NOTES ON BARBULA AND PSEUDOCROSSIDIUM (BRYOPSIDA) IN NORTH AMERICA AND AN ANNOTATED KEY TO THE TAXA

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This preliminary study of Barbula s. lato was prepared in the course of work on taxa of Pottiaceae for the proposed moss floras of Mexico (ed. A.J. Sharp) and of Arctic North America (ed. W.C. Steere, G.S. Mogensen & R.R. Ireland). It is a synthetic treatment based on representative specimens from a wide geographic area and is offered as an alternative to the usual floristic evaluation of species based only on regional collections. In adopting a broader species concept in this and in recent work (Zander, 1977, 1978a, 1978b), I feel that the taxa recognized have gained in biological meaningfulness. Nomenclatural designations for some extreme expressions, permutations of character states, and geographic variants have been lost. But these morphs, in any case, cannot be dealt with by type methodology and the principle of priority, because of lack of clear discontinuities, and must be designated, if at all, by informal names. Gained, hopefully, is a sense of proportion in the recognition of patterns of variation, within and between taxa, that are often interpretable as evolutionary trends or adaptations; the realization that many genera and species of Pottiaceae are widely distributed in the world in geographic patterns often correlating with certain climates or topographic features; and, the practical value of being able to use good technical characters to fairly easily name distinguishable entities in a moss family whose taxonomy has long been reputed to be "cursed" and "difficult and nasty" (Anon., pers. comm.). It is often said that overly broad species concepts are more difficult to correct, at a later time, than overly narrow concepts. However, this is a simplistic view in that most of the effort of present-day revisionary work is in making sense of the overly analytical results of past one-character or regional taxonomy. Such difficulties are discussed as length by Best (1905) who invoked a kind of botanical Manichaicism in early rebellion against atomistic taxonomic attitudes similar to those espoused by Grout (1938a).

"Andro-" and "gynogametophyte" are terms used here instead of "male" and "female plant" because the former terms ought to be used to distinguish sexually differentiated gametophytes (dioicy) while the latter terms refer to sexual differentiation of sporophytes (dioecy). Sporophytes of mosses are always sexless, but the gametophytes may be dioicus or monoicus. Sporophytes of seed-bearing plants may be monoecious or dioecious, but the gametophytes are always dioicous. Dioicy and monoicy are associated with homosporous and the production of gynandrogametophytes, or of both andro- and gynogametophytes, from the same sporangium, but dioecy and monoicy are associated with heterosporous and the production of andro- and
gynogametophytes from different sporangia. Although I consider the substitution of the terms "phyllidium" and "caulidium" for the moss "leaf" and "stem," respectively, to be an unnecessary nicety that does not reflect major genetic differences, the above sexual distinctions are of evolutionary importance and should not be confused or minimized by false homology.

In a study of the very closely related genus *Didymodon* (Zander, 1978a), I supported the use of Saito's (1975) distinctions between *Didymodon* and *Barbula*, which are based largely on gametophyte characters. These were presented in a table. The North American representation of species previously recognized in *Barbula* are here placed in two genera and included in the same key to facilitate identification.

**KEY TO PSEUDOCROSSIDIUM AND SUBGENERA AND SECTIONS OF *BARBULA* IN NORTH AMERICA**

1. Upper leaf margins broadly revolute to spiral-revolute, with cells often more strongly chlorophylllose than medial leaf cells; abaxial stereid band of costa usually strong but adaxial band weak or commonly absent; costa usually excurrent as a stout mucro or short awn. **Pseudocrossidium** Williams

2. Upper leaf margins narrowly recurved to plane, with cell chlorophyll content equal to that of medial cells; both stereid bands usually clearly differentiated, the adaxial usually present though occasionally weak or absent; costa ending below leaf apex, percurrent or excurrent as a mucro. **Barbula** subg. *Hyophiladelphus* (C. Müll.) Zander

3. Leaves lanceolate to ligulate or ovate, costa subpercurrent to excurrent, laminal cells papillose to nearly smooth, either similar on both sides of leaf or more strongly convex adaxially than abaxially but then costa percurrent, annulus persistent. **Barbula** sect. *Hydrogonium* (C. Müll.) K. Saito

4. Leaves firm when wet, upper laminal cells quadrate, papillose, both exposed surfaces similar.
4. Upper leaf margins usually recurved, propagula (when present) small, of 1–10(15) cells; perichaetial leaves seldom strongly differentiated, with cells mostly parenchymatous. ................. Barbula Hedw. sect. Barbula

4. Upper leaf margins plane, propagula (when present) often large, of 4–50 or more cells; perichaetial leaves often convolute-sheathing, with cells highly prosenchymatous. ............... Barbula sect. Convolutae B.S.G.

KEY TO SPECIES AND VARIETIES OF BARBULA AND PSEUDOCROSSIDIUM
IN NORTH AMERICA

1. Leaves spatulate; upper laminal cells adaxially bulging and abaxially flat, epapillose; costa sharply excurrent; annulus revoluble; U.S.A. (Gulf Coast states), Mexico. ...................... 11. B. agraria Hedw.

1. Leaves lanceolate to ligulate or ovate; upper laminal cells superficially similar on both sides of leaf, or adaxially more strongly convex than abaxially but then costa percurrent, usually papillose, seldom smooth or nearly so; costa ending variously; annulus persistent. ...................... 2.

2. Upper laminal cells often lax, quadrat e to rectangular, usually not or weakly papillose, leaves rather flaccid when wet. ................................................ 3.

2. Upper laminal cells firm, quadrat e, usually distinctly papillose, leaves usually firm when wet. .............................. 4.


3. Leaves narrowly lanceolate to long-triangular, margins narrowly recurved to near apex, laminal cells 8–12 µm wide, 1:2:1; Mexico. ............................. 10. B. arcuata Griff.

4. Abaxial costa surface doubly prorulose (i.e. with both ends of rectangular superficial cells protruding) near apex, often with coarsely mamilllose or very rough appearance; leaf base not sheathing; Canada (Alberta), U.S.A. (southeastern and southwestern states), Mexico. ....................... 5. B. indica (Hook.) Spreng.

4. Abaxial costa surface with hollow or solid papillae or epapillose, seldom distinctly prorulose near apex (but then leaf base is strongly sheathing); leaf base occasionally sheathing. ........................................ 5.
5. Leaf apex acute to somewhat blunt, margins plane or weakly recurved below........................................... 6.

5. Leaf apex rounded, margins plane to revolute (apex occasionally acute but then margins recurved above midleaf).................. 8.


6. Costa 1-6 cells subpercurrent, leaf apex entire or occasionally apiculate by a clear or weakly papillose conical cell, leaf base not sheathing; propagula often present, borne on basal rhizoids.............................. 7.

7. Perichaetial leaves acute to abruptly subulate, loosely sheathing; western Canada, western U.S.A. south to Texas................................. 8. B. eustegia Card. & Thér.

7. Perichaetial leaves obtuse to broadly acute, convolute-sheathing; Canada, U.S.A., Mexico............................................................ 7a. B. convoluta Hedw. var. convoluta


8. Leaves apiculate, mucronate, or awned......................... 12.

9. Leaf margins plane or recurved to midleaf, propagula multicellular.................................................. 10.

9. Leaf margins recurved to near apex, propagula unicellular... 11.

10. Propagula borne on basal rhizoids, leaves ligulate to oval, costa usually subpercurrent by 4-8 cells; Canada, U.S.A., Mexico........... 7a. B. convoluta Hedw. var. convoluta p.p.

10. Propagula borne in upper leaf axils, leaves oval, costa subpercurrent by 2-4 cells; Canada (Northwest Territories), U.S.A. (Alaska). 7b. B. convoluta var. gallinula Zander

11. Leaves ovate, marginal cells not differentiated as a border; propagula common, yellow-brown, borne in axillary masses; U.S.A. (North Carolina), Mexico....... 4. B. inaequalifolia Tayl.

11. Leaves ligulate, marginal cells often thick-walled in 2-3 rows; propagula uncommon, red-brown, few in leaf axils; Mexico........... ........................................ 3. B. calcarea Thér.

12. Leaves apiculate or mucronate................................. 13.

13. Leaf margins plane or weakly recurved below midleaf; Canada, U.S.A., Mexico... 7a. *B. convoluta* Hedw. var. *convoluta* p.p.

13. Leaf margins recurved to spiral-revolute, usually to near apex................................................................. 14.

14. Costa with adaxial stereid band distinct; leaf margins narrowly recurved, marginal cells not differentiated.. 15.

14. Costa usually lacking adaxial stereid band; leaf margins broadly recurved to spiral-revolute, cells often weakly papillose on exposed portions of margins, and thin-walled, highly chlorophylllose within the spiralled portion.... 16.

15. Leaf apex obtuse to broadly acute, margins recurved in lower 1/2-2/3; propagula apparently not produced in nature; Canada, U.S.A., Mexico........... 1. *B. unguiculata* Hedw.

15. Leaf apex abruptly rounded to emarginate, margins recurved to near apex; propagula spherical, in leaf axils; Mexico............ ............................... 2. *B. orizabensis* C. Müll.

16. Leaf margins strongly recurved to once (seldom more) revolute, propagula occasionally present on adaxial surface of costa, inner perichaetial leaves convolute-sheathing; Canada (British Columbia, Yukon and Northwest Territories), U.S.A. (Oregon, California).......................... 

............................................................... 12. *P. revolutum* (Brid. in Schrad.) Zander

16. Leaf margins strongly spiral-revolute, propagula absent, inner perichaetial leaves not or little differentiated; U.S.A. (southwestern states), Mexico.......................... .......................... 13. *P. replicatum* (Tayl.) Zander
Type species: Barbula unguiculata Hedw. (lectotype fide Steere, 1938).

The genus Barbula is commonly distinguished from Tortula Hedw. by the presence of two sterieid bands in its costa rather than only one. However, the adaxial sterieid band is often absent in certain species of Barbula. In such cases, the presence of a differentiated epidermis of large-lumened or at least larger-sized cells on the abaxial surface of the costa will distinguish Barbula species. Such an epidermis is not or is only poorly differentiated in Tortula. The North American taxa of Barbula are distinctive and fairly easy to identify by diagnostic characters, although some of the species are polymorphic.

BARBULA Hedw. sect. BARBULA


Additional synonymy is given by van der Wijk, et al. (1959-1969).

Sect. Barbula is characterized by firm leaves; upper leaf margins generally narrowly recurved, occasionally plane; laminal cells papillose; perichaetal leaves seldom strongly differentiated; and, propagula (when present) small, each composed of 1-10(15) cells.


Synonymy is given by Podpýra (1954), Saito (1975) and Steere (1938).

This well-known, common species of ruderal habitats is described and illustrated by most authors of moss identification manuals for temperate zone areas. Barbula unguiculata fo. propagulosa Crum is a synonym of B. indica, q.v. I agree with Cardot (1899) and subsequent authors that Barbula stricta Hedw., Spec. Musc. 119, 1801 (type: U.S.A., Pennsylvania, Muehlenberg s.n., G—holotype) is a synonym of B. unguiculata.
This species is readily distinguished from the similar B. indica by the usually stoutly mucronate costa, which has scattered simple papillae abaxially above midleaf, and the leaf margins more strongly recurved. Barbula unguiculata is rare in Mexico, apparently replaced by the closely related B. orizabensis.

Propagula have never been observed in herbarium collections of B. unguiculata, although occasional swollen ends of rhizoids ("galls" fide Whitehouse, 1973) may mimic rhizoidal propagula (= "tubers" or "brood bodies"). However, specimens cultivated on nutrient agar by D.V. Basile at NY and on moistened perlite by myself at BUF have produced unicellular, green or brown, elliptical propagula, each ca. 20–25 μm long, borne in clusters of uniseriate chains on the ends of long, brown rhizoids arising from the bases of the stems.

   Type: Mexico, Veracruz, Orizaba, Mohr, 1874 (NY—topotype).

   Synonyms: Barbula recurvicospus C. Müll., Bull. Herb. Boiss. 5: 557. 1897. Type: Jamaica, Bridge Hill, Harris 11038 (BM—lectotype), Contenti Road, Harris 10082 (BM—syntype).


   Barbula orizabensis is easily distinguished from B. unguiculata by the characters in the key, although I agree with Theriot (1931) that the two species are closely related. It is described and illustrated by Bartram (1949) and is known from many states in Mexico (Crum, 1951) and from Guatemala (Bartram, 1949) and Jamaica (Crum & Bartram, 1958). It occurs on soil or rock, usually at high elevations. The synonym B. stenotheca was described as a species of Barbula sect. Streblotrichum (= sect. Convolvatae) on account of the convolute-sheathing perichaetial leaves of the type specimen. Species of sect. Barbula occasionally have rather differentiated perichaetia while those of sect. Convolvatae occasionally have undifferentiated perichaetia. On the basis of evaluation of all characters ("Summe der Merkmale" of Loeske, 1910), however, B. orizabensis belongs in sect. Barbula.

   Type: Mexico, Distrito Federal, Desierto, Amable 1620 (PC—lectotype, NY—isotype); Michoacán, Morelia, Loma Santa María, Arsené 4891 (PC—syntype).

Barbula calcar ea was described and illustrated by Theriot (1931) and, as *B. linguaeefolia*, by Bartram (1949). This species is closely related to *B. inaequalifolia*, from which it differs by the characters in the key. The upper leaf margins are occasionally bistrose in small patches and the perichaetial leaves convolute-sheathing in the lower 1/3-2/3. The original description of the synonym *B. linguaeefolia* is incorrect in ascribing plane margins to the type. Propagula were seen only in the lectotype and syntype of *B. calcar ea*. These were found, unattached, in leaf axils, 2-4 per axil, not borne in massive axillary clumps as in *B. inaequali­folia*. I have seen collections of *B. calcar ea* from Mexico (Distrito Federal, Mexico, Michoacán) and Guatemala; these occurred on soil or calcareous rock at 2600-2800 m elevation.


Type: Ecuador, Jameson, 1863 (FH—isotype).

For complete synonymy see Zander (1968).

A description and illustrations were given by Zander (1968), who cited specimens from U.S.A. (North Carolina), Colombia, Ecuador, China, and Java. An additional station has been noted (Zander, 1976) in Chiapas, Mexico. The following collections extend the geographic range of this species: Mexico: Mexico, between Mexico and Puebla, Dull, 1966 (BUF); Michoacán, Uruapan, Fyfe & Fyfe 305la (TENN); Panama: Chiriquí, Volcan Baru, Pineda 964 (MO); Venezuela: Trujillo, Boconó, Paramo de Guirigay, López & Rodríguez 8788—a (FLAS); India: Uttar Pradesh, Kumaun, Debidhura, Pithoragarh, Srivastava L3148 (BUF). The habitat includes roadsides, banks, paramos, on soil, rock, walls, from 700-3100 m elevation. *Husnotiella revoluta* Card. occasionally has axillary masses of unicellular propagula (Bartram, 1926; Zander, 1977) and when sterile may be confused with *B. inaequalifolia*. The former species differs in the following combination of characters states: leaves short-oval to deltoid oval, laminal cell walls evenly thickened, laminal papilae solid, low, broad, simple to multiplex, usually lens-like, and costa with only one stereid band.

In spite of the peristome being red, well developed and twisted 1-4 turns, *B. inaequalifolia* may be better placed in *Bryoerythrophyllum* Chen because of its red coloration and closely hollow-papillose, thin-walled upper leaf cells. It has much the same general appearance as does *Bryoerythrophyllum bolivianum* (C. Müll.) Zander, which, however, has plane margins, lacks propagula, and has the rudimentary peristome typical of *Bryoerythrophyllum* species (Zander, 1978b). This is another confounding example of a moss species with a gametophyte matching the characters of one genus and a sporophyte those of another.


This section is distinguished by the combination of the following character states: leaves firm when wet; plane or weakly recurved leaf margins; papillose laminal cells; adaxial stelar band of costa usually distinct; perichaetial leaves usually convolute-sheathing; and, propagula (when present) often large, composed of 4-50 or more cells.


Barbula cancellata C. Müll., Flora 56: 483. 1873.


Additional synonymy is given by Crum and Steere (1957), Saito (1975) and Steere (1938).

Plants turf-forming, yellow-green to brown; stems seldom branching, to 1.2 cm tall, in transverse section pentagonal, central strand distinct, cortex of smaller, darker cells, epidermis not differentiated; axillary hairs usually of 4-8 uniseriate cells, all clear or the basal 1(-2) with somewhat thickened walls and yellow-brown coloration; tomentum absent. Leaves crowded to rather distant, about equal in size from base to apex, when dry incurved—pressed, often infolded above, occasionally catemulate, when wet erect—
spreading, incurved to plane, ovate to ligulate, occasionally lanceolate or long-triangular, 0.5-1.8 mm long, with a deep, narrow groove adaxially along the costa, margins plane to weakly recurved at midleaf, entire; leaf apex somewhat incurved or weakly cucullate to nearly plane, rarely reflexed, rounded to bluntly acute, apiculate by a clear, not or little papillose, conical cell, rarely muticus; leaf base scarcely differentiated to much broadened, square to rectangular or oval, basal margins not or shortly decurrent; costa usually percurrent or ending 1-4 cells below apex or occasionally excurrent in a short, sharp macro, abaxial superficial cells near apex long- to short-rectangular or quadrate, doubly prorulose (distal and proximal ends of cells protuberant), occasionally nearly smooth or both prorulose and simply papillose, adaxial superficial cells long- to short-rectangular, smooth, or quadrate and papillose in patches above midleaf; costa in transverse section semicircular to elliptical, ventrally flat to convex, lamina inserted at about 90° angle, adaxial epidermis often differentiated as one layer of thin-walled cells, adaxial stereid band absent or weak, guide cells in one layer of 2-4 cells, abaxial stereid band strong, abaxial epidermis undifferentiated or represented by one layer of thick-walled cells with semicircular lumens or with thin walls and circular lumens. Upper laminal cells quadrate, 7-9(10) μm wide, walls thin to evenly thickened, superficially weakly bulging to conic-protuberant, lumens angular, arranged in a weak pattern of longitudinal rows, papillae low-multiplex, mostly hollow, with 4-8 salients per lumen, occasionally coroniform above strongly protuberant cell walls; basal laminal cells medially smooth, 8-12 μm wide, 2-5:1, rectangular, evenly thickened or thin-walled, usually bordered on the margins by 1-4 rows of short-rectangular cells. Propagula often present, borne on stalks in leaf axils issuing just above the axillary hairs, obovoid, clavate, spindle-shaped, elliptical, or spherical, smooth, colliculate or armed with 1-several short, pointed branches, 70-300 μm long, of 8-50 or more cells, green to brown. Dioicus; perichaetium terminal, leaves ovate, entirely prosencho-mateous and convolute-sheathing grading to lanceolate, prosencho-mateous only in the lower 1/3 of the leaf and weakly sheathing, 0.8-2.5(3.0) mm long; perigonia terminal on smaller plants, gémmate, leaves oval.

Seta 0.7-1.3 cm long, red-brown, twisted clockwise; urn 0.8-1.8 mm long, red-brown, smooth when dry, elliptical to ovoid, occasionally curved, neck little differentiated, exothelial cells 18-25 μm wide, 3-6:1, thin- or thick-walled, evenly thickened, stomates present at base of urn, phaneropore, annulus weakly differentiated; peristome inserted on mouth of capsule, of 32 teeth weakly fused in 16 pairs, 0.7-1.7 mm long, teeth linear, densely spiculose, red to orange, with many articulations, little to strongly twisted 0.25-3.0 times, counterclockwise; spores (8)9-12 μm in diameter, smooth to weakly papillose, light brown to yellow-brown; operculum 0.8-1.7 mm long, long- to short-conic, cells twisted counterclockwise. Calyptra 2.0-2.2 mm long, cucullate, usually rough apically with prorulose cells.
The habitat of *B. indica* includes soil, clay, limestone, coral walls, roadbanks, riverbanks, walls, limepit, tree trunks, from near sea level to 3900 m. I have examined specimens from Canada (Alberta), U.S.A. (southeastern and southwestern states and Hawaii), Bermuda, Mexico (Chiapas, Durango, Hidalgo, Jalisco, Morelos, Oaxaca, San Luis Potosí, Sonora, Veracruz), Guatemala, British Honduras, Cuba, Jamaica, Dominican Republic, Haiti, Puerto Rico, St. Lucia, Barbados, St. Jan, New Providence, Martinique, Trinidad, Venezuela, Surinam, Colombia, Peru, Nepal, India, Hong Kong, Japan, Philippines, and New Guinea.

*Barbula indica* (Fig. 1-14) is a polymorphic species, occurring mainly in tropical and warm temperate areas, and includes a profusion of variants with various permutations of character states. Under this name or its synonyms, it is illustrated and described by Saito (1975) and Steere (1938) among others. On account of the considerable synonymy accepted here, a redescription is given above, based on New World specimens. Certain characters that are usually conservative in other species, e.g. length and degree of twisting of peristome teeth, degree of differentiation of perichactial leaves, size, shape and position of propagula, vary markedly. For this reason, synonyms include combinations in other generic names such as *Hydrogonium* (C. Müll.) Jaeg., *Semibarbula* Herz. ex Hilp. and *Strebliotrichum* F. Beauv.

Previous authors have treated the Old World and New World representations as separate entities, although variation is similar throughout the tropics. Saito (1971) reduced certain Asian names to synonyms of the New World *B. cruegeri*, but later (1975) referred these to *B. indica* instead. In North America north of Mexico, *B. indica* has been known under the synonym *B. cruegeri*, as discussed by Steere (1938). Recently, the checklist of Crum et al. (1973) replaced *B. cruegeri* (sensu North American authors) with the name *B. cancellata*, because (H. Crum, pers. comm.) the Texan type of the latter has the small, obovoid propagula characteristic of most collections in North America north of Mexico, while there were indications that *B. cruegeri* (with a type from Trinidad) represents a different, tropical taxon.

There appear to be two major trends in morphological appearance in *B. indica*. *Barbula indica* s. str. has narrowly oval to elliptical leaves, with margins plane or weakly recurved at midleaf, and small, green, obovoid propagula occurring in masses in upper leaf axils. The type from India has propagula 70-90 μm long. This expression is found throughout the range of the species. A somewhat different-looking plant in extreme form is *B. indica* facies "*B. gregaria,*" which was well illustrated by Saito (1975) under the synonym *B. horninervis*. This morph has broadly oval leaves with plane margins and massive, brown, elliptical to spherical, many-celled propagula occurring singly or very few together in upper leaf axils. Facies "*B. gregaria*" is seldom found in temperate areas although it is known from Japan (type of *B. horninervis*) and from Canada.
Vitt 21489–ALTA, Horton 15697–ALTA). A third, less distinctive trend that is widespread in the tropics is the production of propagula, these usually massive, on basal rhizoids, but uncorrelated with leaf morphology. Some of these propagula are apparently formed from an apical cell with two cutting faces and are similar to the "bilateral tubercles" of Leptobryum pyriforme (Hedw.) Wills. illustrated by Berthier (1978). The type of B. cruegeri has elliptical, plane to recurved leaves, and brown tubers borne on rhizoids from lower leaf axils or buried in the soil, ranging from 95-300 μm in length, from 15 to many cells in composition, and obovoid, spindle-like, elliptical or spherical in shape, superficially smooth to colliculate (raspberry-like).

Because of considerable intergradation in characters between these variants, infraspecific categories are not recognized. Individual collections were mostly stenomorphic between plants in expression of particular character states. The characters of the propagula were, however, variable within some collections. In certain specimens, massive propagula on basal rhizoids occurred together with either small, obovoid or massive axillary propagula or with intermediate-sized axillary propagula. Saito (1975) illustrated the Japanese synonym B. horrinervis as having massive, elliptical, apiculate propagula. In fact, in tropical and subtropical areas worldwide, specimens of B. indica may be found with propagula of various sizes and shapes that have one or more apiculi or spines, apically or laterally, resulting in spindle shapes, "ocarina" shapes and "mine" shapes. Saito (1975) also indicated that, in Japan, plants with massive propagula have plane leaf margins (B. horrinervis) and those with small propagula have recurved leaf margins (B. indica), but this correlation is only poorly reflected on a worldwide basis.

Although intergrading variants that are distinctive in the extreme are often recognized, and although the two major variants of B. indica may be biological entities deserving infraspecific scientific names, satisfactory disposition of the multiplicity of taxonomic synonyms following non-discontinuous, non-exclusive criteria (e.g. the "75 percent convention" discussed by Mayr, 1942) is impossible or at least arbitrary, if type methodology is rigorously followed. This is a rather subtle, non-biological, bookkeeping limitation of the Code to practicality of specific and infraspecific concepts.

The term "prorula" referring to a protrusion of the distal or proximal ends of superficial cell walls, or of both (doubly prorulose), was coined by Argent (1973) as pointed out by Manuel (1974). Weber and Simone (1977) suggested the term "scindula" for the same feature, and During (1977, p. 15) further discussed this morphological trait. Above midleaf, the abaxial costal surface of B. indica is usually distinctly doubly prorulose; however, some specimens may have relatively smooth costal surfaces or be covered with quadrate, hollow-papillose cells. Usually, such collections