

The epiphyllous *Radula* (*Radulaceae, Marchantiophyta*) in Thailand, with the description of *Radula grandilobula* sp. nov.

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Abstract – A taxonomic review of the epiphyllous taxa of the genus *Radula* Dumort. in Thailand is presented, based on herbarium specimens and field surveys. Nine species are recognized, including two new records, *R. nymanii* Steph. and *R. stenocalyx* Mont. One new species, *R. grandilobula* Promma et Chantanaorrapint., is described and illustrated. The new species is characterized by the leaf-lobe subtriangular-ovate to falcate-ovate with a narrowly rounded to obtuse apex; the leaf-lobule falcate-ovate, upper half broadly extended, free margin recurved, apex strongly turning away from the stem; and the discoid gemmae occurring perpendicularly on ventral surface of leaf-lobes. A key to species, brief descriptions and illustrations are provided; ecology and geographical distribution of the species are also noted.

Epiphyllous liverworts / Marchantiophyta / new species / *Radula grandilobula* / Thailand

INTRODUCTION

With some 200 currently accepted species, *Radula* Dumort. is one of the largest genera of liverworts. Centers of diversity are the tropical and subtropical regions (Frey & Stech, 2009; Promma & Chantanaorrapint, 2014). Most species are tree trunk and twig epiphytes, and less commonly grow on living leaves or rock. The genus is well characterized and easily recognized by 1) incubous lateral leaves, 2) absence of underleaves, 3) rhizoids restricted to the ventral surface of the leaf lobule, 3) *Radula*-type branching, 4) 1-(4) large oil bodies per leaf cell, and 5) dorsiventrally flattened perianths.

Epiphyllous or foliicolous liverworts grow on living leaves. They are quite common in tropical rain forests with shady areas and long periods of high humidity (Pócs, 1996, 1982; Richards, 1984; Zhu & So, 2001). Many epiphyllous species are restricted to growth on living leaves but some of them are also found on twigs, branches, trunks, or on rocks (von Konrat & Braggins, 1999; Zhu & So, 2001). The present study is based on our observations and field surveys in Thailand, providing evidence that epiphyllous *Radula* species frequently occur in open areas, such as streamsides and forest edges, and from the lowlands to montane forests up to about 2500 m. They share a suite of unique characteristics including small size, highly reduced stems, disc-shaped rhizoid-bundles, long trumpet-shaped perianths which are usually projecting from the substrate, abundant development of sporophytes as

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well as discoid gemmae. Other epiphyllous liverworts show similar morphological adaptations to epiphyllous conditions such as a short life cycle, frequent production of gemmae, and development of rhizoid discs for fixation on the leaf (Zhu & So, 2001; Frahm *et al.*, 2003; Kraichak, 2012; Yu *et al.*, 2014). Moreover, Devos *et al.* (2011) resolved 4 epiphyllous *Radula* species in a well supported monophyletic lineage within subg. *Metaradula*, sister to the remainder of that subgenus. Accordingly, morphological similarity between epiphyllous species such as *R. acuminata* Steph., *R. protensa* Lindenb., *R. nymanii* Steph. can be explained, in part, by their relatedness.

Thailand is well-known as a hotspot of bryophyte diversity (e.g. He *et al.*, 2012, 2013; Kornochalert *et al.*, 2012; Chantanaorrapint & Sridith, 2014; Inuthai *et al.*, 2014; Sukkharak & Chantanaorrapint, 2014). This area is located in both the Indo-Burmese and Sundaland hotspots (Myers *et al.*, 2000), and includes areas identified as the overlapping zone of the Sino-Himalayan and Malesian floristic regions (Smitinand, 1989). Although a revision of the genus *Radula* in Asia was published by Yamada (1979), the epiphyllous *Radula* species from Thailand are still poorly known, reflecting the limited number of bryophyte studies focusing on this country (Sukkharak & Chantanaorrapint, 2014). The first record of epiphyllous *Radula* in Thailand was published by Tixier (1970), who reported *R. acuminata* from Ranong province. So far, six species of epiphyllous *Radula* were reported for the country, namely: *R. acuminata*, *R. assamica* Steph., *R. cavifolia* Hampe ex Gottsche *et al.*, *R. gedena* Gottsche ex Steph., *R. protensa*, and *R. tibiodensis* K.I. Goebel (Kitagawa, 1979; Yamada, 1979; Lai *et al.*, 2008; Sukkharak *et al.*, 2008; Chantanaorrapint & Pócs, 2014). More new records of epiphyllous species can be expected in the unexplored areas, especially in the southern part of Thailand. The purpose of the present paper is to summarize current knowledge on the epiphyllous *Radula* species in Thailand.

MATERIALS AND METHODS

This study is based on recent collections from Thailand as well as herbarium specimens housed in the herbaria BCU, BKF, BM, CMU, EGR, G, HSNU, JE, NICH and PSU. 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. In addition, distribution and ecological data were compiled, brief descriptions, illustrations and a key to species are provided.

TAXONOMIC TREATMENT

Key to species of the epiphyllous *Radula* in Thailand

1. Leaf lobe orbicular, strongly concave; leaf-lobule ca. 4/5 as long as the leaf lobe; gemmae absent.....*R. cavifolia*
1. Leaf lobe ovate, oblong-ovate or suborbicular, nearly plane; leaf-lobules less than 1/2 as long as the leaf lobe; gemmae present.....2

2. Leaf-lobules falcate-ovate or hook-like, apex of lobule spreading or strongly turning away from the stem 3
 3. Gemmae occurring on ventral margins of leaf-lobes, parallel to the surface of leaf-lobes *R. nymanii*
 3. Gemmae occurring perpendicularly on ventral surface of leaf-lobes 4
 4. Leaf-lobules hook-like, upper half narrowly elongate, strongly turning away from the stem, free margin not recurved .. *R. protensa*
 4. Leaf-lobules falcate-ovate, upper half broadly extended, not strongly turning away from the stem, free margin recurved.. *R. grandilobula*
2. Leaf-lobules not as above, apex of lobule never turning away from the stem 5
 5. Gemmae occurring on ventral surface of leaf-lobes *R. acuminata*
 5. Gemmae occurring on margins of leaf-lobes 6
 6. Gemmae occurring perpendicularly on apical margin of leaf-lobe..... *R. tibodensis*
 6. Gemmae occurring on margins of leaf-lobes and parallel to the surface of leaf-lobes 7
 7. Leaf-lobules subtriangular-lingulate or subrhombic with an obtuse apex; gemmae occurring on ventral margins of leaf-lobes *R. assamica*
 7. Leaf-lobules subquadrate to oblong with strongly pronounced mammillose rhizoid-initial area on the inflated carinal region; gemmae occurring on dorsal margins of leaf-lobes..... 8
 8. Cells of leaf lobe usually very irregular in form and size *R. gedena*
 8. Cells of leaf lobe almost equal in form and size *R. stenocalyx*

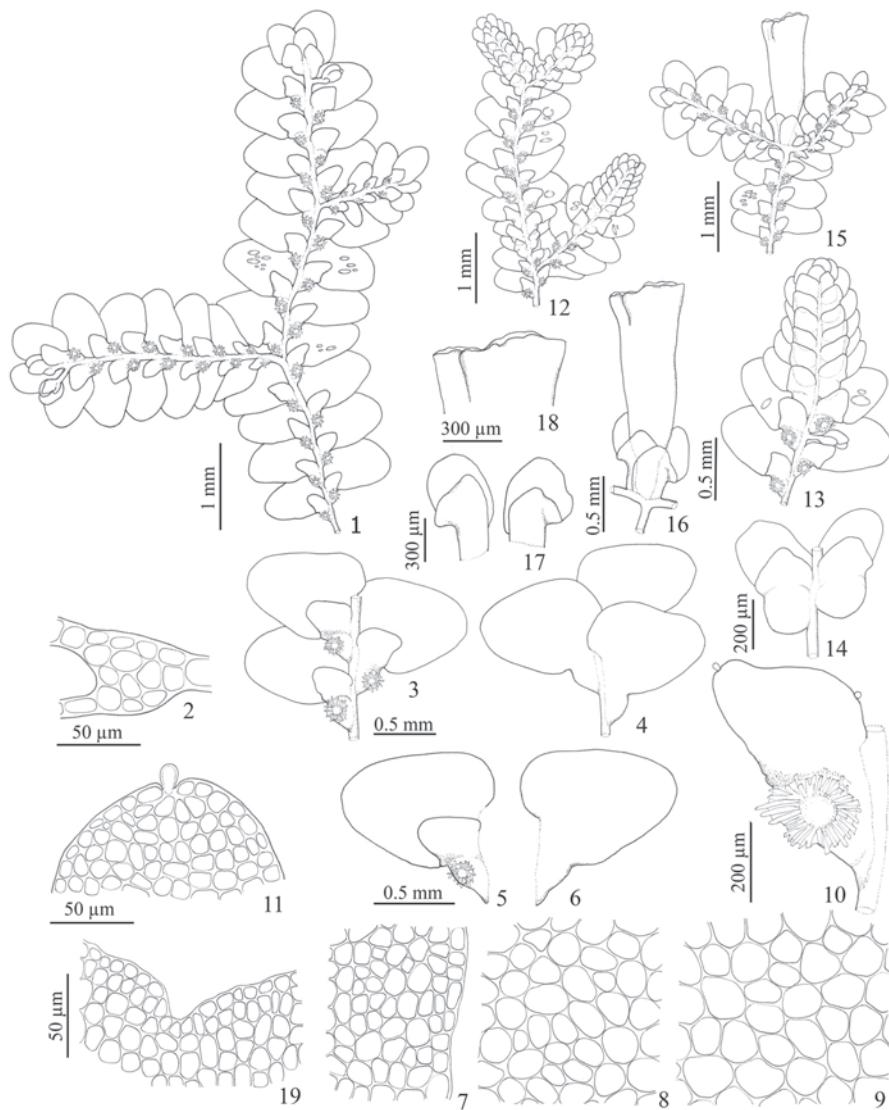
***Radula grandilobula* Promma et Chantanaorr., sp. nov.**

Figs 1-26

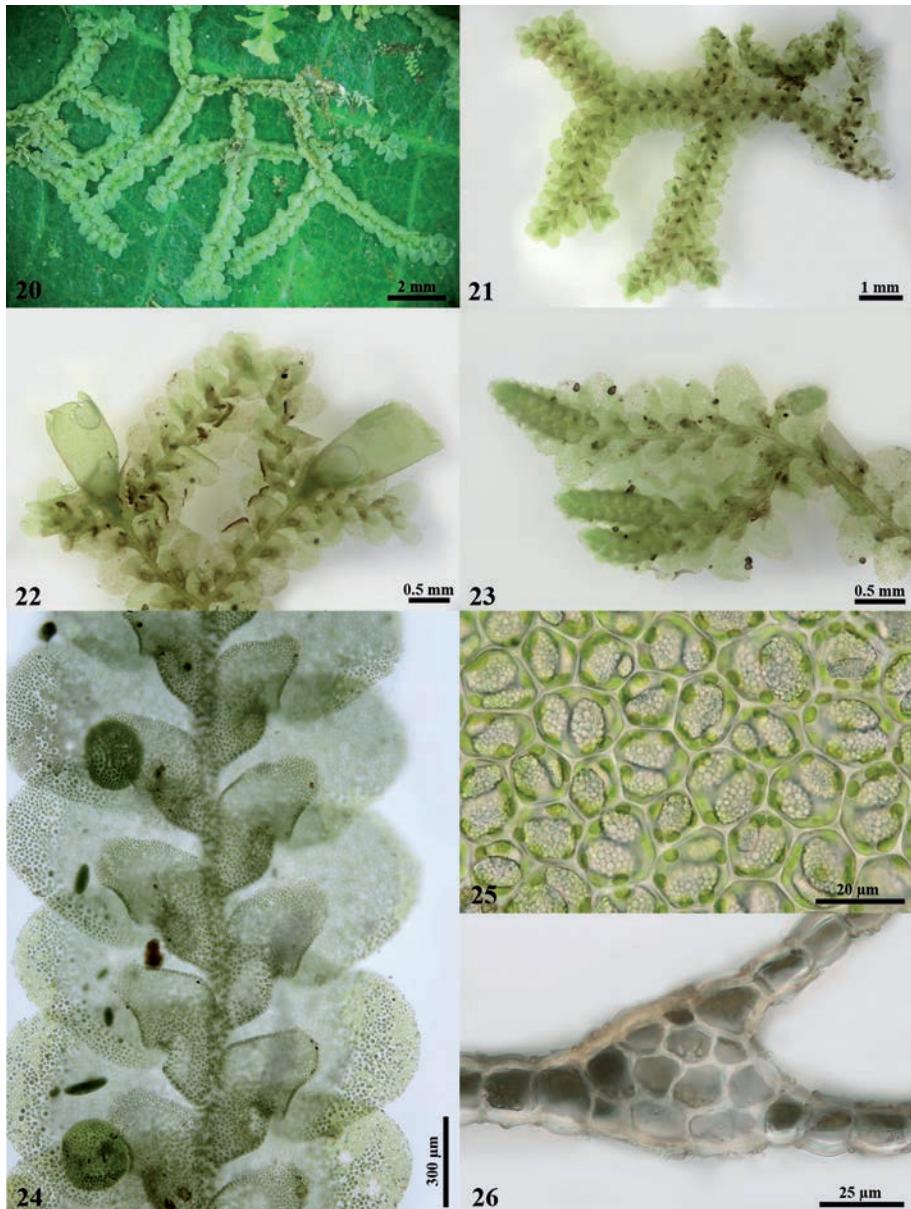
Radula grandilobula is similar to *R. protensa* Lindenb., but differs by large leaf lobules 1/3-2/5 as long as leaf lobes, falcate-ovate, the free margin of the leaf lobule recurved, and lobule apex not abruptly narrowed and turning outwards as in *R. protensa*.

Type: Thailand. Nakhon Si Thammarat, Noppitam, Khao Nan National Park, Huay Kaew Station, Klong Song, 200 m, on leaving leaves, 25 Jan. 2007, *Chantanaorrapint* 1364 (holotype: PSU!, isotypes: BKF!, HSNU!).

Plants medium-sized, 1.25-2 mm wide, green to yellowish green, irregularly pinnately branched. **Stems** in cross-section ca. 45-75 µm in diameter, 4 cells thick, epidermal and medullary cells equal in size and shape, thin-walled, with minute trigones. **Rhizoids** numerous, fasciculate, ± disc-shaped in outline, pale brown, rhizoid-initial area convex on lower part of lobule. **Leaves** moderately imbricate, widely spreading; leaf-lobes subtriangular-ovate to falcate-ovate, 0.7-1.05 mm long, 0.5-0.75 mm wide, apex narrowly rounded to obtuse, margin entire, dorsal base arching and fully covering the stem; marginal cells $7.5-11 \times 9.5-16$ µm, median cells $11-31.5 \times 11.5-23.7$ µm, basal cells $14.3-39.5 \times 14.3-25.3$ µm, thin-walled, with minute or indistinct trigones; cuticle smooth; oil bodies (1-)2 per cell, compound type, grayish to pale brown, ovoid to spherical; leaf-lobules falcate-ovate, ca. 1/3-2/5 of the lobe-length, 0.35-0.67 mm long, 0.2-0.37 mm wide, upper half broadly extended, apex obtuse to rounded, abaxial free margin obliquely straight to slightly arched, usually recurved, adaxial free margin straight and arching toward the bases, usually recurved, base slightly covering the stem, insertions slightly arched, carinal



Figs 1-19. *Radula grandilobula* Promma et Chantanaorr. **1.** Portion of sterile plant. **2.** Cross-section of stem. **3-4.** Portions of sterile plants, **3.** Ventral view, **4.** Dorsal view. **5-6.** Lateral leaves, **5.** Ventral view, **6.** Dorsal view. **7.** Apical cells of leaf lobe. **8.** Median cells of leaf lobe. **9.** Basal cells of leaf lobe. **10.** Leaf-lobule. **11.** Apex of leaf-lobules with hyaline papilla. **12.** Portion of plant with androecia. **13.** Androecium. **14.** Male bracts. **15.** Portion of plant with gynoecium. **16.** Gynoecium. **17.** Female bracts. **18.** Mouth of perianth. **19.** Cells of mouth margin. All from *Chantanaorrapint* 1364 (holotype, PSU).



Figs 20-26. *Radula grandilobula* Promma et Chantanaorr. **20.** Plant habit and habitat. **21.** Portion of sterile plant, ventral view. **22.** Portion of plant with gynoecia. **23.** Portion of plant with androecia. **24.** Portion of sterile plant, ventral view (showing shape of leaf-lobules and position of gemmae). **25.** Median cells of leaf lobe with oil bodies. **26.** Cross-section of stem. All from Chantanaorrapiint & Promma 3486A (paratype, PSU).

region inflated; keel strongly arched, extending at angles of 45°-50° with the stem, sinus acute to subacute. **Asexual reproduction** by discoid gemmae, occurring perpendicularly on ventral surface of leaf-lobes.

Dioicous. **Androecia** terminal or intercalary on stems and branches, with 4-20 pairs of bracts, densely imbricate; bract-lobes 0.42-0.57 mm long, 0.18-0.22 mm wide, ovate to oblong, apex obtuse, margin entire; bract-lobules *ca* 4/6-5/6 of bract-lobe, ovate, apex narrowly obtuse to subacute and somewhat extended, margin entire, keel strongly arched, carinal region strongly inflated. **Gynoecia** terminal on stems and branches, with (1-)2 subfloral innovations; bracts 1 pair, bract-lobes oblong-ovate to obovate-spathulate, 0.63-0.87 mm long, 0.42-0.5 mm wide, apex rounded to obtuse, margin entire, bract-lobules *ca* 1/2 of bract-lobe, oblong, apex obtuse to subacute, keel sinuate; archegonia 8-10 per gynoecium; perianths long trumpet-shaped, 1.46-3.17 mm long, 0.5-0.84 mm wide at middle, mouth 0.63-0.84 mm wide, not two lipped, usually crispate-repand. **Sporophytes** 2.7 mm long; setae very slender, smooth, numerous cell rows, massive, *ca* 1.95 mm long; capsules ovoid-cylindrical, *ca* 0.75 mm long, *ca* 0.2 mm wide; elaters long, *ca* 100-300 µm, tenuous, 2-spiral, smooth, free from sporangium wall; spores large, *ca* 15-20 µm in diameter, subspherical to spherical, papillate.

Etymology: The specific epithet “*grandilobula*” refers to the large sized leaf lobules.

Habitat and ecology: *Radula grandilobula* occurs on living leaves in lowland to lower montane rain forests at altitudes between 130 and 950 m. It may grow associated with *R. nymanii*, *R. protensa* and *R. tjibodensis* on the same leaf.

Distribution: The new species seems to be widely distributed in southern Thailand and may occur in other areas of Peninsular Malaysia as well.

Taxonomic notes: The diagnostic features of *R. grandilobula* are 1) the leaf-lobe subtriangular-ovate to falcate-ovate with a narrowly rounded to obtuse apex, 2) the leaf-lobule large, broadly falcate-ovate, apex not turning away from the stem, upper half broadly extended, free margin usually recurved, and 3) the numerous discoid gemmae occurring perpendicularly on ventral surface of leaf-lobes.

Radula grandilobula is morphologically similar to *R. protensa* in having subtriangular-ovate to falcate-ovate leaf lobes and perpendicular gemmae on the ventral surface of the lobes. *Radula grandilobula*, however, differs from *R. protensa* by lobule shape and spacing. The leaf lobules of the new species are falcate-ovate with broadly extended upper leaf lobule half and an apex not turning away from the stem. In contrast, *R. protensa* has hook-like lobules with a narrowly elongated upper half that is abruptly turning outwards. Furthermore, *R. grandilobula* has recurved, rather than not or slightly incurved free margins of leaf lobules, and obliquely straight to slightly arched, rather than strongly sinuate abaxial free margins.

Radula grandilobula also resembles *R. acuminata*, which also has perpendicular gemmae on ventral surface of leaf-lobes. However the species differ in the shape of their leaf lobules. The main morphological differences between *R. acuminata*, *R. grandilobula* and *R. protensa* are summarized in Table 1.

Additional specimens examined: Nakhon Si Thammarat, Khao Luang National Park, Khao Luang, 937 m, 17 Mar. 2013, Chantanaorrapint & Promma 2162 (PSU, HSNU). Songkhla, Sadao, Ton Nga Chang Wildlife Sanctuary, Pha Dam Waterfall, 100-150 m, 4 Feb. 2014, Chantanaorrapint & Promma 3486A (PSU). Yala, Betong, Ban Chulabhorn Pattana 10, 565 m, 15 Jun. 2013, Chantanaorrapint & Promma 2572B (PSU).

Table 1. Morphological comparison of *Radula grandilobula*, *R. acuminata*, and *R. protensa*

Characters	<i>R. grandilobula</i>	<i>R. acuminata</i>	<i>R. protensa</i>
Cross-section of stems	4 cells thick	4-5 cells thick	4-5 cells thick
Shape of leaf-lobes	subtriangular-ovate to falcate-ovate	falcate-ovate	subtriangular-ovate to falcate-ovate
Oil bodies	(1-2) per cell	1(-2) per cell	1-2 per cell
Leaf-lobules			
shape	falcate-ovate with upper half broadly extended	subquadrate or obliquely quadrate with elongate to blunt tip	hook-like with upper half narrowly elongate
apex	obtuse to rounded, spreading with the stem	obtuse-acute to obtuse, not turning away from the stem	obtuse, strongly turning away from the stem
free margins	usually recurved	slightly incurved or not incurved	slightly incurved or not incurved
abaxial	obliquely straight to slightly arched	nearly straight or slightly arched	strongly sinuate toward the apex
adaxial	straight and arching toward the bases	nearly straight to slightly arched or sinuate toward the arched base	arching toward the base or nearly straight
size	ca. 1/3-2/5 of lobe length	ca. 1/3 of lobe length	ca. 1/3-2/5 of lobe length
Position of gemmae	perpendicular on ventral surface of leaf-lobes	perpendicular on ventral surface of leaf-lobes	perpendicular on ventral surface of leaf-lobes

***Radula acuminata* Steph., Sp. Hepat. 4: 230. 1910**

Type: Vietnam, Tonkin, B. Balansa s.n. (holotype: G!; isotypes: BM!, G!)

Descriptions: Castle (1939: 45), Yamada (1979: 286), Udar & Kumar (1984: 162), Yamada & Piippo (1989: 368), Zhu & So (2001: 60), Dey & Singh (2012: 69)

Illustrations: Castle (1939: 46, fig. 10), Yamada (1979: 287, fig. 47), Udar & Kumar (1984: 163, figs A1-21), Yamada & Piippo (1989: 369, figs 10a, b, e, h, i), Zhu & So (2001: 60, fig. 25), Dey & Singh (2012: 70-71, figs 44-45)

Radula acuminata is the most widely distributed epiphyllous representative of the genus in Thailand. This species is easily recognized by 1) the leaf-lobe falcate-ovate with a narrowly to broadly rounded apex, 2) the leaf-lobule subquadrate or obliquely quadrate with a blunt tip, and 3) the numerous discoid gemmae occurring perpendicularly on the ventral surface of the leaf-lobes. *Radula acuminata* may be confused with *R. assamica* in general appearance, but the latter is distinguished from the former by the leaf-lobule subtriangular-lingulate or subrhombic with an obtuse apex and the discoid gemmae occurring on ventral margins of leaf-lobes and parallel with the surface of them.

Habitat and ecology: In Thailand *Radula acuminata* occurs as an epiphyll in lowland to montane rain forests at altitudes from 200 to 1650 m. This species often grows associated with other epiphyllous liverworts such as *Cololejeunea lanciloba* Steph. and *R. assamica*.

Distribution: India, Thailand, Cambodia, Vietnam, Malay Peninsula, Sumatra, Java, Borneo, New Guinea, Philippines, China, Taiwan, Japan (Yamada, 1979; Udar & Kumar, 1984; Zhu & So, 2001; Dey & Singh, 2012).

Specimens examined: Tak, Umphang, Umphang Wildlife Sanctuary, Thi Lo Su Waterfall, 550-570 m, 25 Oct. 2012, *Chantanaorrapint* 2639, 2640, 2642, 2643, 2644 (PSU), 13 Aug. 2013, *Chantanaorrapint* & *Promma* 2761A, 2765A, 2767A, 2768, 2771A, 2775, 2776, 2779 (PSU). Loei, Dan Sai, Phu Hin Rong Kla National Park, Man Daeng Waterfall, 1650 m, 13 Apr. 2011, *Chantanaorrapint*, *Inuthai* & *Promma* 113 (PSU). Prachin Buri, Khao Yai National Park, Hnong Pling Waterfall, 700-730 m, 18 Feb. 1966, *Touw* 12302 (BKF, L), 19 Nov. 2012, *Chantanaorrapint*, *Inuthai* & *Promma* 495 (PSU), 15 Nov. 2013, *Chantanaorrapint*, *Inuthai* & *Promma* 3319 (PSU). Nakhon Si Thammarat, Khao Luang National Park, Khao Luang, 550-1000 m, 17 Mar. 2013, *Chantanaorrapint* & *Promma* 2166 (PSU), 20 Apr. 2014, *Chantanaorrapint* & *Promma* 3552 (PSU); Khao Nan National Park, 1190 m, 12 Aug. 2007, *Sukkharak* & *Seelanan* 651 (BCU). Trang, Palian, Khao Chedyod, 730-1100 m, 1 May 2014, *Chantanaorrapint* & *Promma* 3730, 3731B, 3732, 3738AA, 3739BB (PSU).

Radula assamica Steph., *Hedwigia* 23: 151. 1884

Type: India, Assam, *W. Griffith* s.n. (holotype: G; isotypes: BM!, G, JE!)

Descriptions: Castle (1939: 41), Yamada (1979: 288), Udar & Kumar (1984: 166), Zhu & So (2001: 65), Dey & Singh (2012: 73)

Illustrations: Castle (1939: 42, fig. 8), Yamada (1979: 288, fig. 48), Udar & Kumar (1984: 167, figs C1-23), Zhu & So (2001: 66, fig. 28), Dey & Singh (2012: 74-75, figs 46-47)

The distinctive features of *Radula assamica* are 1) the leaf-lobe falcate-ovate with an obtuse to rounded-obtuse apex, 2) the leaf-lobule subtriangular-lingulate or subrhombic with an obtuse apex, and 3) the numerous discoid gemmae borne on ventral margins of leaf-lobes and parallel with the surface of them. This species resembles *R. acuminata*, for differences see there.

Habitat and ecology: *Radula assamica* occurs on living leaves and was found in rain forests ranging from 550 to 650 m elevation. This species often grows associated with other *Radula* species such as *R. acuminata* and/or other bryophytes.

Distribution: Sri Lanka, India (Assam), Myanmar, Thailand, Vietnam (Yamada, 1979), China (Zhu & So, 2001).

Specimens examined: Tak, Umphang, Umphang Wildlife Sanctuary, Thi Lo Su Waterfall, 560 m, 13 Aug. 2013, *Chantanaorrapint* & *Promma* 2760, 2765B, 2767B (PSU).

Radula cavifolia Hampe ex Gottsche et al., *Syn. Hepat.*: 259. 1845

Type: Indonesia. Java, “Herb. H[ampe] & G[ottscche]”, collector unknown (holotype: BM; isotypes: S, YU)

Descriptions: Castle (1963: 28 as *R. aneurysmalis* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees), Yamada (1979: 296), Zhu & So (2001: 58)

Illustrations: Castle (1963: 29, fig. 12 as *R. aneurysmalis*), Yamada (1979: 296, fig. 53), Zhu & So (2001: 59, fig. 24), So (2005: 184, figs 6d, e)

Radula cavifolia is rather unique and distinctive among the epiphyllous *Radula* species of Thailand and stands out by the nearly orbicular to ovate and strongly concave leaf-lobes, the strongly inflated, relatively large leaf-lobules (ca. 4/5 of the lobe-length, and ca. 1/3-1/2 as large as the lobe), and the strongly arched leaf keels.

Habitat and ecology: *Radula cavifolia* is a facultative epiphyll, occurring on tree trunks, twigs and living leaves in montane forests at altitudes between 900 and 1800 m.

Distribution: Vietnam, Malay Peninsula, Sumatra, Java, Borneo, Philippines, China, Taiwan, Korea, Japan (Yamada, 1979), Thailand (Kitagawa, 1979).

Specimens examined: Chantaburi, Khao Soi Dao, Khao Soi Dao Wildlife Sanctuary, Khao Soi Dao, 1635 m, 8 Apr. 2012, *Chantanaorrapint*, *Inuthai* & *Promma* 979 (PSU). Nakhon Si Thammarat, Khao Luang National Park, Khao Luang, 1450-1800 m, 18 Mar. 2013, *Chantanaorrapint* & *Promma* 2248A, 2251, 2265C, 2318, 2323, 2325, 2336A, 2349, 2351, 2354, 2356 (PSU), 22 Apr. 2014, *Chantanaorrapint* & *Promma* 3642A, 3654B, 3672, 3673, 3675A, 3687, 3707 (PSU); Khao Nan National Park, Khao Kom, 10 Aug. 2007, *Sukkharak* & *Seelanan* 407 (BCU); Ron Phibun, Khao Ramrome, 935-1000 m, 22 Feb. 2007, *Chantanaorrapint* 1425 (PSU), 29 Oct. 2012, Pócs & Lee 1213/AG, 1213/N (EGR, PSU). Trang, Palian, Khao Chedyod, 1090-1125 m, 23 May 2012, *Chantanaorrapint*, *Inuthai* & *Promma* 1144, 1152, 1173A, 1278C (PSU), 1-3 May 2014, *Chantanaorrapint* & *Promma* 3739AC, 3740A, 3742C, 3744C, 3745A, 3758A, 3789C, 3808C, 3809, 3810 (PSU).

Radula gedena Gottsche ex Steph., *Hedwigia* 23: 146. 1884

Type: Indonesia, Java, “in monte Gede”, C. Solms 32 (isotype: G)

Descriptions: Castle (1967: 51), Yamada (1974: 489; 1979: 289), Zhu & So (2001: 62)

Illustrations: Castle (1967: 51, fig. 23), Yamada (1974: 491, fig. 2; 1979: 290, fig. 49), Zhu & So (2001: 62, fig. 26)

The species is characterized by 1) the ovate to broadly ovate leaf-lobes with rounded apices, 2) the subquadrate to oblong leaf-lobules with a pronounced mammillose rhizoid-initial area on the inflated carinal region, 3) the very irregularly shaped and sized leaf lobe cells, and 4) the numerous discoid gemmae occurring on the dorsal margins of the leaf-lobes and parallel with the surface of them.

Habitat and ecology: *Radula gedena* is a facultative epiphyll, occurring on tree trunks, twigs and living leaves in montane rain forests at altitudes between 1300 and 1500 m. This species was found associated with other *Radula* species such as *R. yangii* K. Yamada and/or other bryophytes.

Distribution: Java, Borneo, Thailand, Japan (Yamada, 1979), China (Zhu & So, 2001), Malaysia (Chuah-Petiot, 2011).

Specimens examined: Nakhon Si Thammarat, Khao Nan National Park, San Yen, ca 1000 m, 21 Apr. 2009, *Chantanaorrapint* SY 5/1 (PSU); Khao Luang National Park, Khao Luang, 1050-1500 m, 17-19 Mar. 2013, *Chantanaorrapint* & *Promma* 2196, 2205, 2247B, 2367B, 2393B (PSU), 21-23 Apr. 2014, *Chantanaorrapint* & *Promma* 3577, 3586B, 3587, 3594B, 3612C, 3643, 3645, 3696A, 3697A (PSU).

Radula nymanii Steph., *Sp. Hepat.* 4: 229. 1910

Figs 27-45

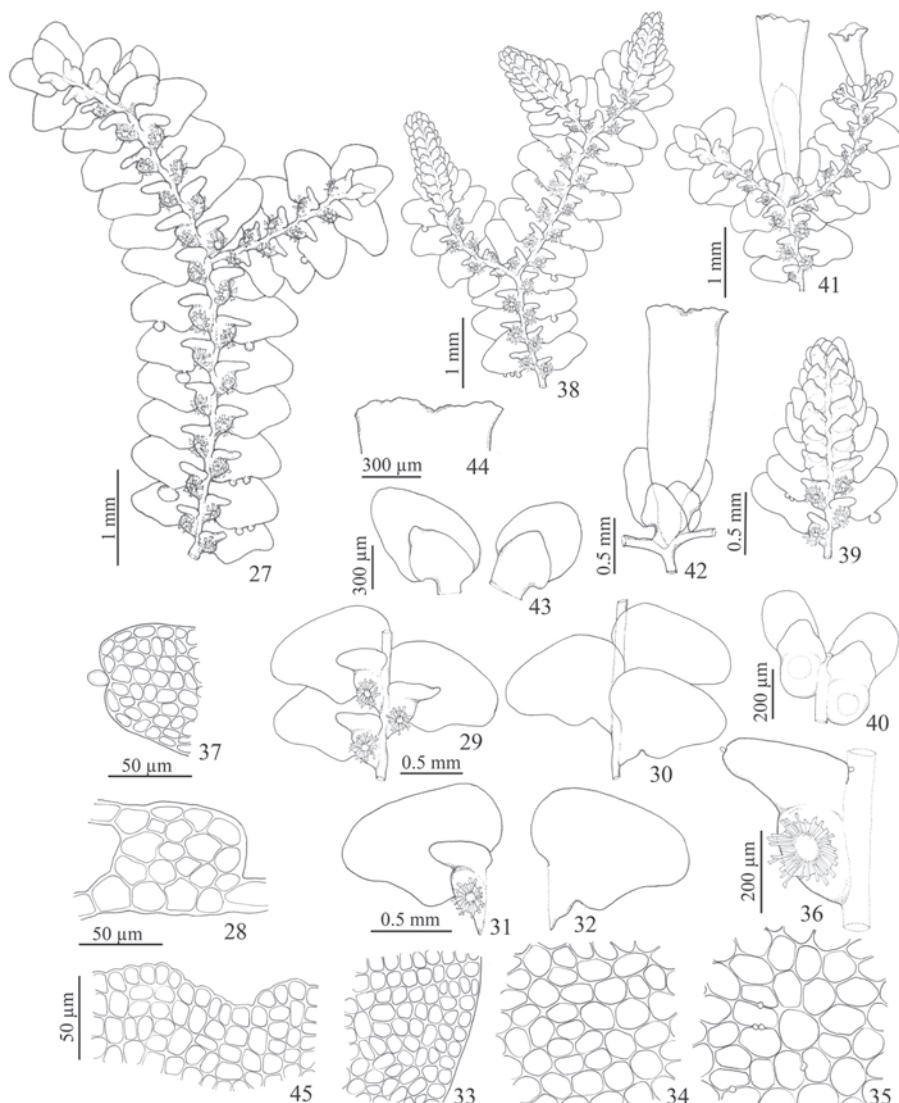
Type: Papua New Guinea, Morobe, Sattelberg, E. O. A. Nyman s.n. (holotype: G!)

Descriptions: Castle (1939: 39), Yamada (1979: 291), Yamada & Piippo (1989: 368)

Illustrations: Castle (1939: 39, fig. 7), Yamada (1979: 291, fig. 50), Yamada & Piippo (1989: 369, figs 10c, d, f, g, j, k), So (2006: 224, fig. 6a)

This species can be recognized by 1) the falcate-ovate leaf-lobe with a narrowly rounded apex, 2) the hook-like leaf-lobules with apices narrowly elongate and then abruptly turning outward, and 3) the numerous discoid gemmae occurring on ventral margins of leaf-lobes and parallel to the surface of leaf-lobes. This species is closely related to *R. protensa* in having hook-like lobules, but the latter differs from the former by the discoid gemmae occurring perpendicularly on the ventral surface of the leaf-lobes.

Habitat and ecology: *Radula nymanii* occurs on living leaves and was usually found along streams in lowland forests ranging from 50 to 600 m elevation. This species often grows associated with other *Radula* species, i.e. *R. protensa* and *R. tjibodensis*, and/or other bryophytes.



Figs 27-45. *Radula nymanii* Steph. **27.** Portion of sterile plant. **28.** Cross-section of stem. **29-30.** Portions of sterile plants. **29.** Ventral view, **30.** Dorsal view. **31-32.** Lateral leaves, **31.** Ventral view, **32.** Dorsal view. **33.** Apical cells of leaf lobe. **34.** Median cells of leaf lobe. **35.** Basal cells of leaf lobe. **36.** Leaf-lobule. **37.** Apex of leaf-lobules with hyaline papilla. **38.** Portion of plant with androecia. **39.** Androecium. **40.** Male bracts. **41.** Portion of plant with gynoecia. **42.** Gynoecium. **43.** Female bracts. **44.** Mouth of perianth. **45.** Cells of mouth margin. All from *Chantanaorrapint, Inuthai & Promma 777* (PSU).

Distribution: Vietnam, Sumatra, Java, Celebes, Borneo, Philippines, China, New Guinea, New Caledonia, Fiji, Samoa, Tahiti, Micronesia (Yamada, 1979), Malaysia (Chuah-Petiot, 2011) **New to Thailand.**

Specimens examined: Phangnga, Mueang, Sa Nang Manora Forest Park, Sa Nang Manora Waterfall, 50 m, 27 Jan. 2008, *Inuthai* 392 (PSU); Takua Pa, Si Phang-nga National Park, Ton Deng Waterfall, 85 m, 3 Aug. 2014, *Chantanaorrapint & Promma* 3882A, 3884A, 3885, 3886C (PSU). Nakhon Si Thammarat, Khao Nan National Park, Huai Kaew Station, Klong Song, 200 m, 25 Jan. 2007, *Chantanaorrapint* 1363 (PSU); Khao Luang National Park, Krung Ching Waterfall, 190-280 m, 19 Dec. 2012, *Chantanaorrapint & Promma* 1805B (PSU), 31 Oct. 2012, Pócs, Taynapuh & Lee 1217/KA (EGR, PSU), 10 Oct. 2014, *Sangrattanaprasert* 209/14A, 220/14BA (PSU). Trang, Palian, Chao Pa Waterfall, 70-260 m, 23 Dec. 2011, *Inuthai* 767A, 768A, 769, 770, 773A, 774, 781, 782 (PSU), 11 Jan. 2012, *Chantanaorrapint, Inuthai & Promma* 777, 779B, 787A, 788A, 789B (PSU), 2 Oct. 2012, *Chantanaorrapint & Promma* 1657, 1659 (PSU), 24 Nov. 2014, *Chantanaorrapint & Promma* 3932, 3935 (PSU). Satun, Thung Wa, Than Plew Waterfall, 50-100 m, 22 Dec. 2011, *Inuthai* 763 (PSU), 12 Jan. 2013, *Chantanaorrapint & Promma* 1836, 1839, 1840 (PSU). Songkhla, Sadao, Ton Nga Chang Wildlife Sanctuary, Pha Dam Waterfall, 100-150 m, 1 Dec. 2011, *Chantanaorrapint, Inuthai & Promma* 532B, 534B, 538B (PSU), 11 Oct. 2013, *Chantanaorrapint, Inuthai & Promma* 3030A, 3031, 3044B, 3048, 3049, 3053A, 3055, 3068A, 3070A (PSU), 4 Feb. 2014, *Chantanaorrapint & Promma* 3486B (PSU). Yala, Betong, Ban Chulabhorn Pattana 10, 500-600 m, 4 Dec. 2011, *Chantanaorrapint & Promma* 608 (PSU), 25 Mar. 2013, *Promma* 18 (PSU), 15 Jun. 2013, *Chantanaorrapint & Promma* 2562, 2572A, 2593, 2625B, 2626C, 2632C, 2641C, 2642C (PSU).

***Radula protensa* Lindenb., in Meissner, Bot. Zeit. 6: 462. 1848**

Figs 46-63

Type: Indonesia, Java, Zollinger H. 577 (isotypes: BM!, PC)

Descriptions: Castle (1939: 43), Yamada (1979: 292), Udar & Kumar (1984: 164), Yamada & Piippo (1989: 370)

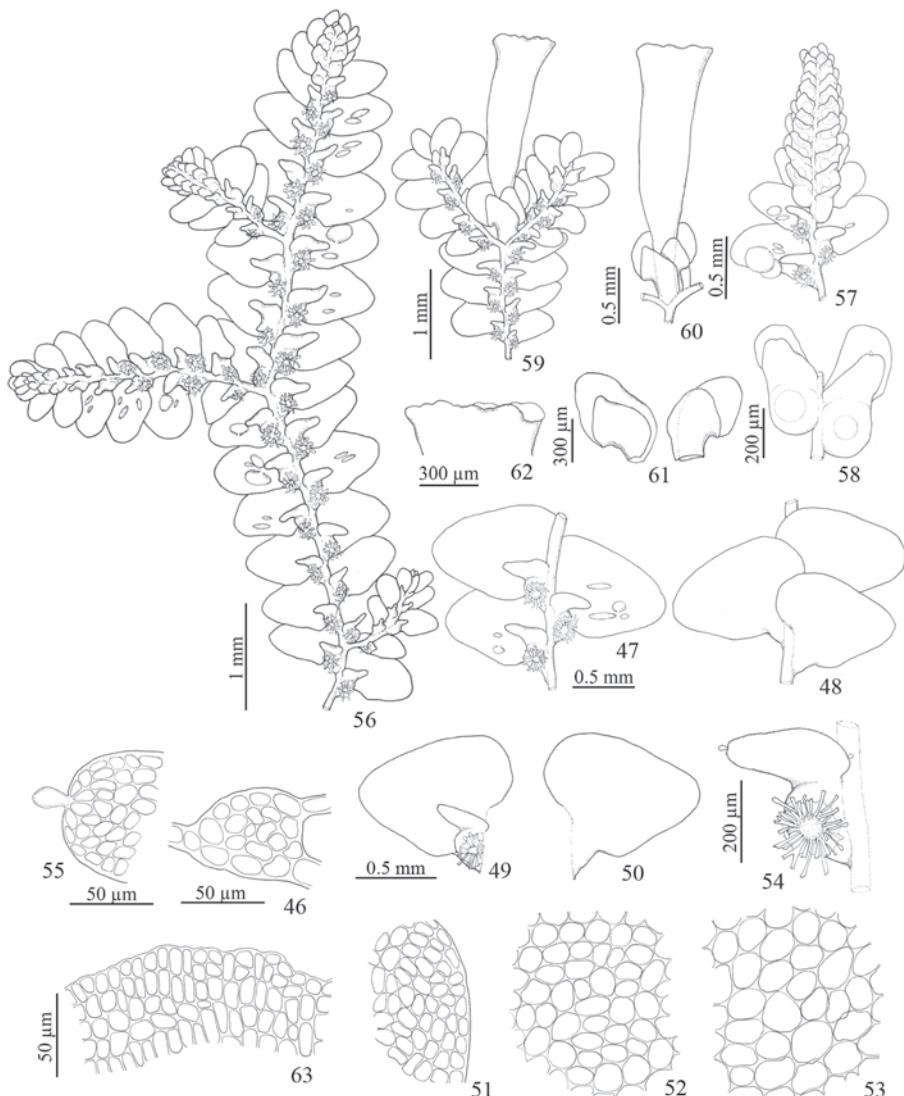
Illustrations: Castle (1939: 44, fig. 9), Yamada (1979: 293, fig. 51), Udar & Kumar (1984: 165, figs B1-22), Yamada & Piippo (1989: 371, Figs 11a, b, e, f, h)

The distinctive features of *Radula protensa* are 1) the falcate-ovate leaf-lobes with a narrowly rounded apex, 2) the hook-like leaf-lobules, with the apex narrowly elongate and then abruptly turning outward, and 3) the numerous discoid gemmae occurring perpendicularly on the ventral surface of leaf-lobes.

Habitat and ecology: *Radula protensa* occurs on living leaves and was usually found along streams in forests ranging from 50-400 m. This species often grows associated with the other *Radula* species, i.e. *R. nymanii* and *R. tibodensis*, and/or other bryophytes.

Distribution: India, Sumatra, Java, Borneo, Philippines, China, Taiwan, New Guinea (Yamada, 1979), Malaysia (Chuah-Petiot, 2011), Thailand (Chantanaorrapint & Pócs, 2014).

Specimens examined: Krabi, Klong Tom, Khao Pra Bang Khram Wildlife Sanctuary, Sra Morakot, 50-100 m, 9 Nov. 2012, Pócs & Somadee 1227/E (EGR, PSU), 20 Jul. 2013, *Chantanaorrapint & Promma* 2647, 2650, 2654, 2655, 2660 (PSU). Nakhon Si Thammarat, Khao Luang National Park, Krung Ching Waterfall, 170-280 m, 19 Dec. 2012, *Chantanaorrapint & Promma* 1802B, 1805A, 1806B, 1807 (PSU), 31 Oct. 2012, Pócs, Taynapuh & Lee 1217/KB (EGR, PSU), 10 Oct. 2014, *Sangrattanaprasert* 209/14B, 213/14, 220/14BB (PSU). Trang, Palian, Chao Pa Waterfall, 70-90 m, 23 Dec. 2011, *Inuthai* 767B, 768B, 773B (PSU), 11 Jan. 2012, *Chantanaorrapint, Inuthai & Promma* 787B, 788B (PSU), 24 Nov. 2014, *Chantanaorrapint & Promma* 3940 (PSU). Songkhla, Sadao, Ton Nga Chang Wildlife Sanctuary, Pha Dam Waterfall, 100-200 m, 4 Feb. 2014, *Chantanaorrapint & Promma* 3486C (PSU); Ton Nga Chang Wildlife Sanctuary, Ton Nga Chang Waterfall, 490 m, 18 Feb. 2015, *Juengprayoon* 195 (PSU). Yala, Betong, Ban Pakbang-Ban Chulabhorn Pattana 10, 350 m, 4 Dec. 2011, *Chantanaorrapint & Promma* 574, 577, 579 (PSU).



Figs 46-63. *Radula protensa* Lindenb. **46.** Cross-section of stem. **47-48.** Portions of sterile plants, **47.** Ventral view, **48.** Dorsal view. **49-50.** Lateral leaves, **49.** Ventral view, **50.** Dorsal view. **51.** Apical cells of leaf lobe. **52.** Median cells of leaf lobe. **53.** Basal cells of leaf lobe. **54.** Leaf-lobule. **55.** Apex of leaf-lobules with hyaline papilla. **56.** Portion of plant with androecia. **57.** Androecium. **58.** Male bracts. **59.** Portion of plant with gynoecium. **60.** Gynoecium. **61.** Female bracts. **62.** Mouth of perianth. **63.** Cells of mouth margin. Figs 46-58. from *Chantanaorrapint & Promma 1850A* (PSU), 59-63. from *Chantanaorrapint & Promma 577* (PSU).

***Radula stenocalyx* Mont., Ann. Sci. Nat., Bot., sér. 4, 3: 315. 1855 Figs 64-83**

Type: French Guiana, Cayenne, *Leprieur* 1395 (types: BM!, YU)

Descriptions: Castle (1939: 36), Yamada (1993: 136), Zhu & So (2001: 63 as *R. tjibodensis*), Dey & Singh (2012: 84 as *R. tjibodensis*)

Illustrations: Castle (1939: 37, fig. 6), Yamada (1993: 135, fig. 53), Zhu & So (2001: 64, fig. 27 as *R. tjibodensis*), Dey & Singh (2012: 85-86, figs 54-55 as *R. tjibodensis*)

The species can be recognized by 1) the broadly ovate to orbiculate leaf-lobes with rounded apex, 2) the somewhat obliquely spreading, subquadrate leaf-lobules with strongly convex and strongly pronounced mammillose rhizoid-initials, and 3) the numerous discoid gemmae occurring on dorsal margins of leaf-lobes, on margins of perianths and male bracts, and being in line with the plant surface.

Radula stenocalyx was previously known as widespread in tropical Africa and America. However, *R. stenocalyx* should be considered as a Pantropic species since specimens from China and Thailand were morphologically inseparable from Neotropical specimens including the type. Asian specimens of this species have probably been confused with *R. tjibodensis* (Zhu & So, 2001; Dey & Singh, 2012). However, *R. stenocalyx* differs from *R. tjibodensis* by the shape of the leaf-lobes and the position of the gemmae.

Habitat and ecology: *Radula stenocalyx* occurs on living leaves and was found in montane forests at altitudes between 1540 and 2550 m.

Distribution: Dominica, Guadeloupe, Trinidad, French Guiana, Brazil, Venezuela, Africa (Castle, 1939), Colombia, Dominica, Guianas (Yamada, 1993), India (Dey & Singh, 2012 as *R. tjibodensis*), China (Zhu & So, 2001 as *R. tjibodensis*) **New to Thailand.**

Specimens examined: China. Yunnan, Gongshan, Dulongjiang, 1450-1500 m, 7 Aug. 1982, *M. Zang* 1609 (HSNU), 2 Aug. 1982, *M. Zang* 2450 (HSNU); Yunan, Pingbian Co., Daweishan Nature Reserve, 1800 m, 14 Nov. 1988, *R.-L. Zhu* 88101 (HSNU); Yunan, Du Long River, 1450 m, 10 Aug. 1982, *D.-C. Zhang* 2417 (HSNU); Xizang, Motuo, Hanmi, s.d., collector unknown s.n. (HSNU); Guizhou, Maolan Nature Reserve, 1800 m, 13 Aug. 1983, *S.-Z. Jiang* 33924 (HSNU). Thailand. Chiang Mai, Chomthong, Doi Inthanon National Park, Mae Jam, 1690 m, 15 Jul. 2012, *Chantanaorrapint, Inuthai & Promma* 1478A, 1479, 1480, 1486 (PSU); Chomthong, Doi Inthanon National Park, Ang Ka, 2535 m, 20 Dec. 2011, *Chantanaorrapint* 2556, 2561 (PSU), 8 Oct. 2012, *Chantanaorrapint & Promma* 1742, 1746, 1746, 1748 (PSU), 4 Apr. 2014, *Chantanaorrapint & Promma*, 3517, 3521 (PSU); Chomthong, Doi Inthanon National Park, Kew Mae Pan, 2205-2220 m, 28 Jun. 2008, *Nathi* 1364 (BCU), 9 Oct. 2012, *Chantanaorrapint & Promma* 1783, 1785, 1786, 1787 (PSU), 4 Apr. 2014, *Chantanaorrapint & Promma*, 3529, 3536, 3537 (PSU); Chom Thong, Royal Agricultural Station Inthanon, 2524-2540 m, 20 Dec. 2011, *R.-L. Zhu* 20111220-144, 20111220-9D (HSNU). Chantaburi, Khao Soi Dao, Khao Soi Dao Wildlife Sanctuary, Khao Soi Dao, 1540-1640 m, 8 Apr. 2012, *Chantanaorrapint, Inuthai & Promma* 933, 960, 962, 964, 966, 968, 974, 982 (PSU).

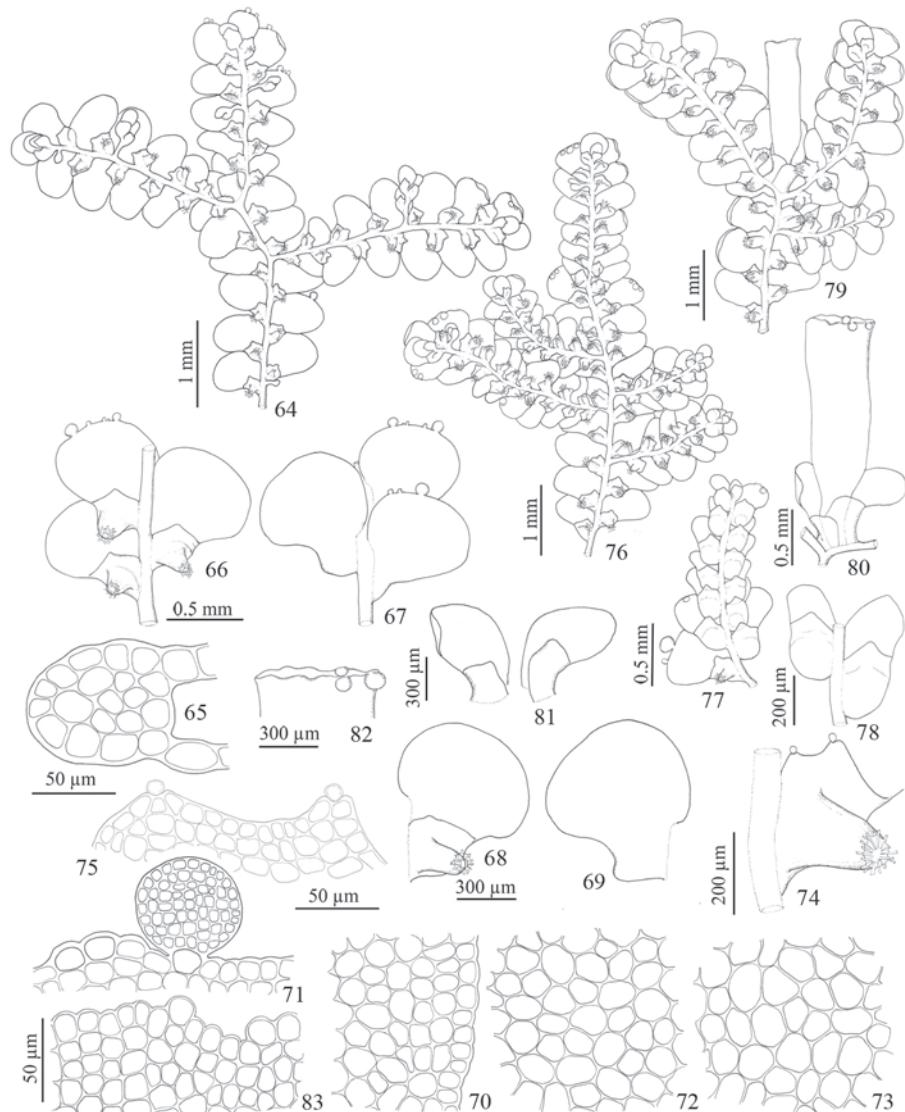
***Radula tjibodensis* K.I.Goebel, Ann. Jard. Bot. Buitenzorg 7: 53. 1888 Figs 84-103**

Type: Indonesia, Java, Tjibodas, *K. Goebel* s.n. (holotype: not located)

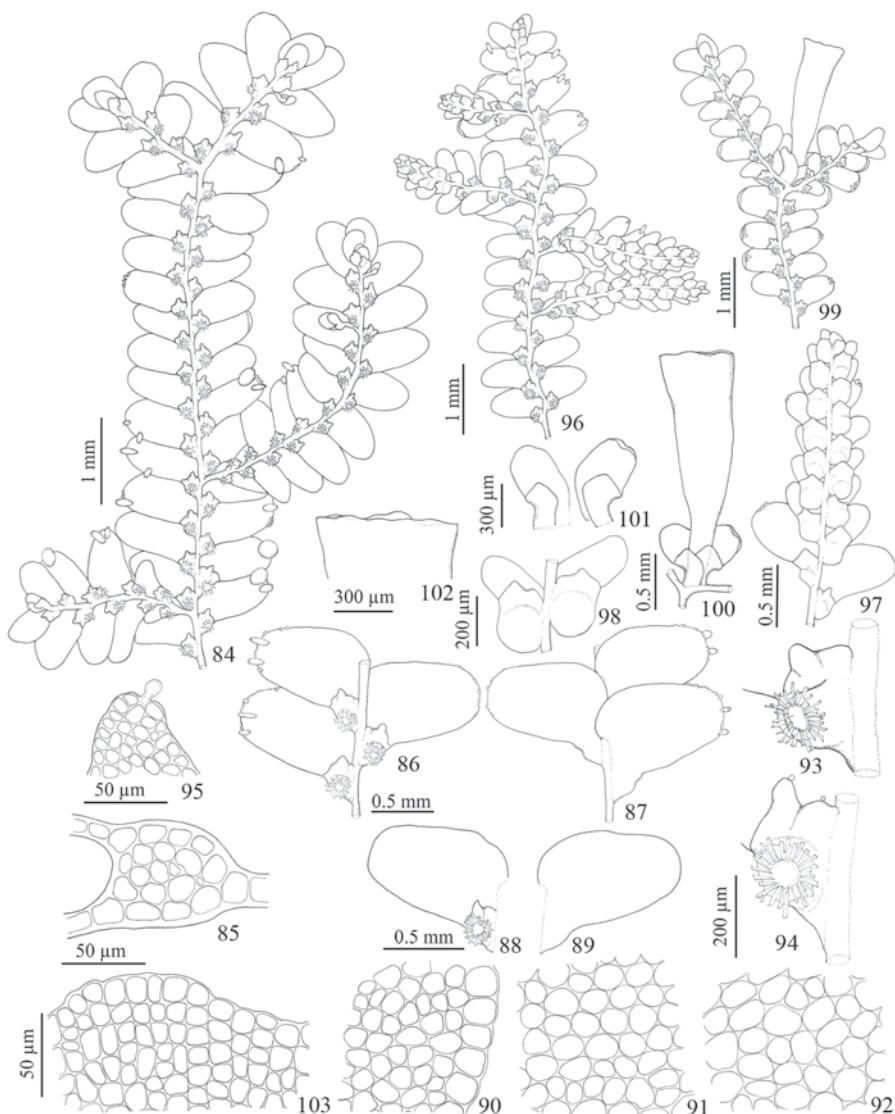
Descriptions: Schiffner (1893: 249), Castle (1939: 32), Yamada (1979: 294), Udar & Kumar (1984: 168), Yamada & Piippo (1989: 368)

Illustrations: Schiffner (1893: 304, taf. 8, figs 9-12), Castle (1939: 33, fig. 5), Yamada (1979: 294, fig. 52), Udar & Kumar (1984: 169, figs D1-10), Yamada & Piippo (1989: 369, figs 10 l-p), So (2006: 227, fig. 7c)

The distinctive features of *Radula tjibodensis* are 1) the narrowly ovate or falcate-ovate to oblong leaf-lobes with narrowly rounded to obtuse apices, 2) the



Figs 64-83. *Radula stenocalyx* Mont. **64.** Portion of sterile plant. **65.** Cross-section of stem. **66-67.** Portions of sterile plants, **66.** Ventral view, **67.** Dorsal view. **68-69.** Lateral leaves, **68.** Ventral view, **69.** Dorsal view. **70.** Apical cells of leaf lobe. **71.** Marginal cells of leaf lobe with gemma. **72.** Median cells of leaf lobe. **73.** Basal cells of leaf lobe. **74.** Leaf-lobule. **75.** Apex of leaf-lobules with hyaline papillae. **76.** Portion of plant with androecium. **77.** Androecium. **78.** Male bracts. **79.** Portion of plant with gynoecium. **80.** Gynoecium. **81.** Female bracts. **82.** Mouth of perianth. **83.** Cells of mouth margin. All from Chantanaorrapint & Promma 1748 (PSU).



Figs 84-103. *Radula tjibodensis* K.I. Goebel. **84.** Portion of sterile plant. **85.** Cross-section of stem. **86-87.** Portions of sterile plants, **86.** Ventral view, **87.** Dorsal view. **88-89.** Lateral leaves, **88.** Ventral view, **89.** Dorsal view. **90.** Apical cells of leaf lobe. **91.** Median cells of leaf lobe. **92.** Basal cells of leaf lobe. **93-94.** Leaf-lobules. **95.** Apex of leaf-lobules with hyaline papilla. **96.** Portion of plant with androecia. **97.** Androecium. **98.** Male bracts. **99.** Portion of plant with gynoecium. **100.** Gynoecium. **101.** Female bracts. **102.** Mouth of perianth. **103.** Cells of Mouth margin. Figs 84-95., 99-103. from Chantanaorrapint, Inuthai & Promma 836 (PSU), 96-98. from Chantanaorrapint, Inuthai & Promma 1349 (PSU).

subquadrate leaf-lobules with a narrowly obtuse to bluntly protruding apex, and 3) the numerous discoid gemmae occurring perpendicularly on apical margins of leaf-lobes. This species can be confused with *R. stenocalyx*; distinguishing character states are listed under the latter species.

Habitat and ecology: *Radula tjbodensis* grows on living leaves and was found in lowland forests to montane rain forests at altitudes between 50 and 1650 m, often associated with *R. protensa* and *R. nymanii*.

Distribution: India, Nepal, Sikkim, Thailand, Vietnam, Malay Peninsula, Sumatra, Java, Borneo, Philippines, New Guinea, Samoa (Yamada, 1979).

Specimens examined: Phangnga, Takua Pa, Si Phang-nga National Park, Ton Deng Waterfall, 85 m, 3 Aug. 2014, Chantanaorrapint & Promma 3880B, 3881A, 3884B, 3886B, 3889B (PSU). Nakhon Si Thammarat, Khao Nan National Park, San Yen, 280-1300 m, 17-22 Apr. 2007, Sukharak & Seelanan 13A, 27, 55A, 96A, 156, 162A (BCU), 25 Jul. 2010, Chantanaorrapint 2244A, 2251A (PSU); Khao Luang National Park, Khao Luang, 700-1700 m, 5-7 Feb. 1966, A. Touw 11895, 11998 (BKF, L), 18 Mar. 2013, Chantanaorrapint & Promma 2281, 2283 (PSU), 21-23 Apr. 2014, Chantanaorrapint & Promma 3601A, 3603, 3607, 3608A, 3615A, 3617A, 3619A, 3700, 3701 (PSU); Khao Luang National Park, Krung Ching Waterfall, 170-190 m, 9 Dec. 2012, Chantanaorrapint & Promma 1802A, 1806A (PSU); Ron Phiboon, Khao Ramrome, 935-1000 m, 22 Feb. 2007, Chantanaorrapint 1422, 1424 (PSU), 15 Dec. 2011, Chantanaorrapint, Inuthai & Promma 738 (PSU), 13 Mar. 2012, Chantanaorrapint, Inuthai & Promma 832, 835A, 836, 837, 838 (PSU), 28 Feb. 2015, Chantanaorrapint & Promma 3951, 3953 (PSU), 27 Oct. 2012, Pócs, Chantanaorrapint & Lee 1209/AR, 1209/U (EGR, PSU). Trang, Palian, Chao Pa Waterfall, 70-100 m, 23 Dec. 2011, Inuthai 773C (PSU), 11 Jan. 2012, Chantanaorrapint, Inuthai & Promma 779A, 789A (PSU); Palian, Khao Chedyod, 550-1120 m, 20-22 May 2012, Chantanaorrapint, Inuthai & Promma 1120A, 1178A, 1205, 1220, 1223A, 1345A, 1348A, 1349, 1350A, 1352C, 1358A, 1367A, 1369, 1371A, 1373AA, 1378A (PSU), 30 Apr.-3 May. 2014, Chantanaorrapint & Promma 3719, 3731A, 3738AB, 3739BA, 3770B, 3780A, 3781A, 3783A, 3784A, 3788A, 3789A, 3790A, 3817B(PSU). Songkhla, Sadao, Ton Nga Chang Wildlife Sanctuary, Pha Dam Waterfall, 135 m, 1 Dec. 2011, Chantanaorrapint, Inuthai & Promma 532A, 534A, 538A (PSU), 11 Oct. 2013, Chantanaorrapint, Inuthai & Promma 3044A, 3053B, 3068B, 3070B (PSU); Ton Nga Chang Wildlife Sanctuary, Tom Nga Chang Waterfall, 940 m, 23 May 2014, Chantanaorrapint & Promma 3870 (PSU). Yala, Betong, Ban Chulabhorn Pattana 10, 550-600 m, 15 Jun. 2013, Chantanaorrapint & Promma 2565, 2598, 2614A, 2615A, 2616A, 2625A, 2626A, 2632A, 2641A, 2642A (PSU).

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