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Didymodon bistratosus (Pottiaceae) in the New World

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Abstract. *New to the Americas from California is* Didymodon bistratosus *J.-P. Hébrard & R. B. Pierrot, differing significantly from congeners by the deep red lower portions of the plant, and 2–3-stratose upper lamina. In California it was found on a sandstone boulder in a mesic oak woodland. Its range worldwide is restricted to California, the Iberian Peninsula and Turkey.*

Keywords. Mosses, *Didymodon*, disjunct, California, Mediterranean vegetation.

A uniquely distinctive *Didymodon* was found by the third author in the Santa Monica Mountains, west of Los Angeles, California. This plant is unlike all other *Didymodon* species previously known from North America and proved to match, in all essentials, specimens of *Didymodon bistratosus* from Mediterranean Europe. Below we describe from North American material how it may be recognized and discuss the origin of the disjunction.

DIDYMODON BISTRATOSUS J.-P. Hébrard & R. B. Pierrot, Nova Hedwigia 59: 354. 1994.

FIGS. 1–8

Plants forming a dense thin turf, *deep green above, strongly reddish brown below.* Stems to 0.2 cm in length, commonly branching; transverse section rounded-pentagonal, hyalodermis absent, sclerodermis weak or absent, cells of inner cylinder 20–25 μm in diam., central strand present, strong; rhizoids few, scattered; axillary hairs 3–5 cells in length, basal cell darker and more thick-walled. Cauline leaves appressed, weakly twisted clockwise or occasionally counterclockwise when dry, spreading and *weakly reflexed above the base* when moist; *long-ovate to elliptic-lanceolate,* adaxial surface broadly channeled at midleaf, concave to occasionally somewhat naviculate apically, usually 1–1.2 mm in length; base weakly differentiated, ovate; margins plane above, recurved below, entire; apex obtuse or acute, occasionally ending in a short, clear, sharp cell. Costa percurrent, *broad,* lacking adaxial outgrowths; adaxial cells at midleaf quadrate-hexagonal, papillose, in 6–8 rows; abaxial cells rounded quadrate-hexagonal; transverse section at midleaf bulging semicircular, occasionally reniform, adaxial epidermis convex, papillose, *adaxial stereid band absent,* guide cells 2–4 in 1 layer, *hydroid strand absent, abaxial stereid band present but very weak,* rounded or elliptic in sectional shape. Basal cells weakly differentiated in small area juxtacostally, very short-rectangular, 10–13 μm in width, 2:1, evenly thickened; upper medial cells rounded-quadrate, 7–10 μm in width, 1:1, *bistratose throughout upper lamina, often tristratose near leaf margins*; *papillae low, fused to a thickened and irregularly shaped lens covering lumen,* cell walls evenly thickened, weakly bulging on both sides of lamina, cells in longitudinal rows, homogeneous in size. Specialized asexual reproduction not seen. Sexual condition dioicous. Perigoniate plants clustered, gemmate, 1 to many perigonia per plant. Perichaetial leaves not or scarcely differentiated, inner leaves weakly sheathing below, archegonia 350–370 μm in length. Seta 0.9–1.3 cm long, reddish brown. Capsule cylindric, 1.2–1.7 mm long, stomata at base of capsule; peristome to 700 μm, of 32 filamentous teeth, twisted about once counterclockwise; *operculum long-conic, slightly curved, 1.1–1.5 mm long, cells twisted counterclockwise.* Calyptra cucullate, smooth, ca. 2–2.4 mm long. KOH laminal color reaction red.

Specimen examined: U.S.A. CALIFORNIA: Los Angeles County, Santa Monica Mountains, Seminole Hotsprings, Mountains Restoration Trust land, edge of old house-pad,

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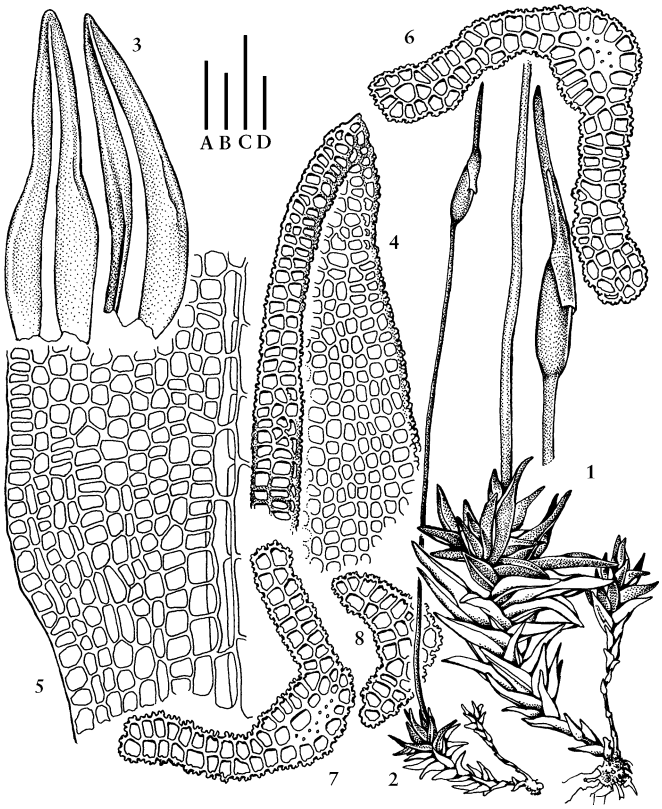

FIGURES 1–8. *Didymodon bistratosus*. — 1–2. Habits with sporophyte. — 3. Two cauline leaves. — 4. Leaf apex. — 5. Basal leaf cells. — 6–7. Transverse sections near midleaf. — 8. Transverse section near leaf apex. Scale bars: A = 1 mm (FIG. 1); B = 1 mm (FIG. 2); C = 0.3 mm (FIG. 3); D = 40 μm (FIGS. 4–8).

UTME 334329, UTMN 3774678 (NAD 27), 34°6.30′ N, 118°47.81′ W (NAD 27) USGS 7.5′ Point Dume Quad., 6 Feb 2005, *T. Sagar 437* (MO).

Habitat: Sandstone boulder, *Quercus agrifolia-Ceanothus spinosus* woodland, with *Dryopteris arguta* (Kaulf.) Maxon and *Pentagramma triangularis* (Kaulf.) Yatsk., elevation 315 m.

Didymodon bistratosus differs from its closest relative, *D. australasiae* (Hook. & Grev.) R. H. Zander, in the strongly bicolorous habit, plants deep green above and densely red below, and the bistratose and occasionally marginally tristratose upper lamina. It belongs, likewise, to sect. *Asteriscium* (Müll. Hal.) R. H. Zander by the absence of an adaxial stereid band and by the abaxial band strongly reduced to a few stereid cells. There are two other *Didymodon* taxa in North America with leaves that can be bistratose. *Didymodon rigidulus* Hedw. var. *subulatus* (Thér. & E. B. Bartram) R. H. Zander is always bistratose, but the costa is excurrent as a subula, and the abaxial stereid band is much stronger. *Didymodon nicholsonii* Culm. is usually defined by a lamina with bistratose margins on long-ovate leaves, but it is occasionally completely bistratose. Here again, the stronger adaxial stereid band rules out *D. bistratosus*. Since one of the defining features of *D. bistratosus* is the bicolorous habit, it is important to note that both *D. nicholsonii* and *D. vinealis* (Brid.) R. H. Zander can exhibit a variety of colors including orange, dark reddish brown, or almost black tints. However, none of these *Didymodon* taxa displays the bicolorous habit of *D. bistratosus*. *Didymodon vinealis* has often been confused with *D. bistratosus* in Europe, but the former is never completely bistratose, and the apical keeling usually creates a ''window'' effect to the upper costa that is diagnostic. *Bryoerythrophyllum columbianum* (F. J. Herm. & E. Lawton) R. H. Zander also has much the same reddish appearance, short leaf shape, and has a similarly broad upper costa, but the lamina is unistratose and the leaf apex of *B. columbianum* is sharply mucronate, rigid, fragile, and comprised of elongate cells.

Didymodon bistratosus was described by Hébrard and Pierrot (1994) from Málaga province, Andalucía, Spain, and subsequently has been found elsewhere in both southern Spain and Portugal (Jiménez 2004; Sérgio et al. 1998). This taxon has been considered an endemic species of the Iberian Peninsula until recently Erdağ and Kürschner

FIGURE 9. Distribution of *Didymodon bistratosus*.

(2005) collected it in southeastern Turkey. Here we report its presence in the New World for first time, from southern California, extending considerably its range (FIG. 9). According to Schofield (1988) the same or similar disjunction between the western coast of North America and the Mediterranean region has been observed in many moss species that occur in areas with a Mediterranean winter-wet, summer-dry climate, such as *Antitrichia californica* Sull., *Claopodium whippleanum* (Sull.) Renauld & Cardot, *Dicranella howei* Renauld & Cardot, *Scleropodium touretii* (Brid.) L. F. Koch, and *Tortula bolanderi* (Lesq. & James) M. Howe.

The species' extreme disjunction between Europe and California could have originated at any time in the past. *Didymodon bistratosus* may have been introduced into southern California recently by human agency. If so, it might become invasive as has *Campylopus introflexus* (Hedw.) Brid., which was first collected in northern California in the 1960s and occurs today as a common, disturbance-oriented species along the Pacific Coast from central California to northern Oregon. Alternatively, it is possible that *D. bistratosus* has arrived naturally during the relatively recent geological history as California and the Mediterranean became similar in climate. Finally, the species could represent an ancient disjunction. If this were so, populations on the two continents would be expected to have diverged genetically in spite of their close morphological similarity as, for example, is demonstrated by the cryptic divergence of the trans-Antarctic populations of *Pyrrhobryum mnioides* (Hook.) Manuel (McDaniel & Shaw 2003), by the higher genetic diversity of *Anacolia menziesii* (Turn.) Paris in North America than in the Mediterranean region (Werner et al. 2003), and by the higher levels of nucleotide diversity in North American plants of the species *Claopodium whippleanum* (Sull.) Renauld & Cardot, *Dicranoweisia cirrata* (Hedw.) Milde, and *Scleropodium touretii* compared to the plants of the same morphospecies from southern Europe (Shaw et al. 2003).

Didymodon bistratosus in Seminole Hotsprings, in the central portion of the coastal Santa Monica Mountains, grows on an apparently native sandstone boulder in an opening in coast live oak (*Quercus agrifolia* Née) woodland with an understory of greenbark ceanothus (*Ceanothus spinosus* Nutt.), toyon [*Heteromeles arbutifolia* (Lindl.) M. Roem.], poison oak [*Toxicodendron diversilobum* (Torr. & A. Gray) Greene], various ferns and forbs. Overall, the Santa Monicas are dominated by chaparral, but these relatively young mountains are dissected by a complex network of mainly seasonal, rather deep and narrow drainages that provide a range of microhabitats including more mesic patches on the north-facing slopes. The *D. bistratosus* station was in a meadow within surrounding oak woodland, and at a short distance from two seasonal drainages contributing to the mesic nature of the area. An overgrown roadbed, built several decades ago, possibly by a homesteader to access one of the seasonal waterfalls, leads past the opening in the oak grove. Close by, a rusted Jeep frame, as well, indicates past disturbance. Part of the small opening was cleared at some point—probably several decades ago—and the boulder may have been pushed

to its present location at that time. Today the rather lovely opening in the woodland is dominated by knee-high *Anthriscus caucalis* M. Bieb. but dotted by fiesta flower [*Pholistoma auritum* (Lindl.) Lilja *ex* Lindbl.], while the small *Cardamine oligosperma* Nutt. clings to the sides of the boulder, finding foothold in the dense, thin *D. bistratosus* mat. On the boulder, the only other bryophyte was *Tortula muralis* Hedw. On soil near by were other locally common species: *Bryum lisae* De Not., *Fissidens sublimbatus* Grout, *Funaria hygrometrica* Hedw., *Scleropodium touretii*, *Timmiella anomala* (Bruch & Schimp.) Limpr., *Asterella californica* (Hampe) Underw., *Riccia nigrella* DC., and *Sphaerocarpos texanus* Austin. Farther out below the surrounding woodland canopy, the most abundant species are *Scleropodium californicum* (Lesq.) Kindb. and *Didymodon vinealis* (Brid.) R. H. Zander. Deeper in the canopy, under the poison oak and greenbark ceanothus, in the mountains where *Didymodon rigidulus* and *D. vinealis* are perhaps the most common mosses, a few more boulders may be found to support *D. bistratosus*, but a more abundant *Scleropodium* species appears to dominate most of the scattered boulders in the area.

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