The Bryum erythrocarpum Complex in China and a Newly Recorded Species: Post-Print

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Date: 2023-08-04T00:00:00+00:00

Abstract

This study employs classical taxonomic methods to investigate the Bryum atrovirens Brid. complex in China, with particular emphasis on the taxonomic value of rhizoidal tuber characteristics. The objectives are to clarify the features and species composition of the Chinese B. atrovirens complex, and to delimit the taxonomic boundaries and geographical distributions among species. The results indicate: (1) The complex comprises nine species in China, namely Bryum apiculatum Schwägr., B. atrovirens Brid., B. bornholmense Wink. & R. Ruthe, B. clavatum (Schimp.) Müll. Hal., B. radiculosum Brid., B. rubens Mitt., B. sauteri Bruch & Schimp., B. stellituber Arts, and B. tuberosum Mohamed & Damanhuri. Among these, B. stellituber represents a newly recorded species in China. Sporophytes of this species were observed for the first time, and rhizoidal tubers were documented in Chinese specimens of B. atrovirens and B. rubens. (2) This group comprises ephemeral plants adapted to temporary environments, reproducing asexually primarily via rhizoidal tubers. The principal diagnostic characters include tuber position, color, shape, size, cell wall thickness, and the degree of protuberance of outer cells. (3) The geographical distribution of each species was established. In conclusion, the Chinese B. atrovirens complex can be rapidly identified based on morphological features of rhizoidal tubers, and the discovery of newly recorded species enriches the bryological knowledge of China.

Full Text

Preamble

The Bryum atrovirens Brid. Complex (Bryaceae, Bryophyta) of China, Including a New Species Record

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Abstract: The Bryum atrovirens Brid. complex in China was critically revised based on morphological evidence, with a focus on the tubers. The aim of the study is to clarify the morphological delimitation and geographical distribution for each recognized species of this complex in China. The results show that: (1) nine species are recognized for the complex in China, namely *B. apiculatum* Schwägr., *B. atrovirens* Brid., *B. bornholmense* Wink. & R. Ruthe, *B. clavatum* (Schimp.) Müll. Hal., *B. radiculosum* Brid., *B. rubens* Mitt., *B. sauteri* Bruch & Schimp., *B. stellituber* Arts and *B. tuberosum* Mohamed & Damanhuri. *B. stellituber* represents a new record for China, whereas sporophytes are for the first time recorded in two populations of the new record, and the rhizoidal tubers of *B. atrovirens* and *B. rubens* are first documented from Chinese material. (2) Species of the *B. atrovirens* Brid. complex are 'ephemeral' colonists adapted to the exploitation of short-lived habitat gaps. Asexual reproduction by means of tubers was observed to be common and numerous. Identification of species within the complex relies heavily on the tuber characteristics, including its distribution (along short or long rhizoids, clustered or not), color, shape, size, cell wall thickness, presence of surface protuberance, and degree of protuberance when present. (3) The distribution at global and Chinese provincial levels for each species is summarized. An identification key to species of the *B. atrovirens* Brid. complex in China is presented. In conclusion, the species identification of the *B. atrovirens* Brid. complex can be rapidly accomplished based on the morphological characteristics exhibited by the tuber. The species newly record adds data for the moss in China.

Key words: *Bryum stellituber* Arts, tubers, *Bryum*, new record, taxonomy

CLC number: Q949.35
Document code: A

The genus *Bryum* is known to comprise 440 species worldwide [**?**, **?**], distributed widely across the globe and commonly found in hills, mountains, forest edges, roadsides, and even periodically disturbed cultivated land. The gametophyte morphology exhibits considerable variation, making it one of the more difficult groups to identify among mosses. Multiple *Bryum* species with rhizoidal tubers were once considered a single species—*Bryum erythrocarpum* Schwägr., nom. illeg. (= *B. atrovirens* Brid.) [**?**, **?**]. Later, Crundwell and Nyholm [**?**] recognized that classification based on variable leaf morphology, costa length, and capsule shape was difficult, while tuber characteristics held greater taxonomic value.

They proposed an informal taxonomic unit—the *B. erythrocarpum* Schwägr. complex (= *B. atrovirens* Brid. complex)—including *B. atrovirens* and related species such as *B. sauteri* Bruch & Schimp., with the most distinctive diagnostic feature being tuber production on rhizoids.

Some scholars have classified *Bryum* at the infrageneric level based on morphological characteristics, placing most species with rhizoidal tubers in either Section *Apalodictyon* Müll. Hal. or Subsection *Apalodictyon* (Müll. Hal.) Podp. [**?**, **?**, **?**, **?**], or in Section *Erythrocarpa* (Kindb.) J.J. Amann [**?**, **?**]. Spence and Ramsay [**?**] proposed the genus *Gemmabryum* J.R. Spence & H.P. Ramsay, which includes most species of the *B. atrovirens* Brid. complex and other *Bryum* species that produce rhizoidal or axillary spherical tubers and share similar gametophytic features. Ochyra et al. [**?**] suggested that if all species with rhizoidal tubers were to be accepted as a single genus, the older name *Osculatia* De Not. should be used. However, molecular phylogenetic studies have shown that these regularly tuber-producing species do not form a monophyletic group [**?**, **?**, **?**]. Consequently, most scholars neither recognize the validity of *Gemmabryum* or *Osculatia* nor adopt infrageneric classifications within *Bryum* [**?**, **?**, **?**, **?**, **?**, **?**, **?**]. Since molecular studies to date have failed to provide clear results for the taxonomy of *Bryum* and its relatives [**?**, **?**], this study adopts a broad concept of *Bryum*, using only *Bryum* as the genus name.

Although the *B. atrovirens* complex is not a natural taxonomic group, tubers serve as a valuable taxonomic character that enables rapid and accurate species identification and have been widely applied in *Bryum* taxonomy [**?**, **?**, **?**, **?**, **?**]. Similar informal complexes such as the *B. billarderii* Schwägr. complex, *B. capillare* Hedw. complex, and *B. bicolor* Dicks. complex have also been used in *Bryum* taxonomic studies [**?**, **?**, **?**, **?**].

Currently, 56 species (including infraspecific taxa) of *Bryum* are known from China [**?**, **?**, **?**, **?**, **?**, **?**], with nearly half capable of asexual reproduction through tuber production [**?**, **?**]. This study aims to: (1) investigate the characteristics and species composition of the *B. atrovirens* complex in China; (2) clarify taxonomic boundaries among species; and (3) determine the ecological and geographical distribution of this group in China.

1 Materials and Methods

The study examined 174 specimens of the *B. atrovirens* complex collected from China. Voucher specimens are deposited in the Herbarium of Jiaozuo Normal College (JZNC) and the Herbarium of Guangxi Institute of Botany (IBK), with additional specimens borrowed from the Herbarium of the Institute of Botany, Chinese Academy of Sciences (PE), the Herbarium of Shenyang Institute of Applied Ecology, Chinese Academy of Sciences (IFP), the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN), the Herbarium of Xinjiang University (XJU), the Herbarium of Hebei Normal University (HBNU), the Herbarium of China Agricultural University (BAU), the Herbarium of Hangzhou

Normal University (HTC), and the Herbarium of Inner Mongolia Normal University (IMNU). Microscopic observation, measurement, photography, and analysis were conducted using a dissecting microscope (Motic SZ45) and a light microscope (Olympus BX51) with an image capture and analysis system (Olympus SC180). Particular attention was paid to rhizoidal tuber characteristics, including size, morphology, color, position on the plant, cell wall thickness, and degree of cell protrusion, to assess their taxonomic value.

2 Results and Analysis

Based on morphological characteristics and species composition criteria for the *B. atrovirens* complex from Europe, Australia, and other regions reported in the literature [**?**, **?**, **?**, **?**, **?**], our morphological study of Chinese species revealed that the complex comprises nine species in China: *B. apiculatum* Schwägr., *B. atrovirens* Brid., *B. bornholmense* Wink. & R. Ruthe, *B. clavatum* (Schimp.) Müll. Hal., *B. radiculosum* Brid., *B. rubens* Mitt., *B. sauteri* Bruch & Schimp., *B. stellituber* Arts, and *B. tuberosum* Mohamed & Damanhuri. Among these, *B. stellituber* collected from Leye County, Guangxi, represents a new record for China, with sporophytes observed for the first time. Previous Chinese literature did not report rhizoidal tuber production in *B. atrovirens* and *B. rubens* [**?**, **?**, **?**]. This study documents tubers in Chinese specimens of both species for the first time, confirming their distribution in China through this diagnostic character.

The main characteristics of the *B. atrovirens* complex are: plants small, 3–15 mm tall. Leaves ovate-lanceolate to lanceolate, erect or erect-spreading when wet, slightly contorted when dry; leaf margins often finely serrulate above, recurved below, with or without differentiated border; costa reddish at base; upper leaf cells elongate-rhomboidal to elongate-hexagonal, becoming shorter and broader toward the base, rectangular to quadrate. Rhizoids often bearing tubers. Dioicous. Capsules cylindrical to ovoid, horizontal to pendulous, yellowish-brown to red; operculum conical, obtuse to short-rostrate; peristome fully developed, endostome segments broadly perforated, basal membrane exceeding half the length of the exostome teeth, cilia with appendages.

Key to the Species of the *Bryum atrovirens* Brid. Complex in China

1. Rhizoidal tubers pyriform, flattened, abundant on short branches of the main rhizoids……**9. *B. tuberosum***

1. Rhizoidal tubers spherical or pyriform, not flattened, abundant or scattered on short branches or long main rhizoids……**2**

2. Surface cells of tuber protuberant, thick-walled, reddish-brown……**3**

2. Surface cells of tuber smooth, thin-walled or slightly thick-walled, yellowish-brown to reddish-brown……**5**

3. Surface cells of tuber conical, strongly protruded; tubers stellate……**1. *B. stellituber***

3. Surface cells of tuber curved, weakly to moderately protruded; tubers globose……**4**

4. Tubers rarely exceed 250 m in diameter, abundant on short branches or single on long rhizoids; often bearing axillary gemmae……**7.** ***B. rubens***

4. Diameter of tubers often exceeds 250 m, scattered on short branches of main rhizoids; axillary gemmae absent……**4.** ***B. bornholmense***

5. Tubers larger, mostly over 120 m in diameter, spheroidal, ovoid or pyriform, thin-walled, yellowish-brown……**6**

5. Tubers smaller, mostly under 120 m in diameter, pyriform or short-claviform, thin-walled or slightly thick-walled, yellowish-brown to reddish-brown……**7**

6. Leaf border not differentiated, costa long-excurrent; tubers spherical……**6.** ***B. radiculosum***

6. Leaf border differentiated, costa short-excurrent; tubers ovoid, occasionally spherical……**3.** ***B. atrovirens***

7. Leaf border differentiated; tubers short-claviform, slightly thick-walled, yellowish-brown……**5.** ***B. clavatum***

7. Leaf border not differentiated; tubers pyriform, thin-walled or slightly thick-walled, yellowish-brown to reddish-brown……**8**

8. Leaves narrowly oblong to elliptic-lanceolate, distinctly keeled and concave, costa percurrent; tubers abundant on short rhizoid branches, rarely on long ones, thin-walled……**2.** ***B. apiculatum***

8. Leaves ovate-lanceolate, flat, costa percurrent, shortly excurrent or aristate; tubers abundant on short branches of main rhizoids, slightly thick-walled……**8.** ***B. sauteri***

2.1 *Bryum stellituber* Arts (New Record, Plate I)

Bryum stellituber Arts, J. Bryol. 19: 453, f. 1–2. 1997.

Plants loosely tufted or solitary, light green, often tinged with red (Plate I: A), becoming reddish-brown with age, leaves evenly distributed on the stem or clustered at the apex. Rhizoids light brown to brown, finely papillose (Plate I: Q). Stems ca. 8 mm tall, often branched. Leaves erect-spreading when wet, not conspicuously contorted when dry; upper stem leaves larger, (2.6–2.9) mm × (0.6–0.8) mm, lower leaves smaller, (1.5) (1.9–2.2) mm × (0.6–0.7) mm, lanceolate, flat or slightly concave, apex acuminate, base narrowly tapered, not decurrent, margins plane above, slightly recurved below (Plate I: I–K), finely serrulate above, entire below (Plate I: I–J); differentiated border distinct, composed of

1–2 rows of narrow, thick-walled cells, yellowish-brown (Plate I: I–K); upper leaf cells elongate-rhomboidal to elongate-hexagonal, thin-walled, (92.3) (46.2–79.8) m × (11.2) 12.1–16.9 m, medial cells larger than upper cells, thin-walled, (47.6–94.3) m × (12.9) 15.3–21.7 m (Plate I: I–J), basal cells rectangular, thin-walled, (43.9–94.8) m × (17.0) 19.1–25.1 (30.1) m (Plate I: K); costa brown to reddish-brown, percurrent to short-excurrent, 66.4–92.4 m wide at base, in cross-section lacking guide cells, with only dorsal stereid bands (Plate I: H). Red to reddish-brown globose tubers abundant or scattered on rhizoids, (95) 145–205 m in diameter, with surface cells extending outward as protuberances of varying heights, conical protuberances up to 37.6 m high, often obtuse at the apex (Plate I: L–Q). Dioicous. Setae 2.1–2.9 cm long, slender, erect, yellowish-brown (Plate I: C). Capsules horizontal to pendulous, cylindrical, 3–4 mm long, yellowish-brown, neck short, narrower than the urn, mouth slightly constricted compared to urn, light brown to dark brown; exothecial cells at mouth elliptical, 2–3 rows of small, transversely elongated cells near the mouth, followed by 4–5 rows of short cells, lower cells arranged longitudinally (Plate I: C–D). Operculum conical, with obtuse apex, red or reddish-brown (Plate I: C); exostome teeth conical, acuminate, papillose on outer surface, lower ca. 2/3 yellowish-brown, upper 1/3 narrowed, hyaline; endostome surface smooth to slightly papillose, pale yellow, hyaline, basal membrane ca. 1/2 the height of the exostome, segments broadly triangular, broadly perforated along the keel, cilia well-developed, 2–3, with long nodulose or appendiculate (Plate I: D). Spores 15–19 m in diameter, coarsely papillose.

The distinctive tuber morphology makes *B. stellituber* easily distinguishable from other *Bryum* species. Although *Bryum jamaicense* Syed has similarly protruding outer cells on tubers [**?**, **?**], that species is related to *B. capillare* Hedw. [**?**, **?**], with ovate to spatulate leaves and a broader differentiated border (2–4 cells vs. 1–2 cells), and significantly larger tubers (190–250 m vs. (95) 145–205 m).

Distribution in China: First record for China, based on specimens collected from two localities in Leye County, Guangxi.
Other distribution: Previously recorded only from the type locality in Uttar Pradesh, India [**?**, **?**].

2.2 *Bryum apiculatum* Schwägr. (Fig. II: A)

Bryum apiculatum Schwägr., Sp. Musc. Frond., Suppl. 1(2): 102, t. 72[top]. 1816. — *Gemmabryum apiculatum* (Schwägr.) J.R. Spence & H.P. Ramsay, Phytologia 87(2): 65. — *Osculatia apiculata* (Schwägr.) Ochyra, Plášek & Bedn.-Ochyra, Acta Mus. Siles. Sci. Nat. 67(1): 75. 2018.

Plants yellowish-green, often tinged with reddish. Leaves narrowly oblong to elliptic-lanceolate, distinctly keeled and concave, border not differentiated, costa percurrent. Tubers abundant, scattered on short rhizoid branches, rarely on long rhizoids, pyriform or irregularly globose, (59–132) m × 48–129 m, yellowish-

brown to reddish-brown, surface cells not protruding, thin-walled, isodiametric.

This species resembles *B. sauteri* in tuber morphology, but its tubers are slightly larger (length exceeding 100 m in larger ones), leaves are distinctly keeled and concave with percurrent costa, whereas *B. sauteri* has smaller tubers (maximum length <90 m), flat leaves, and costa shortly excurrent or aristate.

Distribution in China: Fujian, Guangxi, Hebei, Henan, Xinjiang, Yunnan, Qinghai, Sichuan, Tibet, and Zhejiang [**?**, **?**].
Other distribution: Widely distributed in tropical and subtropical regions, including the Americas (USA, Brazil, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Mexico) [**?**, **?**, **?**, **?**, **?**], Africa (Egypt, Burkina Faso, Central African Republic, Cameroon, Cape Verde, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Lesotho, Mauritius, Madagascar, Mozambique, Namibia, Nigeria, Seychelles, Sierra Leone, Tanzania, Togo, Uganda, Congo, Zambia) [**?**, **?**], South and Southeast Asia (India, Nepal, Sri Lanka, Indonesia, Malaysia, Bangladesh, Thailand, Cambodia, Myanmar, Vietnam, Philippines, Singapore) [**?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**], Australia, Oceania (New Zealand), and Europe (UK) [**?**, **?**].

2.3 *Bryum atrovirens* Brid. (Fig. II: B)

Bryum atrovirens Brid., Muscol. Recent. 2(3): 48. 1803. — *B. erythrocarpum* Schwägr., Sp. Musc. Frond., Suppl. 1 (2): 100. 1816, nom. illeg. — *B. microerythrocarpum* Müll. Hal. & Kindb. in Macoun, Cat. Canad. Pl., Musci 124. 1892.

Leaves evenly arranged on stems, ovate-lanceolate, differentiated border composed of 1–2 rows of elongate cells, costa percurrent to short-excurrent. Capsules cylindrical, yellowish-brown. Tubers on short rhizoid branches, scarce, ovoid or pyriform, occasionally globose, (135–258) m × 109–189 m, yellowish-brown, surface cells not protruding, thin-walled.

This species resembles *B. radiculosum* in tuber morphology, but the latter has globose, smaller tubers (ϕ=120–190 m). *B. radiculosum* is easily distinguished by its leaves lacking a differentiated border and having a long-excurrent costa, whereas *B. atrovirens* has a differentiated border and short-excurrent costa.

Crundwell and Nyholm [**?**] discussed the morphology and distribution of this species under *Bryum erythrocarpum* as a synonym of *B. microerythrocarpum* Müll. Hal. & Kindb., with gametophyte and tuber characteristics identical to those of *B. atrovirens*. Since *B. erythrocarpum* is illegitimate and *B. atrovirens* (1803) predates *B. microerythrocarpum* (1892), the species in question should be *B. atrovirens*.

Distribution in China: Henan, Xinjiang, Shandong, Jiangsu, Zhejiang, Tibet, Hong Kong, Taiwan, Guangxi, Jiangxi, Guizhou, Gansu, Hebei, Hubei, Sichuan, and Macau [**?**, **?**].
Other distribution: Asia (Pakistan, Myanmar, Vietnam, India, Japan)

[?, ?, ?], Africa (Egypt), Europe (UK, Norway, Sweden, Denmark, Germany, Netherlands, Belgium, France, Switzerland, Austria, Poland), Americas (Canada, USA), and Oceania (New Zealand) [?, ?, ?].

2.4 *Bryum bornholmense* Wink. & R. Ruthe (Fig. II: C)

Bryum bornholmense Wink. & R. Ruthe, Hedwigia 38(Beibl. 3): 120. 1899. — *Ptychostomum bornholmense* (Wink. & R. Ruthe) Holyoak & N. Pedersen, J. Bryol. 29: 119. — *Osculatia bornholmensis* (Wink. & R. Ruthe) Ochyra, Plášek & Bedn.-Ochyra, Acta Mus. Siles. Sci. Nat. 67(1): 75. 2018.

Leaves usually evenly arranged on stems, ovate or ovate-lanceolate, differentiated border composed of 2–3 rows of elongate cells, costa excurrent as a mucro. Tubers on short rhizoid branches at stem base, scarce, globose, ϕ=180–390 m, reddish-brown, surface cells slightly protruding, thick-walled.

This species resembles *B. rubens* in gametophyte morphology, and both have larger tubers than other species in the complex. The differences are that *B. bornholmense* has larger, darker tubers with inconspicuously protruding surface cells, borne only on rhizoids, whereas *B. rubens* has relatively smaller tubers (153–291 m), bright red to reddish-brown, with prominently bulging surface cells, and tubers also occur in leaf axils on stems.

Distribution in China: Hebei, Henan, Sichuan, Shandong, Jiangsu, Zhejiang, Guangxi, and Xinjiang.
Other distribution: Multiple European countries (UK, Norway, Sweden, Denmark, Hungary, France) and the Americas (USA, Mexico) [?, ?, ?, ?, ?, ?].

2.5 *Bryum clavatum* (Schimp.) Müll. Hal. (Fig. II: D)

Bryum clavatum (Schimp.) Müll. Hal., Syn. Musc. Frond. 1: 292. 1848. — *Gemmabryum clavatum* (Schimp.) J.R. Spence & H.P. Ramsay, Phytologia 87(2): 66. 2005. — *Osculatia clavatum* (Schimp.) Ochyra, Plášek & Bedn.-Ochyra, Acta Mus. Siles. Sci. Nat., 67(1): 75. 2018.

Plants glossy, reddish. Leaves narrowly oblong to lanceolate, differentiated border distinct, costa short-excurrent, upper and medial leaf cells narrowly elongate-rhomboidal to narrowly hexagonal. Tubers usually solitary at rhizoid tips, occasionally 2 clustered on short branches, scarce, clavate, 84–127 × 73–98 m, brown; surface cells smooth, not protruding, cells near the stalk often elongated, apical cells subisodiametric, slightly thick-walled.

The gametophyte of *B. apiculatum* resembles that of this species, but the former lacks a differentiated border and has a non-excurrent costa, allowing rapid differentiation based on tuber morphology.

Distribution in China: Hainan, Yunnan, and Xinjiang.
Other distribution: Australia, Oceania (New Zealand), South America (Peru,

Chile), and Southeast Asia (Papua New Guinea, Indonesia, Nepal, Philippines) [?, ?, ?, ?].

2.6 *Bryum radiculosum* Brid. (Fig. II: E)

Bryum radiculosum Brid., Muscol. Recent. Suppl. 3: 18. 1817. — *Gemmabryum radiculosum* (Brid.) J.R. Spence & H.P. Ramsay, Phytologia 87(2): 68. 2005. — *Osculatia radiculosa* (Brid.) Ochyra, Plášek & Bedn.-Ochyra, Acta Mus. Siles. Sci. Nat., 67(1): 76. 2018.

Leaves triangular-lanceolate to narrowly lanceolate, border not differentiated, costa short-excurrent, cells narrowly elongate. Tubers on short rhizoid branches, scarce, globose, ϕ=120–190 m, yellowish-brown, surface cells smooth, not protruding, thin-walled.

The distinction between *B. radiculosum* and *B. atrovirens* is discussed above.

Distribution in China: Henan, Jiangsu, Fujian, Tibet, Guangxi, Zhejiang, Yunnan, Hebei, and Xinjiang.
Other distribution: Throughout mainland Europe and islands (UK, Denmark, Slovakia, Romania, Germany, Russian Caucasus, Hungary), Northeast Asia (Japan, Russian Far East), Southwest Asia (Turkey, Israel, Palestine, Lebanon, Saudi Arabia), the Americas (USA, Mexico, Peru, Venezuela, Brazil, Argentina), Africa (Algeria, Egypt, Libya, Morocco, Tunisia, South Africa, Zimbabwe, Namibia), Atlantic islands (Bermuda), and Oceania (New Zealand) [?, ?, ?, ?, ?, ?].

2.7 *Bryum rubens* Mitt. (Plate III: A–C)

Bryum rubens Mitt., Hooker's J. Bot. Kew Gard. Misc., 8: 232. 1856. — *Gemmabryum rubens* (Mitt.) J.R. Spence & H.P. Ramsay, Phytologia 87(2): 68. 2005. — *Ptychostomum rubens* (Mitt.) Holyoak & N. Pedersen, J. Bryol., 29: 120. 2007. — *Osculatia rubens* (Mitt.) Ochyra, Plášek & Bedn.-Ochyra, Acta Mus. Siles. Sci. Nat., 67(1): 76. 2018.

Plants dark green, becoming reddish-brown with age, leaves triangular-lanceolate, differentiated border composed of 1–2(3) rows of thick-walled cells, margins serrulate near apex, costa percurrent to short-excurrent. Tubers globose, clustered on short rhizoid branches at stem base or solitary at tips of long rhizoids, usually small, ϕ=36–96 m, larger ones similar to those in leaf axils; larger tubers (originating from rhizoids) solitary in leaf axils on stems, ϕ=(153) 202–291 m, bright reddish-brown, surface with prominently bulging cells giving a raspberry-like appearance, cells thick-walled.

The distinction between this species and *B. bornholmense* is discussed above.

Distribution in China: Inner Mongolia and Henan [?, ?].
Other distribution: Widespread across Europe (UK, Norway, Finland, Sweden, Estonia, Latvia, Lithuania, Russia, Germany, Switzerland, Spain, Portu-

gal, Hungary), Asia (Turkey, Azerbaijan, Armenia, Pakistan, India, Indonesia, Japan), Africa (South Africa, Tunisia), the Americas (USA, Brazil), Australia, and Oceania (New Zealand) [**?**, **?**, **?**, **?**, **?**, **?**].

2.8 *Bryum sauteri* Bruch & Schimp. (Fig. III: D)

Bryum sauteri Bruch & Schimp. in Bruch et al., Bryol. Eur., fasc. 32(suppl. 1): 10, t. 10. 1846. — *Gemmabryum sauteri* (Bruch & Schimp.) J.R. Spence & H.P. Ramsay, Phytologia 87(2): 68. — *Osculatia sauteri* (Bruch & Schimp.) Ochyra, Plášek & Bedn.-Ochyra, Acta Mus. Siles. Sci. Nat. 67(1): 76. 2018.

Leaves ovate-lanceolate, flat, border not differentiated, costa short-excurrent or aristate. Tubers abundant on short rhizoid branches, pyriform or irregularly globose, (51–90) m × 43–76 m, brown to reddish-brown, surface cells not protruding, cell walls slightly thick; tuber cells large and few in number, only 1–3(4) cells wide.

In the *B. atrovirens* complex, this species has smaller tubers similar to *B. tuberosum* and *B. apiculatum*. It differs from *B. apiculatum* as discussed above. *B. tuberosum* has flattened tubers and differentiated leaf borders, with leaves clustered in a rosette at the stem apex, distinguishing it from *B. sauteri*. Its tubers resemble those of *B. rubens* but lack axillary tubers, and the gametophyte morphology is distinctly different.

Distribution in China: Henan, Zhejiang, Guangxi, Guizhou, Shandong, Xinjiang, Tibet, and Yunnan [**?**, **?**].
Other distribution: Europe (UK, Iceland, Portugal, Spain, Norway, Slovakia, Montenegro, Austria, Belgium, France, Czech Republic, Switzerland, Italy, Russian Caucasus), South Asia (India), Africa (Egypt, South Africa), South America (Ecuador, Chile), Oceania (New Zealand), and Australia [**?**, **?**, **?**, **?**].

2.9 *Bryum tuberosum* Mohamed & Damanhuri (Fig. III: E)

Bryum tuberosum Mohamed & Damanhuri, Bryologist 93: 288, f. 1–10. 1990. — *Osculatia tuberosa* (Mohamed & Damanhuri) Ochyra, Plášek & Bedn.-Ochyra, Acta Mus. Siles. Sci. Nat. 67(1): 76. 2018.

Leaves at stem apex large, densely arranged in a rosette, narrowly ovate to ovate, differentiated border composed of 3–4 rows of cells, costa short-excurrent. Tubers abundant, borne at tips of short rhizoid branches, pyriform or irregularly circular, flattened, 40–70 × 35–57 m, yellowish-brown to reddish-brown, surface cells not protruding, slightly thick-walled; tuber surface only a few cells wide.

Bryum riparium I. Hagen has similar flattened tubers, but the former has taller plants (up to 3 cm) with leaves evenly distributed on stems, whereas the latter has smaller plants with leaves clustered in a rosette at the stem apex.

Distribution in China: Henan, Xinjiang, Guangxi, Zhejiang, and Yunnan.
Other distribution: Malaysia and India [**?**, **?**, **?**].

3 Discussion

3.1 Species Composition of the *B. atrovirens* Complex in China

Rhizoidal tuber production is the most typical but not exclusive feature of the *B. atrovirens* complex. The core species recognized by Crundwell and Nyholm [**?**], Ochi [**?**], and Smith [**?**] include *B. atrovirens*, *B. sauteri*, *B. bornholmense*, *B. radiculosum*, *B. apiculatum*, and *B. rubens*, all of which occur in China. Whether Koponen and Norris [**?**] placed *B. clavatum* together with *B. apiculatum* and *B. atrovirens* (as *B. microerythrocarpum* = *B. atrovirens*) in Section *Apalodictyon*, or Spence and Ramsey [**?**] transferred *B. tuberosum* to *Gemmabryum* based on characteristics of the 'Apiculata' group (rhizoidal tubers and narrow leaf cells), or whether the small, delicate gametophyte with elongate leaf cells and rhizoidal tubers matches the characteristics of the *B. atrovirens* complex, both *B. clavatum* and *B. tuberosum* should belong to this group. *Bryum stellituber* was considered a related species to the *B. atrovirens* complex when described [**?**, **?**], and sporophytes observed in Chinese specimens are consistent with complex characteristics. The *B. rubens* from Wudalianchi, Heilongjiang, was misidentified as *B. capillare* Hedw. [**?**, **?**]. Specimens of *B. rubens* from Inner Mongolia (Heilonglihe National Nature Reserve, Ningcheng County, Chifeng City, Inner Mongolia, Xu Jie 20200717037, 20200717071) lacked tubers [**?**, **?**], whereas specimens from Henan produced abundant tubers, confirming the species' distribution in China.

Although Zhao and Liu [**?**] considered *B. riparium* a species belonging to Section *Apalodictyon*, Smith [**?**] placed it in Subsection *Alpiniformia* due to its larger, robust stature, neither within Section *Apalodictyon* nor the *B. atrovirens* complex. This clearly differs from the small, delicate plants typical of the *B. atrovirens* complex, so it is excluded from this study.

3.2 Rhizoidal Tubers as Stable Taxonomic Characters in the *B. atrovirens* Complex

Rhizoidal tubers in *Bryum* typically occur on underground rhizoids, occasionally on short rhizoids above ground in leaf axils, as in *B. rubens* where some tubers develop on very short rhizoids or initial rhizoid cells at leaf axils above ground. Mature tubers are usually globose, subglobose, or pyriform; when borne on short rhizoid branches, they have a tuber stalk. They are often transparent or grayish-white during early development, becoming yellow, orange, red, or brown at maturity, ranging from tens to hundreds of micrometers in size, and lack leaf primordia. Tuber cells often contain translucent, variably sized spherical oil bodies. In the *B. atrovirens* complex, tuber size, morphology, color, position, and whether constituent cells protrude are relatively stable within species. Whitehouse [**?**] cultured 29 moss species with rhizoidal tubers, including nine species of the *B. atrovirens* complex, on culture media, and found that tuber morphological characteristics showed almost no variation due to environmental factors. Although rhizoidal tubers in the *B. atrovirens* complex may represent

convergent evolution, with similar tubers found in other moss families such as Dicranaceae, Ditrichaceae, Fissidentaceae, and Pottiaceae [**?**, **?**], *Bryum* can be easily distinguished from these groups based on gametophyte characteristics. Therefore, rhizoidal tubers can serve as stable taxonomic characters for the *B. atrovirens* complex.

3.3 Rhizoidal Tuber Production as Ecological Adaptation to Harsh Habitats

Species of the *B. atrovirens* complex are dioicous and mostly grow in grasslands, forest edges, farmland, or garden green spaces. Drought or periodic disturbance results in infrequent sporophyte production. The reproductive strategy shifts from energy-intensive, long-cycle sexual reproduction to less energy-intensive, short-cycle asexual reproduction to rapidly and successfully colonize new habitats [**?**, **?**]. Compared to axillary globose tubers and filamentous gemmae with thin walls, high chloroplast content, and abundant starch, rhizoidal tuber cells are typically thick-walled, low in chloroplasts, and rich in lipid storage [**?**, **?**], enabling maximum drought resistance and greater long-term dormancy capacity. The formation of new gaps or favorable conditions may require long periods, so long-lived propagules are necessary to recolonize habitats. In arid environments, tubers of most moss species can survive for over one year, with tubers of *B. bornholmense* remaining viable after 12 years of herbarium storage [**?**, **?**]. Therefore, dormancy of rhizoidal tubers is an adaptive strategy in transient and variable environments [**?**, **?**].

Species of the *B. atrovirens* complex are ephemeral colonists adapted to temporary environments, reproducing asexually primarily through rhizoidal tubers. Currently, nine species are recognized in China, with *B. stellituber* being a new national record and sporophytes observed for the first time. Rhizoidal tubers of *B. atrovirens* and *B. rubens* are documented from Chinese specimens for the first time. The primary diagnostic features are tuber position, color, shape, size, cell wall thickness, and whether outer cells protrude.

Acknowledgments

We thank Prof. Zhao Jiancheng of Hebei Normal University, Prof. Mamtimin Sulayman of Xinjiang University, Prof. Shao Xiaoming of China Agricultural University, Prof. Wu Yuhuan of Hangzhou Normal University, Prof. Xu Jie of Inner Mongolia Normal University, Dr. Yu Ningning of the Institute of Botany, Chinese Academy of Sciences, Dr. Li Wei of Shenyang Institute of Applied Ecology, Chinese Academy of Sciences, and Dr. Ma Wenzhang of Kunming Institute of Botany, Chinese Academy of Sciences, for their assistance with specimen loans. We also thank the Leye-Fengshan UNESCO Global Geopark Management Bureau and the Yachang Orchid National Nature Reserve Management Center for their support during fieldwork.

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Appendix: Voucher Specimen Information for the *Bryum atrovirens* Complex in China

1. *Bryum stellituber*
Guangxi: Alpine meadow, Caowang Mountain, Yachang Township, Leye County, 106°21 12.57 E, 24°43 57.49 N, on soil, 1822 m, 2020.11.8, Tang QM et al. 20201108-217; Liuxing Tiankeng, Leirong Village, Shuaiba Village, Tongle Town, 106°28 38.23 E, 24°48 40.98 N, on soil, 1188 m, 2018.6.8, Tang QM 20180608-131.

2. *Bryum apiculatum*
Henan: Qinglong Gorge, Jiaozuo City, on thin soil over rock, 700 m, 2004.10.03,

Liu YY 2004100229, 2004100140; Donghe Village, Jingangtai Protection Station, Dabie Mountain Reserve, Shangcheng County, on soil, 230 m, 2016.4.9, Liu YY 16058; Mashankou, Neixiang County, beside ditch, 1960.6.25, Luo JX 144; By water ditch, Taiping Town, Xixia County, on sandy soil, 1960.7.8, Luo JX 175a. Xinjiang: Daqing River, Qinghe County, Altay Mountains, on soil, 1286 m, Mamtimin Sulayman 14886; Shaziquan, Altun Mountain National Nature Reserve, 90°28 E, 37°11 N, on swamp soil, 3940 m, 2011.7.15, Ainiwarjiang Abudurousuli 187; Tula Ranch, Qiemo County, Korla, 86°44 03.62 E, 37°66 56.71 N, on soil by spring, 2910 m, 2017.8.8, Mamtimin 30520, 30521, 30522b; Yixike'ati, Tula Ranch, 87°47 83.36 E, 37°78 71.21 N, aquatic, 3940 m, 2017.8.10, Mamtimin 30569. Zhejiang: Longwang Mountain Nature Reserve, Anji, Huzhou, on rock, 523 m, Wu YH 2017110249; on thin soil over rock, 572 m, Wu YH 2017110273; on rock by roadside, 505 m, Wu YH 2017110315; from Xingchao Village to Wuxi River Bridge, Hongxingping Village, on terraced soil, 261 m, Wu YH 2017070228c, 2017110315; near Xiaoxu Strawberry Farm, Wuyi County, Jinhua City, 119°49 03.48 E, 28°54 47.643 N, on soil by farmland, 66 m, 2021.5.7, Ma XY & Zeng RH 2021050753; along highway from Sanyou Village to Mamian Mountain, Tiantai County, Taizhou City, 120°49 35.18 E, 29°13 49.79 N, on soil in tea plantation, 397 m, 2021.8.14, Ma XY & Tang SF 2021081403b. Tibet: 52 km from Zhongba, 83°32 14.41 E, 29°59 45.07 N, on side of rat burrow, 4591 m, 2019.7.18, Qiao YX 2019p122y008-b. Guangxi: Alpine meadow, Caowang Mountain, Yachang Township, Leye County, 106°21 4.89 E, 24°43 48.51 N, on soil, 1718 m, 2018.10.2, Tang QM & Zhang SY 20181002-322; Cenwanglaoshan Forest Farm, Tianlin County, 1974.10.4, Gao Q 2348. Fujian: Daiyun Mountain, Dehua County, on rock, 302 m, Wu WY & Wang YF 11. Hebei: Wu'an City, on soil, 1140 m, 2005.9.7, Li L 906; Xiaowutai Mountain, Yu County, on soil, 1300 m, 2011.7.13, Niu YL 20111904; 1500 m, 2011.7.8, Niu YL 110004; 2100 m, Niu YL 110015; Zijin Mountain, Xingtai County, on thin soil over rock, 750 m, 2004.4.25, Wang XR 040523-c; Qian Dadi, Tuoliang, Pingshan County, on rock by water, 1450 m, 2004.10.24, Li WQ 040929. Yunnan: Lüchun County, Zang M 148; Laowo Township, Lushui County, 99°02 40.37 E, 25°51 30.14 N, 1452 m, 2007.11.19, Li LB 20073638, 20073637, 20073634, 20073618. Qinghai: Longzang Commune, Xinghai County, 3600 m, Lu FG 036. Sichuan: Erlang Mountain summit, Tianquan County, on soil, 2800 m, Gao Q 17723.

3. *Bryum atrovirens*

Henan: Baoxiao Peak, Jigong Mountain National Nature Reserve, Xinyang City, 114°4 30 E, 31°48 13 N, on rock, 750 m, 2022.6.27, Liu YY 22139b. Tibet: 30 km from Geji County, 81°19 8.18 E, 32°10 38.24 N, on soil by water, 4628 m, 2019.7.24, Fan YJ 2019p166y015, Qiao YX 2019p166y041; 16 km from previous site, 80°6 40.04 E, 32°1 3.74 N, on soil by river, 4336 m, 2019.7.20, Fan YJ 2019p150y008a; 54 km from Shiquanhe, 79°47 28.67 E, 32°54 31.33 N, on grassy slope away from river, 4401 m, 2019.7.21, Fan YJ 2019p155y037a; 52 km from Zhongba, 83°32 14.41 E, 29°59 45.07 N, on sandy soil, 4591 m, 2019.7.18, Qiao YX 2019p122y021a; in rat burrow, Qiao YX 2019p122y012a;

Zhada-Shiquanhe, 40 km from Zhada, 79°59 0.08 E, 31°32 5.73 N, on soil by rock, 4493 m, 2019.7.20, Qiao YX 2019P145Y019; 60 km from Zhada, 80°7 9.81 E, 31°27 6.33 N, on soil under shrub, 4688 m, 2019.7.20, Qiao YX 2019P146Y005-c, 2019P146Y082; 5 km from Zhada-Shiquanhe, 79°48 18.19 E, 31°31 35.6 N, under grass, 3703 m, 2019.7.20, Qiao YX 2019P143Y016, 2019P143Y017; Dêngqên County, on rock, 4000 m, Zang M 5332. Zhejiang: Along highway from Cangxi Village to Shiyan Village, Tiantai County, Taizhou City, 121°06 59.59 E, 29°09 05.96 N, on rock by roadside in shade, 215 m, 2021.7.18, Ma XY & Tang SF 2021071809; Yantan, 120°47 52.45 E, 29°00 00.18 N, on rock on ground, 413 m, 2021.8.15, Ma XY & Tang SF 20210815114; Wuyanling National Nature Reserve, Taishun County, Wenzhou City, 119°40 02.85 E, 27°42 31.86 N, on rock, 717 m, 2020.8.5, Huang WZ et al. 20200805034a; along main road from Lengkeng to Wayaoshang, Anji County, Huzhou City, 119°22 22.62 E, 30°31 06.69 N, on cement by roadside near ditch, 119 m, 2021.8.25, Ma XY & Tang SF 2021082504a; from Xingchao Campground to Baijiling, 119°36 16.44 E, 30°32 34.45 N, on large rock by roadside, 175 m, 2021.8.28, Ma XY & Tang SF 20210828116; along highway from Tongkeng Village to Changpu Bridge, 119°18 40.72 E, 30°35 52.03 N, on sandy soil by highway, 155 m, 2021.8.23, Ma XY & Tang SF 20210823147. Xinjiang: Shaziquan, Altun Mountain National Nature Reserve, 90°28 E, 37°11 N, on swamp soil, 3940 m, 2011.7.15, Ainiwarjiang Abudurousuli 197. Gansu: Qilian Mountains, 2800 m, 1976.6.17, Zhuo ZD 761-013a. Hebei: Zijin Mountain, Xingtai County, on thin soil over rock, 750 m, 2004.4.24, Zhao JC 040509; Yunmeng Mountain, on thin soil over rock, 1000 m, 2001.5.18, Tang WB 100906. Hubei: Shennongjia Forest District, on soil, 1500 m, 2010.5.25, Wang ZJ 1009. Sichuan: Xikou, Dujiangyan City, on tree base in forest, 1350 m, Wang MZ 57313.

4. *Bryum bornholmense*

Henan: Shuihongchi Village, Sili Township, Jiyuan City, on soil under shrub, 1195 m, 2021.5.20, Liu YY 21033; Xiasi Village, Baiyun Town, Song County, 2017.11.12, Liu YY 1740; Baiyun Mountain, on thin soil over rock, 1500 m, 1997, Zhao JC 970141, 971624, 971504; Baoxiao Peak, Jigong Mountain National Nature Reserve, Xinyang City, 114°4 30 E, 31°48 13 N, on rock, 710 m, 2022.6.27, Liu YY 22133; Dongzhai National Nature Reserve, Luoshan County, on rock, 2017.5.20, Liu YY 1721a; Baiyun Protection Station, Lingshan Town, 114°15 2 E, 31°56 54 N, on soil by path, 2019.5.26, Liu YY 19016; on slope, 172 m, 2021.6.19, Liu YY 21086, 21110a; on step soil, 174 m, 2021.6.19, Liu YY 21117b; 177 m, 2021.6.19, Liu YY 21116b; Xiaomagou, 114°16 32.08 E, 31°57 38.71 N, on soil under tea tree, 210 m, 2021.6.19, Liu YY 21057, 21077a; on humus soil, 117 m, 2021.6.19, Liu YY 21061a; Damazhuang, on soil under tea tree, 2021.6.18, Liu YY 21103a; Wangdawan Village, 114°15 46.08 E, 31°56 40.79 N, on *Phyllostachys* root, 174 m, 2021.6.19, Liu YY 21073; by stone road, 174 m, 2021.6.19, Liu YY 21075a, 21091; on step soil, 174 m, 2021.6.19, Liu YY 21076; Jingangtai, Dabie Mountain Nature Reserve, Shangcheng County, 2018.4.21, Liu YY 18009, 18018a; Nianyushan Reservoir, 2018.6.16,

Liu YY 18180b, 18069b; Shenlingzhai Reserve, Luoning County, 2018.7.9, Liu YY 18045; 111°42 42 E, 34°16 9 N, in rock crevice, 580 m, 2019.6.7, Liu YY 19097; Chongdugou, Luanchuan County, Xiefenyai Waterfall, on step, 714 m, 2020.10.25, Liu YY 20172b; on slope, 724 m, 2020.10.25, Liu YY 20183; Lanhong Bridge, 724 m, 2020.10.25, Liu YY 20185; Baisongling Protection Station, Shennong Mountain, Qinyang City, 112°49 E, 35°14 29 N, on soil, 967 m, 2019.9.22, Liu YY 19061, 19067; Fenglin Gorge, Jiaozuo City, on thin soil over rock, 700 m, 2004.5.05, Liu YY 2004100478, 2004100122, 2004100394, 2004100415; Qinglong Gorge, on thin soil over rock, 700 m, Liu YY 2004100229; Yuntai Mountain, Xiuwu County, on soil, 800 m, 2011.11.04, Liu YY 415; Shiren Mountain, Lushan County, on soil, 1670 m, 1997, Zhao JC 971594. Zhejiang: Fugai Mountain National Forest Park, Jiangshan City, on soil, 308 m, Wu YH 2017042108; Dazhou Reservoir, Wen'ao Village, Sanhe Town, Tiantai County, 121°07 56.30 E, 29°03 09.37 N, on rock by roadside, 197 m, 2022.1.21, Ma XY & Xu ZX 2022012140; along river road from Huangjiatang Village to Cui'ao Stream, Leifeng Township, 120°53 48.68 E, 29°05 59.31 N, on dry soil by highway, 97 m, 2021.7.16, Ma XY & Tang SF 2021071627; Huangpu River Source Scenic Area (starting from Mafeng'an Power Station), Anji County, Huzhou City, 119°24 47.90 E, 30°23 56.17 N, on rock wall under forest, 653 m, 2021.5.1, Ma XY & Wang JH 2021050115; along main road from Lengkeng to Wayaoshang, 119°23 18.05 E, 30°32 17.07 N, on slope by roadside, 133 m, 2021.8.25, Ma XY & Tang SF 20210825112. Xinjiang: Bozidun Township, Tomur Peak Nature Reserve, Aksu, Xiaokuzibayi Forest Farm, 80°38 15.5 E, 41°48 55 N, on soil, 2400 m, 2017.6.16, Mamtimin Sulayman 30003. Hebei: Shenxian Mountain, Laiyuan County, on rock, 1500 m, Fan WW 041185; Wudaogou Forest Farm, Weichang County, on soil, 1200 m, Li L 2002-0076; Xingtai County, Tang WB 40503; Longhua County, Liang HZ 41559. Sichuan: Labagou Nature Reserve, Tianquan County, Zhao JC 20070921, 20070926. Guangxi: Along road from Pangtun to Lanjiawan Tiankeng, Yachang Orchid National Nature Reserve, Leye County, 106°22 26.04 E, 24°50 33.39 N, on soil, 1124 m, 2019.10.19, Tang QM & Wei YM 20191019-406.

5. *Bryum clavatum*

Xinjiang: Tastai, Yumin County, Barluk Mountain National Nature Reserve, Tacheng Region, 82°45 18 E, 45°53 45 N, on rock, 1340 m, 2021.7.9, Liu YY 34286a; Yixiekekaxi, Altun Mountain National Nature Reserve, 90°24 E, 37°13 N, on swamp soil, 3930 m, 2011.7.16, Ainiwarjiang Abudurousuli 311. Hainan: Jianfengling, on thin soil over rock, 600 m, Chen BJ 728. Yunnan: Bita Lake, Zhongdian, on soil, 3500 m, Zhang DC 171.

6. *Bryum radiculosum*

Henan: Xiaomagou, Baiyun Protection Station, Dongzhai National Nature Reserve, Luoshan County, 114°16 32.08 E, 31°57 38.71 N, on soil under tea tree, 210 m, 2021.6.19, Liu YY 21060; Damazhuang, on soil under tea tree, 214 m, 2021.6.18, Liu YY 21066; Shenlingzhai, Luoning County, 111°42 4 E, 34°16 15 N, on rock, 650 m, 2018.7.9, Liu YY 18043; Yuntai Mountain, Xiuwu County, on soil, 850 m, 2004.10.18, Liu YY 2004100306. Guangxi:

Alpine meadow, Caowang Mountain, Yachang Township, Leye County, 106°21 13.12 E, 24°43 48.28 N, on soil, 1747 m, 2018.10.02, Tang QM & Zhang SY 20181002-314; 106°21 11.75 E, 24°43 49.05 N, on trunk, 1752 m, 2018.10.02, Tang QM & Zhang SY 20181002-316A; 106°21 4.91 E, 24°43 48.49 N, on soil, 1717 m, 2018.10.02, Tang QM & Zhang SY 20181002-320. Tibet: 60 km from Zhada, 80°7 9.81 E, 31°27 6.33 N, on soil by water, 4688 m, 2019.7.20, Song XT & Qiao YX 2019P146Y079c; 5 km from Pulan County, 81°8 59.93 E, 30°22 37.98 N, on riverbank soil, 4256 m, 2019.7.19, Song XT 2019p137y042b; 21 km from previous site, 85°33 23.57 E, 30°5 0.87 N, in rat burrow, 5325 m, 2019.7.14, Song XT 2019p102y005-a; 32 km from Shiquanhe-Ritu, 79°50 3.63 E, 33°9 38.30 N, on soil by water, 4296 m, 2019.7.21, Fan YJ 2019P154Y010. Zhejiang: Jinghu Dahe Fishing Village, Yuecheng District, Shaoxing City, 120°34 00.60 E, 30°04 44.62 N, on rock by lake shore, 5 m, 2021.4.29, Ma XY & Wang JH 2021042903b; Longwang Mountain Nature Reserve, Anji, Wu YH 20180717001, 20180718063; along road from Niutouwu to reservoir, 119°34 12.44 E, 30°34 43.79 N, on slope by roadside, 62 m, 2021.8.28, Ma XY & Tang SF 2021082856. Xinjiang: Urumqi Botanical Garden, 87°33 09.61 E, 43°53 15.93 N, on rock, 710 m, 2016.4.24, Mamtimin Sulayman 27409, 27413; Shuimogou, 87°39 22.14 E, 43°49 40.15 N, on soil, 818 m, 2016.4.20, Mamtimin Sulayman 27402; 87°39 18.74 E, 43°49 49.42 N, on soil, 810 m, 2016.4.20, Mamtimin Sulayman 27391; Water Park, 87°36 40.90 E, 43°45 08.85 N, on soil, 932 m, 2016.4.14, Mamtimin Sulayman 27285; Tianchi, Tianshan, on rock, 1800 m, Cao T 200369; Yixike'ati, Tula Ranch, Qiemo County, Kunlun Mountains, 87°47 83.36 E, 37°78 71.21 N, on rock, 3940 m, 2017.8.10, Mamtimin Sulayman 30585; Altay Mountains, Qinghe County, on soil, 2100 m, 2009.09, Mamtimin Sulayman 15095; Cele County, aquatic, 2450 m, Mamtimin Sulayman 9500048; 2525 m, Mamtimin Sulayman 9500005. Hebei: Zijin Mountain, Xingtai County, on rock by water, 750 m, 2004.4.24, Wang XR 040503; Xiaowutai Mountain, Yu County, on soil, 1691 m, Niu YL 20108063; Yangjiaping, Zhuolu County, on soil, 700 m, Li LB 20060626; East Peak, Xiaowutai, on soil, 2600 m, Zhao JC 20060732. Yunnan: Gaoligong Mountains, Lushui County, on soil, 2681 m, Li LB 20073056.

7. *Bryum rubens*

Henan: Xihe Scenic Area, Dabie Mountain National Nature Reserve, Shangcheng County, 115°32 2 E, 31°43 25 N, on soil, 421 m, 2019.7.13, Liu YY 19085. Inner Mongolia: Heilonglihe National Nature Reserve, Ningcheng County, Chifeng City, small slope, Xu J 20200717037a; North Yanshan, Sumu Mountain Forest Park, Ulanqab City, Xu J 20200717071a.

8. *Bryum sauteri*

Henan: Huanghualing, Shennong Mountain, Qinyang City, 112°50 E, 35°12 56 N, 1080 m, 2019.5.18, Liu YY 19044; Yuntai Mountain, Xiuwu County, on thin soil over rock, 500 m, 2005.5.11, Liu YY 05411; Fenglin Gorge, Jiaozuo City, on soil, 700 m, 2004.10.11, Liu YY 2004100434; Longyuwan, Luanchuan County, on thin soil over rock, 1650 m, Zhao JC 970510. Zhejiang: Near Fengyang Villa entrance, Lishui City, on rock, 1287 m, Wu YH

2017070505b, 2017070506a; Juebi Qisong scenic spot, Longquan Mountain Scenic Area, on rock, 1401 m, Wu YH 2017070639b; Monkey King Valley, Shiyang Forest Farm, Wencheng County, Wenzhou City, on soil, 1336 m, Wu YH 2017070702b; Laojiashan, Anji County, Huzhou City, 119°15 24.97 E, 30°36 00.71 N, on rock wall by stream, 388 m, 2021.08.23, Ma XY & Tang SF 2021082377. Tibet: 142 km from Zhongba, 82°42 1.19 E, 30°26 14.26 N, on soil, 4775 m, 2019.7.18, Fan YJ 2019P126N3001. Shandong: Mount Tai, on thin soil over rock, Tong ZG 130. Yunnan: Pihe, Fugong County, on thin soil over rock, 1026 m, Cao N 20073341, 20073363, Zhao JC 20073477, 20073332, Li LB 20073323, 20073424. Guangxi: Alpine meadow, Caowang Mountain, Yachang Township, Leye County, 106°21 13.09 E, 24°43 57.61 N, 2019.10.13, on soil, 1820 m, Tang QM & Wei YM 20191013-131; 106°21 19.22 E, 24°43 52.55 N, on soil, 1832 m, Tang QM & Wei YM 20191013-127.

9. *Bryum tuberosum*

Henan: Hui Longsi sample plot, Jingangtai Reserve, Shangcheng County, on soil, 2018.6.17, Liu YY 18064; Nianyushan Reservoir, 2018.6.16, Liu YY 18071b; Fenglin Gorge, Jiaozuo City, on soil, 700 m, 2004.10.11, Liu YY 2004100419, 2004100421. Xinjiang: Xiata Ancient Road, Zhaosu County, Tianshan, 80°49 42 E, 42°28 23 N, on rock, 2740 m, 2017.6.22, Mamtimin Sulayman 30274a. Zhejiang: Longwang Mountain Nature Reserve, Anji, Wu YH 20180718045; Juxi, Cangnan, Wenzhou, on soil, Wu YH 2018041229. Guangxi: Luojiatian Village, Yachang Orchid National Nature Reserve, Leye County, 106°21 55.66 E, 24°46 13.42 N, on soil, 1145 m, 2019.10.20, Tang QM & Wei YM 20191020–475. Yunnan: Xiaomenglun River dam, Mengla County, on sandy soil, 50–551 m, Zhang CG & Cao T 14079.

Note: Figure translations are in progress. See original paper for figures.