
A REVISION OF *DIDYMODON*
SECTION *FALLACES* (MUSCI,
POTTIACEAE) IN EUROPE,
NORTH AFRICA,
MACARONESIA, AND
SOUTHWEST AND
CENTRAL ASIA¹

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ABSTRACT

Didymodon sect. *Fallaces* (Musci, Bryopsida) is taxonomically revised for Europe, North Africa, Macaronesia, and Southwest and Central Asia. Nine species are recognized. *Didymodon planotophaceus*, *D. spadiceus* var. *siluricus*, and *Didymodon ceratodonteus* are newly synonymized with *D. tophaceus*; *D. barbuloides* is a new synonym referred to *D. spadiceus*, and *Trichostomum rigidulum* var. *paludosa* to *D. fallax*. Lectotypes for *Barbula adriatica*, *B. falcifolia*, *B. insidiosa*, *B. kneuckeri*, *B. rigidicaulis*, *B. serpenticaulis*, *B. sinensi-fallax*, *Didymodon barbuloides*, *D. bosniacus*, *D. giganteus*, *D. levieri*, *D. maximus*, *D. rufus*, *D. spadiceus*, *D. spadiceus* var. *siluricus*, *D. tophaceus*, *D. tophaceus* var. *breidlerii*, *Limneria viridula*, and *Trichostomum rigidulum* var. *paludosa* are designated here. *Didymodon asperifolius* and *D. tophaceus* are reported for the first time from the Caucasus and Mauritania respectively. Descriptions, a taxonomic key, as well as LM and SEM photographs are included.

Key words: Asia, *Didymodon*, Europe, Macaronesia, North Africa, Pottiaceae, taxonomy.

Didymodon Hedw. is a genus of the moss family Pottiaceae that includes approximately 122 species worldwide, with the greatest diversity in temperate and mountainous regions (Zander, 1993). The genus was described by Hedwig (1801) to include three species, only one of which is currently accepted in the genus: *D. rigidulus*. The remaining species correspond to genus *Ditrichum* Hampe.

The genus concept of *Didymodon* has been in dispute, especially as regards the morphological delimitation of *Didymodon* versus *Barbula* Hedw. The taxonomic differences between the two genera have long been based on peristome characters: in *Barbula* formed by long and twisted teeth and in *Didymodon* by short and straight teeth. Since these characters separated gametophytically closely related species of the genus *Didymodon* and *Barbula* (e.g., *D. fallax* and *D. spadiceus*), the differentiation between both genera was generally abandoned (Dixon, 1924; Mönkemeyer, 1927; Hilpert, 1933;

Chen, 1941; Nyholm, 1989; Smith, 1978; Kürschner, 2000). Saito (1975) differentiated *Didymodon* and *Barbula* for the first time by gametophytic characters. He principally used the axillary hairs of the leaves for discriminating both genera. The axillary hairs in *Didymodon* have one or two brown basal cells, while in *Barbula* the hairs are hyaline throughout. Later Zander (1993), in his world monograph of the Pottiaceae, expanded the delimitation between *Didymodon* and *Barbula*.

Besides this controversy concerning *Barbula*, the segregation of some *Didymodon* species into other closely related genera, such as *Geheebia* Schimp., *Oxystegus* (Limpr.) Hilp., *Husnotiella* Cardot, and *Trichostomopsis* Cardot, is also of note. However, according to Saito (1975) and Zander (1978, 1993) all of these have the morphological features assigned to *Didymodon*. The molecular data support this opinion. Werner et al. (2004a) sequenced cp *rps4* of *Didymodon rigidulus* Hedw., *Geheebia gigantea* (Funck) Boulay, *Oxystegus sinuosus* (Mitt.)

¹ We thank the curators of the herbaria and the collectors who sent us material on loan: B, BCB, BM, BP, BR, C, CAIA, CAME, CANM, CGE, CLU, COI, DUKE, E, FCO, FI, G, GB, GDA, GJO, GZU, H, HBG, IRAN, JE, L, LE, LISU, M, MA, MO, MUB, NMW, NY, O, PAMP, PC, PO, PRC, RO, S, SINU, SOM, VAL, VIT, W, WB, WU, Z, herbarium T. L. Blockeel, herbarium A. Cogoni, herbarium R. Düll, herbarium W. Frey, herbarium J. Martínez-Abalgar, herbarium R. B. Pierrot, herbarium M. Sabovljevic, herbarium R. Skrzypczak, herbarium C. C. Townsend. This work has been carried out with financial support from MCYT of Spain (Projects BOS2001-0276 and BOS2000-0296-C03-01) and "Fundación Séneca" of Murcia (PI-15/00762/FS/01).

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Hilp., and *Trichostomopsis australasiae* (Hook. & Grev.) H. Rob and observed that all these species are closely related. More precise data have been obtained when sequencing the nrITS region of a high number of taxa, which show that the genus *Didymodon* is monophyletic after including the formerly segregated species and is clearly separated from *Barbula* (Werner et al., 2004b, 2005).

According to Zander (1993) *Didymodon* consists of five sections: section *Asteriscium* (Müll. Hal.) R. H. Zander, section *Fallaces* (De Not.) R. H. Zander, section *Rufidulus* (Chen) R. H. Zander, section *Didymodon*, and section *Vineales* (Steere) R. H. Zander.

Studies of *Didymodon* in Europe are scant, even if we include those of Düll (1984), Düll-Hermanns and Düll (1985), and Kučera (2000), on central European species, and of Kučera (2002), on northern European species. No study has until now included North African taxa or those from Central and Southwest Asia. Recent years have seen the publication of floristic studies or checklist studies in this area (Frey & Kürschner, 1991; Ros et al., 1999; El-Saadawi et al., 1999; Kürschner, 2000; Cano et al., 2002), which have pointed to the existence of numerous endemisms and taxa described or collected once during the first half of the 20th century and then forgotten. Many more works have been published on this genus in North America and Mexico (Zander, 1978, 1981, 1994), East Asia (Chen, 1941), and Japan (Saito, 1975; Noguchi, 1988).

Recognizing the overall scarcity of information, we have carried out a taxonomic revision of the section *Fallaces* in Europe, North Africa, Macaronesia, and Southwestern and Central Asia. Nine species belong to this section in this geographic area: *Didymodon asperifolius* (Mitt.) H. A. Crum, Steere & L. E. Anderson, *D. fallax* (Hedw.) R. H. Zander, *D. ferrugineus* (Schimp. ex Besch.) M. O. Hill, *D. giganteus* (Funck) Jur., *D. maschalogenia* (Renauld & Cardot) Broth., *D. maximus* (Syed & Crundw.) M. O. Hill, *D. spadiceus* (Mitt.) Limpr., *D. tomaculosus* (Blockeel) M. F. V. Corley, and *D. tophaceus* (Brid.) Lisa.

MATERIALS AND METHODS

All available types and numerous collections of *Didymodon* sect. *Fallaces* from Europe, Africa, North America, and Asia have been studied. This revision is based on 1130 specimens deposited in the following institutional and personal herbaria: B, BCB, BM, BP, BR, C, CAIA, CAME, CANM, CGE, CLU, COI, DUKE, E, FCO, FI, G, GB, GDA, GJO, GZU, H, HBG, IRAN, JE, L, LE, LISU, M, MA,

MO, MUB, NMW, NY, O, PAMP, PC, PO, PRC, RO, S, SINU, SOM, VAL, VIT, W, WB, WU, Z, herbarium T. L. Blockeel (Sheffield, United Kingdom), herbarium A. Cogoni (Cagliari, Italy), herbarium R. Düll (Bad Münstereifel, Germany), herbarium W. Frey (Berlin, Germany), herbarium J. Martínez-Abaigar (Logroño, Spain), herbarium R. B. Pierrot (Dolus d'Oléron, France), herbarium M. Sabovljevic (Belgrade, Serbia, and Montenegro), herbarium R. Skrzypczak (Montbrison, France), herbarium C. C. Townsend (Twickenham, London, United Kingdom).

Specimens were examined in a 2% potassium hydroxide solution.

Leaf areolation and ornamentation was studied using a Jeol JSM-6100 SEM at the University of Murcia. The material was fixed in 3% glutaraldehyde with 0.1M cacodylate buffer at 4°C, washed in cacodylate and saccharose buffer, dehydrated in an increasing acetone gradient (30%, 50%, 70%, 90%, 100%), critical-point dried, and sputtered with a gold layer 200–300 Å thick.

World distributions are provided; major political divisions for countries are included when the information was available.

TAXONOMIC HISTORY

Like most of the species of *Didymodon*, those belonging to section *Fallaces* were attributed to different genera (*Trichostomum* Bruch, *Tortula* Hedw., *Geheebia* Schimp.), although, as previously mentioned, these species were especially considered members of the genus *Barbula*. This remained the case until *Didymodon* was delimited morphologically (Saito, 1975; Zander, 1978).

The first subgeneric treatment of *Didymodon* was made by Saito (1975), who recognized two sections for the Japanese species: section *Graciles* (Milde) K. Saito and section *Didymodon*. The section *Graciles* was characterized by the rounded-triangular stem, basal margins of leaves long-decurrent, and cells of the adaxial surface of the costa linear-oblong. This section included *Didymodon giganteus*, *D. eroso-denticulatus*, and *D. rigidicaulis* (Müll. Hal.) K. Saito. Zander (1978) added five species to section *Graciles* (*Didymodon fallax*, *D. laevigatus* (Mitt.) R. H. Zander, *D. michiganensis* K. Saito, *D. leskeoides* K. Saito, and *D. tophaceus*) and expanded the characterization of this section, adding as important characters the spreading to often strongly recurved leaves when moist, unistratose upper laminal cells, and adaxial stereid band usually present. Zander (1979) found an earlier name, *Tortula* sect. *Fallaces* De Not., available at the sectional level for section *Graciles*, so he proposed the new com-

bination *Didymodon* sect. *Fallaces* and synonymized section *Graciles* with this section. Zander (1993) added another morphological character to define the section as the KOH color reaction usually reddish orange and included new species in section *Fallaces*: *Didymodon calycinus* Dixon, *D. ceratodonteus* (Müll. Hal.) Dixon, *D. constrictus* (Mitt.) K. Saito, *D. hastatus* (Mitt.) R. H. Zander, *D. inundatus* (Mitt.) Broth., *D. maximus*, *D. nigrescens* (Mitt.) K. Saito, *D. spadiceus*, *D. tomaculosus*, and *D. waymouthii* (R. Br. bis) R. H. Zander, although he did not provide the number of species worldwide. He also included, exceptionally, *D. asperifolius*, a species with quadrate or shortly rectangular cells on the adaxial surface of the costa. In an evolutionary analysis of the North American species of the genus *Didymodon*, the same author (Zander, 1998) made some changes to his previous proposals, also recognizing the section *Fallaces*, but in a broader sense. He added to this section *D. subandreaeoides* (Kindb.) R. H. Zander; a year later he included this species and *D. nigrescens*, previously considered in section *Fallaces*, in the section *Rufidulus* (Zander, 1999).

This changing situation led us to think that the infrageneric classification in *Didymodon* is difficult to assess based on morphological data. That is because there are no morphological characteristics exclusive of each section, but they are defined by a combination of several features, and often a character is shared by one or more sections.

TAXONOMIC TREATMENT

Didymodon Hedw., Sp. Musc. Frond.: 104. 1801.
TYPE: *Didymodon rigidulus* Hedw. (designated by Steere (1938: 186)).

Trichostomum subg. *Zygotrichodon* Schimp., Syn. Musc. Eur. (ed. 2): 169. 1876. TYPE: *Trichostomum topheaceum* Brid.

Geheebia Schimp., Syn. Musc. Eur. (ed. 2): 233. 1876.
Barbula subg. *Geheebia* (Schimp.) Szafr., Fl. Polska Mchy 1: 213. 1957 [1958]. TYPE: *Geheebia cataractarum* Schimp.

Dactylhymenium Cardot, Rev. Bryol. Lichénol. 36: 72. 1909. TYPE: *Dactylhymenium pringlei* Cardot.

Limneria Stirt., Trans. Bot. Soc. Edinburgh 26: 428. 1915.
TYPE: *Limneria viridula* Stirt.

Prionidium Hilp., Beih. Bot. Centralbl. 50: 640. 1933.
TYPE: *Prionidium setschwanicum* (Broth.) Hilp.

Our own preliminary molecular data (Werner et al., 2005) suggest that the European species of section *Fallaces* seem to be polyphyletic, but no conclusion can be reached until more data are available.

Didymodon sect. **Fallaces** (De Not.) R. H. Zander, Phytologia 44: 209. 1979. *Tortula* sect. *Fallaces* De Not., Mem. Reale Accad. Sci. Torino 40: 287. 1838. *Barbula* sect. *Fallaces* (De Not.) Steere, in Grout, Moss Fl. N. Amer. 1: 174. 1938. *Barbula* subsect. *Fallaciformes* Kindb., Eur. N. Amer. Bryin. 2: 246. 1897.
TYPE: *Barbula fallax* Hedw.

Didymodon sect. *Graciles* (Milde) K. Saito, J. Hattori Bot. Lab. 39: 501. 1975. *Barbula* sect. *Graciles* Milde, Bryol. Siles., 117. 1869. TYPE: *Barbula rigidicaulis* K. Saito.

The species of section *Fallaces* share the following combination of characters: ovate, ovate-lanceolate, or lanceolate leaves (lingulate in *Didymodon tophaceus*) that are erect-patent to squarrose when moist, generally keeled; lamina unistratose, orange to dark red with KOH (*D. maschalogenae* sometimes yellowish), margins weakly to strongly decurrent, plane or recurved from base to ¾ of the leaf, unistratose, not apiculate; costa ending below the apex or percurrent (shortly excurrent in *D. tomaculosus*), ventral cells of the costa in upper leaf elongated (quadrate or shortly rectangular in *D. asperifolius* and *D. tomaculosus*), with generally one layer of guide cells, generally with ventral stereids; upper and middle laminal cells without papillae or with one to three simple or bifurcate papillae per cell; peristome well developed, with straight or spirally twisted teeth.

KEY TO SPECIES OF *DIDYMON* SECT. *FALLACES* IN EUROPE, NORTH AFRICA, MACARONESIA, AND SOUTHWEST AND CENTRAL ASIA

- 1a. Plants with rhizoidal tubers or gemmae in the leaf axils.
 - 2a. Plants with rhizoidal tubers but not gemmae; stems without central strand or weakly differentiated; leaves incurved or spirally twisted, appressed to erect-patent when dry; costa shortly excurrent or percurrent 8. *D. tomaculosus*
 - 2b. Plants with gemmae in the leaf axils, but not rhizoidal tubers; stems with central strand clearly differentiated; leaves catenulate when dry; costa ending below the apex or percurrent 5. *D. maschalogenae*
- 1b. Plants lacking both rhizoidal tubers or gemmae in the leaf axils.
 - 3a. Ventral cells of the costa in upper leaf shortly rectangular to quadrate . . . 1. *D. asperifolius*
 - 3b. Ventral cells of the costa in upper leaf elongated.
 - 4a. Leaves lingulate to oblong-lanceolate, with obtuse or rounded apex; costa generally ending several cells below the apex, very rarely percurrent 9. *D. tophaceus*
 - 4b. Leaves lanceolate, with apex generally

acute (obtuse in *D. spadiceus*); costa ending at the apex or just below the apex.

- 5a. Leaves strongly recurved to squarrose when moist.
 6a. Plants generally to 3 cm high; upper leaves generally to 2 mm long; transverse section of the costa with 2 to 3 guide cells, without ventral stereids
 3. *D. ferrugineus*
 6b. Plants generally more than 3 cm high; upper leaves more than 2 mm long; transverse section of the costa with (3 to) 4 to 8(to 9) guide cells, with 1 to 3 layers of ventral stereids
 6. *D. maximus*
 5b. Leaves erect-patent to spreading, very rarely slightly recurved when moist.
 7a. Plants generally more than 4 cm high; leaves undulate when moist; upper and middle laminal cells strongly sinuous, basal cells pitted 4. *D. giganteus*
 7b. Plants to 4 cm high; leaves not undulate when moist; upper and middle laminal cells not or very slightly sinuous; basal cells not pitted.
 8a. Leaf apex acute; margins recurved from base to $\frac{1}{2}$ or $\frac{3}{4}$; transverse section of the costa with (2 to) 3 to 5(to 6) guide cells; peristome spirally twisted, more than 400–1300(1700) μm long
 2. *D. fallax*
 8b. Leaf apex generally obtuse; margins recurved in the lower half; transverse section of the costa with (4 to) 5 to 9(to 10) guide cells; peristome straight, generally less than (100)135–450(650) μm long
 7. *D. spadiceus*

1. *Didymodon asperifolius* (Mitt.) H. A. Crum, Steere & L. E. Anderson, *Bryologist* 67: 163. 1964. *Barbula asperifolia* Mitt., *J. Linn. Soc., Bot. Suppl.* 1: 34. 1859. TYPE: [India.] “Sikkim, Momay, Regio alp., 15,000 ft.,” *J. D. Hooker s.n.* (lectotype, designated by Li et al. (2001: 157), NY not seen; isotype, BM!). Figure 2A–E.

Didymodon rufus Lorentz, *Bryoth. Eur.*: 621. 1863. TYPE: [Austria.] “In Carinthiae alpe Pasterze,” 1861, *P. G. Lorentz s.n.* (lectotype, designated here, RO!; isotype, PC!).

Barbula sinensi-fallax Müll. Hal., *Nuovo Giorn. Bot. Ital.* 3: 100. 1896. TYPE: “China interior, provincia

Schen-si sept., in monte Thae-pei-san,” Aug. 1894, *J. Giraldis s.n.* (lectotype, designated here, FI!).

Barbula kneuckeri Loeske & Osterwald, *Verh. Bot. Vereins Prov. Brandenburg* 49: 45. 1907. TYPE: [Germany.] “Allgäuer, Nebelhorn, 2200 m,” 17 Aug. 1904, *J. A. Kneucker s.n.* (lectotype, designated here, HBG!).

Plants 1–5 cm high, growing in loose or dense turfs, brown-reddish; *stems* erect or \pm decumbent, simple or branched, without central strand; *rhizoidal tubers* absent. *Leaves* appressed to erect-patent when dry, only the upper leaves slightly twisted, recurved to squarrose, more rarely patent to spreading, not undulate when moist, ovate-lanceolate, gradually narrowed to the apex, keeled, decurrent at base, $1.3\text{--}3 \times 0.5\text{--}0.95$ mm; lamina unistratose, dark red with KOH stain; apex acute; margins entire, sometimes papillose-crenulate, recurved from base to near the apex, sometimes to $\frac{2}{3}$ of the leaf; *costa* 35–75 μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf shortly rectangular to quadrate, papillose, dorsal cells of the costa in upper leaf quadrate, smooth or papillose, in transverse section at leaf base circular, with 2 to 4(to 5) guide cells in 1 layer, 1(to 2) layer of ventral stereids, 1 to 2(to 3) layers of dorsal stereids, ventral epidermis strongly differentiated, papillose, dorsal epidermis differentiated, papillose; *upper and middle laminal cells* rounded, subquadrate or hexagonal, generally oblate, not sinuous, $(3\text{--})5\text{--}12.5 \times 5\text{--}14$ μm , with 1(to 2) simple, tall papillae per cell (sometimes low), thick-walled, collenchymatous; *basal cells* rectangular, quadrate at margins, not sinuous, $(10\text{--})15\text{--}60\text{--}(70) \times (2.5\text{--})5\text{--}12$ μm , forming a \pm differentiated area, smooth, thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicos*. *Sporophyte* not seen.

Habitat and distribution. Granite or calcareous rocks and edges of streams in alpine belt; 2300–3800 m; Africa (O’Shea, 2003), North America, temperate and tropical Asia, Europe. Reported for the first time from the Caucasus.

Discussion. Lorentz published his *Didymodon rufus* in number 621 of *Bryotheca Europaea von Rabenhorst*. We were unable to find any syntype of this exsiccata in B, where the original herbarium of Lorentz is deposited. We did find syntypes in RO and PC. We select as lectotype the syntype kept at RO because it is better preserved.

Barbula sinensi-fallax was described by Müller (1896) from material collected by Giraldis: “Ad latera montis Thae-pei-san.” Müller’s herbarium was deposited at B, but was destroyed in World War II. However, we detected a syntype in Levier’s herbar-

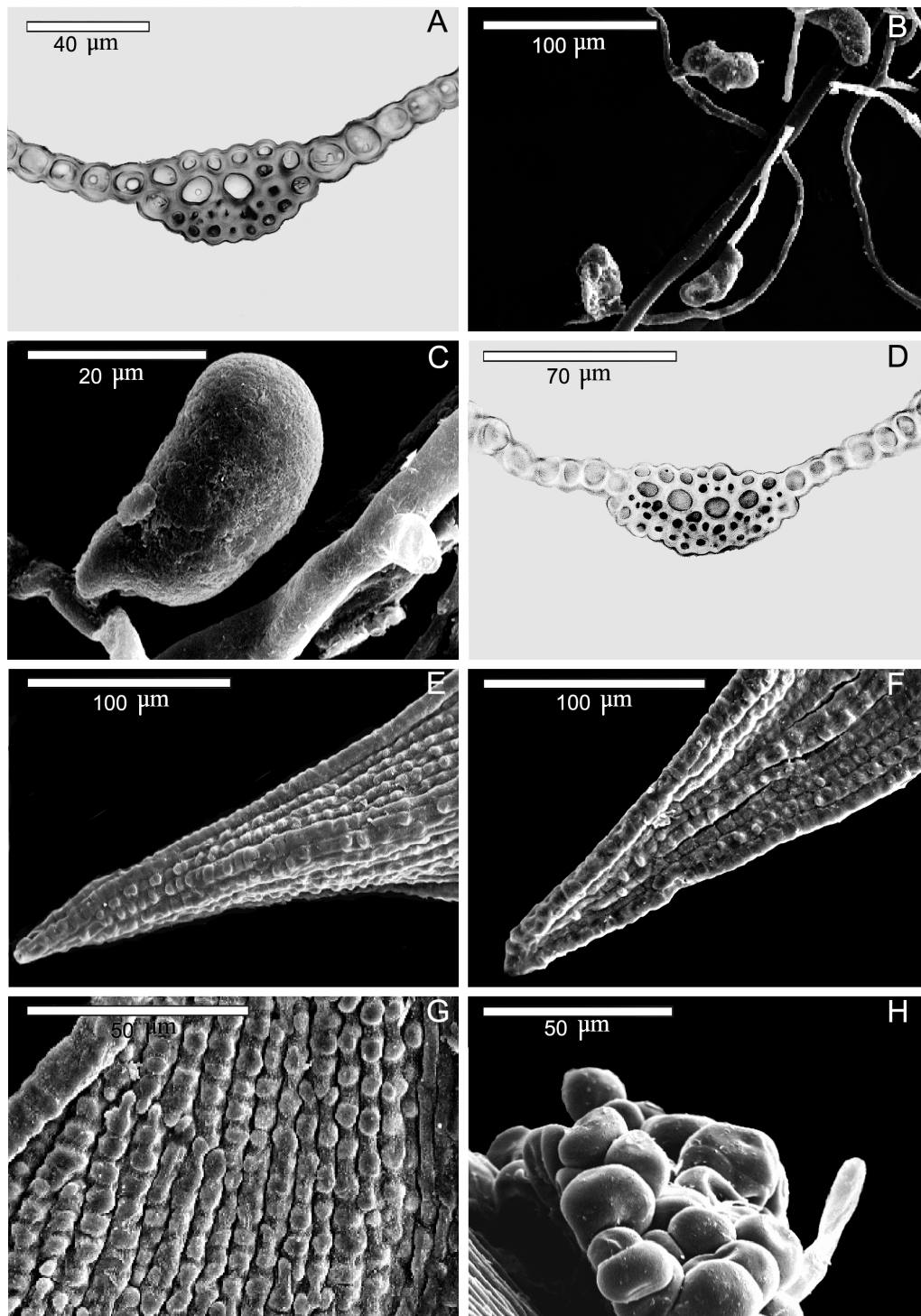


Figure 1. A–C, *Didymodon tomaculosus* (Blockeel & Porley, Hb. Blockeel 31/418). —A. Transverse section of the costa at leaf base. —B. Rhizoidal tubers. —C. Detail of a rhizoidal tuber. D–H, *Didymodon maschalogena* (IRAN 4308). —D. Transverse section of the costa at leaf base. —E. Dorsal surface of leaf apex. —F. Ventral surface of leaf apex. —G. Upper laminal cells. —H. Group of gemmae in the axil of the leaf. Micrographs: A, D: LM; B, C, E–H: SEM.

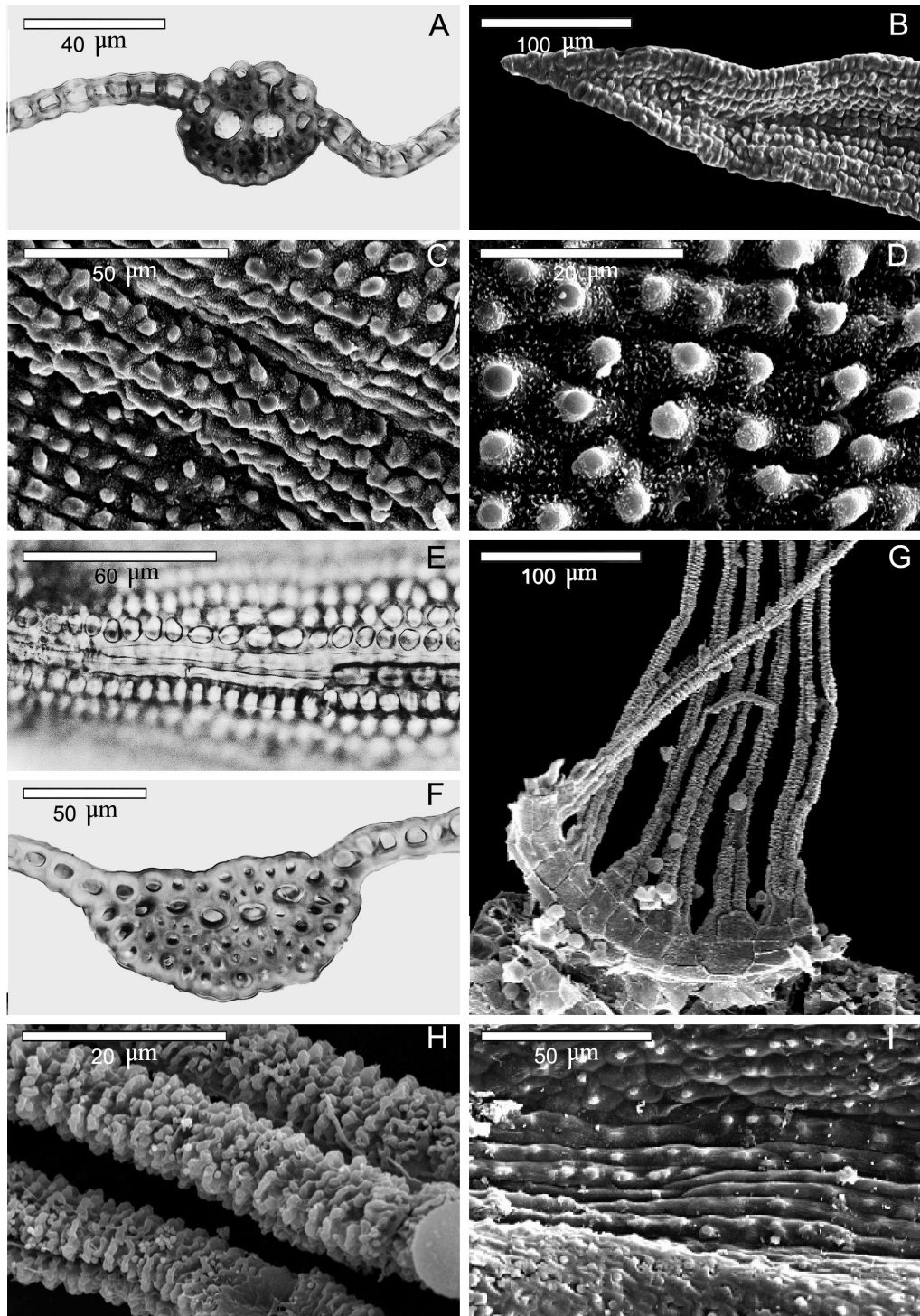


Figure 2. A–E, *Didymodon asperifolius* (Wallace s.n., E). —A. Transverse section of the costa at leaf base. —B. Leaf apex. —C. Ventral surface of the costa in upper leaf. —D. Upper laminal cells. —E. Small band of elongated cells below the apex. F–I, *Didymodon tophaceus* (Cano et al. s.n., MUB 11939). —F. Transverse section of the costa at leaf base. —G. Peristome. —H. Detail of the teeth peristome. —I. Ventral cells of the costa in upper leaf. Micrographs: A, E, F: LM; B–D, G–I: SEM.

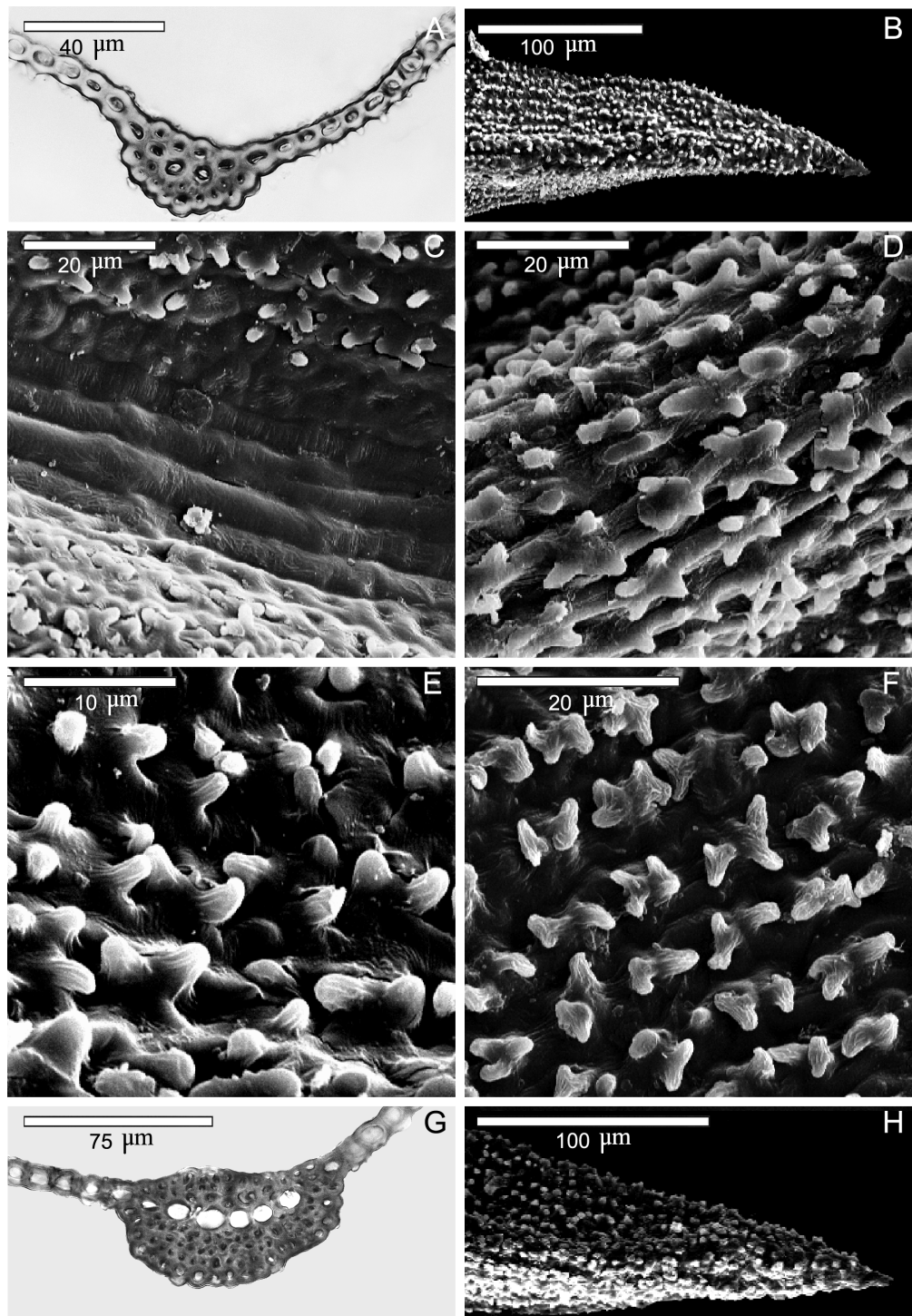


Figure 3. A–E, *Didymodon ferrugineus* (Cano et al. s.n., MUB 8491). —A. Transverse section of the costa at leaf base. —B. Leaf apex. —C. Ventral surface of the costa in upper leaf. —D. Dorsal surface of the costa in upper leaf. —E. Upper laminal cells. F–H, *Didymodon maximus* (Long 14626, E). —F. Upper laminal cells. —G. Transverse section of the costa at leaf base. —H. Leaf apex. Micrographs: A, G: LM; B–F, H: SEM.

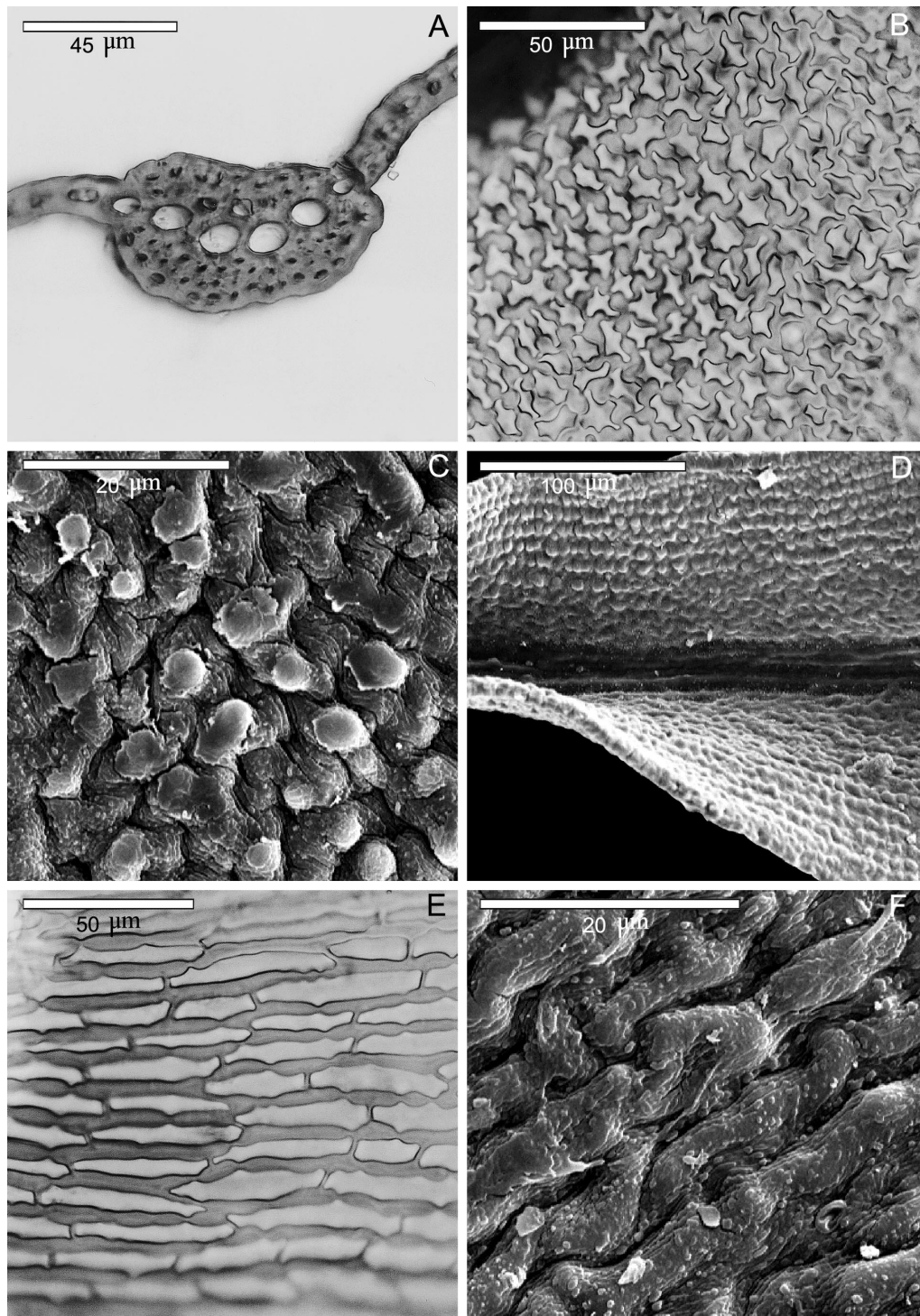


Figure 4. A–F, *Didymodon giganteus* (*Artaria s.n.*, BM). —A. Transverse section of the costa at leaf base. —B, C. Upper laminal cells. —D. Ventral surface of the costa in upper leaf. —E, F. Basal cells. Micrographs: A, B, E: LM; C, D, F: SEM.

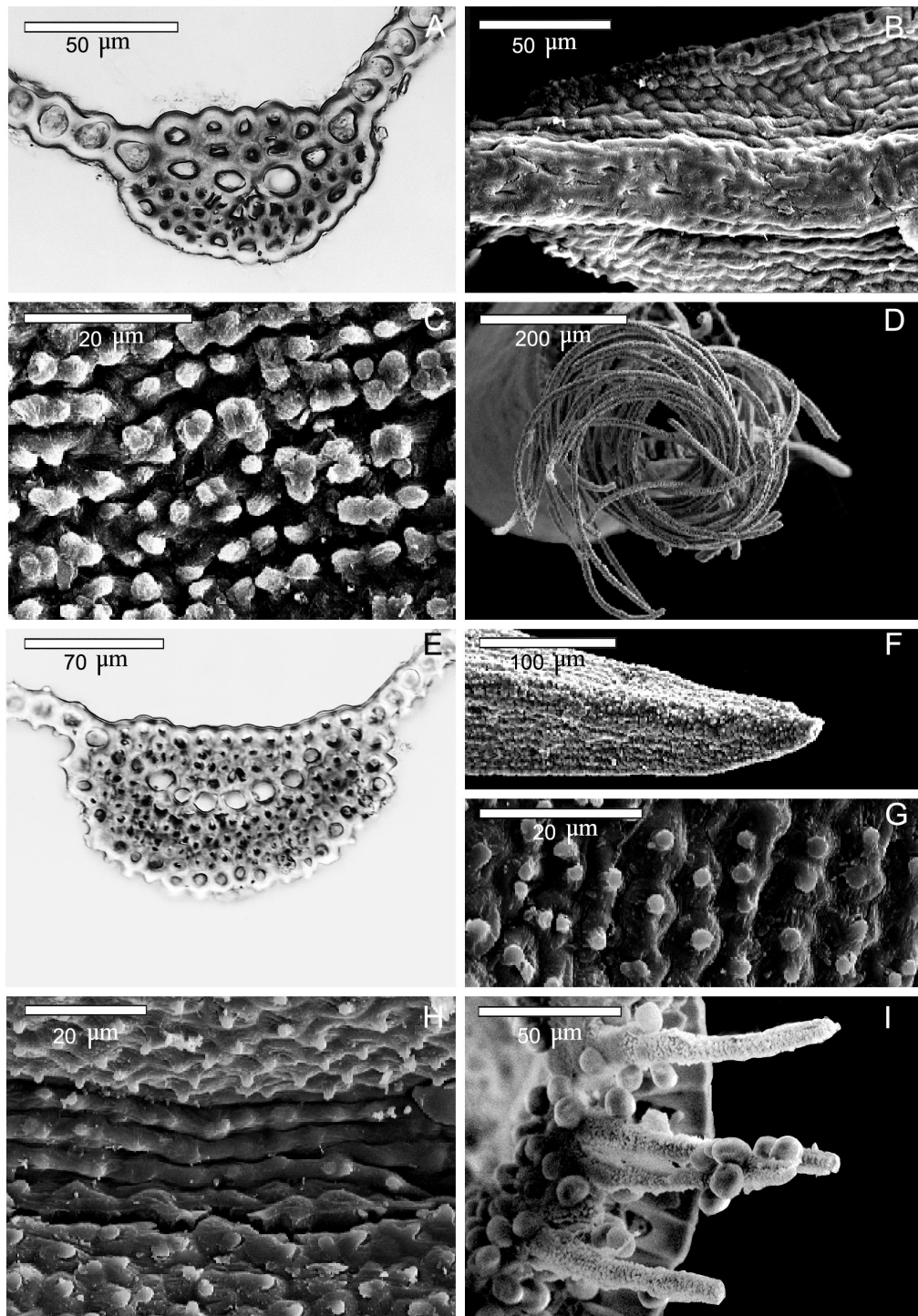


Figure 5. A–D, *Didymodon fallax* (Ros s.n., MUB 13461). —A. Transverse section of the costa at leaf base. —B. Dorsal surface of the costa and laminal cells in upper leaf. —C. Upper laminal cells. —D. Peristome. E–I, *Didymodon spadiceus* (de Miguel s.n., PAMP 2767). —E. Transverse section of the costa at leaf base. —F. Leaf apex. —G. Upper laminal cells. —H. Ventral surface of the costa in upper leaf. —I. Peristome. Micrographs: A, E: LM; B–D, F–I: SEM.

ium at FI that matches the locality indicated in the protologue. We select this material as lectotype.

The protologue of *Barbula kneuckeri* cited two specimens from the same locality: "Nebelhorn, auf Dolomit bei 2000 m am 16 August 1904." One was collected by Kneucker and the other by the authors of the species. Loeske and Osterwald's collections at B were also lost in World War II. A search in the two herbaria where Kneucker's herbarium is kept (KR, H) was unsuccessful. We found a specimen collected by Kneucker at HBG, which totally agrees with the protologue, and we select this latter specimen as lectotype of *Barbula kneuckeri*.

Didymodon asperifolius has an Arctic-Alpine distribution and is uncommon in the area studied, where it is restricted to high mountain ranges (Alps, Pyrenees, Caucasus, Turkistan). *Didymodon asperifolius* shares numerous characters with *D. ferrugineus*, e.g., the shape and disposition of the leaves when moist, apex shape, costa thickness, shape and size of the leaf cells, and color of the lamina with KOH. However, the two species are easily distinguished because *D. ferrugineus* has elongated cells in the upper half of the ventral costa, while in *D. asperifolius* these are quadrate or shortly rectangular. It is important not to confuse this feature with a small band of elongated and translucent cells just below the apex, which most specimens of *D. asperifolius* have. In addition, *D. asperifolius* shows 1 (to 2) simple papillae per cell, while *D. ferrugineus* has 1 to 2 to 4 simple or bifurcated papillae.

No central strand was observed in any of the specimens studied although, according to Zander (1978), they may have such a feature.

Selected specimens examined. KAZAKSTAN. **Alma Ata:** Tianshan Septentrionalis, Montes Transilienses, superior pars vallis Malaja Almaatinka, prope glaciem Tujok-Su, *Lisowski s.n.* (BP 107038). AUSTRIA. **Kärnten:** in Alpe "Fasihaunernik," prope Malta, *Breidler s.n.* (BM). **Steiermark:** Kuppe des Sinabell im Dachsteingebirge bei Schladming, *Baumgartner s.n.* (MO). **Tirol:** Zaythal, Sulden, *Nicholson & Dixon s.n.* (MO). FRANCE. **Savoie:** Col du Petit Mont, Cenis, *Wallace s.n.* (E). ITALY. **Lombardia:** Monte Gavio, *Möller s.n.* (S). **Trentino-Alto Adige:** Tirol, Brenner, *Warnstorf s.n.* (RO). **Valle d'Aosta:** Gressoney-Saint Jean, dalla cima del Grauhaupt, *Carestia s.n.* (RO). RUSSIA. **North Ossetia:** N Ossetian Nature Reserve, upper course of Tsej River, *Abramova s.n.* (SINU). **Dagestan:** Tlyarskij, *Onipchenko s.n.* (SINU). **Karachaevo-Cherkessia:** Malokarachaevsk, Tokhana Gorge, Khudes River upper course, *Onipchenko 30/02* (SINU). SPAIN. **Lérida:** Alta Ribagorça, entre els pics de Coma-lo-Forno i Besiberri Sud, *Ballesteros s.n.* (BCB 28654). SWITZERLAND. **Bern:** Südabhang des Niesen, *Culmann s.n.* (GJO). **Graubünden:** Davos, Rhaetia, *Amann s.n.* (Z). **Valais:** sur La Cabane Britannia, *Amann s.n.* (Z); Südabhang des Saretschpasses, *Culmann s.n.* (Z). CANADA. **Quebec:** Mingan Archipelago Nat.

Park Reserve, Ile Nue de Mingan, *Hedderston 8624* (DUKE).

2. *Didymodon fallax* (Hedw.) R. H. Zander, *Phytologia* 41: 28. 1978. *Barbula fallax* Hedw., *Sp. Musc. Frond.* 120. 1801. *Bryum fallax* (Hedw.) Dicks. ex With., *Syst. Arr. Brit. Pl.* (ed. 4) 3: 816. 1801. *Tortula fallax* (Hedw.) Schrad. ex Turner, *Muscol. Hibern. Spic.* 48. 1804. TYPE: locality not indicated, "Chemnitis lecta" (lectotype, designated by Zander (1978: 28), G!). Figure 5A–D.

Trichostomum rigidulum var. *paludosa* M. T. Lange, *Bot. Tidsskr.* 3: 20. 1869. Syn. nov. TYPE: [Denmark.] "Vejle Fjord," Aug. 1867 (lectotype, designated here, C!).

Barbula adriatica Baumgartner, *Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl.* 92: 325. 1916. TYPE: [Croatia.] "Dalmatien, Insel Lissa, zw. Lissa und Comisa, 50–100 m," 4 Apr. 1910, *J. Baumgartner s.n.* (lectotype, designated here, W!; isotypes, L!, MA!, S!).

Plants 0.3–2.8 cm high, growing in dense or loose turfs, olive-green or brown; *stems* erect, simple or branched, central strand differentiated; *rhizoidal tubers* absent. *Leaves* appressed to erect-patent, incurved when dry, sometimes slightly spirally twisted, erect-patent, spreading or slightly recurved, not undulate when moist, lanceolate to ovate-lanceolate, sometimes keeled, decurrent at base, usually with 2 small plicae at base, 0.6–2.5 × 0.2–0.8 mm; lamina unistratose, reddish orange, rarely yellowish green with KOH stain; apex acute; margins entire, recurved from base to ½ or ¾ of the leaf, sometimes almost plane; *costa* 30–120(–140) µm wide at leaf base, percurrent, ventral cells of the costa in upper leaf elongated, smooth, dorsal cells of the costa in upper leaf shortly quadrate to rectangular, smooth or papillose, in transverse section at leaf base semicircular, with (2 to)3 to 5(to 6) guide cells in 1 layer, (0 to)1 to 2 layers of ventral stereids, (0 to)1 to 3 layers of dorsal stereids, with or without ventral epidermis, smooth, dorsal epidermis differentiated, rarely undifferentiated, smooth or papillose; *upper and middle laminal cells* rounded to hexagonal, oblate or not, not sinuous, (4–)5–15(–18) × (4–)5–13(–17) µm, smooth or with 1 to 3 simple or bifurcate papillae per cell, thick-walled, collenchymatous; *basal cells* rectangular or subquadrate, not sinuous, (7–)10–40(–50) × 5–12.5 µm, smooth, generally thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicous*. *Seta* erect, 0.7–2.3(–2.7) cm long, reddish brown, spirally twisted to left throughout; *capsule* erect or slightly inclined, cylindrical to ellipsoid, 1.1–2.6 × 0.39–0.7 mm, brown; *peristome* of 16 teeth cleft to

near base, filiform, papillose, spirally twisted to the left, 400–1300(–1700) μm long, yellowish brown to reddish brown; *operculum* long conical, 0.9–1.5 mm long; *calyptra* cucullate, 2.4–2.8 mm. *Spores* spherical, 7–12.5 μm diam., weakly papillose, brown-yellowish or yellowish green.

Habitat and distribution. On basic soil (calcareous, clayey, sandy, or nitrified) generally open, more rarely on saline soil, edges of paths, on calcareous and dolomite rocks, fissures or artificial walls; 0–1950 m; Africa, North America (Zander, 2002), South America (Churchill et al., 2000), temperate Asia, Europe.

Discussion. The protologue of *Trichostomum rigidulum* var. *paludosa* includes “Ibaek ved Veile af J. Lange.” In C, we found a sheet from Lange’s herbarium, the label of which matches the locality and collector of the only specimen mentioned in the protologue. We here select this specimen as lectotype. After examining the type material, we conclude that there are no morphological differences between this taxon and *Didymodon fallax*.

The protologue of *Barbula adriatica* includes: “Sant’ Andrea: zwischen Bimbul und Cote 311 m, bei Zankić, 9/VI.1911.” Furthermore, the author mentioned that he had collected this species previously from several places in Istria and Dalmatia. We examined Baumgartner’s herbarium at W, but we did not find any specimen with a label that showed the first locality mentioned in the protologue. However, we found in this herbarium one specimen collected by Baumgartner from Dalmatia in 1910, which is selected as lectotype.

Didymodon fallax is frequently confused with other species in the genus not belonging to section *Fallaces*, especially *D. acutus* (Brid.) K. Saito, because the band of elongated cells on the ventral side of the costa in the upper half of the leaf may be quite small and not clearly distinguishable. It may also be confused with *Ceratodon purpureus* (Hedw.) Brid., which, like the genus *Didymodon*, has axillary hairs with a brown basal cell but which differs from *D. fallax* by the slightly toothed margin near the apex and by the light yellow color of the lamina with KOH. *Didymodon fallax*, on the other hand, has an entire margin, and the reaction with KOH turns the lamina typically a reddish orange or rarely yellowish green.

Selected specimens examined. ALGERIA. **Algiers:** Route de la Mouzaia, *Tixier 6477* (PC). **Blidah:** Blidah, *Graef s.n.* (JE). **Jijel:** Bosque Texenna, *Ros s.n.* (MUB 13147). **Mestghamen:** de Mostaganem a Cap Ivi, *Ros s.n.* (MUB 13146). **Oran:** St. Eugène, *Appert s.n.* (JE). **Relizane:** Oued Rhiou, *Ros s.n.* (MUB 13141). EGYPT. **Fayyum:** Manshy’iet Halpha, *Shabbara 105/86* (CAIA). MO-

ROCCO. **Meknès-Tafilalt:** de Ifrane a Azrou km 9, *Ros s.n.* (MUB 13454). **Oriental:** Nador, *Ros s.n.* (MUB 13461). **Tanger-Tétouan:** El-Fendek, prop de Tetuan, *Brugués s.n.* (BCB 31714). **Taza-Al Hoceima-Taoumate:** Jbel Bouhalla, *Cano et al. s.n.* (MUB 10566). TUNISIA. Kerkouane, *Ros s.n.* (MUB 12512); Djebel Zaghuan, *Poelt 6318* (GZU). GEORGIA. Dzhava, upper course of Liakhvi River, *Dombrowskaya s.n.* (SINU). **South Ossetia Autonomous Oblast:** inter pp. Dzaw et Raro, *Woronow 957* (LE). JORDAN. **Irbid:** Ajlun, Eshtafarineh, *El-Oqlah s.n.* (Hb. Frey 1–4314F, Germany); Jerash, King Talal Dam, *El-Oqlah & Lahham s.n.* (Hb. Frey 1–4312F, Germany). KAZAKHSTAN. **South Kazakh:** Tulubas, the head of Dzhabagly Creek, *Karamysheva s.n.* (LE). LEBANON. Arayeh, Nahr Beirut, *Davis s.n.* (BM, E); above the palace of Beit ed Din, ca. 28 mi. S of Beirut, *Townsend 71/196* (E). TURKEY. **Antalya:** Beymelek Koyer, ca. 20 km WSW of Finike, *Nyholm 690c/72* (S). **Aydin:** 4–5 km from Soke towards Kusadasi, *Wallace s.n.* (NMW). **Balikesir:** Paß über Sindirgi, *Walther 2396a* (HBG). **Bolu:** Abant ca. 30 km SW Bolu, *Nyholm 937/74* (S). **Isparta:** Barla Dagi, W Barlu, *Nyholm 333/72* (S). **Izmir:** ca. 10 km S Selcuk, *Nyholm 79f/72* (S). **Karaman:** Sheyhan, ca. 2 km W Osmaniye near the river Dere, *Bremer & Nyholm 190/78* (S). **Manisa:** 11 km W of Manisa, *Nyholm 1029/71* (S). **Mugla:** Icmeler, near of Marmaris, *Wallace s.n.* (NMW). **Ordu:** Vilayet Ordu, Ünye, *Rubers 4530* (L). UZBEKISTAN: Fergana, *Mafeev s.n.* (LE). ANDORRA. Santa Coloma, Popladó, *Vives s.n.* (BCB 35670). AUSTRIA. **Tirol:** bei Windisch, *Breidler s.n.* (GJO). BELGIUM. Namur, Rochefort, *Vandenbroeck s.n.* (GJO). BOSNIA HERZEGOVINA. Bistrica bei Foca, *Glowacki s.n.* (GJO); Trebevic prope Sarajevo, *Maly s.n.* (HBG). CROATIA. Ragusa, Insel Lapad, *Klofs 4331* (B); Vincural bei Pola, *Glowacki s.n.* (GJO). CYPRUS. Eastern Troodos, N slopes of Mt. Kionia, *Blockeel* (Hb. Blockeel 26/126, United Kingdom). FRANCE. **Alpes Maritimes:** Nice, *Noday s.n.* (S). **Bas-Rhin:** Elsass, Wissemburg, *Winter s.n.* (S). **Côte-d’Or:** Beaune, *Jones s.n.* (E). **Doubs:** Cirque de Consolation N of Morteau, *Touw 13163* (L). **Haute-Corse:** Bastia, Tal des Fango, *Baumgartner s.n.* (W 27254). **Hautes-Pyrénées:** Ruisseau d’Ardalos, *Spruce s.n.* (E). **Herauld:** Castelnau, Jacou, *Barkman 3915* (L). **Landes:** Calcareis, *Berthoumieu s.n.* (S). **Lozère:** Florac, sources du Pecher, *Frahm s.n.* (MUB 1180). **Manche:** Cherbourg, *Corbière s.n.* (S). **Rhône:** Lyon, *Jordan s.n.* (S). **Sarthe:** Carnnes, *Monguillon s.n.* (E). **Vaucluse:** Mont Serein, sous Mont. Ventoux, *Skrzypczak s.n.* (Hb. Skrzypczak 97088, France). GERMANY. **Baden-Württemberg:** Selva Negra, Oberes Enztal, cerca de Gompelscheuer, *Werner s.n.* (MUB 6168). **Bayern:** bei der Tannenber, *Remmler s.n.* (RO). **Brandenburg:** Postdam, *Beinhardt s.n.* (RO). **Hamburg:** Hamburg, *Röll s.n.* (WB). **Hessen:** In month. “Rhön,” *Geheeb s.n.* (RO). **Sachsen:** Dölzig bei Bärwalde, *Ruthe s.n.* (RO). **Thüringen:** Jena, *Röll s.n.* (WB). GREECE. **Crete:** Chania, 8.3 km oberhalb Skinés, *Düll s.n.* (Hb. Düll). **Central Greece and Euboea:** Athens, *Hararas s.n.* (E). **Aegean Islands:** Rhodes, Mount Profitas Elias, *Townsend 71/383* (E). **Ionian Islands:** Corfú, unterhalb Strinilas, *Düll s.n.* (Hb. Düll). **Peloponnese:** Ilia, SE of Vasilakio, Alfios Valley, *Blockeel* (Hb. Blockeel 17/233, United Kingdom). **Thessalia:** Mt. Pelion, *Rechinger 23760* (S). **Thrace:** bei der Lande nördlich von Alexandroupolis, *Rechinger 23744* (S). HUNGARY. **Borsod-Abaúj-Zemplén:** Hegyalja hills, Fináncdomb hill in Tokaj, *Pócs & van Zanten 96107/B* (MO). **Győr-Moson-Sopron:** Sokoró hills, valley Likas Horong, SW from Ravazd, *Pócs &*

van Zanten 9691/DA (MO). **Komárom-Esztergom:** Gerecse Mts., forest W of Tardosbánya, *Pócs & van Zanten 96120/CA* (MO). ITALY. **Puglia:** Puglia, Gargano, *Sabovljevic s.n.* (CAME). **Calabria:** Crotona, Verzino, Grave di Grubbo, *Puntillo s.n.* (CLU B1293). **Campania:** Caserta, *Terracciano s.n.* (RO). **Sardegna:** S. Elia, Cagliari, *Cogoni s.n.* (Hb. Cogoni, Italy). **Emilia-Romagna:** Colli Reggiani ad Dinazzano, *Fiori s.n.* (RO). **Friuli-Venezia Giulia:** Trieste, *Kerner s.n.* (GJO). **Liguria:** San Remo, *Norris s.n.* (JE). **Lombardia:** Como, *Möller s.n.* (S). **Piemonte:** prope Torino, *De Notaris s.n.* (RO). **Sicilia:** Messina, *Zodda s.n.* (S). **Toscana:** Bosco di Larioni, ad orient. Florentiae, *Levier s.n.* (WU). **Trentino-Alto Adige:** Bozen, *Suse s.n.* (S). PORTUGAL. **Algarve:** Fontes Grandes Altas, *Casas et al. s.n.* (LISU 154945). **Beira Litoral:** entre Albergaria dos Doze e Cartania, *Jiménez s.n.* (MUB 12524). **Estremadura:** Serra da Arrábida, Mata do Solitario, *Sérgio s.n.* (COI 485). **Ribatejo:** a 6 km de Permeo para Torres Novas, *Melo s.n.* (LISU). ROMANIA. Moldova, Barnova, *Constantineau s.n.* (WU). RUSSIA. **Adygeya:** Kamennomostskij, Rufabgo Creek valley, *Ignatov s.n.* (SINU). **Karachaev-Cherkessia:** Teberda Nature Reserve, Oriuchat Gorge, *Onipchenko 154/94* (SINU). **Krasnodar Kraj:** Black Sea coast area near Sochi, khosta brach of Caucasian State Reserve, *Ignatov & Ignatova s.n.* (SINU). SERBIA AND MONTENEGRO. **Montenegro:** near Becici SE of Budva, *Touw 7846* (L). **Serbia:** Beska, Srem, *Sabovljevic s.n.* (Hb. Sabovljevic 1014). SLOVAKIA. Velke Zalužie, near Nitra, *Peciar et al. s.n.* (E). SLOVENIA. Wurmberg bei Pettau, *Glowacki s.n.* (GJO, GZU); Fraslan bei Cilli, *Glowacki s.n.* (WU). SPAIN. **Álava:** Amárita, *Heras 995/81* (VIT 1330). **Almería:** Venta de los Yesos, *Guerra s.n.* (MUB 2301). **Asturias:** Caso, Coballes, *Fernández-Ordóñez s.n.* (FCO 291). **Barcelona:** Seva, *Casas s.n.* (BCB 14670). **Cantabria:** Puente Viesgo, *Aedo s.n.* (BCB 30562). **Castellón:** Eslida, *Casañ s.n.* (VAL 3074). **Gerona:** La Molina, *Casas s.n.* (BCB 40007). **Granada:** Sierra Nevada, Barranco de San Juan, *Gil & Martínez s.n.* (GDA 13218). **Huesca:** Valle de Bujaruelo, *Cano et al. s.n.* (MUB 8471). **La Coruña:** Corrubedo, *Reinoso s.n.* (SANT 2757). **Lérida:** Pallars Sobirà, Escart, *Casas s.n.* (BCB 32841). **Málaga:** Marbella by Ronda, *Störmer s.n.* (O). **Murcia:** La Selva, *Ros s.n.* (MUB 368). **Navarra:** Ozcoidi, *Urdino s.n.* (PAMP 2579). **Teruel:** Villarluengo, Muela Mujer, *Puche s.n.* (VAL 2032). **Valencia:** Quesa, carretera a Bicorp, *Puche s.n.* (VAL 5072). **Valladolid:** pr. Portillo, *Cano s.n.* (MUB 15045). **Vizcaya:** Orozco, *Heras 194/86* (VIT 7925). **Zaragoza:** Mequinenza, *Casas s.n.* (BCB 408). SWEDEN. **Skaraborg:** in monte Kinnekulles, Westrogothia, *Zetterstedt s.n.* (RO). **Stockholm:** Stockholm, *Lindberg s.n.* (WU). **Uppsala:** Uppsala, *Zetterstedt s.n.* (GJO). SWITZERLAND. **Bern:** Kandersteg, *Wahnfchaff s.n.* (GJO). UNITED KINGDOM. **England:** Leicester, *Jackson s.n.* (GB).

3. *Didymodon ferrugineus* (Schimp. ex Besch.) M. O. Hill, *J. Bryol.* 11: 599. 1981 [1982]. *Barbula ferruginea* Schimp. ex Besch., *Mém. Soc. Sci. Nat. Cherbourg* 16: 181. 1872. *Triquetrella ferruginea* (Schimp. ex Besch.) Thér., *Smithsonian Misc. Collect.* 85(4): 9. 1931. TYPE: "Mexico," *F. Müller s.n.* (lectotype, designated by Zander (1981: 402), PC!; isotype, BM!). Figure 3A–E.

Barbula rigidicaulis Müll. Hal., *Nuovo Giorn. Bot. Ital.* 4: 255. 1897. TYPE: "China interior, provincia Schensi sept., Pou-o-li," 7 Mar. 1895, *J. Giraldis s.n.* (lectotype, designated here, FI!).

Barbula falcifolia Müll. Hal., *Nuovo Giorn. Bot. Ital.* 4: 257. 1897. TYPE: "China interior, provincia Schensi sept., She-kin-tsuen (Hu-schien)," 28 Dec. 1895, *J. Giraldis s.n.* (lectotype, designated here, H-BR 236005!).

Barbula serpenticaulis Müll. Hal., *Nuovo Giorn. Bot. Ital.* 5: 183. 1898. TYPE: "China interior, provincia Schensi sept., in monte Tui-Kio-san, inter Mnia," 19 Oct. 1896, *J. Giraldis s.n.* (lectotype, designated here, FI!).

Plants (0.5–)0.8–3(–5) cm high, growing in loose turfs, brown-green or reddish brown; *stems* erect or ± decumbent, simple or branched, central strand weakly differentiated; *rhizoidal tubers* absent. *Leaves* appressed or incurved, slightly spirally twisted when dry, mainly the upper leaves, sometimes three-ranked, strongly recurved to squarrose, not undulate when moist, ovate-lanceolate, gradually narrowed to the apex, keeled, long-decurrent at base, (0.5–)0.7–2.0(–2.4) × (0.23–)0.35–0.85 mm; lamina unistratose, dark red with KOH stain; apex acute; margins entire, sometimes papillose-crenulate, recurved in the lower part, plane in the upper part of the leaf; *costa* (25–)30–60(–75) μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf elongated, smooth or papillose, dorsal cells of the costa in upper leaf quadrate, papillose, in transverse section at leaf base semicircular, with 2 to 3 guide cells in 1 layer, without ventral stereids, 0 to 1 layer of dorsal stereids, with or without ventral epidermis, smooth, dorsal epidermis differentiated, papillose or smooth; *upper and middle laminal cells* rounded to irregularly hexagonal, generally oblate, sometimes sinuous, 5–13 × (4–)5–12.5 μm, with (1 to)2 to 4 simple or bifurcate, tall papillae per cell, thick-walled, collenchymatous; *basal cells* shortly rectangular to rectangular, not sinuous, (8–)10–50 × 4–10(–12.5) μm, papillose or smooth, thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicous*. *Sporophyte* not seen.

Habitat and distribution. Calcareous or acidic (granite, schist) rocks with accumulated soil or fissures, artificial walls, soils or taluses generally in shaded places; 20–2000 m; North America (Zander, 2002), Central America (Allen, 2002), temperate and tropical Asia, Europe.

Discussion. *Barbula rigidicaulis* was described by Müller (1896) from material collected by Giraldis: "China interior, prov. Schensi septentr., in loco dicto Pouo-li, Martio 1895." As previously mentioned, Müller's herbarium was lost in World

War II. In Biondi's herbarium at FI, we detected a syntype that matches the locality and date indicated in the protologue. We select this material as lectotype.

In Levier's herbarium at FI we found some of Müller's syntypes of *Barbula falcifolia* collected by Giraldi. We only found three specimens collected by Giraldi, none of which matched the only specimen provided in the protologue. Following Stafleu and Cowan (1981), we checked other herbaria where Müller's material could have been preserved and found a syntype in H-BR from the Bryotheca of Levier, which is in accord with the protologue. This was selected as lectotype.

The protologue of *Barbula serpenticaulis* has the information "China interior, prov. Schen-si sept., in monte Tui-kio-san, Oct. 1896." In Biondi's herbarium at FI we found two syntypes that match the locality and date indicated in the protologue. Both syntypes were collected by Giraldi but on different dates (19 Oct. 1896 and 21 Oct. 1896). We here choose the specimen dated 19 Oct. 1896 because it is better preserved.

Didymodon ferrugineus is characterized by its sometimes 3-ranked leaves that are strongly recurved to squarrose when moist, transverse section of the costa with 2 to 3 guide cells in 1 layer, without ventral stereids, and the strong papillosity of the lamina cells with simple or bifurcate papillae. *Didymodon ferrugineus* may be confused with *D. fallax*, but this latter species is differentiated by having erect-patent to spreading leaves that are rarely slightly recurved, but never squarrose. Furthermore, *D. fallax* generally has 1 to 2 layers of ventral stereids and (2 to)3 to 5(to 6) guide cells in 1 layer, while *D. ferrugineus* lacks ventral stereids and has 2 to 3 guide cells in 1 layer.

None of the specimens studied was fruiting, although according to Zander (1998), in reference to American specimens, the sporophyte is rare and similar to, but often smaller than, that of *D. fallax*.

Selected specimens examined. PAPUA NEW GUINEA. **Morove:** Mt. Sarawaket southern range 4 km SE of Lake Gwam, headwaters of Busu R., *Koponen* 32170 (E). TURKEY. **Trabzon:** Pontic Mts., Black Sea coast, at Sumela monastery by Trabzon, *Papp* s.n. (BP 168092). AUSTRIA. **Salzburg:** Plainerau bei Salzburg, *Zwanziger* s.n. (WU). **Steiermark:** prope Hieflau, *Breidler* s.n. (WU). **Tirol:** Kufstein, *Wahnfchaff* s.n. (HBG). **Vorarlberg:** Kammellbach bei Bregenz, *Blumrich* s.n. (WU). BELGIUM. Vieilles ruines, Liresse, *Belogne* s.n. (HBG). CROATIA. Velebit-Gaviah, Tuljana, Juana bei Medak, *Degen* s.n. (W 22746). CZECH REPUBLIC. Koda, ca. 5 km SE of Beroun, *Townsend* s.n. (E); Tetin, *Bauer* s.n. (GJO). FRANCE. **Alpes-Maritimes:** Tenda, bei Nizza, *Haut* s.n. (S). **Doubs:** Source de la Loue near Ouhans, *Touw* 13234 (L). **Haute-Garonne:** Pyrénées Centrales, vallée

d'Hospice, *Zetterstedt* s.n. (S). **Haute-Savoie:** Saint-Jean-d'Aulps, *Bizot* s.n. (S). **Hautes-Pyrénées:** Pyrénées, Béart, *Spruce* s.n. (S). **Isère:** Villard-de-Lans, *Ravaud* s.n. (LISU 4331). **Savoie:** Mont-Denis, Cret Verdun, *Een* F442 (S). GERMANY. **Baden-Württemberg:** Lichtenstein, *Ros & Werner* s.n. (MUB 17221). **Bayern:** Fränkische Schweiz, Pottenstein, bei der Schüttersmühle, *Elmendorff* s.n. (GJO). GEORGIA. Imeretia, Utseri, in ripa fl. Rion, *Brotherus & Brotherus* s.n. (LE). ITALY. **Friuli-Venezia Giulia:** Peitlstein prope Ampezzo, *Molendo* s.n. (HBG, L, S). **Toscana:** Appenino pistoiese, *Cortini-Pedrotti* s.n. (CAME). **Trentino-Alto Adige:** Brenner-Pass, *Een* s.n. (S). **Veneto:** Vittoria am Monte Canzeglio, *Fleischer* s.n. (BM, WU). RUSSIA. **North Ossetia:** Ossetia, Balta ad fl. Terek, *Brotherus & Brotherus* s.n. (LE). SLOVENIA. Flitsch, *Breidler* s.n. (WU); Fraslan bei Cilli, *Glowacki* s.n. (WU). SPAIN. **Álava:** Zeanuri, Almadin, *Infante* s.n. (VIT). **Barcelona:** Sierra de Montserrat, *Casas* s.n. (BCB 434). **Cantabria:** Picos de Europa, Mts. Refugio Aliva, *Henderson* 2017a (E). **Gerona:** entre Beget y Rocabruna, *Casas* s.n. (BCB 19941). **Guipúzcoa:** Berástegui, Valle de Leizarán, *Heras* 685/92 (VIT 15337). **Huesca:** Escalona, Añisclo, ermita de San Úrbez, *Cano et al.* s.n. (MUB 8491). **León:** Cabrillanes, próximo Caballo, *Muñoz* s.n. (MA 19277). **Lérida:** Lladorre, *Casas* s.n. (PAMP 568). **Lugo:** Ribadeo, Miguxín, *Muñoz* s.n. (MA 17515). **Navarra:** Elzaburu, *Lurso* s.n. (PAMP 5481). **Teruel:** Alcalá de la Selva, *Casas* s.n. (BCB 432). SWITZERLAND. **Bern:** Interlaken nach Därlingen, *Culmann* s.n. (GJO, WU). **Tessin:** Lugano, *Salvatore* s.n. (WU). **Zürich:** Zürich, *Forsder* s.n. (HBG). UNITED KINGDOM. **England:** Cornwall, Penzance, *Curnow* s.n. (GJO). **Northern Ireland:** Marble Arch., *Sérgio & Geisler* s.n. (LISU).

4. *Didymodon giganteus* (Funck) Jur., Laubm.-Fl. Oesterr.-Ung.: 102. 1882. *Barbula gigantea* Funck, Flora 15: 483. 1832. *Grimmia gigantea* (Funck) Schimp., Syn. Musc. Eur.: 695. 1860. *Tortula gigantea* (Funck) Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 21: 250. 1864. *Geheebia gigantea* (Funck) Boulay, Musc. France: 395. 1884. TYPE: [Austria.] "Kärnten, Gössnitzerfall bei Heiligenblut," *J. F. Laurer* s.n. (lectotype, designated here, HBG!). Figure 4A–F.

Didymodon levieri Broth., Nuovo Giorn. Bot. Ital. 13: 256. 1906. TYPE: "China interior, provincia Schen-si septentr. in monte Ki-tou-san," Sep. 1899, *J. Giraldi* s.n. (lectotype, designated here, H-BR 1291005!).

Didymodon subrufus Broth., Symb. Sin. 4: 38. 1929. TYPE: [China.] "Provincia Setschwan austro-occid. in montis Liuku-liangdse, 27°48', inter oppidum Yenyüen et castellum Kwapi, 3700–4200 m," 18 May 1914, *H. F. v. Handel-Mazzetti* 2353 (holotype, H-BR 1291039!).

Plants (3–)7–23 cm high, growing in ± dense turfs, reddish brown or brown-green; *stems* erect or decumbent, irregularly branched, central strand weakly differentiated; *rhizoidal tubers* absent. *Leaves* appressed in the lower part of stem, spirally twisted in the upper part when dry, erect-patent to

spreading, undulate when moist, ovate-lanceolate, gradually narrowed to the apex, sometimes with small plicae at the base, keeled, long-decurrent at base, (2–)2.5–4–5 × 0.7–1.1 mm; lamina unistratose, red with KOH stain; apex acute; margins entire, recurved in lower part, plane in upper part of the leaf; *costa* 42–85 μm wide at leaf base, ending below the apex or percurrent, ventral cells of the *costa* in upper leaf elongated, smooth or papillose, dorsal cells of the *costa* in upper leaf rectangular, papillose, in transverse section at leaf base elliptic to semicircular, with 4 to 6 guide cells in 1 layer, 1 to 2 layers of ventral stereids, sometimes 1 layer of substereids, 1 to 2 layers of dorsal stereids, without ventral epidermis, without dorsal epidermis or weakly differentiated, smooth; *upper and middle laminal cells* oblate, sometimes rounded or rhomboidal, very irregular, strongly sinuous, (3–)4–17.5(–20) × 7.5–20 μm, with 1 to 3 simple or, more rarely, bifurcate, papillae per cell, sometimes apparently absent, thick-walled, strongly collenchymatous; *basal cells* rectangular, becoming shorter toward margins, sinuous, (15–)17.5–55 × 2–8 μm, smooth or papillose, thick-walled, pitted. *Gemmae* in the leaf axils absent. *Dioicous*. *Sporophyte* unknown.

Habitat and distribution. Wet calcareous rocks in waterfalls; 500–2300 m; North America (Zander, 2002), temperate and tropical Asia (Li et al., 2001), Europe.

Discussion. Funck (1832) described *Barbula gigantea* on the basis of two specimens collected by him and Laurer from two different localities “. . . nach Golling. . . ; . . . beim Gösnitzer Wasserfall. . .” We have examined Funck’s herbarium deposited at M but no specimen could be considered to represent a syntype. A search in other herbaria where Funck specimens are kept (BM, BUC, GOET, HAL, JE, TUB) was unsuccessful. Accidentally, we found a specimen collected by Laurer deposited in HBG, whose label shows the second locality mentioned in the protologue. Therefore, we select this material as lectotype.

The protologue of *Didymodon levieri* includes “In monte Ki-tou-san, parcissime; sett. 99.” In Brotherus’s herbarium at H we detected a syntype collected by Giraldi that matches the locality and date indicated in the protologue. We therefore choose this specimen as lectotype.

Since its description by Funck (1832), *Didymodon giganteus* has been included in several genera (*Tortula*, *Grimmia*, *Barbula*), and a monospecific genus (*Geheebia* Schimp.) has even been described for this taxon. Some authors (Corley et al., 1981;

Düll, 1992; Frey et al., 1995; Cortini-Pedrotti, 2001) include this species in the genus *Geheebia*, but others (Saito, 1975; Zander, 1978; Kučera, 2000) consider it within the genus *Didymodon*. A careful study suggests that it does belong to *Didymodon* since it possesses all the morphological characteristics that define this genus. More specifically, *D. giganteus* belongs to section *Fallaces* since it presents the following fundamental characteristics: keeled leaves, decurrent margins, lamina unistratose, elongated cells on the ventral side of the *costa*, and red-staining lamina with KOH. Molecular data obtained from cp *rps4* sequence (Werner et al., 2004a) confirm the close relation between this species and others of the genus *Didymodon* suggested by our morphological study. It should not be considered as a separate genus.

This species is recognizable by its relatively enormous size, as it can reach as much as 23 cm in length, and by its ovate-lanceolate, keeled leaves that have undulate margins in the upper half of the leaf, very sinuous laminal cells, and porous basal cells.

A species with which *Didymodon giganteus* may be confused is *D. maximus*, since both share the same leaf shape, papillosity of the lamina, *costa* thickness, and the red color of the lamina with KOH. However, the wet leaves of *D. giganteus* are erect-patent to spreading, undulate, and (2–)2.5–4.5 mm long. The wet leaves of *D. maximus*, on the other hand, are strongly recurved or squarrose, not undulate, and are smaller in size, (1.2–)1.6–2.8 mm long.

Another close taxon is *Didymodon erosodenticulatus* (Müll. Hal.) K. Saito, a species known only from eastern Asia (China, Japan, Himalayas), where it shares a similar habitat as *D. giganteus*. However, *D. erosodenticulatus* can be differentiated from *D. giganteus* by its toothed, non-undulate upper leaf margin.

Selected specimens examined. AUSTRIA. **Kärnten:** Gössnitzfall näch Heiligenblut, *Handel-Mazzetti s.n.* (GJO, WU). **Niederösterreich:** Silberquelle am Schneeberg, *Handel-Mazzetti s.n.* (WU). **Oberösterreich:** Dachsteingebiet, oberhalb Hallstatt, *Fleischer s.n.* (BM, WU). **Salzburg:** Radstadt Tauern, *Breidler s.n.* (WU). **Steiermark:** inter cataractam “Todtes Weib” at vicum Frein, *Kerner s.n.* (WU). **Tirol:** Prosegg-Klamm, bei Windisch-Matrei, *Baumgartner s.n.* (HBG, WU). FRANCE. **Haute-Garonne:** Val d’Esquierry, *Juin s.n.* (BM, S). **Haute-Savoie:** Samoëns, *Sarrasat s.n.* (GB). **Hautes-Pyrénées:** Cascade du Gros, *Spruce s.n.* (S). GERMANY. **Bayern:** Allgäu, an der strasse von Hindelang nach Hinterstein, *Holler s.n.* (WU). ITALY. **Lombardia:** Como, stravalle bei Torno, *Arteria s.n.* (BM, GZU, M, WU). **Piemonte:** Novara, Bosco di Roncio bei Campello Monti, *Bauer s.n.* (GZU, WU). **Veneto:** “Serai,” prope Sottoguda ditionis venetae, *Mo-*

lendo s.n. (M, W 359094). SLOVENIA. Kranjska gora Krain, *sine collector* (GJO). SLOVAKIA. Bielské Tatry, in monte Zdiarská Vidla, *Smarđa* s.n. (L); Magas Tatra, montis "Stierberg," *Györffy* s.n. (GJO, HBG, WU). SWITZERLAND. **Bern:** Faulhorn, *Grebe* s.n. (GJO). **Glarus:** Glarus, *Culmann* s.n. (WU). **Graubünden:** Vall Roseg, bei Pontresina, *Graef* s.n. (HBG). **Uri:** Klausenpass, *Sérgio* s.n. (LISU). **Valais:** Cascade de Pissevache, *Favrat* s.n. (WU).

5. *Didymodon maschalogenä* (Renaud & Cardot) Broth., Nat. Pflanzenfam. I(3): 1192. 1909. *Barbula maschalogenä* Renaud & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 53. 1905. TYPE: [India.] "Sikkim, Darjeeling," 1901, *G. A. Miller* s.n. (lectotype, designated by Frahm et al. (1996: 137), PC!). Figure 1D–H.

Barbula catenulata Dixon, Anniv. Vol. Bot. Gard. Calcutta: 181. 1942. TYPE: [India.] "Kashmir, Dalhousie," Oct. 1917, *Kinnear 510b* (holotype, BM!).

Didymodon michiganensis (Steere) K. Saito, J. Hattori Bot. Lab. 39: 517. 1975. *Barbula michiganensis* Steere, Moss Fl. N. Amer. 1: 180. 1938. TYPE: [U.S.A.] "Lake Superior at Pictured Rocks, Alger Co., Michigan," 20 Aug. 1935, *G. E. Nichols & W. C. Steere* s.n. (holotype, MICH not seen; isotype, DUKE!).

Plants to 1 cm high, growing in loose turfs, yellow-green; *stems* erect, simple, central strand differentiated; *rhizoidal tubers* absent. *Leaves* catenulate, incurved when dry, erect-patent to spreading, not undulate when moist, ovate to ovate-lanceolate, abruptly narrowed to the apex, keeled in the upper part, decurrent at base, $0.94\text{--}1.27 \times 0.47\text{--}0.65$ mm; lamina unistratose, red or yellowish with KOH stain; apex acuminate; margins entire, recurved from base to 2/3 of the leaf; *costa* $47.5\text{--}75$ μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf elongated, smooth or papillose, dorsal cells of the costa in upper leaf shortly rectangular to quadrate, smooth or papillose, in transverse section at leaf base semi-circular, with 2 to 4 (to 5) guide cells in 1 layer, 0 to 1 layer of ventral stereids, 1 to 2 layers of dorsal stereids, ventral epidermis differentiated, smooth or papillose, dorsal epidermis differentiated, smooth or papillose; *upper and middle laminal cells* rounded, ovoid or oblong, not sinuous, $(3\text{--})4\text{--}10\text{--}(12.5) \times 5\text{--}8\text{--}(10)$ μm , arranged in longitudinal rows, with one low, simple papilla or, more rarely, smooth, thick-walled, collenchymatous; *basal cells* rectangular or shortly rectangular, not sinuous, $(15\text{--})17.5\text{--}37.5\text{--}(50) \times (5\text{--})7.5\text{--}12.5\text{--}(15)$ μm , forming a \pm differentiated area, smooth, thick-walled, not pitted. *Gemmae* multicellular, 2- to 8-celled, borne in the axils of the leaves, abundant, generally spherical, sometimes elliptical, $20\text{--}35\text{--}(45)$ μm

diam., brown, smooth. *Sexual condition* unknown. *Sporophyte* unknown.

Habitat and distribution. On soil; Africa (O'Shea, 2003), North America, temperate and tropical Asia.

Discussion. This species is known from different areas of the world, although it has been reported from a very few scattered localities (Jiménez et al., 2004). It is difficult to confuse with other species of section *Fallaces* since it is the only taxon that has spherical or elliptical axillary gemmae. Another important characteristic of the species is the catenulate position of the leaves when dry, although its most obvious feature is the disposition of the upper and median cells along the lamina in longitudinal rows.

Representative specimen examined. IRAN. Mounts Elburz, *sine collector* (IRAN 4308).

6. *Didymodon maximus* (Syed & Crundw.) M. O. Hill, J. Bryol. 11: 599. 1981 [1982]. *Barbula maxima* Syed & Crundw., J. Bryol. 7: 527. 1973 [1974]. *Barbula reflexa* var. *robusta* Braithw., Brit. Moss Fl. 1: 266. 1887. TYPE: [Ireland.] "Dripping rocks, Ben Bulbin, Sligo," 1871, *D. Moore* s.n. (lectotype, designated here, BM!). Figure 3F–H.

Plants (2–)3–10 cm high, growing in loose turfs, brown-green or reddish brown; *stems* erect, branched, without central strand or weakly differentiated; *rhizoidal tubers* absent. *Leaves* appressed to slightly spirally twisted when dry, strongly recurved to squarrose, not undulate when moist, ovate-lanceolate, gradually narrowed to the apex, keeled, long-decurrent at base, $(1.5\text{--})2\text{--}2.8 \times 0.5\text{--}1.1$ mm; lamina unistratose, dark red with KOH stain; apex acute, rarely obtuse; margins entire or papillose-crenulate, almost plane to recurved in the lower middle part, more rarely in the proximal 3/4 of the leaf; *costa* $40\text{--}90\text{--}(125)$ μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf elongated, smooth or papillose, dorsal cells of the costa in upper leaf rectangular or quadrate, smooth or papillose, in transverse section at leaf base elliptic, with (3 to)4 to 8 (to 9) guide cells in 1 layer, very rarely in 2 layers, 1 to 3 layers of ventral stereids, 1 to 3 (to 4) layers of dorsal stereids, without ventral epidermis or weakly differentiated, smooth or papillose, dorsal epidermis generally differentiated, smooth or papillose; *upper and middle laminal cells* rounded, ovoid or shortly rectangular, oblate or not, sinuous, $(3\text{--})5\text{--}17.5 \times 5\text{--}15$ μm , almost smooth or with 1

to 3 simple or bifurcate, tall papillae per cell, thick-walled, collenchymatous; basal cells rectangular, sometimes sinuous, $12.5\text{--}50 \times 3\text{--}10 \mu\text{m}$, papillose or smooth, thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicous*. *Seta* erect, 1.2 cm long, orange-reddish, spirally twisted to left throughout; *sporophyte* otherwise unknown.

Habitat and distribution. Wet ledges or damp soil at the foot of limestone rocks; North America (Zander, 2002), Europe.

Discussion. Syed and Crundwell (1973) established *Barbula maxima* as a new name on the basis of the type specimen of *Barbula reflexa* var. *robusta*. The protologue of this latter taxon includes: "Limestone rocks at Ben Bulbin, Sligo (Moore)." We have studied the collections of *Barbula reflexa* var. *robusta* in Braithwaite's herbarium in BM, and we found a syntype collected by Moore dated in 1871, which is in complete accordance with the protologue. We therefore select this material as lectotype.

Didymodon maximus is a rare taxon known only from two sites in the northwest of Ireland, one in Alaska, and another in Canada (Northwest Territories) (Zander, 2002). This species demonstrates a distinctive disjunct pattern between western North America and the west of Europe.

Didymodon maximus is close to *D. ferrugineus*, from which it differs almost exclusively in the length of its leaves: (0.5–)0.7–2 mm long in *D. ferrugineus* and (1.5–)2–2.8 mm long in *D. maximus*, and in costa structure: (3 to)4 to 8(to 9) guide cells in 1 layer or more rarely in 2, 1 to 3 layers of ventral stereids, 1 to 3(to 4) layers of dorsal stereids in *D. maximus* compared with the 2 to 3 guide cells arranged in 1 layer, without ventral stereids and 0 to 1 layer of dorsal stereids in *D. ferrugineus*. Furthermore, the plants of *D. maximus*, (0.5–)0.8–4(–5) cm in height, are usually much bigger than plants of *D. ferrugineus*. Syed and Crundwell (1973) stated that *D. maximus* has a clearly developed central strand as opposed to the only slightly differentiated central strand of *D. ferrugineus*, a characteristic they used to differentiate between both taxa. However, all the specimens of *D. maximus* studied by us showed no or, at most, a very slightly differentiated central strand, so that the species could not be separated by reference to this feature.

It was not possible to describe the capsule since the only fertile specimen known (*Long 14626*) has immature or undeveloped capsules.

Didymodon maximus was recently cited from the French Pyrenees (Thouvenot, 2002), but this was

based on an erroneous interpretation of the original citation.

Selected specimens examined. IRELAND. **Leitrim:** Glenade, *Duncan s.n.* (E). **Sligo:** Gleniff above Clogh, below cliffs, *Long 14626* (E).

7. *Didymodon spadiceus* (Mitt.) Limpr., Laubm. Deutschl. 1: 556. 1888. *Tortula spadicea* Mitt., J. Bot. 5: 326. 1867. *Trichostomum spadiceum* (Mitt.) J. E. Zetterst., Kongl. Svenska Vetenskapsakad. Handl. 13(14): 14. 1876. *Barbula spadicea* (Mitt.) Braithw., Brit. Moss Fl. 1: 267. 1887. *Didymodon rigidulus* subsp. *spadiceus* (Mitt.) Adlerz, Bladmossfl. Sver. Lågland 171. 1907. *Barbula rigidula* subsp. *spadicea* (Mitt.) J. J. Amann, Fl. Mouss. Suisse 2: 103. 1918. *Barbula fallax* subsp. *spadicea* (Mitt.) Hillier, Ann. Sci. Univ. Besançon, Sér. 2, Bot.: 48. 1954. TYPE: [United Kingdom.] "Yorkshire, near Bolton Abbey," Oct. 1837, *Wilson s.n.* (lectotype, designated here, NY!). Figure 5E–I.

Barbula insidiosa Jur. & Milde, Hedwigia 8: 97. 1869. TYPE: [Austria.] "Hagenbach bei St. Andrä in Niederösterreich," 25 Apr. 1869, *J. Juratzka s.n.*, Bryoth. Eur. n° 1067 (lectotype, designated here, RO!; isotypes, C!, MO!, WU!).

Didymodon barbulooides Lib. ex Marchal., Bull. Soc. Roy. Bot. Belgique 11: 8. 1872. Syn. nov. TYPE: Locality not indicated, [sine collector] (lectotype, designated here, BR74416!).

Didymodon zetterstedtii Schimp., Syn. Musc. Eur. (ed. 2): 167. 1876. TYPE: [Sweden.] "Kinnekulle," 18 Aug. 1853, *J. E. Zetterstedt 17* (holotype, BM!).

Limneria viridula Stirt., Trans. & Proc. Bot. Soc. Edinburgh 26: 428. 1915. TYPE: [United Kingdom.] "Scotland, near Plockton," Aug. 1914, [sine collector] (lectotype, designated here, Hb. Stirton in BM!).

Plants (0.4–)0.7–4 cm high, growing in \pm dense turfs, brown-green; *stems* erect, simple or branched, central strand differentiated; *rhizoidal tubers* absent. *Leaves* twisted, slightly appressed to incurved when dry, erect-patent to spreading, not undulate when moist, sometimes slightly flexuous, long ovate-lanceolate, gradually narrowed to the apex, not keeled, slightly decurrent at base, (1–)1.5–4(–4.5) \times (0.3–)0.45–1(1.2) mm; lamina unistratose, red-orange with KOH stain; apex obtuse, sometimes acute; margins entire or papillose-crenulate, recurved in the lower middle of the leaf, very rarely to 2/3 of the leaf; *costa* 60–180(–220) μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf elongated, smooth, dorsal cells of the costa in upper leaf shortly quadrate, papillose, in transverse section at leaf base semicircular, with (4 to)5 to 9(to 10) guide

cells in 1 layer, very rarely in two layers, (1 to)2 to 3(to 4) layers of ventral stereids, 2 to 3(to 4) layers of dorsal stereids, without ventral epidermis or weakly differentiated, papillose or smooth, dorsal epidermis differentiated, papillose; *upper and middle laminal cells* ovoid, irregularly rounded or subquadrate, sometimes very slightly sinuous in the middle of the leaf, (4–)5–15 × (4–)5–12.5(–15) μm, with 1 to 3 simple or bifurcate papillae per cell, thick-walled, collenchymatous; *basal cells* rectangular, sometimes slightly sinuous, 10–50 (–65) × 5–12.5 μm, smooth or papillose, generally thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicous*. *Seta* erect, 0.7–2.5 cm long, reddish brown, spirally twisted to left throughout; *capsule* erect or slightly inclined, cylindrical to oblong, 1.3–4.3 × 0.3–0.7 mm, brown; *peristome* of 16 teeth cleft to near base, filiform, smooth or papillose, straight, (100)135–450(650) μm long, brown-reddish; *operculum* long-rostrate, 0.8–1.6 mm long; *calyptra* cucullate, 1.5–3.1 mm. *Spores* spherical, 8–15 μm diam., weakly papillose, brown-green.

Habitat and distribution. On calcareous rocks, more rarely on acidic rocks, on wet taluses at edges of streams and rivers, also on artificial walls; 150–1680 m; temperate Asia, Europe.

Discussion. Mitten (1867) cited several specimens in the protologue of *Tortula spadicea*: “Scotland, Drummond, Yorkshire, near Bolton Abbey, Mr. Wilson. Ireland, Miss Hutchins.” In Mitten’s herbarium at NY we found two syntypes. On the label of one of the specimens was written “Ireland” and in the other “Yorkshire, near Bolton Abbey.” We select this latter specimen as lectotype since it is better preserved.

In the protologue of *Barbula insidiosa*, Juratzka (1869) cited material from different localities: “Grunauer bei Hirschberg in Schlesien (Ilgner); Wien (Juratzka); Meran (Milde); Westphalen: Sauerland (H. Müller).” The same author also mentioned that some material of this taxon was going to be issued in *Rabenhorst Bryotheca Europaea* (Nr. 1067). We did not find any syntype in W, where the Juratzka specimens are deposited. However, we have located several specimens of Rabenhorst’s *exsiccatae* in different herbaria (C, MO, RO, WU). We select the specimen deposited in WU because it is better conserved than the other specimens.

Didymodon barbuloides was described by Marchal (1872) on the basis of several specimens collected by Libert. The protologue of this taxon does not include any reference to the locality or localities of the collection: “In rupibus arenariis umbrosis. Autumno.” We found a syntype at BR,

where the original herbaria of Libert and Marchal are kept. This specimen is in accordance with the protologue so we select it as lectotype. After examining this material, we conclude that there are no significant morphological differences between this taxon and *D. spadiceus*.

The protologue of *Limneria viridula* includes “It grows in several places on the west coast of Scotland, but most luxuriantly near the base of the famous Duncraig.” We have checked Stirton’s herbarium in GLAM, but found no material suitable for a lectotype. According to Staffleu and Cowan (1986), some of Stirton’s material can be found in BM. We located two possible specimens from the Stirton herbarium in BM whose label shows the same locality (Scotland, near Plockton). One of these specimens corresponds to *Didymodon insulanus* (De Not.) M. O. Hill, so we choose as lectotype the other material, which is in accordance with the protologue.

Didymodon spadiceus is characterized by its erect-patent to spreading leaves when moist, their long ovate-lanceolate shape and generally obtuse apex, margins recurved in the lower half of the leaf, occasionally to 2/3 of the leaf, and the transverse section of costa showing generally 1 layer of (4 to)5 to 9(to 10) guide cells. In addition, the sporophyte has short peristome teeth (100–)135–450(–650) μm that are long and straight.

Occasionally especially large specimens of *D. fallax* may be found in mountainous regions, with long, ovate-lanceolate leaves, stout costa more than 100 μm wide at base, and strongly papillose laminal cells with bifurcated papillae and slightly sinuous lumens [*Casas et al. s.n.* (BCB 32841)], which are difficult to distinguish from *D. spadiceus*. The sporophytes of these two species, however, are clearly different.

Selected specimens examined. IRAN. **Mazandaran:** in valle fluvii Talar inter Abbasabad et Cahi, *Rechinger* 2268 (W); above Shahi, Caspian coast, *Agnew s.n.* (NMW). AN-DORRA. La Massana Parish, Arinsal, *Townsend* 98/118 (E). AUSTRIA. **Kärnten:** Feistritz-Thale, *Robic s.n.* (WU). **Niederösterreich:** Helenenthal bei Baden, *Handel-Mazzetti s.n.* (WU). **Steiermark:** Salzaufener beim Holzrechen, *Baumgartner s.n.* (WU). **Tirol:** Nord-Tirol, Sellrain, *Handel-Mazzetti s.n.* (WU). **Vorarlberg:** Feldkirch, *Handel-Mazzetti s.n.* (WU). BOSNIA HERZEGOVINA. Bistrica bei Foca, *Glowacki s.n.* (GJO); Lapesnica bei Sarajevo, *Glowacki s.n.* (GJO). BULGARIA. **Plovdiv:** Mt. Rhodope centralis, Er-Kjupria, *Petrov s.n.* (SOM). CROATIA. Istrien, Draga-Tal bei Vermo, *Glowacki s.n.* (GJO); Velebit-Gaviah, Tuljana bei Medak, *Baumgartner s.n.* (W 23154). CZECH REPUBLIC. Moldau bei Stechowitz, *Bauer s.n.* (HBG). FRANCE. **Doubs:** Cirque de Consolation N of Morteau, *Touv* 13166 (L). **Haute-Savoie:** Fessey, *Puget s.n.* (S). **Hautes-Pyrénées:** Labassère, V. de Béart, G. de Valentin, *Spruce s.n.* (S). **Isère:** Le Bourg

d'Arud, cascade du ruisseau de la Pisse au Sud du village, *De Sloover s.n.* (MO). **Jura:** Source de l'Ain, *Cuynet s.n.* (BCB 1749). **Meuse:** Vallée de Froide, Fontaine, *Cardot s.n.* (MO). **Pyrénées Orientales:** Amélie-les-Bains, *Buterte s.n.* (S). **Pyrénées-Atlantiques:** Beost, *Spruce s.n.* (S). **Sarthe:** Le Mans francs à l'Epau, *Monguillon s.n.* (WU). **Tarn-et-Garonne:** Pyrénées Centrales, Cascade de Montauban, *Zetterstedt s.n.* (S). **GEORGIA.** **Abkhazia:** Tsebelda, *Kopakovskij s.n.* (LE); Angrestiae Pelznir, *Woronow s.n.* (LE). **GERMANY.** **Bayern:** prope Wildflecken, *Geheeb s.n.* (RO). **Brandenburg:** Potsdam, *Giordano s.n.* (RO). **Hesse:** prope Rengersfeld (mont. Rhon), *Geheeb s.n.* (RO). **Nordrhein-Westfalen:** bei Alme, *Grebe s.n.* (WU). **Sachsen:** Kirnitzschtal, *Riehmer s.n.* (GJO). **Sachsen-Anhalt:** Harz, Treseburg, *Loeske s.n.* (WU). **Thüringen:** Walpernhain prope Orterfeld, *Schliephacke s.n.* (RO). **GREECE.** **Macedonia:** Pieria, Olympo, Umgebung der Primias-Wasserfälle, straßenende Lithodorion, *Düll s.n.* (Hb. Düll); 2 km SW Veria, *Wolff & Loosjes 4* (L). **HUNGARY.** **Borsod-Abaúj-Zemplén:** Borsod, prope Hamor, *Boros s.n.* (MO). **Budapest:** Budapest, *Pest, Boros s.n.* (MO). **ITALY.** **Friuli-Venezia Giulia:** strasse von Maggio gegen Venzzone, *Breidler s.n.* (GJO). **Lazio:** Roma, Circo Romano, *Poli s.n.* (RO). **Lombardia:** Bellagio, *Giovani s.n.* (S). **Trentino-Alto Adige:** Monte Bondone, *Cortini-Pedrotti s.n.* (CAME). **Umbria:** Interamna (RO). **ROMANIA.** **Harghita:** Transilvania, Ciuc, prope balneas Borsec, *Demeter s.n.* (MO). **RUSSIA.** **Adygeya:** Caucasian Reserve, Maikop, in Zhelobnaya River, *Vasilieva s.n.* (LE). **SERBIA AND MONTENEGRO.** **Montenegro:** Kom, *Glowacki s.n.* (GJO); Monastir Morački, *Glowacki s.n.* (GJO). **SLOVENIA.** Gebiet von Görz bei Flitsch, *Breidler s.n.* (GJO). **SPAIN.** **Álava:** Aspárrena, Andoin, La Tobería, *Heras 782/82* (VIT 2198). **Asturias:** Somiedo, carretera al Puerto, pr. Gúa, *Muñoz s.n.* (MA 16434). **Baleares:** Mallorca, cruce de carretera Sacalobra y carretera a Pollensa, *Cano et al. s.n.* (MUB 11938). **Canabria:** Camaleño, próximo las Ilces, *Muñoz s.n.* (MA 19194). **Cuenca:** Hoz de Beteta, Río Guadiela, *Fuertes-Lasala & Silva s.n.* (MA 306). **Gerona:** El Coll, *Vives s.n.* (BCB 35617). **Guipúzcoa:** Aya, Barranco de Azolaras, *Heras 1450/95* (VIT 19655). **Huesca:** Valle de Pineta, Bielsa, *Casas s.n.* (BCB 49867). **León:** Villablino, *Allorge & Allorge s.n.* (B). **Navarra:** Arbayún, *de Miguel s.n.* (PAMP 2767). **Vizcaya:** Orozco, Urigoiti, torrentera de Aldabide, *Heras 421/90* (VIT 13663). **SWEDEN.** **Östergötland:** Väversunda, Anudden, W Mt. Omberg, *Hallingbäck 38779* (MUB 14118). **UNITED KINGDOM.** **England:** prope Burnley, *Nowell s.n.* (RO).

- 8. *Didymodon tomaculosus*** (Blockeel) M. F. V. Corley, *J. Bryol.* 11: 649. 1981 [1982]. *Barbula tomaculosa* Blockeel, *J. Bryol.* 11: 583. 1981. TYPE: [United Kingdom.] "Midgley near Wakefield," 6 Jan. 1980, *T. L. Blockeel s.n.* (holotype, CGE!; isotype, Hb. T. L. Blockeel!). Figure 1A–C.

Plants 0.2–0.9 cm high, growing in very loose turfs, dark green or reddish brown; *stems* erect, simple, without central strand or weakly differentiated; *rhizoidal tubers* underground or on rhizoids on lower stem, multicellular, with one or several shining globules per cell, rounded to elongate, straight or

variously curved, 30–145 × 22–45 μm, brown, smooth. *Leaves* sparse along the stem, incurved or spirally twisted, appressed to erect-patent when dry, patent to spreading, more rarely recurved, not undulate when moist, lanceolate to ovate-lanceolate, acuminate, generally keeled in the upper part, slightly decurrent at base, 0.7–2.1 × 0.25–0.58 mm; lamina unistratose, yellow to reddish orange with KOH stain; apex acute; margins entire, recurved from base to ¾ of the leaf; *costa* 30–87.5 μm wide at leaf base, shortly excurrent or percurrent, ventral cells of the costa in upper leaf quadrate or rectangular, smooth, dorsal cells of the costa in upper leaf quadrate or rectangular, smooth, sometimes with low papillae, in transverse section at leaf base semicircular or elliptic, with 2 to 4 (to 5) guide cells in 1 layer, without ventral stereids, 1 (to 2) layers of dorsal stereids, ventral epidermis differentiated, smooth, dorsal epidermis differentiated, smooth; *upper and middle laminal cells* quadrate to shortly rectangular, oblate or not, not sinuous, 5–17.5 × 5–12.5 μm, smooth or with low papillae, thin-walled or slightly thickened, collenchymatous; *basal cells* quadrate to rectangular, not sinuous, 10–37.5 × 5–10 μm, smooth, thin-walled, not pitted. *Gemmae* in the axils of the leaves absent. *Dioicous*. *Sporophyte* unknown.

Habitat and distribution. Arable fields; Europe.

Discussion. A rare taxon known from very few stations in the United Kingdom and only two localities in Ireland (Hill et al., 1992). The Irish collections consist of poor material detected under the microscope and appear to have come from a more friable soil than the English plants (Hill et al., 1992). This was considered an endemic to the British Isles until Koperski et al. (2000) cited it from one site in the south of Germany.

Didymodon tomaculosus is principally characterized by the presence of numerous rhizoidal tubers that are subterranean or on the rhizoids on lower stems. Stems have a weakly differentiated, sometimes absent, central strand and widely spaced leaves along the stem. The costa is shortly excurrent or percurrent, without ventral stereids, the lamina cells are generally smooth although they may show low papillae, which can only be observed in cross section.

Didymodon tomaculosus forms small turfs loosely interwoven with other mosses. This habit and its small size, together with its morphological similarity to *D. fallax*, mean that the taxon may easily be confused with *D. fallax* or even completely overlooked. *Didymodon tomaculosus* differs from *D. fallax* mainly by having square or shortly rectangular

cells on the ventral side of the costa in the upper half of the leaf (vs. elongated in *D. fallax*) and by the presence of rhizoidal tubers (vs. absent).

Selected specimens examined. UNITED KINGDOM. **England:** Derbyshire, near Pebley Pond, N of Barlborough, *Blokeel s.n.* (Hb. Blokeel, United Kingdom); Wakefield, near Wintersett reservoir, *Blokeel & Porley s.n.* (Hb. Blokeel 31/418, United Kingdom); Leeds, Temple Newsam, *Blokeel s.n.* (Hb. Blokeel, United Kingdom).

9. *Didymodon tophaceus* (Brid.) Lisa, Elenc. Musch.: 31. 1837. *Trichostomum tophaceum* Brid., Muscol. Recent. Suppl. 4: 84. 1818 [1819]. *Anacalypta tophacea* (Brid.) Fürnr., Flora 12: 31. 1829. *Didymodon trifarius* var. *tophaceus* (Brid.) Mont., Arch. Bot. (Paris) 1: 140. 1833. *Trichostomum trifarium* var. *tophaceum* (Brid.) Fior.-Mazz., Specim. Bryol. Rom. (ed. 2): 14. 1841. *Barbula tophacea* (Brid.) Mitt., J. Proc. Linn. Soc., Bot. 1: 35. 1859. TYPE: [Germany.] "Comburgi," Feb. 1808, [sine collector] (lectotype, designated here, Hb. Bridel in B!). Figure 2F–I.

Didymodon ceratodonteus (Müll. Hal.) Dixon, Kongel. Norske Vidensk. Selsk. Skr. 1932: 7. 1932. Syn. nov. *Pottia ceratodonteia* Müll. Hal., Syn. Musc. Frond. 1: 564. 1849. TYPE: [South Africa.] "Philippstown Kattrivier," C. F. Ecklon *s.n.* (lectotype, designated by Magill (1981: 233), BM!).

Didymodon spadiceus var. *siluricus* Velen., Rozpr. Česká Akad. Věd, Tř. 2, Vědy Mat. Přír. 6: 152. 1897. Syn. nov. TYPE: [Czech Republic.] "Proti Libsicum," Mar. 1893, J. Velenovský *s.n.* (lectotype, designated here, PRC!).

Didymodon tophaceus var. *breidleri* E. Bauer, Lotos 47: 138. 1899. TYPE: [Czech Republic.] "Bohemia centr. Rinnal gegenüber Libsitz," Aug. 1897, E. Bauer *s.n.* (lectotype, designated here, HBG!; isotypes, GJO!, PR!).

Didymodon bosniacus Glow., Verh. Zool.-Bot. Ges. Wien 56: 196. 1906. TYPE: [Bosnia Herzegovina.] "Bosnien, Pliva-Masserfall bei Zajce," 25 July 1904, J. Glowacki *s.n.* (lectotype, designated here, GJO!).

Didymodon planotophaceus J. Froehl., Ann. Naturh. Mus. Wien 59: 118. 1953. Syn. nov. TYPE: [Iran.] "Prov. Luristan, Bisheh, 50 km a Khorramabad orientem versus, ca. 1200–1400 m," 14–16 July 1948, K. H. Rechinger 7407 (holotype, S!; isotypes, B!, E!, G!, H!, MO!, NY!, Z!).

Plants 0.3–4(–6) cm high, growing in dense turfs or cushions, olive-green or brown; *stems* erect, simple or branched, central strand differentiated; *rhizoidal tubers* absent. *Leaves* appressed, slightly incurved or patent when dry, erect-patent to spreading, not undulate when moist, lingulate, lanceolate or oblong-lanceolate, not keeled, decurrent at base, (0.3–)0.5–2.2(–3) × (0.15–)0.23–0.8 mm; lamina unistratose, brown-orange or more rarely

yellowish with KOH stain; apex obtuse or rounded, sometimes broadly acute and rarely apiculate; margins entire or papillose-crenulate in upper leaf, plane or weakly recurved from base to ½ or ¾ of the leaf; *costa* (30–)50–130(–145) μm wide at leaf base, ending several cells below the apex, very rarely percurrent, ventral cells of the costa in upper leaf elongated, smooth, dorsal cells of the costa in upper leaf quadrate to rectangular, smooth or papillose, in transverse section at leaf base semicircular, with 2 to 6 guide cells in 1 layer, 0 to 2(to 3) layers of ventral stereids, sometimes 1 layer of substereids, 1 to 3 layers of dorsal stereids, with or without ventral epidermis, smooth, dorsal epidermis differentiated, smooth or papillose; *upper and middle laminal cells* subquadrate to irregularly hexagonal, sometimes shortly rectangular, oblate or not, not sinuous, 5–27(–36) × (4–)5–15(–25) μm, with 1 to 2 generally low, sometimes tall, simple or bifurcate papillae per cell, sometimes apparently absent, thick-walled, collenchymatous; *basal cells* rectangular or shortly rectangular, not sinuous, (7.5–)10–75(–100) × (4–)5–15 μm, smooth or papillose, generally thick-walled, not pitted. *Gemmae* in the axils of the leaves absent. *Dioicous*. *Seta* erect, 0.6–1.9 cm long, red, spirally twisted to left throughout; *capsule* erect or slightly inclined, shortly cylindrical to ovoid, (0.7–)1–2.5 × 0.4–0.86(–1) mm, brown-reddish; *peristome* of 16 teeth irregularly cleft to near base, filiform, papillose, straight, (60–)90–400(–450) μm long, yellowish brown; *operculum* rostrate or long-rostrate, (0.5–)0.7–1.5 mm long; *calyptra* cucullate, 1.2–2.4 mm. *Spores* spherical, 7–18 μm diam., weakly papillose to almost smooth, yellowish brown.

Habitat and distribution. Calcareous rocks or seeping banks by running water that can be occasionally submerged; 0–2900 m; Africa, North America, South America (Churchill et al., 2000), temperate Asia, tropical Asia (Li et al., 2001), Europe. Reported for the first time in Mauritania.

Discussion. The protologue of *Didymodon tophaceus* includes: "in Germania visam clar. Fröhlich Comburgi Suevorum Februario 1808 legit." In Herbarium Bridel at B there are two sheets with the same locality of the original description, but only one shows the date of collection. We select this latter specimen as lectotype.

In the protologue of *Didymodon spadiceus* var. *siluricus*, Velenovský (1897) cited several specimens from different localities. We examined Velenovský's herbarium at PRC in order to locate original material. We found only one specimen whose locality was mentioned in the original description,

so we selected this material as lectotype. The study of this specimen showed that its differential characters are within the usual range of variation of *D. tophaceus*, and it is considered synonymous with the latter species.

In PR, where the original herbarium of Bauer is deposited, we only found a sheet of *Didymodon tophaceus* var. *breidlerii*, which belonged to Bauer's *Bryotheca Bohemica* (no. 221). The label matches the locality of the only material mentioned in the protologue; however, the date of collection is later than the publication of this species. On the other hand, we found another specimen collected by Bauer at HBG whose label shows the locality mentioned in the protologue and with a date prior to its publication (August 1827). Therefore, we chose this exemplar as lectotype.

We have studied Glowacki's herbarium at GJO and found two syntypes of *Didymodon bosniacus*. On the label of both specimens was written "Bosnien, Pliva-Masserfall bei Zajce," and they are in total accord with the protologue. We select the specimen marked Nr. 25181/6513 as lectotype since it is better preserved.

Because of the leaf shape, *D. tophaceus* may be confused with *D. luridus* Hornsch., although the papillosity of the lamina cells and the presence of elongate cells on the ventral side of the costa on the upper half of the leaf help distinguish *D. tophaceus* since in *D. luridus* the lamina cells are smooth and the cells of the ventral side of the costa are quadrate.

Didymodon sicculus M. J. Cano, Ros, García-Zamora & J. Guerra is frequently confused with *D. tophaceus*, since they both have the same type of papillosity and apex shape. However, *D. tophaceus* has elongated cells in the ventral side of the costa on the upper half of the leaf, while the cells in *D. sicculus* are quadrate or shortly rectangular. Furthermore, their respective habitats markedly differ, *D. sicculus* being terricolous and growing in dry places, while *D. tophaceus* grows on calcareous rocks over which water runs or in very wet places.

Pottia ceratodonteia Müll. Hal. was described by Müller (1849) and was later transferred to *Didymodon* by Dixon as *D. ceratodonteus*, a name that has been widely used in bryological literature (Magill, 1981; O'Shea, 2003). After studying the type material of *P. ceratodonteia* we think there are no sufficiently important morphological differences to separate this material from *D. tophaceus*. Therefore, *P. ceratodonteia* is proposed as a new synonym of *D. tophaceus*.

Didymodon planotophaceus J. Froehl. was described by Froehlich (1950) from eastern Iran

(province of Lorestan) and has not since been collected. According to Froehlich, *D. planotophaceus* is close to *D. tophaceus*, from which it differs by having flat margins and smooth lamina cells. A study of the type material has shown that the same stem may present leaves with both smooth and papillose lamina cells, which is common in *D. tophaceus*. The flat or curved margin also falls within the normal variability of this species. We conclude, therefore, that there are no significant morphological differences between this taxon and *D. tophaceus*, so it should be regarded as being synonymous with the latter.

Side (1983) described the presence of rhizoidal tubers formed of a simple row of cells in several examples from the south of England. Also long leaf structures on the leaf axils, in the form of axillary hairs, and designated teratological axillary hairs, have been described by Allen (1992) in specimens from Arkansas (U.S.A.). These may reach almost three-quarters of the length of the leaves. No type of asexual reproduction was observed in the specimens studied.

Selected specimens examined. ALGERIA. **Algiers:** Philippeville, *Glin s.n.* (S). **Constantine:** prope Constantine, *Appert s.n.* (JE). **M'Sila:** Oasis de Bou Saïda, *Broeksmitt s.n.* (L). **Oran:** St. Eugène, *Appert s.n.* (JE). **Tamanghasset:** Zentralsahara, Hoggar Gebirge, Gueltas von Issakarassene, *Frahm s.n.* (MO, NY). **Tizi-Ouzou:** Tizi-Ouzou, *Appert s.n.* (B, JE). EGYPT. **Ad Daqahliyah:** in einem Ausstich bei Matarieh, *Fleischer s.n.* (BP 79949, C, WU, Z). **Al-Wadi Al-Jadid:** Farafra Oasis, *Abou-Salama U-978c* (CAIA). **Alexandria:** Faculty of Science, Alexandria University, *Shabbara s.n.* (CAIA). **Gizeh:** Memphis, *Een s.n.* (S). **Ismailia:** Ismailia, *Een s.n.* (S). **Sinai:** Gebel Saint Katherine, *Abou-Salama U-892b* (CAIA). **Suez:** Eastern Desert, 116 km E of Cairo along the road to Suez, *Een E058* (S). LIBYA. Tripolitania, Bu Gheilam, *Cavara s.n.* (S). MOROCCO. **Fès-Boulmane:** Jbel Bou Iblane, entre el puerto de Tizi-n'Tiskine y Taffert, *Ros et al. s.n.* (MUB 13453). **Taza-Al Hoceima-Taoumate:** Jbel Bouhalla, *Cano et al. s.n.* (MUB 10611). MAURITANIA. **Adrar:** barranco de Illij, *González-Mancebo & Ros s.n.* (MUB 14511). AFGHANISTAN. **Bamian:** inter jugum Kota Deraz Kol et Panjao prope pagum Mandigak, *Rechinger 19763* (S). **Helmand:** in der Nähe von Kabul bei Gulbach, *Gilli s.n.* (S). **Kabul:** Band-e-Amir, *Furse & Furse s.n.* (L). ARMENIA. Montes "Karabakhskoie najorge," Goris, in vicinitate pagi vetusbi Khondzoresk, *Vasák s.n.* (GZU). GEORGIA. Borshom pr. fl. Kura, *Brotherus s.n.* (GJO, LE); Imeretia, inter Oni & Utseri, pr. fl. Rion, *Brotherus s.n.* (Z). IRAN. **Gilan:** bei Enseli am Caspischen Meer, *Pichler s.n.* (GJO, WU). **Mazandaran:** Babil, *Starmuahlner s.n.* (S); in valle fluvii Talar inter Abbasabad at Cahi, *Rechinger 2264* (S). IRAQ. **As Sulaymaniyah:** inter Kirkuk et Sulaymaniyah, *Rechinger 15731* (S). **Dahuk:** Solav, Dohuk, *Ráshic s.n.* (E). ISRAEL. **Hazafon:** Upper Galilea, Wadi Karen, *Nachmony 97a* (E). JORDAN. **Al Karak:** Wadi Arava, Fenan in direction to Dana, *Baierle s.n.* (B, Hb. Frey 86-182, Germany). **Irbid:** El-Mashara, *El-Oqlah s.n.* (Hb. Frey 1-4641F, Germany).

SYRIA. **Halab:** Beilan, *Hausknecht s.n.* (BM, JE). TAJIKISTAN. Darvazskogo, p. Odi-Hingou, *Mamatkulov 7392* (LE). TURKMENISTAN. Turkestan, regio Transkaspica, Karakalinsk, *Tschernjekorskaja 435* (GB, LE, S); SW Kopet-Dagh [Mts.], Kara-Kala, *Seyphulin s.n.* (LE). TURKEY. **Adana:** Saimbeyli, *Davis 19889* (E). **Antalya:** ca. 20 km from Manavgat, on road to Ahseki, *Nyholm & Crundwell 1243* (E). **Artvin:** Artvin, *Nyholm 563/74* (S). **Bilecik:** Bilecik, *Bornmüller 13183* (B, HBG, Z). **Denizli:** Honaz Dag, *Walther s.n.* (Hb. Düll). **Khrammaras:** Taurus Cataonicus, in mote Wank Dag prope Malatja, *Handel-Mazzetti 2507* (W). **Konya:** near Aksehir Gölü ca. 10 km N Aksehir, *Crundwell et al. 472a/72* (S). **Manisa:** 11 km W of Manisa, *Nyholm 1029/71b* (S). **Mugla:** ca. 2 km E of Cetibeli ca. 13 km N of Marmaris, *Nyholm 487b/71* (S). **Neveir:** Gülschir und dem kl. Dorf Alkan am SE-Rande des Hirkadag-Massivs, *Becker s.n.* (Hb. Düll). **Ordu:** Vilayet Ordu, Ünye, Black Sea coast, *Rubers 5038* (L). **Sinop:** above the Black Sea shore on the NW side of the Sinop, *Townsend 88/140*, United Kingdom). ALBANIA. **Dürres:** Durazzo, *Kórpáti s.n.* (BP 64449). **Tirana:** Tirana, *Kórpáti s.n.* (BP 64421). AUSTRIA. **Steiermark:** Ennsthal, bei Wölkenstein, *Breidler s.n.* (GJO). **Tirol:** Innsbruck, *Luisier s.n.* (PO 2183). BOSNIA HERZEGOVINA. Kiseljak bei Žepče, *Glowacki s.n.* (GJO, GZU). BULGARIA. **Burgas:** Mt. Strandza, prope Sinemorets, *Petrov s.n.* (SOM). **Khaskovo:** Mt. Rhodope, prope Kardzali, *Ganeva s.n.* (SOM). CROATIA. Dalmatien, bei Makarska südöstlich von Baskovic, *Froehlich s.n.* (S); Drubrovnik, *Pierrot & Pierrot 73076* (Hb. Pierrot, France). CYPRUS. Kyrenia, *Düll s.n.* (Hb. Düll). FRANCE. **Alpes Maritimes:** La Bocca, dans la Frayere, *Pierrot 55313* (Hb. Pierrot, France). **Ardèche:** Beaulieu, *Jaderholm s.n.* (GB, S). **Bouchés du Rhône:** Aix-en-Provence, Pied de la Sainte Victoire, *Skrzypczak s.n.* (Hb. Skrzypczak 97110, France). **Corse-du-Sud:** Festung Bonifacio an der Südspitze von Korsika, *Hübschmann s.n.* (B). **Deux-Sevres:** Vignes près Thouars, *Biget s.n.* (BCB 1761). **Haute-Corse:** Castirla d'Corde, *Lévier s.n.* (S). **Hérault:** Salasc, *Pierrot & Pierrot 92112* (Hb. Pierrot, France). **Ille-et-Vilaine:** Le Vivier, nord for Dol, *Størmer s.n.* (O). **Loiret:** Lettaure, *Thériot s.n.* (S). **Manche:** Cherbourg, *Le Jolis s.n.* (S). **Nord:** Dunkerque, *Lesdain s.n.* (S). **Tarn:** Albi, *Sudre s.n.* (BC). **Var:** Flassans-sur-Issole, *Skrzypczak s.n.* (Hb. Skrzypczak, France). **Vaucluse:** Bonnieux, *Ros s.n.* (MUB 1075). **Vendée:** Les Sables-d'Olonne, *Charrier s.n.* (O). GERMANY. **Bayern:** Friedrichsthal bei Baireuth, *Walther s.n.* (MO). **Hamburg:** bei Bergedorf, *Jaap s.n.* (WU). **Sachsen:** Leipzig, bei Beucha, *Kepsch s.n.* (C). GREECE. **Crete:** Iraklión, 1.5 km oberh. Gonies, Dornstrauch-Shibljak, *Düll s.n.* (Hb. Düll). **Central Greece and Euboea:** Elis, Paralimni, *Rechinger s.n.* (S). **Aegean Islands:** Patmos, on hillside ca. 1 km NW of the harbour of Scala, *Townsend 70/167* (E). **Ionian Islands:** Corfú, bei Nimfes, *Düll s.n.* (Hb. Düll). **Macedonia:** Athos, bei Pródromos, *Rauh s.n.* (B, JE). **Peloponnese:** Lakonia, Mistras, near Sparti, *Blockeel* (Hb. Blockeel 17/094, United Kingdom). **Thessalia:** *Rechinger 23750* (S). HUNGARY. **Bács-Kiskun:** lacu Szappaszék prope Fülöpháza, *Papp s.n.* (BP 168084). **Budapest:** Budapest, *Boros s.n.* (C, MO). **Jász-Nagykunszabolcs:** Montes Gyalui havasok, vallis rivi Melegsamos, *Vajda s.n.* (MO). **Liptauer:** Weidengrunde beim Bade Luaski, *Schulz s.n.* (GJO). ITALY. **Abruzzo:** Santuario Collelongo, *Düll s.n.* (Hb. Düll). **Calabria:** Catanzaro, *Micheletti s.n.* (BM, C, HBG, JE, M). **Campania:** Fuorigrotta, *Giordano s.n.* (S). **Emilia-Romagna:** presso la fonti nei colli de Sassuolo, *Fiori s.n.*

(RO). **Friuli-Venezia Giulia:** Triest, *Hausknecht s.n.* (JE). **Lazio:** Roma, Fontanile ad aqua Traversa, *Cuboni s.n.* (RO). **Liguria:** Zoagli, *Maggio s.n.* (RO). **Lombardia:** Bergamo, Val Gandino, Lefte, *Corti s.n.* (CANM 127401). **Marche:** Piceno, *Orsini s.n.* (RO). **Sardegna:** Tacco di Osimi, *Cogoni s.n.* (Herb Cogoni, Italy). **Sicilia:** Taormina, *Trautmann s.n.* (GB, S). **Toscana:** Gorgonia, *Arcangeti s.n.* (S). **Trentino-Alto Adige:** Castelfondo, prope pontem Novellae, *Evers s.n.* (GZU). **Umbria:** bei Montone, *Hemeyers s.n.* (O). **Veneto:** Tacquitara, Barbargia, *Marcucci s.n.* (JE, M). MACEDONIA. Cerna, *Herzog 644* (JE); Zaduka, *Herzog 638* (JE). MALTA. Buskett, *Mifsud s.n.* (MUB 12542). PORTUGAL. **Algarve:** Lagoa, Senhora da Rocha, Vale do Engenho, *Sérgio et al. s.n.* (LISU 155068). **Alto Alentejo:** Castelo de Vide, Termas de Fadagosa, *Sérgio s.n.* (LISU). **Azores:** S. Miguel, road from Furnas to Ribeira Quente, *Crundwell 1424* (E). **Baixo Alentejo:** Herdade da Ribeira Abaixo, *Garcia s.n.* (LISU 171238). **Beira Litoral:** cerca de S. Bento, *Sérgio s.n.* (COI 169). **Douro Litoral:** Arca de Água, arredores do Porto, *Machado s.n.* (PO 731). **Estremadura:** Aricino, *Machado s.n.* (PO 729). **Madeira:** Deserta Grande, ribeiro do Pedregal, *Nóbrega s.n.* (LISU 162110). **Mihno:** Mole-do, *Machado s.n.* (PO 733). **Ribatejo:** Águas-Belas, *Barros s.n.* (LISU 64473). RUSSIA. **Adygeya:** Prov. Kuban, Maikop, *Schapchnikov s.n.* (LE). **North Ossetia:** pr. fl. Ardon, *Brotherus s.n.* (Z). **Krasnodar Kraj:** Khosta, in faucibus fluminis Macesta prope pagum Izmailovka, *Vasák s.n.* (GZU). **Stavropol Kraj:** Kislovodsk Town, *Schteynberg s.n.* (LE). SERBIA AND MONTENEGRO. **Montenegro:** Duboko an der Mrtvica goom, *Glowacki s.n.* (GJO). SPAIN. **Asturias:** Colunga, Playa "La Griega," *Muñoz s.n.* (MA 16438). **Barcelona:** Gavá, *Casas s.n.* (BCB 49825). **Cádiz:** Ronda, *Pierrot & Pierrot 68071* (Hb. Pierrot, France). **Cantabria:** Arnauero, Playa de la Arena, *Muñoz s.n.* (MA 16439). **Castellón:** Ares del Maestre, *Guara s.n.* (VAL 3460). **Córdoba:** Sierra de Córdoba, bei Córdoba, *Fleischer s.n.* (C, M, WU). **Jaén:** Sierra de Segura, Las Acebeas, *Gil s.n.* (GDA 22350). **La Coruña:** Corrubedo, Laguna de Carregal, *Reinoso s.n.* (SANT 2756). **La Rioja:** Anguiano, *García s.n.* (Hb. Martínez-Abajigar, Spain). **Las Palmas:** Fuerteventura, betw. Tetir La Matilla, *Crundwell 1175* (E). **Lérida:** Balaguer, *Casas s.n.* (BCB 37744). **Murcia:** Pliego, Fuente de la Teja, *Ros & Aboal s.n.* (MUB 536). **Santa Cruz de Tenerife:** Tenerife, 1 km E of Puerto de la Cruz, *Crundwell 301* (E, NY). **Teruel:** Alcalá de la Selva, *Varo et al. s.n.* (GDA 13407). SWEDEN. **Jönköping:** Småland, Visingsö, *Arvén s.n.* (WU). **Värmland:** Skane, *Berggren s.n.* (WU). **Västergötland:** Vestrogothiae, Bellin, *Lindberg s.n.* (WU). SWITZERLAND. **Aargau:** Aarufer bei Brugg, *Geheeb s.n.* (RO). **Tessin:** Bellinzona, *Jägglé s.n.* (GB). UNITED KINGDOM. **England:** Warrington, Yorkshire, *Schimper s.n.* (RO). U.S.A. **Maine:** Knox, Rockport Town, Goose River, *Allen 25750* (MUB 18989).

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