



A revision of the genus *Anthoceros* (Anthocerotaceae, Anthocerotophyta) in China

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Abstract

The genus *Anthoceros* (Anthocerotaceae, Anthocerotopsida) in China is reviewed. Five species and one variety are recognized. *Anthoceros alpinus*, *A. bharadwajii*, and *A. subtilis*, are reported new to China. *Aspiromitus areolatus* and *Anthoceros esquirolii* are proposed as new synonyms of *Folioceros fuciformis* and *Phaeoceros carolinianus*, respectively. A key to the species of *Anthoceros* in China is provided.

Key words: *Anthoceros alpinus*, *A. bharadwajii*, *A. subtilis*, hornworts, new synonym

Introduction

Hornworts (Anthocerotophyta) represent a key group in the understanding of evolution of plant form because they are hypothesized to be sister to the tracheophytes (Qiu *et al.* 2006). An estimate of 200–250 species of hornworts exist worldwide (Villarreal *et al.* 2010; Garcia *et al.* 2012; Villarreal *et al.* 2012). *Anthoceros* Linnaeus (1753: 1139) is the largest genus of hornworts, with ca. 83 species (Villarreal *et al.* 2010). With a global distribution, the centres of diversity in the genus are in the Neotropics and tropical Africa and Asia.

Anthoceros formosae Stephani (1916: 1002) was the first species of the genus described from China, based on U.J. Faurie's collection from Taiwan. Seven years later Stephani (1923) described two new species from China: *Anthoceros esquirolii* Stephani (1923: 427) [= *Phaeoceros carolinianus* (Michaux 1803: 280) Proskauer (1951: 347) (present study)] and *A. subalpinus* Stephani (1923: 429) [= *Phaeoceros subalpinus* (Steph.) Udar & Singh (1981: 257)]. Khanna (1938) added two *Anthoceros* species to the Chinese flora: *A. fulvisporus* Stephani (1912: 306) [= *Phaeoceros fulvisporus* (Steph.) Hasegawa (1993a: 52)] and *A. chungii* Khanna (1938: 316) (a new species). Lai and Wang-Yang (1976) reported four species from Taiwan: *A. formosae* [= *A. angustus* Stephani (1916: 1001)], *A. miyabenus* Stephani (1897: 85) [= *Folioceros fuciformis* (Mont.) Bharadwaj (1975: 227) (Piippo 1990)], *A. nagasakiensis* Stephani (1916: 1005) [= *A. agrestis* Paton (1979: 257)] (Stotler & Crandall-Stotler 2003) and *A. vesiculosus* Austin (1874: 17) [= *Folioceros vesiculosus* (Austin) Bharadwaj (1975: 227)]. Hsu (1979) listed nine *Anthoceros* species, including several invalid names, in his checklist of bryophytes in China (see section below under "Synonyms, doubtful and excluded records"). Hasegawa (1993b) made a taxonomic revision of Taiwanese Anthocerotae, and confirmed six species of *Anthoceros* in Taiwan, including a new species [*A. verruculosus* Hasegawa (1993b: 103)] and a new variety [*A. fusiformis* Aust. var. *taiwanensis* Hasegawa (1993b: 100)]. Since 1995, numerous publications have contributed to the knowledge of the *Anthoceros* flora in China (So 1996; Zhu & So 1996; Gao & Cao 2000; Guo & Zhang 2001; Gao & Lai 2003; Wu *et al.* 2006; Zhang & Chen 2006; Zhang & Wu 2006; Wu & But 2009; Wang *et al.* 2011).

Although Piippo (1990) listed 19 names of *Anthoceros*, including seven accepted species and Gao & Wu (2010) reported six species of *Anthoceros* in China, no taxonomic revision of the genus is available. Here we present a revision of *Anthoceros* in China. During our recent examination of specimens, we identified three new records of *Anthoceros* in China: *A. alpinus* Stephani (1923: 425), a critically endangered species known only from the type locality in India (Singh 2008), *A. bharadwajii* Udar & Asthana (1985: 484) and *A. subtilis* Stephani (1916: 1003). An examination of type specimens revealed that *Aspiromitus areolatus* Stephani (1916: 969) and *Anthoceros esquirolii* are synonymous with *Folioceros fuciformis* and *Phaeoceros carolinianus*, respectively. Therefore, five species and one variety of *Anthoceros* from China are recognized in this paper with illustrations of five species and descriptions of the three species new to China.

Generic description

Anthoceros L., Sp. Pl. 1139. 1753. emend. Proskauer, Bull. Torrey Bot. Club 78: 346. 1951. Type species: — *Anthoceros punctatus* Linnaeus (1753: 1139).

Thalli small to medium-sized, light green, orbicular to strap-shaped, more or less lobed along margins, ecostate, with mucilage-containing schizogenous cavities; dorsal surface of thallus crispate (lamellate) or smooth, cells of upper epidermal layer with 1 (–4) chloroplast per cell, pyrenoid present, absent or with a starch-free area. *Nostoc* colonies scattered within ventral thallus. Androecia irregularly distributed or arranged along median line, antheridia numerous (up to 66) per cavity with a jacket of four tiers of cells and a long stalk. Involucre erect, cylindrical. Capsule erect, projecting from involucre and bivalved, dehiscing longitudinally from apex to base, with stomata epidermally, cells of epidermal layer rectangular, columella well-developed. Spores smoky gray, dark brown to blackish with a defined trilete mark; ornamentation spinose, punctuate, baculate, jagged or lamellate. Pseudoelaters 1–4 (–5) cells long, thin-walled, sometimes with irregular bands of thickenings.

Anthoceros, a large genus of hornworts that contains about 83 species, is often found on soil and rocks in primarily pantropical regions (Villarreal *et al.* 2010), and includes nine species in India (Asthana & Srivastava 1991) and five species in Japan (Katagiri & Furuki 2012). In China, five species and one variety are recognized here and they are separated in the following key.

Key to species of *Anthoceros* in China

- 1 Thalli with numerous subspherical to pillow-form gemmae along front margins *A. angustus*
- 1 Thalli without gemmae 2
- 2 Dorsal surfaces of thallus lamellate or plicate; proximal surfaces of spores without smooth area along trilete marks 3
- 3 Dorsal surfaces of thallus usually densely complicate lamellate; proximal surfaces of spores with distinct foveate-reticulate ornamentation, but not papillose *A. punctatus*
- 3 Dorsal surfaces of thallus rather distinctly plicate but not lamellate; proximal surfaces of spores with papillose to spinulose ornamentation *A. subtilis*
- 2 Dorsal surfaces of thallus not lamellate or plicate; proximal surfaces of spores with distinct smooth area along trilete marks 4
- 4 Thalli strap-shaped, somewhat flabellate; spores with roughened spinate to spinulate outgrowths/lamellae on distal surface *A. fusiformis* var. *taiwanensis*
- 4 Thalli not strap-shaped; spores with reticuloid projections on distal surface 5
- 5 Spores 40–61 μm in diameter, distal surface with closely studded blunt projections forming reticuloid-semireticulate pattern *A. alpinus*
- 5 Spores 35–54 μm in diameter, distal surface with spinulate-blunt projections forming pseudolamellate-lamellate pattern *A. bharadwajii*

Anthoceros alpinus Steph., Sp. Hepat. 6: 425. 1923.

Type:—INDIA. Oriental. Mussoorie, ca. 7000 ft., October 1879, *J.F. Duthie s.n.* (holotype G-12759!).

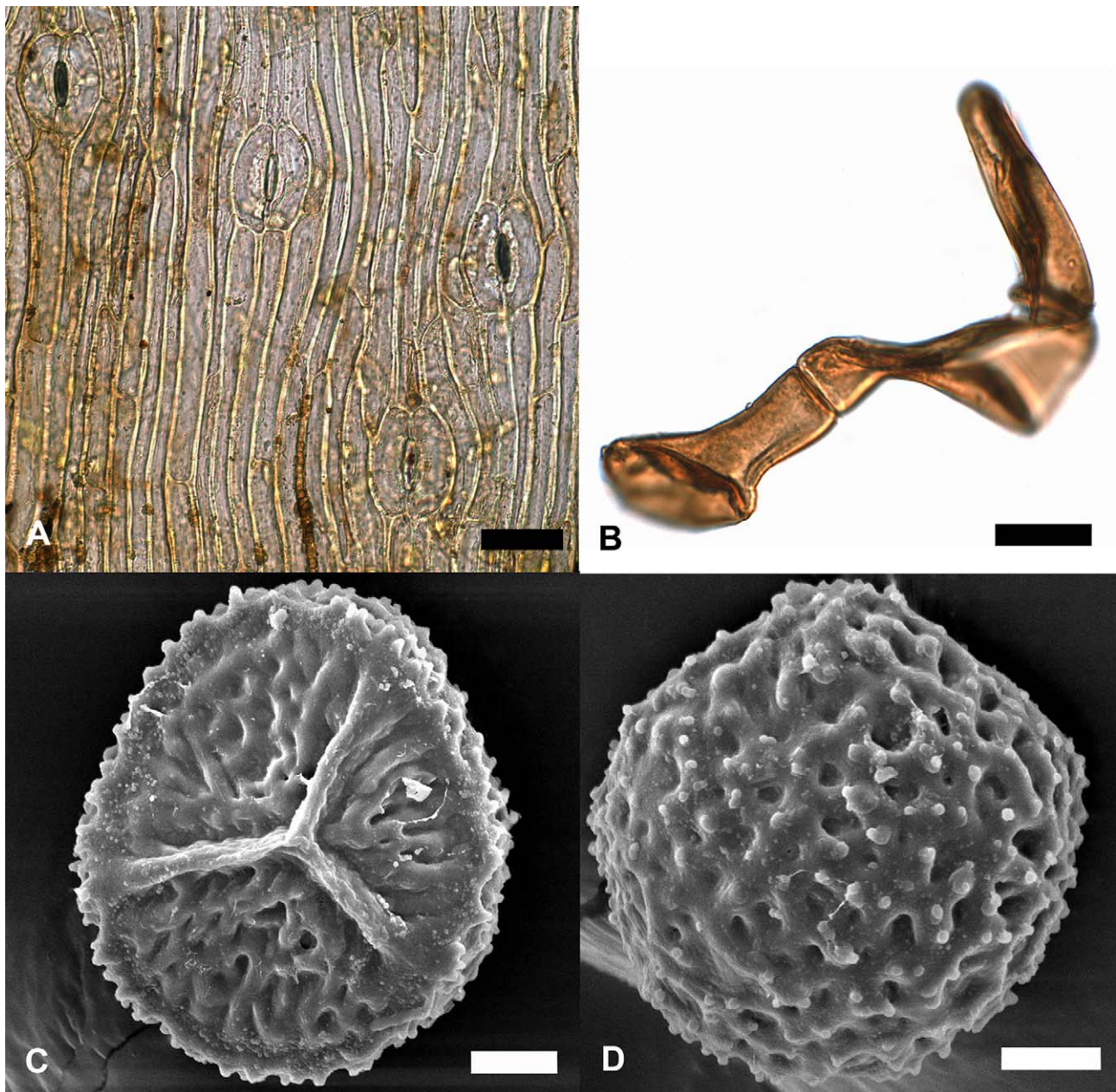


FIGURE 1. *Anthoceros alpinus* Steph. A. Thin-walled epidermis of capsule with stomata. B. Pseudoelater with thin-walls and irregular thickenings. C. SEM (scanning electron microscope) micrograph showing proximal spore face with a prominent trilete mark and narrow surrounding strip that is ornamentation-free (smooth). D. SEM micrograph showing distal face of spore with semi-reticulate pattern comprising ridges ornamented with blunt and round-headed knobs. All from *D.G. Long 18961* (E). Scale bars: A=50 µm; B=20 µm; C, D=10 µm.

Thalli medium-sized, in rosettes, ecostate, thallus lobes tapering, up to 6 mm long and 4 mm wide at apex, spongy. *Nostoc* colonies uncommon, scattered across the ventral side of thallus. Dioicous (?). Antheridia not seen. Involucre cylindrical, erect, up to 3 mm high, smooth at mouth. Capsules frequent, up to 3 cm long, bivalved, with well-developed columella. Epidermal cells of capsule walls rectangular to narrow rectangular, $36\text{--}197 \times 9\text{--}29$ µm, thick-walled, stomata scattered, $42\text{--}70 \times 40\text{--}44$ µm, each stoma with two reniform guard cells surrounded by 5–7 cells; cells of the inner lining layer of capsule walls rectangular, $27\text{--}100 \times 26\text{--}50$ µm, sometimes with irregular dark thin bands on tangential walls. Spores blackish-brown, 40–61 µm in diameter, sporoderm with closely studded blunt projections forming a reticuloid-semireticulate pattern, proximal face

with a prominent trilete mark bordered by a distinct unsculptured streak, 2–8 µm wide. Pseudoelaters blackish brown, 93–146 µm long, usually 2–4 cells long, cells narrowly rectangular, mostly 25–58 × 10–24 µm, thin walled, sometimes with irregular thickenings.

Anthoceros alpinus was first collected by J.F. Duthie from Mussoorie of India in 1879 (Stephani 1923). It seems that no more collections were made until Asthana and Nath (2004) rediscovered it from Nainital of India in 1991. Due to development, especially the road construction, *A. alpinus* is threatened with the loss of habitat, and has been added to the critically endangered list of India bryophytes by Singh (2008). Here, we report this species (Fig. 1) as a new record to China. The collection was made by D.G. Long at an altitude of 2653 m from Yunnan in 1990.

The length of pseudoelaters in *Anthoceros alpinus* is variable; pseudoelaters from the type specimen are 65–97 µm long, but they are usually 93–146 µm long in Chinese material (Fig. 1 B). Under the scanning electron microscope (SEM), the proximal surface of spores of *A. alpinus* exhibits a conspicuous trilete mark bordered by an unsculptured streak (Fig. 1 C). The sporoderm has a distinct semi-reticulate pattern comprising prominent ridges ornamented with blunt and round-headed projections (Fig. 1 D). These ridges form imperfect reticulations enclosing lumina and pits at some places. The sporoderm is clearly devoid of any sharp projections over the irregularly running ridges which enclose variously shaped lumina all over its surface.

Although three taxa of *Anthoceros* in China, *A. alpinus*, *A. bharadwajii* and *A. fusiformis* var. *taiwanensis* resemble each other by the sporoderm ornamentation with distinct smooth strips along the trilete mark, *A. alpinus* is easily distinguished by spore characteristics as described above. *Anthoceros bharadwajii* possesses a reticuloid-pseudolamellate sporoderm on small spores (35–54 µm in diameter). *Anthoceros fusiformis* var. *taiwanensis* is characterized by scattered spinate to spinulate outgrowths that are united at the base on the proximal surface of spores, and spinate to spinulate lamellae on distal ornamentation (Hasegawa 1993b).

Habitat:—Known only on soil in temple grounds, at 2635 m in China and roadside ridges in temperate habitats between 2100–2350 m in India.

Distribution:—China (Yunnan) and India.

Representative specimen examined:—CHINA. Yunnan: Yulong Naxi Autonomous Co., *Camellia* Temple N of Lijiang, on shady wall in temple grounds, 2635 m, 9 October 1990, *D.G. Long 18961* (E).

Anthoceros angustus Steph., Sp. Hepat. 5: 1001. 1916.

Type:—INDIA. Sikkim-Himalaya, prope Kurseong, 1000 m, 1897, *Rev. Bretaudeau 1239* (holotype G-12816!).

= *Anthoceros formosae* Steph., Sp. Hepat. 5: 1002. 1916. ≡ *Aspiromitus formosae* (Steph.) R.M.Schust., Hepat. Anthocerotae N. Amer. 6: 742, 785. 1992. Type:—CHINA. Taiwan. “Kushaku”, 6 June 1903, *U.J. Faurie 49* (holotype G-19002!).

= *Anthoceros grosseinvolucratus* Steph., Sp. Hepat. 6: 426. 1923. Type:—INDIA. Sikkim Himalayas, s.d., *J.D. Hooker s.n.* (holotype G-16583!).

= *Anthoceros formosae* Steph. fo. *gemmulosus* S.Hatt., Bull. Tokyo Sci. Mus. 11: 182. 1944. ≡ *Anthoceros gemmulosus* (S.Hatt.) Schiffn. & Pandé ex Bharadw., J. Indian Bot. Soc. 37: 76. 1958. Type:—JAPAN. Hyuga, Minami-nakagun, Obi, Ohte, *S. Hattori 2563* (lectotype designated by Hasegawa (1984) TNS).

Description:—Hasegawa (1984), Asthana & Srivastava (1991).

Anthoceros angustus is characterized by the presence of subspherical to pillow-form gemmae that are spongy, cavernous and densely crowded along the apical margin of the thallus (Fig. 2 A–C). This species is highly variation in spore architecture, as described and illustrated by Asthana & Srivastava (1991). Proximal surfaces of spores in Chinese samples are sparsely papillate to spinulate (Fig. 2 I, K), but in type specimens sometimes with few false lamellae formed by several closely studded spines (Fig. 2 N, O). On the distal spore surface, the distribution of false lamellae is dense (Fig. 2 J, M) or dispersed (Fig. 2 L, P). Asthana and Srivastava (1991) reported the lack of a distinct pyrenoid in chloroplasts. Ultrastructural studies, however, confirm the presence of a pyrenoid-like area (Renzaglia *et al.* 2009). Chloroplasts in Chinese samples possess

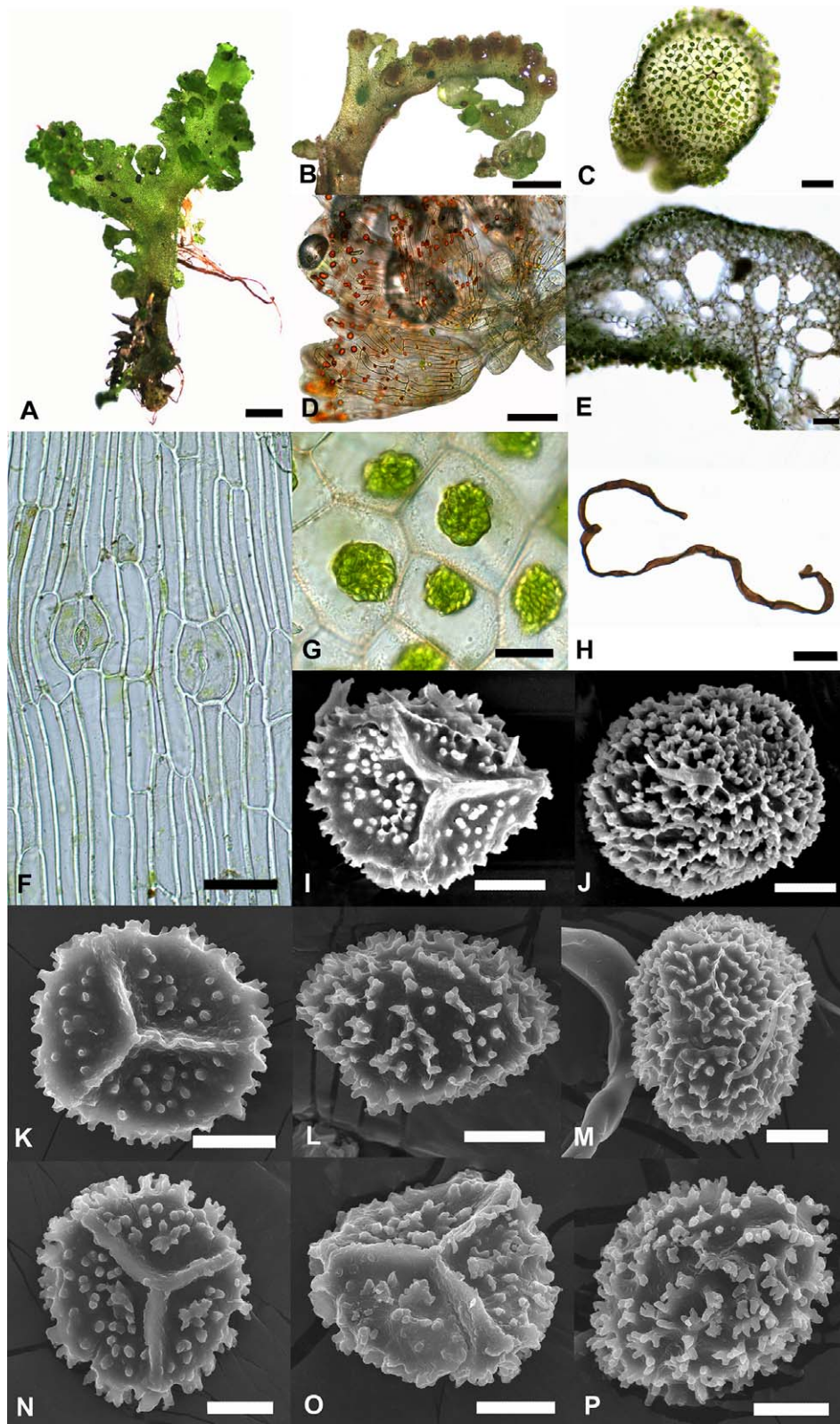


FIGURE 2. *Anthoceros angustus* Steph. A. Thallus with marginal gemmae. B. Male thallus, with androecia linearly arranged along the median line. C. Gemma. D. Dehiscent antheridia with orange chromoplasts in jacket cells. E. Transverse section of thallus showing large mucilage cavities. F. Elongated epidermal cells of a young capsule, showing thin-walled cells and two stomata. G. Epidermis of thallus, showing solitary chloroplasts with starch granules. H. Elongated, thin-walled pseudoeleter. I, K, N, O. SEM micrographs showing proximal spore faces with distinct trilete marks and shortly papillate to spinulate-blunt protuberances. J, L, M, P. SEM micrographs showing distal spore faces with adherent studded spines forming a false lamellate pattern. A and C–M from *T. Peng & J. Wang 20110520-8* (HSNU), B and D from *T. Peng & J. Wang 20111011-9* (HSNU), N–P from *Rev. Breteau 1239* (holotype of *Anthoceros angustus*: G-12816). Scale bars: A, B=1 mm; C, E=100 μ m; D, F, H=50 μ m; G, I–P=10 μ m.

abundant starch granules (Fig. 2 G), as reported by Vaughn *et al.* (1992) and Renzaglia *et al.* (2009). *Anthoceros angustus* is similar to *A. subtilis* in sporoderm architecture, but the two species can be separated by the sporoderm architecture on distal surface under SEM. *Anthoceros angustus* has several closely studded spines forming false lamellate patterns on distal surface of spores (Fig. 2 J, L, M, P), while *A. subtilis* has frequent bifurcated spines (Fig. 5 E). Moreover, *A. angustus* has conspicuously longer pseudoelaters (240–496 µm) (Fig. 2 H) than *A. subtilis* (77–199 µm) (Fig. 5 C).

Habitat:—On soil, wet rocks and sandy soil at 707–2460 m.

Distribution:—China [Fujian, Hunan, Sichuan, Taiwan (Piippo 1990 as *A. formosae*; Hasegawa 1992, 1993b; Gao & Cao 2000 as *A. formosae*; Lin 2000 as *A. formosae*; Gao & Lai 2003 as *A. formosae*; Zhang & Wu 2006 as *A. formosae*; Gao & Wu 2010 as *A. formosae*), Xizang, Yunnan], Bhutan, India, Japan and Nepal (Hasegawa 1993b).

Representative specimens examined:—CHINA. Fujian: Dehua Co., Daiyunshan Nature Reserve, Yanghui Village, beside the farm, on soil, 920 m, 3 July 2010, X.-Q. Zhang *et al.* 20100703-63B (HSNU); Hunan: Yongshun Co., township government of Xiaoxi to Xiaoxidukou, on soil, 200 m, 8 May 1999, T. Cao 990601 (IFP); Sichuan: Muli Tibertan Autonomous Co., No. 913 field, 2460 m, 26 August 1983, K.-K. Chen 598 (IFP); Xizang: Motuo Co., suburban district of County seat, on sandy soil on slope, 857 m, 29°23.224'N, 95°21.803'E, 16 October 2011, T. Peng & J. Wang 20111016-5B (HSNU), Madi Village, on rock with a thin layer of soil by road, 982 m, 29°23.857'N, 95°22.911'E, 16 October 2011, T. Peng & J. Wang 20111016-7B, 20111016-9B (HSNU); Yunnan: Fumin Co., Yongding, 1985, Y.-K. Yang 139 (IFP), Yuanyang Co., Fengchunling, Laocaozhai, on rock by forest, 9 June 1974, M. Zang 4827 (IFP), Gongshan Co., Cikai North Road, on soil, 1515 m, 27°44.962'N, 98°39.872'E, 20 May 2011, T. Peng & J. Wang 20110520-8, 20110520-10B, 20110520-11A, 20110520-13A, 20110520-15 (HSNU), Dulong Xiang, west slope of Gaoligong Shan, Irrawadi catchment, east bank of Dulong Jiang on road to Hongxin Qiao just south of Bapo, degraded valley slope with secondary scrub, on face of road cut, 1391 m, 27°44.187'N, 98°21.003'E, 3 November 2004, D.G. Long 33859 (E), Fugong Co., Gaoligong Shan Range, southern end of the Hengduan Shan. Nu Jiang (Salween River) watershed, 1725 m, 27°07.303'N, 98°49.595'E, 25 April 2004, J.R. Shevock 25091 (E), Jinping Co., Fenshuiling Nature Reserve, on soil, 1975 m, 22°51'49.25"N, 103°13'32.86"E, 24 November 2012, J. Wang *et al.* 20121124-80229 (HSNU), Lvchuan Co., from Lvchun to Jinping, near stream, on soil, 1616 m, 22°52'00.34"N, 102°32'18.22"E, 23 November 2012, J. Wang *et al.* 20121123-80 (HSNU), Tengchong Co., Shangying Xiang, Datianpo Cun, west slope of Gaoligong Shan, on road from Bawan to Tengchong, 7 km above Dahaoping, Roadside in evergreen Lithocarpus/Lauraceae/bamboo forest, on damp soil bank, 2130 m, 24°56'52"N, 98°44'46"E, 18 October 2003, D.G. Long 32410B (E), Jinghong City, Nabanhe National Nature Reserve, from Xiaonuoshangzhai to Guomenshan Reserve Station, on soil by road, 1240 m, 7 January 2006, T. Cao & G.-Y. Song 060545 (HSNU). BHUTAN. Punakha District: Mo Chu valley below Tashithang, Wet evergreen broad-leaved forest, on damp gravelly bank, 1630 m, 27°44'31"N, 89°44'18"E, 26 September 1999, D.G. Long 28789A (E). NEPAL. Sankhuwasabha District: forested slopes above Tashigaon, degraded evergreen Quercus lamellosa forest, on damp gravelly bank, 2240 m, 27°37'N, 87°14'E, 24 September 1991, D.G. Long 20541 (E).

Anthoceros bharadwajii Udar & A.K.Asthana, Proc. Indian Natl. Sci. Acad. B 51(4): 484. 1985.

Type:—INDIA. Kerala, Trichur, ca. 1500 m, September 1982, R. Udar & party, 5446/82 (holotype LWU).

Thalli medium-sized, ecostate, often radially oriented to fan-shaped with slight to deeply dissected lobes at margins, thalli up to 13 mm long and 3–10 mm wide, 0.2–0.3 mm thick; spongy; dorsal epidermis of thallus with single chloroplast per cell, cells irregular in shape, each measuring 25–36 µm across with a central dark pyrenoid region. Dioicous (?). Antheridia not seen. Involucre cylindrical, erect, up to 5 mm high, narrow at mouth. Capsules erect, up to 3.5 cm, bivalved, with well-developed columella. Epidermal cells of capsule rectangular to narrow rectangular, 91–242 × 8–15 µm, thick-walled, stomata scattered, 56–87 × 33–43 µm,

each with two reniform guard cells surrounded by 5–7 cells; cells of the inner lining layer of capsule walls rectangular, $40\text{--}75 \times 28\text{--}41 \mu\text{m}$, sometimes with irregular dark thin bands on tangential walls. Spores brown-dark, brown, $35\text{--}54 \mu\text{m}$ in diameter with spinulate blunt projections forming a pseudolamellate pattern; proximal faces marked with distinct trilete mark, bordered on both sides by $2\text{--}5 \mu\text{m}$ wide unsculptured strip, trilete marks reaching periphery or terminating shortly before periphery. Pseudoelaters light-brown, $102\text{--}270 \mu\text{m}$ long, usually 4 cells long, cells narrowly rectangular, mostly $43\text{--}76 \times 8\text{--}21 \mu\text{m}$, thin-walled, sometimes branched.

This species, known previously only from India (Western Himalayas, Eastern Himalayas, South India (Asthana & Srivastava 1991) and Great Himalayan National Park (Singh & Singh 2008), is newly reported for China and known from Yunnan province.

Anthoceros bharadwajii is similar to *A. alpinus* and *A. fusiformis* var. *taiwanensis* in spore architecture (Fig. 3). The differences between *A. bharadwajii* and *A. alpinus* were discussed under *A. alpinus*. *Anthoceros bharadwajii* resembles *A. fusiformis* var. *taiwanensis* on sporoderm ornamentation with distinct smooth strips along trilete marks. *A. bharadwajii* is distinct in the possession of spores with pseudolamellate sporodermis (Fig. 3 D, E). Thalli of *A. fusiformis* var. *taiwanensis* are strap-shaped and further separate the species (Hasegawa 1993b).

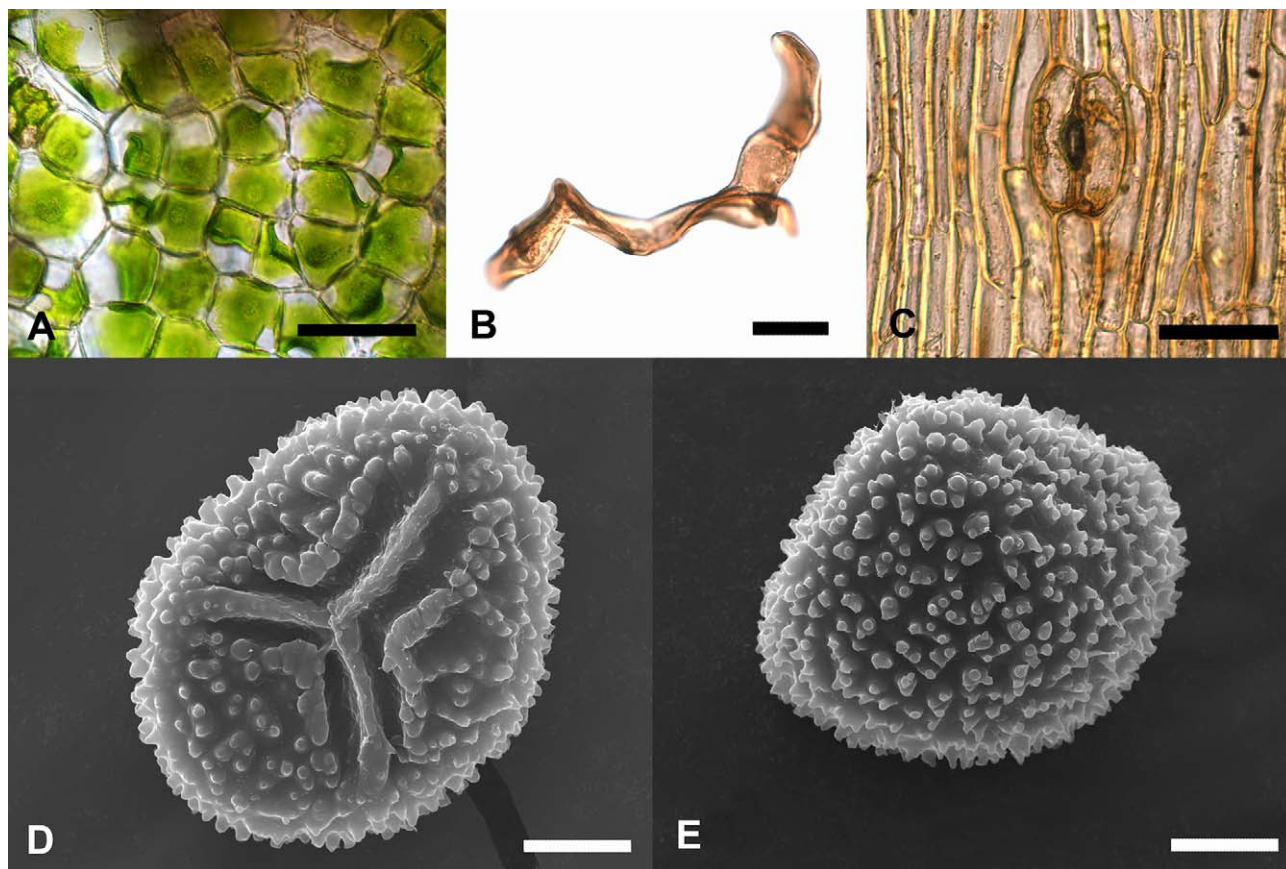


FIGURE 3. *Anthoceros bharadwajii* Udar & A.K.Asthana. A. Dorsal epidermis of thallus with solitary chloroplasts spread across cells and round, central pyrenoids. B. Pseudoelater with thin-walls and irregular thickenings. C. Capsule epidermis with thin-walled cells and a stoma. D. SEM micrograph showing proximal face of spore marked by a distinct trilete mark and parallel wide unsculptured strips. E. SEM micrograph showing distal spore face with densely studded tuberculate-baculate projections. A–C from Y. Yu 20100920-8 (HSNU), D and E from D.-K. Li 03264 (SHM). Scale bars: A, C=50 μm ; B =20 μm ; D, E=10 μm .

Habitat:—Mostly on soil near roads, rarely on wet rock at 1470–2550 m in China.

Distribution:—China (Yunnan) and India.

Representative specimens examined:—CHINA. Yunnan: Anning Co., Caoxi Temple, Zhenzhu Spring, on soil in forest, 13 October 1976, *D.-K. Li 03264* (SHM), Bijiang Co., Gaoligongshan, Pianma to Tingming Lake, 30 July 1978, *M. Zang 5734_1* (IFP), Gaoligongshan, Gubaofeng, on wet rock, 14 July 1978, *M. Zang 5501* (IFP), Baoshan Co. (Longyan Qu), Mangkuan Xiang, east slope of Gaoligong Shan, between Hanlong Village and Shaoxiangpingxi near Baihualing, Subtropical forest slopes with cultivated areas and *Juglans* trees, on soil bank by path, under *Artemisia*, 1545 m, 25°17'38.9"N, 98°47'54.7"E, 12 October 2007, *D.G. Long & J. Shevock 37521* (E), Cangyuan Wazu Autonomous Co., Bianfudong, 3 September 1980, *S.-Y. Zeng 80-1375* (IFP), 10 October 1980, *S.-Y. Zeng 80-1813* (IFP), Binchuan Co., Zhongyuanshan, on soil, 2 October 1991, *X.-Y. Jia 910186, 910186-1* (IFP), Gongshan Co., Bingzhongluo Village, from Jiasheng Village to Dulongjiang, on soil by road, 1846 m, 20 September 2010, *Y. Yu 20100920-7, 20100920-8* (HSNU), Gengma Daizu-Wazu Autonomous Co., Banwang Village, 29 August 1980, *S.-M. Yu 80-1190* (IFP), Jingdong Co., Ailaoshan Nature Reserve, Xujiaba, from Ecology station to Bojiba, beside a ditch, on soil, 2512 m, 24°33'42"N, 101°00'07"E, 23 November 2010, *Y.-F. Wang 67B* (HSNU), beside the Tea Garden, on soil, 2486 m, 24°32'52"N, 101°01'38"E, 24 November 2010, *Y.-F. Wang III* (HSNU), Kunming City, Jindian Temple, on soil by road, 21 September 1976, *D.-K. Li 02571* (HSNU), Lvchuan Co., Lieshimu, on wet soil, 14 September 1973, *M. Zang & X.-R. Xu 14* (IFP), Yulong Naxizu Autonomous Co., Yulongxueshan, 6 August 1985, *X.-J. Li 85556* (IFP), Tengchong Co., Qushi Xiang, Yong'an Cun, Longchuan Jiang valley, east fork of Longchuan Jiang at Yonganqiao Bridge, river bank with exposed granite rocks and scrub, on gravelly bank of road cutting, 1470 m, 25°19'29"N, 98°36'33"E, 22 October 2003, *D.G. Long 32514* (E), Xundian Huizu and Yizu Autonomous Co., Qinglong Temple, on soil by railway, 1920 m, 1 November 1977, *W.-X. Xu 77006* (IFP), Songming Co., on soil, September 1979, *G.-H. Feng 6* (IFP), Menghai Co., Manxinglongla, near the mountain, on soil, 1840 m, 9 January 2006, *T. Cao & G.-Y. Song 060913B* (HSNU). NEPAL. Taplejung District: Tamur River near Hellok, cultivated slopes, on terrace bank, 1670 m, 27°30'N, 87°47'E, 4 September 1989, *D.G. Long 16597* (E).

Anthoceros fusiformis Austin var. *taiwanensis* J.Haseg., Acta Phytotax. Geobot. 44(2): 100. 1993.

Type:—CHINA. Taiwan, Chiayi Hsien, Mt. Ali, Mt. Tsu-Tson-san, 2300–2900 m, *S. Kurokawa 4004* (holotype TNS).

Description:—Hasegawa (1993b).

Illustrations:—Hasegawa (1993b, p. 100, fig. 1).

Anthoceros fusiformis var. *taiwanensis* is characterized and recognized by strap-shaped thalli, dark brown spores, 32–42 µm in diameter, the proximal surfaces of spores with distinct and wider smooth strips along the trilete marks, spores with spinulate-lamellate outgrowths (Hasegawa 1993b).

Habitat:—2300–2900 m in Taiwan (Hasegawa 1993b).

Distribution:—China (Hasegawa 1993b). A rare species, known only from Mt. Ali and Mt. Tsu-Tson-san, Chiayi Hsien in Taiwan.

Anthoceros punctatus L., Sp. Pl. 2: 1139. 1753.

= *Anthoceros crispulus* (Mont.) Douin, Rev. Bryol. 32: 27. 1905. (fide Stotler & Crandall-Stotler 2005).

For further synonyms, see Proskauer (1958).

Description:—Hasegawa (1984); Asthana & Srivastava (1991).

Selected Illustrations:—Hasegawa (1984, p. 255, figs. 5), Proskauer (1958, p. 1308, figs. 510).

Anthoceros punctatus (Fig. 4) is the most common species of *Anthoceros* in China. The main features include 1) thalli usually in rosettes, monoicous, up to 1.7 cm in diam, with dense complicate lamellae (Fig. 4 A, B), 2) spores reticulate over distal and proximal faces, proximal surfaces foveate-reticulate, without spines (Fig. 4 J), trilete mark distinctly ridged often reaching to the periphery (Fig. 4 J), and distal surfaces spinulate and reticulate, combined at base and apically bifurcated spinulate on the knots of reticulation (Fig. 4 K), and 3) antheridia body 58–72 × 101–158 µm, stalk 19–20 × 40–93 µm (Fig. 4 E).

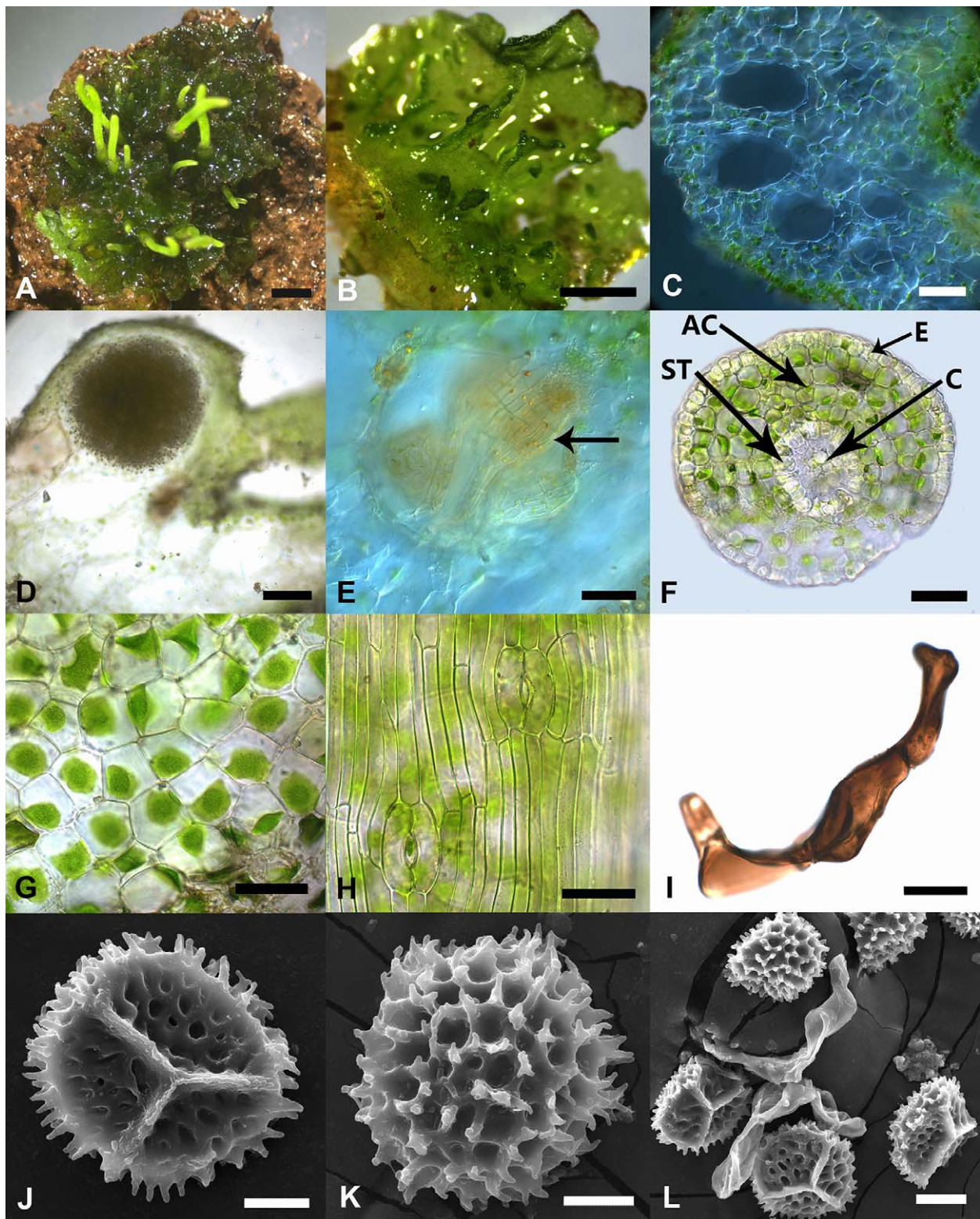


FIGURE 4. *Anthoceros punctatus* L. A. Thalli with immature light green sporophytes. B. Dorsal lamellae on thallus. C. Transverse section of thallus showing large mucilage cavities. D. *Nostoc* colony within ventral thallus in transverse section. E. Transverse section of thallus showing one antheridial cavity with four antheridia (arrow). F. Transverse section of a young sporophyte with a central columella (C), single-layered sporogenous tissue (ST), four-layers of assimilative cells (AC) and non-photosynthetic epidermis (E). G. Dorsal thallus epidermis with a single chloroplast. H. Thin-walled epidermis of capsule with stomata. I. Three-celled pseudoelater, showing thin-walls and irregular thickenings. J. SEM micrograph showing proximal spore face with distinct trilete mark and reticulations (foveate-reticulate). K. SEM micrograph showing distal spore face which is spinulate and reticulate with bold spinulate ridges, spines subacute at apex with rounded heads, occasionally bifurcating. L. SEM micrograph showing spores and pseudoelaters. A–I from T. Peng 20110220-11 (HSNU), J–L from D.-K. Li & C.-H. Gao 07035 (SHM). Scale bars: A=2 mm; B=1 mm; C=100 μ m; D=200 μ m; E–H=50 μ m; I, L=20 μ m; J, K=10 μ m.

Anthoceros punctatus is morphologically similar to *A. agrestis* except that the latter has smaller mature thalli (0.6–1.5 cm in diameter in *A. agrestis*; up to 1.7 cm in diameter in *A. punctatus*) and antheridia (body 45–56 × 56–88 µm, stalk 8–20 × 20–48 µm in *A. agrestis*; body 58–72 × 101–158 µm, stalk 19–20 × 40–93 µm in *A. punctatus*) (Paton 1979).

Habitat:—Mostly on soil, rarely on wet rock at 100–2795 m in China.

Distribution:—China [Anhui (So 1996), Fujian, Guangdong (So 1996), Guizhou, Heilongjiang (Piippo 1990; Gao & Wu 2010), Hong Kong, Hubei (Zhao *et al.* 2002; Xiong & Yang 2006 as *Anthoceros* (sic) *punctatus*), Jiangsu (Zhang & Lai 1993), Jiangxi (Li & Ji 1991 as *A. crispulus*; Ji 1993 as *A. crispulus*; Ji 1994 as *A. crispulus*; Fang *et al.* 1998; Ji *et al.* 2001), Jilin (Piippo 1990; Gao & Wu 2010), Liaoning (Piippo 1990), Shaanxi, Shanghai (Zhang & Lai 1993), Taiwan (Piippo 1990; Hasegawa 1993b; So 1995; Lin 2000; Gao & Wu 2010), Yunnan, Zhejiang], India, Japan, Indonesia Java, Europe, Nepal, North America, South America (Hasegawa 1984).

Representative specimens examined:—CHINA. Fujian: Dehua Co., Daiyunshan Nature Reserve, Nancheng Town, beside the field, on soil, 319 m, 25°37.646'N, 118°23.148'E, 4 April 2010, *R.-L. Zhu et al.* 20100404-22 (HSNU); Guizhou: Libo Co., Maolan National Nature Reserve, Laqiaozhai, Hydrology Monitoring Point, low-lying land, on soil, 638 m, 25°18.001'N, 107°17.965'E, 22 February 2011, *T. Peng* 20110222-1, 20110222-3, 20110222-6 (HSNU), Liangzaixin, low-lying land, on soil, 725 m, 25°16.976'N, 107°56.689'E, 20 February 2011, *T. Peng* 20110220-10, 20110220-11, 20110220-37C (HSNU); Shaanxi: Chenggu Co., Tianming Village, Jiuba, on rock by ditch, 570 m, 30 March 1990, *M.-X. Zhang & M. Wang* 2614 (XBGH); Hong Kong: Lantau Island, near the Dankness Channel, 4 March 1988, *C.-H. Gao* 27197 (SHM); Yunnan: Gongshan Co., Cikai town, Jishudi Village, Service Station of the village, behind the mountain, on sandy soil, 1568 m, 27°45.386'N, 98°39.523'E, 20 May 2011, *T. Peng & J. Wang* 20110520-25, 20110520-26B (HSNU), Cikai North Road, on soil, 1515 m, 27°44.962'N, 98°39.872'E, 20 May 2011, *T. Peng & J. Wang* 20110520-10C, 20110520-13B (HSNU), Menghai Co., Jiangbian, on dry branch, 24 February 1979, *G.-C. Zhang & T. Cao* 14504 (IFP); Zhejiang: Dongyang City, Qianxiang Town, Sanbao Village, on rock with a thin layer of soil, 1 May 2011, *J. Wang* 20110501-1B (HSNU), Zhoushan City, Putuoshan, near the Damiaoqian, 200 m, 12 May 1979, *D.-K. Li & C.-H. Gao* 6989 (SHM), from Fayu Temple to Foding, 100 m, 14 May 1979, *D.-K. Li & C.-H. Gao* 07035 (SHM), Shengzhou City, Guimen, Jiexi, Shijing, Zhuyuwankou, on soil in farmland, 2 June 2005, *R.-L. Zhu* 20050602-1 (HSNU), Linan Co., Xitianmushan Nature Reserve, 8 May 1991, *R.-L. Zhu* 91037 (HSNU). NEPAL. Taplejung District: Ridge NE of Gupha Pokhari, mixed *Rhododendron* forest, on rocky bank by path, 2795 m, 27°17'N, 87°32'E, 25 October 1991, *D.G. Long* 21553 (E).

Anthoceros subtilis Steph., Sp. Hepat. 5: 1003. 1916.

Type:—INDIA. South Canara, Mangalore, August 1907, *R. Pflleiderer* 6127 (holotype G-12823!).

= *Anthoceros subbrevis* Haseg., J. Hattori Bot. Lab. 57: 261. 1984. Type:—JAPAN. Miyazaki Pref., Nichinan-shi, Nagayoshi, on soil, *J. Hasegawa* 7770 (holotype KYO). (fide Hasegawa 1998).

= *Anthoceros brunneus* Steph., Sp. Hepat. 5: 1004. 1916. Type:—VIETNAM. Tonkin, s.d., *H.F. Bon* 1290 (holotype G!).

= *Anthoceros fuscus* Steph., Sp. Hepat. 5: 1004. 1916. Type:—VIETNAM. Thua Thien Hue, Annam, September 1908, *P.A. Ebenhardt* 224 (holotype G-12818!).

= *Anthoceros notothyloides* Steph., Sp. Hepat. 6: 426. 1923. Type:—INDIA. South Canara, Mangalore, September 1906, *R.J. Pflleiderer* 5004 (holotype G-12822!).

Thalli orbicular, small, usually about 6 mm in diameter, light green to deep, cavernous, spongy, ecostate, deeply separate formed fan-shaped to obcuneate lobes, dorsal surfaces significantly plicate without lamellae, and margins always lobulate irregularly. *Nostoc* colonies scattered in ventral side of thallus. Dioicous (?). Androecia not seen. Involucre cylindrical, erect, up to 2.5 mm high, nearly smooth at mouth. Capsules mostly 1–1.9 cm long, bivalved, with well-developed columella. Epidermal cells of capsule walls rectangular to narrow rectangular, 99–112 × 13–19 µm, thick-walled, stomata scattered, 46–52 × 33–44 µm, each stoma with two reniform guard cells surrounded by 5–8 cells; cells of the inner lining of capsule walls rectangular, 19–42 × 22–33 µm, sometimes with irregular dark thin bands on tangential walls. Spores brown to dark-

brown, 35–44 μm in diameter, with spinulate-baculate projections, often apically bifurcated, on proximal surfaces, triradiate marks distinct, attaining to the equator, with spinulose-lamellate, distal surfaces roughened with papillate to spinulose outgrowths often united at the base, more densely spinulate than proximal face. Pseudoelaters light brown, 77–199 μm long, usually 2–3 cells long, thin walled, sometimes with irregular bands of thickenings.

In China, *Anthoceros subtilis* somewhat resembles *A. angustus* on the sporoderm ornamentation (Fig. 5). For their differences, see *A. angustus*.

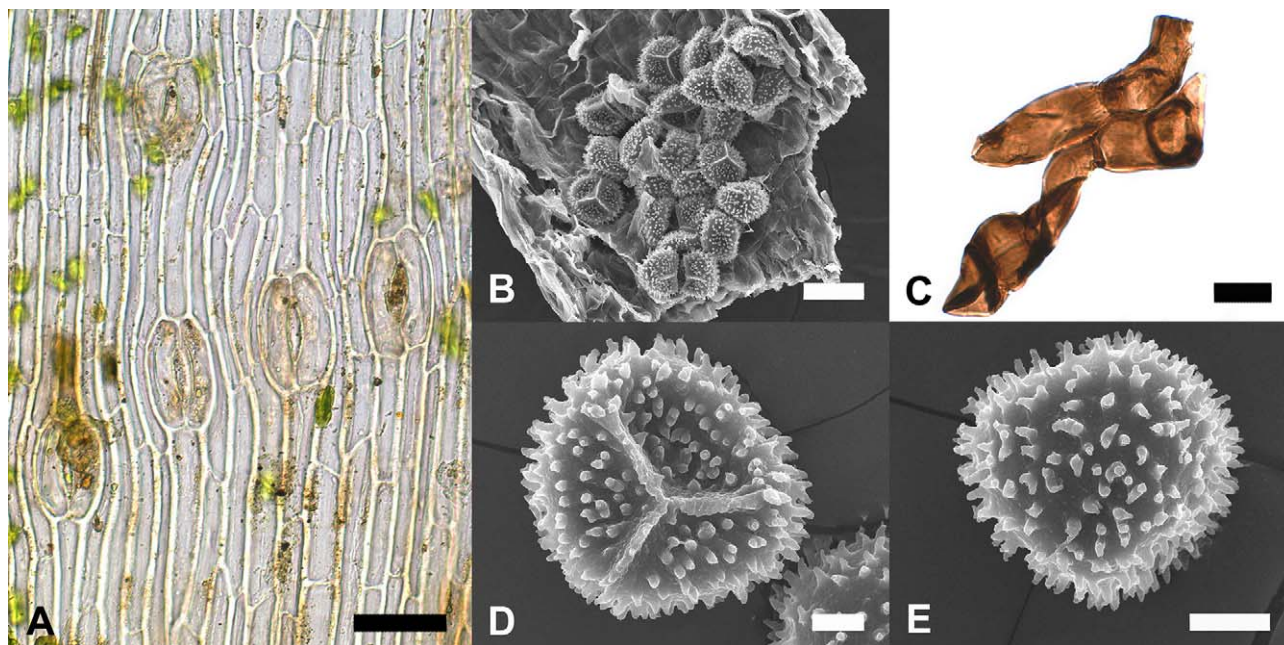


FIGURE 5. *Anthoceros subtilis* Steph. A. Capsule epidermis with thin walls and stomata. B. SEM micrograph showing sporophyte fragment with tetrads and pseudoelaters. C. Pseudoelaters with thin-walls and irregular thickenings. D. SEM micrograph showing proximal face of spore which is spinulose and has distinct trilete mark. E. SEM micrograph showing distal spore face which is papillate to spinulose with spines often united at the base. All from *R.-H. Dai PX95106* (GACP). Scale bars: A, C=50 μm ; B, D, E=10 μm .

Habitat:—Mostly on soil, rarely on rock at 10–2000 m in China.

Distribution:—China (Guizhou, Heilongjiang, Jilin, Liaoning and Yunnan), India [Maharashtra, Karnataka, South Canara (Asthana & Srivastava 1991)], Japan, Nepal (Hasegawa 1998), Thailand, Vietnam [Annam (Asthana & Srivastava 1991)].

Representative specimens examined:—CHINA. Guizhou: Panxian Co., Shiqiao, 23 August 1995, *R.-H. Dai PX95106* (GACP); Heilongjiang: Shangzhi Co., Maoershan, on soil, 21 August 1959, *Q. Gao et al. 269* (IFP), 31 October 1985, *S.-Y. Zeng 85-63* (IFP), September 1959, *5051* (IFP); Jilin: Linjiang City, mountainside of Maoershan, corn field, on soil, 7 September 1963, *Q. Gao 7723* (IFP); Liaoning: Dalian City, Longhe, 29 August 1987, *X.-Y. Jia 870041* (IFP), Kuandian Manzu Autonomous Co., Baishilizi Nature Reserve, Heigou corn field, 22 September 1987, *T. Cao & S.-Z. Wang 38643, 38644* (IFP), on soil, *T. Cao & S.-Z. Wang 38663* (IFP), Benxi Co., Xiamatang town, on soil, 16 September 1975, *Q. Gao 13407* (IFP), Xiamatang Town, on soil in broomcorn field, 16 September 1975, *Q. Gao 13398* (IFP), Huanren Co., Laotudingzi National Nature Reserve, Tianqiaohegou, on soil, 500 m, 26 September 1986, *T. Cao & J.-Y. Feng 471A* (IFP), Shenyang City, shoreside of Hunhe, broomcorn field, on soil, *Q. Gao 7041* (IFP), Yunnan: Bijiang Co., Gaoligongshan, Pianma to Tingming lake, 30 July 1987, *M. Zang 5734* (IFP), Cangyuan Wazu Autonomous Co., 8 September 1980, *S.-Y. Zeng 80-1848* (IFP), Bianfudong, on rock, 3 September 1980, *S.-M. Yu 80-1389* (IFP), Dali City, Tsang (Cang) Shan, path from Shi Jo Village to Huadianba, on damp bank in village, 2000 m, 16 October 1990, *D.G. Long 19198* (E), Ruili City, Nongdao, on soil behind the Leiyun, 14 July 1977, *X.-J. Li 172* (IFP), Denggashan, 13 August 1980, *X.-J. Li 80-825A* (IFP), Nongdao Town, Leiyun Village, on wet soil by forest edge, 150 m, *X.-J. Li 165* (IFP), Songming Co., Meiziqing, September 1979, *G.-*

H. Feng 7 (IFP), Tengchong Co., Chengguan commune, on soil, 7 August 1980, X.-J. Li 80-715 (IFP). THAILAND. Chiang Mai Province: Chom Thong District, Royal Agricultural Station Inthanon, on soil, 1300 m, 18°54.278'N, 98°51.842'E, 20 December 2011, R.-L. Zhu 20111220-42 (HSNU).

Synonyms, doubtful and excluded records

Anthoceros agrestis Paton, *J. Bryol.* 10: 257. 1979.

Anthoceros agrestis was reported from Taiwan by Lai & Wang-Yang (1976) as *A. nagasakiensis* which was reduced to a synonym of *Anthoceros agrestis* by Stotler & Crandall-Stotler (2003). The recent report of this species by Wang *et al.* (2011) was based on Lai & Wang-Yang (1976). Unfortunately, no material of this species was available for the present study.

Anthoceros appendiculatus Steph., *Bot. Jahrb. Syst.* 23: 315. 1896. = *Folioceros appendiculatu* (Steph.) J.Haseg., *J. Hattori Bot. Lab.* 60: 382. 1986. (cf. Hasegawa 1986).

Anthoceros areolatus (Steph.) Hsu, comb. inval.

This combination was first presented in Hsu (1979)'s checklist. It is considered to be invalid due to the lack of a basionym citation. The basionym "*Aspiromitus areolatus* Steph., *Sp. Hepat.* 5: 969. 1916" is a synonym of *Folioceros fuciformis*. For details, see below *Aspiromitus areolatus*.

Anthoceros areolatus (Steph.) P.C.Chen, comb. inval.

Gao & Wu (2010) listed *Anthoceros areolatus* (Steph.) P.C.Chen, but no valid literature about this species was found. Thus, *Anthoceros areolatus* (Steph.) P.C.Chen, is an invalid name.

Anthoceros chinensis (Steph.) Hsu, comb. inval.

The combination made by Hsu (1979) is invalid because no basionym was cited. The basionym "*Aspiromitus chinensis* Steph., *Sp. Hepat.* 5: 969. 1916." is a synonym of *Phaeoceros carolinianus* (Michaux) Prosk. (Hasegawa 1991). For details, see below *Aspiromitus chinensis* Steph.

Anthoceros chungii Khanna, *J. Indian Bot. Soc.* 17: 316. 1938.

Anthoceros chungii was reported as a new species from Kiangsi (Jiangxi), China by Khanna (1938). It is known only from the type, which we were not able to examine. According to the protologue (Khanna 1938), *A. chungii* is characterized by strap-shaped thalli and light brown spores without a distinct triradiate mark. The typical *Anthoceros* grows in rosettes and has dark brown spores with a distinct trilete mark. A further study may indicate that *Anthoceros chungii* is a member of *Folioceros*.

Anthoceros dichotomus Raddi, *Atti Accad. Sci. Siena* 10: 289. 1808. = *Phymatoceros bulbiculosus* (Brot.) Stotler, W.T.Doyle & Crand.-Stotl., *Phytologia* 87(2): 115. 2005. (cf. Stotler & Crandall-Stotler 2005).

Anthoceros esquirolii Steph., *Sp. Hepat.* 6: 427. 1923. = *Phaeoceros esquirolii* (Steph.) Udari et D.K.Singh 1981. Type:—China. Siang Chou, *Esquirol* 2653pp (holotype G-18896!). = *Phaeoceros carolinianus* (Michaux) Prosk., *Bull. Torrey Bot. Club* 78: 347. 1951, *syn. nov.*

Anthoceros esquirolii is monoicous, with thalli medium-size to large, strap-shaped to suborbicular, ecostate, solid, androecia scattered, involucre solitary, erect, cylindrical, capsules bivalved and twisted, with stomata, spores yellow, trilete marks distinct, proximal surfaces minutely papillate in center of each face, distal surfaces densely papillate, pseudoelaters 2–4 cells long, thin-walled. We found that these characters are identical to those of *Phaeoceros carolinianus*. Thus, *Anthoceros esquirolii* is considered to be conspecific with *P. carolinianus*, a widespread species.

Anthoceros fusiformis Austin, Bull. Torrey Bot. Club. 6: 28. 1875.

Anthoceros fusiformis occurs disjunctly on both sides of the Pacific Ocean, from Japan and North America. Yang (1960) reported *Anthoceros fusiformis* from Taiwan. This might be an error referring to *Folioceros fuciformis*, as suggested by Piippo (1990). Unfortunately, there is no material of this species available to study.

Anthoceros glandulosus Lehm. & Lindenb., Nov. Stirp. Pug. 4: 26. 1832. ≡ *Folioceros glandulosus* (Lehm. & Lindenb.) Bharadwaj, Geophytology 2(1): 82. 1972. (cf. Asthana & Srivastava 1991).

Anthoceros laevis L., Sp. Pl. 1139. 1753. ≡ *Phaeoceros laevis* (L.) Prosk., Bull. Torrey Bot. Club 78: 347. 1951. (cf. Proskauer 1951).

Anthoceros miyabenus Steph., Bull. Herb. Boissier 5: 85. 1897. = *Folioceros fuciformis* (Mont.) D.C.Bharadwaj, Geophytology 1(1): 13. 1971. (cf. Bharadwaj 1971; Hasegawa 1984).

Anthoceros pearsonii M.Howe, Bull. Torrey Bot. Club 25: 8. 1898. ≡ *Phaeoceros pearsonii* (M.Howe) Prosk., Bull. Torrey Bot. Club 78: 347. 1951. (cf. Proskauer 1951).

Anthoceros szechuenensis P.C.Chen

Although this name was listed from China by Hsu (1979), Wu *et al.* (1984), Piippo (1990) and Gao & Wu (2010), the name has not been validly published.

Aspiromitus areolatus Steph., Sp. Hepat. 5: 969. 1916. Type:—China. *M.E. Wichura s.n.* (holotype G-20763!) = *Folioceros fuciformis* (Mont.) D.C.Bharadwaj, Geophytology 1(1): 13. 1971, *syn. nov.*

Our examination of the type reveals the following features: thallus monoicous, strap-shaped, ecostate, cavernous, somewhat regularly and pinnately lobed, dorsal surfaces of lobes nearly smooth or slightly lamellate along incisions, androecia scattered, solitary erect cylindrical involucre, bivalved and twisted capsules, stoma composed of two reniform guard cell surrounded by 5–7 cells, brown spores with indistinct or vestigial trilete marks, proximal spore surface densely papillate to baculate, distal surface grossly baculate, pseudoelaters 2–4 celled, strongly thick-walled. These characters are identical to those of *Folioceros fuciformis*. There are no differences between the two species and we consider them conspecific.

Aspiromitus chinensis Steph., Sp. Hepat. 5: 969. 1916. Type:—China, Yunnan, Ta-pin-tze, 900 m, *Delavay 1622* (holotype G-20498!) = *Phaeoceros carolinianus* (Michaux) Prosk., Bull. Torrey Bot. Club 78: 347. 1951. (Hasegawa 1991).

Acknowledgments

We extend appreciation to the curators and staff of E, G, HIRO, HSNU, IFP, SHM, SHTU, SZG, GACP, L, NICH, and NY for making specimens including types available for study through loans or visits. This research was sponsored by the National Natural Science Foundation of China (no. 31170190), the Special Program for the National Basic Work of the Ministry of Science and Technology, China (No. 2012FY110600), 211 Project for the East China Normal University and the Science and Technology Foundation of Guizhou (no. J[2008]2096). Special thanks to D. Long for loaning his collections for our study, J.C. Villarreal and Si He for reading and correcting the earlier manuscript, anonymous reviewers and the associate editor (Karen Renzaglia) for helpful comments and improvements on the manuscript.

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