A taxonomic revision of *Dicranodontium* (Musci)

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The 39 species of *Dicranodontium* which are currently included in the genus are critically revised and reduced to 7. Dicranodontium fleischerianum Schultze-Motel could not be separated from D. uncinatum (Harv.) Jaeg. and is regarded as synonymous with the latter. Dicranodontium dimorphum Mitt. has proven to be synonymous with D. didictyon (Mitt.) Jaeg., D. meridionale Bartr. with D. pulchroalare Broth., D. ceylonense Fleisch., D. subasperum Williams and D. perviride Dix. & P. Varde are synonymous with D. denudatum (Brid.) Britt., D. subintegrifolium Broth., D. attenuatum (Mitt.) Wils., D. caespitosum (Mitt.) Par. and D. decipiens (Mitt.) Mitt. ex Broth. are synonymous with D. didymodon (Griff.) Par., D. blindioides (Besch.) Broth., D. sparsum Dix. are synonymous with D. uncinatum (Harv.) Jaeg. Dicranodontium sinense (C. Müll.) Par. is identical with Campylopus japonicus Broth. and recognized as Campylopus sinensis (C. Müll.) J.-P. Frahm comb. nov. Dicranodontium falcatum Broth. (described as endemic from Hawaii) is synonymous with D. porodictyon Card. & Thér. from China, D. tanganyikae J. Tayl. & P. Varde is identical with Campylopus flexuosus (Hedw.) Brid. var. incacorralis (Herz.) J.-P. Frahm, D. humilis P. Varde is a species of Blindia, D. interruptum P. Varde is identical with Bryohumbertia filifolia (Hornsch.) J.-P. Frahm, D. horricuspis Card. and D. capillifolium (Dix.) Takaki are synonymous with D. asperulum (Mitt.) Broth. Dicranodontium brasiliense Herz. is placed as subspecies in D. pulchroalare. Dicranodontium intermedium Allen is placed into Atractylocarpus and recognized as A. intermedius (Allen) J.-P. Frahm comb. nov. Dicranodontium insularum Bartr. and D. tristaniense Dix. & Thér. belong to Dicranoloma. Dicranodontium tenii Broth. described from China is identical with Dicranum hamulosum Mitt. from Japan. Dicranodontium tenuinerve Dix. & Sak. described from Japan is identical with Bryohumbertia subcomosa (Dix.) J.-P. Frahm. Dicranodontium filifolium Broth. seems not to belong to this genus, but its systematic position is dubious. Dicranodontium subporodictyon Broth. is transferred to the genus Dicranum Hedw. and recognized as D. subporodictyon (Broth.) Gao. The types of Dicranodontium tapes (C. Müll.) Par. and D. papillifolium Gao were not available, but it is very unlikely that these species belong to this genus.

Key words: Dicranaceae, Dicranodontium, Musci, nomenclature, taxonomy

INTRODUCTION

Dicranodontium is a genus of the Dicranaceae subfam. Campylopodioideae. This subfamily comprises the genera Atractylocarpus, Bryohumbertia, Campylopus, Dicranodontium, Pilopogon and Sphaerothecium (Frahm 1991). All of these genera except Dicranodontium have been revised (Atractylocarpus: Padberg & Frahm 1986, Bryohumbertia: Frahm 1982, Pilopogon: Frahm 1983, Sphaerothecium: Frahm 1986; Campylopus was revised in numerous single publications). The present publication will complete the treatments of genera of Campylopodioideae.

Seventy-four species of Dicranodontium and 32 infraspecific taxa are listed in Index Muscorum (Van der Wijk et al. 1959), and 35 of them were accepted. Two species were added in the additions to the Index Muscorum 1963-89 (Crosby et al. 1992), one species was later described by Allen (1994) and another species was transferred to Dicranodontium from Campylopus by Frahm (1994). Two species were excluded from the genus by Frahm (1991), resulting in a total of 39 species. For comparison: Brotherus (1901) recognized 18 species within the genus in the first edition of the "Natürlichen Pflanzenfamilien" and 21 species in the second edition (Brotherus 1924). Except for the species occurring in Canada (Ireland 1987), this genus has so far not been revised.

The purpose of this paper is to give a worldwide overview of the genus and a critical revision of the taxa. Therefore the majority of infraspecific taxa are not treated, of which 32 were described. Furthermore, a revision of all taxa which were previously placed by other authors into different genera has been omitted.

Dicranodontium species are difficult to separate from those of Campylopus, Dicranum, Atractylocarpus or Bryohumbertia. This is shown by the fact that 12 species of Dicranodontium were originally described as species of Campylopus or Dicranum or more rarely Paraleucobryum and Dicranella and 17 species described as Dicranodontium were later transferred to Campylopus, Atractylocarpus, Campylopodium, Paraleucobryum, Dicranella or Dicranoloma. Some species of Dicranodontium (those without enlarged or incrassate and pitted juxtacostal cells) resemble Atractylocarpus in the gametophyte (Padberg & Frahm 1986) and can hardly be distinguished without sporophytes. Only the sporophytes differ. In Atractylocarpus, the setae are long, 15–25 mm, erect when dry and flexuous when wet, in Dicranodontium the setae are shorter, 6-15 mm long, flexuous when dry but cygneous when wet and or in the young state. This difference is certainly not satisfying, especially when specimens are sterile. Therefore Atractylocarpus and Dicranodontium were synonymized by Williams (1913). This view was followed by Allen (1994) in his treatment of the Central American Dicranaceae, and it was used to support a new species, Dicranodontium intermedium, which is autoicous like Atractylocarpus but has cygneous setae like Dicranodontium. However, if this view is accepted, Dicranodontium has also consequently to be synonymized with Campylopus because it differs from certain species of Campylopus only by its longer upper laminal cells; Pilopogon must be synonymized with *Campylopus* because it differs from *Campy*lopus only by its straight setae and long sheathing perichaetial leaves; Bryohumbertia must be united with Campylopus because it does not differ gametophytically from the latter but only in some capsule characters; and Sphaerothecium must be included in Campylopus because it differs only in the larger spores. This would create a large and unwieldy genus comprising all genera so far included in the subfamily with several hundred species, for pragmatic reasons alone this does not seem to be an advantage.

In spite of their anatomical similarities, *Dicranodontium* and *Atractylocarpus* differ in their ranges in that *Dicranodontium* is holarctic in distribution, reaching the tropics only in SE-Asia and in the Andes but *Atractylocarpus* occurs worldwide in the high montane or alpine belt.

TAXONOMIC TREATMENT

Dicranodontium B.S.G.

Bryol. Eur. 1: 159, 1847.

Type: *Dicranodontium longirostre* (Web. & Mohr) B.S.G. (= *D. denudatum*).

Plants erect, in dense cushions. Leaves erect, sinuose to falcato-secund or hamate, from a sheathing concave base narrowed into a long often tubulose setaceous tip. Lamina short, reaching only 1/4 of leaf length. Costa filling (1/4–)1/3

of the leaf width, in transverse section with a ventral layer of epidermal cells, a ventral stereid band, a median row of large deuter cells, a dorsal stereid band and a dorsal layer of epidermal cells, excurrent, serrate to serrulate all around in the upper part or rarely (in *D. didymodon*) almost smooth. Alar cells differentiated, thin-walled, hyaline or reddish, inflated or not, sometimes auriculate. Inner basal laminal (juxtacostal) cells inflated, hyaline, sharply delimited from the outer cells or not. Outer laminal cells smaller and narrower, forming a distinct limbidium or not. Upper laminal cells rectangular to elongate rectangular.

Dioicous. Seta flexuous when dry, cygneous when moist or young, 0.6–1.5 cm long. Capsule short cylindrical, erect, smooth, weakly furrowed when empty. Operculum longly rostrate, as long or almost as long as the capsule. Annulus absent. Peristome teeth 16, typically dicranoid, divided to the base, striate at base and papillose at tips. Calyptra cucullate, usually smooth or rarely ciliate.

Vegetative propagation by means of deciduous leaves or leaf tips. Deciduous leaves are very typical for most species of the genus and are expressed in the epithet "denudatum". The leaves can be deciduous in such a number that large parts of the stem are defoliate. The stem looks then like a *Picea*-branch without needles.

As in many other dioicous genera, sporophytes are produced infrequently, perhaps due to the lack of male plants, which are smaller. Sterile populations usually consist entirely of female plants.

All species treated here in *Dicranodontium* are very similar in appearence; they have a very short lamina, long subula, a similar transverse section of the costa and also similar sporophytic characters (length of seta and shape of capsule). Therefore there are only a few differentiating characters remaining to separate species, e.g. the shape of the inner basal laminal cells or the denticulation of the subula. Because of the small number of differentiating characters, there are fewer combinations of characters possible than species described and thus a reduction of the species number could be expected.

The leaves can be circinate, falcate or almost straight and flexuose in the same species; there are always falcate forms known in species which usually have straight and flexuose leaves and "subfalcatum" forms in species with usually circinate leaves. Therefore no illustrations of the habit of the species are provided here.

The presence/absence, size or form of the alar cells, which is often used in the literature to differentiate species, is not used here since this character proved to be too variable.

A main source of confusion in the genus has been the description of the inner basal laminal cells. They are described as distinctly or indistinctly differentiated from the outer ones. In Dicranodontium asperulum, D. didictyon, D. meridionale, D. porodictyon and D. uncinatum they are as conspicuous as in the leaf base of Calymperaceae. They are usually thin-walled, hyaline, translucent, much enlarged and distinctly and very abruptly differentiated from the narrow elongate cells at the margins. In contrast, the inner basal laminal cells of D. denudatum and D. divmodon are larger than the outer ones, but not differentiated in colour from the outer ones. The transition to the outer basal laminal cells is more gradual. The inner ones are usually thick-walled but not pitted. The shape of the inner basal laminal cells is the only character which seems to group the genus into natural units and can therefore be used for a infrageneric classification.

The upper laminal cells are usually described as elongate in this genus, a character, which differentiates it from related genera such as *Campylopus*. However, if this character is studied carefully, it turns out that the upper laminal cells of *Dicranodontium denudatum* are sometimes only about 5 times longer than broad, those of *D. didictyon* are only 5–7 times longer as broad, and some species such as *D. uncinatum* have almost no upper laminal cells. In this case the subula is excurrent above the leaf shoulders. Really long upper laminal cells (12:1) are only found in *D. pulchroalare*.

The costa has principally the same structure in all species with a median row of guide cells, ventral and dorsal layers of stereids and ventral and dorsal rows of epidermal cells. The latter will distinguish *Dicranodontium* from species of *Campylopus* with two stereid bands or also most species of *Dicranum*. The ventral layer of stereids can be almost as broad as the costa (e.g. in *Dicranodontium asperulum*, *D. pulchroalare*, *D. porodictyon* and *D. uncinatum*) or shorter (e.g. in *D. denudatum*, *D. didymodon*, *D. didictyon*). In the latter case, the stereid band is visible in the costa as a dark band and the costa seems to be ill defined. A broad ventral stereid band is found in species with hyaline inner basal laminal cells and a narrow ventral stereid band is found in species without hyaline inner laminal cells. The single exception to this is *D. didictyon*, which has a narrow stereid band but large hyaline inner basal laminal cells.

The subula is 4–5 times longer than the lamina, which is also a character that helps to distinguish *Dicranodontium* from related genera. It is almost smooth in *D. didymodon*, but serrate in all other species. The subula of *D. asperulum* is said to be serrate all around, but this is principally also the case in all other species, at least in the uppermost part of the subula. The subula of *D. asperulum* is, however, serrate all the way down. The intensity of serration can vary greatly even in leaves from the same plant.

Dicranodontium is vegetatively very similar to certain species of Campylopus and those species of Dicranum with a broad costa. It can be distinguished from these genera by its elongate upper laminal cells and its leaf shape which has a short lamina and a long subula about four times longer than the lamina. From species of Campylopus with dorsal and ventral stereid bands in the costa it is also distinguished by its costal morphology as seen in the transverse section. In Dicranodontium there are distinct ventral and dorsal epidermal cells in Dicranodontium and a multilayered band of ventral stereids, however, in Campylopus, the ventral stereids are single layered, or if multilayered, lack an outer epidermal layer. Also the leaf shape seems to differentiate Dicranodontium from these genera. The lamina is very short, only 1/4-1/5 of the leaf length, and quickly narrowed into the long subula, and the leaf base is concave and sheathing the stem. The alar cells are usually fugacious and remain attached to the stem when the leaves are stripped off or when the leaves have fallen off.

Sporophytically, *Dicranodontium* resembles *Bryohumbertia* in a smooth calyptra, an operculum, which is as long as the capsule, and a relatively long seta (as compared with *Campylopus*) which is sinuose in the upper part. The capsules of species of *Dicranodontium* are, however, cylindrical and the seta is not twisted.

Key to the species of Dicranodontium

1.	Inner basal laminal cells large, hyaline, thin-walled, strongly contrasting with the smaller, chlorophyllose outer cells
1.	Inner basal laminal cells not strongly contrasting with
	the outer ones
	2. Leaf margin toothed almost to the leaf base. Subula serrate all around 1. <i>D. asperulum</i>
	2. Leaf toothed only in the upper third of the subula
3.	Robust plants, 4–10 cm high. Ventral stereid bands in transverse section of the costa as broad as the costa4
3.	Slender plants, up to 5 cm high, in appearence much
	like D. denudatum but with enlarged hyaline juxtacostal
	cells. Ventral stereid band in transverse section of the
	costa only in the middle of the costa 3. D. didictyon
	4. Lamina extending almost to the apex in a very nar-
	row band 1-4 cells wide, denticulate at margins
	4. Lamina not extending to the apex in a narrow band
	at margins
5.	Upper laminal cells pitted 6. D. pulchro-alare
5.	Upper laminal cells not pitted 5. D. porodictyon
	6. Upper third of subula denticulate all around
	2. D. denudatum
	6. Upper third of subula almost smooth to finely ser-
	rulate 4. D. didymodon

Dicranodontium asperulum (Mitt.) Broth. (Fig. 1)

Nat. Pfl. 10: 336. 1901.

Dicranum asperulum Mitt., J. Linn. Soc. Bot. Suppl. 1: 22. 1859. — Campylopus asperulus (Mitt.) Kindb., Bih. K. Svensk. Vet. Ak. Handl. 7: 88. 1883. — Type: India. "In Himalayae orient. reg. temp., Sikkim" J. D. Hooker 18, 29 (NY, lectotypus nov.).

Dicranodontium aristatum Schimp., Syn. 695. 1860 (fide Williams, N. Am. Fl. 15: 152. 1913). — Didymodon aristatum Lindb., Musc. Scand. 25. 1879. — Type: Germany. Bohemia, "Bekleidet in ungeheurer Menge die Sandsteinfelsen von Merkersdorf und Adersbach in Böhmen …, im Mai 1860 ges. von Dr. Milde." (isotypes H-SOL, H).

Dicranodontium lutescens Schimp. ex Mol., Jahresber, Naturw. Ver. Passau 10: 49. 1875 (*fide* Braithw., Brit. Moss. Fl. 1: 159. 1883). — Type not seen.

Dicranum virginicum Aust., Bot. Gaz. 4: 150. 1879 (fide Williams, N. Am. Fl. 15: 152. 1913). — Campylopus virginicus (Aust.) Lesq. & Jam., Man. 80. 1884. — Type: USA. Virginia, Mt. Rogers, Small 77 (isotype H).

Dicranodontium horricuspis Card., Rev. Bryol. 28: 113. 1901, syn. nov. — Type: Indonesia. Sulawesi, Bua-Kräng, 5 000–7 000 ft., Fruhstorfer s. n. (holotype PC).

Brothera capillifolia Dix., J. Bombay Nat. Hist. Soc. 39: 774. 1937, syn. nov. — Dicranodontium capillifolium (Dix.) Takaki, J. Hattori Bot. Lab. 31: 292. 1968. — Type:

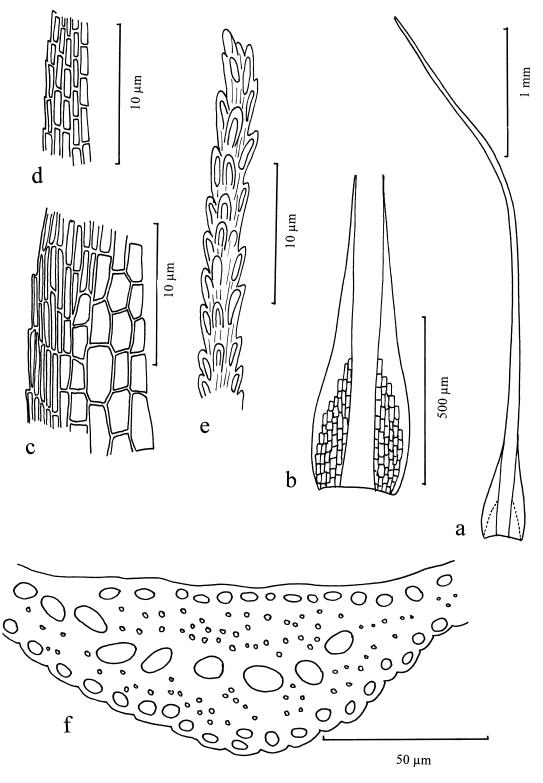


Fig. 1. *Dicranodontium asperulum* (Mitt.) Broth. (type of *D. aristatum* Schimp., H-SOL). — a: Leaf. — b: Leaf base. — c: Basal laminal cells. — d: Upper laminal cells. — e: Leaf apex. — f: Transverse section of costa.

India. Assam, Aka Hills, 1933, Bor & Piri s. n. (holotype BM).

Plants usually very tall, to 10 cm high, yellowish green, in dense tufts, slender with small leaves, densely foliate, erect, more or less appressed (as plants grown on sandstone such as the type of *D. aristatum*) or robust, distantly foliate with sinuose or homomallous leaves. Leaves 5– 6 mm. Margin finely toothed almost to the leaf base. Lamina reaching only 1/4 of the leaf length. Alar cells fugacious, hyaline. Inner basal laminal cells enlarged, hyaline, well separated from the narrow, longer, chlorophyllose outer ones. Middle laminal cells rectangular, incrassate, not pitted.

Sporophyte rarely found. Seta 1.5–2 cm long, sinuous when moist. Capsule oblong, 1.5–2 mm long. Operculum longly rostrate, almost the length of the urn. Spores 13 mm.

Illustrations: Grout (1937): pl. 44; Gangulee (1971): fig. 152; Nyholm (1954): fig. 33B; Crum & Anderson (1981): fig. 104; Gangulee (1971): fig. 149 as *D. capillifolium*; Takaki (1968): fig. 4 as *D. capillifolium*.

This species usually is easily recognized by its long arista, which is serrate all around (as a rat's tail file, as expressed in the species names asperulum and aristatum), therefore the leaf apex is not canaliculate as in most other species of the genus, and the leaf margin is denticulate to the base. There are rarely forms with almost smooth or only finely denticulate leaves, which can be identified, however, by the large hyaline inner basal laminal cells in combination with very slender, almost erect leaves. Furthermore, the leaves are usually (and very unusual for the genus) upright and erect patent to appressed. There are also forms with curved leaves ("Dicranodontium aristatum var. falcatum"). But these, however, are sometimes found in the same collection sites and seem to represent only modifications. The character strongly serrate vs. almost smooth leaf apex is not correlated with these forms.

The arista is sometimes extremely fine and long, in which case it is often curled.

The protologue of *Dicranodontium asperulum* includes two syntypes, *Hooker 18* and *29*. The herbarium of Mitten, however, includes only no. 29, which is therefore chosen as lectotype.

As pointed out by Frahm (1994), *Dicranodontium capillifolium* was described from Assam as species of *Brothera*. Takaki (1968) in a study of the genus *Brothera* transferred it to *Dicranodontium*. The species was only known from the type locality in Assam, but recently it has been reported from several localities in Sichuan and Yunnan, China (Frahm 1994). These records belong, however, to forms of *Dicranodontium denudatum*, in which the leaf apex ends in a very long and fine subula which partially consists of a single row of cells. This feature, however, is found only in the uppermost leaves of a plant. The other leaves are less long and resemble those of "typical" *Dicranodontium denudatum*. Furthermore, the leaf anatomy of the long-pointed leaves is not different from those from *D. denudatum*.

The range of *Dicranodontium asperulum* is mainly holarctic. It is, however, found in SE-Asia in Nepal, Sikkim, Yunnan, Taiwan and in Sulawesi (type of *D. horricuspis*). Although only known from this single record in Sulawesi, its identity is unquestionable.

Habitat: on siliceous rocks (sandstone, gneiss, granite) in cool, humid montane areas, based on the size and quantity of herbarium specimens, often in large masses.

Distribution: North America, Appalachian Mtns. (Georgia, North Carolina, Tennessee, Virginia, Pennsylvania), Canada (British Columbia), Alaska. Europe (Scotland, Norway, Germany, Czech Republic, Poland, Slowakia, Austria, Switzerland, Italy). Himalayan region (India, Nepal, Sikkim), China (Sichuan, Yunnan), Sulawesi, Taiwan, Japan.

Specimens examined. — Norway. Söndhordaland, Stöle, Wulfsberg 22 (H-SOL); Hordaland, Tyeskaret, Kotilainen s. n. (H); Aalesund, Berggren s. n. 1868 (H, H-SOL); Ryfylke, Trafjord, Bryhn s. n. 1889 (H); Bergen, Wulfsberg 12 (H, H-SOL); Rogerland, Dirdal, Persson s. n. (H). Scotland. Glasgow, Linnox Castle, McKinley s. n., Bryotheca europ. 940 (H-SOL); Ben Voirloch, Schimper s. n., Hunt s. n. (H, H-SOL); Perthshire, Stuearchroin, Meldrum s. n. (H). Highland Region, Seven Sisters National Park near Shiel Bridge, Frahm s. n. (hb. Frahm). Germany. Franken, Nusshard, Molendo s. n. (H-SOL). Sachsen, Zittauer Gebirge, am Töpfer bei Oybin, Kopsch 316 (hb. Frahm). Elbsandsteingebirge, Teufelsgrund, Siegel s. n. (hb. Frahm). Czekia. Adersbach, Milde s. n. (H-BR); auf Glimmerschieder der Hohen Seewand bei Eisenstein im Böhmerwalde, Bryotheca Bohemia 110 (H); "Enge Stiege" in der böhm. Schweiz, an Sandstein, Schiffner s.n. (H); auf Sandstein im Khaatale bei Schönlinde, Bryotheca Bohemica 16 (H); Böhmerwald, Plöckenstein, Kujala s. n. 1926 (H). Adrspachske skaly, in saxis arenaceis prope pag. Janovice, Musci cechosl. exsicc.

502, 539, 936, 944, 1172. (H). Teplice, Pilous 329, 936 (hb. Frahm). Poland. Sudetes, monts Góry Stolowe, Lisowski 58386, 64204 (H,U). Tatra Mtns., Mt. Zolta Turnia, Bryotheca Polonica 1365 (H); an Sandsteinfelsen des "Wilden Loches" bei Cudowa, Milde s. n. (H-SOL), ibidem, Bryotheca Silesiaca 56 (H). Austria. Salzburg, Ammersbach Schwartz s. n. (H-SOL); Krimmler Wasserfall, Schwab s. n. (hb. Frahm); bei Wagrain, Schwab s. n. (hb. Frahm). Kaprun, Breidler s. n. as D. denudatum forma (H-SOL). Steyermark, St. Nikolai, Breidler s. n. (H, H-SOL); Gneissblöcke im Ingeringgraben in der Gaal, Breidler s. n. (H); Gneisfelsen am Fuße des Mittelbergs bei Schladming, Breidler s. n. (H); Oberthal bei Schladming, Breidler s. n. (H); am Fuß de Metterberges bei Schladming, Breidler s. n. (H). Nord-Tirol, am Weg nach Gerlos im Zillerthal zw. dem "Ötschen" und Gmünd, Kalkschiefer, Handel-Mazzetti s. n. (H). Tirol, in valle Gschnitz ad alpem Lapones, Kerner, Fl. Exsicc, Austr.-Hung. 731 (H,U). Switzerland. Bei Splügen 1 800 m, Holler s. n. 1867 (H). Italy. Como. Valsassina, Alpe di sasso 1 600 m, Bryoth. Europ. meridion. 215 (H). Ukraine. Yaremche, Lazarenko s. n. (H). U.S.A. Pennsylvania, Franklin Co., Jerusalem, Collins 1615 (H). Virginia, White Top, Britton 198 (H-BR); Tucker Co., Blackwater Falls near Davis, Anderson 21870 (DUKE), Ray 11282 (F). Smyth Co., Summit of White Rock Mtn., Small s. n. as D. longirostre (DUKE); Mt. Rogers, Small, Mosses of the Southern United States 77 (H). North Carolina, Burke Co., Table Rock W Morgantown, Anderson 22221 (F, FLAS, H, U), 15103 (DUKE); Yancy Co., Balsam Cone Mt. near Busick, Anderson 12755 (DUKE, F, H, U); Yancey Co., Mt. Mitchell, Anderson 15001 (DUKE, H) 9475 (DUKE); Swain Co., Porters Gap, Anderson 4357 (DUKE); Jackson Co., Maidenhair Falls, Anderson 10274 (DUKE); Grandfather Mtn., Anderson 12717, 12744 (DUKE); Macon Co., Highland Falls, Anderson 10411 (DUKE); Linville Falls, Anderson 15014 (DUKE), Sharp 325, Clebsch BR12 (F). Chestnut Bold, Grout s. n. as Campylopus virginicus (DUKE). Klingman's Peak, Schallert 59, Musci Europ. Bore. Amer. 485 (DUKE, H). Tennessee, Sevier Co., Great Smoky Mtns. Nat. Park near Newfound Gap, Schofield 10501 (DUKE, F, H, U); ibid. Mont Le Conte, Delgadillo 1509 (hb. Frahm), Anderson 20838 (DUKE); 1/2 mi below Alum Cave, Sharp 4752 as D. denudatum (DUKE), Schofield 10581 (DUKE); near Ramsay Cascades, Norris 63-282 (DUKE); Ramsay Prong above Greenbrier, Sharp 3660 (DUKE, F); Ramsey Cascades, Sharp 3594 (F). Carter Co., Roan Mtn., Sharp 34463 (DUKE); Roaring Fork Creek, Sharp 344994 (DUKE). Near Siler's Bald, Schofield 9444 (DUKE). Rainbow Falls, Schofield 10670 (DUKE). Canada. Brit. Columbia, Queen Charlotte Islands, Graham I., Persson s. n. 1957 (H); Graham Isl. Gudal Creek, Schofield 33538 as D. denudatum (DUKE); Moresby Isl., Anna Inlet, Schofield 24353 (DUKE); NW coast of Moresby Isl., Schofield 15495 (DUKE); Blue Heron Cove, Schofield 31344 (DUKE). Rainbow Lake 20 km E of Prince Rupert, Schofield 20830 as D. denudatum (DUKE); Prince Rupert Reservoir, Boas 59 (DUKE). India. Tassangse, hb. Griffith (NY). Sikkim. Yalloong hills, Hooker (H-SOL). Nepal. Between Dor and Chauke 2 850 m, Iwatsuki 451 (H). China. Sichuan, Wolong, Wu Yi Ping, *Eggers CHI 3*/43 (hb. Frahm). **Taiwan.** Prov. Ako, Mt. Daibu, *Matsuda 1252* (H). **Japan.** Hondo, Shimotsuka, *Sakurai 847* as *D. uncinatum* (H). Honshu, Nagano Pref., Mt. Gakidake, alpine region 2 500 m, *Takaki 12722* (H).

Dicranodontium denudatum (Brid.) Britt. (Fig. 2)

in Williams, N. Am. Fl. 15: 151. 1913. — Dicranum denudatum Brid., Musc. Rec. 1: 184. 1806. — Campylopus denudatus (Brid.) Kindb., Bih. K. Svensk Vet. Ak. Handl. 7: 87. 1883. — Didymodon denudatus (Brid.) Lindb., Musc. Scand. 25. 1879. — Types: "Ad ligna putrescentia et rupes madidas prope Dietharz Thuringiae ... In Bugesiae montibus etiam legit Déjean. Ex Helvetia etiam misit Schleicher in valle Solaley supra Bex ad rupes crescens." (lectotypus nov., G).

Didymodon longirostris Web. & Mohr, Bot. Taschenb. 155, 463. 1807 (fide Williams, N. Am. Fl. 15: 151. 1913). — Cynodontium longirostris (Web. & Mohr) Schwaegr., Spec. Musc. Suppl. 1: 111. 1811. — Dicranodontium longirostre (Web. & Mohr) B.S.G., Bryol. Eur. 1: 158. 1847. — Campylopus longirostris (Web. & Mohr) Sendtn., Flora 31: 215. 1848. — Trichostomum longirostris (Web. & Mohr) Hartm., Handb. Skand. Fl. ed. 5: 385. 1849. — Dicranum longirostre (Web. & Mohr) Kindb., Eur. N. Am. Bryin. 2: 190. 1897. — Type: "Ñad trunc. putr., in sylv. subalp. com. Glatz, in Sudet." (type could not be located).

Dicranum chionophilum C. Müll., Syn. Musc. fr. 1: 398. 1848 (fide Robinson, Bryologist 70: 11. 1967). — Campylopus chionophilus (C. Müll.) Mitt., J. Linn. Soc. Bot. 12: 81. 1869. — Type: Venezuela. Méerida, Funck & Schlim s. n. (holotype destroyed at B, lectotypus NY).

Campylopus alpinus Schimp., Musc. Eur. Nov. Bryol. Eur. Suppl. Campyl. 1–2: 5. 1864. — *Dicranodontium alpinum* (Schimp.) Loeske et Podp., Zpravy Komm. Prir. Pozk. Moravy Odd Bot. 2: 54. 1906. — *Dicranodontium denudatum* ssp. *alpinum* (Schimp.) Giac., Atti Ist. Bot. Univ. Lab. Critt. Pavia ser. 5, 4: 193. 1947. — *Dicranodontium denudatum* var. *alpinum* (Schimp.) Hag. K. Norsk Vid. Selsk. Skrift. 1914: 56. 1915. — Type: "Cambrovalliae alp.", *Schimper s. n.* (isotype H-SOL).

Campylopus flexuosus (Hedw.) Brid. var. pachyneuron Mol., Ber. Naturh. Ver. Augsburg 18: 139. 1865 (fide Milde, Bot. Zeit. 28: 416. 1870). — Campylopus pachyneuros (Mol.) Walth. & Mol., Laubm. Oberfrank. 106. 1868. — Campylopus alpinus Schimp. var. pachyneuros (Mol.) Mol., Jahresber. Naturh. Ver. Passau 10: 51. 1875. — Dicranum pachyneuron (Mol.) Kindb., Eur. N. Am. Bryin. 2: 190. 1897. — Type not seen.

Dicranum notabile Stirt. Scott. Natural. 8: 257. 1886 (fide Williams, N. Am. Fl. 15: 151, 1913). — Type not seen.

Dicranodontium virginicum Britt. in Millsp., Bull. West Virginia Agric. Exp. Stat. 24: 488. 1892 (*fide* Williams, N. Am. Fl. 15: 151. 1913). — Type not seen.

Dicranodontium millsphaugii Britt. in Millsp., Bull. West Virginia Agric. Exp. Stat. 24: 488. 1892 (fide Williams,

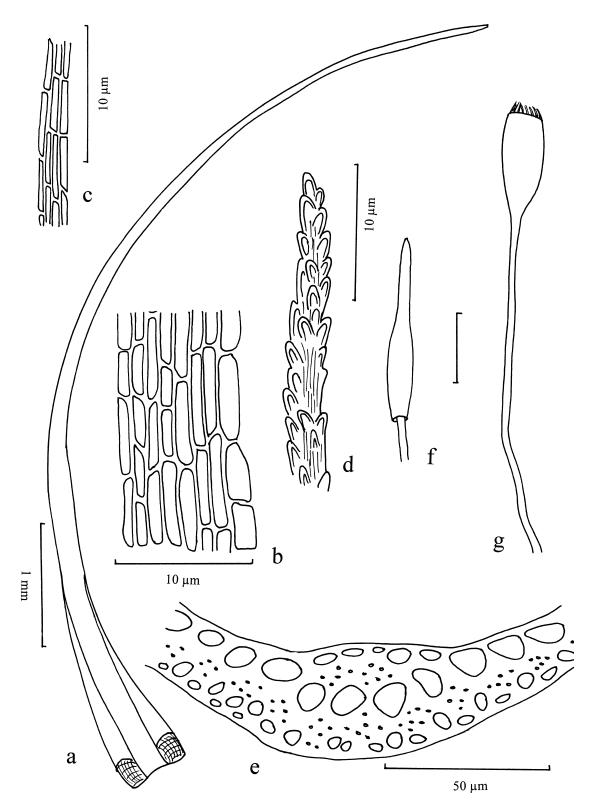


Fig. 2. *Dicranodontium denudatum* (Brid.) Britt. (Musci Acroc. Bor. Amer. 102, H-BR). — a: Leaf. — b: Basal laminal cells. — c: Upper laminal cells. — d: Leaf apex. — e: Transverse section of costa. — f: Calyptra. — g: Sporophyte.

N. Am. Fl. 15: 151. 1913). — Type: USA. West Virginia, Tibb's Run, Monongahela, on sandstone boulders in woods, *Millspaugh 1596* (isotype H-BR).

Dicranodontium subasperum Williams, Bull. New York Bot. Gard. 8: 337. 1914, syn. nov. — Type: Philippines. Luzon, Mt. Santo Tomas, Williams 1846 (isotypes H, H-BR).

Dicranodontium ceylonense Fleisch. in Dix., J. Bot. 53: 260. 1915, syn. nov. — Type: Sri Lanka. "Berg Naminacula auf der Spitze am Erdboden 2 000 m. Musci Arch. Ind. 452" (isotype H-BR).

Dicranodontium perviride Dix. & P. Varde, Rev. Bryol. 52: 38. 1925. — Type: India. Madras, Palni-Hills, Pérumal, *Foreau* 277 (not seen).

Campylopus intermedius Wils. in Hunt, Mem. Lit. Phil. Soc. Manchester er. 3, 3: 234. 1867, *nom. nud.*

Dicranodontium uncinatulum C. Müll. in Jaeg., Verh. S. Gall. Naturw. Ges. 1877–78: 645. 1880, *nom. nud.* — Material: Japan. "Niko trans Yokohama", *Schaal s. n.* (not seen).

Plants in silky dark green tufts, to 8 cm tall (usually 2-4 cm), tomentose below. Stems distantly foliate, often partially or totally denudated of leaves. Comal leaves sometimes caducous and covering the tufts with loose leaves, with a much longer subula and a different structure of the costa as described for D. fleischerianum by Tan (1983). Leaves 5-7 mm long, short and slightly curved or flexuose and with relatively short subula, which is only 1.5 times longer than the lamina, or longer and falcate-secund with longer subula, often deciduous, from sheathing, concave base narrowed into a long channelled subula. Costa covering 1/4-1/3 of leaf base, indistinctly limited from the lamina, often with a dark stripe in the middle caused by the ventral stereid band and a gradual transition to the lamina, excurrent in a more or less denticulate apex. Alar cells thin-walled, inflated, reddish or hyaline. Basal laminal cells rectangular, thick-walled, 3-5 times longer as wide, rarely pitted, narrower and thinner at margins, the inner and outer ones not strongly differentiated. Upper laminal cells firm walled, ca. 5-10 times longer than broad.

Seta 6–10 mm long, erect, twisted and flexuose, curved when wet in young sporophytes. Capsule oblong, ovoid, elliptic to short cylindric, 1.5– 2 mm long, smooth. Operculum as long as the capsule. Calyptra smooth at base. Spores 10–15 mm.

Illustrations: Grout (1937): pl. 43; Crum & Anderson (1981): fig. 103; Bartram (1939): fig. 49 as *D. subasperum*; Frahm (1991): fig. 142. The illustration in Gangulee (1971: fig. 150), drawn from a Japanese specimen, shows a leaf

with a relatively narrow costa, a lamina reaching far up the leaf with almost quadrate upper laminal cells and the leaves crisped when dry. It does not fit this species but was probably drawn from a species of *Dicranum*.

There are no specimens of *Dicranodontium denudatum* in the Bridel-Herbarium in B, however, one of the syntypes cited in the protologue is in G, and this specimen is proposed as lectotype.

Dicranodontium denudatum is very variable in appearence. The variation ranges from small plants with almost erect and relatively short pointed leaves to robust plants with distinctly falcate leaves. Dicranodontium didymodon seems only to differ by its smooth leaf tips.

Campylopus alpinus (D. denudatum var. *alpinum)* consists of plants in dense tufts with almost erect, shorter pointed leaves, which are only slightly curved at the stem tips. The plants give the impression of a species of *Campylopus* and can only be distinguished when sterile by its longer upper laminal cells, which are about ten times longer as wide. These plants also much resemble *Dicranodontium subporodictyon* in appearence. The latter has, however, strongly porose laminal cells. This type of variation is often seen in alpine expressions of many other species, and so this taxon is not given taxonomic rank.

According to Eddy (1988), *Dicranodontium* subasperum cannot be distinguished from stressed or juvenile forms of *D. uncinatum*. The inner basal cells of *D. subasperum* are, however, "merging rather gradually into the narrow marginal cells" (Eddy 1988), but are distinct in *D. uncinatum*. *D. subasperum* is not treated here as a form of *D. uncinatum*, since this character seems to be a fundamentally different character state within the genus.

The authors of *Dicranodontium perviride* compare the species with *D. sparsum*, from which it differs by a less broad limbidium at the leaf margins, and *D. ceylonense*, from which it differs by a scabrous subula. Both *D. sparsum* and *D. ceylonense* are synonymous of *D. denudatum*. These characters are regarded as relatively unimportant for delimiting a species and therefore also *D. perviride* is provisionally placed here into the synonymy of *D. denudatum*.

Habitat: on siliceous rocks and boulders (sandstone, granite), on rotten wood and tree stumps in humid habitats from the submontane to the alpine belt. Distribution: Holarctic; Eurasia (Europe, Caucasus, Himalaya, Siberia, China, Japan), south to India, Sri Lanka and the Philippines, North America, Newfoundland, Ontario, British Colombia, from there through the Rocky Mountains south to Central and South America (Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Venezuela, Bolivia, here newly recorded for Peru).

Selected specimens examined. — Norway. Wulfsberg 17 (H-SOL). Sweden. Småland, Barkeryd, Arnell s. n. (H-SOL). Germany. Oberpfalz, Gnadenberg, Arnold s. n. (H-SOL). Austria. Rekawinkel nächst Wien, Juratzka s. n. (H-SOL). France. Pyrenees, Vallée de Lutour, Spruce s. n. (H-SOL). Czechia. Tatra, Bryoth. europ. 799 (H-SOL). Poland. West Carpthians, Muci macroregioni merid. Polon. 230 (H). England. Lancashire, Hunt s. n. (H-SOL). Belgium. Stavelot pres de Liege, Mansion 536A (H). Italy. Bozen, Radein, Eggers It10,7 (hb. Frahm). Switzerland. Berner Oberland, Haslital, Guttannen, Frahm 79880 (hb. Frahm). Spain. Burgos, Frahm s. n. (hb. Frahm). Turkey. Distr. Trapezunt, prope oppidum Goerele, Handel-Mazzetti 842 (H-BR). USA. Pennsylvania, Bradford, McKean Viaduct, Musci Acrocarpi Boreali Americani 102 (H-BR); New Hampshire, Waterville, Lorenz 69 (H-BR). North Carolina, Macon Co., Devils Courthouse, Frahm 803055 (B, hb. Frahm); Transsylvania Co., Bearwallow Creek, Anderson 12816 (DUKE); Burke Co., Lenville Falls, Frahm s. n. (hb. Frahm). Georgia, Tallulah Falls, Mosses of the Southern United States 11 as Dicranodontium millspaughii (U, hb. Frahm), Small 9649 (NY, hb. Frahm). Virginia, Mt. Rogers, Mosses of the Southern United States 77 as Campylopus virginicus (hb. Frahm). Tennessee, Sevier Co., Great Smoky Mtns. Nat. Park, Delgadillo 1492 (hb. Frahm). Colorado, Larimer Co., Rocky Mtns. Nat. Park, Frahm 84475 (hb. Frahm). Ohio, Hocking Co., Conkle's Hollow, Conard s. n. (B); Alaska, Glenn Highway mile 67, Steere 12599 (hb. Frahm). Canada. British Columbia. Queen Charlotte Islands, Graham Isl., Goose Bay, Schofield 37167 (U). Vancouver Isl., Effingham Inlet, Schofield 75853 (U); Prince Rupert Area, Pitt Island, Vitt 24342 (U). Newfoundland, Fortune Bay and Hermitage, Tuomikoski 1495 (H), ibidem Brassard 10580 (U). Mexico. Oaxaca, 48 km NE de Llano de las Flores, Delgadillo 830 (H, hb. Frahm). Veracruz, Orizaba, Andrew B 543 (F). Guatemala. Argueta, Bernoulii & Cario s. n. (GOET). East of Totonicapán, Sharp 2600 (FLAS). Huehuetenango, above San Mateo, Sharp 4951 (F). Chiquimula, SE of Concepción de las Minas, Steyermark 31000 (F). Honduras. Morazán, slopes of Cerro Uynca, Standley & Williams 760 (F). Nicaragua. Upper slope of volcan Mambacho, Croat 39150 (MO. hb. Frahm). Costa Rica. Herédia, Vara Blanca, Bishop s. n. (FLAS). Vicinity of Laguna Barba, Crosby 9854 (MO). Venezuela. Distr. Libertador, Sierra Nevada de Merida, Griffin et al. 1741 (hb. Frahm). Bolivar, Mt. Roraima, Steyermark 58924b (F). Miranda, Pico de Naiguará, Stevermark 62968 (F). Peru. Cuzco, Pachu Picchu, Hegewald 8770, Frahm 823997 (hb. Frahm). Bolivia. La Paz, Nevado Jankho Uma, Lewis 79-

1430A (F, hb. Frahm). Russia. Caucasus, Radscha inter Uzeni et Glola, Brotherus s. n. (H-BR); bei Hudryubsch, Nordmann s. n. 1836 (-BR). Abchasia, Sommier & Levier Iter Caucasicum 406, 454 (H-BR). Altai, Artybasch, Verastschagin s. n. (H-BR); Siberia, Minusinak, Argunoff 68 (H-BR). India. Kodaikanal, Palni Hills, leg. Foreau 1934, Musci Selecti et Critici 171 as D. sparsum (H), ibidem, Residue of "Musci Madurensis Indiae meridionalis Exsiccata" as D. sparsum (H, NY). Sikkim. Senchal Range, Hartless 2207, as D. dimorphum (H-BR); Bata Shay 5 000 ft., Hartless 2725 as D. dimorphum (H-BR); prope Kurseong 6 000 ft., Decoly & Schaul 2555 as D. dimorphum (H-BR); Jose bungalow, Long 7546 as D. dimorphum (H-BR); prope Kurseong, Chattakpur, Decoly & Schaul 2546 bis, 2547 bis as D. dimorphum (H-BR); Darjeeling 7 000 ft., Weber van Bosse 665 as D. dimorphum (H-BR). China. Sichuan, Ma Er Kang Co., Mt. Meng Bi, He 31143 (H). Wen-chuan Co., Wo-long Nature reservetaion, Jian-shing 3708 (H). Japan. Prov. Iszu, Mt. Amagi, Tishiba 1622 (H-BR); Prov. Iyo, Shinotayama, Ogata s. n. (H-BR); Prov. Musasi, Mt. Takao, Sasaoka (H-BR). Taiwan. Prov. Taityn, Onae, Suzuki s. n. (H-BR); Prov. Yamashiro, Mt. Hie, Takahashi 1605 (H-BR); Prov. Kii, Mt. Ando, Minakata 975 (H-BR). Honshu, Gifu-ken, San-notani, Musci Japonici Exs. 1613 (hb. Frahm).

Dicranodontium didictyon (Mitt.) Jaeg. (Fig. 3)

Verh. S. Gall. Naturw. Ges. 1877–78: 380. 1880. — *Dicranum didictyon* ("*dicticyon*") Mitt., J. Linn. Soc. Bot. Suppl. 1: 21. 1859. — *Campylopus didictyon* (Mitt.) Jaeg., Verh. S. Gall. Naturw. Ges. 1870–71: 434. 1872. — Type: India. "In Himalayae orient. reg. temp., Sikkim, J. D. H. (No. 27, 27b, 51, 51b)." (All syntypes in NY; specimen *51* chosen as lectotype here.)

Dicranodontium dimorphum Mitt. in Ren. & Card. Bull. Soc. R. Bot. Belg. 38: 8. 1900, *syn. nov.* — Types: "India orientalis: Bhotan (leg ...?); Sikkim: Darjeeling (rev. L. Stevens; miss Walker)" (isotype H-BR).

Plants 1–5 cm high, tomentose below. Leaves more (at stem tips) or less falcate, 4–5 mm long. Alar cells reddish or hyaline, not protuberant. Inner basal laminal cells hyaline, enlarged, rectangular (1:2–5), sometimes double-layered, distinct from the outer narrow basal laminal cells which form a border of 10–12 cell rows. Upper laminal cells (= continuation of the limbidium) incrassate, elongate.

Seta 5 mm long, erect, flexuose. Capsule 0.75 mm long. Operculum and Calyptra not seen.

Illustration: Gangulee (1971): fig. 157.

This species has the appearence of *Dicranodontium denudatum* and has therefore often been

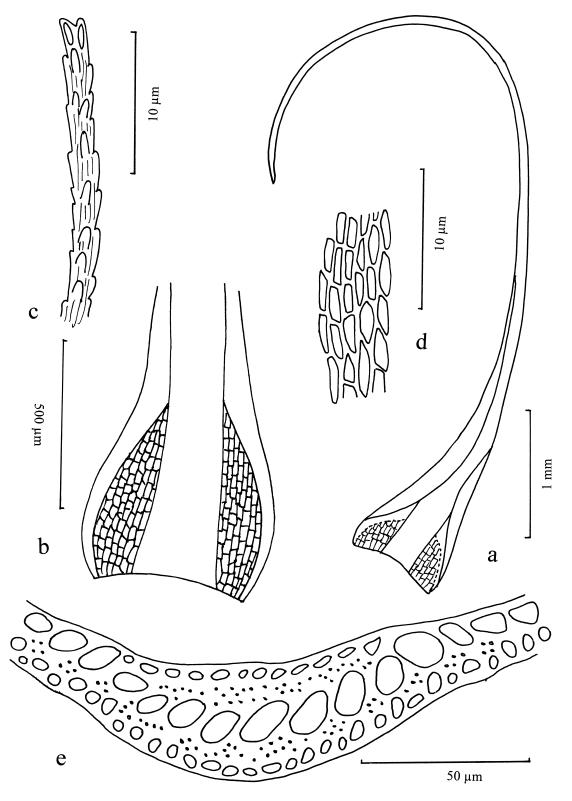


Fig. 3. Dicranodontium didictyon (Mitt.) Jaeg. (isotype of D. dimorphum Mitt., H-BR). — a: Leaf. — b: Leaf base. - c: Leaf apex. - d: Upper laminal cells. - e: Transverse section of costa.

confused with the latter, especially because both species occur together in parts of the Himalaya and can hardly be distinguished macroscopically. It differs, however, microscopically by the enlarged hyaline and well differentiated inner basal laminal cells.

The enlarged hyaline inner basal laminal cells are shared with *Dicranodontium uncinatum*. This seems to be the reason that *D. didictyon* (or its synonym *D. dimorphum*) has been reported from within the range of *D. uncinatum* in tropical SE-Asia. *Dicranodontium uncinatum* is, however, more robust and has a different transverse section of the costa. The transverse section of *D. didictyon* resembles that of *D. denudatum* with a small group of ventral stereids in the middle of the costa, whereas the ventral stereids of *D. uncinatum* cover the whole costa.

The authors of *Dicranodontium dimorphum* compare this species with *D. didictyon* ("D. dicticyoni (sic) valde affinis"), from which *D. dimorphum* is distinguished by a couple of quantitative characters such as smaller size, narrower and longer, less dentate leaves, narrower laminal cells, shorter seta and smaller capsule. Gangulee (1971) differentiates *D. dimorphum* from *D. didictyon* in his key by weakly delimited lower pale cells and a smooth leaf tip. These characters are not sufficient to separate the two species. Therefore *D. dimorphum* is regarded as a synonym of *D. didictyon*.

Habitat: on rotten wood and ground.

Distribution: N India, China (Sichuan, first record from Yunnan).

Specimens examined. — India. Sikkim, Tongloo, Kurz 2107 as D. attenuatum (H-BR); Rhambhi 1 829 m, Long 7887 as D. dimorphum (H-BR); Senchal Range, Hartless 2206 as D. dimorphum (H-BR); prope Kurseong, Decoly & Schaul 2548 bis as D. dimorphum (H-BR). Darjeeling, Stevens 4–6 (H-BR); Thareg 3 353 m, Long 7552 (H-BR); Ghoom Ridge, Hartless 2205 (H-BR). China. Sichuan. Setschwan, in montium Daliang-schan, Handel-Mazzetti 1531 (H-BR); inter Yenyüen et Yungning, Handel-Mazzetti 2946 (H-BR). Yunnan. prope fines Tibeto-Birmanicas inter fluvios Lu-djiang et Djiou-djiang, Handel-Mazzetti 9247, 9491, 9350, (H) as D. armatum.

Dicranodontium didymodon (Griff.) Par. (Fig. 4)

Ind. Bryol. 338. 1896. — *Dicranum didymodon* Griff. Calcutta J. Nat. Hist. 2: 499. 1842. — *Campylous didymodon* (Griff.) Jaeg., Verh. S. Gall. Naturw. Ges. 1870–71: 434. 1872. — Type: India. "In sylvis Myrung et ad truncos in pinetis Moflong" *Griffith s. n.* (isotype H-SOL).

Dicranum attenuatum Mitt., J. Linn. Soc. Bot. 1: 22. 1859, syn. nov. — Dicranella attenuata (Mitt.) Jaeg., Verh. S. Gall. Naturw. Ges. 1870–71: 375. 1872. — Dicranodontium attenuatum (Mitt.) Wils. ex Jaeg., Verh. S. Gall. Naturw. Ges. 1877–78: 380. 1880. — Type: India. "In Himalayae orient. reg. temp., Sikkim" Hooker 78b (holotype NY).

Dicranum caespitosum Mitt., J. Proc. Linn. Soc. Bot. Suppl. 1: 22. 1859. — Campylopus caespitosus (Mitt.) Jaeg., Verh. S. Gall. Naturw. Ges. 1870–71: 434. 1872. — Dicranodontium caespitosum (Mitt.) Par., Ind. Bryol. 337. 1898. — Type: India. "In Himalayae orient. reg. temp., Sikkim" J. D. Hooker 11 (holotype NY).

Dicranodontium subintegrifolium Broth., Sitzungsber. Ak. Wiss. Win Math.-Nat. Kl. 133: 562. 1924, *syn. nov.* — Type: China. Yunnan "bor.-occid.: In montis Yülung-schan prope urbem Lidjiang silvis mixtis temperatis ad rivum Beschui, ad ligna putrida; ca. 2 950–3 050 m" *Handel-Mazzetti 4217* (holotype H).

Dicranum decipiens Mitt., J. Linn. Soc. Bot. Suppl. 1: 16. 1859, syn. nov. — Dicranodontium decipiens (Mitt.) Mitt. ex Broth., Nat. Pfl. ed. 2, 10: 190. 1924. — Type: India. "In Himalayae orient. reg. temp., Sikkim" Hooker 87; in mont. Khasia, reg. subtrop., inter D. fragile", Hooker 87b (holotype NY, the specimen is labelled 87).

Campylopus longigemmatus Gao in Gao, Zhang & Cao, Acta Bot. Yunnan 3: 392. 1981. — *Dicranodontium longigemmatum* (Gao) J.-P. Frahm, Crypt. Bryol. Lich. 15: 196, 1994. — Type: Tibet. Cona Xian, on rotten wood, 2 900 m, *Chen 5152a* (holotype ISPH, not seen; isotype PE).

Plants 0.5-2(-3) cm high. Leaves up to 6 mm long, falcate secund especially at stem tips, from an ovate, concave base quickly contracted into a long, tubulose subula. Costa filling 1/3-1/2 of the leaf base or more, often with a dark line in the middle, excurrent into a subula, which is very minutely serrulate in the upper part or almost smooth. Alar cells inflated, lax, sometimes auriculate, hyaline and thin-walled. Inner laminal cells incrassate, short rectangular (1:2–5), hardly pitted, much larger than the outer basal laminal cells but not very sharply separated from them. Upper laminal cells elongate rectangular, 10-12:1.

Seta 8–10 mm long. Capsule 1.5 mm long, oblong or short cylindrical. Calyptra smooth at base.

Illustrations: Gangulee (1971): fig. 148 as *D. decipiens*, fig. 147 as *D. attenuatum*, fig. 154 (see note below), fig. 156 as *D. caespitosum*.

This species is conspicuously small and slender, distinctly more slender than *Dicranodontium denudatum*. Microscopically it is easily recog-

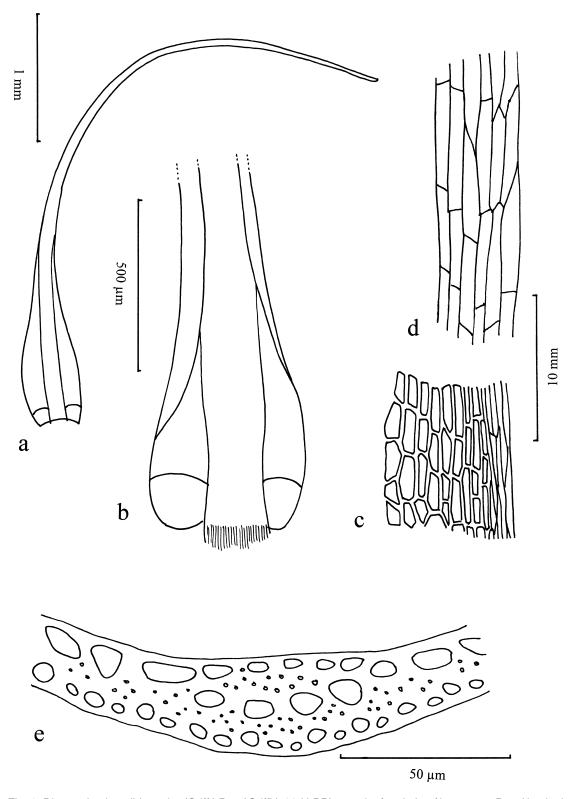


Fig. 4. *Dicranodontium didymodon* (Griff.) Par. (*Griffith 32*, H-BR). — a: leaf. — b: Leaf base. — c: Basal laminal cells. — d: Upper laminal cells. — e: Transverse section of costa.

nized by the almost smooth subula, a character found within the genus only in this species. It has, however, a much more slender habit (and has therefore been described as *Dicranella attenuata*). Even the tallest plants seen (material named *Dicranodontium birmense* by Brotherus) look therefore different from *D. denudatum*.

The species has been described under several names, but all from the same range. Gangulee (1971) separated *Dicranodontium decipiens* and *D. attenuatum* from *D. didymodon* by "comparatively slender or low plants" and the couplet, which should have differentiated *D. decipiens* and *D. attenuatum* contains no alternative to distinguish both species.

Dicranodontium longigemmatum was described as species of Campylopus and was transferred to Dicranodontium by Frahm (1985) based on an isotype kept in the herbarium of Beijing (PE), since the type was not available. The isotype as well as other specimens from PE are, however, not in accordance with the protologue, which could not be obtained at that time. The illustration of this species in the protologue indicates that it is indeed a species of Campylopus. The specimens of D. longigemmatum from PE cited by Frahm (1994) as well as the isotype belong to Dicranodontium didymodon.

Ganguleee (1971) describes and illustrates *Griffith 32*, which differs from the type and the specimen *Griffith 32* in H-SOL by a narrow costa, filling only 1/6 of the leaf base, a long cylindric capsule and erect-patent leaves.

Habitat: on ground, rotten wood, and bark of trees between 200 and 3 900 m altitude.

Distribution: Himalaya (Darjeeling, Sikkim, Bhutan, here newly recorded to Nepal), where it seems to be quite frequent, China (Yunnan), Thailand, Burma.

Specimens examined. — India. Sikkim, Kurseong 6 800 ft., Decoly 270b as D. caespitosum (H-BR). Khasia, Moflong, Griffith 124 as D. caespitosum (H-BR). Kambachen, rocks in woods 11 000 ft. unknown collctor no. 87 as D. decipiens (H-BR); Punjab, Simla, Mt. Jako 7 700 ft., Gollan 6393 (H-BR). Darjeeling, without locality, Long 6189 as D. "asperulum" (H-BR). Himalaya, Jaunsar, Duthié s. n. as D. longirostre (H-BR). Himalaya, Reang, on trees 600–700 ft., Long 7547 as D. attenuatum (H-BR), ibid. on rock 600 ft., Long 7545 as D. attenuatum (H-BR). On trees, Long 6187 as D. attenuatum (H-BR), Sikkim, prope Kurseong alt. 1 900 m, Bretaudeau 1696 as D. attenuatum (H-BR), ibid. 7 000 ft., Decoly & Schaul 2556, 2557 as D. attenuatum (H-BR), ibid. 6 900 ft., Decoly 269 as D. attenuatum (H-BR), Mussoorie, near summit of Witche's Hill 6 200 ft., Gollan 63911 as D. attenuatum (H-BR), Mussoorie, Nag Tiba 8 000 ft., Rhada Lal 4115 as D. attenuatum (H-BR), ibid. 10 000 ft, Rhada Lal 4134 as D. attenuatum (H-BR), Tikri Garhwal 10 000-11 000 ft., Bahadru 6232, 6330, 6331,6337 as D. attenuatum (H-BR). Bhutan. Rydong, 10 000 ft., Griffith 31 (H-BR); Khasia, Griffith 32 (H-SOL); inter Maria Basti and Labar, 5 000-6 000 ft., Durel 31 (H-BR); above Sara 7 000-8000 ft., Griffith 33 as D. attenuatum (H-BR), without locality, Griffith 33 as D. attenuatum (H-SOL). Nepal. Between Basantapur and Dor, Iwatsuki 330 (H) as D. denudatum. Thailand. Doi Suthep at Chiengmai, Larsen et al. 2504 (H, MO) as D. uncinatum. Burma. Bhamo, Birmania sup., on trees, Khairuddin 3216, 3220 (H-BR) as Dicranodontium birmense Broth. nom. nud. China. Sichuan, inter oppidum Yenyüen et castellum Kwapi, Handel-Mazzetti 2321 (H-BR). Yunnan, in montium inter Dali, Handel-Mazzetti 6584 as D. caespitosum (H-BR); in montis Dji-schan, Handel-Mazzetti 6390 as D. caespitosum (H-BR). Bijang, Zang 5412, 5941 (PE, hb. Frahm); Weixi, Zhang 208a (PE, hb. Frahm); Gongshan, Zang 744 (PE, hb. Frahm); Zhong Tian, Li 81-1097 (PE, hb. Frahm); Degin, Wang 81-2361, Zang 8430a (PE, hb. Frahm); Lijiang, Li 80-141 (PE, hb. Frahm); Yangbi, vicinity of Xueshanhe, Redfearn et al. 202 (MO, hb. Frahm); vicinity of Dapingzi, Redfearn et al 607 (MO, hb. Frahm).

Dicranodontium porodictyon Card. & Thér. (Fig. 5)

Bull. Ac. Inst. Geogr. Bot. 21: 269. 1911. — Type: China. Prov. Kouy, *Fortunet s. n.* (isotype H-BR).

Dicranodontium falcatum Broth., Bishop Mus. Bull. 40: 7. 1927, syn. nov. — Type: USA. Hawaii, W-Maui, Baldwin 108 (holotype H-BR).

Dicranodontium hawaiicum Broth., Bishop Mus. Bull. 40: 8. 1927 (fide Bartram, Bishop Mus. Bull. 101: 47. 1933). — Type: USA. Hawaii, Kuhui, *Skottsberg 1570* (holotype H-BR).

Plants to 8 cm high, erect, in tufts, reddish tomentose below. Leaves up to 9 mm long, flexuose (type of *D. hawaiicum*) or falcate (type of *D. falcatum*), concave at base, quickly narrowed into a long, setaceous apex. Costa filling one third of leaf base, excurrent, finely denticulate in the upper part. Lamina reaching 1/4 of leaf length. Alar cells large, hyaline or reddish. Inner basal laminal cells enlarged in a short group, shortly rectangular (1:2–5), hyaline and thin-walled and also incrassate and pitted. Outer basal and middle laminal cells elongate, incrassate and pitted. Upper laminal cells linear, incrassate.

Sporophyte not known.

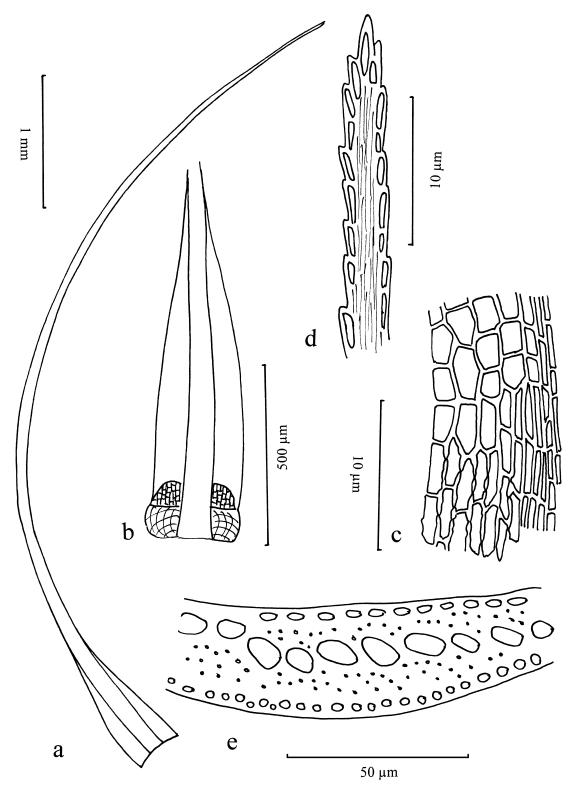


Fig. 5. Dicranodontium porodictyon Card. & Thér. (isotype, H-BR). — a: Leaf. — b: Leaf base. — c: Basal laminal cells. — d: Leaf apex. — e: Transverse section of costa.

Illustrations: Bartram (1933): fig. 29 as D. falcatum.

A species which is easily recognized by its strongly porose basal laminal cells. The species was known only from the Chinese type specimen until it was discovered that specimens collected in the Himalaya as *Dicranodontium macroalare* and the species described from Hawaii as *D. falcatum* or *D. hawaiicum* are conspecific. The records from Hawaii are much more numerous than those from Asia.

Habitat: on trees and wet peaty banks. Distribution: India (Sikkim), China, Hawaii.

Specimens examined. — USA. Hawaii, swamps of Kohala, Rack s. n. as D. falcatum (H-BR), Kohala Mtns., Alakahi trail, Bishop & Herbst s. n. (U). Maui, Baldwin 247, 1138, 1141 as D. falcatum (H-BR), Haleakala, Skottsberg 1177, 1178 as D. falcatum (H-BR), Puu Kukui, Skottsberg 1630 as D. falcatum (H-BR), Oahu, Baldwin 1696 as D. falcatum (H-BR). Kohalu, Upper Kamakua ditch, Selling 4664 as D. falcatum (H); Oahu, N Waianae Mtns., Bryoph. Hawaiica Exsicc. 53 as D. falcatum (H, MICH, U); Puu Kaala, Hoe 483 (MICH). Maui, Kula Pipe Line Trail, Bartram 570 as D. falcatum (H), ibidem Hoe 373 (MICH); Puu Kukui, Cranwell 4058 as D. falcatum (H); Alakai swamp, Selling 4288 as D. falcatum (H); Oahu, Kipapa Gulch, Hosaka s. n. as D. falcatum (H). Maui, Haleakala Nat. Park, Vitt 14860 (ALTA, hb. Frahm). India. Sikkim, Shikar Jum 3 505 m, Long 7886 as D. macroalare (H-BR). Senchal Range 8 000 ft., Hartless 2209 (H-BR). China. See type cited above.

Dicranodontium pulchroalare Broth. (Fig. 6)

Trans. Linn. Soc. London Bot. ser. 2, 6: 89. 1901. — Type: Venezuela. Mt. Roraima, *McConnell & Quelch 345* (*lecto-typus* H-BR).

Dicranodontium meridionale Bartr. Contr. U.S. Nat. Herb. 26: 65. 1928, syn. nov. — Type: Costa Rica. Prov. Heredia, Cerra de las Caricias north of San Isidro, Stanley & Valerio 52296 (holotype FH, isotypes H-BR, NY, US). Paratypes: Costa Rica. Heredia, Cerro de las Lajas, Standley & Valerio 51647 (H-BR, NY, US); Cerro de Zurqui, Standley & Valerio 50492 (NY, US), 50284 (H-BR, US), 50491a (FH); Cerro de las Caricias, Standley & Valerio 52234 (US).

Plants to 10 cm long, distantly foliate, in loose tufts. Stems tomentose below. Leaves erect spreading or curved, 8-10(-12) mm long, longly setaceous, canaliculate at base. Costa excurrent in a long awn which is densely spinulose all around in the upper third. Lamina reaching only 1/4 of leaf length. Alar cells reddish or hyaline, large, thin-walled, inner basal laminal cells enlarged, shortly rectangular (1:2–5), thin-walled and hya-

line, in older leaves also incrassate and pitted, but always distinct from the outer laminal cells, which are narrow elongate, firm-walled and pitted. Middle laminal cells as outer basal laminal cells. Upper laminal cells elongate, 7–12: 1, firm-walled, slightly pitted.

Seta 9 mm long. Capsule oval. Spores $13-15 \,\mu$ m.

Illustrations: Frahm (1991): fig. 143 as *D. meridionale*, fig. 144.

Dicranodontium meridionale and D. pulchroalare were accepted as separate species in the treatment of the Campylopodioideae in the Flora Neotropica series (Frahm 1991). The latter species was only known from the type locality and recorded from an additional collection in Costa Rica. However, D. pulchroalare differs only by its larger size and pitted inner basal laminal cells. The first character is merely a quantitative character and cannot be used to differentiate at the species level. The second character is also found in large forms of D. uncinatum and seems to be an effect of the larger size.

Often it is difficult to distinguish this species from *Dicranodontium uncinatum* because the leaf anatomy of both species is very similar. *Dicranodontium pulchroalare* has erect-spreading, patent or appressed and slightly curved leaves, *D. uncinatum* has usually circinate leaves, but the *D. fleischerianum* expression in the tropics also appressed and slightly curved leaves. A character differentiating both species is a small band of 1– 4 laminal cells extending up the leaf in *D. uncinatum*, which is denticulate at margins.

Brotherus was not sure where to place this species when he described it. The specimens in his herbarium are labelled as "*Campylopus perauriculatus*", "*Atractylocarpus perauriculatus*" and "*Dicranodontium pulchro-alare*". The enlarged inner basal laminal cells in combination with the elongate laminal cells and the long serrulate leaf apex make it, however, most probable that this species belongs to *Dicranodontium*.

Dicranodontium denudatum and *D. pulchroalare* have several times been collected at the same localities.

Dicranodontium pulchroalare was found only a few times with sporophytes and is usually sterile, which is surprising considering its relatively large range.

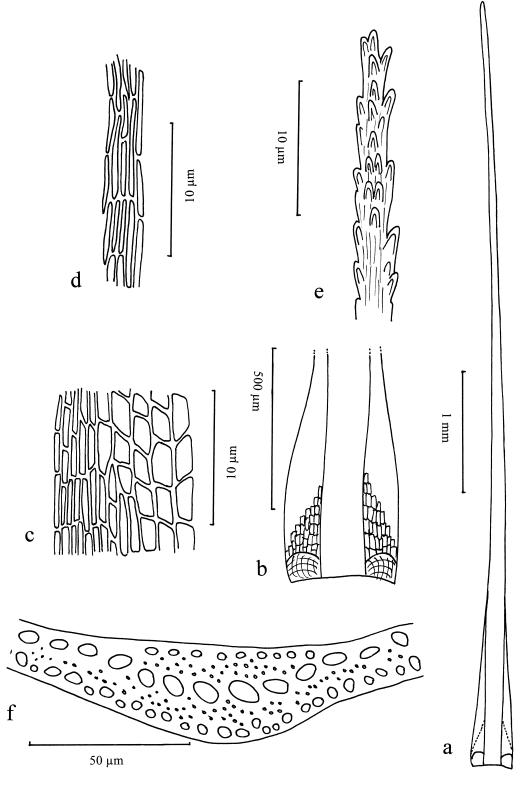


Fig. 6. *Dicranodontium pulchroalare* Broth. (syntype of *D. meridionale* Bartr., H-BR). — a: Leaf. — b: Leaf base. — c: Basal laminal cells. — d: Upper laminal cells. — e: Leaf apex. — f: Transverse section of costa.

Habitat: on soil, rocks and rotten wood at elevations from 1 100–2 600 m.

Distribution: Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, Colombia, Peru, Bolivia, here newly recorded for Ecuador and Mexico.

Specimens examined. — Mexico. Oaxaca, Ixtlán, 11 km N of high point at Cerro Pelón, Mickel & Hellwig 24243 (NY, hb. Frahm). Guatemala. Huehuetenango, above San Mateo, Sharp 4954 (DUKE). Honduras. Cerro Uyuea, Zamorano, Morazán, Carlson 2485 (MICH, hb. Frahm). Costa Rica. Vicinity of Laguna Barba, Crosby 9854 (MO. hb. Frahm). Alajuela, Orilla de Riachuela, Griffin & Araya 53 (FLAS). Heredia, Cerros de Zurgui, Stanndley 50492 (NY). Cerro de las Lajas N of San Isidro, Standley & Valerio 51647 (NY). Barba, Alfaro 1219 (F). Rio Patria 12 km above San Rafael, Richards R5847 (MICH). Venezuela. Amazonas, Cerro Duida, Buck & Brewer 15535 (NY). Colombia. Antioquia, Sonsón, Churchill & Sastre-De Jesus 12922 (H). Riseralda, Sta. Rosa de Cabal, Wolf 731 (U). Ecuador. Pichincha, road from Lloa to Rio Cristal, Frahm 119 (hb. Frahm). Peru. Machu Picchu, Hegewald 8828 (hb. Frahm). Huayna Picchu, Menzel P-287 (hb. Frahm). Bolivia. La Paz Prov. Murillo, E-side of canyon of Rio Zongo, Lewis 82-554, 82-530, 82-573, 82-576 (H, hb. Frahm), 82-557, 82-577, 82-546 (hb. Frahm). Cochabamba, Prov. Chapare, Rio Khuri Nof Corani, Lewis 79-2376 (hb. Frahm).

Dicranodontium pulchroalare ssp. *brasiliense* (Herz.) Frahm, *comb. et stat. nov*.

Dicranodontium brasiliense Herz., Hedwigia 67: 254. 1927. — Type: Brazil. Serra dos Orgaos, *v. Lützelburg 6519* (holotype JE).

Illustrations: Frahm (1991) fig. 140.

Dicranodontium brasiliense differs from *D. pulchroalare* only in the falcate leaves and the less serrate leaf tip, as already mentioned by Frahm (1991). Therefore it is regarded as a vicariant subspecies of the latter in SE-Brazil.

Distribution: Known only from the type locality.

Dicranodontium uncinatum (Harv.) Jaeg. (Fig. 7)

Verh. S. Gall. Naturw. Ges. 1877–78: 380. 1880. — *Thy-sanomitrium uncinatum* Harv. in Hook., Icon Pl. Rar. 1: 22. 1836. — *Dicranum uncinatum* (Harv.) C. Müll., Syn. Musc. 1: 404. 1848. — *Didymodon uncinatus* (Harv.) Lindb., Bot. Not. 1883: 19. 1883. — Type: Nepal. *Wallich s. n.* (isotype H-SOL).

Campylopus nitidus Dozy & Molk., Musci Fr. Ined. Arch. Ind. 5: 139. 1847, *syn. nov.* — *Dicranum nitidum* (Dozy & Molk.) Dozy & Molk., Pl. Jungh. 3: 330. 1854. — *Dicranodontium nitidum* (Dozy & Molk) Fleisch., Musci Fl. Buitenzorg 1: 87. 1904, *hom. illeg. pro D. nitidum* Jam., Bull. Torrey Bot. Cl. 6: 34. 1875 (= *Paraleucobryum longifolium* (Hedw.) Loeske). — *Dicranodontium fleischerianum* Schultze-Motel, Taxon 12: 127. 1963. — Type: Indonesia. "Java, in M. Pangerango, ex hb. Mkb." (probable isotype H-BR).

Dicranum circinatum Wils., Bryol. Brit. 76. 1855 hom. illeg. (fide Mitt. in Braithw., J. Bot. 8: 230. 1870). — Dicranodontium longirostre var. circinatum (Wils.) Milde, Bot. Zeit 28: 417. 1870. — Dicranodontium circinatum (Wils.) Schimp., Syn. ed. 2: 100. 1876. — Type: Scotland. Ben Voirlich by Loch Lomond, Greville s. n. (isotypes H-SOL).

Dicranodontium circinatum var. subfalcatum Limpr., Laubm. Deutschl. 1: 411. 1887. — Dicranodontium subfalcatum (Limpr.) Loeske & Osterw. in Bauer, Musci Eur. Exsicc. ser. 16: 792. 1912. — Type: Switzerland. "im Murgthale 1 500 m bei St. Gallen", Jäger s. n. (isotype H),

Dicranum blindioides Besch., Rev. Bryol. 18: 88. 1891, syn. nov. — Dicranodontium blindioides (Besch.) Broth., Nat. Pfl. 1(3): 336. 1901. — Type: China. Yunnan, Delavay 4859 (isotype H).

Campylopus batjanensis Broth. in Warburg, Monsunia 1: 42. 1899 (*fide* Fleischer, Musci Fl. Buitenzorg 1: 89. 1904). — *Dicranodontium batjanense* (Broth.) Broth., Nat. Pfl. 1(3): 336. 1901. — Type: Indonesia. "Archip. Ind. or., Batjan, Mt. Sibella", *Warburg s. n.* (holotype H-BR).

Dicranodontium forbesii Broth. ex Fleisch., Musci Fl. Buitenzorg 1: 90. 1904, cf. Tan (1983) as synonym of D. fleischerianum var. clemensiae and Eddy (1988). — Type: Indonesia. Java, Forbes s. n. (holotype H-BR).

Dicranodontium sparsum Dix., J. Bot. 53: 260. 1915, *syn. nov.* — Type: Sri Lanka. On bank near waterfall, Nuwara Eliya, *Binstead* 383 (isotype H-BR).

Dicranodontium nitidum var. longisetum Broth., Mitt. Inst. Allg. Bot. Hamburg 7: 116. 1928. — Dicranodontium blindioides (Besch.) Broth. var. robustum Broth., Symb. Sin. 4: 20. 1929, syn. nov. — Type: China. Yunnan, prope fines Tibeto-Birmanicas in convalle fluvii Dijou-djiang, Handel-Mazzetti 9333 (holotype H-BR).

Dicranodontium nitidum Fleisch. var. clemensiae Bartr., Philipp. J. Sci. 61: 236. 1936. — Dicranodontium fleischerianum Schultze-Motel var. clemensiae (Bartr.) Schultze-Motel, Taxon 12: 127. 1963. — Type: Malaysia. N-Borneo, Mt. Kinabalu elev. 7 000–8 000 ft., in dense masses on trail and trees, *Clemens 51029* (holotype FH, not seen), *Clemens 51045* (paratype H-BR).

Dicranodontium merrillii Broth. ex Bartr., Philipp. J. Sci. 68: 47. 1939. — Dicranodontium uncinatum (Harv.) Jaeg. var. merrillii (Broth. ex Bartr.) Bartr., Philipp. J. Sci. 68: 47. 1939. — Dicranodontium fleischerianum Schultze-Motel var. clemensiae (Bartr.) Schultze-Motel fo. merrillii (Bartr.) Tan, Ann. Bot. Fennici 20: 234. 1983. — Type: Philippines. Luzon, Mt. Santo Tomas, Merrill 4900 (isotype H-BR).

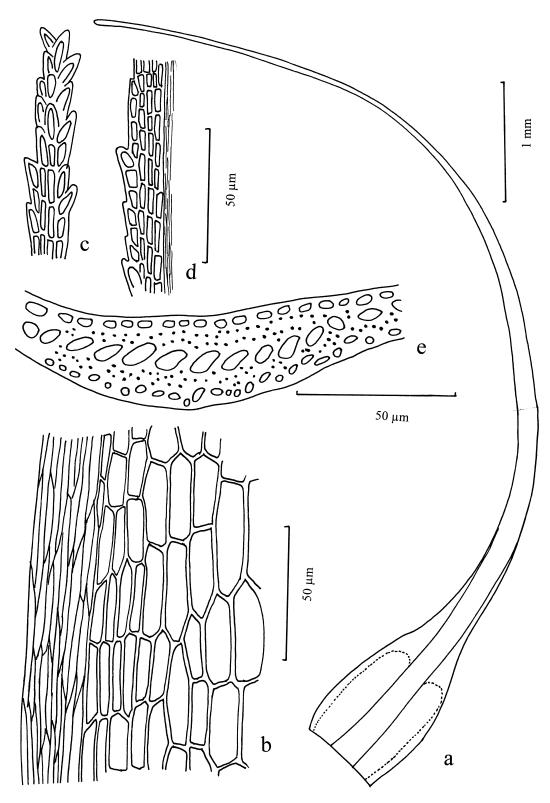


Fig. 7. *Dicranodontium uncinatum* (Harv.) Jaeg. (*Durel 26*, H-BR). — a: Leaf. — b: Basal laminal cells. — c: Leaf apex. — d: Margin of upper part of the leaf. — e: Transverse section of costa.

Dicranodontium fleischerianum Schultze-Motel var. longisetum (Broth.) Touw, J. Hattori Bot. Lab. 44: 152. 1978. — Type: Malaysia. Borneo, Mt. Kinabalu, *Clemens 10741* (holotype H-BR).

Plants 6-10(-20) cm long, in golden green, glossy tufts, tomentose below, larger plants prostrate, ascending with stem tips. Leaves up to 12 mm long, with broad sheathing base of 1/4-1/5 leaf length, circinate, setaceous, curved and homomallous or slightly curved and stronger curved at stem tips or almost erect and only slightly sinuose. Costa filling 1/3 of the leaf base, excurrent in a fine subula which is serrulate down to the middle. Alar cells hyaline and thin-walled, inflated, often remaining at the stem. Inner basal laminal cells conspicuous, forming a large group of hyaline, rectangular (1:3-5) cells which are sharply delimited from the outer and upper laminal cells. Outer laminal cells in 10-12 rows very narrow and linear. Upper laminal cells two-layered, merging with the costa which is indistinctly delimited (as in *Chorisodontium*), thick-walled and pitted.

Seta 10–15 mm long, erect, sinuose. Capsule 2 mm long, ovoid to short cylindrical, smooth or slightly ribbed. Operculum nearly as long as the capsule, obliquely rostrate. Calyptra ciliate at base, however, the cilia are falling off soon which can give the impression of a smooth calyptra.

Illustrations: Nyholm (1954): fig. 33A; Gangulee (1971): fig. 155 (does not seem to fit the species), fig. 153 as *D. fleischerianum*; Fleischer (1900–1902): fig. 9 as *D. nitidum*; Tan (1983): figs. 1–5.

This species is very easily recognized by its robust size (it is apparently the largest species within the genus), in its typical expression with circinate leaves. The plants named *Dicranodontium fleischerianum* have falcate but not circinate, weakly falcate or almost straight leaves. Some specimens from Europe grow in dense tufts and have less strongly curved leaves (var. *subfalcatum* Limpr.). Such less falcate forms seem to occur at higher elevations and can be compared with alpine forms of *D. denudatum*.

I was not able to sufficiently separate *Dicranodontium uncinatum* and *D. fleischerianum*. Both species have been reported from SE-Asia. Tan (1983) states that "the two species can be difficult to separate in some collections." In keys (Fleischer 1901–1902, Gangulee 1971), "*D. fleischerianum* is generally distinguished from *D. un*- cinatum by the absence of distinctly auriculate alar regions and the less falcate-secund leaves" (Tan 1983). This character seems, however, very variable. (If this interpretation is followed, several specimens of D. uncinatum from Europe must be transferred to D. fleischerianum.) For a time I thought I could separate both species by a new character, i.e. by the way that D. fleischerianum seems to have transparent upper laminal cells just above the inflated inner basal laminal cells, that extend up along the costa. In D. uncinatum, these cells above the inflated alar cells do not extend far up along the costa but are contracted and form a small leaf shoulder. These cells are two-layered and opaque and not transparent. Using this difference it turned out that all specimens from tropical SE-Asia could be attributed to D. fleischerianum. However, some specimens from the holarctic such as D. uncinatum var. subfalcatum showed the character typical for D. fleischerianum, too, and therefore I concluded that both species are the same.

Dicranodontium uncinatum has a unique character within the genus, which has not been mentioned in the literature. This is a small border of 1–4 laminal cells extending up the leaf to the leaf apex with the exception of the uppermost third of the subula.

Tan (1983) recognized *Dicranodontium flei*scherianum var. clemensiae (Bartr.) Schultze-Motel at a varietal level and placed *D. forbesii* as a synonym to this variety. Var. clemensiae was distinguished by the sharply delimited inner basal laminal cells, whereas the inner basal laminal cells of the var. *fleischerianum* gradually merge into the adjacent cells. Tan apparently did not compare the var. clemensiae with the type of the typical variety. It appears that var. clemensiae represents larger plants and the var. *fleischerianum* smaller plants. Therefore I agree with Eddy (1988) and Norris and Koponen (1990) in not distinguishing this variety.

The type of *Dicranodontium fleischerianum* var. *longisetum* (Broth.) Touw has 15-mm long setae, which seem to be usual for this species and therefore seems not to need recognition.

Eddy (1988) put *Dicranodontium novoguineense* Broth. & Geheeb into the synonymy of *D. uncinatum*, but I agree with Norris and Koponen (1990) that it is identical with the species formerly described as *Atractylocarpus comosus* Dix. and is better accepted as *Atractylocarpus novoguineensis* (Broth. & Geh.) Norris & T. Kop.

Dicranodontium sparsum consists of very "sparse" plants which are a few millimeters high. The leaves show distinct hyaline enlarged cells at base. Since the leaf apices are serrate, it is supposed that the species was described from young plants of *Dicranodontium uncinatum*. *Dicranodontium didictyon* resembles it better in size but has almost smooth leaf apices.

Dicranodontium uncinatum was originally described as species of *Thysanomitrion* because of the ciliate base of its calyptra. It is apparently the only species of *Dicranodontium* with a ciliate calyptra.

Dicranodontium uncinatum was erroneously cited as an illegitimate homonym by the authors of the Index of Mosses (Crosby *et al.* 1992).

Habitat: on damp, shaded silicious rocks and cliffs in cool montane regions, in the southern Himalaya (Sikkim) also on trees, in tropical regions on rocks, rotten wood and soil in montane rainforests. In Scotland often together with species of similar distribution such as *Pleurozia purpurea*, *Breutelia chrysocoma*, *Campylopus schwarzii* and also *Dicranodontium asperulum* According to the quantities collected in some places apparently growing in large masses.

Distribution: Atlantic parts of Europe (Scotland, Norway), Sudetes, Alps (Austria, Switzerland); West Coast of North America (British Columbia); Japan, Taiwan, Himalaya (Nepal, Sikkim, Bhutan, N-Burma). Sri Lanka, Java, Sulawesi, Burma, Borneo, Philippines, tropical to subtropical China (Hainan, Yunnan).

Specimens examined. - Scotland. Hunt s. n. (H); Ben More, Meldram s. n. (H); Loch Assynt, Sutherland, Duncan s. n. (H); Ben Lawers, Hunt s. n. (H); Argylshire, Ballachulish, Binstead s. n. (H); Ben Voirloch, Hunt s. n. (H), Greville s. n. (H-SOL). Norway. Rogaland, Olten, Dirdal, Persson s. n. (H); Bergen, Isdalen, Jörgensen s. n. (H); Hordaland, Fitjar, Levag, Störmer s. n. (H); Rugsund, Wulfsberg s. n. (H-SOL); Stavanger, Kaalaas s. n. (H-SOL); Hordaland, Os, nar Mösnecken, Persson s. n. (H); Stavanger, Nyman s. n. (H); Suedal, Bryhn s. n. (H); Nordfjord, Rugsund, Wulfsberg s. n. (H). Poland. Karkonosze, Bryotheca Polonica 309 (H). Austria. Salzburg, Krimmler Fälle, Handel-Mazzetti s. n. (H), Breidler s. n. (H-SOL); Tirol, St. Anton am Arlberg, Musci europ. exsicc. 729 (H). Styria, Saeltertal, Dürrmosssteig, Breidler s. n. (H); St. Nikolai, Breidler s. n. (H, H-SOL), Flora Exsiccata Austro-Hungarica 1126 (H); Kaltenbachalm bei Sölk, Breidler s. n. (H-SOL); Steiermark, Hex-

stein bei Irdning, Breidler s. n. as D. denudatum (H-SOL); Prenneggthal bei Schladming, Breidler s. n. (H-SOL). Canada. British Columbia, Queen Charlotte Isl., Schofield 45087 (H); Graham Isl., Dawson Inlet, Persson s. n. as D. denudatum (H). Moresby Isl., Takakia Lake 10 miles S of Moresby Logging Camp, Schofield 25076 (NY). Peel Inlet, Schofield 30477 (NY, U), 30761 (NY). Japan. Yakushima Isl., Bryophyta selecta exsiccata 433 (H); Saitama Pref., Chichibu Mtns., near Jumonji Pass, Bryoph. Sel. Exsicc. 185 (H); Kyushu, Kumamoto Pref., Mt. Ichibusa, Mayebara 22912 (H); Tokushima Pref., Mt. Tsurugi, Koponen 36550 (H, hb. Frahm). Bhutan. Inter Maria Basti et Labar, Durel 26 as D. didictyon (H-BR). Nepal. Between Ghopte and Gosa, Iwatsuki 993 (H). India. Darjeeling, Phalut, Hara et al. 200936 (H). Siri 7 000 ft., Gambler 10070 as D. didictyon (H-BR); Beang, on trees 600 ft., Long 7543 (H-BR); Thallut 11 880 ft., Long 7551 as D. didictyon (H-BR); prope Kurseong 1 900 m, Bretaudeau 1706 as D. didictyon (H-BR); ibid., Mahaldaram 6 800 ft., Decoly & Schaul 2558 as D. didictyon (H-BR); ibid. Decoly 270 (H-BR). Tiger Hill, Fleischer B 3240 (H). China. Yunnan, "prope fines Tibeto-Birmanicas in convalle fluvii Djiou-djang ... supra vicum Schutsche", Handel-Mazzetti 9451 (H-BR) as D. blindioides. Hainan, on trees alt. 1 500 m, McClure 8696 as D. forbesii rev. Tan (H-BR). Sichuan, Omei Shan, along trail to Golden Summit, Redfearn 34688 (SMS, hb. Frahm). Sri Lanka. Horton Plains, Kryptogamae Exs. 1690 (H); Central Province, without collector (H-BR); an Felsen der Name-Bya Schlucht bei Nuwara Eliya, Herzog 161 (H-BR). Nuwara Eliya, v. Hübschmann s. n. (hb. Frahm); ibidem Eggers SL 5,6, SL9,1 (hb. Frahm). Indonesia. Java. Prov. Preanger, Tjibodas, Cryptog. Exsicc. 3876 (H); Tjibodas, Nyman s. n. 1898 (H-BR); Tjiburrum 1 700 m, Musci Arch. Indici 119 (H-BR); ibid. Nyman 110 (H-BR); ibid. Schiffner s. n. (S, hb. Frahm); Pangerango, Kurz 875, 658, Wichura 2508, 2509, Didrichsen s. n., Möller 342, 343, Nyman 38, 40, Fleischer s. n., Musci Arch. Indici 120 (H-BR); Salak, Möller 353 (H-BR) as D. forbesii. Sulawesi. Pik von Bonthavn, Warburg s. n. (H-BR). Burma. Nattorang 7 000 ft., Kurz 2877 as D. didictyon (H-BR). Saw Chaung, Chin Hills, Dickason 8556 (H). Siam, Hosseus s. n. as D. dimorphum (H-BR). Malaysia. Borneo. Mt. Kinabalu Park, Bryoph. Selecta exsiccata 831, 983 (H); Clemens 10741, 10742 (H-BR), Meijer s. n. (S, hb. Frahm). Philippines. Luzon, Mt. Tabayoc, Jacobs B 566 (H, L); Mindanao, Mt. Lipa, Ramos 37165 (H-BR); Luzon, Benguet, Pauai, Clemens 9313, McGregor 8699 as D. didictyon rev. Tan (H-BR); Prov. of Laguna, Mt. Banajao, Robinson 6593 as D. didictyon (H-BR). Mt. Polia, Ifugae Prov., Pancho 4802 (FLAS). Taiwan. Prov. Taityn, Mt. Nobo, Suzuki 2668 as D. subuncinatum (H-BR). Mt. Tai-ping-shan, Ilan Co., Chuang 2060 (H). Prov. Takao, Mt. Daibu, Simada 3809 (H).

GEOGRAPHIC DISTRIBUTION

The genus *Dicranodontium* is mainly holarctic in distribution. There are two species in North

America (*D. denudatum* and *D. asperulum*), three in Europe (the latter two plus *D. uncinatum*), however, twenty-three were described from the Himalayas and adjacent China, which raised much confusion and much more than half of the specimens from this area needed to be revised. Even after the revision, there are 5 species (*D. asperulum*, *D. denudatum*, *D. didictyon*, *D. didymodon* and *D. uncinatum*) occurring together in the small region of Sikkim. Gangulee (1971) has pointed out that the species within the genus *Dicranodontium* are heavily concentrated in Asia.

It is conspicuous that the three species occurring in the temperate latitudes of the northern hemisphere belong to two different sections of the genus. These species are also those with the largest ranges, covering the entire holarctic, although the ranges are fragmentary, probably as a result of the Quaternary climate changes. It can be supposed that these species were the ancestors, from which the other species derived, e.g. *Dicranodontium didictyon* from *D. uncinatum* and *D. didymodon* from *D. denudatum* in the region from Sikkim to Yunnan.

Dicranodontium denudatum is the most frequent and most widespread species of the three species occurring in the temperate region of the holarctic. It is not only very frequent in western Europe but is also found in Russia (Moscow, Altai Mtns.).

Dicranodontium asperulum and D. uncinatum have a very similar distribution in the northern hemisphere and are occasionally even found together. The highly disjunct range comprises British Columbia, Scotland and Norway as well as in Japan, which could be interpreted as a relictical range from the Tertiary in an area, which was not ice covered during glaciation, similar to the range of *Campylopus atrovirens*. However, both species of *Dicranodontium* are also found in Central Europe (Alps, Tatra), which corroborates this hypothesis.

All species of *Dicranodontium* described from the southern hemisphere and tropical Africa were misplaced in this genus.

EXCLUDED SPECIES

Dicranodontium asperifolium (Mitt.) Broth.

Nat. Pfl. ed. 2, 10: 190. 1924. — *Campylopus asperifolius* Mitten, J. Linn. Soc. Bot. 12: 79. 1869. = *Campylopus asperifolius* Mitt. (*fide* Frahm, Lindbergia 7: 29. 1981).

Dicranodontium australe Dix.

New Zealand Inst. Bull. 3: 92. 1923. — Type: New Zealand. South Fjord, Lake Te Anam, *R. Brown ter. s. n.* (isotype H-BR). = *Dicranoloma menziesii* (Hook. f. & Wils.) Par. (*fide* Sainsbury, Bryologist 49: 101. 1946).

Dicranodontium brachydictyon Broth.

Philipp. J. Sci. 31: 278. 1926. = *Campylopus hemitrichius* (C. Müll.) Jaeg. (*fide* Bartram, Mosses of the Philippines: 41. 1939).

Dicranodontium costaricense (C. Müll.) Williams

N. Am. Fl. 15: 153. 1913. — *Leptotrichum costaricense* C. Müll., Bot. Zeit. 16: 161. 1858. = *Atractylocarpus costaricensis* (C. Müll.) Williams, Bryologist 31: 110. 1928.

Dicranodontium filifolium Broth.

Symb. Sin. 4: 20. 1929. — Type: China. Hunan "in monte Yün-schan prope urbem Wukang, in silva elata frondosa umbrosa ad cort. viv. Fagi longipetiolatae. 1 250 m", *Handel-Mazzetti 1250* (holotype H-BR).

Although the leaves of the type specimen have a rather broad costa (1/4 of the leaf width at leaf base), the upper laminal cells are short rectangular (1:2) to almost quadrate and extend nearly to the leaf tip, and the basal laminal cells are short rectangular and very strongly incrassate. The most conspicuous character of this species is that the comal leaves end in a very long subula which is 5–7 times longer than the lamina. The type material is sterile and therefore the systematic position of this species remains unclear.

Dicranodontium humile P. Varde

Rev. Bryol. Lich. 19: 145. 1950. — Type: Uganda. Kigasi Distr., Mt. Muhadara, alpine region, on moist steep rock surface in a small ravine on the western slope of the mountain 3 925 m, *Hedberg 2192* (holotype PC).

This species, which is known only sterile and only from the type specimen, is certainly no *Dicranodontium*. Its costa fills only 1/10 of the leaf width, the subula is short, smooth (denticulate only in the extreme apex), the basal laminal cells are homogenous thick walled and incrassate and not differentiated in inner and outer ones. The large inflated alar cells indicate that it is probably a species of *Blindia*, perhaps *B. acuta* (Hedw.) B.S.G., which is known from higher elevations in Central Africa.

Dicranodontium insularum Bartr.

Rev. Bryol. Lich. 28: 209. 1959. — Type: Gough Island, *van der Werve 51* (isotype H). = The isotype belongs to *Dicranoloma*.

Dicranodontium intermedium Allen

Novon 2: 1. 1991. — Type: Panama. Chiriqui, Volcán Barú, 1 800–3 400 m, *Allen 9123* (holotype MO). Paratypes: Panama. Chiriqui, Volcán Baru, *Allen 9127, 9132, Davidse* & D'Arcy 102901 (MO).

The epithet refers to the intermediate position between Atractylocarpus and Dicranodontium. The species is autoicous like Atractylocarpus but has cygneous setae like Dicranodontium. Compared with all other species included here in Dicranodontium, the species lacks however, ventral and dorsal epidermal cells in transverse section of the costa as in Atractylocarpus. It has furthermore thick-walled, pitted inner basal laminal cells, a character, which is not present in Dicranodontium but which is found in Atractylocarpus neocaledonicus Broth. For these reasons, I place Dicranodontium intermedium in Atractylocarpus, although the cygneous seta clearly shows that the systematic placement of this species is still problematical.

Atractylocarpus intermedius (Allen) J.-P. Frahm comb. nov.

(Dicranodontium intermedium Allen, Novon 2:1. 1991.)

Allen (1994) includes *Atractylocarpus* in *Dicranodontium* as Williams (1913) did. This eliminates the problem with the generic position.

Dicranodontium interruptum P. Varde

Rev. Bryol. Lich. 19: 145. 1950. — Type: Madagascar. Contreforts occidentaux du massif de Marojejy (Nord-Est) près du col de Doanyanala, forêt ombrophile sur latérite de gneiss 800–1 200 m, *Humbert* 10936 (holotype PC). = *Bryohumbertia* cf. *filifolia* (Hornsch.) J.-P. Frahm.

It could be concluded from its epithet that this species is not a Dicranodontium but belongs to Bryohumbertia, because the interrupted foliate stems are highly characteristic for the latter genus. The exact identity of D. interruptum is not known since the genus Bryohumbertia lacks a worldwide revision and the situation in Africa is very puzzling. There are three species recognized worldwide: B. filifolia (Hornsch.) J.-P. Frahm in the Neotropics, B. flavicoma (C. Müll.) J.-P. Frahm in tropical Africa and B. subcomosa (Dix.) J.-P. Frahm in SE and E-Asia. Bryohumbertia filifolia usually consists of large plants with several tufts of verticillate leaves. In contrast, Bryohumbertia flavicoma consists of small plants which have only a basal rosette of leaves or one comal tuft in addition. Bryohumbertia subcomosa resembles B. flavicoma. In the neotropics there exists, however, a small form within the range of B. filifolia, which resembles B. flavicoma or B. subcomosa. This is presently regarded as B. filifolia var. humilis (Mont.) J.-P. Frahm. At present it is not known whether B. filifolia var. humilis is a separate species or not and whether B. flavicoma and B. subcomosa are identical with the latter. Most confusing is the very rare presence of B. filifolialike plants in Africa. It is not known whether these belong to B. filifolia from the neotropics or whether these are larger forms of *B. flavicoma*. The type of Dicranodontium interruptum consists of such large B. filifolia-like plants which are 7 times interrupted foliate.

Dicranodontium novo-guineense Broth. & Geh.

Öfv. Finsk. Vet. Soc. Förh. 37: 154. 1895. = Atractylocarpus novo-guineense (Broth. & Geh.) Norris & T. Kop. (fide Norris & Koponen 1990). According to Eddy (1988), it is probably synonymous with *Dicranodontium uncinatum*, but I agree with Norris and Koponen (1990) in placing this species in *Atractylocarpus*.

Dicranodontium papillifolium Gao Chien

In Gao Chien *et al.*, Acta Bot. Yunnan 3: 393. 1981. — Type: China. Xizang, Distr. Yadong Xian 2 700 m, *Chen* 7799 (holotype IFP, isotype KUN). Type material was not available on request. This species is described as having papillose leaves, a character which would be unique in this genus and which makes it very unlikely that this species belongs to *Dicranodontium*. Specimens named *D. papillifolium* in PE, of which the labels written in Chinese could not be transcribed, belong to *D. asperulum*.

Dicranodontium schwabei Herz. & Thér.

Beih. Bot. Centralbl. 60B: 21. 1939. — Type: Chile. Aysén, Istmo de Ofqui, *Grosse s. n.* (holotype JE). = *Chorisodontium* sp. (cf. Frahm 1991).

Dicranodontium setosum Williams

Bull. Torrey Bot. Cl. 34: 570. 1908. — Type: Colombia. Páramo de Buena Vista, *Pittier 2060* (holotype NY, isotype PC). = *Atractylocarpus longisetus* (Hook.) Bartr. (*fide* Frahm 1991).

Dicranodontium sinense (C. Müll.) Par.

Ind. Bryol. Suppl. 119. 1900. — *Dicranum sinense* C. Müll. Nuov. Giorn. Bot. Ital. n. ser. 4: 249. 1897. — Type: China. "China interior, provincia Schen-si sept., in monte Ki-san", *Giraldi 1490 (lectotypus nov.* H-BR).

This species should be referred to *Campylopus japonicus* Broth. because of its quadrate upper laminal cells and the almost smooth long leaf tip. For the distribution of *C. japonicus* in China, see Frahm (1992). Since the epithet "sinense" has the priority, a new combination must be introduced:

Campylopus sinensis (C. Müll.) J.-P. Frahm, *comb. nov.*

Dicranum sinense C. Müll. Nuov. Giorn. Bot. Ital. n. ser. 4: 249. 1897. — Campylopus japonicus Broth., Hedwigia 38: 207. 1899, syn. nov.

Dicranodontium sordidum (Mitt.) Gangulee

Nova Hedwigia 12: 429. 1966. — Dicranum sordidum Wils. ex Mitt., J. Proc. Linn. Soc. Bot. Suppl. 1: 18. 1859. — Blindia sordida (Mitt.) C. Müll., Bot. Zeit. 22: 349. 1864. — Campylopus sordidus (Mitt.) Jaeg., Verh. S. Gall. Naturw. Ges. 1870–71: 434. 1872. According to the authors of the Index Muscorum (Van der Wijk *et al.* 1959), this species is *Blindia sordida*. However, Bartlett and Vitt (1986) state in their monograph of *Blindia* that the type (not seen) is dicranoid and not seligeroid. So this problem needs further study.

Dicranodontium subporodictyon Broth.

Symb. Sin. 4: 20. 1929. — Type: China. Yunnan, "Schutsche prope fines Tibetico-Birmanicas in convalle fl. Ivravaddi, 2 000 m", *Handel-Mazzetti 9433* (holotype H-BR, isotype H).

Dicranum subporodityon (Broth.) Gao

Flora Bryoph. Sin. 1: 307, 1994.

This species differs from all other species of *Dicranodontium* by (1) a lamina which reaches 2/5 of the leaf length and therefore the leaves lack a long subula, (2) reddish, inflated, not fugacious alar cells, (3) not deciduous leaves, (4) a relatively narrow costa, which fills only 1/4 of the leaf base, and which is indistinctly confined and widened in the part of the leaf where it fills the subula (as in the genus *Chorisodontium*), (5) strongly incrassate and pitted basal laminal cells, (6) gradually tapering leaves as already noticed by Corley and Wallace (1974), and (6) relatively short incrassate and pitted upper laminal cells. The sporophyte is not known.

Illustrations: Corley and Wallace (1974): fig. 1.

Gao placed this species in *Dicranum*. *Dicranodontium subporodictyon* differs in fact from other species of the genus by so many characters, that it cannot be kept in the genus. Its generic placement is, however, dubious due to the lack of sporophytes.

There are several species of *Dicranum* (*Orthodicranum* viz. *Crassidicranum*) in E-Asia such as *D. leiodontium* Card. and D. *hamulosum* Mitt. in Japan, to which *Dicranum subporodictyon* seems to be related, however, this complex is in urgent need of a revision. Brotherus (1924) established a subgenus *Pseudochorisodontium* within *Dicranum*, which reminds one of the *Chorisodontium*like costa of *D. subporodictyon*, but the four species put by Brotherus in this subgenus (two of them from E-Asia) have a very narrow costa.

This species was described and previously known only from Yunnan. In 1971, E. C. Wallace collected a specimen in Scotland, which he suspected to be a Campylopus, but could not name. He sent a sample to the author as well as other bryologists, who regarded it as a Dicranodontium, perhaps a form of D. denudatum. Later M. F. V. Corley compared it with specimens of Dicranodontium kept in the British Museum and found that the Scottish specimen was identical with D. subporodictyon from Yunnan. The description of the Scottish specimen given by Corley and Wallace (1974) differs from the type by scanty tomentum and the indication of 1-2 rows of upper laminal cells in the upper half of the leaf. They mention, however, a conspicuous character of D. subporodictyon, a dark stripe in the middle of the costa. According to herbarium specimens, W. B. Schofield had collected this species in British Columbia in 1962 and then later in 1964 and 1968. As shown from his labels, he had also named it first as Campylopus sp. Furthermore, an unnamed specimen collected by W. C. Steere in 1949 could be identified as Dicranodontium subporodictyon. It is recorded here for the first time for Alaska viz. the United States.

Although all specimens named *Dicranodontium denudatum* var. *alpinum* from Scotland and several from other regions (e.g. Norway) were examined, no additional record of *Dicranum subporodictyon* from Europe could be found.

The disjunction between Scotland and the Himalayas viz. Yunnan is also met in the hepatics Mastigophora woodsii, Bazzania pearsonii, Anastrophyllum donianum, A. joergensenii, Plagiochila carringtonii, Scapania ornithopodioides, S. nimbosa, Pleurozia purpurea, and in the mosses Campylopus schwarzii and Leptodontium recurvifolium (Corley & Wallace 1974).

Habitat: on wet siliceous rocks.

Distribution: China, Alaska, Brit. Columbia, Scotland.

Specimens examined. — Scotland. Above Kniloch Hourn, West Inverness, Wallace s. n. (hb. Frahm). Canada. Brit. Columbia, Queen Charlotte Islands., Graham Isl., Goose Cove, Schofield 37198 (H, U, hb. Frahm); S. E. Moresby Isl., Bigsby Inlet, Schofield 24064; Chaatl Isl., Schofield 18666 (H); Moresby Isl., mouth of Tasu Sound, Schofield 84011 (H), 73669 (U). USA. Alaska, mouth of Kings River at junction with Matanuska River, Glenn Highway mi 67, Steere 12549 det. Frahm (NY).

Dicranodontium tanganyikae J. Tayl. & P. Varde

Kew Bull. 1954: 506, 1954. — Tanzania. Type: Tanganyika, Lupanga Peak 4 000 ft., *Burtt 4713* (holotype PC).

The sterile type specimen of this species, which is known only from the type, does not belong to *Dicranodontium* because of its short (1:1.5–2) upper laminal cells. But it is identical with *Campylopus flexuosus* (Hedw.) Brid. var. *incacorralis* (Herz.) J.-P. Frahm, an alpine variety known from the Andes and the afro-alpine regions.

Dicranodontium tapes (C. Müll.) Par.

Ind. Bryol. 120. 1900. — *Dicranum tapes* C. Müll., Hedwigia 36: 348. 1897. — Type: Australia. Tasmania, Deal Island, *Dobson s. n.* (not available).

Dicranodontium tenii Broth. & Herz.

Hedwigia 65: 150. 1925. — Type: China. Yunnan, "Umgegend von Pe yen tsin auf faulem Holz ca. 3 000 m, *Ten 36* (holotype H-BR).

This species seems to be identical with *Dicranum hamulosum* Mitt. (*Orthodicranum hamulosum* (Mitt.) Broth.) described from Japan and so far recorded as endemic from Japan. However, the systematic position of this species as well as other E-Asian species of *Dicranum* such as *D. leiodontium* Card. is dubious. Noguchi (1987) notes for instance that "*D. leiodontium* is very similar to *Dicranodontium*." The plants have leaves with broad costae and short upper laminal cells and thus resemble certain species of *Campylopus* but have setae 10–15 mm long which are flexuose when moist, capsules with long operculum and thus resemble *Dicranodontium*.

Dicranodontium tenuinerve Dix. & Sak.

Bot. Mag. Tokyo 50: 514. 1936. — Type: Japan. Kuisiu, Mt. Takakuma, *Doi 3536* (holotype BM).

Although described from Japan, this species was not treated by Noguchi (1987). Surprisingly, the type specimen turned out to be *Bryohumbertia subcomosa* (Dix.) J.-P. Frahm (= *B. walkeri* (Mitt.) J.-P. Frahm), a SE-Asian species, which was recorded first for Japan by Frahm and Deguchi (1987). The leaves can be superficially compared with those of *Dicranodontium*. They end in a long dentate arista and have large inflated alar cells, however, the upper laminal cellas are not longly rectangular or linear but only shortly rectangular.

Dicranodontium tristaniense Dix. & Thér.

in Christ., Res. Norw. Sc. Exp. Tristan da Cunha 48: 21. 1960. — Types: Tristan da Cunha, forest west of 3rd Gulch 550–600 m, *Christophersen & Mejland 940* (type), *ibid. 933b 935*. Crater, 1 900 m,754 (paratypes).

As mentioned by Dixon in the protologue (or by Bartram, who edited the publication after the death of Dixon?), this species differs from all other species of *Dicranodontium* by an erect seta, "which shows no sign of curving when moistened", and the peristome teeth are not divided to the base. It is furthermore evident from the description, that this species has an annulus. Therefore it is probably not a species of *Dicranodontium* but more likely a *Dicranoloma* or *Chorisodontium*.

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