plate 9 *Trismegistia calderensis* var. *rigida* (plants with developed alar cells)

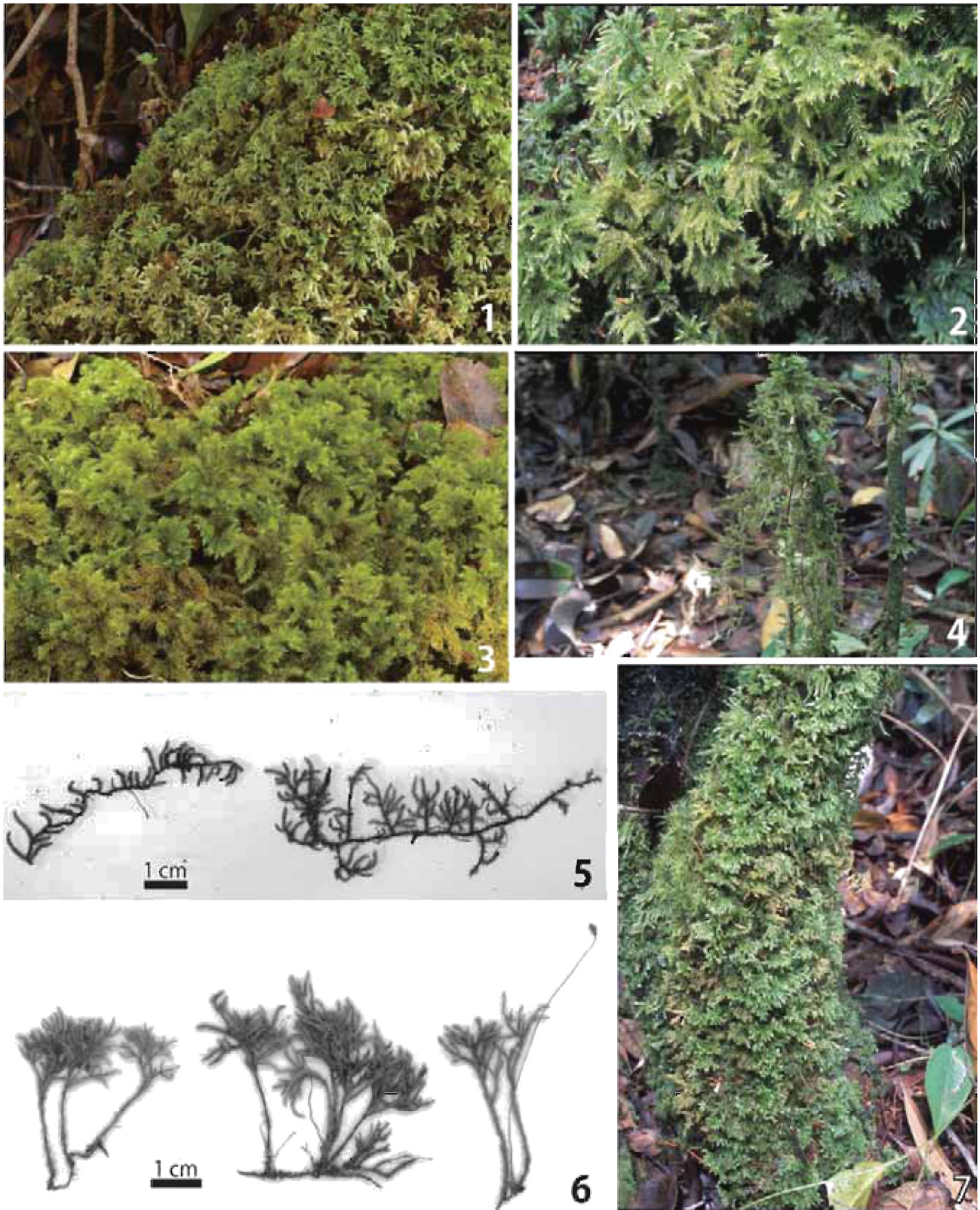


Plate 10 *Trismegistia calderensis* var. *subintegrifolia* (plants and habitat)

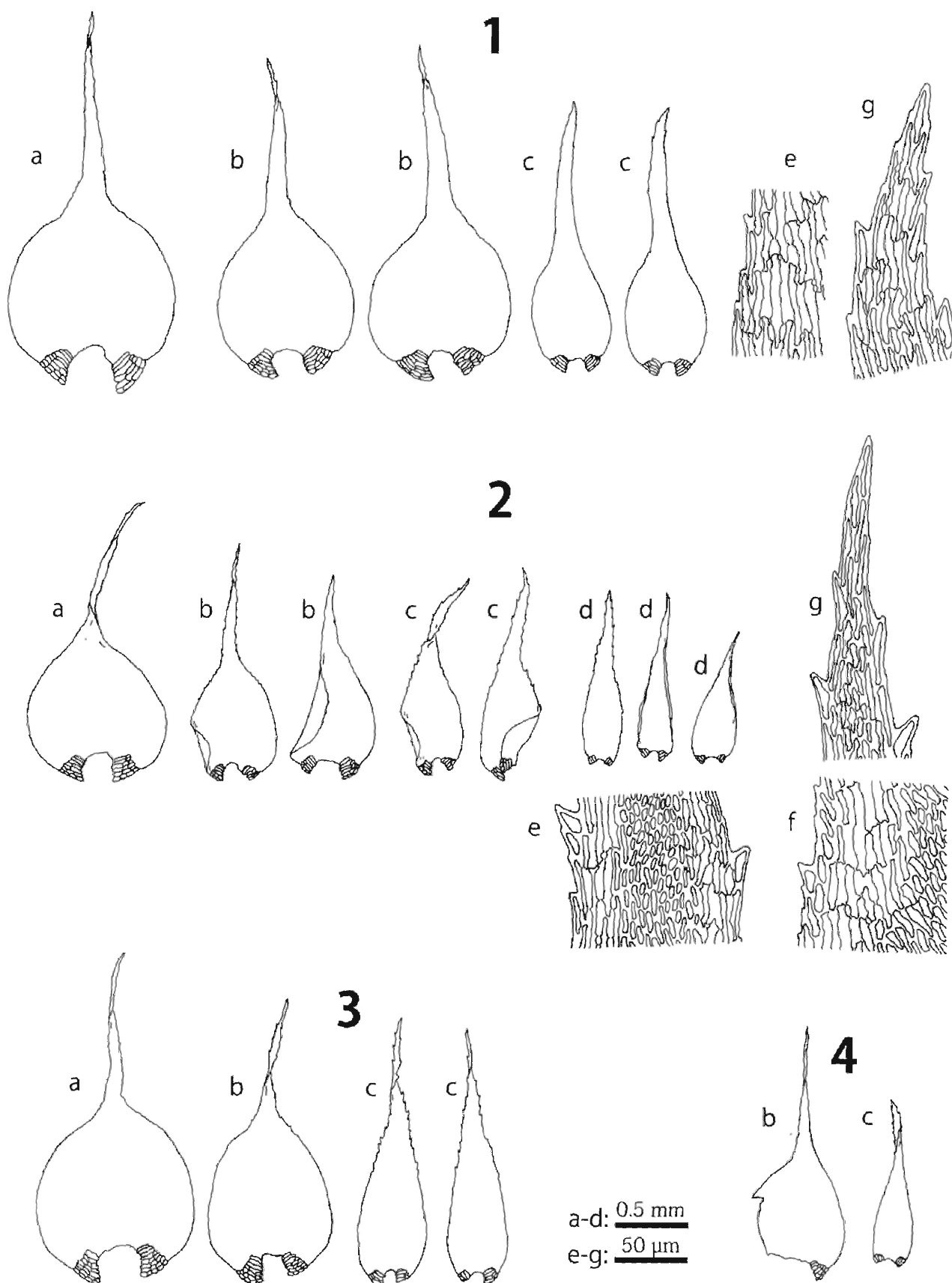


Plate 11 *Trismegistia calderensis* var. *subintegrifolia* (variation)

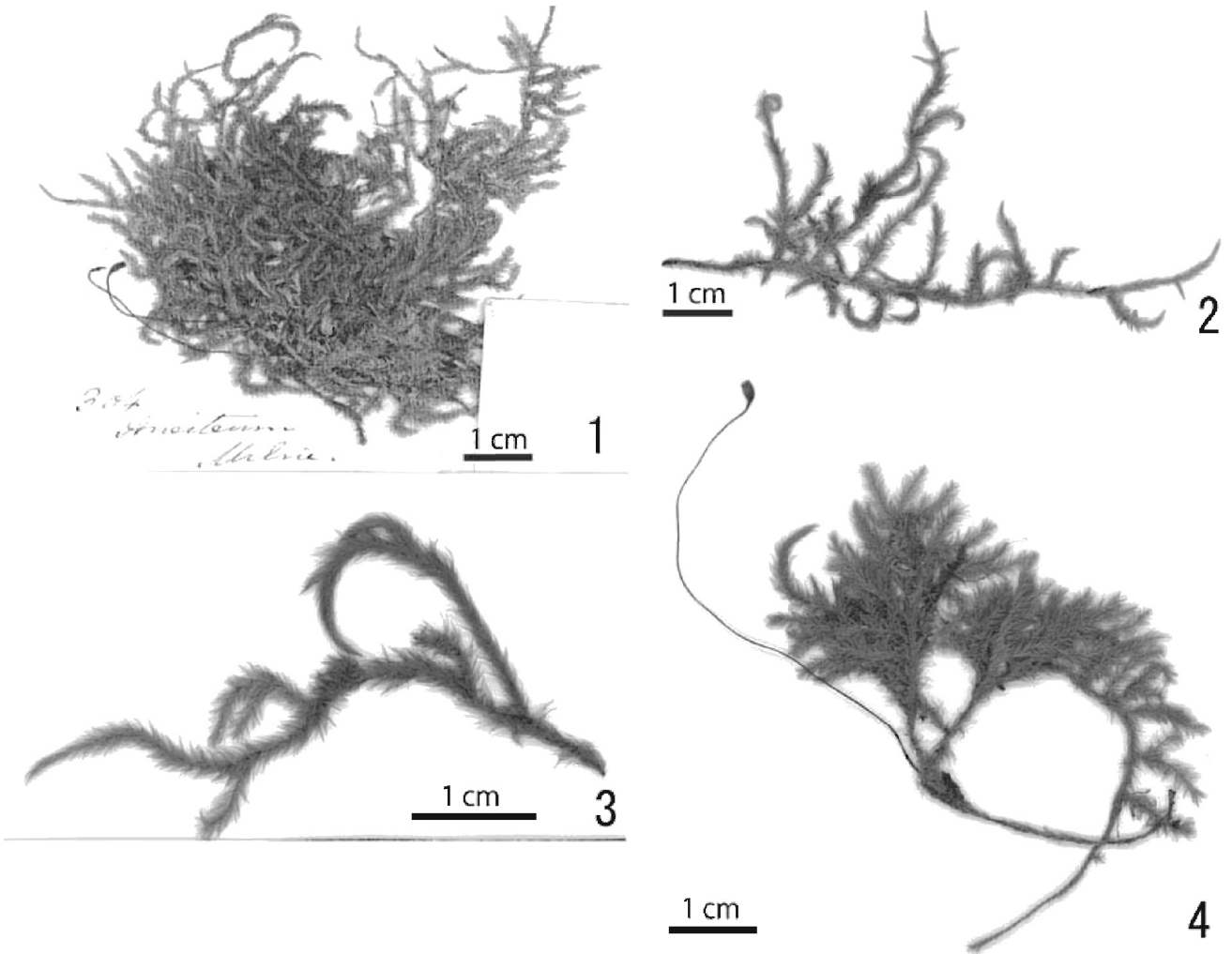


Plate 12 *Trismegistia complanatulula* (plants)

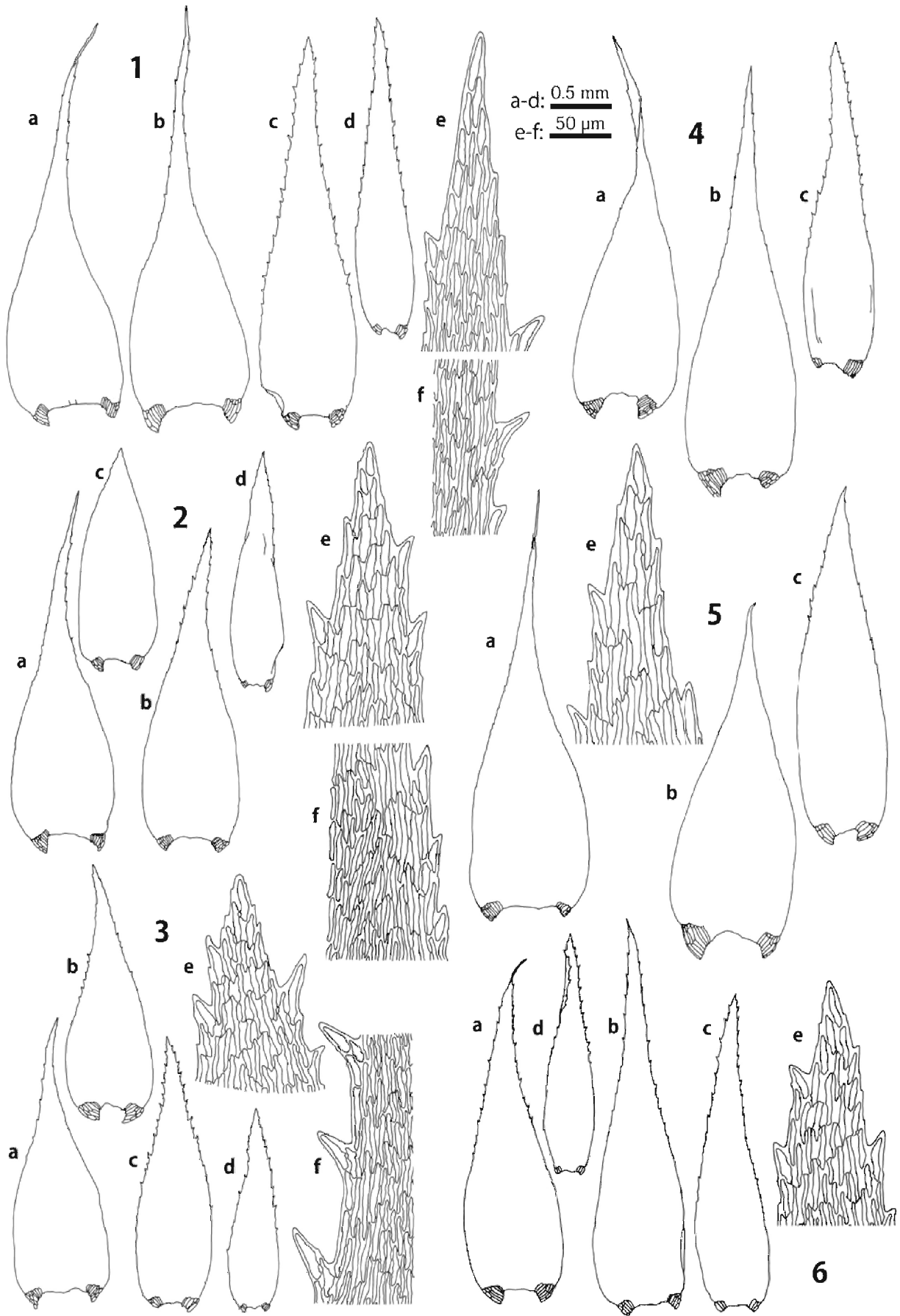


Plate 13 *Trismegistia complanatula* (variation)

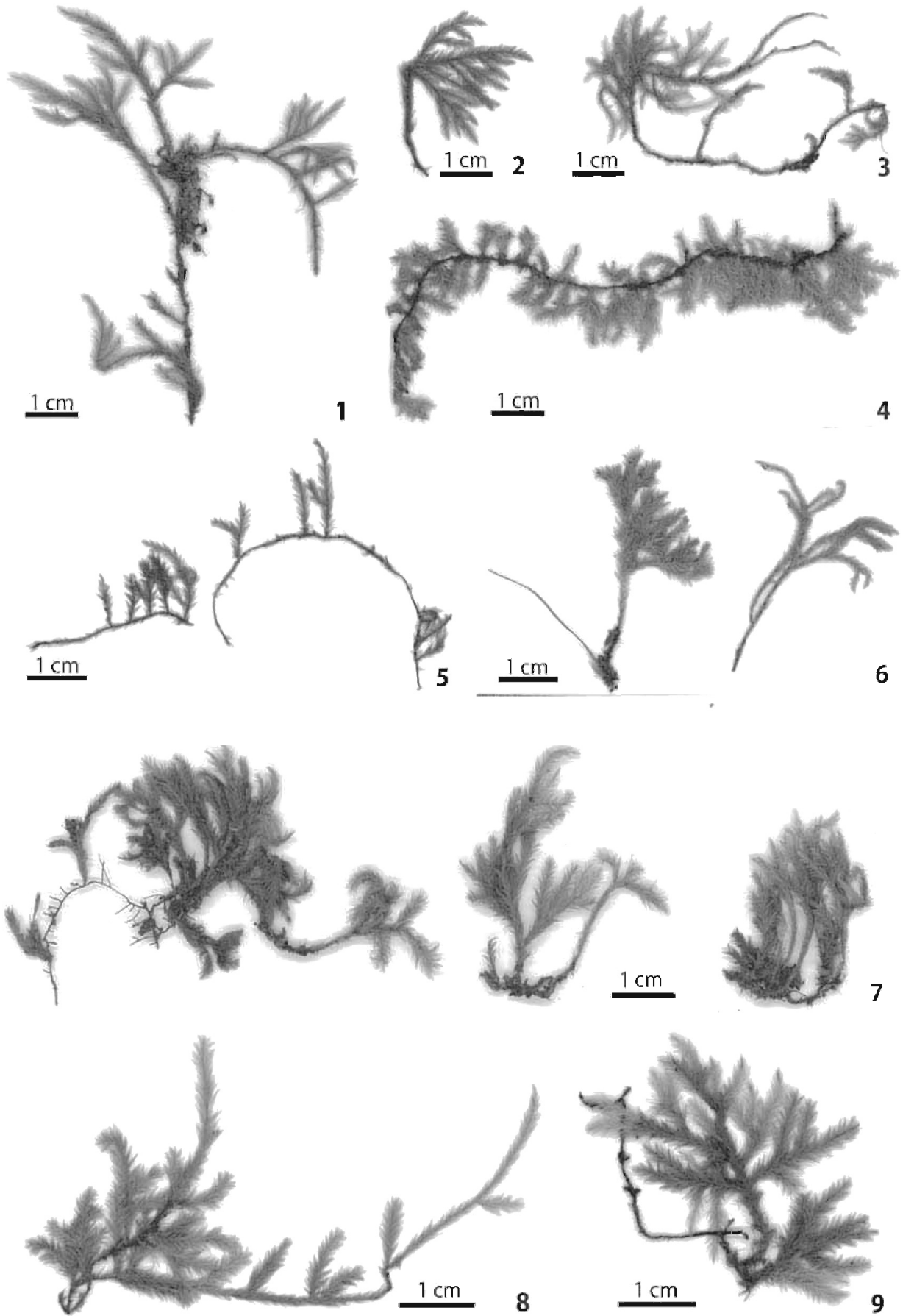


Plate 14 *Trismegistia lancifolia* var. *lancifolia* (variation of plants)



Plate 15 *Trismegistia lancifolia* var. *lancifolia* (plants and habitat)

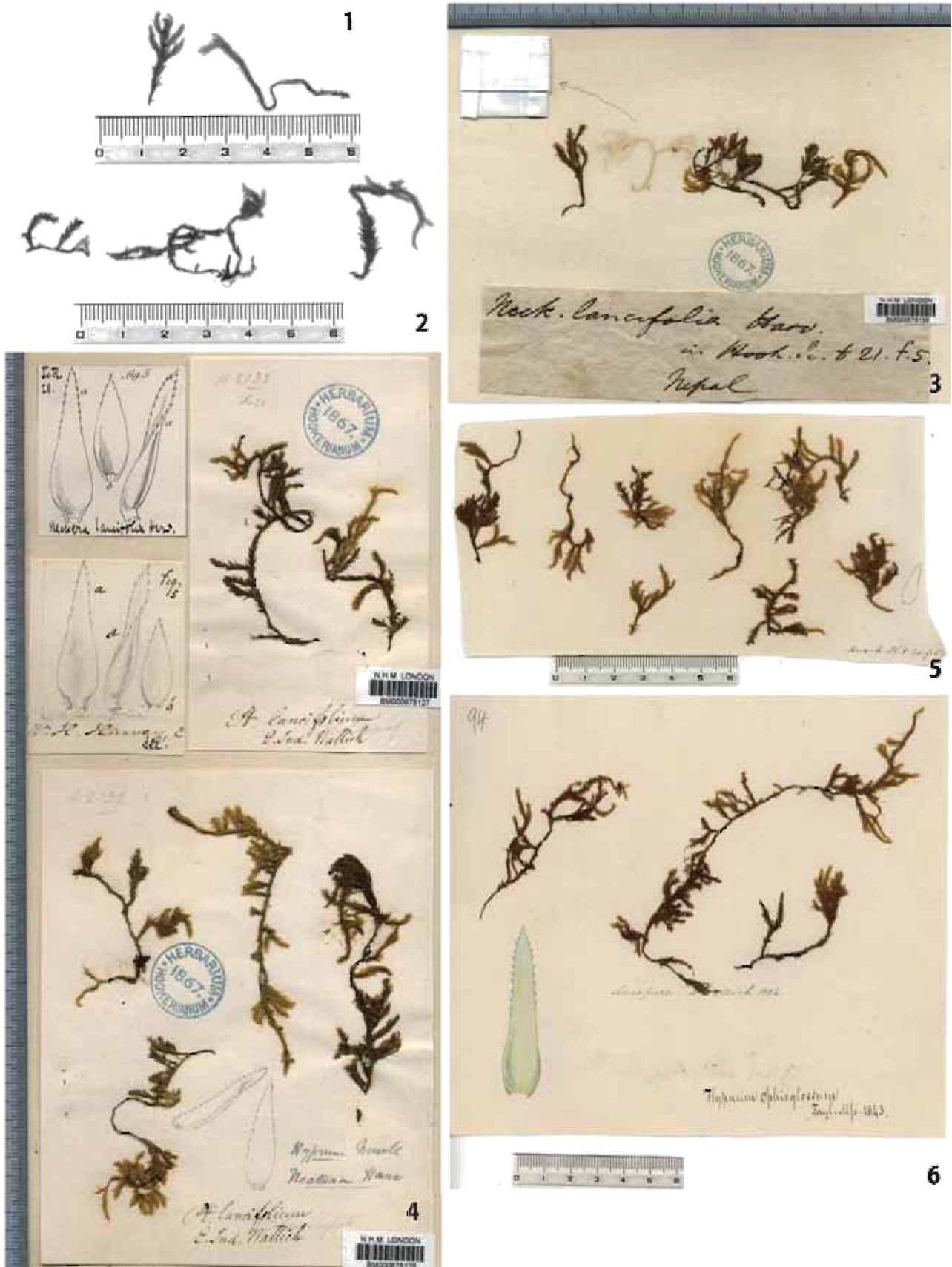


Plate 16 *Trismegistia lancifolia* var. *lancifolia* (type materials of *Neckera lancifolia*)

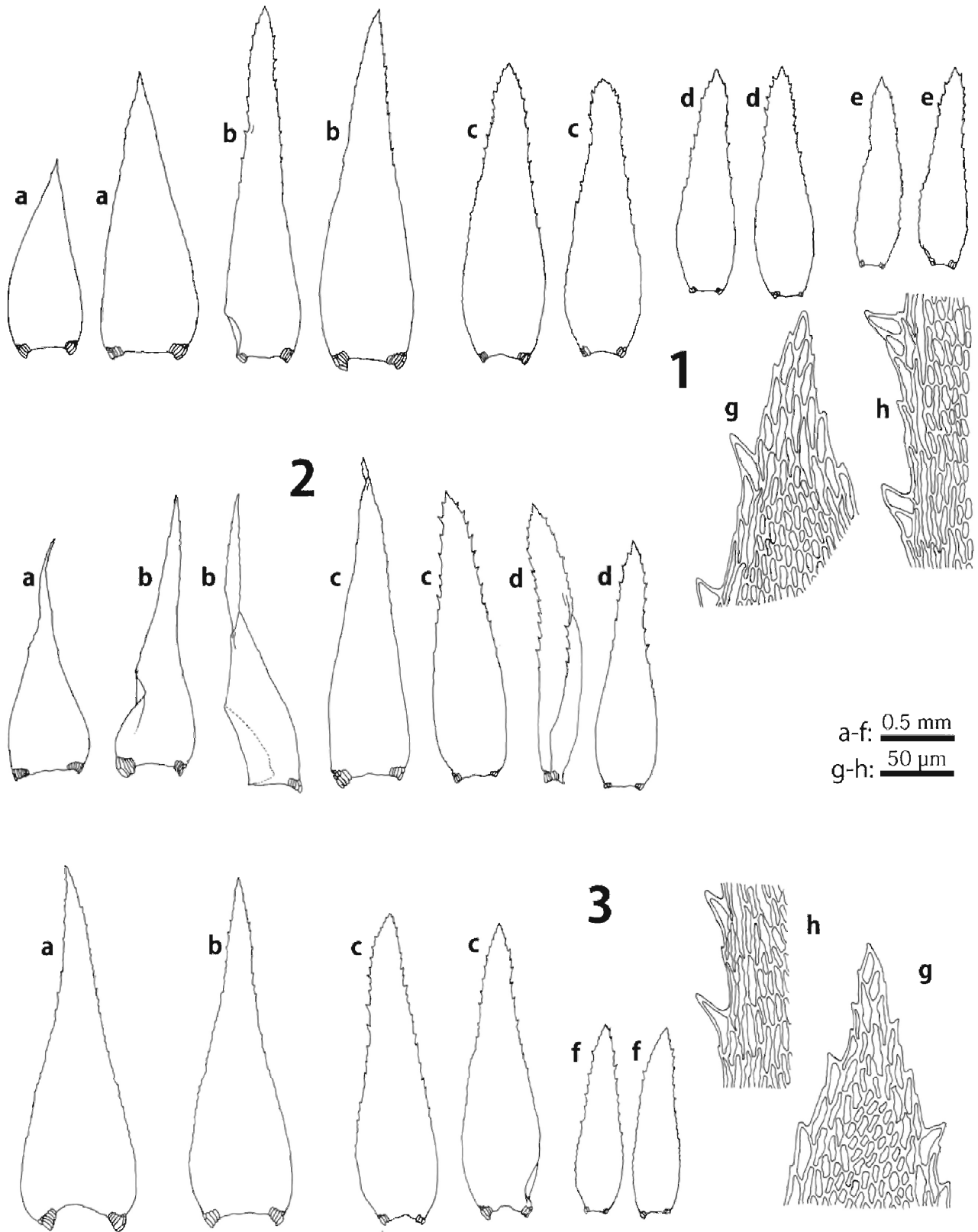


Plate 17 *Trismegistia lancifolia* var. *lancifolia* (type materials of *Neckera lancifolia*)