

The identity of *Grimmia andreaeoides* Limpr. and *Didymodon subandreaeoides* (Kindb.) R.H.Zander

JAN KUČERA¹ and HERIBERT KÖCKINGER²

¹University of South Bohemia, Czech Republic and ²Karl-Franzens-Universität Graz, Austria

SUMMARY

Didymodon subandreaeoides (Kindb.) R.H.Zander, known to-date from north-western North America and the Beringian part of Arctic Russia, is identical to the earlier described European taxon *Didymodon rigidulus* subsp. *andreaeoides* (Limpr.) Wijk & Margad. (*Grimmia andreaeoides* Limpr.). Nomenclatural history of both taxa and an amended description with illustrations are given, and the variability, differentiation, ecology and distribution are discussed. The typification of all known synonyms is provided.

KEYWORDS: *Grimmia andreaeoides* Limpr., moss taxonomy, nomenclature, typification, ecology.

INTRODUCTION

The results of the first author's taxonomic studies of the *Didymodon rigidulus* group in Europe have led to the conclusion that *D. rigidulus* ssp. *andreaeoides* (Limpr.) Wijk & Margad. is specifically distinct from *D. rigidulus* Hedw. The same opinion, based on field experience in the Eastern Alps, is held by HK. The reasons for separating the two taxa include numerous taxonomically important morphological and anatomical details, contrasting ecology, existence of mixed stands, and distinctive electrophoretic isozyme patterns that will be described in another publication.

The search for the correct species name (*Didymodon andreaeoides* has already been used, *D. andreaeoides* Cardot & Broth., based on a different type) necessitated checking the type of *Didymodon subandreaeoides* (Kindb.) R.H.Zander. The types of the two taxa of Kindberg earlier synonymized by Steere (1938) — *Barbula subandreaeoides* and *Barbula andreaeoides* — were found to be fully identical with the type of the European *Grimmia andreaeoides* Limpr. For nomenclatural reasons, discussed in Zander (1978), the correct name of this taxon is *Didymodon subandreaeoides* (Kindb.) R.H.Zander. It has to be noted that the view that these three taxa could be identical had already been expressed by W. Schultze-Motel on his revision labels (apparently unpublished). He, too, studied the types of *Barbula andreaeoides* and *B. subandreaeoides* in S at the time of his studies on the costate *Andreaea* species (as

putative synonyms of *Andreaea rothii* F.Weber & D.Mohr).

NOMENCLATURAL HISTORY

The distinctiveness of *Didymodon subandreaeoides*, under its earlier names, has been repeatedly doubted by European authors. The discoveror of the species, Breidler, having sent two specimens to Limpricht, who later based his description of *G. andreaeoides* on them, labeled one of them (selected here as the lectotype) '*Didymodon rigidulus* forma *gemmaipara*'. In contrast, Sebillé (1908), who had found the species in the French Alps, confirmed its position within *Grimmia*. The view that the taxon could merely be a form of *Didymodon rigidulus* was again expressed by Culmann in Amann & Meylan (1918). In the same year Culmann made *G. andreaeoides* a subspecies of *Barbula rigidula* (Hedw.) Mitt. It is interesting to note that Culmann's opinions were evidently based on a misinterpretation. JK was able to study the collections of '*Grimmia andreaeoides*' in Z and found that the specimens interpreted as being transitional between *Didymodon rigidulus* and '*Grimmia andreaeoides*' by Culmann were in fact either pure specimens of *Didymodon subandreaeoides* or mixed stands of both species, without any trace of transitions. Such mixed stands are not rare in the Alps. Loeske (1930) later had the same opinion as Culmann. Jones & Warburg (1950) went still further in viewing '*Grimmia*

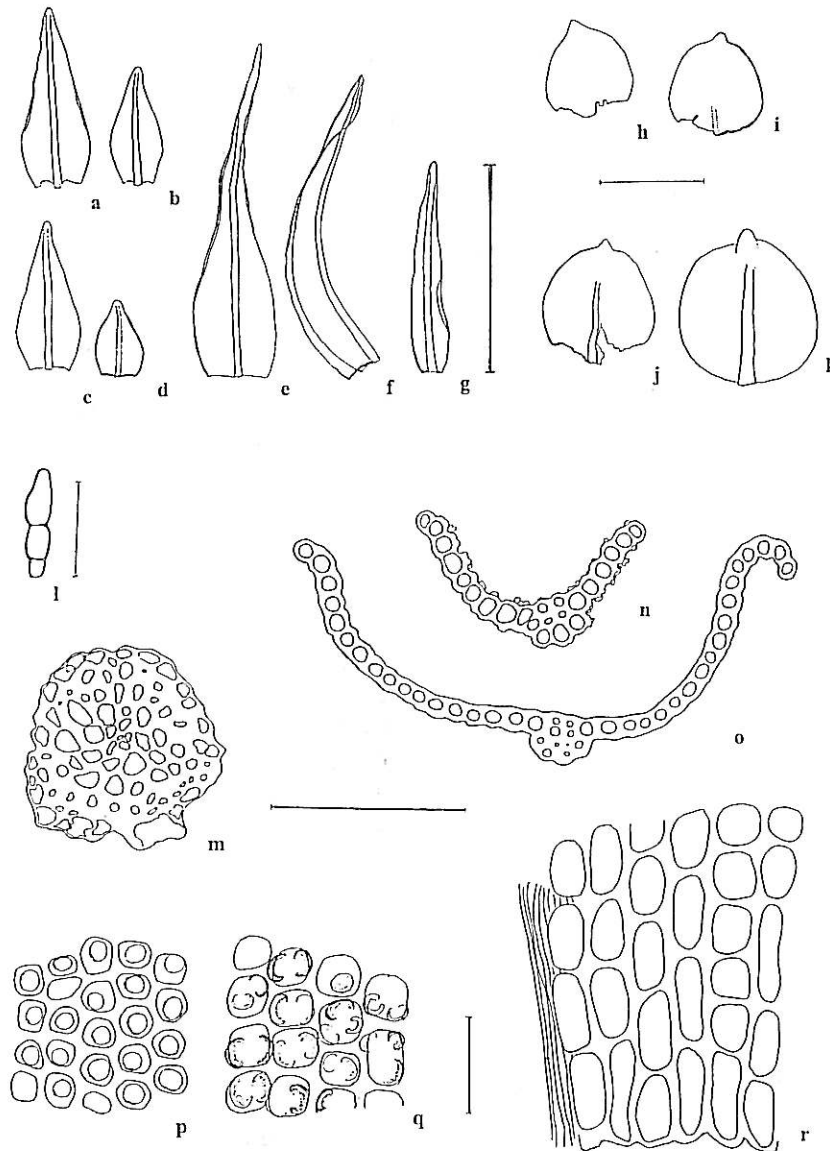


Figure 1. *Didymodon subandreaeoides* (Kindb.) R. H. Zander: a-d, vegetative leaves; e-f, outer perichaetial leaves; g, inner perichaetial leaf; h-k, basal flagellum leaves; l, axillary hair; m, stem cross-section; n, leaf cross-section in the upper part; o, leaf cross-section in the lower part; p-q, upper lamina cells; r, basal lamina cells. [a-b, g: Köckinger 97-626; c-d, r: Köckinger 97-494; e-f, m-o: Kučera E2724; h-l: Kučera E1601; p: Köckinger 97-539; q: Köckinger 97-441]. Scale bars: a-g, 1 mm; h-k, 200 µm; l, 50 µm; m-o, 100 µm; p-r, 20 µm.

andreaeoides' as 'merely an abnormal growth-form of *Barbula rigidula*'. To support their opinion, they noted the presence of gemmae in the leaf axils of plants collected in the Snowdon area (Wales, United Kingdom) originally by D.A. Jones and later by themselves. We also had the opportunity to study the specimen collected on Snowdon by D.A. Jones which is housed at E. This single and unfortunately small specimen indeed combines the characters of both *D. rigidulus* and *D. subandreaeoides* but differs from both taxa in important details. We are convinced that this poor material cannot be unequivocally assigned to either species. Probably the last author who dealt taxonomically with '*Grimmia andreaeoides*' was Pilous (1958) who studied plants from the Belianské Tatry Mts. (Slovakia). He compared them

with *Molendia tenuinervis* Limpr. and came to the conclusion the taxa are closely related and that their morphological characters intergrade to such an extent that '*Grimmia andreaeoides*' should be viewed only as a form of *Molendia tenuinervis* (the two new combinations he made in his paper were however invalid). It is true that the leaf shape of both taxa is extremely similar, however, the crucial differences between the genera *Molendia* and *Didymodon*, e.g. the position of gametangia, were unfortunately not taken into account. Since then the existence of '*Grimmia andreaeoides*' has been almost forgotten. British authors (Smith, 1980; Corley *et al.*, 1981) and Maier & Geissler (1995) viewed it as a synonym of *Didymodon rigidulus*. German authors (Düll, 1984; Frahm & Frey 1992; Frey *et al.*, 1995) mostly

neglected the taxon although Düll (1991) later noted that *D. rigidulus* ssp. *andreaeoides* 'is a remarkable taxon'.

Didymodon subandreaeoides had a similar history of neglect and reinstatement in America. In 1905, N.C. Kindberg described, among other taxa from British Columbia, two new members of the genus *Barbula* — *B. andreaeoides* and *B. subandreaeoides*, differing in minor details of leaf shape. They were put into synonymy with *Andreaea rothii* by Steere (1938) and therefore nearly forgotten for the next forty years. Later, however, Steere (1978) changed his mind and pointed out that *Barbula andreaeoides* was a distinct species. Zander (1978) accepted his view and placed the species in the genus *Didymodon*, following the generic concept of Saito (1975). The justification of accepting *Didymodon subandreaeoides* as a distinct species in North America has not been doubted in the last twenty years as far as we know.

AMENDED DESCRIPTION OF *DIDYMODON SUBANDREAEIOIDES* (Fig. 1)

***Didymodon subandreaeoides* (Kindb.) R. H. Zander**, *Phytologia* 41 (1): 23. 1978

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

Type: Canada, Brit. Columbia, Joho valley, rocks. 6.8.1904 leg. J. Macoun. S, reg. nr. B3378 (lectotype, here designated). **Syntype:** Canada, Brit. Columbia, Pipestone Pass, 7000 ft, rocks. 5.7.1904 leg. J. Macoun, three duplicates in S.

Synonyms:

Grimmia andreaeoides Limpr., *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz* 1: 776–777. 1888, **syn. nov.**

(*Didymodon rigidulus* subsp. *andreaeoides* (Limpr.) Wijk & Margad., *Taxon* 9: 50. 1960. *Barbula rigidula* subsp. *andreaeoides* (Limpr.) Culm., *Revue Bryologique* 40: 42. 1912).

Type: [Austria] Tirol: Kitzbühler Horn, Thonschiefer u. Kalk, 1990 m. 13.8.1882 leg. J. Breidler (sub *Didymodon rigidulus* forma *gemmaipara?*), BP. (lectotype, here designated).

Syntype: Salzburg: Keeskar im Obersulzbachthal im Pinzgau, 26–2700 m. 14.8.1879 leg. J. Breidler, BP. isosyntype JE.

Barbula andreaeoides Kindb., *Rev. Bryol.* 32: 36. 1905.

TYPE: Canada, Brit. Columbia, McArthur Pass, 7500 ft, rocks. 10.8.1904 leg. J. Macoun, herb. S, reg. Nr. B3375. (Lectotype, here designated; 2 isoelectotypes in S!)

Plants in dense low cushions or tufts, dull reddish brown, ferruginous or dark brown, young or shaded parts dull green. *Stems* ± erect, irregularly branching, with numerous flagelliform innovations, about 5 to 10 mm long including the dead parts of the stems. Cross-

section ± rounded pentagonal, only to 0.15 mm in diameter, central strand absent or vestigial, inner cortex formed by thick-walled cells, their walls brownish, sclerodermis absent, weak hyalodermis of enlarged, less thickened cells present. *Axillary hairs* 40–80 µm long, 3–4 celled, basal cell short, brownish. *Leaves* appressed, sometimes slightly spiralled around stem when dry, erect-spreading when moist, (0.3–) 0.5–0.9 (–1.1) mm long and 0.25–0.35 mm wide, 1.5–2.5 times longer than wide, larger leaves from ovate-elongate base obtusely lanceolate, shorter leaves essentially ovate, obtusely keeled to U-shaped in cross-section, apex usually obtuse. Leaves of deciduous flagelliform innovations markedly concave, cochleariform, suborbicular, often wider than long, obtusely apiculate, frequently grading to the normal shape upwards, if the flagellum does not drop off. *Costa* weak, 20–45 µm wide near base, slightly widening towards the upper part of leaf, typically ending 1–4 cells below apex but sometimes percurrent or obtusely excurrent up to 20% of the leaf length, especially in the perichaetial leaves. Costa of the basal flagellum leaves greatly reduced to entirely absent. Costal superficial cells continuous from lamina both ventrally and dorsally, isodiametric in about the upper two-thirds of the leaf length, shortly rectangular in the basal third. Cross section elliptical, in basal part flat on the ventral side, showing ventrally and dorsally developed epidermis, inner cells in usually one row, essentially undifferentiated, of the substereid type or as guide cells, in larger leaves sometimes several dorsal stereids present. *Margins* entire or papillose or mammillose crenulate, recurved from about $\frac{1}{4}$ to $\frac{2}{3}$ of the leaf length but often plane (about $\frac{1}{3}$ of the studied leaves), always plane on the flagellum leaves, unistratose or rarely bistratose near apex. Upper lamina cells isodiametric, ± rounded, slightly to heavily thick-walled, (6–) 8–12 (–17) µm wide (the walls constituting 10–35% of the cells width), more or less papillose with conical or C-shaped papillae, especially in the apical region, rarely smooth. Cells of the basal flagellum leaves smooth. Basal paracostal cells shortly rectangular, (5–) 8–12 (–19) µm wide and (8–) 9–25 (–35) µm long (the walls constituting 15–40% of the cell width), (0.7–) 1.1–2.0 (–4.0):1, mixed with angular cells especially on the transition towards the upper cells, brownish, with thick walls, smooth. Towards margins cells shorter, sometimes wider than long. *Vegetative propagation* by means of deciduous flagella in leaf axils. Apparently dioicous. *Archegonia* terminal, up to ca 550 µm long, surrounded by usually conspicuously larger perichaetial leaves (to 1.5 mm) with more excurrent costa. *Antheridia* and *sporophytes* unknown.

VARIABILITY

The plant is usually described as not being variable but it is in fact highly polymorphic in some characters. These include in particular the form and length of the leaves, the

degree of excurrent of the costa, the papillosity of the leaf cells and the width of the cell walls and cell size (see description).

The most constant characters are the cross-section of stem and leaf costa, brownish colour, and the presence of flagelliform innovations in the leaf axils with suborbicular and cochleariform proximal leaves. In the course of our studies, two highly deviant forms were found, which cannot at present be assigned to either *D. subandreaeoides* or another species of the genus with security, due to the scarcity of the available material and the absence of transitive forms. One of them, known to-date from two sites in the Austrian Alps approaches *Didymodon asperifolius* (Mitt.) H. A. Crum, Steere & L. E. Anderson in its habit and dimensions, the other from Clogwyn du'r Arddu (Wales, U.K.) mentioned above is in habit and anatomical and morphological details identical to *D. subandreaeoides* but its numerous axillary gemmae of *Didymodon rigidulus*-type do not fit its known variability.

DIFFERENTIATION

D. subandreaeoides is most likely to be confused with the most closely related *Didymodon* species — *D. rigidulus* and *D. asperifolius*, with which it also often occurs. It differs from the first mainly in (1) the constant presence of axillary flagella with reduced ovate to suborbicular concave leaves with plane and unistratose margins, (2) the absence of axillary gemmae (provided that the above mentioned specimen from Wales does not belong to *D. subandreaeoides*), (3) the shape of basal cells, which are usually hyaline (including the cell walls) and less thickened in *D. rigidulus*, and (4) the stem cross section, which in *D. rigidulus* shows a distinct central strand, no hyalodermis and \pm thin walled cells of the inner cortex. Also the papillosity of the upper cells, costa cross-section, and usually unistratose margins of *D. subandreaeoides* differ from *D. rigidulus* but the evaluation of these characters may require some experience with the variability of both taxa.

Distinction from *D. asperifolius* may prove much more difficult in individual cases (particularly if the deviant plants from the Austrian Alps belong to *D. subandreaeoides*), although this is usually a much coarser plant. In *D. asperifolius*, specialized vegetative propagation is unknown, the leaf bases are more constricted, and the basal paracostal cells are typically much longer. Also, the costa in *D. asperifolius* is somewhat stronger, never excurrent, with well differentiated guide cells, both ventral and dorsal stereids, and the apex is always acute (it may however become eroded in both species). The stem cross-section does not show any trace of hyalodermis. The ferruginous coloration is essentially identical in both species. Confusion is further possible with other less related or unrelated taxa — *Molendoa tenuinervis* (whether this is a distinct taxon or only a modification of *M. hornschi* (Hook.) Lindb. ex Limpr.), and diverse *Schistidium* and

Grimmia species. From *Molendoa tenuinervis*, which may have precisely the same leaf shape, it differs mainly in the position of gametangia (which are on short lateral branches in *Molendoa*), in the basal cells, hyaline and less thickened in *Molendoa*, in the upper cells, more heavily papillose and \pm thin walled in *Molendoa*, in the specialized vegetative propagation, unknown in *Molendoa tenuinervis*, and the colour, which is usually dull or bluish green in *Molendoa tenuinervis*. From the superficially similar *Schistidium* and *Grimmia* species with muticous leaves, which might occur in similar habitats, it differs among other characters in the costa cross-section (homogeneous in *Schistidium* or with a hydroid strand in *Grimmia*, not biconvex in any of the species with muticous leaves).

ECOLOGY

Didymodon subandreaeoides is an alpine species in Central Europe (the localities usually lie at between 900 and 3000 m, but a single locality at only 550 m is known in Slovakia), in Northern America also growing at low altitudes in tundra. It generally grows on rocks; in the Alps and Carpathians mainly on calcareous schist, marble, limestone, dolomite, greenstone and similar types of base-rich bedrock. It avoids poor siliceous rocks like gneiss or granite. From our experience in Europe, it seems to avoid carbonate rocks without a distinct content of silicates at lower altitudes, whereas in the upper alpine zone its ecological amplitude is much wider, tolerating pure limestone and dolomite. The species prefers dry and sunny, S.-, S.W.- and S.E.-facing rock walls and ledges. In the upper alpine zone it also occurs on N.-facing slopes, colonizing vertical and inclined rock faces. At somewhat protected sites, particularly below the tree-line, it is able to grow directly on rough surfaces, otherwise it usually becomes established in small fissures. Frequently, especially in exposed alpine habitats, the flagella regenerate within or among the cushions of basiphilous *Grimmia* (*G. tergestina* Tomm. ex Bruch, Schimper & W. Gümbel, *G. poecilostoma* Cardot & Sebillé, *G. anodon* Bruch & Schimp.) or *Schistidium* spp. (*S. robustum* (Nees & Hornsch.) H. H. Blom, *S. atrofussum* (Schimp.) Limpr., *S. brunnescens* Limpr. subsp. *brunnescens* and others). *D. subandreaeoides* is generally restricted to habitats which are not or only temporarily covered by snow in winter. Therefore it avoids boulders unless these are sufficiently large and exposed to the wind. As far as we know, *D. subandreaeoides* has never been found in man-made habitats.

Although *D. subandreaeoides* is a rather delicate plant, it expands its cushions due to the massive development of branches from the leaf axils at the expenses of the 'host' species, which is not infrequently displaced completely. The species is normally not overgrown by larger or competitively stronger mosses but sometimes it might be overgrown by lichens. As the rhizoidal development is limited, the larger and \pm isolated cushions become unstable and

drop off. *D. subandreaeoides* is never the dominant species, even in its optimum habitats.

Infrageneric mixed stands occur rather frequently, particularly with *D. rigidulus*, *D. icmadophilus* (Schimp. ex Müll. Hal.) K. Saito and the ecologically close but rare *D. johansenii* (R. S. Williams) H. A. Crum, in the upper alpine zone also with *D. asperifolius*. Other commonly associated species are the above mentioned *Grimmia* and *Schistidium* species, *Tortella tortuosa* (Hedw.) Limpr., *T. bambergensis* (Schimp.) Broth., *Ditrichum flexicaule* (Schwägr.) Hampe, *Orthotrichum cupulatum* Hoffm. ex Brid., *Pseudoleskeella catenulata* (Brid. ex Schrad.) Kindb. or *Hypnum vaucheri* Lesq. On N-facing slopes in the upper alpine zone of the limestone mountains of the Eastern Alps it is frequently and typically associated with *Schistidium grande* Poelt. On periodically irrigated, sloping rock surfaces it sometimes grows within extensive stands of *Schistidium brunnescens* subsp. *brunnescens*. The companions on subneutral rocks may be moderately acidophilous mosses like *Grimmia unicolor* Hook. or *G. funalis* (Schwägr.) Bruch & Schimp.

DISTRIBUTION

The distribution area of *D. subandreaeoides* includes the Beringian part of Arctic Russia (Ignatov & Afonina, 1992), north-western North America (from Alaska along the Cordillera mountain range south to Colorado: Zander, 1998), the French, Swiss, German, and Austrian Alps (no specimens yet seen from the Italian territory), and the Carpathians (Belianské Tatry and Malá Fatra Mts. in Slovakia, Făgăraș Mts. in Romania, it can be expected also in the Ukrainian Carpathians). The distribution pattern implies that the taxon is rather old (as it is absent from areas glaciated during the Pleistocene like Scandinavia and Siberia) and seems to prefer areas with continental climatic conditions.

SELECTED SPECIMENS STUDIED

CANADA: British Columbia: Joho valley, rocks. 6.8.1904 leg. J. Macoun (S); Pipestone Pass, 7000 ft, rocks. 5.7.1904 leg. J. Macoun (S); McArthur's Pass, 7500 ft, rocks. 10.8.1904 leg. J. Macoun (S). **Yukon:** Bonnet Plume Range, Pinguicula Lake: 64°42'N, 133°26'W, 2800–3200 ft elev. On NE facing slope of mtn, at NW end of lake, in calcareous, alpine tundra with mesic limestone outcrops, 21.7.1976 leg. D. H. Vitt (S).

AUSTRIA: Carinthia: Hohe Tauern: Franz-Josefs-Höhe, 1904 leg. Nicholson & Dixon (FI) — Winkl, path Gößnitzfall-Bruchetalm, 1400–1450 m, Kučera E1591, E1601 (PR); Gurktaler Alpen: Rinsennock, SE-Seite des Gipfels, 2320–2330 m, Köckinger (GZU). **Upper Austria:** Warscheneck, ca. 2350 m, Köckinger 98-523 (GZU). **Salzburg:** Hohe Tauern: Keeskar im Obersulzbachthal im Pinzgau, 26–2700 m, 1879 leg. J. Breidler (BP, JE); Radstädter Tauern, W Weißbeck, Südhang unterh. der Riedlingscharte, ca. 2180 m, Köckinger 97-539 (GZU) — E Zalußenalm, S-Hang der Plankowitz-

spitze, ca. 1800 m, Köckinger 97-626 (GZU). **Styria:** Schladinger Tauern: Schiedeck, 2300–2330 m, Köckinger 88-112.2 (GZU) — Steinkarhöhe, N der Unt. Klafferscharte, ca. 2250 m, Köckinger 97-135.3 (GZU); Dachstein-Massiv: Eselstein, ca. 2350–2500 m, Köckinger 93-811, 93-817 (GZU); Rottenmanner Tauern: Kl. Geierkogel E. Hochschwung, ca. 1800 m, Köckinger 97-441, 97-494 (GZU); Hochschwab-Gruppe: Polster, SE side, ca. 1650 m, Köckinger 98-495 (GZU); Eisenerzer Alpen: S slopes of Mt. Wildfeld, 1690 m, Kučera E2767, E2774, E2776 (PR), Köckinger 98-929 (GZU); Wölzer Tauern: Gaistrumer Ofen bei Oberwölz, ca. 1000 m, Köckinger 96-302 (GZU). **Tyrol:** Kitzbühler Horn, 1990 m, 1882 leg. J. Breidler (BP); Allgäuer Alpen: Schochenalptal, 1520 m, 1996 leg. A. Schäfer-Verwimp (herb. Schäfer-Verwimp 19633); Hohe Tauern: Granatspitzgruppe: 1 km W Sudetendeutsche Hütte, ca. 2550 m, Köckinger 96-952 (GZU); Venedigergruppe: zwischen Zunagl und Muswand W Hinterbichl, ca. 2350 m, Köckinger 97-1180 (GZU); Glocknergruppe: Rocks NE Lucknerhaus, 2100 m, Kučera E2724 (PR).

FRANCE: Savoie: Dans le forêt de Zertan près Pralognan, 1907 leg. Sebelles (Z, PC); Peisey, 1930 leg. Abbé Guillaumet (PC).

GERMANY: Bavaria: Gipfel der Hochplatte, 1550 m, 1910 leg. H. Paul (M); Estergebirge, Krottenkopf, 1961 leg. J. Poelt (GZU); Zugspitze, 2900 m, 1997 leg. M. Preußing; Berchtesgaden, bei Funtensee, ca. 1630 m, 1920 leg. Th. Herzog (BP, JE); Kreis Garmisch-Partenkirchen: Osterfelder-Sattel zum Längenfelder, ca. 1860 m, 1989 leg. R. Lotto (herb. Meinunger); Kreis Füssen: Branderschrofen E Hohenschwangau, ca. 1750 m, 1996 leg. L. Meinunger (herb. Meinunger); Kreis Miesbach: Trainsjoch S Bayrischzell, ca. 1700 m, 1995 leg. L. Meinunger (herb. Meinunger).

ROMANIA: Făgăraș Mts., mons Királykő prope Zărnești, ca. 1500 m, 1962 leg. L. Vajda (BP).

SLOVAKIA: Bešeňová, travertines, ca. 550 m, 1958 leg. Z. Pilous (herb. Pilous); Belianské Tatry Mts.: sub monte Muráň, ca. 1680 m, 1946 leg. Z. Pilous (Z, PR); Mons Javorinka prope Podspády, 1500 m, 1962 leg. Á. Boros (BP); Hohe Tatra, Tokarnyn Wrch (= Tokáreň ca. 1200 m), 1906 leg. Györfly (JE). Malá Fatra Mts.: Chleb — skály na vrcholu, vápenec, 1951 leg. Z. Pilous (BRNM).

SWITZERLAND: Bern: Am Fuß des Eiger — Rotstock, ca. 2350 m, 1920 leg. Th. Herzog (JE); Kl. Scheidegg, ca. 2100 m, 1920 leg. Th. Herzog (JE); Gipfel des Männlichen, 2340 m, 1909 Culmann (Z); Unterhalb des Lauchenhorns am Faulhornweg, 2050 m, 1912 Culmann (Z); Klus bei Kandersteg, 1360 m, 1909 Culmann (Z). **Obwalden:** Schiessplang, 2120 m, 1931 P. Fintan Greter (Z). **Valais:** Chaurion, 2400 m, 1902 leg. Amann (Z); Pont de Nant, 10.6.1894, unsigned (LAU).

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TAXONOMIC ADDITIONS AND CHANGES: *Didymodon subandreaeoides* (Kindb.) R. H. Zander (syn. *Grimmia andreaeoides* Limpr.).

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J. KUČERA, University of South Bohemia, Faculty of Biological Sciences, Department of Botany, Branišovská 31, CZ-37005 České Budějovice, Czech Republic. E-mail: kucera@tix.bf.jcu.cz
H. KÖCKINGER, Karl-Franzens-Universität Graz, Institut für Botanik, Holteigasse 6, A-8010 Graz, Austria.