Taiwania, 59(4): 340– 347, 2014
DOI: 10.6165/tai.2014.59.4.340

RESEARCH ARTICLE

Taxonomic Studies on Thai Anthocerotophyta I. The Genera *Dendroceros* and *Megaceros* (Dendrocerotaceae)

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(Manuscript received 11 June 2014; accepted 10 Auguster 2014)

ABSTRACT: A taxonomic review of the hornwort genera *Dendroceros* Nees and *Megaceros* Campb. in Thailand is presented, based on herbarium specimens and field surveys. Three species are recognized, namely *D. cucullatus* Steph., *D. suplanus* Steph. and *M. flagellaris* (Mitt.) Steph. A key, descriptions and line drawings and notes on the ecology and geographical distribution of the species are provided.

KEY WORDS: bryophyte, *Dendroceros*, hornworts, *Megaceros*, taxonomy, Thailand.

INTRODUCTION

The division Anthocerotophyta (hornworts) is the smallest group of bryophytes, comprising 10 genera (including: *Anthoceros* L., *Foliioceros* D.C. Bhardwaj, *Dendroceros* Nees, *Leiosporoceros* Hässel, *Megaceros* Campb., *Nothoceros* (R.M. Schust.) J. Haseg., *Notothylas* Sull. ex A. Gray, *Phaeoceros* Prosk., *Phaeomegaceros* Duff et al. and *Phymatoceros* Stotler *et al.*) (Li *et al.*, 2011; Villarreal, per. com.) with probably 200–250 species (Duff *et al.*, 2007; Villarreal *et al.*, 2010). The diagnostic characters of the hornworts are: horn-like sporophyte that lacks seta, the presence of a basal meristem and dehiscence along one or two vertical lines. The gametophyte is always thalloid, mostly uniplastidic containing pyrenoids (Villarreal *et al.*, 2010). Hornworts are widely distributed in tropical and temperate zones, with higher species diversity in the tropical and austral temperate regions, perhaps reflecting a taxonomic bias to well-studied areas. Hornworts typically grown on mostly moist mineral soil of banks and cliffs, cultivated land and splashed rocks along streams (Frey & Stech, 2005; Villarreal *et al.*, 2010).

The genera *Dendroceros* and *Megaceros* belong to the family Dendrocerotaceae (Milde) Hässel, and they share the following characters: capsule without stomata, pseudoelaters bearing helicoidal thickening bands and a single antheridium per chamber (Hässel de Menéndez, 1988; Villarreal *et al.*, 2010). These two sister genera are reciprocally monophyletic and differ by gametophyte and spore features. *Dendroceros* is characterized by the presence of costa and unistratose thallus wings and having a single chloroplast per cell with a distinctive pyrenoid with protein incrustations. In contrast, *Megaceros* species have a broad and ecostate thallus and each cell contains 1–8 chloroplasts (Villarreal *et al.*, 2010). The spores of *Dendroceros* are multicellular and endosporic, while those of *Megaceros* are unicellular and exosporic (Renzanglia, 1978; Villarreal *et al.*, 2012).

In Thailand, the rather poorly known bryoflora is reflected on the few hornwort reports for the country (Sukkharak and Chantanaorrapint, 2014). Hasegawa (1983) studied the genus *Megaceros* in Asia, and confirmed that *M. flagellaris* (Mitt.) Steph. is present in Thailand. Lai *et al.* (2008) published an updated checklist of liverworts and hornworts of Thailand, and added *D. suplanus* Steph. to the Thai flora. Recently, Chantanaorrapint *et al.* (2014) reported *D. cucullatus* Steph. for Thailand. The aim of the present study is to contribute new knowledge for the taxonomic account of hornworts in the Flora of Thailand.

TAXONOMIC TREATMENT

This study is based on recent collections from Thailand as well as herbarium specimens in BCU, BKF, CMU, G, KLU, L, PSU and SING. Morphological and anatomical characters were studied using stereo and compound microscopes. The distinctive characters of the species were illustrated with the aid of an Olympus drawing tube. Mature spores were removed from sporangia and mounted on double-stick cellophane adhesive tape affixed on stubs. Spores were then plated with a thin layer of gold and examined with JEOL JSM-5410 LV scanning electron microscope. In addition, distribution and ecological data were compiled, descriptions, illustrations and a key to species are provided.

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RESULTS AND DISCUSSION

In this study two species of *Dendroceros* and one species of *Megaceros* are described and illustrated from Thailand. The species are *D. cucullatus* Steph., *D. suplanus* Steph. and *M. flagellaris* (Mitt.) Steph. Based on the localities from the field surveys and herbarium specimens, it has been concluded that the genus *Dendroceros* has limited distribution in the southern half of the country, whereas *M. flagellaris* is widely distributed occurring in 5 floristic regions including the northern, eastern, south-eastern, south-western and peninsular regions (Fig. 1). The peninsular region exhibits great diversity of species (Fig. 1), probably due to its more humid climate and less disturbed forests. According to their habitat and forest type, Thai *Dendroceros* are either epiphytes or epiphyllous, found in humid montane forest or cloud forest, from 1000 to 1700 m a.s.l., whilst *M. flagellaris* is usually found on wet rocks along stream in shady areas from lowland to over 2300 m a.s.l.

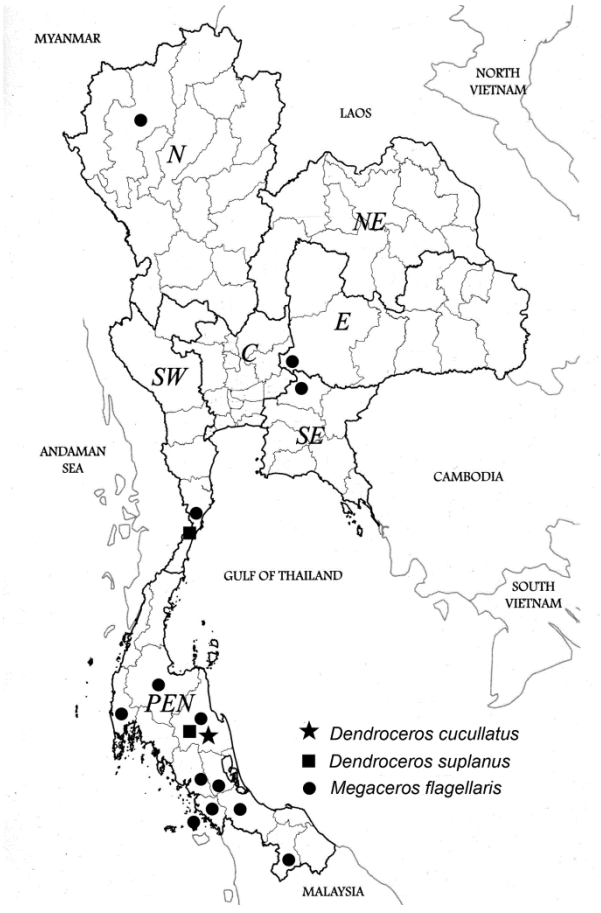


Fig. 1. Distribution of the species of Dendrocerotaceae in Thailand. Thai Floristic regions N= Northern, NE= North-Eastern, E= Eastern, SE= South-Eastern, C= Central, SW= South-Western, PEN= Peninsular.

Keys to species of Thai Dendrocerotaceae

1. Plants usually growing on wet rocks; thalli broad, without costa; spores unicellular at maturity…… ***Megaceros flagellaris***
1. Plants growing on bark or leaves; thalli narrower, with costa; spores multicellular at maturity……..2.
2. Costa cavernous; lamina strongly crispate to galeate; spore consist of more than 10 cells…… ***Dendroceros cucullatus***
2. Costa solid, lamina plane to crispate; spore consist of *ca.* 10 cells ……..……. ***Dendroceros subplanus***

Dendroceros cucullatus Steph., Sp. Hepat. 6: 429. 1923. Type: Philippines. Mindanao, Butuan Subprovince, 15 m, on tree trunk, Mar-Jul 1911, *C. M. Weber 1341* (holotype G!).

Figs. 2 & 5A–B.

Thalli pale green when fresh, pale brown to blackish when dry, medium-sized, up to 15 mm long, 1.6–2.5 mm wide, irregularly subpinnately branched or sometimes subdichotomously branched; costa rather broad, 0.5–1 mm wide, in transverse section more or less flat dorsally and convex ventrally, cavernous, lacunae 20–90 μm in diameter, arranged in 1–2 rows of larger lacunae together with additional smaller ones; lamina unistratose, strongly crispate or forming a hood-like structure, with large perforation especially conspicuous near margin, margins nearly entire; epidermal cells 20–25 × 25–35 μm at margin, 25–35 × 30–40 μm from middle to costa, thin- to slightly thick-walled, trigone-like structures rather large, triangular to triangular-cordate. *Rhizoids* colorless, scattered on ventral side of costa, inner wall smooth. *Nostoc* colonies embedded in the thallus, scattered on both dorsal and ventral sides of costa, especially in its older parts.

Monoicous. *Androecia* scattered on main branches; antheridia solitary, rounded-ovoid, 200–250 μm in diameter. *Involucres* erect, cylindrical, 5–7 mm long, surface bearing small scales. *Capsules* slender, up to 15 mm long, dehiscing into two valves when mature; stomata absent; epidermal cells rectangular, 35–55 × 20–25 μm, with narrow lumens and strongly thickened walls, prorate at the tips of cells. *Spores* subglobose to rounded-triangular, various in size depending on developmental stage, 55–75 μm in diameter, green, multicellular with numerous cells; distal surface spinulose, the surface between spinules with irregularly ridges; proximal surface of the irregular ridges with wart-like structures. *Pseudoelaters* pale brown, unbranched, *ca.* 450 μm long, ca. 10 μm wide, with a single helicoidal band.

Habitat and ecology: *Dendroceros cucullatus* grows on living leaves, branches and tree trunks in humid montane forest at *ca.* 1000 m a.s.l., and is associated with other liverworts, especially with *Cheilolejeunea trapezi*a (Nees) R.M. Schust. & Kachroo, *Colura conica* (Sande Lac.) K.I. Goebel, *Drepanolejeunea levicornua*

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Steph., *Metalejeunea cucullata* (Reinw. *et al.*) Grolle, and *Lejeunea* spp. In Thailand, the species is known only from the summit of Mt. Khao Ramrome, Nakhon Si Thammarat but might have a wider.

Distribution: Philippines and Thailand.

Specimens examined: **THAILAND:** Nakhon Si Thammarat, Ron Phibun, summit of Khao Ramrome Mt., 08°14'18"N, 99°48'182"E, 1000 m, 13 May 2007, *Chantanaorrapint 1666* (PSU); 24 Aug 2007, *Chantanaorrapint 2007*, *2008* (PSU); 12 Mar 2013, *Chantanaorrapint & Promma 2096* (BKF, PSU).

Note: *Dendroceros cucullatus* was considered as a synonym of *D. difficilis* Steph. by Hasegawa (1980). However, a detailed analysis of the type materials and additional specimens clearly indicates that *D. cucullatus* is a distinct species, which can be easily distinguished from *D. difficilis* by its thallus margin, structure of costa and epidermal cells of capsule (Chantanaorrapint *et al.*, 2014). This species is well characterized and easily recognized by the following characters 1) costa with schizogenous cavities, 2) thallus lamina strongly galeate with entire margins and 3) the spore is covered by densely arranged wart-like structures on its proximal surface.

Dendroceros subplanus Steph., Sitzungsb. Naturf. Ges. Leipzig 36: 20, 1909. Type: Indonesia. Java, s.d. leg. *Solms 26c* (holotype G!).

Figs. 3 & 5C–D.

Thalli dark green, somewhat brownish when dry, to 14 mm long, 1.5–2.5 mm wide, dichotomously to subdichotomously branched, branches strap-shaped; costa narrow, 0.35–0.65 mm wide, in transverse section 6–9 cells thick, solid, nearly flat dorsally and strongly convex ventrally, slightly and evenly thick-walled, epidermal cells scarcely differentiated; lamina unistratose, rather broad, nearly flat, rarely lobed, sometimes undulate to crispate around the thallus apex, margins entire; lamina cells hexagonal to rounded, 20–35 μm in diameter, trigone-like structures rather large, usually with conspicuous perforations, especially near margin of the lamina. *Rhizoids* colorless or pale brown, scattered on ventral side of costa, inner wall smooth. *Nostoc* colonies embedded in thallus, scattered along both ventral and dorsal side of the costa, especially in older parts.

Monoicous. *Androecia* scattered, monandrous; antheridia broadly ovoid, *ca.* 200 μm in diameter. *Involucres* erect, cylindrical, 5–7 mm long, nearly smooth, sometimes with flattened scales. *Capsules* slender, up to 30 mm, bivalved when mature; stomata absent; epidermal cells rectangular, 35–60 × 20–25 μm, with narrow lumens and strongly thickened walls. *Spores* subglobose to rounded-triangular, various in size depending on developmental stage, 35–60 μm in diameter, green, multicellular, consist of ca. 10 cells; distal surface spinulose, the surface between spinules irregularly vermiculate; proximal surface coarsely vermiculate. *Pseudoelaters* pale brown, unbranched, ca. 450 μm long, *ca.* 10 μm wide, with a single helicoidal band.

Habitat and Ecology: In Thailand *Dendroceros subplanus* typically grows on twigs and branches in montane rain forests (1000–1700 m a.s.l.).

Distribution: Indonesia (Java, Sumatra), Papua New Guinea (Piippo, 1993) and Thailand.

Specimens examined: **THAILAND**: Prachuap Khiri Khan, Huai Yang Waterfall national park, summit of Khao Luang, 1100 m, 22 May 2010, *Chantanaorrapint 2415* (PSU); 26 May 2011, *Chantanaorrapint, Inuthai & Promma 1050* (PSU). PENINSULAR: Nakhon Si Thammarat, Khao Luang national park, Khao Luang, 1000 m, 4 Feb 1966, *Touw 11588* (BKF, L); Khao Nan national park, San Yen, 1200 m, 19 Apr 2007, *Chantanaorrapint 1507*, *1513* (PSU); 20 Apr 2007, *Chantanaorrapint 1568* (PSU), *Sukkharak & Seelanan 107* (BCU); 21 Apr 2007, *Chantanaorrapint 1645* (PSU); Khao Nan Yai, 1400 m, 21 Jun 2007, *Kidyoo 998* (PSU); 23 Jun 2007, *Sukkharak s.n.* (BCU).

Notes: The distinctive features of *Dendroceros subplanus* are 1) costa solid without schizogenous cavities, 2) thallus lamina nearly flat with many small perforations and 3) the spore ornamentation coarsely vermiculate on the proximal surface. *Dendroceros subplanus* is closely related to *D. tubercularis* S.Hatt., in having solid costa, thallus lamina with many small perforations and thallus margin nearly entire. However, the later differs from the former by thallus lamina stronger crispate at the apex. Hasegawa (1980) noted that *D. tubercularis* perhaps conspecific with *D. subplanus*.

Megaceros flagellaris (Mitt.) Steph., Sp. Hepat. 5: 951. 1916. Basionym: *Anthoceros flagellaris* Mitt. in Seemann, Flora Vitiensis: 419. 1873. Type: Samoa. *R.T. Powell s.n.* (lectotype designated by Proskauer, NY).

Figs. 4 & 5E–F.

Thalli dark green when moist, dull green to blackish brown when dry, more or less dichotomously branched, usually forming dense mats more than 10 cm wide; the thallus solid, ecostate, variable in shape from broad irregular straps or fans, often with short lateral branches; in transverse section 7–14 cells thick in the middle, 1–4 cells thick along the margin; thallus margin irregularly crenate, dentate or fringed; dorsal surface smooth, epidermal cells in surface-view quadrate, hexagonal or rectangular, 25–60 × 15–30 μm, rather thin-walled, usually with 1–2 chloroplasts per cell. *Rhizoids* few, scattered along the median part of the ventral surface, hyaline to pale brown, often branched near the apex. *Nostoc* colonies embedded in thallus, slightly protruding, recognized externally as scattered dark-brown to blackish dots on the ventral side.

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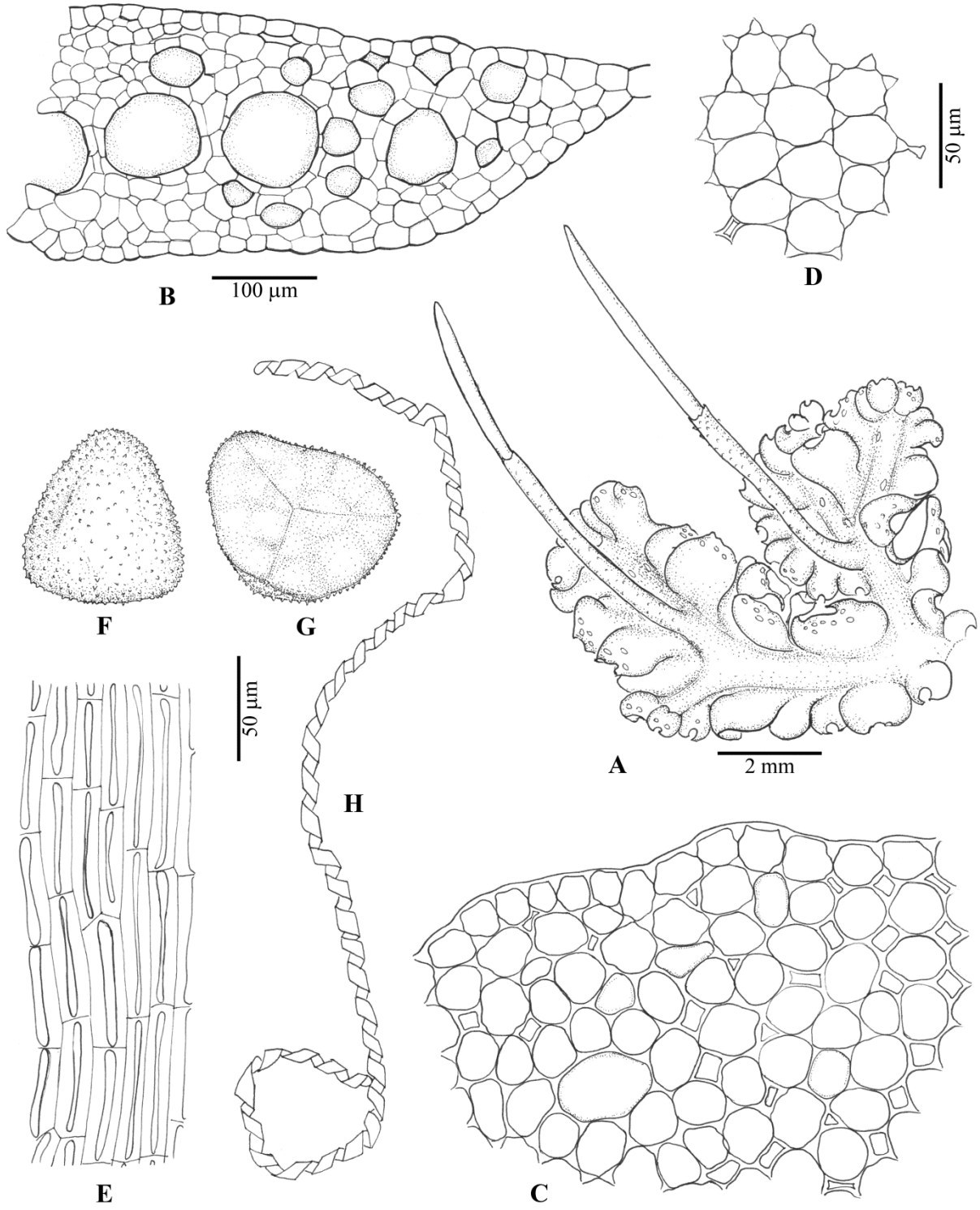


Fig. 2. ***Dendroceros cucullatus*** **Steph. A: Thallus with sporophyte. B: Transverse section of costa. C, D: Cells of thallus lamina; C: from margin, D: from middle. E: Epidermal cells of capsule. F, G: Spores; F. distal view, G. proximal view. H: Pseudoelater. All from** ***Chantanaorrapint & Promma 2096.***

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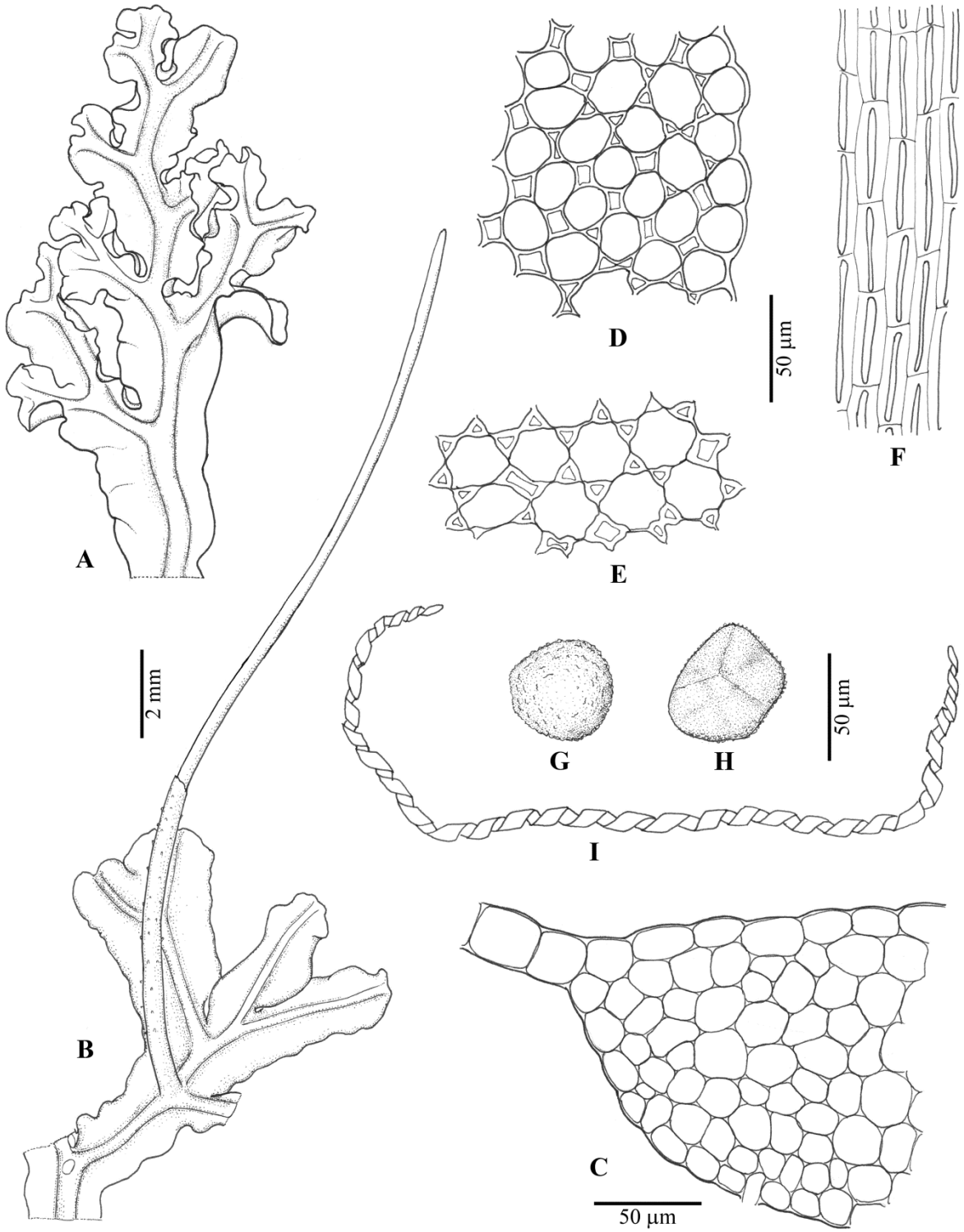


Fig. 3. ***Dendroceros subplanus*** **Steph. A: Sterile thallus. B: Thallus with sporophyte. C: Transverse section of costa. D, E: Cells of thallus lamina; D. from margin, E. from middle. F: Epidermal cells of capsule. G, H: Spores; G. distal view, H. proximal view. I: Pseudoelater. All from** ***Chantanaorrapint 1513*****.**

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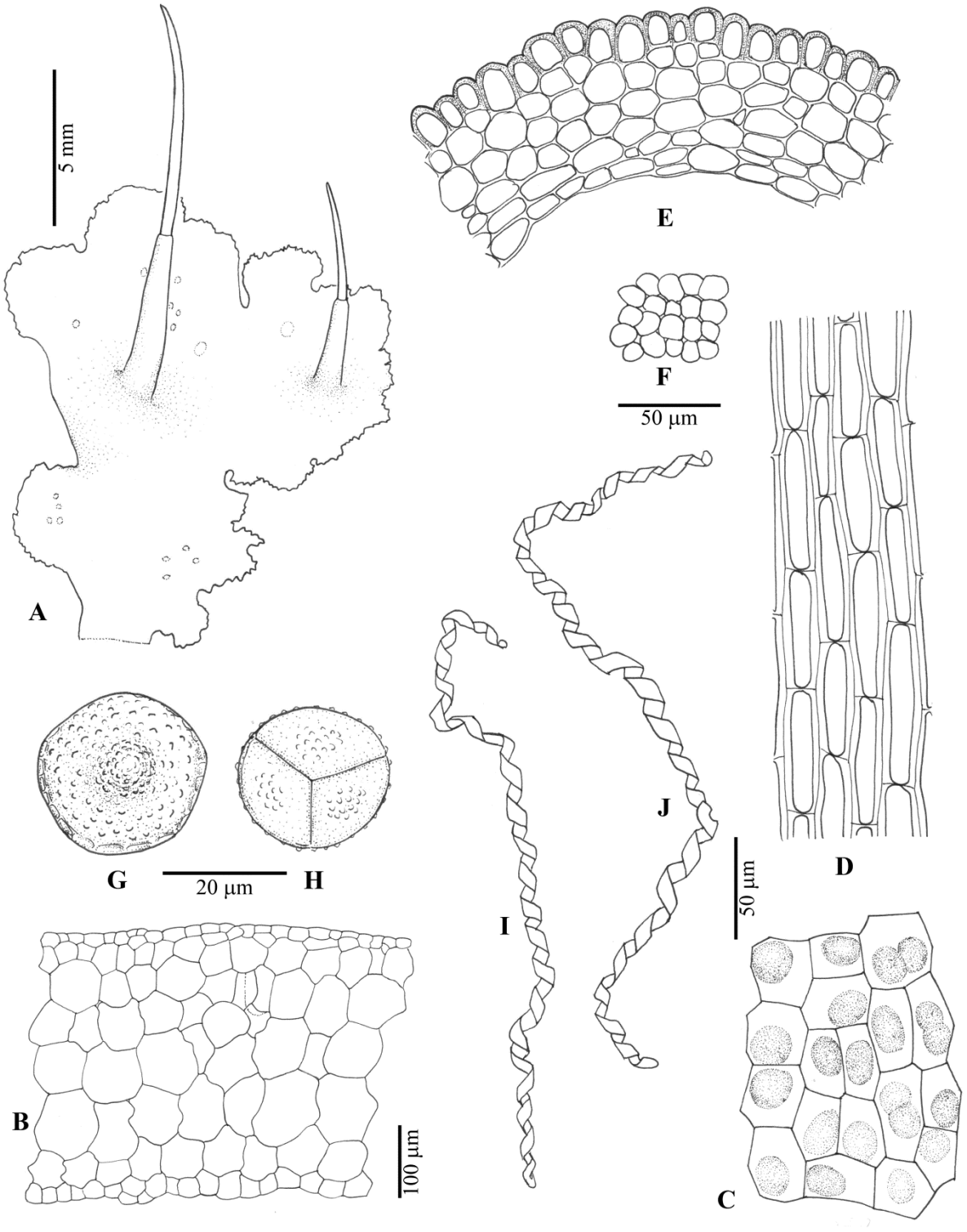


Fig. 4. ***Megaceros flagellaris*** **(Mitt.) Steph. A: Thallus with sporophyte. B: Transverse section of thallus at middle part. C: Dorsal epidermal cells of thallus. D: Epidermal cells of capsule. E: Transverse section of capsule wall. F: Transverse section of collumella. G, H: Spores; G. distal view, H. proximal view. I, J: Pseudoelaters. All from** ***Chantanaorrapint & Promma 2428*****.**

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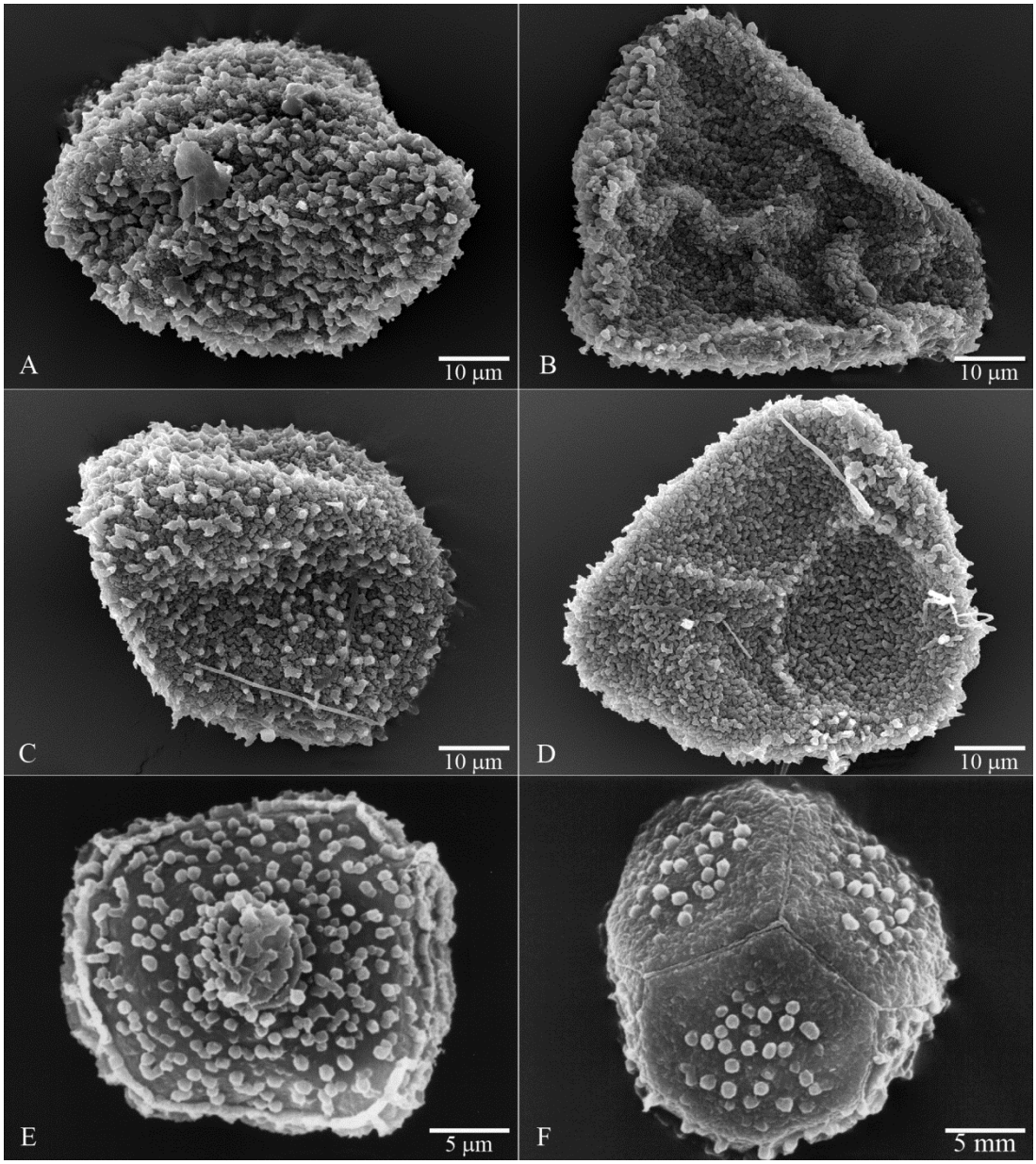


Fig. 5. SEM photos of spores. A, B: *Dendroceros cucullatus* Steph., A. Distal view of spore, B. Proximal view of spore. C, D: *Dendroceros subplanus* Steph., C. Distal view of spore, D. Proximal view of spore. E, F: *Megaceros flagellaris* (Mitt.) Steph., E. Distal view of spore, F. Proximal view of spore.

Monoicous. *Androecia* aggregated in lateral branches or scattered on main branches, monandrous; antheridia subglobose, ca 250 μm in diameter. *Involucres* solitary, erect, cylindrical, sometimes attenuate, 5–10 mm high, smooth. *Capsules* up to 5 cm long, usually dehiscent along one suture but sometimes bivalved; columella consisting of 20 cells in transverse section, assimilative layer 4–5(–6) cell layers; epidermal cells of capsule elongate-rectangular, 45–70 × 15–20 μm, thick-walled, stomata lacking. *Spores* greenish, with thin exine, globose to rounded-tetrahedral but often somewhat irregular in shape, mostly 20–28.5 μm in diameter; distal face with a central hump surrounded by abundant verrucose projections; proximal face with a faint trilete mark, each facet with group of granulose projections in the centre; equatorial region irregular reticulate. *Pseudoelaters* pale brown, unbranched, 200–350 μm long, with a single helicoidal band.

Habitat: In Thailand, *Megaceros flagellaris* is common, growing on wet rocks along stream in shady

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areas, and was found in lowland forest to upper montane forest at altitude of 100–2300 m a.s.l. This species usually associated with *Heteroscyphus argutus* (Reinw. et al.) Schiffn. and *H. coalitus* (Hook.) Schiffn.

Distribution: *Megaceros flagellaris* is widely distributed in Angola, Australia (Queensland), China, Hawaii India, Indonesia, Japan, Philippines, New Caledonia, New Guinea, New Zealand, Samoa, Tahiti, Tanzania and Thailand (Hasegawa, 1983, 1995; Campbell, 1984; Garcia *et al.*, 2012; Cargill *et al.*, 2013).

Specimens examined: **THAILAND**. Chaing Mai, Doi Inthanon National Park, ca 2500 m, in dense moist evergreen forest, 19 Dec 1965, *Tagawa & Kitagawa T2957* (BKF), 19 Dec 1965, *Tagawa & Kitagawa T3116* (BKF); Gew Mae Pan, 2300 m, 10 Nov 2011, *Chantanaorrapint & Inuthai 258* (PSU); Doi Suthep-Pui National Park, 850 m, 12 Nov 2011, *Chantanaorrapint & Inuthai 341* (PSU). Prachinburi, Khao Yai National Park, Hnong Pling, 730 m, 19 Nov 2011, *Chantanaorrapint, Inuthai & Promma 485, 491* (PSU); 15 Nov 2013, *Chantanaorrapint, Inuthai & Promma 3320* (PSU). Prachuap Khiri Khan, Huai Yang Waterfall National Park, summit of Khao Luang, 1100 m, 10 Aug 2001, *Chantanaorrapint 628* (PSU). Nakhon Si Thammarat, Khao Luang, 800–1000 m, 22 Jan 1966, *Tagawa & Kitagawa T5359* (BKF), 19 Mar 2013, *Chantanaorrapint & Promma 2428* (PSU); Khao Nan National Park, Klong Kan station, 300 m, 25 Dec 2006, *Chantanaorrapint 1331* (PSU), San Yen, 1200 m, 20 Apr 2007, *Chantanaorrapint 1586* (PSU);Trang, Khao Jed Yod, 800–1000 m, 22 May 2012, *Chantanaorrapint, Inuthai & Promma 1376* (PSU); Satun, Than Plew waterfall, 10 Aug 2011, *Chantanaorrapint 2444* (PSU); Songkhla, Ton Nga Chang Wildlife Sanctuary, 130 m, 1 Dec 2012, *Chantanaorrapint Inuthai & Promma 533* (PSU); Yala, Betong, 600 m, *Chantanaorrapint & Promma 621* (PSU), 15 Jun 2013, *Chantanaorrapint & Promma 2635* (PSU).

Notes: *Megaceros flagellaris* is easily separated from other members of the genus by its spore ornamentation having reticulate pattern around the equatorial region (Fig. 5E). Hasegawa (1983) reduced several species of *Megaceros* from South-east Asia and the Pacific Island as *M. flagellaris* (including: *M. caledonicus* Steph., *M. celebensis* Steph., *M. grandis* (Å ngstr.) Steph., *M. monandrus* Steph., *M. monospirus* Steph., *M. muriculatus* Steph., *M. novaeguineae* Steph., *M. nymanii* Steph., *M. parvisporous* Steph., *M. salakensis* Campb., *M. stahlii* Steph., *M. tjibodensis* Camp. and *M. vesconianus* Gott. ex Besch.). Recently, a reexamination of the type specimens, however, reveals that *M. tjibodensis* is quite different from *M. flagellaris* in spore ornamentation (Cargill *et al.*, 2013).

ACKNOWLEDGMENTS

The author would like to thank Prof. Dr. T. Pócs (EGR) and Assoc. Prof. Dr Kitichate Sridith (PSU) for their valuable comments on the first draft of the manuscript, Dr. J. C. Villarreal (M) and Dr. D.C. Cargill (CAMB) for literatures. Thank also go to the curators and staffs of BCU, BKF, CMU, G, HSNU, KLU, L, PSU and SING for making specimens including types available for study through loans or visits. This work was supported by the Faculty of Science Research Fund, Prince of Songkla University.

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