TORTELLA BAMBERGERI IN NORTH AMERICA AND AN EVALUATION OF ITS TAXONOMY

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ABSTRACT - *Tortella bambergeri* (Schimp.) Broth. is shown to include *T. brotheri* (Lindb. ex Broth.) Broth. as a new synonym. A new description is made based largely on gametophytic traits. A key distinguishes it from closely related species. Previously considered a European endemic, *T. bambergeri* is newly reported for North America from four stations in Connecticut, Maine, Vermont, and Michigan in the United States. *Tortella tortuosa* var. *fragilifolia* (Jur.) Lindb. appears to have no distinction from the typical variety except for an exceptional degree of fragility.

KEYWORDS - *Tortella bambergeri, T. brotheri, T. tortuosa var. fragilifolia*, taxonomy, North America, bryology

INTRODUCTION

In my 1989 treatment of the genus *Tortella* (Lindb.) Limpr. for North America (Eckel 1998), *Tortella bambergeri* (Schimp.) Broth. was not recognized. This species was not generally accepted for Europe, having been synonymized with *Tortella tortuosa* (Hedw.) Limpr. by Mönkemeyer (1927, p. 270), and it was not included in the European checklist (Corley, et al. 1981), It also did not appear in the Flora of North America (Eckel, 2007).

But Duell (1984) did include *Tortella tortuosa* var. *bambergeri* (Schimp.) in his distribution of European Mosses, and Duell and Meinunger (1989) restored the status of the variety to the species level for their moss flora of Germany. Bosanquet (2006) then presented a detailed description of the species as it occurred in the British Isles. Soon after, additional papers were published on the species in Spain by Brugués et al. (2009) and the Caucasus by Ignatova and Doroshina (2008).

In May, 2006, Mr. Heribert Köckinger of Austria began a communication with the author regarding *Tortella alpicola* Dix., *T. bambergeri* and other *Tortella* (Lindb.) Limpr. species from Austria. He first suggested to me that the description and report of *Tortella tortuosa* var. *fragilifolia* (Jur.) Lindb. for North America presented (Eckel, 1998) might be *Tortella bambergeri*. Ignatova and Doroshina (2008) also ventured the same speculation. When I discussed var. *fragilifolia* in 1998, the characteristics of *Tortella tortuosa* presented in the literature made it desirable to include variation in stem and leaf sections in the characterization of the species *sensu lato*. The present paper incorporates research on the genus since 1998.

TAXONOMY

Schimper (1876) originally described *Tortella bambergeri* as a *Trichostomum* Bruch. He compared *Trichostomum bambergeri* with *T. brachydontium* Bruch in F. Müll., but noted the sharp V-shaped demarcation between the chlorophyllose cells of the lamina and the hyaline cells of the base was similar to those of *Barbula fragilis* (= *Tortella fragilis* (Drumm.) Limpr.). Apparently the two characteristics essential in the delimitation of *Trichostomum bambergeri* and its then placement in *Trichostomum* were two: the presence of a multicellular stem central strand, and, the "Peristome teeth very long, erect, supported by a basal membrane, divided to the base in two very delicate purplish crura composed of laterally compressed sides, scarcely papillose," that is, the peristome teeth were straight (erect) (Schimper 1876).

Limpricht's (1888) treatment of the mosses of Germany, Austria and Switzerland continued to recognize *Trichostomum bambergeri*. His treatment of *Tortella tortuosa* L., fully described several forms of variation. Although he noted the stem central strand in *Trichostomum bambergeri*, he also indicated that the central strand was absent in *T. tortuosa*, that the long peristome of *T. tortuosa* displayed

three turns, and was red and "lang papillose," i.e. spiculose (Limpricht 1888).

The lectotype of the genus *Trichostomum* is *T. brachydontium* Bruch, one of the species with which Schimper compared his new *T. bambergeri*. Although Brotherus (1892) modified the generic concept of *Trichostomum* from Limpricht's (1888) treatment (Crum & Anderson 1981), by the time of Brotherus Brotherus' contribution to Engler & Prantl's Natürlichen Pflanzenfamilien (Brotherus, V. F. 1902–1909), *T. bambergeri* was transferred to *Tortella* where it has since remained.

In the next edition of Engler and Prantl, Brotherus (1924–1925) wrote that *Tortella bambergeri* was part of a group that included *T. nitida* (Lindb.) Broth., *T. aprica* (Müll. Hal.) Broth. and *T. limbata* (Schiffn.) Geh. & Herz., that were characterized by pulvinate sods and white-shining costae when dry. It is also included in a group of *Tortella* with peristome teeth where twisting is marginal or rudimentary, in contrast to a much larger group with the peristome teeth that twist around their axis once or several times, of which *Tortella tortuosa* is a central example.

Mönkemeyer (1927) soon stated, however, that *Tortella bambergeri* was one of numerous forms of *Tortella tortuosa*, being a rigid, fragile plant ("starre, brüchige Form"), and even though the peristome teeth, together with the cells of the operculum, were wound [only] one half turn to the left, the plants were otherwise indistinct from *T. tortuosa*. He did not describe, nor did he illustrate, the condition of the stem central strand for *T. tortuosa*, but incorrectly depicted the hyaline basal "V" portion having an acute angle at the apex of the basal cells along the costa rather than the leaf margin.

Frahm (in Frey et al., 1995, p. 185), persisted in synonymizing *T. bambergeri* with *T. tortuosa*, considering the erect character of the peristome insignificant for distinguishing it as a species (according to Bosanquet 2006). However, Frahm accepted the species as distinct in the "Moosflora" series, e.g. ed. 4 (Frahm 2004, p. 304) and also in its earlier issue in Frahm (1983). The description in the latter booklet indicated that the species is similar to *Tortella tortuosa*, but the leaves are rigid, fragile, the stems have a central strand, and the peristome teeth are wound only one half turn. As Bosanquet (2006) noted, Mönkemeyer's opinion served to synonymize *Tortella bambergeri* with *T. tortuosa* in the Index Muscorum (Wijk et al. 1969).

As the primary couplet in their key to the genus *Tortella* of Baden-Wuerttemberg, Nebel and Phillipi (2000) perhaps first introduced the vegetative character of short, quadrate, papillose cells completely or in patches on the ventral side of the leaf costa at leaf-middle, keying to *T. bambergeri, T. fragilis, T. tortuosa, T. humilis* and *T. flavovirens*. The contrasting couplet was that the ventral surface is covered exclusively with elongate, narrow smooth cells (*T. densa* and *T. inclinata*). *Tortella fragilis* and *T. bambergeri* are separated by their fragile leaves, and then *T. fragilis* has no stem central strand, but *T. bambergeri* does.

In their description of *Tortella bambergeri*, Nebel and Phillipi also noted that on the ventral side of the costa, and in the upper part of the leaf also on the dorsal side, the costa is covered with short, more or less quadrate, papillose cells; they indicated that the green upper laminal cells are sharply distinguished from the hyaline basal cells. Sporophytes were not observed.

The character of the peristome—usually not observed by authors subsequent to Schimper, such as Limpricht (1888) who described the peristome in square brackets ["peristome with a basal membrane, the teeth erect, very long, divided to the base into 2 very delicate, empurpled, scarcely papillose crura"]—is not described in recent collections in Germany, Russia and Spain (Frahm & Frey, 2004; Frey, et al., 1995; Nebel & Philippi, 2000; Ignatova & Doroshina, 2008; Brugués, et al. 2009). Fruiting material is not indicated except for a "fruiting specimen, collected by R. Hall in August 1951…present in the NMW Herbarium" (Bosanquet 2006). Bosanquet (2006) described the peristome teeth as "350–365 µm long, narrow, papillose; peristome almost straight or twisted through 180°…".

The character most in support of placing *T. bambergeri* in *Tortella* is the V-shaped demarcation of the abrupt transition of papillose, quadrate laminal cells and the hyaline, smooth, elongate basal cell region.

HOLOTYPES OF *TORTELLA BAMBERGERI AND T. BROTHERI*

The holo- and isotypes of *Tortella bambergeri* in the collections at state in full (BM), were not available to Bosanquet (2006) when he published his paper for the British Isles species . His belief that the species had been collected in Britain was founded on the opinion of Dr. J. Kučera "based on his experience of the species in the Czech Republic" (Bosanquet 2006). By this time, bryologists in Central and Northern continental Europe (e.g. Duell, 1984; Duell & Meinunger,1989; Frahm & Frey, 2004; Nebel & Philippi, 2000) had adopted the name *T. bambergeri* to associate with the characters delineated by Bosanquet (2006). Two additional papers were later published for collections sharing these characteristics in the Caucasus (Ignatova & Doroshina, 2008) and the Iberian peninsula (Brugués et al., 2009).

However, after examining the holo- and isotype of *Tortella bambergeri* at BM, it is evident that characteristics initially described by Schimper did not entirely fit the characteristics for plants described by Bosanquet (2006) and in subsequent papers. There are no quadrate papillose cells on either the ventral or dorsal side of the distal part of the costa in leaves of the type. On the other hand, Schimper's protologue indicated a stem central strand, and this character was indeed found in the type material. Schimper also described the peristome of *T. bambergeri* as having long, erect teeth (not twisted), which matches Bosanquet's description of "almost straight or twisted through 180°".

The European *Tortella brotheri* (Lindb. ex Broth.) Broth is based on a suite of specimens collected in the Caucasus and these also display the characters outlined by Bosanquet and others, but are contradictory in some aspects such as the peristome teeth sometimes being wound twice, and red and papillose instead of
the scarcely twisted, scarcely papillose condition.

The collection of syntypes published in the protologue of *Tortella brotheri,* as *Mollia brotheri* Lindb. ex Broth. (Brotherus 1892), were examined in a collection of specimens curated at Helsinki (H), and which derive from the herbaria of both Brotherus and Lindberg. *Tortella brotheri* has long been considered a synonym of *T. tortuosa* in the Russian floristic literature (e.g. Ignatov & Ignatova, 2003).

Ignatova and Doroshina (2008) felt that their recent specimens from the Caucasus were *Tortella bambergeri*. They examined, however, two syntypes of *T. brotheri* at LE: one was considered by them to be *T. tortuosa* (Imeretia, Utzeri pr. fl. Rion, V. F. Brotherus), the other *T. bambergeri* (Ossetia, ad fl. Didi Liachva, A. H. & V. F. Brotherus 17. VII. 1881). In the absence of access to additional syntypes for *T. brotheri*, they speculated, that *T. brotheri* was indeed a synonym of *Tortella tortuosa*, because of the "smooth and shiny costa mentioned in the protologue [of *T. brotheri*, which] contradicts characters established for *T. bambergeri*" (Ignatova & Dorshina, 2008).

After studying 12 syntype specimens of *Tortella brotheri* borrowed from H, and, as the author (Brotherus) did not indicate a preference among the specimens cited in his protologue, I have chosen a syntype specimen from the herbarium of Brotherus, the author (not Lindberg), to lectotypify the species. There is an apparent duplicate (an isolectotype) in the Lindberg herbarium and both specimens are fruiting.

***Tortella brotheri* (Lindb. ex Broth.) Broth.,** Nat. Pflanzenfam. 1(3): 397. 1902. (Basionym: *Mollia brotheri* Lind. ex Broth., Acta Soc. Sci. Fenn. 19(12): 46. 1892). Lectotype (here designated): [Imeretia:] Caucasus, Mekvena, ad fl. Rion, ad saxa calcar. umbr., 4/6 1877, leg. V. F. Brotherus "c.fr." (H-BR–lectotypus). Isolectotype: Imeretia: Mekvena, ad saxa umbr. calcarea. 1877. 4 Junii, V. F. Brotherus [No.] 30 "c.fr."(H-SOL–isolectotype).

Other syntypes of *Tortella brotheri* are as follows. All syntypes are taxonomically *Tortella bambergeri* except the last (= *Tortella tortuosa*): **(1)** [Imeretia:] Caucasus: Mekvena, in valle fl. Rion, ad saxa calc. umbr., 6/6 1877, leg.

V. F. Brotherus (H-BR). **(2)** [Imeretia:] Caucasus: Atschara, ad fl. Rion, ad rup. calc., 10/6 1877, leg. V. F. Brotherus (H-BR). **(3)** [Imeretia:] Caucasus, Tsessi, in valle fl. Rion, ad rupes siccas calc., 28/6 1877, leg. V. F. Brotherus (H-BR). **(4)** [Letschgum:] Caucasus, Radscha, Uzeri, ad saxa calcarea, 7/7 1877, leg. V. F. Brotherus "c.fr." (H-BR). **(5)** Ossetia:] Caucasus: [Khtsoue] "Zkwe," ad fl. Didi Liachva, leg. V. F. Brotherus, 17/7 1881, leg. V. F. Brotherus (H-BR). **(6)** Ossetia: [Khtsoue] "Zkwe," ad fl. Didi Liachva, 1881. 17/VII, A. H. & V. F. Brotherus. Plantae Caucasicae No. 30 (H-SOL). **(7)** Imeretia: Mekvena, ad saxa umbr. calcarea, 1877 6 Junii, V. F. Brotherus [No.] 34 (H-SOL). **(8)** Imeretia: Tsessi, ad rupes siccos calc., 1877 28/VI, V. F. Brotherus [No.] 124, (H-BR; H-SOL). **(9)** Imeretia: Uzeri, ad saxa calcarea, 1877 7 Julii, V. F Brotherus [No.] 32 "n.sp. c.fr." (H-SOL). **(10)** Syntype here identified taxonomically as *Tortella tortuosa*: [Letschgum:] Caucasus, Muri, pr. fl. [Tshenis?] [Tschali?], 15/6 1877, leg. V. F. Brotherus (H-BR).

The protologue appears to have been written by Brotherus because Brotherus' (1892) publication appeared after Lindberg died (in 1889). In the introduction to the 1892 publication, Brotherus stated that Lindberg would contribute descriptions of new species (but he did not), while Brotherus would discuss the phytogeography. Under "*Mollia Brotheri* Lindb." in the protologue to the species, Brotherus wrote "n. sp. in sched.", that is, Brotherus knew Lindberg wanted a new species, but only because he had indicated it on a label. The description of the species may be said to be Brotherus' guess as to the characters Lindberg used to identify the specimens as new. Consequently Brotherus' protologue may have introduced ambiguities. For example, there is no mention of a stem central strand, emphasis is given to the shining, smooth costa. The only critical difference from *Mollia* (i.e. *Tortella*) *tortuosa* was a small size, a vivid greenness, shining turfs and a dorsal nerve extremely shiny. He stated that the peristome teeth were many times convolute, pale red, and densely and high-papillose.

Eleven of the 12 syntypes (including the lectotype) of *Tortella brotheri* studied here were nearly identical to recent gametophyte descriptions, such as those of Bosanquet (2006) for *Tortella bambergeri*. One syntype (see above) was *Tortella tortuosa.* A syntype (not seen) at LE [Imeretia, Utzeri prope fluminem Rion, V. F. Brotherus, 7.VII.1871] (sic 1877?) was reported as *T. tortuosa* by Ignatova and Doroshina (2008).

DIFFERENTIATION

It is curious that, in the literature published since Schimper's 1876 protologue based on the holotype, very few specimens could be found to exactly correspond to Schimper's name (*T. bambergeri*), and there are no reports of any authentic specimens identified by Schimper, who died four years after his publication.

Limpricht, for example, in 1888 gave an extended description of *Trichostomum bambergeri* and included an illustration. He first indicated that the leaves were fragile (brüchig). He included an illustration of the cross section of the distal portion of a cauline leaf. The section looks like that of the syntypes of *Tortella brotheri* (with a ventral epidermis of papillose cells), not of the holotype of *T. bambergeri* (with the smooth ventral stereid band exposed. Limpricht stated that only a few sterile specimens were seen for his flora of Germany, Austria and Switzerland. His description of the peristome is placed in square brackets as a quote from Schimper's protologue.

In 1904, Roth also described the leaf cross section of *T. bambergeri* and included "differentiierten Aussenzellen" in addition to guide cells and two stereid bands. Roth mentioned that collections of this species were few, although he did not indicate how many additional specimens he saw. He described the peristome teeth but not whether they were twisted. He illustrated a distal leaf cross section with a ventral epidermis.

Historical problems with both taxa (*T. bambergeri*, *T. brotheri*), including poor quality of the protologues, the seemingly depauperate nature of the holotype of *T. bambergeri*, and the few specimens cited in the early floristic literature, may have contributed to their inclusion in *T. tortuosa* by Mönkemeyer (1927) and subsequent authors.

I was initially inclined to cite *Tortella brotheri* as the more appropriate name for specimens recently published as *T. bambergeri* due to the absence of certain characters in Schimper's holotype of the latter species, I decided that the holotype of the early name *T. bambergeri* was depauperate, although within the range of variation of *T. brotheri*. Based on the holotype of *T. bambergeri*, the syntypes of *T. brotheri*, and various European specimens identified as *T. bambergeri* at NY, the following characters are fundamental to *Tortella bambergeri* (including *T. brotheri* as a synonym):

1) The stem central strand is universally present. In one collection, there was no obvious central strand in the main or primary stem, but a clear one in sections of both the two subsequent branches. These hydroid strands were clear and unambiguous. This feature occurs in all material attributable taxonomically to *T. bambergeri*.

2) The leaves are not only fragile in all specimens, but they are transversely truncated near the apex, as though the apex were deciduous, not just fragile.

3) No ventral or dorsal epidermis was noted in sections of the apex of leaves of the holotype of *T. bambergeri*, but the smooth ventral stereid layer was exposed to a width of 1–2(–3) cells with no quadrate, papillose cells on the dorsal side of the costa— a characteristic of *Tortella tortuosa*. Most other specimens identified as *Tortella bambergeri* in this study had parenchyma cells as epidermal layers on the costa, including all but two of the syntypes of *T. brotheri*. Sections of the leaf laminae of the holotype, however, did display bistratose pairs of cells, most frequently asymmetrically adjacent to the costa, and often near mid-lamina or at the margin on one or both sides. This character is easily overlooked, but it taxonomically unifies the type material of the two species and the material in North America.

As for the peristome reportedly being erect or somehow not twisted as much as is the case in *Tortella tortuosa*, or being pale or scarcely papillose, intact peristomes seen in those few specimens with fruiting material all showed peristomes twisted at least once and as many as two times in at least one capsule of a collection—enough to suggest that although the peristome twist in *T. bambergeri* may not be as extreme as in *T. tortuosa*, the twist may attain up to 2 revolutions. In the protologue of Brotherus'(1892) *Mollia brotheri*, the peristome teeth were described as "pluries convolutis". The peristome teeth of *Tortella tortuosa* are often cited as twisted 2–3 times, but more recent authors usually describe them as generally "twisted" or "spirally wound together" (Crum & Anderson, 1981). In one specimen of *Tortella tortuosa* seen from the state of Tennessee, the peristome was indeed tightly wound 2–3 times.

DESCRIPTION OF *TORTELLA BAMBERGERI*

With the establishment of *Tortella bambergeri* as a distinct species with a specific array of characters, *T. tortuosa* var. *fragilifolia* as discussed in my 1998 paper mostly describes *T. bambergeri* in the New World. Consequently, the var. *fragilifolia* seems to have no distinction from the typical variety except for an exceptional degree of fragility which may be due to environmental factors, such as aridity.

***Tortella bambergeri* (Schimp.) Broth.,** Nat. Pflanzernfam. 1(3): 397, fig. 2. 1902.

Type: Italy, southern Tyrol, near Meran, Castle Rametz, on the outer walls (battlements), Bamberger, 1853 (BM, herb. Schimper—holotype; BM, herb. Hampe—isotype). "In muris arcis Rametz prope Meran Tyrolis meridionalis ubi clar. Bamberger anno 1853 legit" (Schimper, 1876).

Basionym: *Trichostomum bambergeri* Schimp., Syn. Musc. Eur. (ed.2): 173. 1876.

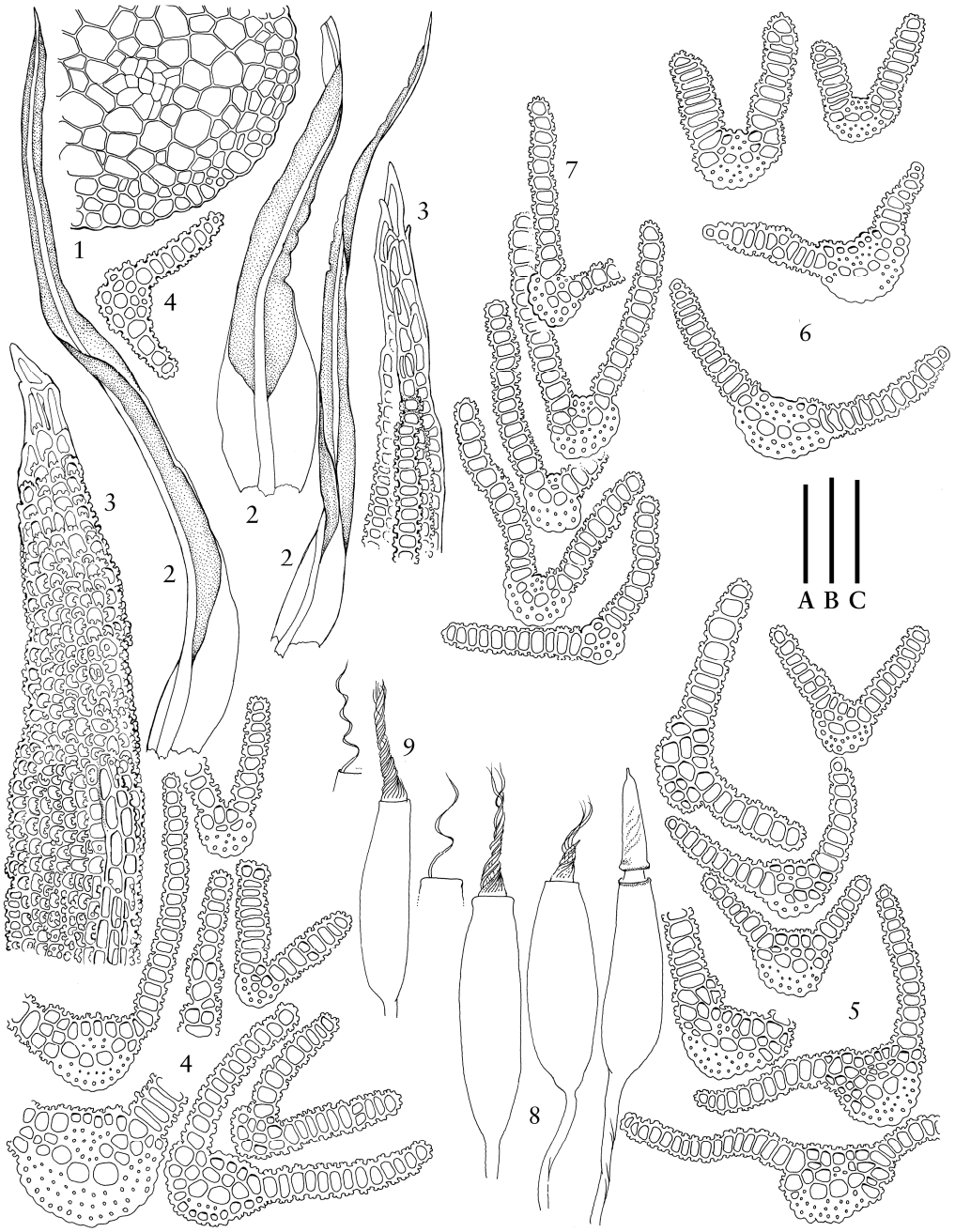

Plate 1 - *Tortella bambergeri* (Schimp.) Broth. 1. Stem section with central strand. 2. Three leaves. 3. Two leaf apices showing variation. 4. Eight leaf sections near apex. (Figs. 1–4 from Maine: Ledlie 1894.) 5. Seven leaf sections near apex of various of the syntypes of *T. brotheri*. 6. Four leaf sections near apex of the holotype of *T. bambergeri*. 7. Five leaf sections near apex of *T. tortuosa*. 8. Three capsules of *T. bambergeri* from syntypes of *T. brotheri*. 9. Capsule of *T. tortuosa*. Scale bars: A = 0.5 mm for fig. 2. B = 50 µm for figs. 1, 3–7. C = 1 mm for figs. 8–9.

Mollia bambergeri (Schimp.) Braithw., Brit. Moss Fl. 1: 230. 1885.

Tortella tortuosa var. *bambergeri* (Schimp.) Duell, Bryol. Beitr. 4: 89. 1984.

Tortella brotheri (Lindb. ex Broth.) Broth., Nat. Pflanzenfam. 1(3): 397. 1902, **syn. nov.**

Basionym: *Mollia brotheri* Lind. ex Broth., Acta Soc. Sci. Fenn. 19(12): 46. 1892.

The following description is based on the holo- and isotypes of *Tortella bambergeri*, and all European and American specimens seen:

Plants medium-sized, 1.6–2.2 mm tall, in dense, moderately loose tufts, dull, sordid, olive-green above, occasionally deep emerald green, buff to blackish brown at the base, with exposed dorsal side of costae luminous, yellow-stramineous.

Stems erect, simple or more often branching, closely invested with leaves, densely foliose-comose at the stem apices, strongly red-tomentose along stem to the bases of uppermost leaves; central strand present, in section with a radius of 4–5 cells in the central cylinder, well differentiated in a cluster of often from 12–16 relatively thin-walled cells of smaller dimension than the central cylinder cells.

Leaves 4–5(–5.5) mm long, 0.45–0.5(–0.6) mm wide, strongly crisped and undulate when dry, loosely intricate-circinate and moderately undulate when moist, especially in older leaves and, in the comal region, with moderately undulate leaf bases grading into stiffer distal part; generally *fragile leaf apices* mostly absent in lower (older) leaves and in many comal (young) leaves, the lamina friable in rectangular patches, often with linear rifts in intact leaves; elongate comal leaves ranging from rather broadly lanceolate above a somewhat wider base, becoming gradually narrower and long-linear or awl-shaped as leaves occur nearer to a perichaetium; a few rigid, long awl-shaped leaves may protrude above the comal leaves as filiform elements, usually indicating the presence of a perichaetium; cauline leaves generally keeled-canaliculate in the apex to broadly canaliculate below, sometimes cucullate-acuminate; a proximal 1/4–1/5 part commonly distinguishable, often separated from the distal 3/4 by a shoulder; often the distal part contracted at a midpoint, separating a somewhat undulate lower portion narrowing from a flat distal portion, somewhat rigid with parallel sides; uppermost ca. 0.10 of leaf may be broken off as a unit of 500–750 μm and it is in this region that quadrate, papillose cells may cover both the abaxial and adaxial surfaces of the costa; **laminal margins** weakly and sporadically incurved, bordered with distinctly smaller cells in leaves in the distal part of the lamina and in leaves with increasing proximity to the perichaetium to somewhat elongate and smooth in one row, distal margins rounded-crenulate by papillose cell ends; **leaf base** erect, broadly ovate to rectangular with shoulders near or above the distal end of region of hyaline basal cells, ca. 0.20–0.25 of the leaf length; **basal cells** abruptly differentiated from distal cells, occasionally gradually differentiated mid-lamina or distal cells penetrating the basal region in lines, thin, lax, hyaline, firmer near the costa, flaccid throughout, especially on the margins, boundary forming an oblique line, rising distally on the margins, both sides of the lamina together showing a V-shaped region of yellowish to sometimes white-hyaline cells in leaves from the same stem; **costa** strong, in surface view *dorsally* stramineous and shining, smooth to the excurrency, or in many leaves with quadrate papillose cells, as in the lamina, immediately below the cusp to various lengths from 0.10 part of the leaf, and, in intermediate awl-shaped perichaetial leaves to nearly the entire length of the leaf; costa *ventrally* medially covered by quadrate papillose cells, with the stereid layer discontinuously exposed apically in a very narrow gap of one or rarely two stereid cells in width, costa excurrent as a smooth to denticulate (by extension of the distal cell ends) multicellular, mucronate to long-subulate apiculus; **costal section** usually lunate, occasionally circular, with a well-developed stramineous ventral and dorsal stereid layer separated by a layer of guide cells, ventrally nearly always with a continuous layer of quadrate, papillose, chlorophyllose cells as an epidermal layer, dorsally the epidermal layer of quadrate papillose cells is usually absent or present on the costa adjacent to the laminal cells,

the dorsal stereid layer exposed by up to three cells to entirely covering the dorsal surface of the costa in the extreme apical regions in leaves, as in the outer perichaetial leaves, when parenchyma cells occur on both surfaces of the costa there is no defined stereid layer and the section is entirely of parenchyma (apparent guide cells plus epidermal) cells, in richly chlorophyllose plants the entire section may appear green, rather than with yellow stereid layers; **laminal cells** distally generally unistratose, asymmetrically sometimes with bistratose cell pairs adjacent to the costa or in mid-lamina, rarely at the margin, rounded quadrate-hexagonal, 7–10 µm, bifid-papillose.

Dioicous. **Perigoniate plants** not seen; **perichaetia** terminal on stem and on subterminal innovations, occasionally with up to three perichaetia on each branch of a stem; archegonia relatively long, 700–800 µm; **perichaetial leaves** 0.45–2 mm, with a border of elongate, smooth, hyaline cells, distally becoming nearly smooth with proximity to the archegonia; perichaetial leaves in unfertilized perichaetia forming a complex from short, completely smooth, elaminated, awl-shaped and colorless leaves adjacent to the archegonia to increasingly broadening and laminated with green, quadrate, papillose cells, the subulate apices extending down the margin of perichaetial leaves partly to completely to the hyaline leaf base, very narrow with generally parallel sides; outer perichaetial leaves as long as the cauline, to 2 mm, but narrower, sometimes covered completely on the dorsal surface with green, papillose, parenchyma cells.

Seta reddish yellow in lower parts to paler yellow below the purplish base of the capsule, (9–)10–11(–20) mm, erect. **Capsule** cylindric, often slightly gibbous, to 2.5 mm, orange-yellow with a purplish base and red-purple mouth; peristome teeth (0.5–)1(–2) times wound to the right, ca. 1 mm long, deteriorated peristomes appearing less twisted, teeth appearing pale, but under compound microscope red and with high papillae. **Operculum** to 1 mm, red-purple at mouth, shortly apiculate. **Spores** 10–12 µm.

KEY DISTINGUISHING *TORTELLA FRAGILIS, T. BAMBERGERI* AND *T. TORTUOSA*

1. Dry vegetative leaves at stem apex spirally incurved and contorted but always mixed with erect, strict, glistening setaceous leaf tips, vegetative leaf apices shining, ending in fragile, long-linear, rounded-trigonous, multicellular propaguloid tips; leaf apices in section bistratose symmetrically next to the costa, distally extending to the margins, lamina and costal layers becoming undifferentiated in the propaguloid tips; stem central strand absent. .....*Tortella fragilis*

1. Dry vegetative leaves at stem apex with all apices spirally incurved and contorted but without erect glistening setaceous leaf tips, vegetative leaf apices dull (except for the costa), and may be fragile, but without obvious propaguloid modifications; leaf apices in section unistratose or asymmetrically bistratose in laminal patches, lamina and costal layers mostly differentiated in the leaf apices; stem central strand present or absent 2

2. *Stem* with distinct central strand*; leaf generally canaliculate* throughout, *lamina at apex* occasionally bistratose in cell-pairs or asymmetrically next to the costa*; costal cross section* in the apical portion of the leaf generally semicircular to elliptical*; papillose ventral epidermal cells* present nearly or absolutely throughout the ventral surface of the costa near the apex, *ventral stereid band* disappearing in apical quarter of the leaf or less; *quadrate, papillose epidermal cells* in a small patch sometimes on the dorsal costa immediately below the mucro especially in perichaetial leaves (best seen in surface view), *section of extreme apex* occasionally without stereid layers*; leaf apices* regularly fallen away in a clean horizontal line as propagules*; peristomes* 0.5–1 (-2) times generally loosely twisted.
…….....*Tortella bambergeri*

2. *Stem* without distinct central strand; *leaf keeled in distal half, lamina at apex* never bistratose; *costal cross*

section in the apical portion of the leaf circular*; papillose ventral epidermal cells* absent on costa in distal quarter of leaf, *ventral and dorsal stereid band* present throughout, ventral stereid band exposed in upper quarter of the leaf in a narrow channel as smooth, elongate cells*; quadrate papillose epidermal cells* absent on dorsal costal surface throughout the leaf including the apex; *section of extreme apex* consisting of stereid and guide cells only, occasionally the ventral stereid layer disappearing and the guide cells comprising the ventral surface*; leaf apices* may be absent through erosion in fragile leaves, not evidently as propagules*; peristomes* 2–3 times generally tightly twisted.

….……*Tortella tortuosa*

NORTH AMERICAN *TORTELLA BAMBERGERI* COLLECTIONS

U.S.A.: Connecticut. On trap rock, West Rock near New Haven, O. D. Allen, Nov. 17, 1879, ex herb. J. A. Allen (NY), as *Tortella tortuosa.* **Maine.** Oxford Co., Sumner, Labrador Pond, base of large boulder at pond edge; 44°23'50"N, 70°25'27"W, 478 feet; Patricia Ledlie 1894, August 28, 2002 (MO) as *Tortella tortuosa.* **Vermont.** Town of Newfane, soapstone quarry, on rock in more or less open woods, Aug., 1939, Inez M. Haring, s.n. (MO "no. 17501" herb. Fay Macfadden; NY; CANM) as *Tortella tortuosa* var. *fragilifolia, T. nitida.* **Michigan.** Emmet Co., Cecil Bay; on sand, C. Berg 26 July 1961 (NY) as *Tortella tortuosa,* mixed with *Tortella fragilis.*

Trichostomum tenuirostre (Hook. & Tayl.) Lindb. mimics *Tortella bambergeri* almost perfectly, especially in having quadrate papillose cells in the apex on both the ventral and dorsal surfaces of the leaf, and on losing the ventral stereid band in the same region. Superficially, when dry, the habit mimics also in its spirally circinate leaves and transversely fragile leaf tips. The most salient differences are immediately seen in the absence of cauline tomentum, universally present on all three species of *Tortella* in the key; the leaves are always short-mucronate and never long-acuminate or subulate; the hyaline basal cells in some leaves may seem to match *Tortella tortuosa* by extending up the margin in one or two rows, but there are always some leaves where the cells are gradually transitional with the distal cells completely to the margin. More study is necessary to evaluate the presence or absence of a stem central strand or the nature of the stem cross-section, and also aspects of the peristome, which is always much shorter than those of the three species of *Tortella* discussed in this paper. *Trichostomum tenuirostre* also has a peculiarly irregular manner of narrowing the leaves toward the apex by abandoning a marginal row of cells, hence creating a "step," resembling a knitter terminating a row, or "decreasing," by knitting two stitches together. Sometimes the row discontinuously reemerges distally, only to vanish again, creating another marginal irregularity.

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