Revision of Asian *Herbertus* (Herbertaceae, Marchantiophyta)

Aino Juslén

*Botanical Museum, P.O. Box 7, FI-00014 University of Helsinki, and Department of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland*

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Based on a study of approximately 1300 herbarium specimens, 12 species are recognized in the genus *Herbertus* Gray (Herbertaceae, Marchantiophyta) in Asia: *H. aduncus* (Dicks.) Gray subsp. *aduncus*, *H. armitanus* (Steph.) H.A. Mill., *H. buchii* Juslén sp. nova, *H. ceylanicus* (Steph.) Abeyw., *H. circinatus* (Steph.) H.A. Mill., *H. dicranus* (Taylor ex Gottsche et al.) Trevis, *H. guangdongii* P.J. Lin & Piippo, *H. kurzii* (Steph.) R.S. Chopra, *H. longispinus* Jack & Step., *H. pilifer* (Steph.) H.A. Mill, *H. ramosus* (Steph.) H.A. Mill., and *H. sendtneri* (Nees) Lindb. Nine binomials are proposed as new synonyms. *Herbertus subrotundatus* X. Fu & Y.J. Yi does not belong to the genus *Herbertus*. The ranges of *H. aduncus* subsp. *aduncus*, *H. dicranus*, and *H. sendtneri* extend to other continents in addition to Asia. Four species are shared by Asia and Australasia. The distribution areas of five species are restricted to Asia. Of those five, two are known only from their type localities: *H. buchii* from Amur province, Russia, and *H. guangdongii* from Hainan Island, China. A key to the species is presented. Descriptions, illustrations, and distribution maps are presented for each species.

Key words: distribution, *Herbertus*, liverwort, nomenclature, taxonomy

**Introduction**

**Background**

This paper is a revision of species of *Herbertus* reported from Asia. The study covers the areas As 1, As 2, As 3, and As 4 excluding Papua New Guinea (see van der Wijk et al. 1959). *Herbertus* is a well-defined liverwort genus with erect growth form, ventral intercalary branching (occasionally also *Frullania* type (Fulford 1963, Gradstein 2001)), transversely inserted, deeply bifid, usually conspicuously falcato-secund, often asymmetric leaves with a conspicuous vitta. Underleaves are similar to lateral leaves, but slightly smaller and more symmetrical than lateral leaves. Cell walls have large trigones and intermediate thickenings. Species delimitation is still very problematic because of the large morphological variation observed. Complicated nomenclature has also caused much confusion. Schuster (2000) stated that no competent revision has been made and a revision should be presented before publication of keys for the genus. He introduced several potentially useful characters for future studies (Schuster 2000).
Species of *Herbertus* grow in humid areas, that have not been glaciated during Pleistocene. The plants often establish extensive hummocks. *Herbertus* grow on rock faces, boulders, on tree bases, trunks, and branches, and also on litter; often amongst mosses. In Asia the species often remain infertile. In this study twelve *Herbertus* species are accepted for Asia.

**Historical outline**

Gray (1821) established the genus *Herbertus* in his *Natural Arrangement of British Plants*. He described this new genus based on *Jungermannia adunca* Dicks., as *Herbertus aduncus* (Dicks.) Gray. Almost simultaneously Dumortier (1822) introduced the genus *Schisma*, with the species *Schisma 'adunca'*(Dicks.) Dumort., *S. 'juniperina'*(Sw.) Dumort. and *S. 'concinnata'*(Lightf.) Dumort., based on *Jungermannia adunca*, *J. juniperina* Sw. and *J. concinnata* Lightf., respectively. Later, he made changes under the same generic name (Dumortier 1831). Dumortier did not pay attention to Gray’s genus until 1874, when he rejected the name *Herbertus* because of its masculine form and synonymized it with his own genus *Schisma*. *Herbertus* was also overlooked by Nees von Esenbeck (1833, 1838) who considered *Schisma* to be the valid name and even discussed synonymizing *Schisma* under *Mastigophora* Nees. In the *Synopsis Hepaticarum* both *Schisma* and *Mastigophora* were treated as part of the genus *Sendtnera* Endl. (Gottsche *et al*. 1844–1847). Among 18 species of *Sendtnera*, six species belonging to the group now considered as *Herbertus* were listed. Carruthers (1865) reminded that Gray’s (1821) generic name *Herbertus* should have the priority. Carrington (1870) preferred and suggested the female form ‘*Herbertia*’ (nom. illeg., non Sweet 1827). Subsequently, Lindberg (in Lindberg & Lackström 1874) proposed the name in the form ‘*Herberta*’. This was in use until 1975 when the name *Herbertus* was accepted as valid following decision by the ICBN (Florschütz & Grolle 1975). Schiffner (1898) recognized ‘*Herberta adunca’* (Dicks.) Gray and ‘*H. dicrana’* (Taylor ex Gottsche *et al.*.) Trevis. in his *Hepaticarum Archipelagi Indici*. However, Stephani (1909) continued using the name *Schisma* for the 71 mostly geographically very limited species he listed.

Evans (1917) reviewed the early history of the genus and presented a valuable evaluation of characters revising species from Europe, Canada and the United States. At that time 75 species were recognized worldwide. Later, Stephani (1922) described even more species, raising the total number to 86. For a long time after Evans (1917), only Schuster (1957) dealt with the comparative taxonomy of the genus. Both predicted a mass reduction of the number of species. Until now the number of *Herbertus* species published amounts to ca. 100 (Bonner 1966, Geissler & Bischler 1990), and new species were described even recently (e.g. Kumar & Manocha 2000, Yi *et al*. 2001). However, Gradstein (2001) gave a conservative but altogether more realistic worldwide estimation of 25 species.

Asian Herbertus

The first Asian species was *Schimzeria dicranus* Taylor (= *H. dicranus* (Taylor ex Gottsche et al.) Trevis.) described from Nepal (Gottsche et al. 1844–1847). Already Montagne (1842) mentioned *Schisma juniperina* var. *sanguineum* from Neelgherries (= Nilgiri), India. At the variety level, it is not valid as an earliest Asian species name. Jack and Stephani (1892) described ‘Herberta longispina’ Jack & Steph. from the Philippines. Schifflner (1893) discussed ‘*H. pilifera’* from Ambon Island, Indonesia, under the name ‘Herberta longispina’. *Schisma piliferum* was validly published only by Stephani (1909). Stephani (1895) described the first species from China, *H. chinensis* Steph., *H. delavayi* Steph., and *H. wichurae* Stephani (1909) added many taxa to the genus: *Schisma giraldae*um Steph. from China, *S. ceylanicum* Steph. and *S. perrottetii* Steph. from Ceylon (= Sri Lanka), *S. kurzii* Steph. from the Himalayas, *S. sikkimens* Steph. and *S. nilgerriense* Steph. from India, *S. javanicum* Steph. and *S. ramosum* Steph. from Java, Indonesia, and *S. decurrens* Steph. from the Philippines. The next species described from Asia was *Schisma sakuraii* Warnst. (Warnstorf 1915). Herzog (1921) described *S. divaricatum* from Seram Island, Indonesia. Stephani (1922) added *S. fleischeri* Steph., *S. fragile* Steph., *S. gracile* Steph., *S. himalayum* Steph., and *S. pinnatum* Steph. from India and *S. pusillum* Steph. from South Korea. Nicholson (in Nicholson et al. 1930) published ‘Herberta handelii’ Nichols. from Yunnan, China, and Herzog (1932) ‘*H. angustissima’* Herzog from the Philippines. Horikawa (1934) listed six species, five of them new, ‘Herberta imbricata’, ‘*H. longifolia*’, ‘*H. minima*’, ‘*H. minor*’, and ‘*H. remotiusculifolia*’. Herzog (1939) mentioned ‘*H. lonchobasis*’, ‘*H. nicholsonii*’, and ‘*H. mastigophoroides*’ as herbarium names in his paper dealing with Himalayan bryophyte collections. Chopra (1943) wrote a census of Indian hepatics, and made the combination ‘*H. kurzii*’ (Steph.) R.S. Chopra. Hattori (1947) made a new combination ‘*H. sakuraii*’ (Warnst.) S. Hatt., and two forms under ‘*H. sakuraii*’, fo. ‘pusilla’ and fo. ‘remoutiusculifolia’. In 1955 Hattori listed *H. pusilla*, *H. remotiusculifolia*, ‘*H. minor*’, and ‘*H. minima*’ as synonyms of *H. aduncus* subsp. *aduncus*. *Herbertus maximus* (nom. nud.) was mentioned by Yang (1960) from Taiwan, but Piippo (1990) was not able to find a description under that name.

Miller (1965) published a review of *Herbertus* in the tropical Pacific and Asia, which, however, did not solve the taxonomy of the genus (see Schuster 2000). He listed 48 species from tropical Pacific and Asia. ‘*Herbertus lonchobasis*’, and ‘*H. mastigophoroides*’ from India, Himalayas, and ‘*H. nepalensis*’ from Nepal were presented as new Asian species and ‘*H. darjeelingensis*’ was published as nom. nov. for *Schisma gracile* Steph. (non *Schisma gracile* Montague). Later Miller (1968) published further notes on *Herbertus*.

Hattori (1966, 1971, 1975) dealt with species of *Herbertus* in the series on the flora of the eastern Himalaya. He synonymized ‘*H. handelii*’ and ‘*H. imbricata*’ with ‘*H. kurzii*’, and *H. delavayi* with *H. sendmieri* (Hattori 1966), and described ‘*Herberta giralda*na var. *verruculosa*’ from Bhutan (Hattori 1971). In the third report Hattori (1975) reduced this variety under ‘*Herberta giralda*na’. Del Rosario (1971) described *H. milleriana* from the Philippines, and later he studied the *Herbertus* flora of the Philippines (Del Rosario 1975). Tixier (1972) reported ‘*H. cf. minima*’ Horik. from the Philippines. According to Inoue (1974) the type specimen of ‘*H. minima*’ proved it to be synonymous with ‘*H. sakuraii*’ and not with *H. aduncus* as was assumed since Hattori (1955). Inoue (1977) also published one of the few studies of the Asian *Herbertus*. There he synonymized several species under *H. dicranus* and *H. sakuraii*. *Index of Bryological List, China*, reported 15 species from China, but several earlier taxonomical changes were neglected (Hsu 1979). Chang (in Gao & Zhang 1981) described *H. suafangnessis* from Heilongjiang and *H. aduncus f. minor* from Liaoning.


**Material and methods**

Approximately 1300 *Herbertus* specimens were examined for the present study. The specimens were borrowed from B, BM, C, DUKE, G, GOET, FH, H, HIRO, JE, L, LE, MANCH, M, MU, NICH, NY, PC, PNH, S, U, UC, and Z.

Initially the specimens were studied in dry condition to observe the leaf arrangement. Other characters were studied from shoots soaked in water. The leaf apices in old specimens are often very fragile, but they possess important characters, such as the apex shape and number of uniseriate cells. In badly fragmented specimens finding even a single lateral leaf with undamaged leaf apex was sometimes impossible. Cross-sections of stems were made manually by holding the shoot with forceps and cutting the stem with a razor blade. They were always made from the middle part of stem.

The length and width of the leaves were measured according to the standard introduced by Van Reenen (1982). The cell-counts presented for dorsal basal lamina, between sinus and vitta bifurcation point, and from height and width of stem cross-section are from a direct line. The cell sizes refer to the lumen. The illustrations are based on microscope drawings made with a drawing tube. I have also listed selected illustrations from the earlier literature, which succeed in showing the important features of taxa. Representative specimens examined are listed shortly, showing only one specimen per country or per
Taxonomic treatment

Key to the species of *Herbertus* in Asia

1. Leaf lobes strongly circinate .......................... *H. circinatus*
2. Leaf lobes falcate or straight .......................... 2
3. Leaf lobe apices piliferous ............................. 3
4. Leaf lobe apices not piliferous ........................ 4
5. Vitta very indistinct, bifurcating above mid basal lamina .......................................................... *H. guangdongii*
6. Vitta strong, bifurcating below or by the mid basal lamina .................................................. *H. armitanus*
7. Leaves ± straight .................................................. 7
8. Leaves falcate .......................................................... 8
9. Leaf length–width ratio 1.0–1.3(–1.5)  ......... *H. sendmeri*
10. Leaf length width ratio > 1.8 ......................... 10
11. Vitta indistinct, bifurcating near the base or well below mid lamina, leaf length–width ratio 2.6–2.7 ...... .............................................. *H. buchii*
12. Vitta bifurcating by mid or above basal lamina, leaf length–width ratio 1.8–4.0 .................. 9
13. Leaf lobes long and narrow, (2–)3–7 uniseriate cells in the apex, leaf length–width ratio 2.6–4.0 ....... *H. aduncus*
14. Leaf lobes broad, 2–3 uniseriate cells in the apex, leaf length–width ratio 1.8–2.5 ......................... *H. ceylanicus*
15. Leaf margins often with coarse appendices, leaf length–width ratio 1.0–1.2(–1.5), leaf lobes broadly acute or triangular, stem cross-section triangular or rounded ................................................................... *H. sendmeri*
16. Leaf margins without coarse appendices, leaf length–width ratio 1.3–3.7, leaf lobes lanceolate, acute, stem cross section oval .......................................................... 11
17. Margins of underleaf lobes often serrate, leaf length–width ratio 1.3–2.0, vitta deeply grooved below .......... .................................................. *H. kurzii*
18. Margins of underleaves not serrate, leaf length–width ratio 1.5–3.7, vitta often strong, but not deeply grooved .............................. 12
19. Basal disc moderately expanded, cells of the basal lamina 10–13 × 12–25 µm ................................. *H. dicranus*
20. Basal disc conspicuously expanded, cells of the basal lamina 15–20 × 30–35 µm ........................ *H. ramosus*

Asian species of *Herbertus*

*Herbertus aduncus* (Dicks.) Gray subsp. *aduncus*


*Herbertus remotiusculifolius* (*‘Herberta remotiusculifolia’*) Horik., J. Sci. Hiroshima Univ. ser. B, div. 2, 2: 209. 1934. — *Herbertia sakuraii f. remotiusculifolius* (*Herberta sakuraii f. remotiusculifolia*) (Horik.) S. Hatt., J. Hattori Bot. Lab. 2: 6. 1947. — Type: China. Taiwan, Prov. Tainoku, Mt. Taiheizan, Minamoto, Toganooodumi-Mururoau, 1932 Horikawa 9405 (holotype HIRO!). — Synonymized by Hattori (1947: 6) as *‘H. sakuraii fo. remotiusculifolia’, (1955: 81), as *‘H. sakuraii’*. There are three different species in the specimens. One was described and illustrated by Horikawa (1934) and it belongs to *H. aduncus subsp. aduncus*. But also leaves of *H. dicranus* and *H. kurzii* can be found in the same mixed state. The illustrations of *H. aduncus* and *H. dicranus* were published earlier (Juslén 2004).

Nomenclature follows the latest edition of Greuter et al. (2000). Authors’ names are abbreviated according to Brummit and Powell (1992). Herbarium abbreviations follow Holmgren et al. (1990)
specimen. *Herbertus kurzii* (as *H. imbricata* Horik.) was noted also by H. A. Miller (1965). The origin of this mixture remains a puzzle. However, the specimens annotated as *H. remotiusculifolius* are *H. aduncus*.


Plant size very variable, small to medium-sized, green, brown, yellowish, rarely reddish, 2–8 cm long. Stem cross-section often rounded, or oval, 0.1–0.35 × 0.1–0.3 mm. Leaves ± imbricate, erect, ± straight and almost symmetrical, basal lamina hardly expanded, in dorsal side 3–7(–8) cells wide, leaf length 0.5–2.5 mm, width 0.3–0.9 mm, leaf length–width ratio 2.6–4.0; bifid usually to ca. 3/4, lobes long and narrow, 8–24 cells wide at lobe base, 4–8 cells wide at point half way towards apex, lobe apex acute, with (2–)4–7 uniseriate cells and (2–)4–7 rows below apex two cells wide, leaf margin usually plane, slime papillae few and sessile if present; vitta not very strong, extending to 2/5–4/5 of lobe, vitta cells 10–18 × 28–63 μm in mid basal lamina, bifurcating usually above mid basal lamina, 3–8(–10) cells between sinus and vitta bifurcation point, 10–20 × 12–30 μm; basal lamina cells 10–12 × 12–23 μm, usually with triangular trigones; underleaves smaller and symmetrical.

Dioecious. Intercalary androecia with bracts in 4–6 pairs, not falcate and not as deeply lobed as leaves, margins occasionally denticular. Bracteoles similar to bracts. Terminal gyroecia with similar bracts and bracteoles bifid to ca. half of their length, margins denticulate. Perianth ovate, narrowed to mouth, divided into 6 lobes. Sporophytes seen only in North American specimens. For further description see Schuster (1966).

**SELECTED ILLUSTRATIONS:** Horikawa 1934: 210 (fig. 36) as *H. remotiusculifolia*; Schuster 1957: 139 (fig. 4: 3–14) as *H. sakuraii* subsp. *sakuraii*.

The type specimen of *Herbertus aduncus* is poor, only one shoot mounted on herbarium sheet. Proskauer (1962) assumed that it was collected from Western North America, despite the original description “*alpibus Scoticis*”. Indeed, the lectotype resembles other North American *H. aduncus* subsp. *aduncus* specimens. It has a sporophyte and shortly stalked slime papillae, whereas Asian *H. aduncus* subsp. *aduncus* seldom has either of them. The other *Herbertus* shoot on the same herbarium sheet is *H. aduncus* subsp. *tenuis* or *H. dicranus*. Already Proskauer wrote a note attached to herbarium sheet that only the shoot with sporophyte should be considered as the type; he commented that the other shoot might or might not be of the same species. *Herbertus aduncus* subsp. *aduncus* occurs in western North America and Asia. *Herbertus aduncus* subsp. *hutchinsiae* grows in Europe (Paton 1999), and *H. aduncus* subsp. *tenuis* in the Appalachian mountains, U.S.A. (Schuster 1966).

*Herbertus aduncus* subsp. *aduncus* is distributed from North America to eastern Asia and the Himalayan area. The species has been reported altogether from eight provinces of China (Piippo 1990, Fang et al. 1998, Justén 2004). The record published in the present paper from Sichuan, China is new for the province (see Piippo et al. 1997). *Herbertus aduncus* grows on tree trunks and rocks. It has been collected from 180 m in U.S.A to 3600 m in the Himalayas. However, it does not reach as high elevations as the other species of the Himalayan area: *H. dicranus*, *H. kurzii* and *H. sendtneri*.

Some of the specimens earlier identified as *H. fragilis* were very fragile indeed. Despite the almost leafless shoots, I was in most cases able to remove one or few leaves or at least parts of leaves for examination. In addition to its fragility *H. fragilis* does not show other specific features and the type specimen of *H. fragilis* is *H. aduncus* subsp. *aduncus*. However, many of the specimens identified as *H. fragilis* proved to be *H. dicranus*.

**TOTAL DISTRIBUTION** (Fig. 1): Am 1: Canada, USA; As 2: China, Japan, South Korea; As 3: Bhutan, India, Nepal.

Plants medium-sized to robust, brown, with some orange, purple or green, 5–10(–15) cm. Stem cross-section oval or flattened oval 0.2–0.6 × 0.15–0.45 mm. Leaves ± imbricate, falcate and almost symmetrical, basal lamina expanded, in dorsal side 5–16(–23) cells wide, leaf length 1.3–3.5 mm, width 0.3–1.5 mm, length–width ratio 2.3–7.2; bifid 2/3–3/4 of leaf length, lobes linear-lanceolate, 8–37 cells wide at lobe base, 6–12 cells wide at point half way towards apex, lobe apices acuminate, with 3–9 short or somewhat elongated uniseriate cells and 1–9 rows below apex two cells wide, leaf margins usually with sessile or up to 4 cells long stalked slime papillae; vitta strong, extending mostly to apex or at least half of lobe, vitta cells 10–20 × 33–108 µm in mid basal lamina, bifurcating at half or a little lower of mid basal lamina, 7–22 cells between sinus and vitta bifurcation point, 7–17 × 10–34 µm; basal lamina cells 8–23 × 14–42 µm, with small to medium-sized trigones; underleaves smaller and symmetrical. Sex organs not seen.

**Selected Illustrations:** Piippo 1984: 27 (fig. 5).

Piippo (1984) and So (2003) studied *H. armitanus* in the Australasian area and concluded that
the species is common and very variable in size, leaf shape, and size of trigones in New Guinea. Characteristic for the species are the sharp acuminate leaf lobes pointing in different directions. The leaf lobe apex cells are 3–9 in number, and they may be elongated. The *H. armitanus* records are mostly from wood, but rarely also from rock. It grows at 1260–3000 m in Asia and even higher, to 3600 m, in Papua New Guinea (see also Piippo 1984 and So 2003).

**TOTAL DISTRIBUTION** (Fig. 3): As 3: Thailand, Vietnam; As 4: Indonesia, Papua New Guinea, the Philippines.


**Herbertus buchii** Juslén, *sp. nova* (Fig. 4)

Plantae graciles, foliis parum secundis penitus bilobatis, foliis apice fere obtusis cellulis 1–4 uniseriatis, vittis non distinctis, prope basin laminae bifurcatis, 14–16 cellulis inter sinum et punctum bifurcationis, cellulis basalibus aliis 10 µm longis et 10 µm latis, folia inferiora non secunda.


**ETYMOLOGY**. Named in honour of Prof. Hans Buch (1883–1964), distinguished Finnish hepaticologist, who described this species as new in herbarium already in 1929.

Plants medium-sized, orange brown, 3–7 cm long. Stem cross-section oval; 0.35–0.4 × 0.2–0.32 mm. Leaves ± imbricate, ± straight and almost symmetrical, basal lamina somewhat expanded, in dorsal side ca. 15 cells wide, leaf length 1.6–3 mm, width 0.6–1.1 mm, length–width ratio 2.6–2.7; bifid more than half, lobes broadly acute, 20–22 cells wide at lobe base and 11–12 cells wide at point half way towards
Fig. 3. Distribution of *Herbertus armitanus*, *H. buchii*, *H. guangdongii*, and *H. kurzii*. Solid circles = *H. armitanus*, square = *H. buchii*, open circle = *H. guangdongii*, asterisks = *H. kurzii*.

Fig. 4. — a–k: *Herbertus buchii* (from holotype H-317965). — a: Habit. — b: Part of the shoot, side view. — c: Part of the shoot, ventral view. — d and e: Leaves. — f and g: Underleaves. — h and i: Leaf apices. — j: Cells in sinus. — k: Cells of basal lamina and vitta. — l–u: *Herbertus ceylanicus* (from isolecotype MANCH-10675). — l: Habit. — m: Part of the shoot, dorsal view. — n: Part of the shoot, ventral view. — o and p: Leaves. — q: Underleaf. — r and s: Leaf apices. — t: Cells in sinus. — u: Cells of basal lamina and vitta. Use the 0.5 cm scale for a and l, the 1 mm scale for b, c, m and n, the 0.5 mm scale for d–g and o–q, and the 50 µm scale for h–k and r–u.
apex, lobe apex shortly acute, somewhat blunt in appearance, with 1–4 uniseriate cells and 4 rows below apex two cells wide; leaf margins with a few slime papillae; vitta not conspicuous, extending to beyond half of lobe, vitta cells 11–14 × 56–75 µm in mid basal lamina, bifurcating near base of lamina or well below mid basal lamina, 14–16 cells between sinus and vitta bifurcation point, 11–17 × 11–17 µm; basal lamina cells ca. 10 × 10 µm, with large trigones; underleaves smaller and symmetrical. Sex organs not seen.

My examinations support Prof. Buch’s concept of an independent species. The collection locality in the Stanovoy Mountain Range, Dzhiktangra River, is ca. 300 km W from the Sea of Okhotsk. According to Qian et al. (2003), the area belongs to the Upper Amur geographical region, which has continental to subcontinental climate with severe winters. The climate of Upper Amur region is influenced by the Pacific air masses. Box and Choi (2003) describe a high annual moisture index for the area. The region is poorly collected, and H. buchii can be expected to be found elsewhere in the Russian Far East. Characteristics of H. buchii are the straight deeply bifurcated leaves, with equally thick lobes, lobe apices blunt in appearance, and an indistinctive vitta that bifurcates near the base of the basal lamina.

**TOTAL DISTRIBUTION** (Fig. 3): As 1: Russia, Amur Region, known only from type.

*Herbertus ceylanicus* (Steph.) Abeyw. (Fig. 4)


Plants medium-sized, dark or olive brown or greenish, 2–4 cm long. Stem cross-section oval or rounded, 0.2–0.45 mm × 0.15–0.3 mm. Leaves imbricate, ± straight and almost symmetrical, basal lamina somewhat expanded, in dorsal side 5–9 cells wide, leaf length 1–2.6 mm, width 0.4–0.6 mm, length–width ratio 1.8–2.5; bifid 2/3–3/4 of leaf length, lobes broad and straight, 12–19 cells wide at lobe base and 7–12 cells wide at point half way towards apex, lobe apex acute, with 2–3 uniseriate cells and 2–5 rows below apex two cells wide; leaf margin with sessile or up to 2 cells long stalked slime papillae; vitta quite strong in basal part, not grooved, extending only somewhat beyond half of lobe, vitta cells 11–20 × 28–80 µm in mid basal lamina, bifurcating in mid basal lamina, or even near base, 5–18 cells between sinus and vitta bifurcation point, 8–17 × 11–34 µm; basal lamina cells ca. 11–17 × 11–28 µm, with medium-sized trigones; underleaves smaller and symmetrical. Pouched male bracts in 3–6 pairs, bracteoles similar to bracts. Female plants not seen.

**SELECTED ILLUSTRATIONS**: Miller 1965: 349 (fig. 28), 351 (fig. 32).

The description of *Herbertus ceylanicus* by Miller (1965) fits well my own observations. The species can be identified based on straight leaves, acute broad lobes and relatively narrow basal lamina. The colour is often greenish or olive-brown. Miller (1965) assumed *H. ceylanicus* to grow on soil. However, all the specimens I have seen with the substrate given in the label data, were from tree trunks. *Herbertus ceylanicus* is distributed at elevations of 1200–2600 m in tropical Southeast Asia.

**TOTAL DISTRIBUTION** (Fig. 5): As 3: Sri Lanka, As 4: Indonesia, Malaysia.

**REPRESENTATIVE SPECIMENS EXAMINED. — As 3**: Sri Lanka. Nuwara Eliya District, on tree, 1978 *Ruinard 17/36* (L-0410294); Horton Plains, 1846 *Gardner*, hb. William Mitten 1906 no. 106, (NY). As 4: *Indonesia*. Sumatra, Bukit Besar, 1899 *Giesenhagen* (M-0025120!, det. Stephani as ’*Schisma adunca* ’); Flores, Manggarai Prov., Poco Rii mountain ridge, Ruteng, on isolated trees at margin between evergreen forest and slope grassland, sunny, open, dry, 1750 m, 1988 *Touw & Snoek* 23294 (L-0410308). **Malaysia.** Peninsular Malaysia, Pahang, Genting Highlands, Gunung Ulu Kali, summit region, mossy forest, hanging down from small twigs, ca. 1.5 m above the forest floor, 1750 m, 1997 *Klaazenga 111* (L-0094017).

*Herbertus circinatus* (Steph.) H.A. Mill. (Fig. 6)

*J. Hattori Bot. Lab. 28: 318. 1965 (‘Herberta circinata’).
Plants medium-sized to very large, reddish or orange brown, 8–13 cm long. Stem cross section oval, 0.4–0.6 mm × 0.3–0.4 mm. Leaves closely imbricate, strongly circinate, asymmetrical, basal lamina expanded, in dorsal side 8–25 cells wide, leaf length 2.7–3.5 mm, width 0.8–1.4 mm, leaf length–width ratio 1.9–4.0; bifid 1/2–2/3, lobes 17–29 cells wide at lobe base and 12–16 cells wide at point half way towards apex, lobe apex acuminate, with 2–6 uniseriate cells and 3–6 rows below apex two cells wide; leaf margins often with up to 8 cells long stalked slime papillae; vitta very strong, extending to apex of leaf, vitta cells 10–20 × 28–80 µm in mid basal lamina, bifurcating in ca. 2/3 basal lamina, 12–14 cells between sinus and vitta bifurcation point, 8–14 × 20–40 µm; basal lamina cells ca. 10–17 × 20–40 µm, with large trigones; under-leaves smaller and symmetrical, not circinate. Sex organs not seen. So (2003) described terminal gynoecia surrounded by several whorls of bracts remarkably larger than lateral leaves.


**Herbertus dicranus** (Taylor ex Gottsche et al.) Trevis.


Schisma sakuraii Warnst., Hedwigia 57: 69. 1915. —


Herbertus (‘Herberta’) nichollsonii Herzog, Ann. Bryol. 12: 80. 1939, nom. nud. — Orig. coll.: India. Himalaja, Tsomgo Lake zwischen Gangtok und Natu La, 3800 m, 1937 Trol 10 (JE!, MU!).

Plants highly variable, from thin and slender to very robust, green, olive, brown or distinctly red to reddish black, 4–13 cm long. Stem cross-section oval, 0.2–0.7 × 0.1–0.5 mm. Leaves imbricate, ± falcate and asymmetrical, with ± strongly expanded dorsal lamina base (4–)6–20 cells wide, leaf length 0.6–6 mm, width 0.2–2.2 mm, leaf length–width ratio 1.8–3.7; bifid usually, to ca. 3/5, lobes widely acute, 10–35 cells wide at lobe base and (6–)7–22 cells wide below apex two cells wide, leaf margins plane, entire or ± lobate, with few sessile or shortly-stalked basal slime papillae; vitta conspicuous, extending to 1/2–4/5 of lobe, vitta cells 12–15 × 30–68 µm in mid basal lamina, bifurcating usually well below or sometimes at mid basal lamina, 8–29 cells between sinus and vitta bifurcation point, 10–20 × 12–30 µm, basal lamina cells 10–13 × 12–25 µm, often with distinct nodulose trigones; underleaves somewhat smaller and ± symmetrical; pouched male bracts in 4–6 pairs, bracteoles similar, 6-laciniate perianth lobed to almost half, uppermost female bracts deeply plicate, bract lobe and basal lamina margins serrulate or denticulate. Sporophyte not seen.
Herbertus dicranus is the most common species in Asia and extremely variable morphologically. At its one extreme it is relatively small, hardly falcate, with thin leaf lobes and little expanded basal lamina. That kind of *H. dicranus* is mostly found in Japan and China, and the plants are sometimes difficult to differentiate from *H. aduncus*, which has, however, no expansion of basal lamina, and no vitta bifurcation point in the upper part of the basal lamina. Its leaves are straight, and the leaf lobes have more numerous uniseriate cells (see also Juslén 2004). At the other extreme *H. dicranus* is robust, often red-coloured with falcate broad leaves, and with large basal lamina expansions. *Herbertus dicranus* grows on different substrates from tree trunks to banks and boulders at elevations from 800 m in the Japanese mountains up to 5000 m in the Himalayas.

I was able to study material from 11 provinces of China. The records from Guangxi, Henan, and Jiangxi are new for these provinces. The specimens studied from Hunan are listed in Juslén (2004). According to the checklist by Piippo (1990), *H. dicranus* occurs also in Xizang (Tibet), Fujian, and Zhejiang. Altogether *H. dicranus* is now known from 14 provinces of China.

Hodgetts (2001) lectotypified a *H. sakuraii* (Warnst.) S. Hatt. specimen in MAK. However, Miller (1965) examined the specimen from Sakurai’s herbarium, which is located in MAK. That is a valid lectotypification. During the course of the present study I was able to study a specimen from B, which contains the original notes and illustrations by Warnstorf. Apparently it is the original type of *H. sakuraii* (Warnst.) S. Hatt., that has been thought to be destroyed during World War II (see Hodgetts 2001). As Warnstorf did not specify the holotype, the specimen in B remains as an islectotype.

Hattori (1984) restudied the type from B, and criticized the short description and original drawings by Warnstorf (1915). Hattori (1984) argued that basal discs are shown too narrow in Warnstorf’s illustrations, and suggested that it might be due to imperfect separation of leaves from the shoots. Furthermore, Hattori (1984) estimated that photographic illustrations of *H. sakuraii* leaves in Miller’s (1965) revision were not typical *H. sakuraii* but possibly from undeveloped or atypically small leaves. Hattori (1984) confirmed that in his publication from 1947, fig. 1 (p. 4) actually shows *H. sakuraii*, but the name *H. longifissa* was used. In the same paper, figs. 2 (p. 5) and 3 (p. 7) show *H. aduncus* even though it is given there as *H. sakuraii* (Hattori 1947). Hattori (1984) illustrated typical leaves of *H. sakuraii* from the type specimen in B. He stated that typical leaves of *H. sakuraii* can also be found in the Illustrations of Japanese Hepaticae (Inoue 1974). The description and illustrations of *H. sakuraii* by Hattori (1984) as well as the examination of the specimen in B well support the synonymization of *H. sakuraii* with *H. dicranus* by Hodgetts (2003). Furthermore, the molecular phylogeny of Feldberg and Heinrichs (2005b) supports the inclusion of *H. sakuraii* within *H. dicranus*.

Schuster (1957) published a specimen from Japan as *Herbertus sakuraii* subsp. *sakuraii*. His identification was based on the prevailing concept of *H. sakuraii*. Miller and Scott (1960) studied a specimen from Sakurai’s herbarium, which, however, was not the type. They discussed the identity of *H. sakuraii* (1960) and Miller (1962) the identity of *H. aduncus*. Furthermore, Proskauer (1962) published Dickson’s type of *H. aduncus*. Schuster (1966) discussed the nomenclature and accepted the nomenclatural changes made by Miller and Scott (1960), Miller (1962), and Proskauer (1962). After all, *H. sakuraii* subsp. *sakuraii* R.M. Schust. ended up being called ‘Herberta adunca’ (Dicks.) Gray subsp. *schusteri* (H.A. Mill. & E.B. Scott) H.A. Mill. Schuster (1966) reminded that the publications cited above did not deal with comparative taxonomy of the plants, but only speculated with nomenclatural points. According to my examination of a large amount of Asian and American specimens, the type specimen of ‘Herberta adunca’ (Dicks.) Gray subsp. *schusteri* (H.A. Mill. & E.B. Scott) H.A. Mill. is *H. dicranus*. It is also very similar to the Japanese type specimen of *H. sakuraii* from B.

Herzog (1939) considered that six different species exist in the Himalayan area. He thought that none of the ‘species’ belong to *Herbertus dicranus*, which is one of the six species listed
by Herzog. However, within the variation of *H. dicranus* in its whole distribution area, all of Herzog’s six species are conspecific with *H. dicranus*, except *H. fragilis* that belongs to *H. aduncus*. Earlier, I synonymized *H. lonchobasis* H.A. Mill. including the herbarium names ‘*Herberta lonchobasis*’ Herzog & W.E. Nicholson and ‘*Herberta nicholsonii*’ Herzog (see Herzog 1939) with *H. dicranus* (Juslén 2004). One of Herzog’s (1939) herbarium names described as a species by Miller (1965), *H. mastigophoroides* H.A. Mill., is now reduced under synonymy of *H. dicranus*. *Herbertus himalayanus* was earlier synonymized with *H. sakuraii* (Inoue 1977) and *H. sakuraii* with *H. dicranus* (Hodgetts 2003). I have not seen the type specimen of *H. millerianus*. However, the specimen I studied (Miller 10442, MO-4416272) was collected from the same area simultaneously with the type (Del Rosario 1971, 1975). Based on my study, although exceptionally robust, *H. millerianus* is conspecific with *H. dicranus*.

Most of the records of *Herbertus subdentatus* (Steph.) Fulford from Africa and South America were left without a name as the type specimen proved not to be similar to other records (see Hodgetts 2003). Hodgetts (2003) identified all specimens of *H. subdentatus non* (Steph.) Fulford as *H. dicranus*. However, Feldberg et al. (2004) in their molecular study showed that South American *H. subdentatus* specimens fall in the same clade with Austrian *H. sendtneri*. They named the South American *H. subdentatus* records as *H. sendtneri*. They also rejected the synonymy of *H. borealis* with *H. dicranus* based on their phylogenetic results, which showed *H. borealis* to be a sister to *H. stramineus*. A sample of African *H. subdentatus auct. non* (Steph.) Fulford was included in my phylogenetic study, and it belongs to the same unresolved clade with several species, e.g. *H. dicranus* from China (Juslén 2006).

**TOTAL DISTRIBUTION (Fig. 7):** Am 1: Canada, USA; Afr 2: DR Congo, Kenya, Rwanda, Tanzania, Uganda (Wiggington & Grolle 1996); Afr 3: Madeira, Mauritius, Réunion (Grolle 1995); Oc: Hawaii, New Caledonia (Miller et al. 1983); As 2: China, Japan; As 3: Bhutan, India, Nepal, Sri Lanka, Thailand, Vietnam; As 4: Indonesia, Malaysia, the Philippines.

Chuan, 1960 Tu 3019 (H-3173861 as H. chinensis); Jiangxi. Yanshan Co., Wuyishan National Nature Reserve, warm temperate (subtropical) zone, on boulder, 1580 m, 1993 Ji 4858 (H); Shaanxi. Tai-Bai-shan, on rock, 3100 m, 1957 Lee 802 (H-3173909); Sichuan. 3600–3900 m, 1914 Handel-Mazzetti (FH as H. sikkimensis). Taiwan. Nantou, Along highway 14 just west of Yuanshan near km post 24 between Wushe and Mt. Hohuan saddle, west of taroko National Park boundary, Tsuga chinensis forest with Rhododendron, on metamorphic rock, 2800 m, 1999 Shevock 17905 (UC-1739888); Yunnan. On boulder, 2750 m, Long 18965 (JE). Japan. Kyushu. Hondo, Shimotsuke, Nikko, pr. Catar. D. Kirifuri, rupicola, skiphila, 1933 Sakurai (UC-526944, as H. longifissa); Shikoku, Ehime-ken (Prov. Iyo), Mt. Onijago-Hazegamori, (FH as H-3173861); Sichuan. 3600–3900 m, 1914 Herbertus kurzii (Steph.) R.S. Chopra (Fig. 8)

Herbertus kurzii (Steph.) R.S. Chopra (Fig. 8)


Plants medium-sized, to large, often robust, dark brown, blackish, often with deep purple, reddish or orange, 5–16 cm long. Stem cross-section oval, 0.2–0.45 × 0.2–0.35 mm. Leaves imbricate, falcate, basal lamina strongly expanded, in dorsal side 8–25 cells wide, leaf length 0.85–2.0 mm, width 0.5–1.2 mm, leaf length–width ratio 1.25–2.0; bifid 1/2–2/3 of leaf length, lobes lan-

Herbertus guangdongii P.J. Lin & Piippo (Fig. 8)


Plants medium-sized, rather robust, reddish brown, 3–7 cm long. Stem cross-section oval, ca. 0.25 × 0.2 mm. Leaves imbricate, somewhat falcate, basal lamina ± expanded, in dorsal side ca. 10 cells wide, leaf length 1.8–2 mm, width 0.7–0.8 mm, leaf length–width ratio 2.5; bifid ca. 2/3 of leaf length, lobes lanceolate, 10 cells wide at lobe base and 8 cells wide at point half way towards apex, lobe apex acuminate, with 2–7 uniseriate cells and ca. 3 rows below apex two cells wide; leaf margins rarely with slime papillae; vitta very indistinct, disappearing below half of lobe, vitta cells 14–17 × 50–60 µm in mid basal lamina, bifurcating above mid basal lamina, 6–7 cells between sinus and vitta bifurcation point, 8–17 × 17–28 µm; basal lamina cells ca. 14 × 28 µm, with large trigones; underleaves smaller and more symmetrical. Sex organs not seen.

SELECTED ILLUSTRATIONS: Lin et al. 1992: 205 (fig. 2f–k).

Herbertus guangdongii can be identified by very indistinct vitta, slight constriction at the base of the leaf lobes, and leaf lobes abruptly narrowing at apices to 2–7 elongated uniseriate cells. I have seen only few specimens of Herbertus from Hainan and only the type specimen of H. guangdongii. In order to confirm the status of this species and its relationships with other species of the genus more specimens would be needed.

TOTAL DISTRIBUTION (Fig. 3): As 2: China, Hainan, known only from the type.

Plants medium-sized to large, often robust, dark brown, blackish, often with deep purple, reddish or orange, 5–16 cm long. Stem cross-section oval, 0.2–0.45 × 0.2–0.35 mm. Leaves imbricate, falcate, basal lamina strongly expanded, in dorsal side 8–25 cells wide, leaf length 0.85–2.0 mm, width 0.5–1.2 mm, leaf length–width ratio 1.25–2.0; bifid 1/2–2/3 of leaf length, lobes lan-
ceolate, 12–35 cells wide at lobe base and 7–20 cells wide at point half way towards apex, lobe apex broadly acute, with 1–4(–7) uniseriate cells and 1–5 rows below apex two cells wide; leaf margins with sessile or shortly stalked (1–2 cells long stalks) slime papillae, rarely without slime papillae; vitta strong below, grooved, extending below half or a little beyond half of lobe, vitta cells 10–28 × 40–85 µm in mid basal lamina, bifurcating in mid basal lamina, rarely near base, (6–)9–30 cells between sinus and vitta bifurcation point, 8–20 × 11–28 µm; basal lamina cells 8–17 × 14–36 µm, with medium-sized or large trigones; underleaves somewhat smaller and more symmetrical, lobe margins often toothed. Sex organs not seen.

**Selected Illustrations:** Miller 1965: 387 (figs. 99–102); Inoue 1977: 6 (fig. 4).

*Herbertus kurzii* was described from the Himalayas by Stephani (1909). Miller (1965) mentioned that it is known only from type specimen. I was able to study a large number of additional specimens from the Himalayas. Hattori (1966) synonymized *H. handelii* from Yunnan,
China and *H. imbricatus* from Taiwan with *H. kurzii*. The holotype of *H. kurzii* is badly fragmented, but the examination proved it to be conspecific with specimens of *H. nepalensis* described by Miller (1965). The type specimen of *H. nepalensis* shows particularly clearly the toothed or serrate upper margins of underleaves. In most specimens of *H. kurzii* underleaf margins are not serrate but only malformed or occasional teeth are visible in underleaf margins. However, in addition to serrate underleaf margins, *H. kurzii* is relatively easily identified by its deeply plicate leaves and relatively large leaves with small (< 2) lateral leaf length–width ratio. It has been collected both on tree trunks and on rocks, only from ca. 4000 m and even higher altitudes from the Himalayas. I have not seen additional specimens from Yunnan or Taiwan.

**TOTAL DISTRIBUTION** (Fig. 3): As 2: China; As 3: Bhutan, India, Nepal.

**REPRESENTATIVE SPECIMENS EXAMINED.** — As 3: Bhutan. Thimphu district, slope on S side of Jange Tsho, *Rhododendron aeruginosum* scrub, on branch of Rhododendron, ca. 3940 m, 1999 Long 28864 (H, as *H. delavayi*). India. Sikkim, West District, Between Dzongri and Prek Chhu, open hillside with dwarf *Rhododendron*, on boulder, alt ca. 4000 m, 1992 Long 22651 (H). Nepal. Tributary of Simbu Khola on S side of Yalung Glacier, steep rocky valley in mossy block scree, ca. 4400 m, 1989 Long 17097 (JE).

**Herbertus longispinus** Jack & Steph. (Fig. 9)


Plants medium-sized to large, sometimes robust, brown, reddish or orange brown, 8–13 cm. Stem cross-section oval or flattened oval, 0.25–0.5 mm × 0.2–0.35 mm. Leaves distant or imbricate, strongly falcate, squarrose or spreading, basal lamina hardly expanded, in dorsal side 3–11 cells wide, leaf length 1.6–4.0 mm, width 0.35–0.7 mm, leaf length–width ratio 4.1–5.9; bifid 2/3–5/6 of leaf length, lobes long linear, 10–17 cells wide at lobe base and 7–10 cells wide at point half way towards apex, lobe apex long, slender, piliferous, with 5–15 not elongated uniseriate cells and 3–17 rows below apex two cells wide; leaf margin with a few slime papillae; vitta quite strong, grooved, extending to apex of lobe, vitta cells 8–20 µm × 55–85 µm in mid basal lamina, bifurcating above or in mid basal lamina, 5–15 cells between sinus and vitta bifurcation point, 8–22 µm × 14–28 µm; basal lamina cells 11–17 × 11–28 µm, with small or medium-sized trigones; underleaves smaller and more straight; 6-laciniate perianth lobed to half of length, uppermost female bracts deeply plicate, bract lobe and basal lamina margins serrulate or denticulate. Male sex organs and sporophyte not seen.

**SELECTED ILLUSTRATIONS:** Miller 1965: 400 (fig. 125, as *H. angustissima*), 404–405 (figs. 131–132).

The leaves of *Herbertus longispinus* are deeply bifid, the leaf lobes are extremely long, ending with 5–15 not very strongly elongated uniseriate cells, 2–3 times longer than wide, below that the lobe is up to 17 rows two cells wide; the basal lamina is hardly expanded. The type locality of both *Herbertus longispinus* and *H. angustissimus* are in the Philippines. Already So (2003) suspected them to be conspecific and *H. angustissimus* is now synonymized with *H. longispinus*. All the leaf measurements of the taxa are very similar. Mostly, there is variation in density of leaves and falcatedness of leaves from imbricated, falcated (e.g. the type specimen of *H. longispinus*) to ± spreading and very sparse and brittle leaves (e.g. the type specimen of *H. angustissimus*). Based on the studied specimens the latter form seems to be more common. *Herbertus longispinus* grows both on trees and rocks, but the substrate does not seem to explain the variation. It occurs at elevations from 1200 m to 3000 m.

**TOTAL DISTRIBUTION** (Fig. 10): As 2: Taiwan; As 4: Indonesia, Malaysia, the Philippines.

**REPRESENTATIVE SPECIMENS EXAMINED.** — As 2: China. Taiwan, Chi-tou to Chi-ti, Nantou Co., on humus, 1200–1800 m, 1968 Chuang & Schofield 492 (as *H. dicranus* det. by Lee) (NY). As 4: Indonesia. On cliff, 1963 Iwatsuki 533 (H); 6500 ft, 1962 Meijer BI1697 (L-0410312); Flores, on bark,
Fig. 9. Herbertus longispinus (a–g, i and j from lectotype, G; h from isolectotype PC). — a: Habit. — b: Part of the shoot, dorsal view. — c: Part of the shoot, ventral view. — d and e: Leaves. — f: Underleaf. — g and h: Leaf apices. — i: Cells in sinus. — j: Cells of basal lamina and vitta. Use the 1 cm scale for a, the shorter 1 mm scale for b and c, the longer 1 mm scale for d–f, and the 50 µm scale for g–j.


**Herbertus pilifer** (Steph.) H.A. Mill. (Fig. 11)


Plants medium-sized, orange or reddish brown, sometimes with greyish or deep purple colour, 3–8 cm. Stem cross-section oval, 0.25–0.35 × 0.2–0.25 mm. Leaves imbricate, somewhat falcate, basal lamina not much expanded, in dorsal side 5–8 cells wide, leaf length 1.7–2.6 mm, width 0.4–0.6 mm, length–width ratio 4.1–4.6; bifid 2/3–3/4 of leaf length, lobes narrowly lanceolate, 12–17 cells wide at lobe base and 5–9 cells wide at point half way towards apex, lobe apex piliferous, with 6–9 uniseriate strongly elongated cells, and 2–7 rows below apex two cells wide; leaf margin with stalked slime papilla, stalks up to 8 cells long, sometimes margins without slime papilla; vitta not strong in basal part, but extending to apex of lobe, vitta cells 14–20 µm × 55–80 µm in mid basal lamina, bifurcating below mid basal lamina, 8–16 cells between sinus and vitta bifurcation point, 14–20 µm × 14–20 µm; basal lamina cells ca. 14 µm × 14–40 µm, with large trigones; underleaves smaller and symmetrical. Sex organs not seen.
Herbertus pilifer resembles *H. longispinus*, but it can be identified by very piliferous leaf apices, which end in 6–9 very strongly elongated uniseriate cells, the uniseriate cells being 5–6 times longer than wide. In Meijer’s specimens from Borneo, collected from ultrabasic area, the lumens of leaf apex cells are reduced to only narrow lines ca. 10 times longer than wide. The leaf apices of those plants are extreme as well, being very sharp in their appearance. Furthermore, the basal lamina of *H. pilifer* is even less expanded than that of *H. longispinus*. The substrates of *H. pilifer* are poorly indicated in

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**Selected Illustrations:** Miller 1965: 409 (fig. 138); Piippo 1984: 28 (fig. 6).

**Fig. 10.** Distribution of *Herbertus longispinus* and *H. sendtneri*. Circles = *H. longispinus*, asterisks = *H. sendtneri*.

**Fig. 11.** *Herbertus pilifer* (a–c, e, g, i and j from Kluiving 1453, H; d, f, h from L-0410297). — a: Habit. — b: Part of the shoot, dorsal view. — c: Part of the shoot, ventral view. — d and e: Leaves. — f: Underleaf. — g and h: Leaf apices. — i: Cells in sinus. — j: Cells of basal lamina and vitta. Use the 1 cm scale for a, the shorter 1 mm scale for b and c, the longer 1 mm scale for d–f, and the 50 µm scale for g–j.
the specimens that I have examined. The species grows at the elevations of 1000–3500 m.

**TOTAL DISTRIBUTION** (Fig. 12): As 4: Indonesia, Malaysia, Papua New Guinea.


**Herbertus ramosus** (Steph.) H.A. Mill. (Fig. 13)


Plants medium-sized to large, sometimes robust, brown, reddish or orange brown. Stem cross-section oval, 0.4–0.6 × 0.25–0.5 mm. Leaves imbricate, falcate, basal lamina strongly expanded, in dorsal side 8–24 cells wide, leaf length 1.0–2.8 mm, width 0.7–1.2 mm, leaf length–width ratio 1.5–2.5 (~3.5); bifid 1/2–3/4 of leaf length, lobes broadly lanceolate, 15–34 cells wide at lobe base and 9–16 cells wide at point half way towards apex, lobe apex acute, with 4–8 uniseriate cells and 2–7 rows below apex two cells wide; leaf margins with sessile or shortly stalked (1–2 cells long stalks) slime papillae, rarely without slime papillae; vitta strong, grooved, extending to half or somewhat beyond half of lobe, vitta cells 11–20 µm × 28–87 µm in mid basal lamina, bifurcating below mid basal lamina or near base, 14–26 cells between sinus and vitta bifurcation point, 8–17 × 8–31 µm; basal lamina cells 11–17 × 11–34 µm, with large trigones; underleaves smaller and more symmetrical. Gynoecia terminal, with several pairs of female bracts, innermost bract bifid to its half, length ca. 3.5 mm, oblong; perianth ca. 4.5 mm long, mouth lobes acuminate. Sporophyte described by So (2003).

**SELECTED ILLUSTRATIONS:** Miller 1965: 384 (fig. 95, as ‘H. javanica’); So 2003: 16 (fig. 3).

So (2003) synonymized Herbertus javanicus (Steph.) H.A. Mill. with H. ramosus (Steph.) H.A. Mill. Both were originally described from Java, and my examination of holotypes of both H. ramosus and H. javanicus confirmed this synonymization.

Characteristic for H. ramosus are falcato-secund leaf lobes, the dorsal basal lamina often much wider than the ventral one, and broad lanceolate lobes. The leaves are often so wide that the leaf length–width ratio is smaller than in most of the Asian species. Herbertus ramosus is a common species in Indonesia extending to

Fig. 12. Distribution of Herbertus pilifer and H. ramosus. Circles = H. pilifer, squares = H. ramosus.
New Guinea (So 2003). *Herbertus javanicus* is a common name in specimens due to Schiffner’s large collections from 1893 and 1894, with duplicates in various herbaria under this name. Study of these specimens revealed that in addition to *H. javanicus* (≡ *H. ramosus*) they contain also *H. armitanus* and *H. ceylanicus*. I have examined specimens at elevations 1200–3300 m growing on tree trunks and roots, but So (2003) also reported specimens growing on peat and on ground at above 4000 m from West Irian, Indonesia, and from Papua New Guinea. One peculiar specimen collected by Harder *et al.* from Vietnam grew on limestone. The shoots are robust, the basal laminae of the leaves are largely expanded, the vitta poorly defined, and most conspicuously the lobes are often unequally divided to three lobes both in lateral and underleaves. I suspect that these peculiar features might be due to the substrate.

**TOTAL DISTRIBUTION** (Fig. 12): As 3: Sri Lanka, Thailand, Vietnam; As 4: Indonesia, Papua New Guinea.

**REPRESENTATIVE SPECIMENS EXAMINED.** — As 3: **Sri Lanka.** 1865 Beccari (L-0278232). **Thailand.** Mt. Luang, on trunk, 1650–1700 m, 1966 Touw 11719 (BM-000745144). **Vietnam.** Ha Giang, Quang Ba District, Bat Dai Son, in primary forest on limestone with Biota sp., Fraxinus, Quercus, and Pseudotsuga, Taxus and Acer dominants, collections along ridge and below peak, and some on slopes with broadleafed, deciduous forest with some coniferous spp., 1100–1200 m, 2000 Harder, Hiep & Averyanov 5093 (MO-5244366). As 4: **Indonesia.** Java, montis Pangerango, 2975 m, 9 May 1894 Schiffner (B-300230210); Sulawesi (Celebes), on trunk, 2360 m, 1981 Johansson, Nybom & Riebe 452 (L-0410317); Borneo, Korthals (BM-000825739, H-SOL 2303013, H-SOL 2303024).


Plants small to medium-sized, dark or orange brown, 2–6 cm long. Stem cross-section tri-
angular to somewhat rounded, 8–11(–14) cells wide and 8–12 cells high, 0.15–0.45 × 0.2–0.4 mm size. Leaves ± imbricate, erect, falcate or ± straight, asymmetrical, basal lamina expanded, in dorsal side 9–21 cells wide, size of those cells 3–5 × 3–6 µm, leaf length 0.7–2.5 mm, width 0.5–2.0 mm, leaf length–width ratio 1.0–1.3(–1.5); bifid 2/5–2/3; lobes from broad acute to triangular, 10–26 cells wide at lobe base and 9–20 cells wide at point half way towards apex, lobe apex quite blunt, with 1–4(–6) uniseriate cells and 1–3(–5) rows below apex two cells wide; leaf margins often with coarse appendages, slime papillae from sessile to stalked with two cells; vitta not strong or distinct only below, extending usually just to bifid part of leaf or to half of lobe, vitta cells 14–20 × 40–90 µm in mid basal lamina, bifurcating in mid basal lamina, 1/4–4/5 of length of basal lamina from sinus, (5–)7–15(–19) cells between sinus and vitta bifurcation point, 11–28 × 11–33, basal lamina cells 11–17 × 11–22 µm, often with distinctive trigones; underleaves smaller and more symmetrical. Sex organs not seen.

**Selected Illustrations:** Miller 1965: 392 (fig. 109) as ‘H. delavayi’; Meinunger & Köckinger 2002: 40 (fig. 3).

The species is easily recognized by small length–width ratio of leaves, weakly falcato-second leaves, with often coarse marginal appendages, very few uniseriate cells in the leaf lobe apices, the weak vitta, and triangular or somewhat rounded cross-section. Nees (1838) described Schisma sendtneri from the Austrian Alps, where the present European distribution is restricted. Herbertus sendtneri has not been found again from the old locality in Thuringian Forest, and is regarded as extinct in Germany (Meinunger & Köckinger 2002). In the Himalayas H. sendtneri is widely distributed: in Bhutan, India, and Nepal. Hattori (1966) synonymized Chinese H. delavayi with H. sendtneri. During the present study also additional localities for H. sendtneri were discovered from Yunnan. In Asia H. sendtneri occurs at high elevations, i.e. 2500–4900 m. It grows on rocks and boulders, banks and on tree trunks as well; often together with mosses. Miller (1965) cited the specimen 1471 in G as “type”, and 1472 as paratype for H. delavayi. They were labeled as collected in 1889 by Delavay from the type locality. However, H. delavayi was described already in 1895 by Stephani who referred to “Herb. Paris” in his description. Therefore the specimen in PC is to be considered as a holotype of H. delavayi and a specimen in BM (000661074) as an isotype. The specimens in G are paratypes.
Morphology of *Herbertus sendtneri* seem to be quite identical in different parts of its scattered range. However, in the study based on nuclear ITS, and 5,8S sequences, Feldberg *et al.* (2004) showed that *H. sendtneri* from the Alps belongs to the same clade with *H. azoricus* (Steph.) Richards and a South American species earlier called *H. subdentatus* (auct. non (Steph.) Fulford; see also Hodgetts 2003). They synonymized *H. azoricus* with *H. sendtneri* and named South American *H. subdentatus* auct. non (Steph.) Fulford records as *H. sendtneri* as well. In my phylogenetic analysis based on nuclear ITS2, chloroplast trnL-F, and morphology *H. sendtneri* from the Himalayas and *H. subdentatus* from South America were resolved as sister species (Juslén 2006). Feldberg *et al.* (2004) accept a broad morphological definition for *H. sendtneri* as *H. azoricus* and *H. subdentatus* auct. non (Steph.) Fulford differ remarkably from Austrian, Himalayan, and Chinese *H. sendtneri* in their morphology. Recently they have added several South American *Herbertus* binomials under synonymy of *H. sendtneri* (Feldberg & Heinrichs 2005a).

Koponen (1992) discussed the disjunctive distributions between European and East Asiatic floras. She stated that such taxonomic connections are rare, but some examples exist. Koponen (1992) synonymized morphologically identical *Tayloria delavayi* and *T. rudolphiana* that occur disjunctly in Yunnan and in the Alps. Judging from the known disjunct distributions of liveworts, the range of *H. sendtneri* in Austria, the Himalayas, China, the Azores, and South America would be exceptional (see Schofield & Crum 1972, Koponen 1992). The species concept should be further tested with comprehensive sampling including Asian *H. sendtneri*.

**TOTAL DISTRIBUTION** (Fig. 10): **As 2:** China; **As 3:** Bhutan, India, Nepal; **Eur:** Austria. 

**REPRESENTATIVE SPECIMENS EXAMINED.** — **As 2:** China. Yunnan, Yulong Shan, mountain ridge above Wo Tu Di, on mossy rocks in gully with *Rhododendron adenogynum*, 4000 m, 1990 Long 19047 (JE). **As 3:** Bhutan. Haa district, summit of Chetlai La, on boulder, 3890 m, 1999 Long 28730 (H). **India.** Singalila Ridge, Tarupani, 4300 m, 1980 Pradhan Rai 193 (B-300230827); Sikkim, on cliff, 4775 m, 1996 Long 26630 (H as *H. delavayi*); on boulder, 3965 m, 1992 Long 22568 (H). **Nepal.** Sinion La, exposed rocky ridge, amongst boulders, ca. 4525 m, 1989 Long 16994 (JE). **Eur:** Austria. Innsbruck, Rosskogel, 2000 m, 1991 Melick 910746 (H. Van Melick personal collection); Tirol, 2000 m, 1923 Berger (H-3174066).

**Excluded taxa**

*Herbertus subrotundatus* X. Fu & Y.J. Yi


*Herbertus subrotundatus* does not belong to *Herbertus*. It lacks the trigonous cell walls and intermediate thickenings characteristic for the genus. Furthermore, the vitta is very indistinctive. The specimen available for this study is extremely small and fragile, and based on observations of the sole specimen I was not able to draw further conclusions about the identity of the species.

*Herbertus gymnocoloides* was introduced without a Latin description. I was not able to detect other references to *H. gymnocoloides*. The illustrations given for *H. gymnocoloides* are exactly similar as those for *H. subrotundatus* in Yi *et al.* (2001). Therefore, *H. gymnocoloides* is regarded as an invalid name of *H. subrotundatus*.

**Taxa not available for study**

*Herbertus mehrae* D. Kumar & N. Manocha, nom. inval.


*Herbertus udarii* D. Kumar & N. Manocha

Geophytology 29: 105. 2000. — **Type:** India. West Bengal, Darjeeling, Ray Ville Road. 1969 Udar, Srivastava & Kumar (holotype LWU-1400/69).

**Discussion**

Miller (1965) listed 47 species and one uncertain species from Asia, Australasia, and Pacific
Islands excluding Australia and New Zealand. So (2003) accepted eight species from Australasia and South Pacific including Australia and New Zealand. The present study covered Asia, but not Australasia, Pacific Islands, Australia or New Zealand; 12 species are accepted. Together, So (2003) and the present study recognize 16 species from Asia, Australasia and the South Pacific. This is in agreement with several statements that have predicted a mass reduction of species in Herbertus (Evans 1917, Schuster 1957, Gradstein 2001). Miller (1965) also proposed a division of Herbertus to five sections. However, my examination of Asian Herbertus gives no support to that proposal.

The ranges of Herbertus aduncus subsp. aduncus, H. dicranus, and H. sendtneri extend to other continents in addition to Asia. Four species, H. armitanus, H. circinatus, H. pilifer, and H. ramosus, occur in Australasia as well (So 2003). The distribution areas of five species, H. buchii, H. ceylanicus, H. guangdongii, H. kurzii, and H. longispinus, are restricted to Asia. Within the area covered by the present study, Herbertus is most extensively collected from the Himalayas, and the genus can be considered well known in the area. Herbertus flora is richest in the diverse tropical Indo-Malayan region. However, the collections still do not cover the area comprehensively.

Numerous specimens from Asia have been earlier named as Herbertus longifissus. However, H. longifissus is a species occurring only in Melanesia (So 2003). So (2003) mentioned that the range of Asian specimens named as H. longifissus revealed to be H. sakuraii (= H. dicranus), and I agree. Two Asian species, H. buchii from Amur, Siberia and H. guangdongii, from Hainan, China, are known only from the types. Gambaryan (1992) analyzed the hepatic flora of Russian Far East, including the collection locality of H. buchii, and found it unique in many respects. She also pointed out the irregular and insufficient study of this area. Lin et al. (1992) stated that also the bryoflora of the Hainan island still remains poorly known. Another example of rarely collected, but distinctive Herbertus species beyond the focus of this study is the New Caledonian endemic H. leratii (Steph.) H.A. Mill. It has been collected only twice in the early 1900s from Mt. Mou (So 2003). I was able to examine a recent collection from Mt. Panié, New Caledonia (1999 van der Werff & McPherson I6020A, MO-5224932), which is H. leratii.

Herbertus is known to be morphologically an extremely plastic genus. Feldberg and Heinrichs (2005b) discussed the problems of delimitation of the species. They especially pointed out the difficulties in circumscription of Asian and Holartic species. Earlier taxonomists used narrow species concepts (Stephani 1895, 1898–1924, Miller 1965). I have applied a wider species concept as in accordance with more recent studies (Inoue 1977, So 2003). The sexual organs seem to be rare in Herbertus and their limited study did not offer new insights into species delimitation. I was not able to study material fresh enough to enable observation of the oil bodies. An additional character to be studied from Asian species is leaf cell surface structure as seen in the SEM micrographs used e.g. by So (2003), Feldberg et al. (2004), and Feldberg and Heinrichs (2005a). The lack of stable morphological characters obviously creates problems in identification of some intermediate forms. However, based on my experience, Herbertus species can be satisfactorily circumscribed by studying an extensive amount of specimens. In order to recognize monophyletic species, the species boundaries here presented are to be further tested by comparison of morphology and molecular topologies, and first of all, by combining evidence from all available sources.

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