

A new evaluation of the genus *Trichostomopsis* (Pottiaceae, Bryophyta)

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New taxonomic data are provided for the genus *Didymodon*, after a revision of the species treated as *Trichostomopsis*. Only two species are now recognized: *D. australasiae* and *D. umbrosus*. *Trichostomopsis curvipes* and *T. trivialis* recognized by previous authors are reduced to synonyms of *D. umbrosus*, while *Trichostomopsis haussknechtii* is synonymized with *D. australasiae*. Other taxa studied, such as *Barbula bistrata*, *B. incrassata*, *B. linguaecuspis*, *Tortula cabulica*, *T. cucullifolia* and *T. geniculata*, have been synonymized with *D. australasiae*. *Didymodon torquescens* is proposed as a synonym of *D. revolutus*. Lectotypes for *Barbula ecuadoriensis*, *B. haussknechtii*, *B. incrassata*, *B. linguaecuspis*, *B. nanocaulis*, *B. poeppigiana*, *B. rufiseta*, *B. trichostomacea*, *B. trivialis*, *Didymodon patentifolius*, *D. subtropaceus*, *Tortula geniculata*, *Trichostomopsis crispifolia*, and *Trichostomum fuscescens* are proposed. Morphological descriptions, distribution data, illustrations, LM and SEM photographs of the species recognized are included. © 2005 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2005, 147, 117–127.

ADDITIONAL KEYWORDS: *Didymodon* – musci – nomenclature – taxonomy.

INTRODUCTION

The genus *Trichostomopsis* Cardot was described by Cardot (1909) to accommodate the new species *T. crispifolia* Cardot from Mexico. This genus was mainly distinguished on the basis of its smooth laminal cells, plane margins, lax, hyaline basal cells, and bistratose apex and margins in the upper part. Since then, however, its systematic position has been controversial. Some authors treat it as belonging to independent genera, *Asteriscium* (Müll. Hal.) Hilp. *nom. illeg.* non *Asteriscium* Cham. & Schldl., *Trichostomopsis* or *Didymodon* Hedw.

Hilpert (1933) proposed segregating the species of *Barbula* sect. *Asteriscium* into a separate genus that he called *Asteriscium*, in which he also included *Trichostomopsis crispifolia*, the only species belonging to this genus at that time, because he observed no differences in the shape of leaves and cells of the lamina and costa anatomy between both genera. Nevertheless the name *Asteriscium* cannot be used for a genus of mosses because it was previously used to designate a

genus of vascular plants. Grout (1939) recognized three species in *Trichostomopsis* and maintained that this genus has affinities with *Barbula*, *Trichostomum* and *Didymodon* but proposed as differentiating characteristics, the bistratose margins and single stereid band in the costa. Later the genus *Trichostomopsis* was revised by Robinson (1970) in North America and the southern hemisphere. In this work he accepted five species: *T. australasiae* (Hook. & Grev.) H. Rob., *T. curvipes* (Müll. Hal.) H. Rob., *T. fayae* Grout, *T. trivialis* (Müll. Hal.) H. Rob. and *T. umbrosa* (Müll. Hal.) H. Rob. The same author considered *Trichostomopsis* to be closely related to *Barbula* but stated that the former can be distinguished from it by its hyaline and very lax basal cells, bistratose upper leaf margins, costa with a single dorsal stereid band and without ventral stereids, and the scarcely twisted peristome teeth. In the same year, *Barbula haussknechtii* Jur. & Milde and *Trichostomum aaronis* Lorentz were transferred into *Trichostomopsis* by Agnew & Townsend (1970). This work together with that of Casas (1970), who reported for the first time *T. australasiae* from Spain, extended the distribution area of this genus to Asia and Europe, respectively. Up to then, *Trichosto-*

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mopsis was known only in the Old World from the Canary Islands.

Zander (1978) synonymized *Trichostomopsis* with *Didymodon*, which was later included by Zander (1981, 1993) and Guerra & Ros (1987) within the section *Asteriscium* (Müll. Hal.) R. H. Zander of *Didymodon*. Also, the taxonomic treatments of Kučera (2000), Jiménez, Ros & Cano (2003) and Jiménez, 2004) treat them as belonging to *Didymodon*. However, many authors (Magill, 1981; Düll, 1992; Frey *et al.*, 1995; Kürschner, 2000; Cortini-Pedrotti, 2001; Allen, 2002) preferred to treat both genera distinctly. In this work the genus *Trichostomopsis* has been considered part of *Didymodon* since no taxonomic characters of sufficient significance have been observed to separate both genera. Also molecular data obtained by chloroplast *rps4* gene sequences (Werner *et al.*, 2004b) and by the nuclear ITS1 and ITS2 genic region sequences (O. Werner, J. A. Jiménez, R. M. Ros, M. J. Cano & J. Guerra, unpubl. data) confirm the close relationship between the species treated as *Trichostomopsis* and others of the genus *Didymodon*, as is also suggested by morphological studies. There is no reason therefore to consider it as a separate genus. The combination of characters present in the species of *Trichostomopsis* (stem occasionally with hyalodermis, bistratose upper leaf margins and very lax hyaline basal cells) allows its placement in a separate group within *Didymodon*. At present, based on these characters and according to Zander (1993) *D. australasiae* (Hook. & Grev.) R. H. Zander and *D. umbrosus* (Müll. Hal.) R. H. Zander are included within the section *Asteriscium*. However, recent molecular data based on ITS sequences show that *D. paramicola* (H. Rob.) O. Werner, J. A. Jiménez & Ros and *D. bistratosus* Hébr. & R. B. Pierrot, which do not match totally with the diagnostic characters provided by Zander (1993) for section *Asteriscium*, are surprisingly related with *D. australasiae* and *D. umbrosus* (Werner *et al.*, 2004a). Also, the rest of the sections proposed for *Didymodon* are not supported by the morphological and molecular data (Jiménez, 2003; O. Werner, J. A. Jiménez, R. M. Ros, M. J. Cano & J. Guerra, unpubl. data). Therefore, further studies for all the species of this genus should be carried out in order to clarify the infrageneric classification of this genus.

The aim of this paper was to attempt, through a morphological study, to clarify the validity of the different species treated at present within *Trichostomop-*

sis (*T. aaronis* (Lorentz) S. Agnew & C. C. Towns., *T. australasiae*, *T. curvipes*, *T. haussknechtii* (Jur. & Milde) S. Agnew & C. C. Towns., *T. umbrosa* and *T. trivialis*).

MATERIAL AND METHODS

In the present study the type specimens of all the published names in *Trichostomopsis* have been studied, whenever they could be located. Numerous collections from throughout the world have been studied. This revision is based on 380 specimens from the following institutional and personal herbaria: BM, BP, CHR, DUKE, E, FH, GOET, H, JE, LE, LISU, M, MA, MEXU, MGC, MUB, NY, PAL, PC, PRE, TFC, W, herbarium T. L. Blockeel, herbarium W. Frey, herbarium R. Skrzypczak.

All specimens were examined in potassium hydroxide solution at 2%.

Microscopic examinations and measurements were taken with an Olympus-BH2 light microscope, while microphotographs were obtained with an Olympus PM-10AK camera mounted on this microscope. The leaf surface was studied using a Jeol JSM-6100 SEM. The material was fixed in 3% glutaraldehyde with 0.1 M cacodylate buffer at 4°C, washed in cacodylate and saccharose buffer, dehydrated in an increasing acetone gradient (30%, 50%, 70%, 90% and 100%), critical-point dried and sputtered with a gold layer 200–300 Å thick.

RESULTS

After the morphological study of the species, only two species were recognized: *Didymodon australasiae* and *D. umbrosus*.

The key below is proposed to distinguish them:

Didymodon australasiae (Hook. & Grev.) R. H. Zander, *Phytologia* 41: 21. 1978. *Tortula australasiae* Hook. & Grev., *Edinburgh J. Sci.* 1: 301. 1824. Type: [Australia] 'King George's Sound, New Holland' 1791, A. Menzies *s.n.* [Lectotype: BM!, designated by Guerra & Ros (1987)]. (Figs 5, 6, 7, 8, 9)

Barbula poeppigiana Müll. Hal., *Linnaea* 17: 585. 1843. Type: 'Chili australis' 1828, C. Poeppig 4 [Lectotype: H!, here designated].

Tortula geniculata Mont., *Ann. Sci. Nat., Bot.* 4: 107. 1845. Type: 'Chili' C. Gay *s.n.* [Lectotype: PC!, here designated] **syn. nov.**

Stems without hyalodermis or occasionally present in patches; leaves oblong-lanceolate to lanceolate, ovate or triangulate; marginal basal cells not or weakly differentiated, quadrate to shortly rectangular	1. <i>D. australasiae</i>
Stems with hyalodermis; leaves long-lanceolate; marginal basal cells clearly differentiated, long-rectangular to elongate in 2–6 rows	2. <i>D. umbrosus</i>

- Barbula rufiseta* Taylor, J. Bot. 5: 51. 1846. Type: [Australia] 'Swan River' 1843, *J. Drummond s.n.* [Lectotype FH!, here designated; isoelectotype, BM!].
- Barbula graminicolor* Müll. Hal., Syn. musc. frond. 1: 611. 1849. Type: 'Chili ad terram loc. umbros. Racangua' vi.1828, *C. Bertero s.n.* [Lectotype: PC! designated by Zander (1981); isoelectotype, BM!].
- Trichostomum fuscescens* Hook. f. & Wilson, Fl. nov.-zel. 2: 73. 1854. Type: 'N. Zealand' *J. D. Hooker 358* [Lectotype: BM!, here designated].
- Barbula decolorans* Hampe, Ann. Sci. Nat., Bot. 3: 348. 1865. Type: [Colombia] 'Bogotá, Guadalupe, ad Barrancas, 3100 m' viii.1863, *A. Lindig s.n.* [Holotype: BM!].
- Trichostomum aaronis* Lorentz, Abh. Königl. Akad. Wiss. Berlin 1867: 29. 1868. Type: [Jordan] 'facing Ain el 'Enoqiyya, 2 km NNE of Azraq ed Druz' 30.iv.1965, *C. C. Townsend 65/447* [Neotype: BM!, designated by Guerra & Ros (1987); isoneotype, E!].
- Barbula haussknechtii* Jur. & Milde, Verh. K. K. Zool.-Bot. Ges. Wien 20: 593. 1870. Type: [Iran] 'Schahpur' *C. Haussknecht s.n.* [Lectotype: W!, here designated; isoelectotype, JE!] **syn. nov.**
- Barbula incrassata* Lindb., Acad. Soc. Sci. Fenn. 19: 57. 1892. Type: [Georgia] 'Caucasus, Kobi ad fl. Terek' v.1877, *V. F. Brotherus s.n.* [Lectotype: H!, here designated; isoelectotype: S!] **syn. nov.**
- Barbula acrophylla* Müll. Hal., *Hedwigia* 37: 127. 1898. Type: 'Australia Felix, Grampians, Mt. William' *D. Sullivan s.n.* [Lectotype: H!, designated by Sollman (2002)].
- Barbula nanocaulis* Müll. Hal., *Hedwigia* 37: 125. 1898. Type: [Australia] 'Tasmania, Eagle Hawk' 29.x.1889 [Lectotype: H!, here designated].
- Barbula trichostomacea* Müll. Hal., *Hedwigia* 38: 108. 1899. Type: [South Africa] 'Rondebosh' *A. Rehmann 97* [Lectotype: NY!, here designated; isoelectotype, PRE].
- Didymodon subtrophaceus* R. S. Williams, *Bull. New York Bot. Gard.* 3: 119. 1903. Type: [Bolivia] 'La Paz, 12000 ft.' 18.viii.1901, *R. S. Williams 2869* [Lectotype: NY!, here designated].
- Didymodon craspedophyllus* Cardot, *Rev. Bryol.* 36: 81. 1909. Type: 'Mexique, Etat de Jalisco, Barranca of Guadalajara, 4000 ft.' 1908, *C. G. Pringle 15227* [Holotype: PC!].
- Didymodon diaphanobasis* Cardot, *Rev. Bryol.* 37: 125. 1910. Type: 'Mexique, Etat de Mexico, Ixtaccihuatl' 1909, *C. A. Purpus 3721* [Holotype: PC!].
- Tortula hellenica* Schiff. & Baumgartner, Verh. Zool.-Bot. Ges. Wien 69: 332, Abb. 7, 1920. Type: 'Griechenland, Santorin, Phira-Hagios Elias' iv.1911, *V. Schiffner 226* [Lectotype: FH!, designated by Sollman (1984)].
- Tortula hellenica* var. *brevifolia* Schiff. & Baumgartner, Verh. Zool.-Bot. Ges. Wien 69: 332, Abb 7, 1920. Type: 'Griechenland, Attika, Athen, im Parthenon auf der Akropolis, an der Stelle wo das Fundament der Pallas Athene von Phidias war' iv.1911, *V. Schiffner 133* [Holotype: FH!].
- Barbula linguaecuspis* Broth., *Rev. Bryol.* 47: 8. 1920. Type: 'Ecuador SW, Azuay, secus rivulum collis supra Cañar, 3200 m' 16.i.1909, *M. Allioni s.n.* [Lectotype: H!, here designated] **syn. nov.**
- Barbula ecuadoriensis* Broth., *Rev. Bryol.* 47: 8. 1920. Type: 'Ecuador, distr. Azuay, vias campestras prope Cañar, 3150 m' 16.i.1909, *M. Allioni s.n.* [Lectotype: H!, here designated].
- Didymodon patentifolius* Thér., *Smithsonian Misc. Collect.* 85: 15. 1931. Type: 'Mexique, Vallée de México, Xoquiapán' 22.i.1924, *B. Amable 1676* [Lectotype: PC!, here designated].
- Trichostomopsis brevifolia* E. B. Bartram, *Bryologist* 34: 61. 1932. Type: [USA] 'Tuna Canyon, Los Angeles Co. California' iii.1931, *F. A. MacFadden 8107* [Holotype: FH!; isotype, NY!].
- Trichostomopsis fayae* Grout, *Moss fl. N. Amer.* 1: 228. 1939. Type: [USA] 'California, Los Angeles Co., San Fernando Valley', 9.v.1932, *F. A. MacFadden 8172* [Holotype: DUKE!].
- Tortula cabulica* J. Froehl., *Mitt. Thüring. Bot. Ges.* 1(2-3): 61. 1955. Type: 'Afghanistan: bei Kabul, W-Hang des Scher Darwasah, 1840 m', 31.iii.1950, *A. Gilli M33c* [Holotype: W!] **syn. nov.**
- Tortula cucullifolia* J. Froehl., *Mitt. Thüring. Bot. Ges.* 1(2-3): 62. 1955. Type: 'Afghanistan: Berg bei der Hängebrücke über den Kabulfluss zwischen Dschelalabad und Laghman, 650 m' 14.ii.1950, *A. Gilli M31* [Holotype: W!] **syn. nov.**
- Barbula bistrata* Rungby, *Bot. Not.* 112: 81. 1959. Type: [Iraq] 'prope Mosul', 8.iii.1956, *S. Rungby 1784* [Holotype: C!] **syn. nov.**

PLANTS 0.2–1.6(2.3) cm high, growing in dense turfs, dark-green, brown-green or blackish-green. STEMS erect, simple or branched, without hyalodermis or irregularly differentiated, central strand differentiated. RHIZOIDAL TUBERS underground, multicellular, rounded to elongate, 25–150 × 12.5–50 µm, brown, smooth. LEAVES crisped, twisted or incurved when dry, erect-patent to spreading when moist, ovate, triangulate, oblong-lanceolate to lanceolate, 0.6–2.6 × 0.2–0.55 mm; lamina unistratose, more rarely regular or irregularly bistratose in the upper third of the leaf, green to yellow, rarely orange-reddish with KOH; apex rounded to acute, sometimes cucullate; margins entire or papillose-crenulate, plane, sometimes lightly recurved in the upper middle of the leaf, bi- to tristratose in the upper middle of the leaf; costa 35–125 µm wide at leaf base, ending below the apex or percurrent, occasionally weakly spurred above midleaf; ventral cells of the costa, in the upper middle

of the leaf, quadrate to shortly rectangular, papillose; dorsal cells of the costa, in the upper middle of the leaf, quadrate to elongate, smooth or papillose, in cross section at leaf base semicircular or elliptical; with 1–2 layers of guide cells, with 2–6 cells in each one of them, without ventral stereids, 1–3 layers of dorsal stereids, generally without hydroids, ventral surface cells layer usually bulging, smooth or papillose, dorsal surface cells differentiated or not, smooth or papillose; upper and middle laminal cells rounded, subquadrate or shortly rectangular, oblate or not, $5\text{--}17.5(25) \times 7.5\text{--}20(22.5)$ μm , with 1–3 simple or bifurcate papillae per cell, sometimes smooth, generally thick-walled; basal cells quadrate to rectangular $(7.5)10\text{--}75 \times 7.5\text{--}20$ μm , differentiated, hyaline, smooth, thin-walled; marginal basal cells not or hardly differentiated, quadrate to shortly rectangular. Dioecious. SETA erect, 0.5–2 cm long, brown-reddish to yellow. CAPSULE erect, cylindrical to elliptical, $0.85\text{--}2 \times 0.4\text{--}0.8$ mm, brown to brown-reddish. PERISTOME of 32 filiform teeth, papillose, straight or slightly twisted, 250–850 μm long, occasionally rudimentary, brown-yellowish. OPERCULUM long rostrate $(0.45)0.65\text{--}1.1(1.4)$ mm long. CALYPTRA cucullate, 1.6–3 mm. SPORES spherical, 7.5–15 μm in diameter, weakly papillose, green-yellowish to brown.

Habitat: On calcareous or acidic rocks, artificial walls, soils and taluses (stony, gypsiferous, loamy, sandy, nitrified), edges of paths, generally in dry places during great part of the year; 0–4560 m.

Distribution: Europe; Africa; America; south-west and central Asia; Australia; New Zealand. This taxon is reported for the first time from Brazil, Kazakhstan, Portugal and Oman.

Selected specimens examined: AFGHANISTAN: BAGHLAN, in valle fluvii Qunduz inter Doshi et Doab, 800–1300 m, 11.vi.1962, *Rehinger 19659* (W). KANDAHAR, 55 km W von Kandahar, 900 m, 9.iii.1969, *Breckle s.n.* (HERB. W. FREY). MAZAR-I-SHARIF, in faucibus fluvii Balkh supra Aq Kupruk, 700–800 m, 7–8.vi.1962, *Rehinger 19669* (W). ALGERIA: CONSTANTINE, El Kantara, 6.iv.1985, *Ros s.n.* (MUB 4001). AUSTRALIA: SOUTH AUSTRALIA, Mount Gambier (GOET). VICTORIA, Moyston, *Sullivan 537* (H). BOLIVIA: LA PAZ, Battallias river, 3900 m, 24.viii.1901, *Williams 1712* (NY). BRAZIL: RIO GRANDE DO SUL, Caçapava do Sul, Ruínas do Forte, 15.xi.1987, *Wasum et al. s.n.* (MA 7275). COLOMBIA: CUNDINAMARCA, Nova Granata, Guadalupe, 3200 m, viii.1863, *Lindig 2020a* (BM). CHILE: ANTOFAGASTA (II REGIÓN), Toconao, $23^{\circ}11'S$, $68^{\circ}00'W$, 2480 m, 28.xi.2001, *Cano 292* (MUB 13546). BIOBÍO (VIII REGIÓN), Talcahuano, $36^{\circ}43'S$, $73^{\circ}06'W$, 28 m,

3.xi.2001, *Cano 8a* (MUB 16413). COQUIMBO (IV REGIÓN), Pichidanguí, $32^{\circ}09'S$, $71^{\circ}30'W$, 70 m, 11.xi.2001, *Cano 122a* (MUB 16408). LA ARAUCANÍA (IX REGIÓN), pr. Coi Coi, La Lobería, $38^{\circ}50'S$, $73^{\circ}28'W$, 21.xii.2001, *Cano 452* (MUB 15678). MAGALLANES (XII REGIÓN), Prov. Última Esperanza, pr. Parque Nacional Torre del Paine, $51^{\circ}07'S$, $73^{\circ}07'W$, 70 m, 22.i.2002, *Cano 695c* (MUB 16402). O'HIGGINS (VI REGIÓN), Rancagua, a 15 km de mina La Juanita, $34^{\circ}14'S$, $70^{\circ}25'W$, 1035 m, 8.xii.2001, *Cano 326a* (MUB 16406). REGIÓN METROPOLITANA DE SANTIAGO, Baños de Colina, $33^{\circ}11'S$, $70^{\circ}36'W$, 945 m, 8.ix.2001, *Cano 23* (MUB 16405). TARAPACÁ (I REGIÓN), pr. Putre, $18^{\circ}12'S$, $69^{\circ}32'W$, 3720 m, 24.xi.2001, *Cano 214a* (MUB 12702). VALPARAÍSO (V REGIÓN), Papudo, $32^{\circ}30'S$, $71^{\circ}26'W$, 1 m, 11.xi.2001, *Cano 112* (MUB 16404). ECUADOR: PICHINCHA, Quito, 2500–3000 m, v.1920, *Holmgren s.n.* (H). EGYPT: SINAI, Jebel Musa, ravine 500 m N. of St. Catherine's Monastery, 1600–1800 m, 4.iv.1982, *Frahm 825109* (E). FRANCE: ALPES-MARITIMES, Nice, Le Château, 11.iv.2001, *Skrzypczak* (HERB. R. SKRZYPCZAK 1087). PYRÉNÉES ORIENTALES, Collioure, 17.ii.2004, *Skrzypczak* (HERB. R. SKRZYPCZAK 4005a). GREECE: CENTRAL GREECE AND EUBOEA, Atenas, Acrópolis, 350 m, 14.iii.1999, *Cano et al. s.n.* (MUB 12092). PELOPONNESE, Argolida, ancient Epidavros, iii.1988, *Blockeel* (HERB. T. L. BLOCKEEL 17/291 A). IRAQ: AL ANBAR, Western Desert, 50 km N of Rutba, at edge of Gara depression, v.1963, *Agnew s.n.* (E). AT TAÍMIN, Kirkuk Liwa, Ain Dibbis, N. of Kirkuk, 26.xii.1962, *Agnew s.n.* (E). BAGDAD, Hilla Liwa, Iskanderiya, 6.i.1963, *Agnew s.n.* (E). DILAYA, Anaiza, 28.v.1962, *S. Agnew s.n.* (E). DULAIM, Habbaniya plateau, N.-facing, 31.i.1958, *Agnew s.n.* (E). NINAWA, Mosul Liwa, between Hatra and Sharqat, 24.iii.1961, *Agnew s.n.* (E). ISRAEL: Straße nach Jerusalem, abzweig Mishor Adummin, 300 m, 3.v.1989, *Frey & Kürschner 89–90* (HERB. W. FREY). Straße Jerusalem-Jericho, Abzw. Nahal Perat, hang am Kibuz Jericho, 200 m, 1.v.1989, *Frey & Kürschner 89–63* (HERB. W. FREY). ITALY: SICILY, Palermo, chiesa de S. Domenico, *Dia s.n.* (PAL). Agrigento, Via Impera, 29.xii.1999, *Ruggiano s.n.* (PAL). JORDAN: 'AMMAN, above Wadi Aseikhim, c. 13 km ENE of Azraq ed Druz and 6 km SSE of Jebel Aseikhim, less than 0.5 km from the edge of the lava desert, 6.v.1965, *Townsend 65/437* (E). AL KARAK, Wadi Arava, Fenan, Khirbet el-Ghewebe, 320 m, 5.iii.1986, *Baiede & Kürschner 86–15* (HERB. W. FREY). AL MAFRAQ, the ruined Roman fort on Jebel Aseikhim, on the western side, 630 m, 2.v.1965, *Townsend 65/458* (E). MA'AN, Petra, iii.1967, *Hepper 3387* (E). KAZAKHSTAN: CHIMKENT, inter diversoria Belyye Vody et Antonovka inter Chimkent et Aulie Ata, 18.v.1896, *Brotherus s.n.* (H). LEBANON: Ruins of Baalbek, 24.iv.1967, *Townsend s.n.* (E). LESOTHO:

- 9 km N of Matebeng, S of Sehonghong along Mountain Road, 1.xii.1977, *Magill 4255* (PRE). MEXICO: DISTRITO FEDERAL, Bosque de Tlalpan, 19°17'N, 99°10'W, 2300 m, 5.x.2001, *Delgadillo s.n.* (MEXU 6655a). GUANAJUATO, Sierra de Pénjamo, 9 km SW de Cuéramo, 20°37'N, 101°41'W, 1920 m, 31.x.1993, *Delgadillo s.n.* (MEXU 5836). HIDALGO, Cima del Cerro Xihuingo al N de Tepeapulco, 19°48'N, 98°33'W, 2980 m, 10.x.1986, *Cárdenas s.n.* (MEXU 4607). IMBABURA, Ibarra, garden of the Hosteria Chervali, 2270 m, 15.vii.1991, *Arts s.n.* (MEXU 15004). JALISCO, Ixtlahuacán de los Membrillos, 37 km SE of Guadalajara on the road to Chapala, 20°21'N, 103°14'W, 27.xii.1969, *Delgadillo s.n.* (MEXU 2773). MÉXICO, ladera Oeste del Popocatepetl, 3.viii.1968, *Delgadillo s.n.* (MEXU 2226). PUEBLA, Pico de Orizaba, laderas W, cerca del rancho Miguel Hidalgo, 19°03'N, 97°19'W, 3300 m, 26.iv.1982, *De Luna s.n.* (MEXU 687a). TLAXCALA, 8 km E de Calpulalpan, 19°35'N, 98°38'W, 2560 m, 11.xi.1987, *Cárdenas s.n.* (MEXU 4608a). VERACRUZ, 5 km S de Altotonga, 19°43'N, 97°14'W, 28.x.1979, *Delgadillo s.n.* (MEXU 3887b). MOROCCO: GUELMIM, Ifrane de l'Anti-Atlas, 29°11'N, 9°32'W, 750 m, 5.iii.2001, *Cano & Muñoz s.n.* (MUB 11667). MARRAKECH-TENSIFT-AL HAOUZ, Alto Atlas, Toubkal, subida desde Armt hacia el refugio de Neltner, 2175 m, 19.vi.1998, *Cano et al. s.n.* (MUB 8386). SOUSS MASSA-DRAË, Tizi-n'Tagounit, 1600 m, 19.vi.2000, *Draper et al. s.n.* (MUB 13244). TANGER-TÉTOUAN, Cap Spartel, 14.iv.1984, *Ros s.n.* (MUB 12849). NEW ZEALAND: AUCKLAND, Rangitoto, 21.viii.1933, *Moore 597* (CHR). CANTERBURY, Bealey state Forest Park, 985 m, 16.iv.1989, *Huang 385* (CHR). HAWKE'S BAY, Kiwi, Wairoa, 5.ix.1926, *Hodgson 138* (CHR). NELSON, Nelson, 4.ii.1930, *Sainsbury 1271* (CHR). OTAGO, Dunedin, Yard area, 26.vi.1933, *Simpson 77* (CHR). SOUTHLAND, Auckland Islands, Enderby Island, 13.xii.1972, *Vitt 8851* (CHR). WELLINGTON, Cape Terawhiti, 18.ix.1937, *Healy s.n.* (CHR). OMAN: Khasab road below Jebal Harim, near Jiddat al Sahasa, 1450 m, 23.x.1984, *Miller 6712c* (E). As Sayh, 1120 m, 26.xii.1984, *Gallagher 7429c* (E). PORTUGAL: MADEIRA, Isla de Madeira, Pico das Torres, 32°44'N, 16°56'W, 1580 m, 27.viii.2003, *Cano 1330* (MUB 15626). SAUDI ARABIA: ASIR, Sawdah Mountains 25 km NNW of Abha, 2650 m, 27.xi.1981, *Frey & Kürschner 81-832b* (HERB. W. FREY). AL MADINAH, Jabal Radhua, 1280 m, x.1985, *Collenette s.n.* (E). AR RIYAD, zwischen Salbukh und Qarineh, 60 km NNW Riyadh, 650 m, 26.iii.1981, *Frey & Kürschner 81-109b* (E). HA'IL, Jabal Ibrahim, off the Taif-Al Baha road, 2290 m, 17.iii.1987, *Collenette 6095d* (E). SOUTH AFRICA: NORTHERN CAPE, 15 km S of Noupoot along N1, 5 km N of Hanover turnoff, 16.i.1979, *Magill 5843* (PRE). WESTERN CAPE, Cape Town, *Rehmann 98* (NY). SPAIN: ALBACETE, Cancarix, 550 m, 17.iii.1996, *Ros & Guerra s.n.* (MUB 6049). ALICANTE, Sierra de Callosa, Callosa de Segura, Barranco de Enmedio, 250 m, 17.iv.1993, *Cano s.n.* (MUB 4905). ALMERÍA, Tabernas, Venta de los Yesos, 500 m, 20.ix.1989, *Martínez-Sánchez et al. s.n.* (MUB 4694). CÁDIZ, Cádiz, muralla de la ciudad, 36°32'N, 6°17'W, 5 m, 1.i.2004, *Cano 1385* (MUB 15935). CIUDAD REAL, pr. Picón, 39°30'N, 4°06'W, 810 m, 1.v.2004, *Cano 1529* (MUB 16851). CÓRDOBA, Facultad de Veterinaria, 6.iii.1977, *Oliva s.n.* (HERB. R. OLIVA 560). GRANADA, Sierra Nevada, Alpujarras, Barranco de la Salud, 1000 m, 16.iv.1998, *Ros & Werner s.n.* (MUB 16837). LAS PALMAS, GRAN CANARIA, kilometre 43-44 south on road from San Mateo, 975 m, 27.i.1975, *Redfearn et al. 30151* (NY). MÁLAGA, Sierra de Mijas, 24.i.1986, *Trigo & Guerra s.n.* (MGC 1533). MELILLA, Melilla, 12.iv.1985, *Ros s.n.* (MUB 12421). MURCIA, Moratalla, Benizar, Rincón de las Cuevas, 38°16'N, 1°59'W, 950 m, 11.iv.2003, *Jiménez et al. s.n.* (MUB 15416). SANTA CRUZ DE TENERIFE, La Gomera, Parque Nacional de Garajonay, próximo a Igualero, 1350 m, 16.iv.2000, *Losada & Rodríguez s.n.* (TFC 11806). TUNISIA: Zwischen Gafsa und Bir El Afey, 25.iii.1985, *Frahm 844511 A* (E). TURKEY: ADIYAMAN, Nemrut hill at Adiyaman, Arsameia archaeological site, 800 m, 29.vii.2001, *Papp s.n.* (BP). TURKMENISTAN: TURKESTAN, Zakaspijskaya oblast, Krasnovodsk [Turkmenbsi], 15.iv.1914, *Davilov 5* (LE). Turkestanania, regio Transkaspica, Key-Dag prope lacum in specia, 26.iv.1914, *Davilov 6* (S). USA: CALIFORNIA, Stanislas county, south-facing ridgetop low on alquist trail, Henry Coe state park, 450 m, 19.iv.1998, *Whittemore s.n.* (MUB 9976). UZBEKISTAN: BUCHARA, montes Kajkitan, 30.vii.1906, *Roshewitz s.n.* (M). Tuiny-Tau Mts., near Amu-Darya River, 30.iii.1906, *Roshewitz s.n.* (LE). VENEZUELA: MÉRIDA, Camino a la Laguna Negra, 3700 m, 18.i.2004, *Nuñez & Martínez-Abaigar s.n.* (MUB 19119). YEMEN: AL MAHWIT, Bait Taiz, Jebel Meisar, 3200 m, 20.vi.1980, *Wood 3324 A* (E). SAN'A, J. Nabi Shwaib above Metna, 3000 m, 20.ix.1978, *Miller 606-b* (E).

DISCUSSION

Trichostomum aaronis was described by Lorentz (1867) and was later reported from different countries of North Africa, south-western Europe and south-western and central Asia (Guerra & Ros, 1987; Townsend, 1987; Frey & Kürschner, 1991; Dia & Raimondo, 1994). According to Guerra & Ros (1987) and Frey & Kürschner (1993), *D. aaronis* is differentiated from *D. australasiae* by its shortly ovate or oblong-lanceolate leaves, which are widest at midleaf, obtuse apex, quadrate to rounded ventral cells of the costa and quadrate to shortly rectangular marginal basal

cells. Examination of the type material of *D. aaronis* and numerous material from Asia, Africa and Europe showed that its differential characters are within the usual range of variation of *D. australasiae* (Jiménez, 2004).

Both *Barbula bistrata* Rungby and *Tortula cabulica* J. Froehl. were synonymized by Agnew & Townsend (1970) as *D. aaronis*. After studying the type specimens we concluded that there are no morphological differences to separate these taxa from *D. australasiae*.

Barbula haussknechtii Jur. & Milde is known, in addition to the type locality, from very few localities in Kuwait, Iraq, Afghanistan and Syria (Frey & Kürschner, 1991; Kürschner, 1996). According to Agnew & Vondráček (1975), this species is very close to *D. aaronis*, from which it differs almost exclusively in the marginal basal cells. These cells are almost linear, four or more times longer than wide in *D. haussknechtii* while in *D. aaronis* are shortly rectangular and up to three times longer than wide. A study of the type of *B. haussknechtii* and most of the specimens cited under this name has shown that the shape of marginal basal cells in both taxa is the same and that there are no characters of sufficient taxonomic value to substantiate the specific status of this species. So, we concluded that *B. haussknechtii* is the same taxa as *D. aaronis* and therefore as *D. australasiae*.

Barbula incrassata Lindb. and *Tortula cucullifolia* J. Froehl. were described by Brotherus (1892) and Froehlich (1955) from Georgia and Afghanistan, respectively, and have not been collected again since. After examining the type material from both specimens, we conclude that there are no significant morphological differences between these taxa and *D. australasiae*.

Didymodon umbrosus (Müll. Hal.) R. H. Zander, *Phytologia* 41: 22. 1978.

Barbula umbrosa Müll. Hal., *Linnaea* 42: 340. 1879.

Type: [Argentina] 'ad muros pr. Córdoba' 1870, *P. G. Lorentz s.n.* [Lectotype: NY!, designated by Guerra & Ros (1987); isolectotype: HGB!]. (Figs 1–4, 9)

Barbula curvipes Müll. Hal., *Linnaea* 42: 344. 1879.

Type: 'Argentina, Siambon' 1872, *P. G. Lorentz s.n.* [Lectotype: NY!, here designated] **syn. nov.**

Barbula trivialis Müll. Hal., *Hedwigia* 38: 107. 1899.

Type: [South Africa] 'Orange Free State, Kadziberg' 1875, *A. Rehmann 99* [Lectotype: NY!, here designated; isolectotype: PRE!] **syn. nov.**

Trichostomopsis crispifolia Cardot, *Rev. Bryol.* 36: 74.

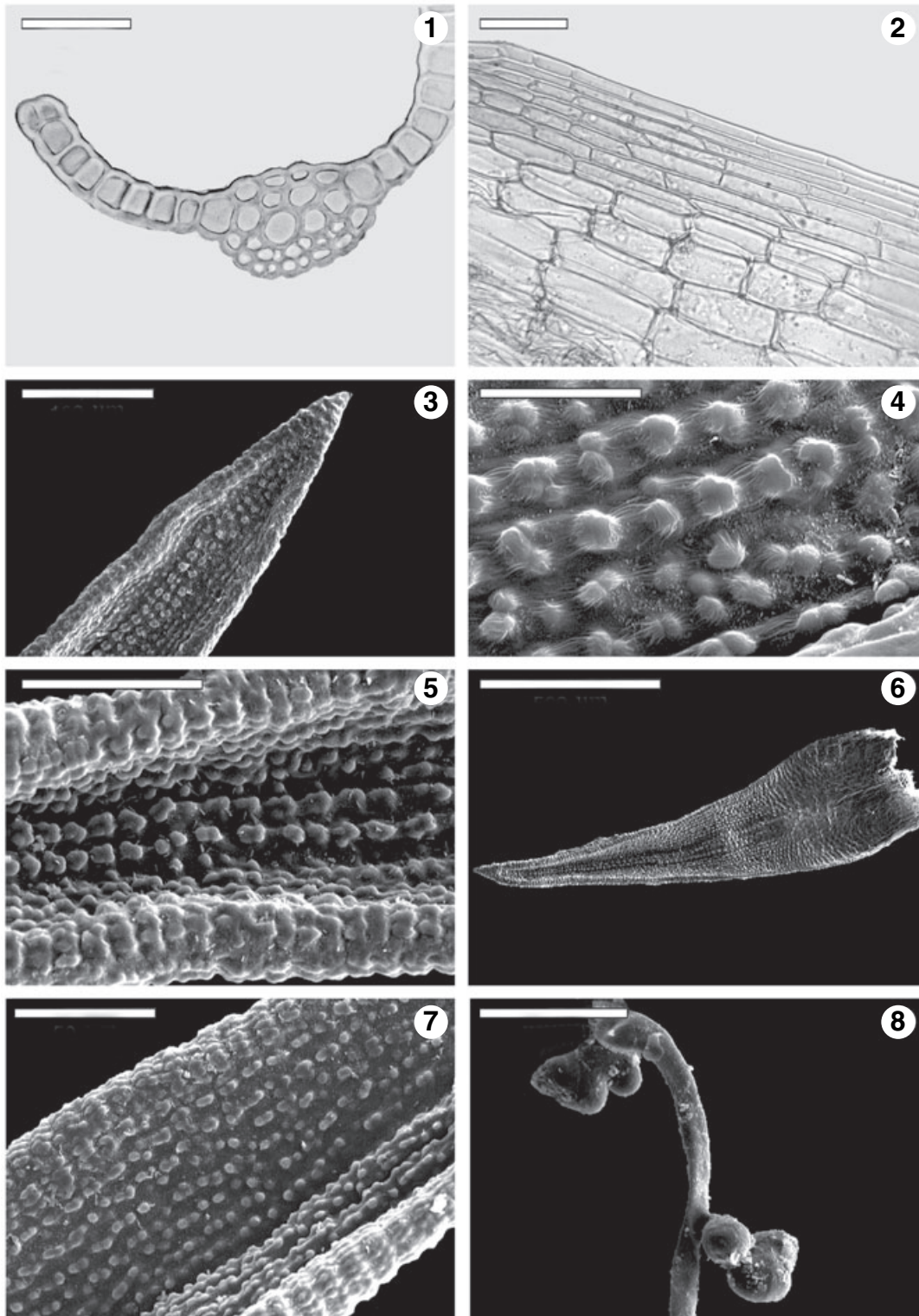
1909. Type: [Mexico] 'Hidalgo, Tula, 6800 ft.' 9.x.1908, *C. G. Pringle 15273* [Lectotype: PC!, here designated; isolectotype: NY!].

Asteriscium flavisetum Herzog, *Repert. Spec. Nov. Regni Veg.* 55: 18. 1952. Type: [Argentina] 'Prov. Salta, Departamento Iruya, Lomas de Abra, Grande nördl. von Orán' 29.vi.1933, *C. C. Hosseus 147* [Holotype: JE!].

PLANTS 0.2–1 cm high, growing in dense turfs, glaucous, bright green to olive-green. STEMS erect, simple or branched, with hyalodermis, central strand differentiated. RHIZOIDAL TUBERS underground, multicellular, rounded to elongate, 25–190 × 15–40 µm, brown, smooth. LEAVES crisped, twisted or incurved when dry, spreading to slightly recurved when moist, long-lanceolate (0.8)1.2–3 × 0.25–0.7 mm; lamina unistratose, more rarely regular or irregularly bistratose in the upper third of the leaf, green-yellowish or yellow with KOH; apex acute or obtuse; margins entire, generally plane, bi- to tristratose in the upper middle of the leaf; costa 30–85 µm wide at leaf base, ending below the apex or percurrent, occasionally weakly spurred above midleaf; ventral cells of the costa, in the upper middle of the leaf, quadrate to elongate, papillose; dorsal cells of the costa, in the upper middle of the leaf, elongate, seldom shortly rectangular or quadrate, smooth or papillose; in cross section at leaf base semicircular or elliptical; with 1–2 layers of guide cells, with 3–6 cells in each one of them, without ventral stereids, 1–2 layers of dorsal stereids, generally without hydroids, ventral surface cells layer rarely bulging, smooth or papillose, dorsal surface cells differentiated or not, smooth or papillose; upper and middle laminal cells rounded, subquadrate or rectangular, oblate or not, 5–15(20) × (5)7.5–12.5(15) µm, with 1–3 simple or bifurcate papillae per cell, sometimes smooth, generally thick-walled; basal cells rectangular, 25–80(100) × 10–20(30) µm, differentiated, hyaline, smooth, generally inflated, thin-walled; marginal basal cells differentiated, long-rectangular to elongate in 2–6 rows. Dioecious. SETA erect, 0.7–1.3 cm long, brown-reddish to yellow. CAPSULE erect, cylindrical, 0.7–2 × 0.4–0.7 mm, brown to brown-reddish. PERISTOME of 32 filiform teeth, papillose, straight or slightly twisted, 350–900 µm long, occasionally rudimentary, brown-yellowish. OPERCULUM long rostrate, 0.8–1.4 mm long. CALYPTRA cucullate, 1.6–2.2 mm. SPORES spherical, 7.5–12.5 µm in diameter, weakly papillose, brown to brown-yellowish.

Habitat: Soils and taluses generally nitrified, calcareous rocks and artificial walls; 0–2385 m.

Distribution: South Africa; Europe; South America; North America. This taxon is reported for the first time from Africa (South Africa).



Figures 1–8. *Didymodon umbrosus* (Figs 1–4 from MUB 2258). Fig. 1. Cross-section at upper leaf. Scale bar = 25 μ m. Fig. 2. Marginal basal cells. Scale bar = 40 μ m. Fig. 3. Leaf apex. Scale bar = 100 μ m. Fig. 4. Upper laminal cells. Scale bar = 20 μ m. *Didymodon australasiae* (Figs 5, 7, 8 from MUB 15416; Fig. 6 from MUB 12820). Fig. 5. Ventral surface of the costa in the upper middle of the leaf. Scale bar = 50 μ m. Fig. 6. Leaf. Scale bar = 500 μ m. Fig. 7. Upper laminal cells. Scale bar = 50 μ m. Fig. 8. Rhizoidal tubers. Scale bar = 50 μ m.

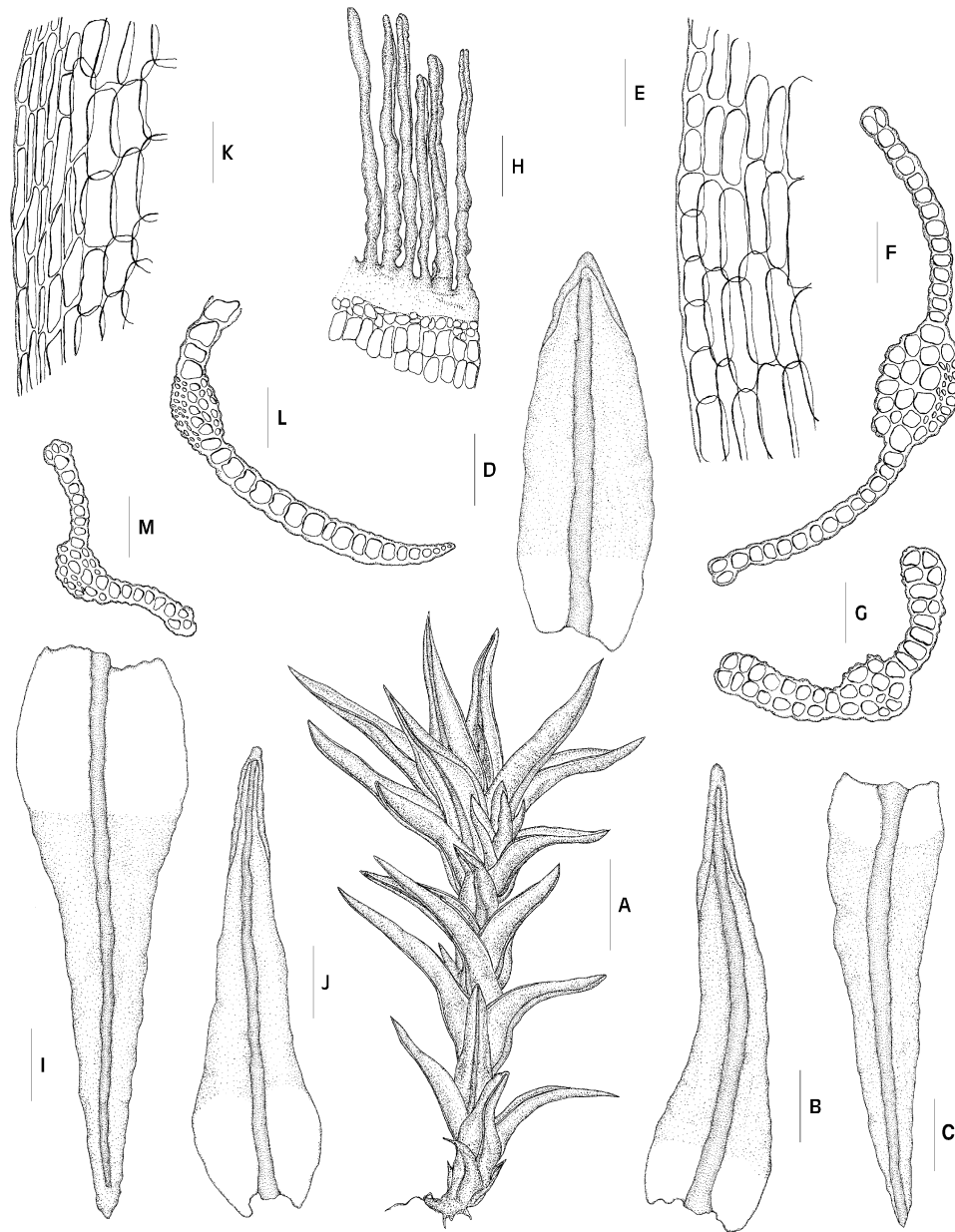


Figure 9. *Didymodon australasiae* (A–C, E–G from MUB 15416; D from MUB 6049; H from *Townsend 78/108-E*). A, habit when wet. Scale bar = 1.2 mm. B, C, D, leaves. Scale bar = 0.2 mm. E, marginal basal cells. Scale bar = 30 µm. F, G, leaf cross-sections. Scale bar = 50 µm. H, peristome teeth. Scale bar = 120 µm. *Didymodon umbrosus* (I–M from MGC 745). I, J, leaves. Scale bar = 0.3 mm. K, marginal basal cells. Scale bar = 30 µm; L, M, leaf cross-sections. Scale bar = 40 µm.

DISCUSSION

Barbula trivialis was described by Müller (1899). It has been considered as a South African endemic until Casas & Oliva (1982) and Guerra & Ros (1987) reported it from central and southern Spain. Later, it has been collected from Jordan (Frey & Kürschner, 1993), France (Skrzypczak & Pierrot, 2001) and Greece (Blockeel *et al.*, 2002). Robinson (1970), in his

revision of *Trichostomopsis*, distinguished *D. trivialis* from *D. umbrosus* only in the width of its upper laminal cells, 7–8 µm in *D. trivialis* and 9–14 µm in *D. umbrosus*. After studying the type material of *B. trivialis*, we concluded that the differential characters provided for this taxon do not allow its separation from *D. umbrosus*, since the width of the upper laminal cells overlap in both species. Therefore, there is no

reason to maintain *B. trivialis* as an independent taxon from *D. umbrosus*.

Guerra & Ros (1987) stated that *D. trivialis* was characterized by deltoid-lanceolate leaves, gradually narrowed from half to apex and widest in the upper third, entire margins and shortly rectangular marginal basal cells. After studying the specimens cited as *D. trivialis* from France, Greece and Spain, all of them have been identified as *D. australasiae* and not as *D. umbrosus*. It was not possible to study the specimens reported by Frey & Kürschner (1993) from Jordan but, according to the description provided in that work, this, too, seems to be *D. australasiae*.

Trichostomopsis curvipes is the only species belonging to the genus *Trichostomopsis* that had not been transferred to *Didymodon* by any author. This taxon has been considered as an Argentinean endemic since Müller (1879) described it from Tucumán province, and since then it has not been collected again. Robinson (1970) recognizes this species as a good taxon but closely related to *T. umbrosa* and *T. trivialis*. In fact, he considered that these three species could be separated from the rest of the species of *Trichostomopsis* by their adaxial cells of the costa which are smaller than the guide cells and the many rows of narrow marginal cells on the leaf base. However, according to Robinson (1970) *T. curvipes* can be distinguished from *T. umbrosa* and *T. trivialis* by its finely papillose laminal cells. After examining the only three samples collected from this species, we have been able to confirm that this taxon belongs to the genus *Didymodon*. Furthermore, no morphological differences allow this taxon to be separated from *D. umbrosus*, since this kind of papillosity can appear in *D. umbrosus* too.

Selected specimens examined: ARGENTINA. CÓRDOBA: Ascochinga, 1871, *Lorentz s.n.* (NY). Tulumba, vi.1871, *Lorentz s.n.* (NY). FRANCE. ALPES-MARITIMES: Nice, Èze, 25.x.2002, Skrzypczak (HERB. R. SKRZYPCZAK 2473). Nice, Le Château, 17.vi.1995, SKRZYPCZAK (HERB. R. SKRZYPCZAK 95600). HÉRAULT: nord de Béziers, 18.iv.2002, Skrzypczak (HERB. R. SKRZYPCZAK 2141). PYRÉNÉES ORIENTALES: Saint-Cyprien, Etang du Canet, 2004, *Skrzypczak* (HERB. R. Skrzypczak 4001). MEXICO. ZACATECAS: 3 km W de Concepción del Oro, 2385 m, 27.iii.1981, *Cárdenas s.n.* (MEXU 1159). PORTUGAL. ESTREMADURA: Lisboa, Jardim Botânico, 24.viii.1978, *Sérgio s.n.* (MUB 2258). Serra dos Candeeiros, entre Porto de Mós e Mendiga, en 362, km 11.6, 1977, *Mendes s.n.* (LISU 154213). Setúbal, Serra da Arrábida, Formosinho, 1982, *Sérgio & Sim-Sim* (LISU 152427). SPAIN. BARCELONA: Barcelona, calle Verdi 154, 15.iii.1970 (MGC 745). USA. CALIFORNIA: Los Angeles Co., Montrose, 1961 W. Verdugo Blvd, 25.vi.1953, *McFadden 2170* (E).

OTHER TAXA RELATED WITH *TRICHOSTOMOPSIS*

Didymodon torquescens Cardot, Rev. Bryol. 36: 83. 1909.

Cardot (1909) described this species on the basis of the following characters: leaves spirally contorted when dry, margins plane in the lower part but strongly revolute from over base to apex and rudimentary peristome. Bartram (1926) transferred it to the genus *Husnotiella* Cardot, opinion shared by Grout (1939). Later Zander (1981) considered *Husnotiella torquescens* Cardot as a synonym of *Didymodon australasiae*. After a study of the type material (Mexico: 'Etat de Michoacan, Morelia Bosque de San Pedro', 1908, *M. Solorzano s.n.*, holotype PC!) we believe that this taxon is morphologically different from *D. australasiae*. Although some samples of *D. australasiae* may resemble *D. revolutus* Cardot, this specimen shows typical characters of *D. revolutus*, including a costa ending below the apex and strongly spurred above midleaf, guide cells in one layer, without ventral stereids, 1(2) layers of dorsal stereids, and ventral epidermis with a pad of cells (Jiménez *et al.*, 2003). The linear-lanceolate leaves and generally acute or apiculate apices, which is not very common in *D. revolutus*, are the only features that suggest this might not be as *D. revolutus*. However, the characters previously mentioned in addition to the strongly revolute margins and rudimentary peristome show that *D. torquescens* is a synonym of *D. revolutus*.

Trichostomum calcicola Hampe, Icon. Musc. 29. 1844.

The original publication where *Trichostomum calcicola* was described (Hampe, 1844) consisted only of a plate without any information about the locality, collector or date. Sollman (1995) examined two possible Australian specimens, deposited in the Herbarium Hampe in BM, which could belong to the type material. In this work Sollman selected as lectotype material the sample marked 'Preiss 2455' and he stated that both samples were common forms of *Didymodon australasiae*. Indeed, these specimens have features, such as the bistratose margins in the upper middle of the leaves and hyaline basal cells, which are typical of *D. australasiae*. However, after studying the anatomy of the leaf costa we have observed that this is different with respect to *D. australasiae*. Both specimens have one layer of the guide cells and 1–2 layers of ventral stereids, while *D. australasiae* may have 1–2 layers of guide cells but lacks ventral stereids. In our opinion, this single discrepancy is sufficient for *T. calcicola* not to be included in the list of synonyms of *D. australasiae*. On the other hand we have not been able to assign it to any of the species of *Didymodon* known, so that these samples could correspond to a

well differentiated taxon of the genus *Didymodon*. Nevertheless for its confirmation, a deeper study and examination of numerous Australian collections is necessary.

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