NEW COMBINATIONS IN *DIDYMODON* (MUSCI) AND A KEY TO THE TAXA IN NORTH AMERICA NORTH OF MEXICO

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In the course of studies on the Pottiaceae, I have become convinced that the distinctions made by Saito (1975) between the genera *Barbula* Hedw. and *Didymodon* Hedw. are valid. As was discussed by Crundwell and Nyholm (1965), taxonomic differences between the two genera have been based largely on peristome characters, the former having long, twisted teeth, the latter with short, straight to weakly twisted teeth. These distinctions have never been totally satisfactory as species that are gametophytically closely related to some *Barbula* species have short, nearly straight peristome teeth while others with close relationship to *Didymodon* species have elongate, twisted peristomes. As the genera are closely related, many authors (e.g. Chen 1941, Dixon 1924, Nyholm 1956, Savicz-Ljubitzkaja & Smirnova 1970) have simply treated all species as *Barbula*. Saito (1975) proposed several distinctions between the two genera based largely on gametophytic characters, some of which had been previously discussed by Hilpert (1933), that serve to separate easily the species into two natural groups. Table 1 compares the major distinguishing features of *Barbula* and *Didymodon*. I agree with Hilpert (1933) that the species now recognized in *Bryoerythrophyllum* Chen (= *Didymodon* subg. *Erythrophyllum* Limpr.) are more closely related to *Barbula* than to *Didymodon*. *Trichostomopsis* Card. and *Geheebia* Schimp. are here treated as synonyms of *Didymodon*.

Many taxa now recognized in *Barbula* are better placed in *Didymodon*. Saito (1975) made several transfers involving Asiatic taxa that reflect his generic concepts but certain American and European taxa remain without appropriate combinations. Based on studies of specimens from ALA, ALTA, BUF, CANM, FH, MICH, NY, PC, S-PA, TENN, UBC, US and other herbaria, the following key, new combinations and discussion is presented hopefully as a coherent concept of *Didymodon* in North America north of Mexico.

All of the species of *Didymodon* that are represented by more than a few collections show a degree of variation in characters here considered critical for identification. Regionality of the species supports an assumption of genetic differentiation; however, this may turn out to be best recognized as race formation within widely distributed polymorphic species. To alert plant geographers as to which species are relatively well known and which are possibly artifacts, the following terms are used here. Species

Table 1. Summary of important distinctions between the genera Didymodon and Barbula in North America north of Mexico.

	Didymodon	Barbula
Leaf shape	usually lanceolate to long-lanceolate	usually ovate to long-elliptical
Cells of axillary hairs	hyaline except a yellow-brown basal cell	all cells often hyaline
Basal laminal cells	usually little differentiated, green and short-rectangular	usually strongly differentiated, hyaline and elongate
Abaxial superficial cells of costa above mid-leaf	quadrate to occasionally elongate	short-rectangular to elongate, rarely quadrate
Laminal papillae	absent or simple or rarely multiplex; solid	usually multiplex, rarely C-shaped, simple or absent; often hollow
Propagula, when present	green, thin-walled, of 1-10 cells	green to yellow- or red-brown, thin- to thick-walled, of 1-50 or more cells
Peristome teeth	absent or rudimentary to long and twisted	short and weakly twisted to long and twisted

that are suspected to be "pigeonhole" taxonomic concepts (Grout 1938), that is, segregates from a continuum of morphological variation, e.g. on a stature gradient (Zander 1977), have their names followed by the annotation "columb." for "columbarium," a dove cote. Some species have been studied only in limited geographic areas and are suspected to be the same as other species elsewhere in the world. The names of these narrowly conceived species are followed by "paroch." for "parochialis." Most species of Pottiaceae that are known only from local floristic studies are parochial species and should not be cited in studies of plant geography without much reservation. I find that only study of intraspecific variation of a species and of related species on a worldwide basis can provide a sense of proportion that allows the kind of taxonomic appraisal that satisfactorily reflects evolutionary and migratory history. Until a taxonomic study is made at the world level, preferably with ancillary experimental culture work, difficulties in routine identification of Didymodon species

Table 2. Suggested parallel trends in speciation in three sections of Didymodon.

	sect. Didymodon	sect. Vineales	sect. Graciles
Plants red-brown	D. nigrescens	D. asperifolius	D. laevigatus
Leaves short-lanceolate	D. acutus	D. brachyphyllus	D. michiganensis
Leaves long-lanceolate	D. umbrosus	D. vinealis var. flaccidus	D. giganteus
Leaf apex differentiated as a propagulum	D. johansenii	D. sinuosus	—
Leaf cells porose	D. johansenii	—	D. giganteus
Propagula present in leaf axils	D. rigidulus	D. reedii	D. michiganensis
Hygrophilic species	D. luridus	—	D. tophaceus

must be expected when using this key and those of other authors due to unusual combinations of character states or to intermediate states.

Variation in degree of peristome development is common in Didymodon and has led to confusion in generic limits. Qualitative characters of the peristome are relatively conservative and are appropriately emphasized at the family level in moss taxonomy (Crosby 1974). However, peristome morphology and other sporophyte characters may be variable in a quantitative sense. The few phenological survey studies that have been done show that the sporophytes of common, temperate zone species of Pottiaceae (and of other families) take 5-12 months to mature (Grimme 1903, Krieger 1915). Also, the capsule anatomy differentiates throughout much of the period of seta elongation (Wijk 1932) although final stages happen very quickly (Kreulen 1975). Surely developmental processes of the sporophyte should be commonly affected, especially in species of Pottiaceae growing in environmentally variable habitats, in regard to relative size and size-dependent elaboration of the peristome, perhaps in response to varying amounts of available photosynthate. Hilpert (1933) asserted that peristome ornamentation is never quantitatively exactly alike between individuals of the same species in the Pottiaceae and considered variation between species in peristome development to be related to environmental influences of the habitat. In both Didymodon and

Barbula, long peristomes usually have well developed basal membranes and sharply differentiated, filamentuous, spiculose peristome teeth. Short peristomes have poorly differentiated basal membranes and long-subulate, spiculose to papillose teeth. In most species, peristomes are rather fragile and are often broken off in old capsules. Didymodon vinealis var. vinealis has perhaps the best developed peristome in the genus, twisted occasionally to 2.5 turns. Barbula species may have rather short, nearly straight teeth grading to long and twisted to 2.5 turns. Great variation in peristome development within species is common in both Didymodon and Barbula and may be correlated with control of spore dispersal appropriate for various environments. Also, Lazarenko (1957) has emphasized the importance in spore liberation of fragile peristome teeth in the genus Callicladium (Hypnaceae).

Variation in presence and in degree of differentiation of the adaxial stereid band has also been a source of confusion, as noted by Saito (1975). The long-held importance of costal anatomy as a character distinguishing the tribes Pottieae and Barbuleae is not to be denied, but has led to misplaced emphasis on this character in the Barbuleae in which great variation of costal anatomy occurs between species and even within species. In many species of Didymodon, there may be either one or two stereid bands present in the costa. In D. vinealis, the adaxial stereid band is usually represented by 2-4 widely lumened, slightly thick-walled cells of about the same diameter as the cells of the costal epidermis and only slightly smaller than the guide cells. The genera Trichostomopsis Card. and Husnotiella Card. were both placed in the Pottieae by Grout (1939) as they characteristically have only one stereid band in the costa. However, Robinson (1970) recognized the relationship of Trichostomopsis near Barbula, and I here place it in synonymy with Didymodon; Husnotiella is actually very close in relationship to Didymodon and should be treated in the Barbuleae.

Illustrations, descriptions, further discussion of variation, and additional synonymy for most of the species dealt with here are given by Chen (1941), Dixon (1924), Nyholm (1956), Podpěra (1954), Saito (1975) and Steere (1938a, 1938b) inter alios.

KEY TO DIDYMODON TAXA IN NORTH AMERICA NORTH OF MEXICO

1. Leaf tips caducous or very fragile..... 2.

1. Leaf tips with intact apices or these merely occasionally broken..... 5.

2. All leaf apices absent in mature leaves, deciduous early, apical cells near leaf apex weakly conic-mamillose; U.S.A. (Alaska), Europe, U.S.S.R..... ..... 14. D. sinuosus (Mitt.) Delogn.

2. Leaf apices mostly present in mature leaves, merely fragile or deciduous late, upper laminal cells smooth to papillose..... 3.

3. Leaves long-triangular, usually deeply grooved along the costa adaxially, costa percurrent to short-excurrent, laminal papillae irregular to multiplex; western North America..... ..... 13. D. occidentalis Zander

3. Leaves ovate- to long-lanceolate, broadly and weakly concave, not medially grooved, costa long-excurrent, laminal papillae absent to low and mostly simple..... 4.

4. Leaf apices swollen and notched, upper laminal cells usually with porose walls and angular lumina; U.S.A. (Alaska), Canada (Yukon, Northwest Territories), U.S.S.R.. ..... 4. D. johansenii (Williams) Crum

4. Leaf apices narrow, entire, upper laminal cells usually evenly thickened and with rounded-quadrate or oval lumina; northern areas and at high elevations in North America, Europe, Asia..... 1b. D. acutus var. icmadophilus (Schimp. ex C.M.) Zander

5. Plants red- to black-brown, leaves not keeled or highly recurved, margins finely crenulate by bulging cell walls, usually plane above midleaf, costae thin, 2-3 cells wide above midleaf, laminal papillae absent to massive and lens-shaped..6.

5. Plants without this exact combination of characters..... 8.

6. Leaves dimorphic: cochleariform, epapillose leaves present on fragile branchlets or portions of some stems; U.S.A. (Alaska, Colorado), Canada (Yukon, Northwest Territories, British Columbia, Alberta)..... ..... 9. D. subandreaeoides (Kindb.) Zander

6. Leaves monomorphic..... 7.

7. Plants often fruiting, leaf apices acute, propagula absent; northwestern North America, Guatemala, India, China..... ..... 7. D. nigrescens (Mitt.) K. Saito

7. Plants sterile, leaf apices obtuse, unicellular propagula present in clusters in the leaf axils; Canada (Yukon, Northwest Territories), U.S.S.R..... ..... 8. D. perobtusus Broth.

8. Costa with elongate superficial adaxial cells, upper laminal cells unistratose..... 9.

8. Costa with quadrate superficial adaxial cells, or, if elongate, then upper leaf margins bistratose..... 14.

9. Leaf base auriculate or weakly winged at insertion, apex often whip-like, long-acuminate; Canada (Northwest Territories), India, Japan... 20. D. leskeoides K. Saito

9. Leaf base not sharply flairing, apex obtuse to short-acuminate..... 10.

10. Leaves ovate to long-elliptical, apex often obtuse, costa often ending before the apex; widely distributed ..... 21. D. tophaceus (Brid.) Lisa

10. Leaves short- to long-lanceolate, apex acute, costa subpercurrent to short-excurrent..... 11.

11. Plants usually propaguliferous, leaves catenulate when dry, laminal cells in obvious longitudinal rows; U.S.A. (Michigan), Canada (Northwest Territories), Mexico, India (Assam), Japan.. ..... 16. D. michiganensis (Steere) K. Saito

11. Plants lacking propagula, leaves appressed-incurved to weakly spreading when dry, laminal cells somewhat staggered..... 12.

12. Plants small, leaves to 2.5 mm long, laminal cells usually 8–10 µm wide; widely distributed..... ..... 17. D. fallax (Hedw.) Zander

12. Plants large, leaves to 5.0 mm long, laminal cells usually 10–14 µm wide..... 13.

13. Leaf margins usually edentate, upper laminal cells with thick, porose cell walls; U.S.A. (Alaska), Canada (Northwest Territories, British Columbia), Europe, U.S.S.R., China, Japan..... 19. D. giganteus (Funck) Jur.

13. Leaf margins occasionally weakly dentate, upper laminal cells with angular lumina but walls not or little porose; widely distributed..... 18. D. rigidicaulis (C. Muell.) K. Saito

14. Leaves with a narrow, adaxial, medial channel, apex often apiculate by a conical cell, margins usually recurved, often to near the apex..... 15.

14. Leaves lacking an adaxial, medial channel, apex seldom apiculate by a conical cell, margins plane to recurved below midleaf..... 19.

15. Leaves red-brown, strongly recurved and keeled when moist, papillae when present simple, stem central strand usually absent; subalpine and subarctic areas of the Northern Hemisphere... 15. D. asperifolius (Mitt.) Crum, Steere & Anders.

15. Leaves green to yellow- or red-brown, spreading to weakly recurved and weakly keeled when moist, papillae when present bifid to multiplex, stem central strand present..... 16.

16. Leaves deltoid to short-lanceolate, margins recurved to near the apex, apices of some leaves obtuse; western U.S.A..... 10. D. brachyphyllus (Sull. in Whipple) Zander

16. Leaves short- to long-lanceolate or long-triangular, margins recurved near base to lower 2/3 of leaf, apices of all leaves acute..... 17.

17. Leaves long-triangular, apices often fragile and bistratose at least in patches, basal cells quadrate to short-rectangular, peristome absent or rudimentary; range: see 3a..... 13. D. occidentalis Zander

17. Leaves lanceolate, apices little thickened or fragile, basal cells short- to long-rectangular, peristome weakly to strongly developed..... 18.

18. Leaves to 2.5 mm long, straight to curved; widely distributed in western North America, Europe, Asia, Africa... 12a. D. vinealis (Brid.) Zander var. vinealis

18. Leaves to 5 mm long, flexuous; western North America, Europe, Asia, Africa..... ..... 12b. D. vinealis var. flaccidus (B.S.G.) Zander

19. Axillary propagula present..... 20.

19. Axillary propagula absent..... 21.

20. Propagula all multicellular, leaf apex acute; widely distributed..... 2. D. rigidulus Hedw.

20. Propagula mostly unicellular, leaf apex broadly obtuse; range: see 7b... 8. D. perobtusus Broth.

21. Upper leaf lamina bistratose..... 22.

21. Upper leaf lamina unistratose..... 25.

22. Upper leaf lamina entirely bistratose; U.S.A. (Arizona), Mexico..... 3. D. mexicanus var. subulatus Thér. & Bartr. ex Bartr.

22. Upper leaf lamina bistratose along margins..... 23.

23. Basal laminal cells with firm, weakly to strongly thickened walls, differentiated usually only medially; range: see 20a... ..... 2. D. rigidulus Hedw.

23. Basal laminal cells thin-walled and usually somewhat inflated, often bulging-rectangular, differentiated across leaf base.... ..... 24.

24. Leaves long-lanceolate, usually smooth or weakly papillose, marginal basal cells narrowly rectangular in 2-4 rows, adaxial superficial cells of costa usually elongate, stem with hyalodermis; U.S.A. (California), Mexico, Uruguay, Argentina... 6. D. umbrosus (C. Muell.) Zander

24. Leaves short-lanceolate, smooth to strongly papillose, marginal basal cells not or weakly differentiated from the medial, adaxial superficial cells of costa quadrate, stem lacking hyalodermis or this weakly differentiated; western U.S.A., Mexico, Andes of South America, Australasia, South Africa..... ..... 5. D. australasii (Hook. & Grev.) Zander

25. Plants flagellate, leaves strongly appressed when dry, linear-lanceolate, costa long-excurrent; Canada (Northwest Territories), China..... ..... 1c. D. acutus var. ditrichoides (Broth.) Zander

25. Plants not flagellate, leaves appressed-incurved to weakly twisted and weakly spreading when dry, short- to long-lanceolate, costa short- to long-excurrent..... 27.

26. Costa short-excurrent, entire; widely distributed..... ..... 1a. D. acutus (Brid.) K. Saito var. acutus

26. Costa long-excurrent, often fragile; northern areas and at high elevations in North America, Europe, Asia..... 1b. D. acutus var. icmadophilus (Schimp. ex C.M.) Zander

The taxa in Didymodon are here placed in three sections. Each section has what appear to be parallel trends in morphological variation among the species as summarized in Table 2.

DIDYMODON Hedw. sect. DIDYMODON, Spec. Musc. 104. 1801.
Type: D. rigidulus Hedw.

Synonyms: Barbula sect. Asteriscium C. Muell., Linnaea 42: 342. 1872, syn. nov. Type: Barbula umbrosa C. Muell.
Trichostomopsis Card., Rev. Bryol. 36: 73. 1909, syn. nov. Type: T. crispifolia Card.
Asteriscium (C. Muell.) Hilp., Beih. Bot. Centralbl. 50(3): 618. 1935, hom. illeg. non Cham. & Schlecht. Linnaea 1: 254. 1826.
For additional synonymy see Saito (1975).

This group is essentially that which Steere (1938a) discussed as Barbula sect. Acutae Steere, nom. illeg. (fide Index Muscorum, Wijk et al. 1959-1969), but with the addition of several species including two previously placed in Trichostomopsis. The section is characterized by the leaves appressed to spreading when moist, weakly concave, margins not or weakly decurrent, plane to recurved below, seldom apiculate, the costa percurrent to more usually excurrent, the upper laminal cells often bistratose, seldom papillose but if so then papillae usually simple to bifid, irregular to hemispherical, 1-4 over each lumen, the adaxial superficial cells of the costa quadrate above midleaf in at least some plants of all species, and the adaxial stereid band usually absent. The peristome is usually rather short and little twisted, occasionally to 1.5 or 2.0 turns. Spores mature in various seasons depending on the species.

1a. Didymodon acutus (Brid.) K. Saito var. acutus [columb.]

This taxon, while common in Mexico, is only occasional although widely distributed in the United States. Barbula bescherellei Sauerb. in Jaeg., considered "...scarcely more than a vigorous form of B. acuta..." by Crum (1969), is a synonym.

1b. Didymodon acutus var. icmadophilus (Schimp. ex C. Muell.) Zander, comb. nov. [columb.]

Basionym: Barbula icmadophila Schimp. ex C. Muell., Synop. Musc. 1: 614. 1849.
Synonym: Barbula acuta var. icmadophila (Schimp. ex C. Muell.) Crum, Bryologist 72: 241. 1969.

This is an often robust, northern and western-montane expression of D. acutus. I agree with Crum (1969) that it should be treated at the varietal level.

1c. Didymodon acutus var. ditrichoides (Broth.) Zander, comb. & stat. nov. [columb.]

Basionym: Barbula ditrichoides Broth., Sitzungsb. Akad. Wiss. Wien Math. Nat. Kl. 133: 566. 1924.

This appears to be a highly reduced, flagellate version of the var. icmadophilus but it has an easily recognized, distinctive appearance. It is known from montane China (Chen 1941) and was recently collected in Canada: Northwest Territories, Nahanni Range, just N of Peak, 61° 43'N, 123° 20'W, dry, N-facing alpine tundra with limestone rock outcrops, 1090 m elev., Vitt 20294 (ALTA).

2. Didymodon rigidulus Hedw.

This species is quite close in relationship to D. acutus, differing in most collections in the broader leaf apex, which is bistratose at least marginally, and in the presence of axillary propagula. However, some specimens are intermediate in character state combinations and may be interpreted as either D. acutus with propagula or as D. rigidulus lacking propagula. The axillary propagula are said by Steere (1938b) to be a constant feature of D. rigidulus; however, western collections often lack them, as attested by Flowers (1973) and Weber (1973). There are two specimens labeled as D. rigidulus in the Hedwig-Schwaegrichen herbarium at G. One of these is apparently the type from Germany: "Lipsiae in ponte ad Kuhthurum lect.," and is good material of D. rigidulus with propagula present. The collection from U.S.A.: "specimen e Pensylvaniae a. repta," is D. fallax.

3. Didymodon mexicanus var. subulatus Thér. & Bartr. ex Bartr. [columb. & paroch.]

This may be viewed as an expression of D. acutus var. icmadophilus with bistratose upper leaf laminae. Collections intermediate in character between these two taxa are easily referred to D. rigidulus (without propagula).

4. Didymodon johansenii (Williams) Crum

This is an essentially boreal, circumarctic species. The distribution is summarized by Packer and Vitt (1974) and Steere (1978). Didymodon acutus var. icmadophilus may be confused with this species as the leaf apices are often quite fragile; Steere (1938b) remarked on the fragility of the leaf tips of D. rigidulus, another possible source of confusion. However, D. johansenii differs from both species in that the leaf apices are swollen, constricted or notched and the laminal cell walls are often thickened-porose above midleaf.

5. Didymodon australasii (Hook. & Grev.) Zander, comb. nov.

Basionym: Tortula australasiae Hook. & Grev., Edinburgh Jour. Sci. 1: 301. 1824.
Synonyms: Didymodon diaphanobasis Card., Rev. Bryol. 37: 125. 1910.
Barbula australasiae (Hook. & Grev.) Brid., Bryol. Univ. 1: 828. 1827.
Trichostomopsis brevifolia Bartr., Bryologist 34: 61. 1932.
Trichostomopsis diaphanobasis (Card.) Grout, Moss Fl. N. Amer. 1: 228. 1939.
Trichostomopsis fayae Grout, Moss Fl. N. Amer. 1: 228. 1939, syn. nov.
Trichostomopsis australasiae (Hook. & Grev.) H. Robins., Phytologia 20: 187. 1970.

Robinson (1970) gave a long list of additional synonyms for this species in his revision of Trichostomopsis. This species is similar and probably closely related to D. rigidulus by the areolation and laminal papillae, the bistratose upper laminal margins, and the transverse section of the costa showing only an abaxial stereid band (the adaxial stereid band is only occasionally present in D. rigidulus) and 2-3 adaxial layers of wide-lumened, isodiametric adaxial cells. Comparison of the illustrations of the transverse sections given by Flowers (1973) for D. rigidulus and by Grout (1939) and Lawton (1971) for synonyms of D. australasii demonstrates this. Didymodon australasii differs from D. rigidulus in the dry, often desert habitat, the leaves usually with broadly acute and somewhat cucullate apices, the costa seldom excurrent, the basal laminal cells usually thin-walled and hyaline, and propagula absent.

As is common in desert species of Pottiaceae, the costa often bulges adaxially. Didymodon umbrosus is closely related and occasionally intergrades with D. australasii Although it has bistratose upper laminal margins, D. umbrosus usually may be distinguished from the above two species by the long-subulate leaf shape, the usually elongate adaxial superficial costal cells, the inflated basal cells, and the distinct hyalodermis of the stem. The few specimens of Trichostomopsis aaronis (Lor.) Agnew & Towns. and T. haussknechtii (Jur. & Milde) Agnew & Towns. from Iraq that I have examined (at MO) are apparently the same as D. australasii though further study is needed before synonymy is justified.

6. Didymodon umbrosus (C. Muell.) Zander, comb. nov. [columb.]

Basionym: Barbula (Asteriscium) umbrosa C. Muell., Linnaea 42: 340. 1879.
Synonyms: Trichostomopsis crispifolia Card., Rev. Bryol. 36: 74. 1909.
Trichostomopsis umbrosa (C. Muell.) H. Robins., Phytologia 20: 185. 1970.

Further synonymy is given by Robinson (1970). Trichostomopsis crispifolia Card. (isotype!—NY), the generitype of Trichostomopsis Card., is included and Trichostomopsis thus becomes a synonym of Didymodon. Didymodon umbrosus is unusual in the sect. Didymodon in having usually rather large, 10-13 µm wide, short-rectangular, porose upper leaf cells (approached by those of D. johansenii), the elongate adaxial superficial costal cells, and in the distinct hyalodermis of the stem. It appears to intergrade in these characters, however, with D. australasii (q.v.). It is the largest of the species of sect. Didymodon, but is apparently lacking in the Pacific Northwest where the most robust species of sect. Vineales and sect. Graciles are found. This may be due to different climatic factors needed to induce or allow selection for large size in sect. Didymodon. Didymodon incrassato-limbatus Card. of Mexico (probably a synonym of D. nicholsonii Culm. of Europe) also has long-lanceolate leaves but the laminal cells are usually small, 7-9 µm wide, quadrate to hexagonal and thin-walled, often bistratose in medial patches, the adaxial costal cells are quadrate, the basal laminal cells are not distinctly inflated and the hyalodermis is not or only poorly differentiated.

7. Didymodon nigrescens (Mitt.) K. Saito

This species is discussed and illustrated by Saito (1975). Steere (1978) reported it from Alaska and British Columbia as new to North America. American synonyms that may be added to the list of Saito (1975) are Barbula rufofusca Lawt. & Herm. (holotype!—US) from Alaska and B. bunneola C. Muell. (isotype!—NY) of Guatemala. It is now known in the New World from Central America and from

many collections from hyperoceanic and montane areas of northwestern North America. This and the following two species are closely related by the red coloration of the plants, the upper leaf margins crenulate by bulging cell walls, and the costa very thin, often with elongate adaxial cells. A paper dealing with these three species giving descriptions and details of geographic range and ecology is being prepared with Dr. W.C. Steere. Although in the sect. Vineales, D. asperifolius is similar in many characters, but may be easily distinguished by its recurved leaves with margins usually recurved to near the apex.

8. Didymodon perobtusus Broth.

This species is similar to D. tophaceus in the costa ending often 4-6 cells below a broadly obtuse apex, but is closely related to D. nigrescens and D. subandreaeoides by the reddish coloration, crenulate leaf apices and the thin costa that may have elongate adaxial cells. Its known range includes U.S.S.R.: Mongolia (holotype!—H), and Canada: Yukon, Firth River basin, near mouth of Mancha Creek, calcareous bluff, Sharp MC-58152a (NY); Northwest Territories, Mackenzie Distr., Nahanni National Park, Virginia Falls, mist zone, Scotter 22433 (NY). The former Canadian collection has been reported previously by Steere (1978). This species may have a close relationship with Husnotiella revoluta Card. of Middle America, which has similarly shaped but marginally revolute leaves, and, as noted by Bartram (1926) and Zander (1968), may also produce unicellular propagula in axillary clusters. Didymodon perobtusus is very similar to Barbula uruguayensis Broth. (isotype!—NY) of Uruguay, which has similar propagula but differs mainly in the green coloration and the areolation being nearer that of D. tophaceus in the unistratose lamina and the weakly colored cell walls that do not bulge along the upper leaf margin.

9. Didymodon subandreaeoides (Kindb.) Zander, comb. nov.

Basionym: Barbula subandreaeoides Kindb., Rev. Bryol. 32: 36. 1905.
Synonym: Barbula andreaeoides Kindb., Rev. Bryol. 32: 36. 1905.

As Steere (1978) has noted, Barbula andreaeoides represents a good species, and is not a synonym of Andreaea rothii Web. & Mohr as once though (Steere 1938a). Because the combination in Didymodon is occupied by an earlier name, the synonym B. subandreaeoides, published at the same time, is here transferred to Didymodon rather than provide a new name for B. andreaeoides. Sporophytes are not known for this species and reproduction is apparently asexual by fragile branches with cochleariform leaves. The heteromorphic leaves are quite distinctive, showing often on the same branch a sharp change from a series of ovoid, weakly

concave, strongly papillose leaves to a series of cochleariform, deeply concave, non-papillose, smaller leaves. The developmental switching mechanism that determines leaf morphology may be similar in sharp response to that governing heterophylly in amphibious Ranunculus species.

DIDYMODON sect. VINEALES (Steere) Zander, comb. nov.

Basionym: Barbula sect. Vineales Steere in Grout, Moss Fl. N. Amer. 1: 174. 1938.
Synonym: Barbula sect. Rubiginosae Steere in Grout, Moss Fl. N. Amer. 1: 174. 1938.

This section is characterized by the leaves spreading to wide-spreading and occasionally recurved when moist, concave across the leaf to keeled and narrowly channeled along the adaxial surface of the costa, margins weakly decurrent to strongly so in robust plants, weakly recurved below to recurved or revolute to near the apex, often apiculate by a conical cell, the costa usually percurrent to shortly excurrent in a broad mucro, the upper laminal cells occasionally bistratose along the leaf margins, epapillose to papillae simple, irregular to spiculose-multiplex, 1-4 over each lumen, the adaxial superficial cells of the costa quadrate in the upper half of the leaf and the adaxial stereid band often absent. The peristome is absent or rudimentary to well developed and twisted to 2.5 turns. Spores mature usually in spring, also summer.

10. Didymodon brachyphyllus (Sull. in Whippl.) Zander, comb. nov. [columb.]

Basionym: Barbula brachyphylla Sull. in Whippl., Rep. Pacif. Railr. Route Surv. Bot. 4: 186. 1856.

I agree with Steere (1938a) that this species "...is apparently the most reduced form of the extremely variable B. vinealis-B. cylindrica complex...." The leaf apex is often broadly obtuse in some leaves of a collection. Flowers (1973) appears to have included this species within his concept of D. vinealis.

11. Didymodon reedii H. Robins. [columb. & paroch.]

This species was described from material from Maryland (holotype!—US), which matches very nearly specimens of the western D. brachyphyllus. The eastern material differs mainly in being propaguliferous. Recent collections from Colorado (Larimer Co., 6.5 km NNW of Livermore, Hermann 26986—USFS; Yuma Co., 3.2 km S of Bonny Reservoir, Hermann 23531—MICH, USFS) also prove to be D. reedii. Synonymy of the two names is probable, although the

presence in Maryland of a species from this western North American section of Didymodon is surprising. Additionally, the Asiatic D. tectorum (C. Muell.) K. Saito, illustrated by Saito (1975), is probably synonymous with D. reedii, antedating it, but is itself antedated by D. brachyphyllus. Didymodon cordatus Jur. of Europe is related but may be distinguished by the massive costa. More satisfactory resolution of these taxa awaits revisionary study.

12a. Didymodon vinealis (Brid.) Zander, comb. nov., var. vinealis

Basionym: Barbula vinealis Brid., Bryol. Univ. 1: 830. 1827.

Some specimens with bistratose margins are confused in herbaria with D. rigidulus; however, the leaves narrowly channeled along the costa, the highly recurved leaf margins and the percurrent or shortly excurrent costa are diagnostic. Saito (1975) may have recognized D. vinealis under the name D. constrictus (Mitt.) K. Saito, judging from his key, description and illustrations. Specimens with rather thin cell walls are easily recognized by the usually papillose upper laminal cells, and the costa with a crescent-shaped abaxial stereid band, the adaxial stereid band usually lacking and represented by 1(-2) layers of wide lumened cells of about the same diameter as those of the adaxial costal epidermis. Of the species of Didymodon studied, D. vinealis is most closely related to Barbula in the often relatively long and twisted peristome, the distinctive adaxial medial laminal groove along the coata in well developed plants, and the laminal papillae being often multiplex.

12b. Didymodon vinealis var. flaccidus (B.S.G.) Zander, comb. nov. [columb.]

Basionym: Barbula vinealis var. flaccida B.S.G., Bryol. Eur. 2: 86. 1842 (fasc. 13-15 Mon. 24).
Synonym: Barbula cylindrica (Tayl.) Schimp. in Boul., Fl. Crypt. Est Muscin. 430. 1872.

Steere (1938a) treated this taxon as Barbula cylindrica and noted that some robust collections from British Columbia were much larger than any European specimens he had seen. Regional climate is probably a deciding factor in selection or expression of degree of robustness, as is also likely with robust forms of D. rigidicaulis.

13. Didymodon occidentalis Zander, nom. nov. [columb.]

Name replaced: Barbula rubiginosa Mitt., Jour. Linn. Soc. Bot. 8: 27. 1864 (non Didymodon rubiginosus (C. Muell.) Broth., Nat. Pfl. 1(3): 405. 1902).

I have seen specimens of D. occidentalis from British Columbia, Oregon and California. The apex of the leaf is fragile, often broken or knobby, the costa is evenly stout to near the apex and is in a rather deep adaxial laminal groove, and the lamina near the leaf apex is bistratose, at least in patches. This species is closely related to and transitional between D. vinealis and D. sinuosus. Although the few capsules of D. occidentalis that I have seen lack peristomes and Steere (1938a) described the species as eperistomate, Lawton (1971) notes that a rudimentary peristome may be present.

14. Didymodon sinuosus (Mitt.) Delogn.

Under the synonym Barbula sinuosa (Mitt.) Grav., several European authors (Demaret & Castagne 1964, Husnot 1884-1894, Moenkemeyer 1927, Podpěra 1954) have indicated, at least by juxtaposition of names in manuals, that D. sinuosus is closely related to D. vinealis. Although Dixon (1924) could find no definite alliance, I agree with the former authors. This obligate apomict is related to D. vinealis through D. occidentalis, which may have sporophytes and has merely fragile leaf apices. Didymodon sinuosus has been found in North America only in Alaska (Zander 1978b) and may be easily confused with D. johansenii from which it may be distinguished by the characters cited in the key.

15. Didymodon asperifolius (Mitt.) Crum, Steere & Anderson

This species was discussed by Steere (1938b) under the synonym D. rufus Lor. Contrary to Saito's (1975) key and description, the central strand of the stem is occasionally present, although weak. This is an arctic-alpine species paralleling similar reddish-brown northern or montane expressions in the other sections of Didymodon. Didymodon asperifolius may possibly be better placed in sect. Graciles because of the recurved leaves and simple laminal papillae.

DIDYMODON sect. GRACILES (Milde) K. Saito, Jour. Hattori Bot. Lab. 39: 504. 1975. Type: D. rigidicaulis (C. Muell.) Saito

Synonym: Barbula sect. Fallaces Steere in Grout, Moss Fl. N. Amer. 1: 174. 1938, syn. nov.

For additional synonymy, see Saito's (1975) treatment. This section is characterized by the leaves spreading to often strongly recurved when moist, concave to keeled, margins weakly to strongly decurrent, plane to recurved in lower 2/3, not apiculate, the costa ending below the apex to shortly excurrent, the upper laminal cells unistratose, epapillose to papillae simple, hemispherical or occasionally conic-spiculate, usually 1-2 over each lumen, the adaxial superficial cells of the costa short-rectangular to elongate in the upper half of the leaf and the adaxial stereid band usually present. The peristome is rudimentary to well developed and twisted to 2 turns. Spores mature usually in winter or spring. Unlike sect. Didymodon and sect. Vineales, there is no tendency toward bistratose upper laminal cells or very fragile or caducous leaf apices. Saito (1975) recognized only two sections of Didymodon in Japan, this and sect. Didymodon. The latter included species that I here place in sect. Vineales. Admittedly, the sect. Graciles is more distinctive in character than the sect. Vineales.

16. Didymodon michiganensis (Steere) K. Saito [columb.]

In addition to the type locality in Michigan, this species has been reported from a very few scattered localities worldwide: Mexico (Bowers & Sharp 1975), Assam (Robinson 1968) and Japan (Saito 1975). Polytopic origin due to unusual environmental conditions that may have evoked, from the related widespread species D. fallax, both a usually repressed potential to form propagula and to produce the characteristic gametophore morphology would be a hypothesis that might explain the spotty distribution. However, a specimen that has the gametophore characters of D. michiganensis that are described in the key but lacking propagula has been collected in Canada: Northwest Territories, Mackenzie District, Virginia Falls, spray zone, Scotter 22277 (NY). Thus, propagula production and gametophore morphology are not necessarily tied and the situation may not have a simple explanation. The relationship of propaguliferous and non-propaguliferous expressions of D. michiganensis with D. fallax may be similar in evolutionary origin to the relationship of D. brachyphyllus and D. reedii with D. vinealis.

17. Didymodon fallax (Hedw.) Zander, comb. nov.

Basionym: Barbula fallax Hedw., Spec. Musc. 120. 1801.

There are three specimens named as Barbula fallax in the Hedwig-Schwaegrichen herbarium at G. The lectotype, labeled "Barbula fallase Hedw. St. Crypt. Vol. 1. p. 62. t. 24. Chemnitis lecta," is of operculate, fruiting plants of B. fallax that are well within the concept of the species described by Steere (1938a) and which is recognized in the present study. Another specimen, labeled "Barbula fallase Hedw. St. Crypt. Bryum Delen. 46 ese ipso cryptg. Herbario," is of deoperculate plants of D. rigidulus that lack propagula. A third, labeled "Barbula fallax e Brid. Br. imberbe...Ehrhardt," consists of dioicous (!) plants of Bryoerythrophyllum recurvirostrum (Hedw.) Chen (not B. rubrum (Jur.) Chen cf. Zander 1978a). Following recommendation 7B of the 1969 I.C.B.N., my choice of the first specimen as lectotype preserves current usage, is in consonance with the protologue, and, of the three specimens, in fact fits the protologue best. The species D. fallax, D. rigidicaulis and D. giganteus in North America are possibly better recognized as a single polymorphic species because of the large number of plants that are intermediate in character.

18. Didymodon rigidicaulis (C. Muell.) K. Saito [columb.]

This taxon has been treated as the synonym (see Saito 1975) Barbula reflexa (Brid.) Brid. in most American manuals. It is a species intermediate in character between D. fallax and D. giganteus. Very large forms in the Pacific Northwest occasionally grade into D. giganteus or have margins weakly dentate above midleaf, approaching the Asiatic D. eroso-denticulatus (C. Muell.) K. Saito. Similar large forms described as Barbula maxima Syed & Crundw. (Ireland: Sligo Co., Crundwell & Warburg, 1962—NY), occur in western Ireland. The disjunction of these unusually robust expressions parallels an East-West intercontinental disjunction of the Andean species Bryoerythrophyllum jamesonii (Tayl.) Crum, which has been collected in the Queen Charlotte Islands of British Columbia and in Scotland (Zander 1978a), being one of many examples of species disjunctive in range between northern areas of marine or hyperoceanic climate with precipitation maxima in winter. Regional climate probably has allowed expression or selection for large size, which has reached an end point in the B. fallax complex in D. giganteus. Didymodon rigidicaulis is often reddish in coloration, paralleling reddish forms in other sections of the genus.

Another, more consistently reddish species of the sect. Graciles is:

Didymodon laevigatus (Mitt.) Zander, comb. nov.

Basionym: Tortula laevigata Mitt., Jour. Linn. Soc. Bot. 12: 160. 1869.

This species is Andean, Middle American montane and West Indian in range and differs from D. rigidicaulis by the long-lanceolate leaves, acuminate from a broad leaf base, spreading but not or only weakly recurved when moist, upper laminal cells 8-10 µm wide, very thick-walled and lumina round to oval or rounded-trapezoidial, epapillose. The lectotype (by Steere 1948) and syntype specimens at NY(!) are far more robust—the plants reaching to 8 cm long—than specimens I have seen from Costa Rica: Cartago Prov., Cerro de la Muerte, King C-1276 (US) or Jamaica: Morce's Gap, Britton 161 (NY), which do not exceed 2.5 cm in length. A combination in Didymodon is made here as the species is apparently rather widely distributed and may well occur north of Mexico. It may be distinguished from specimens of the reddish species D. nigrescens that have elongate adaxial costal cells by the entire leaf margins and the strong costa, which is usually 3-5 cells wide adaxially above midleaf.

19. Didymodon giganteus (Funck) Jur. [columb.]

Collections of this species from Alaska intergrade somewhat with D. rigidicaulis and also have occasional denticulations on the upper leaf margins. Mainly on account of the highly porose or trigonous upper leaf cells, some authors recognize this species in the monotypic genus Geheebia Schimp. but it certainly belongs in the D. fallax complex. Both D. giganteus and D. rigidicaulis have leaf cells usually somewhat larger (10-14 µm wide) than those of D. fallax (8-10 µm wide).

20. Didymodon leskeoides K. Saito

This boreal-montane species differs from D. fallax by the often flagellate stem apices, the auricled basal leaf margins and the often long, whip-like acumination of the leaf apex (illustrated by Saito 1975). It was described only recently by Saito (1975) from Japan, and I have seen collections from India: N. Uttar Pradesh, above Almora, Pindari Glacier, Srivastava 2839 (BUF) and Canada: Northwest Territories, South Nahanni R., Virginia Falls, spray zone, Scotter 22439 (NY); Nahanni Mtns., N slope, alpine tundra, Vitt 20251 (ALTA).

21. Didymodon tophaceus (Brid.) Lisa

This is a polymorphic species usually found on calcareous rock in seepage or in other wet sites. Variation in peristome development is considerable and is discussed by Andrews (1941). All American specimens that I have seen may be referred to the sect. Graciles in possessing leaves often apically denticulate when robust, the elongate adaxial costal cells, the often strong adaxial stereid band, the large leaf cells often 12-14 µm wide with rounded lumina and simple, hemispherical to rounded-conic papillae that often occur singly over each lumen. Also, authors of major identification manuals have reported that the spores mature usually in winter, or occasionally spring, in the north temperate zone. The large decurrencies emphasized as a taxonomic character for D. tophaceus by Conard (1945) are described as characteristic for sect. Graciles by Saito (1975); however, as Conard notes (1951) such decurrencies are often present in species placed here in sect. Vineales, namely D. occidentalis and D. vinealis. Some American authors recognize D. luridus Hornsch. in Spreng. (= D. trifarius of most authors but not Hedwig, fide Zander 1978c) as a good species, placing it close to D. tophaceus in relationship. I agree with Crum, Steere and Anderson (1973) that true D. luridus has not been found in North America north of Mexico. Judging from European collections at BUF, D. luridus is unrelated to D. tophaceus, being in sect. Didymodon very near D. acutus. Its spores mature at the same time as those of D. tophaceus but this is perhaps an adaptation to the similar, nearly constantly moist habitat. Some collections of small plants of D. tophaceus may be similar to D. luridus in bearing leaves appressed when dry, little recurved when moist, short-ovate and acute, costa short-excurrent or percurrent; however, D. luridus differs in the leaf cells being very small, 7-9 µm wide, evenly quadrate (to hexagonal), and the superficial cells of both adaxial and abaxial sides of the costa being similar to the laminal cells, quadrate at least in the upper 1/2 of the costa. Most plants of D. tophaceus can be readily distinguished from D. luridus under the dissecting microscope by the often blackish color of some leaves, the leaves spreading and curled when dry and often recurved when moist, with strong, often reddish costae and blunt leaf apices.

EXCLUDED SPECIES

Didymodon columbianus Herm. & Lawt. is now treated as a species in the genus Bryoerythrophyllum (Zander 1978a). I agree with Crum, Steere and Anderson (1973) that the Florida collection of D. fuscoviridus Card. reported by Reese (1956) is D. rigidulus. Didymodon parvulus (Kindb.) E.G. Britt. is Distichium inclinatum (Hedw.) B.S.G. (fide Steere & Crum 1977).

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