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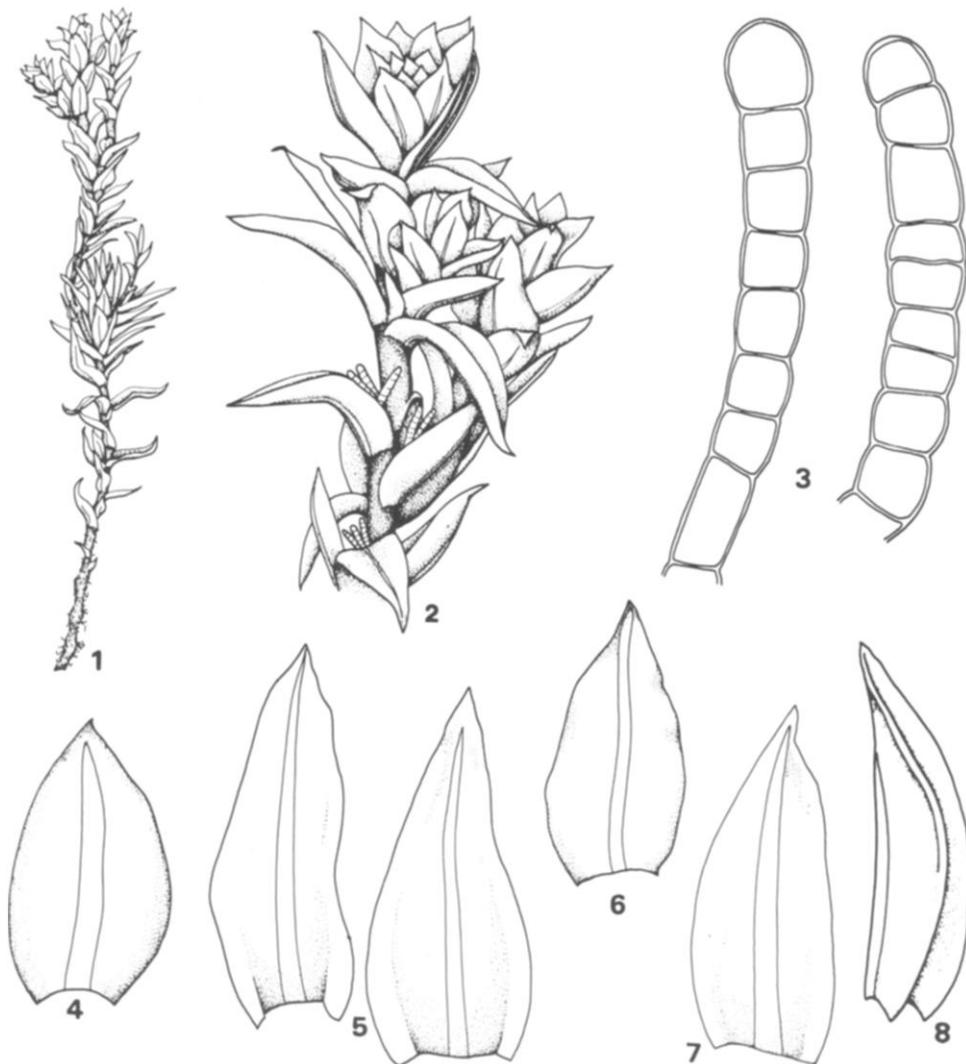
Propaguliferous *Ceratodon purpureus* in Riparian Environments

Abstract. *Some North American riparian populations of Ceratodon purpureus (Hedw.) Brid. are characterized by filamentous propagula that are borne most abundantly on stems of sterile plants. The plants are similar to the type of C. dimorphus Philib., which the authors consider a synonym of the polymorphic C. purpureus.*

Ceratodon purpureus (Hedw.) Brid. (Ditrichaceae) is a cosmopolitan, weedy, highly polymorphic acrocarpus moss exhibiting forms and habitat preferences of such diversity that it may be referred to either the stress-tolerant or the ruderal category of primary adaptive strategy described by Grime (1977). Though morphological variability is considerable (Index Muscorum, Wijk et al., 1959–1969, lists three subspecies and 36 varieties worldwide as good taxa), the characteristic capsules, the general appearance of the plant, the leaf margins serrulate above and the laminal areolation of regularly quadrate, smooth cells is usually sufficient for identification. Taxonomic appraisals of specific and infraspecific categories in *Ceratodon* vary considerably (cf. Britton, 1913; Crum et al., 1973; Grout, 1936; Nyholm, 1954). Dixon (1924), Flowers (1973) and Ireland (1971) agree that much phenotypic intergradation, involving many characters, occurs in *C. purpureus*.

The senior author discovered a propaguliferous variant (Fig. 1–8) of *Ceratodon purpureus* in Pennsylvania, similar to that described by Ireland (1971), which was referred to the forma *dimorphus* (Philib.) Mönk. In a subsequent survey of collections of *Ceratodon purpureus* at BUF and CANM, we found several specimens, from scattered riparian stations in North America, that bore filamentous propagula. No tubers (=brood bodies of some authors) were seen on basal rhizoids, confirming Whitehouse's (1976) evaluation that all previous reports of these for *C. purpureus* are to be discounted as very doubtful or as mistakes. The propagula are borne directly on the stem (Fig. 2) in small clusters of 1–10 in., and just above the leaf axils. They are most frequent on older portions of the stems. The axillary hairs are quite different, being composed of long, narrow, echlorophyllose cells with the basal cell usually thicker-walled, and originate only from the upper segment of the adaxial leaf base (as illustrated by Saito, 1975, for *Barbula unguiculata* Hedw.). The propagula are green to light brown, filamentous to occasionally clavate, occasionally with 1–2 short lateral branches, mostly 150–190 μm long, composed of (4)6–8(15) uniseriate, thin-walled, short-cylindrical cells, each cell about as wide as long, occasionally with longitudinal internal walls. The transverse walls are often darker brown than the superficial walls. At times the propagula are rather dark brown, but they lack the thickened walls of what are usually interpreted as perennating bodies. Also, the internal oil (refractive) globules typical of rhizoidal propagula of other moss species are lacking or few and small. Sometimes the propagula are composed of long-cylindrical cells and look much like protonema and, indeed, may be developing into such.

The plants with propagula are generally sterile with flaccid, incurved, acute, ovate-lanceolate leaves (usually shorter and broader than those on plants without propagula), each with a percurrent costa and plane to recurved margins. Although the plants with



FIGURES 1-8. *Ceratodon purpureus* (Hedw.) Brid., propaguliferous plants. — 1. Habit, $\times 6$. — 2. Portion of stem with propagula, $\times 25$. — 3. Propagula, $\times 290$. — 4. Leaf (abaxial surface), $\times 50$. — 5. Leaves (adaxial surface), $\times 50$. — 6. Leaf (abaxial surface), $\times 50$. — 7. Leaf (adaxial surface), $\times 50$. — 8. Leaf (lateral view), $\times 50$. Figures 1-5 from *Ireland 5579*; 6-8 from *Zander 4127*. Illustrations by Linda Ley.

that combination of characters at first appeared to us to be a taxon distinct from *C. purpureus*, it was discovered upon the examination of herbarium collections that intergradations occurred in all of these morphological features. No consistency in gametophore characteristics would allow referral of all propaguliferous specimens to any one infraspecific category. Most of them appear to fit the description and plants of an isotype, var. *dimorphus* (Philib.) Mönk. ex Geh., which we now believe is a synonym of *C. purpureus*. It is recognized as distinct in the checklist of Crum et al.

(1973). The isotype of *C. dimorphus* Philib. (Switzerland: Simplon Pass, Valaise, 2000 m, *Philibert*, 4 August 1887, in CANM was found to have propagula even though they are not described in the protologue of the species.

We agree with Andrews (1932) that *Mielichhoferia recurvifolia* Kindb. of British Columbia, Canada, is *Ceratodon purpureus*. The sterile plants of the isotype at CANM possess the leaf shape and propagula described above. The propagula are borne in large clusters, are well developed and often branched (with the appearance of those of *Hyophila involuta* (Hook.) Jaeg. & Sauerb.).

Mass collections (Zander & Eckel 4664, 4665) of *Ceratodon purpureus* at the Snyder County, Pennsylvania, station where propaguliferous plants had been found about a year earlier revealed that plants bearing abundant propagula characteristically appear in 1–3 cm wide clumps in crevices of the exposed E-facing vertical sides of a huge boulder about 1.5–2.5 m above the (non-flood) waterline. The plants are sterile and have ovate-lanceolate leaves with percurrent or subpercurrent costae, which is typical of most propaguliferous specimens from elsewhere in North America. The only fertile plants at this station grow in a broad, 5–20 cm wide turf on soil in less exposed positions 3–6 m from the river. This turf consists of sterile plants mixed with antheridial and archegonial plants, many of the latter bear young sporophytes in the spike stage of development. The leaves of the fertile plants are somewhat longer and narrower than those of the sterile; however, some archegonial plants bear propagula, though scantily. The presence of propagula in both fertile and sterile plants and the characteristic riparian habitat point to the possibility of some degree of ecotypic differentiation of propaguliferous expressions of *Ceratodon purpureus*. However, some herbarium specimens were seen that have flaccid, incurved, ovate-lanceolate leaves but lack propagula entirely and occur in both riparian and non-riparian habitats. The observed partial phenotypic segregation at the Pennsylvania site into mostly propaguliferous, sterile clumps on the exposed riverside rock face and mostly non-propaguliferous, often fertile turf in more protected areas may be due to some environmental effect, although this could also be caused by chance juxtaposition of two genetically different populations or by ecotypic differentiation. Experimental study of propaguliferous populations of *C. purpureus* would be worthwhile.

Many authors note that the asexually reproducing expressions of some species are associated with certain environments; for instance, Griffin (1977) found that *Leiomela bartramoides* (Hook.) Par. varies considerably in production of deciduous leaves, and collections with such asexual diaspores come mostly from exposed rock surfaces. Whitehouse (1973) reported that the tubers of *Ditrichum pusillum* (Hedw.) Britt. were less frequent on fertile plants. The propaguliferous variety of *Dicranum speirophyllum* Mont. is always sterile and occurs in more stressed, exposed habitats than does the frequently fruiting non-propaguliferous variety (Bartram, 1933; Hoe, pers. comm.). In some cases, sexual-asexual dimorphism may be environmentally triggered. For example, the leaves of *Tortella fragilis* (Drumm.) Limpr. have fragile, thickened, propaguloid apices. However, plants of both var. *fragilis* and var. *tortelloides* Zander & Hoe, when transferred to humid growth chambers, formed new lateral branches with leaves similar to those of *T. tortuosa* (Hedw.) Limpr., a closely related species that lacks modification of the leaf apices (Zander, unpubl.; Zander & Hoe, 1979). Although propaguliferous expressions are often recognized as taxa distinct from similar but non-propaguliferous morphotypes, simple, multicellular propagula have been induced in culture in several *Barbula* species for which these previously had been unknown (Maheu, 1908). In *Eucladium verticillatum* (Brid.) B.S.G., propagula

have been only rarely seen—Dalby (1966) and Dunk and Dunk (1973) report their occurrence in cave populations; however, Saito (1972, 1975) has forced production of rhizoidal propagula in this species in culture.

The habitat of the propaguliferous expression of *Ceratodon purpureus* is largely riverbanks, but occasionally lakeshores, found on limestone, red shale, gneiss, stone wall, soil and a wooden bridge, from near sea level to 2280 m elevation. It apparently has no distinctive geographic range different from that of the non-propaguliferous facies.

Out of 1014 specimens of *C. purpureus* examined in the herbaria of CANM and BUF, only 10 propaguliferous specimens were discovered. This small figure is undoubtedly not representative of the abundance of the propaguliferous plants in nature, since collectors are usually selective in choosing largely well-developed plants with sporophytes, and it is these plants that normally lack propagula. To determine true abundance, sampling studies would be required whereby entire colonies of *C. purpureus* are searched for propaguliferous plants.

In summary, we believe the following should be considered synonyms of *Ceratodon purpureus* (Hedw.) Brid.: *C. dimorphus* Philib., Rev. Bryol. 15: 28, 1888; *C. purpureus* subsp. *dimorphus* (Philib.) Limpr., Laubm. Deutschl. 3: 683, 1901; *C. purpureus* var. *dimorphus* (Philib.) Mönk. in Geh., Allg. Bot. Zeitschr. 15: 92, 1909; *C. purpureus* fo. *dimorphus* (Philib.) Mönk., Laubm. Eur. 158, 1927; *Mielichhoferia recurvifolia* Kindb., Rev. Bryol. 35: 36, 1905.

Propaguliferous North American specimens of Ceratodon purpureus.—U.S.A. ARIZONA: COCOCINO CO., Oak Creek Gorge, West Fork, *Zander 4142* (BUF). NEW YORK: CHENANGO CO., NE of North Norwich, between Chenango R. and canal towpath, *Glowny*, 1971 (BUF); NIAGARA CO., Goat I., Niagara Falls, *Zander 4127* (BUF, CANM). PENNSYLVANIA: NORTHUMBERLAND CO., ca. 1.5 km S of village of Fisher's Landing, roadside of Penn. Rt. 147 above Susquehanna R., *Zander & Eckel 4661* (BUF, CANM, PAC); SNYDER CO., picnic area ca. 1.5 km N of Juniata Co. line, roadside of U.S. Rt. 15, riverside of Susquehanna R., *Zander 4630* (14 March 1977) (BUF, CANM, PAC); same location, *Zander & Eckel 4664, 4665* (16 April 1978) (BUF, CANM, PAC). WASHINGTON: KING CO., ca. 16 km NW of Redmond, *Ireland 5579* (CANM). CANADA. BRITISH COLUMBIA: foot of Lake Agnes, *Macoun*, 1904 (CANM—isotype of *Mielichhoferia recurvifolia* Kindb.). ONTARIO: Parry Sound District, Patterson Twp., Scott's Dam, Restoule R., just W of Restoule Prov. Park, *Cook 2008* (CANM). QUEBEC: PONTIAC CO., Mansfield Twp., escarpment ca. 1.8 km NW of Fort Coulonge, 45°54'N, 76°48'W, *Ley*, 19 Sept. 1978 (CANM).

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Some Mosses from British Honduras

Abstract. Two relatively small collections of mosses from British Honduras yielded 51 species, of which 23 apparently have not been reported previously from this country. In addition to being closely related to that of Guatemala, the moss flora of British Honduras also demonstrates close affinities with the West Indian moss flora.

In spite of its small size—or perhaps because of it—British Honduras has not received the thorough bryological exploration which has been given to neighboring Guatemala (Bartram, 1949). The last reports on the mosses of British Honduras were published more than thirty years ago (Bartram, 1932, 1934; Steere 1934, 1937, 1946) and were based on collections made by non-bryologists in conjunction with work on other groups of plants.

During the first half of 1934, William A. Schipp of Belize worked with the British Honduras-Guatemala Border Survey. He made a relatively small collection of bryophytes. Although his field labels refer only to the survey camps by number without coordinates or other data, the approximate altitudes reaching nearly 1000 m above sea level would suggest that he was working in the more mountainous areas of the southwestern British Honduras border. Due to the lack of a professional bryologist at the New York Botanical Garden at that time, this collection was placed in storage. It came to light only very recently, and the specimens are now deposited at NY. A more recent collection, from farther east and at lower elevations, was made by the late Marian