The Genus *Colura* (Dumort.) Dumort. (Lejeuneaceae, Marchantiophyta) in Malesian Region

Jiroat Sangrattanaprasert

A Thesis Submitted in Fulfillment of the Requirements for the Degree of Doctor of Philosophy in Biology

Prince of Songkla University

2019

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I hereby certify that this work has not been accepted in substance for any degree, and is not being currently submitted in candidature for any degree.

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ชื่อวิทยานิพนธ์ ลิเวอร์เวิร์ตสกุล *Colura* (Dumort.) Dumort. (Lejeuneaceae, Marchantiophyta) ในภูมิภาคมาเลเซียน
ผู้เขียน นายจิโรจน์ แสงรัตนประเสริฐ
สาขาวิชา ชีววิทยา
ปีการศึกษา 2561

บทคัดย่อ

การศึกษาทบทวนด้านอนุกรมวิธานของลิเวอร์เวิร์ตสกุล *Colura* (Dumort.) Dumort. ในภูมิภาคมาเลเซียนด้วยการศึกษาตัวอย่างที่เก็บรักษาในพิพิธภัณฑ์พืชต่าง ๆ และตัวอย่างที่เก็บในภาคสนามระหว่างเดือนมิถุนายน พ.ศ. 2556 ถึงเดือนมกราคม พ.ศ. 2561 การประเมินความสัมพันธ์ทางวิวัฒนาการของระดับต่ำกว่าสกุลจากการวิเคราะห์ชุดข้อมูลโมเลกุลรวม (nrITS *trnL–F* และ *rbcL*) ด้วยวิธี Maximum parsimony Maximum likelihood และ Bayesian inference สนับสนุนการแบ่งสกุล *Colura* เป็น 2 สกุลย่อย คือ สกุลย่อย *Colura* และสกุลย่อย *Glotta* Grolle *et* R.L.Zhu นอกจากนี้ *Macrocolura sagittistipula* (Spruce) R.M.Schust. ควรจัดไว้เป็นสมาชิกของสกุล *Colura* ดังเดิม ผลการศึกษาความสัมพันธ์ทางวิวัฒนาการของ *C. inflata* K.I.Goebel และชนิดใกล้เคียง พบว่า *C. inflata* มีความแตกต่างแยกเป็นชนิดชัดเจน ในขณะที่ *C. corniantha* Grolle และ *C. siamensis* Jovet-Ast เป็นชนิดเดียวกัน ในการศึกษาทบทวนพบลิเวอร์เวิร์ตสกุล *Colura* ทั้งสิ้น 34 ชนิด ในจำนวนนี้เป็นพืชชนิดใหม่ 1 ชนิด คือ *C. sigmoidea* Sangratt. *et al*. และพืชที่มีรายงานใหม่ 4 ชนิด (*C. calyptrifolia*, *C. corniantha*, *C. medusa*, and *C. valida*) นอกจากนี้ *C. cymbalifera* Herzog *et* Jovet-Ast และ *C. siamensis* จัดเป็นชื่อพ้องของ *C. hemisphaerica* Jovet-Ast และ *C. corniantha* ตามลำดับ ในการศึกษาครั้งนี้ได้จัดทำรูปวิธานระบุชนิด คำบรรยาย และภาพวาดลายเส้น ของทั้ง 34 ชนิด พร้อมทั้งข้อมูลสภาพแหล่งอาศัย ลักษณะทางนิเวศวิทยา และการกระจายพันธุ์ของแต่ละชนิด ลิเวอร์เวิร์ตสกุล *Colura* พบเจริญบนใบไม้เป็นหลัก บางชนิดพบเจริญบนกิ่งหรือเปลือกไม้ พบได้ตั้งแต่ความสูงใกล้ระดับทะเลถึงความสูง 2900 เมตรจากระดับทะเล ลิเวอร์เวิร์ตสกุลนี้ส่วนใหญ่ (26 ชนิด) พบกระจายพันธุ์ในป่าดิบเขาระดับต่ำถึงป่าดิบเขา เมื่อพิจารณาขอบเขตการกระจายพันธุ์ทางภูมิศาสตร์ของสกุล *Colura* ทั้ง 34 ชนิด สามารถแบ่งออกเป็น 5 กลุ่ม ดังนี้ เขตร้อน-กึ่งเขตร้อนทั่วโลกและเขตอบอุ่น (5.88%) เอเชียเขตร้อนและกึ่งเขตร้อน–ออสตราเลเซีย–แปซิฟิก (35.29%) มาเลเซียน (47.05%) อินโดจีน–สุมาตรา (8.82%) และพืชถิ่นเดียวในเกาะมะลุกุ ประเทศอินโดนีเซีย (3.94%)

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Author Mr. Jiroat Sangrattanaprasert
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ABSTRACT

A taxonomic revision of the genus *Colura* in Malesian region is presented based on specimens from herbaria and field collections carried out from June 2013 to January 2018. The infrageneric phylogenetic relationships of *Colura* species are assessed. The combined molecular data (nrITS, *trnL–F*, and *rbcL*) were analysed using Maximum parsimony, Maximum likelihood, and Bayesian inference. The resulted topology supports the classification of the genus *Colura* into 2 subgenera: *Colura* and *Glotta* Grolle *et* R.L.Zhu. In addition, *Macrocolura sagittistipula* (Spruce) R.M.Schust. should be retained as a member of the genus *Colura*. Besides, the phylogenetic relationships of *C. inflata* K.I.Goebel and it related species was also investigated. The analyses indicate that *C. inflata* is a distinct species, while *C. corniantha* Grolle and *C. siamensis* Jovet-Ast are a conspecific. In this revision, 34 species of *Colura* are recognised, including one new species, *C. sigmoidea* Sangratt. *et al*. and four new records (*C. calyptrifolia, C. corniantha, C. medusa,* and *C. valida*). Moreover, *Colura cymbalifera* Herzog *et* Jovet-Ast and *C. siamensis* were treated as synonyms of *C. hemisphaerica* Jovet-Ast and *C. corniantha*, respectively. A key to species, descriptions and illustrations are provided. Habitats, ecology, and geographical distributions are also presented. The majority of the species are epiphylls with some species growing on branch or bark. The total altitudinal range of the genus extends from near sea level to 2900 m in elevation. Almost all *Colura* species (26 species) are found distributed in lower montane to montane rain forests. Among phytogeography, five groups are classified including 1) Pantropic-Subtropic and Temperate (5.88%), 2) Asia Tropical and Subtropical–Australasia–Pacific (35.29%), 3) Malesia (47.05%), 4) Indo-china–Sumatra (8.82%), and 5) Endemic of Maluku Islands (Indonesia) (3.94%).

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CONTENTS

	Page
CONTENTS	VIII
LIST OF TABLES	X
LIST OF FIGURES	XI
CHAPTER	
1. INTRODUCTION	1
The taxonomic history of the genus *Colura*	2
The phylogenetic position of the genus *Colura*	3
Infrageneric classification of the genus *Colura*	4
Previous studies of the genus *Colura* in Malesian region and adjacent areas	5
Some taxonomic problems in the genus *Colura*	10
Study area	12
Objectives	14
2. MORPHOLOGY AND ANATOMY	15
2.1 Introduction	15
2.2 Morphological and anatomical study	16
2.2.1 Plant materials	16
2.2.2 Laboratory study	16
2.3 Results	17
2.4 Discussions	38
3. MOLECULAR PHYLOGENY	41
3.1 Introduction	41
3.2 Materials and methods	43
3.2.1 Taxon and character sampling	43
3.2.2 DNA extraction, amplification, and sequencing	45
3.2.3 Phylogenetic analyses	45
3.3 Results	46
3.4 Discussions	51
3.4.1 Phylogenetic relationship of the infrageneric classification	51

CONTENTS (CONT.)

	Page
3.4.2 *Colura inflata* and related species	54
3.4.3 Cryptic species	55
4. TAXONOMIC TREATMENTS	56
4.1 Introduction	56
4.2 Materials and methods	57
4.3 Results and discussions	58
4.3.1 Taxonomic treatment	61
4.3.2 Excluded species	208
4.3.3 Geographical distribution of *Colura* in Malesian region	209
4.3.4 Altitudinal distribution of the genus *Colura* in Malesian region	209
4.3.5 Microhabitats	209
4.3.6 Phytogeography	210
5. SUMMARY	213
Suggestions for further studies	214
REFFERENCES	215
VITAE	226

LIST OF TABLES

Table		Page
1.1	The species number of *Colura* recorded in Malesia and adjacent areas.	10
3.1	List of taxa used in the present study, including information about locality, information and deposited herbaria of voucher specimens, as well as their GenBank Accession numbers.	47
3.2	Primer sequences used for PCR amplification and sequencing.	50
4.1	Habitats, elevations and forest types of *Colura* species recorded in Malesian region.	60

LIST OF FIGURES

Figure		Page
1.1	Position of *Colura* in Lejeuneaceae phylogeny	6
1.2	Phylogeny of the genus *Colura*, showing four sections belonging to two subgenera and position of genus *Macrocolura*	7
1.3	Outline map showing the Malesian boundary	12
1.4	Outline map of Southeast Asia showing the four biodiversity hotspots	13
2.1	Habitats and habits	18
2.2	Stems in transection showing 7 cortical and 3 medullary cells	19
2.3	Branching of *Colura acroloba* under Scanning Electron Microscope (SEM)	19
2.4	Portions of plants in ventral view showing uniform lateral leaves	20
2.5	Lateral leaves, ventral view	21
2.6	Valves and valve frames of genus *Colura* investigating by SEM	23
2.7	Valve types	24
2.8	Valve frames	25
2.9	Leaf cells	26
2.10	Leaf cell surface under the SEM technique showing smooth cuticle	27
2.11	Oil bodies of *Colura* species	28
2.12	The variation of underleaves in the genus *Colura*	29
2.13	Androecia of *Colura* species	30
2.14	The variations of the androecia	31
2.15	The variations of perianths and beaks	33
2.16	Sporangia of *Colura apiculata*	34
2.17	The mature sporophytes of genus *Colura*	35
2.18	Elaters of the sporangium in genus *Colura*	36
2.19	Spore ornamentations of the genus *Colura*	37
2.20	Gemmae of genus *Colura*	38
2.21	The comparison between lobule valve of *Pleurozia* and *Colura*	40
3.1	The significant characters of *Colura* section *Heterophyllum* Jovet-Ast	44
3.2	Morphological comparison within *Colura inflata* complex	44

LIST OF FIGURES (CONT.)

Figure		Page
3.3	Maximum likelihood phylogenetic reconstruction of the genus *Colura*, inferred from combined dataset (nrITS, *trnL-trnF*, and *rbcL*)	51
3.4	The comparison of perianth keel apices of *Colura corniantha* and *C. siamensis* showing the presence/absence of apical teeth	55
4.1	Methods of measurement in *Colura*	59
4.2	*Colura acroloba* (Prantl) Jovet-Ast	146
4.3	*Colura acroloba* (Prantl) Jovet-Ast	147
4.4	*Colura apiculata* (Schiffn.)	148
4.5	*Colura apiculata* (Schiffn.)	149
4.6	*Colura ari* (Steph.) Steph.	150
4.7	*Colura ari* (Steph.) Steph.	151
4.8	*Colura bisvoluta* Herzog *et* Jovet-Ast	152
4.9	*Colura bisvoluta* Herzog *et* Jovet-Ast	153
4.10	*Colura brevistyla* Herzog	154
4.11	*Colura calyptrifolia* (Hook.) Dumort.	155
4.12	*Colura clementis* Grolle	156
4.13	*Colura conica* (Sande Lac.) K.I.Goebel	157
4.14	*Colura conica* (Sande Lac.) K.I.Goebel	158
4.15	*Colura corniantha* Grolle	159
4.16	*Colura corniantha* Grolle	160
4.17	*Colura corynophora* (Nees, Lindenb. *et* Gottsche) Trevis.	161
4.18	*Colura corynophora* (Nees, Lindenb. *et* Gottsche) Trevis.	162
4.19	*Colura crenulata* Grolle	163
4.20	*Colura crenulata* Grolle	164
4.21	*Colura cristata* Jovet-Ast	165
4.22	*Colura cristata* Jovet-Ast	166
4.23	*Colura denticulata* Jovet-Ast	167
4.24	*Colura denticulata* Jovet-Ast	168

LIST OF FIGURES (CONT.)

Figure		Page
4.25	*Colura galeata* Jovet-Ast	169
4.26	*Colura galeata* Jovet-Ast	170
4.27	*Colura hemisphaerica* Jovet-Ast	171
4.28	*Colura hemisphaerica* Jovet-Ast	172
4.29	*Colura herzogii* Jovet-Ast	173
4.30	*Colura herzogii* Jovet-Ast	174
4.31	*Colura imperfecta* Steph.	175
4.32	*Colura imperfecta* Steph.	176
4.33	*Colura inflata* K.I.Goebel	177
4.34	*Colura inflata* K.I.Goebel	178
4.35	*Colura junghuhniana* (Prantl) Steph.	179
4.36	*Colura junghuhniana* (Prantl) Steph.	180
4.37	*Colura karstenii* K.I.Goebel	181
4.38	*Colura karstenii* K.I.Goebel	182
4.39	*Colura maxima* Jovet-Ast	183
4.40	*Colura medusa* J.Eggers *et* Pócs	184
4.41	*Colura medusa* J.Eggers *et* Pócs	185
4.42	*Colura meijeri* Jovet-Ast	186
4.43	*Colura meijeri* Jovet-Ast	187
4.44	*Colura mosenii* Steph.	188
4.45	*Colura ornata* K.I.Goebel	189
4.46	*Colura ornata* K.I.Goebel	190
4.47	*Colura palawanensis* Jovet-Ast	191
4.48	*Colura palawanensis* Jovet-Ast	192
4.49	*Colura pallida* Steph.	193
4.50	*Colura pallida* Steph.	194
4.51	*Colura pluridentata* Jovet-Ast	195
4.52	*Colura pluridentata* Jovet-Ast	196

LIST OF FIGURES (CONT.)

Figure		Page
4.53	*Colura sigmoidea* Sangratt., Chantanaorr. *et* R.L.Zhu	197
4.54	*Colura speciosa* Jovet-Ast	198
4.55	*Colura speciosa* Jovet-Ast	199
4.56	*Colura superba* (Mont.) Steph.	200
4.57	*Colura superba* (Mont.) Steph.	201
4.58	*Colura tenuicornis* (A.Evans) Steph.	202
4.59	*Colura tenuicornis* (A.Evans) Steph.	203
4.60	*Colura valida* Jovet-Ast	204
4.61	*Colura valida* Jovet-Ast	205
4.62	*Colura verdoornii* Herzog *et* Jovet-Ast	206
4.63	*Colura verdoornii* Herzog *et* Jovet-Ast	207
4.64	The distribution patterns of *Colura* species in Malesia.	212
4.65	The distribution patterns of *Colura* species in Malesia.	212

CHAPTER 1

INTRODUCTION

The genus *Colura* (Dumort.) Dumort. was first described by Dumortier (1831) as a section of *Lejeunea* Lib. and was subsequently raised to the generic rank by Dumortier (1835), based on *C. calyptrifolia* (Hook.) Dumort. This genus belongs to Lejeuneaceae Cavers, which is the largest family of the liverworts with more than 1800 species belonging to ca. 70 genera (Zhu *et al*. 2017), and was placed in subfamily Lejeuneoideae C.Massal, tribe Lejeuneeae Dumort., subtribe Cololejeuneinae Gradst., based on molecular and morphological evidence (Gradstein 2013). *Colura* contains 83 accepted taxa (Söderström *et al*. 2016), of these 39 species are endemic (Pócs 1996). The genus is mainly distributed in the tropical and subtropical regions (Jovet-Ast 1954, Pócs 1996). The species of *Colura* are easily recognised by underleaf deeply bilobed, one per lateral leaf; leaf lobules tubular to cylindrical, usually broadening distally and terminating in a sac; lobule sac with a valve and a pore (Mizutani 1961, Barthlott *et al*. 2000, Zhu & So 2001, Frey & Stech 2009, Sangrattanaprasert *et al*. 2017). Most species of *Colura* are epiphyllous plants, occasionally on small twigs and bark, and growing in sunny areas in various habitats from lowland to highland montane rain forests.

Tropical Asia consists of 4 regions, i.e., Indian Subcontinent, Indo-China, Malesia and Papuasia (Brummitt 2001). Malesian region is one of the most important area which includes three biodiversity hotspots: Philippines, Sundaland and Wallacea (Myers *et al*. 2000). Moreover, the highest number of the genus *Colura* was also reported in these areas (Pócs 1996). Although a comprehensive taxonomic revision of *Colura* was published by Jovet-Ast (1953), several new species have been described recently (Pócs & Eggers 2007, Pócs 2013, Sangrattanaprasert *et al*. 2019a) as well as new distribution records were still reported from the unexplored areas (e.g. Pócs *et al*. 2011, Pócs & Podani 2015, Pócs & Lee 2016, Sangrattanaprasert *et al*. 2017, 2018, 2019a, 2019b (in press)). Furthermore, the taxonomic statuses of some species

complexes are still unclear, so the revision of this genus in Malesian region is needed to fulfill gaps of knowledge and for a better understanding.

The taxonomic history of the genus *Colura*

At first, *Colura* was first established as sect. *Colura* Dumort. belonging to genus *Lejeunea* in 1831, but Dumortier (1835) afterwards raised this section to be a generic rank in *Recueil d'Observations sur les Jungermanniacées*, and *C. calyptrifolia* was designated as a type of genus.

Subsequently, Spruce (1884) divided the genus *Lejeunea* into 38 subgenera in which subg. *Coluro-Lejeunea* was coined invalidly because the inclusion of the hyphen (Söderström *et al*. 2015). Although the genus *Colurolejeunea* was validated later by Stephani (1891), it was an obligate synonym of the genus *Colura*, because of these two genera share the same type (Bonner 1963, Söderström *et al*. 2015). The genus *Colurolejeunea* had been treated as a synonym of *Colura* by Jovet-Ast (1953), consequently.

Stephani (1916) recognised 28 species of *Colura* worldwide and published in Species Hepaticarum. The species were ranged regionally into Africa (2 species), Tropical America (7 species), Antarctica (2 species), Asia and Oceania (16 species), and Europe (1 species). At that time, he also provided short descriptions of all species including 10 new species.

Jovet-Ast (1948) described *C. rhynchophora* collected from Guadeloupe. After that, Jovet-Ast (1953) published a monograph of *Colura*, in which 53 species were recognized included their descriptions and line drawings. Among these 22 species were first proposed and a combination of *C. acroloba* was made. Moreover, she also divided the genus into six sections based mainly on the lobule valve characters. One year later, a supplementary of the monograph including a description of a new proposed species (*C. denticulata* Jovet-Ast) and suggestions on the evolution of lobule valve compared with valve of *Pleurozia gigantea* (F.Weber) Lindb. (Pleuroziaceae Müll.Frib.) and the relationships of six sections were published (Jovet-Ast 1954). Continuously, 16 species and 1 variety of *Colura* were first described from many countries, i.e., Australia, Cambodia, Indonesia, Madagascar, Malaysia, New

Caledonia, New Zealand, Tanzania, Thailand, and Vietnam (Jovet-Ast 1956, 1958a, 1961, 1967a, 1967b, 1976, 1980, 1983, Jovet-Ast & Tixier 1958). In 1980, she constructed a key to species of nine taxa belonged to sect. *Oidocorys* and disscussed about their distribution as well. Besides, more distribution data of *Colura* species were reported continuously (Jovet-Ast 1958b, 1961, 1967a, 1967b, 1976, 1980, Jovet-Ast & Tixier 1958).

The phylogenetic position of the genus *Colura*

Over the past two decades, the phylogenetic taxonomy based on molecular data became the main tool used for resolving many taxonomic problems. Many bryologists have used phylogenetic reconstruction to resolve taxonomic position and classification (Lewis *et al*. 1997, Shaw & Renzaglia 2004, Crandall-Stotler *et al*. 2009). Moreover, the phylogenetic relationships within the family Lejeuneaceae had been analyzed (Ahonen *et al*. 2003, Gradstein *et al*. 2003, 2006, Groth-Malonek *et al*. 2004, Wilson *et al*. 2007). The results showed that the genus *Colura* nested within subfamily Lejeuneoideae, tribe Lejeuneeae, subtribe Cololejeuneinae (the largest subtribe of the family) (Fig. 1.1) (Gradstein 2013, Heinrichs *et al*. 2014a, 2014b). The subtribe Cololejeuneinae comprises 12 genera, namely *Aphanotropis* Herzog, *Austrolejeunea* R.M.Schust., *Calatholejeunea* K.I.Goebel, *Cololejeunea* (Spruce) Schiffn., *Colura*, *Diplasiolejeunea* (Spruce) Schiffn., *Haplolejeunea* Grolle, *Macrocolura* R.M.Schust., *Myriocoleopsis* Schiffn., *Schusterolejeunea* Grolle, *Siphonolejeunea* Herzog, and *Tuyamaella* S.Hatt (Gradstein 2013).

The closest morphologically related genus to *Colura* is *Macrocolura*, which shares many similar characters with the former genus, such as the presence of one underleaf per lateral leaf and the presence of apical lobule sac with a valve covering sac pore. However, *Macrocolura* is distinguished by underleaf insertion being invertedly J-shaped, convex underleaf with two short straight forward lobes, asymmetrical underleaves, and the presence of rhizoid fascicule at the middle of underleaves (Grolle & Zhu 2002). Furthermore, *Colura* is also morphologically similar to *Diplasiolejeunea* in having one underleaf per each lateral leaf, however the latter differs from *Colura* by the absence of apical sac at leaf apex and the presence of

ocelli in leaf lobes (Zhu & So 2001). Based on the molecular phylogeny, there are two genera placed as a sister clade with *Colura-Macrocolura* clade, namely *Myriocoleopsis* and *Siphonolejeunea* (Fig. 1.1). The genus *Myriocoleopsis* is strongly distinguished from *Colura* by stem in transection having 5 cortical cells and 1 medullary cell, the absence of underleaf, and leaf lobule being reduced or absent. The genus *Siphonolejeunea* shares some characters with *Colura*, such as stem in transection having 7 cortical cells and 3 medullary cells, underleaf being bilobed with deep lobe, underleaf lobe being triangular or lanceolate, and the absence of ocelli; *Siphonolejeunea*, however, differs from *Colura* by presence of 1 underleaf per a pair of lateral leaves, having oblong lobule without forming the apical lobule sac, and absence of lobule valve.

Infrageneric classification of the genus *Colura*

Based on lateral leaf features, valve types, and perianth characters, Jovet-Ast (1953) divided *Colura* into six sections: sect. *Eucolura* Jovet-Ast, sect. *Gamolepis* Jovet-Ast, sect. *Heterophyllum* Jovet-Ast, sect. *Lingua* Jovet-Ast, sect. *Macrorhamphus* Jovet-Ast, and sect. *Oidocorys* Jovet-Ast. All six section names, nevertheless, were invalid due to the lack of Latin diagnosis. The sect. *Macrorhamphus*, moreover, was invalid because this section includes the generitype, *C. calyptrifolia*, so it needs to be changed to sect. *Colura* legally (Grolle 1965). Moreover, adding prefix *Eu-* to the name of subdivision of genus as the sect. *Eucolura* was illegal. Therefore, Grolle (1965) established a replacement name, sect. *Harmophyllum* Grolle, and also provided its Latin description. The sect. *Oidocorys* Jovet-Ast *ex* Grolle was validly reestablished by providing a Latin description later (Grolle 1969). Then, the validation of two sections (*Gamolepis* & *Heterophyllum*) were made (Jovet-Ast 1983).

Afterwards, Grolle & Zhu (2002) agreed with Schuster (1994) to segregate *Macrocolura* from *Colura* sect. *Lingua* subsect. 1 by Schuster (1994) and they raised subsect. 2 of sect. *Lingua* to sect. *Glotta* Grolle *et* R.L.Zhu. Moreover, they proposed two subgenera, *viz*., subg. *Colura* and subg. *Glotta* Grolle *et* R.L.Zhu, based on the presence and absence of hinge cells of valve. The conspectus and key to subgenera

and sections as well as list of species under the appropriate sections were provided further. Thus, the genus *Colura* have been divided into two subgenera and six sections: subg. *Colura* including sect. *Colura*, *Gamolepis*, *Harmophyllum*, and *Oidocorys* and subg. *Glotta* including sect. *Glotta* and *Heterophyllum*.

Although the comprehensive phylogenetic study within the subdivisions of the genus *Colura* never been conducted hitherto, some species representative four sections (*Colura*, *Harmophyllum*, *Heterophyllum*, and *Oidocorys*) have been analysed by Heinrichs *et al*. (2012). In that work, the resulted topology also revealed that subg. *Colura* and sect. *Heterophyllum* was non-monophyletic (Fig. 1.2). However, their analysis included members from only four sections, so the members from the two remaining sections (*Gamolepis* and *Glotta*) are needed for a more comprehensive study.

Previous studies of the genus *Colura* in Malesian region and adjacent areas

The study of the genus *Colura* in Tropical Asia was started with an account of *Colura* worldwide which includes Asia and Oceania regions (Stephani 1916), and at that time Stephani also proposed six species of *Colura* from these areas. Then, Jovet-Ast (1953) described and illustrated 23 *Colura* species in her monograph. Among these, 14 species belonging to five sections (*Colura*, *Gamolepis*, *Glotta*, *Harmophyllum*, and *Heterophyllum*) in Tropical Asia were proposed, and all eight species members belonging to sect. *Heterophyllum* were found in Southeast Asia. Later, Pócs (1996) investigated the epiphyllous liverworts worldwide. The results showed the highest species number (224 species) of epiphyllous liverworts represented in Malesia and the highest number of the genus *Colura* (28 species) was also reported from this region.

In Cambodia, Jovet-Ast (1958a) described a species, namely *C. fastigata* Jovet-Ast collected from Kampong Som. Then, Tixier (1975) conducted a preliminary study of bryophytes and furnished a species list of mosses (48 species) and liverworts (43 species) including three *Colura* species: *C. acroloba* (Prantl) Jovet-Ast, *C. conica* (Sande Lac.) K.I.Goebel, and *C. corynophora* (Nees, Lindenb. *et* Gottsche) Trevis.

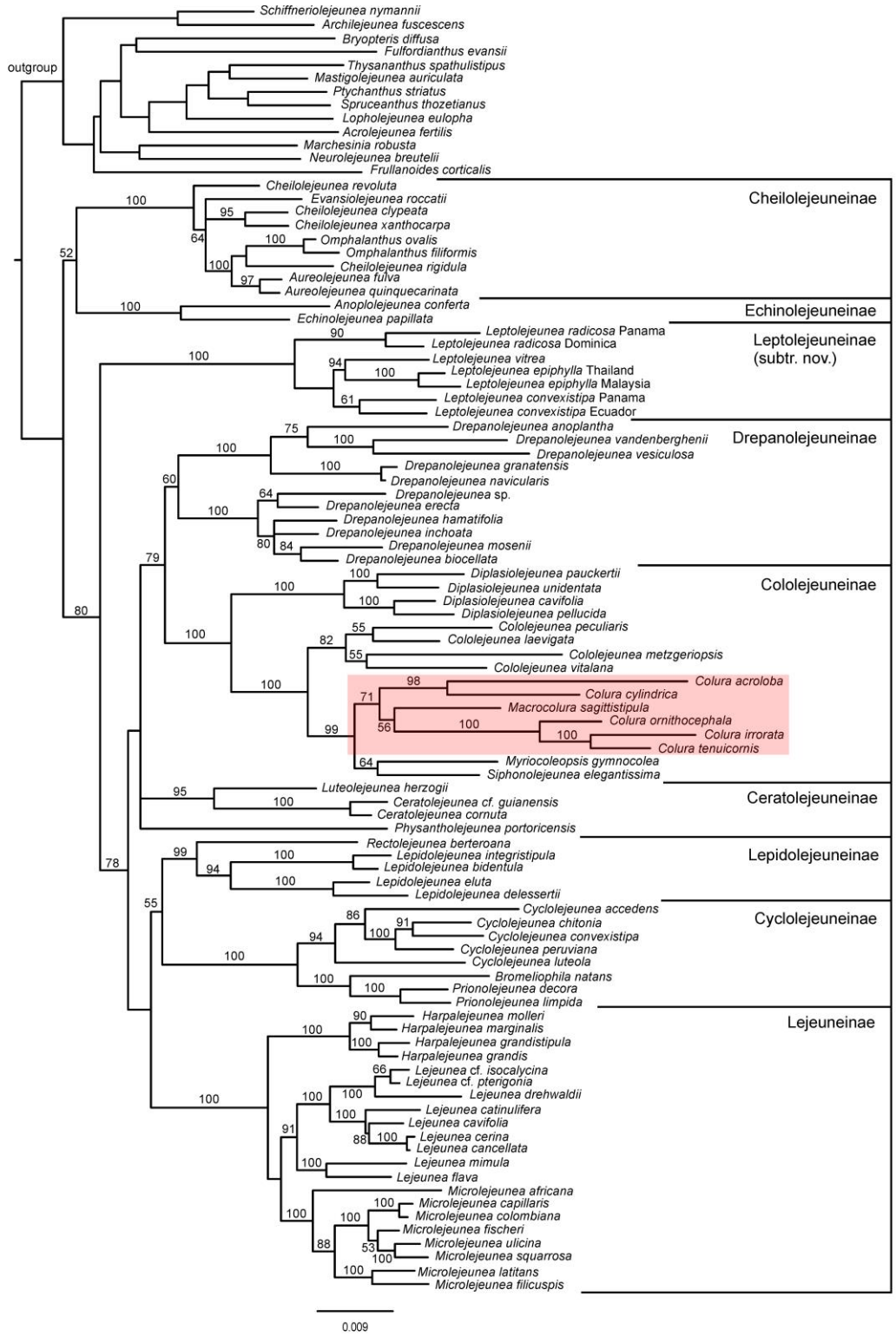

Fig. 1.1 Position of *Colura* in Lejeuneaceae phylogeny. Modified from Heinrichs *et al*. (2014a).

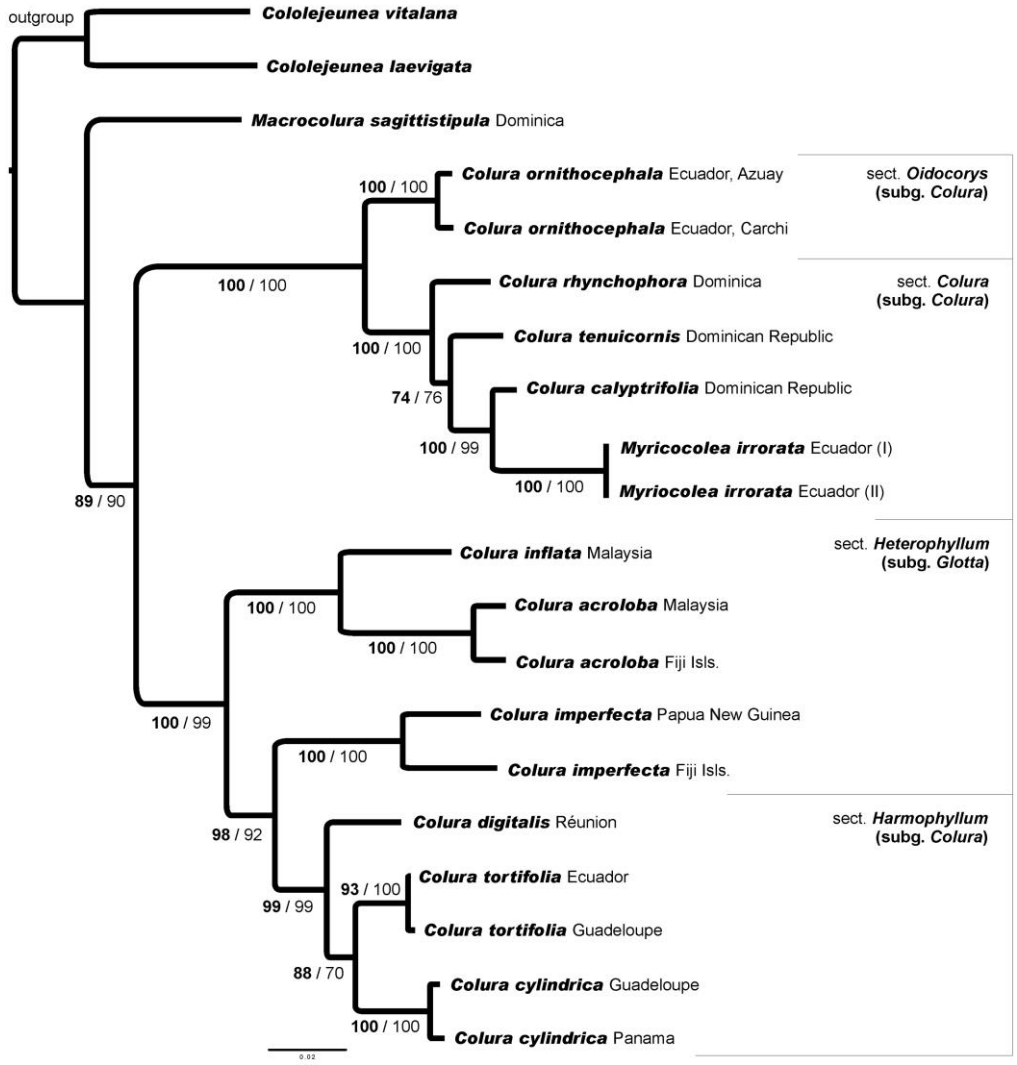

Fig. 1.2 Phylogeny of the genus *Colura*, showing four sections belonging to two subgenera and position of genus *Macrocolura*. Modified from Heinrichs *et al*. (2012).

For Chinese bryoflora, Zhu & So (2001) investigated epiphyllous liverworts. Seven species of *Colura* were reported along with the description of the genus and key to species. Wang *et al*. (2011) updated checklist of liverworts and hornworts in Taiwan. The present list contains 512 species of liverwort belonging to 116 genera in 52 families, of which three species of *Colura*, *viz*., *C. acroloba*, *C. inuii* Horik. and *C. tenuicornis* (A.Evans) Steph. were included. Two year later, Yang *et al*. (2013) revised the genus *Colura* in Taiwan, two more additional species, namely *C.*

calyptrifolia and *C. conica* were reported. Full descriptions and key to species of *Colura* in Taiwan were also given.

For Indian bryoflora, seven species of *Colura* were reported, including *C. acroloba*, *C. apiculata* (Schiffn.) Steph. (as *C. leratii* (Steph.) Steph.), *C. ari* (Steph.) Steph., *C. calyptrifolia*, *C. conica*, *C. pluridentata* Jovet-Ast, and *C. tenuicornis* (Lal 1977, 2003, Udar & Awasthi 1985, Singh 1996, Asthana & Shukla 2010, Singh & Barbhuiya 2012, Dey & Singh 2016).

For Indonesia, there are 16 *Colura* species were reported, including *C. acroloba*, *C. ari*, *C. apiculata*, *C. conica*, *C. corynophora*, *C. denticulata*, *C. hemisphaerica* Jovet-Ast, *C. herzogii* Jovet-Ast, *C. imperfecta* Steph., *C. inflata* K.I.Goebel, *C. junghuhniana* (Prantl.) Steph., *C. meijeri* Jovet-Ast, *C. mosenii* Steph., *C. ornata* K.I.Goebel, *C. superba* (Mont.) Steph., and *C. tenuicornis* (Sande Lacoste 1864, Stephani 1890, 1896, 1916, Schiffner 1893b, 1898, 1900, van Leeuwen 1936, Jovet-Ast 1953, 1954, Bonner 1963, Geissler & Bischler 1987, Pócs *et al*. 1994, Zhu & So 2001).

In Japan, Mizutani (1961) published the revision of Lejeuneaceae composing of *Colura tenuicornis* and *C. meijeri*. The key to species, descriptions, and illustrations were also equipped.

Pócs (2012) studied on small collections of epiphyllous liverworts from Laos and reported *Colura tenuicornis*, new for the country.

In Malaysia, Kitagawa (1969) collected hepatic samples from Penang, Malaysia and reported two species of *Colura*, *viz*., *C. acutifolia* Jovet-Ast and *C. corynophora*. Then, Chuah-Petiot (2011) provided the liverwort and hornwort checklist in Malaysia comprising 17 species of *Colura*. Recently, the investigation epiphyllous liverwort in Malay Peninsula reported three new species records of *Colura* (*C. brevistyla* Herzog., *C. mosenii*, and *C. speciosa* Jovet-Ast) (Pócs & Lee 2016).

Based on literature and field collections, Pócs (2013) reported 25 species of *Colura* in Papua New Guinea and neighboring areas. Of these, four new species were

described included: *C. koponenii* Pócs, *C. medusa* Eggers *et* Pócs, *C. mizutanii* Pócs, and *C. norrisii* Pócs.

Tan & Engel (1986) published the checklist of Philippine liverworts on the basis of previous reports, and six species of *Colura* were listed composed of *C. acroloba*, *C. ari*, *C. conica*, *C. corynophora*, *C. ornata*, and *C. palawanensis* Jovet-Ast.

The examinations of *Colura* in Sri Lanka (Ceylon) were started by Herzog (1921) describing *C. brevistyla*. After that, ten new species records of *Colura* in Sri Lanka were found continuously, namely, *C. acroloba*, *C. ari*, *C. calyptrifolia*, *C. conica*, *C. corynophora*, *C. greig-smithii* Jovet-Ast, *C. meijeri*, *C. ornata*, *C. tenuicornis*, and *C. verdoornii* Herzog *et* Jovet-Ast (Jovet-Ast 1953, Onraedt 1979, 1981, Eggers & Schäfer-Verwimp 1987).

For bryoflora of Thailand, Lai *et al*. (2008) published an updated checklist of liverworts and hornworts in Thailand. Within the account, there are six species of *Colura*, *viz*., *C. acroloba*, *C. conica*, *C. corynophora*, *C. siamensis* Jovet-Ast, *C. superba* and *C. tixieri* Jovet-Ast. Then, Chantanaorrapint & Pócs (2014) enumerated the liverwort taxa new to Thailand in which four additional *Colura* species, *C. apiculate* (as *C. leratii*), *C. brevistyla*, *C. ornata*, and *C. pallida* Steph., were also recorded. Later, Pócs & Podani (2015) reported *C. ari* and *C. imperfecta* from southern Thailand.

For Vietnam bryoflora, Pócs & Ninh (2005) collected the hepatic plants on the biodiversity framework (ASEAN-ARBC) from Vu Quang Nature Reserve in central Vietnam, and *Colura brevistyla* was found as a new record to Vietnam. Later, Pócs & Ninh (2012) reported epiphyllous liverworts from Cát Tiên National Park, southern Vietnam. They found 21 species of epiphyllous liverworts including two species of *Colura*, *viz*., *C. conica* and *C. ornata*, the latter was a new for bryoflora of Vietnam. Pócs *et al*. (2013) examined epiphyllous liverworts in Bidoup-Núi Bà National Park, central Vietnam; two species of *Colura* were found: *C. acroloba* and *C. superba*. Lately, Shu *et al*. (2017) updated checklist of liverworts and hornworts in Vietnam and reported 17 species of *Colura* included one new record, *C. inuii*.

As the conclusion, the numbers of species reported in Malesian region and adjacent areas were enumerated in Table 1.1.

Table 1.1 The species number of *Colura* recorded in Malesia and adjacent areas.

Country	Number of species recorded	References
Cambodia	4	Jovet-Ast (1958a), Tixier (1975)
China	8	Zhu & So (2001), Wang *et al*. (2011), Yang *et al*. (2013)
India	7	Lal (1977, 2003), Udar & Awasthi (1985), Singh (1996), Asthana & Shukla (2010), Singh & Barbhuiya (2012), Dey & Singh (2016)
Indonesia	16	Sande Lacoste (1864), Stephani (1890, 1896, 1916), Schiffner (1893b, 1898, 1900), van Leeuwen (1936), Jovet-Ast (1953, 1954), Bonner (1963), Geissler & Bischler (1987), Pócs *et al*. (1994), Zhu & So (2001)
Japan	2	Mizutani (1961)
Laos	1	Pócs (2012)
Malaysia	20	Kitagawa (1969), Chuah-Petiot (2011), Pócs & Lee (2016)
Philippines	6	Tan & Engel (1986)
Papua New Guinea	25	Pócs (2013)
Sri Lanka	11	Herzog (1921), Jovet-Ast (1953), Onraedt (1979, 1981), Eggers & Schäfer-Verwimp (1987)
Thailand	12	Lai *et al*. (2008), Chantanaorrapint & Pócs (2014), Pócs & Podani (2015)
Vietnam	17	Pócs & Ninh (2005, 2012), Pócs *et al*. (2013), Shu *et al*. (2017)

Some taxonomic problems in the genus *Colura*

Although a comprehensive taxonomic revision of *Colura* has been done by Jovet-Ast (1953) and various regional treatments were published (e.g. Jovet-Ast 1958b, 1961, 1983, Zhu & So 2001, Grolle & Zhu 2002, Pócs & Eggers 2007, Pócs 2013), many taxonomic problems of the genus still remain. Several species show

morphological similarities among them, for example in *C. hemisphaerica* and *C. cymbalifera* Herzog *et* Jovet-Ast in which distinguished morphological characters of these two species were remarked (Jovet-Ast 1953). Moreover, there is one species complex which displays the ambiguous boundaries between species that is *Colura inflata* complex, including *C. inflata*, *C. corniantha* Grolle, and *C. siamensis*. The three species in this complex share the common characters of heterophyllous leaves and strongly inflated perianth-keels; however, *Colura corniantha* differs from *C. inflata* in having apical teeth at perianth-keels (absent in *C. inflata*) (Jovet-Ast 1961). *Colura siamensis* differs from *C. inflata* in saccate leaves often smaller than non-saccate leaves (saccate leaves as large as non-saccate leaves in *C. inflata*) and leaf margin slightly entire to dentate (denticulate in *C. inflata*) (Jovet-Ast 1967a). Jovet-Ast (1967a) mentioned that these three closely related species may be conspecific, thus additional specimens and molecular data are needed for the species delimitation within the complex. Fortunately, this complex group is distributed from South Vietnam, Northeast Thailand to Indonesia (Sumatra); consequently, the additional materials can be collected for investigation.

Moreover, Schuster (1984) mentioned two characters of *C. lyrata* Steph. (species belongs to sect. *Lingua* subsect. 1 by Jovet-Ast (1953)) distinguished from other species in the genus by bilateral asymmetry underleaves and botryoidal oil bodies. Later, he treated *C. lyarata* under the new generic name, *Macrocolura* in 1992. However, the genus *Macrocolura* was invalid at first, so it was validated by Schuster (1994) with the Latin description. Nevertheless, Schäfer-Verwimp (1999) demonstrated that the botryoidal oil bodies of *Macrocolura lyrata* (Steph.) R.M.Schust. cannot serve for the generic separation because this type of oil bodies can be also found in some *Colura* species (Gradstein *et al*. 1977, Kis & Pócs 1997) as well as the underleaf character does not warrant generic separation as different types of underleaves also occur in other genera, such as *Diplasiolejeunea*. Therefore, Schäfer-Verwimp (1999) rejected Schuster's treatment in his work. There are some molecular works which include *Macrocolura lyrata* and a few *Coulra* species in the phylogenetic analyses (Heinrichs *et al*. 2012, 2014a, 2014b, Gradstein *et al*. 2018). The results revealed that *Macrocolura lyrata* was placed sister to *Colura* clade (Fig.

1.2). For resolve the taxonomic position, it should be reinvestigated by expanding the number of the *Colura* specimens (Heinrichs *et al*. 2012).

Study area

The Malesian region is located in the Southeast Asia. Based on the recent definition, this area comprised Borneo, Cocos Island, Java, Lesser Sunda Island, Malaya, Maluku, Philippines, Sulawesi, Sumatra and Christmas Island (Brummit 2001). However, Thai Peninsula is also included for this work. The northern border of Malesian region is between the Philippines and Taiwan, and the southern boundary is between Lesser Sunda and Australia. The western border is between Sumatra and Nicobar Islands. The most eastern of Malesian region used to include Papua New Guinea (van Steenis 1950), but in the present definition, the Papua New Guinea was excluded (Brummit 2001). Thus, the eastern limit of the Malesian region is between Maluku and New Guinea (Fig. 1.3).

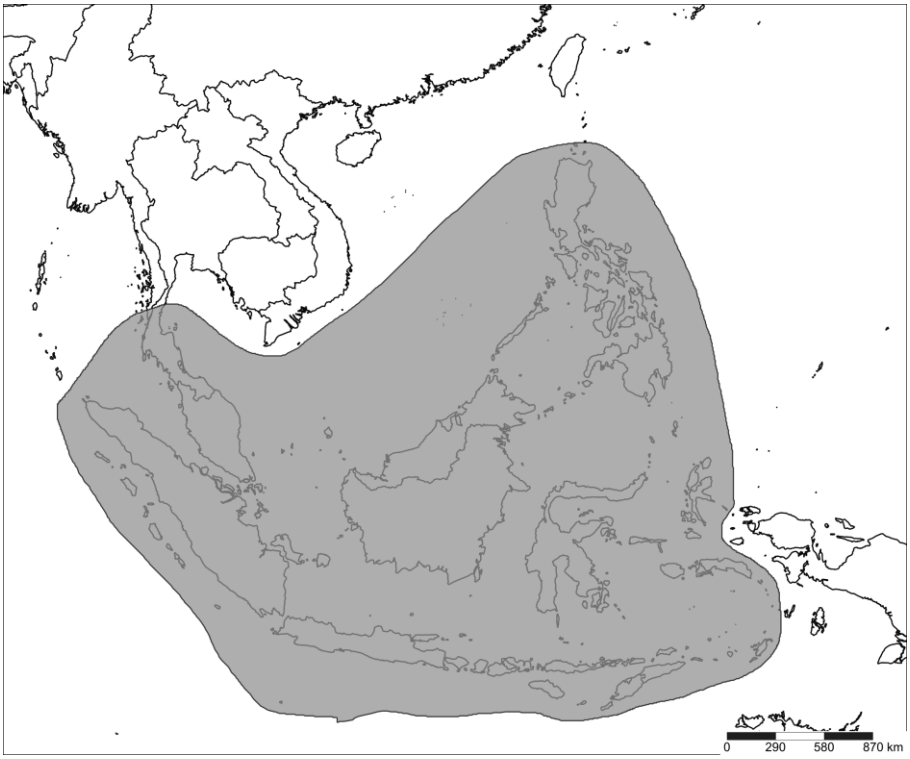

Fig. 1.3 Outline map showing the Malesian boundary adapted from Brummit (2001). Map was created with SimpleMappr (http://www.simplemappr.net).

Moreover, the Malesia is the phytogeographic region consists of three biodiversity hotspots, *viz*., Sundaland, Philippines and Wallacea (Fig. 1.4) (Myers *et al*. 2000, Woodruff 2010). The great variation in topographic features of Malesian region has resulted in a large diversity of plant communities rich in microhabitats for bryophytes (Pócs 1982). Besides, the most areas within this region have an everwet climate (van Welzen *et al*. 2005). Hence, the number of epiphyllous and corticolous liverwort taxa must be higher than other areas (Gradstein & Pócs 1989, Pócs 1996). According to the investigation of the epiphyllous liverwort diversity by Pócs (1996), the highest species number, both total (28 species) and endemic (6 species), of *Colura* was also found in Malesian region. Hence, this area is interesting for revising the genus.

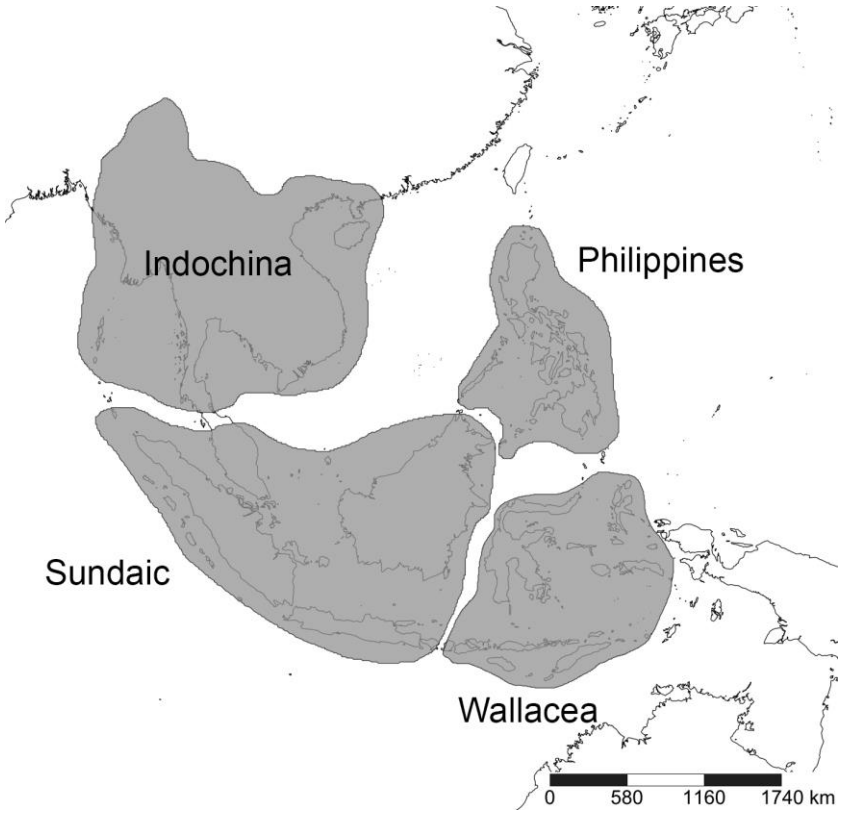

Fig. 1.4 Outline map of Southeast Asia showing the four biodiversity hotspots. According to some authorities the Indochina and Sundaic (Sundaland) bioregions meet on the Thai-Malay peninsula at the Kangar-Pattani Line; others place the transition near the Isthmus of Kra. The Sundaic and Wallacea bioregions meet at Wallace's Line between Borneo and Sulawesi (Modified from Woodruff 2010). Map was created with SimpleMappr (http://www.simplemappr.net).

Objectives

1. To examine species delimitation with *Colura inflata* complex.

2. To reinvestigate the infrageneric classification of *Colura* based on the molecular and morphological data.

3. To revise the genus *Colura* in Malesian region based on herbarium specimens and recent collections from the field surveys.

4. To provide a key constructed for identifying species within the genus *Colura* in Malesian region together with detailed descriptions and line drawing of all taxa.

CHAPTER 2

MORPHOLOGY AND ANATOMY

2.1 Introduction

The molecular phylogenetic data revealed that the genus *Colura* is closely related with genus *Macrocolura* within subtribe Cololejeuneinae (Gradstein *et al*. 2003, Gradstein 2013). The genera belonged to this subtribe shared synapomorphies, that are the narrow transverse leaf insertion and broadly quadrate-shaped sporangial hinge (Gradstein 2013).

The genus *Colura* differs from *Macrocolura*, the most closely related genus by insertion of underleaves being invertedly J-shaped, asymmetrical underleaves, and rhizoid fascicule originating at the middle of underleaves (Grolle & Zhu 2002). *Colura* is also morphologically similar to *Diplasiolejeunea* by stem consisting of 7 cortical and 3 medullary cells in transection, branching of *Lejeunea*-type, one bilobed underleaf per each leaf, and asexual reproduction by discoid gemmae; nevertheless, the genus *Colura* differs from the other one by the presence of enlarged lobule sac at the lobule apex and the presence of a valve covering a sac pore (Zhu & So 2001).

Jovet-Ast (1954) discussed about lobule valve of *Colura* comparing with valve of genus *Pleurozia*. She suggested that their valve characters are strongly similar in morphology and physiology, even though those two genera are not closely related. She also mentioned that *Pleurozia*'s valve shares similarity with valve of *Colura* sect. *Lingua* (=sect. *Glotta*) in having large size consisting of many cells and the absence of hinge cells; this may indicate that valves of species within sect. *Lingua* are the most primitive in the genus.

Even though the genus *Colura* had been monographed by Jovet-Ast (1953), the reproductive organs and sporophytes of many species are still unknown, and oil bodies are problematic to examine in the dried herbarium specimens. Therefore, the investigation both gametophyte and sporophyte features from fresh materials are essential and useful for classification and identification in generic and species levels.

2.2 Morphological and anatomical study

2.2.1 Plant materials

Morphological and anatomical details of all *Colura* species in the present study were described based on herbarium vouchers and field survey specimens in Malesia.

Herbarium specimens, including types, of Malesian *Colura* housed in BCU, BKF, BM, BO, CMU, E, EGR, HSNU, JE, KLU, L, MO, PC, and SING were investigated (herbarium code following Thiers (2018)). Moreover, explorations and field surveys were carried out in Thailand and some places in Peninsular Malaysia and Indonesia (Java), between June 2013 and January 2018. The study sites were selected based on previous reports and other unexplored areas where provided the appropriate habitats from lowland to highland montane rainforest.

2.2.2 Laboratory study

All specimens of the genus *Colura* were examined with the Olympus SZH10 stereo and Olympus CH30 upright microscopes. The morphological characters of all species were observed, measured, and described. Illustrations of significant characters of all species were made with the upright microscope with an attached Olympus drawing tube. Vegetative and reproductive structures were taken from mature plants. The specimens were turgid by a drop of water before measurement and illustration. The measurements always represent the observed morphological variation of plants.

Some microcharacters, e.g., leaf surface and spore ornamentation were examined with a FEI Quanta 400 scanning electron microscope (SEM). All of specimens were prepared by dissection and dehydration before placing them in critical point drying machine (CPD). After that, the dried specimens were mounted on double-stick cellophane adhesive tape affixed on stubs. Then, the specimens were plated with a thin layer of gold and examined by the SEM.

2.3 Results

Growth habit

The member of genus *Colura* in Malesian region commonly occur in loose to dense mats on living leaves (Fig. 2.1A–E). However, the highland species such as *C. calyptrifolia*, *C. hemisphaerica* (Fig. 2.1F), *C. junghuhniana*, *C. karstenii* (Fig. 2.1G), *C. tenuicornis*, and *C. valida* (Fig. 2.1H) can usually be found growing on branches or bark of tree trunks.

Colour and size

Plants are yellowish green or bright green to rarely dark green (*C. meijeri*, *C. karstenii*, Fig. 2.1G) when fresh. When drying, they become pale or dark brown. Most species of *Colura* in Malesian region are rather small and delicate plants, usually less than 2 mm wide. The smallest species is *C. medusa* (0.4–0.56 mm wide) and the largest is *C. karstenii* (2–5 mm wide).

Rhizoids

Rhizoids are unicellular and colorless. They are produced by rhizoid initial cells at the base of underleaves (Fig. 2.3B).

Stems

For species of Malesian *Colura*, stems are yellowish-green to pale green in color and elliptic to circular in transverse section. The stems consist of 7 rows of cortical cells (epidermal cells) surrounding 3 medullary cells (Fig. 2.2). The cortical cells are usually larger than the medullary cells. The cortical cells are little or no thick-walled. Trigones and intermediate thickenings in cortical and medullary cells are distinctly small or absent. The ventral merophyte of the main stem is usually 2 cells wide in all *Colura* species.

Vegetative branching

The vegetative branches of *Colura* are *Lejeunea*-type, the branch originating from a cortical cell covered by the brace cells (the collar initial cells) (Crandall-

Stotler 1972). The base of lateral branch is surrounded by collar (gyrothecal) and branch diverges from the main stem axis at about 90° (Fig. 2.3).

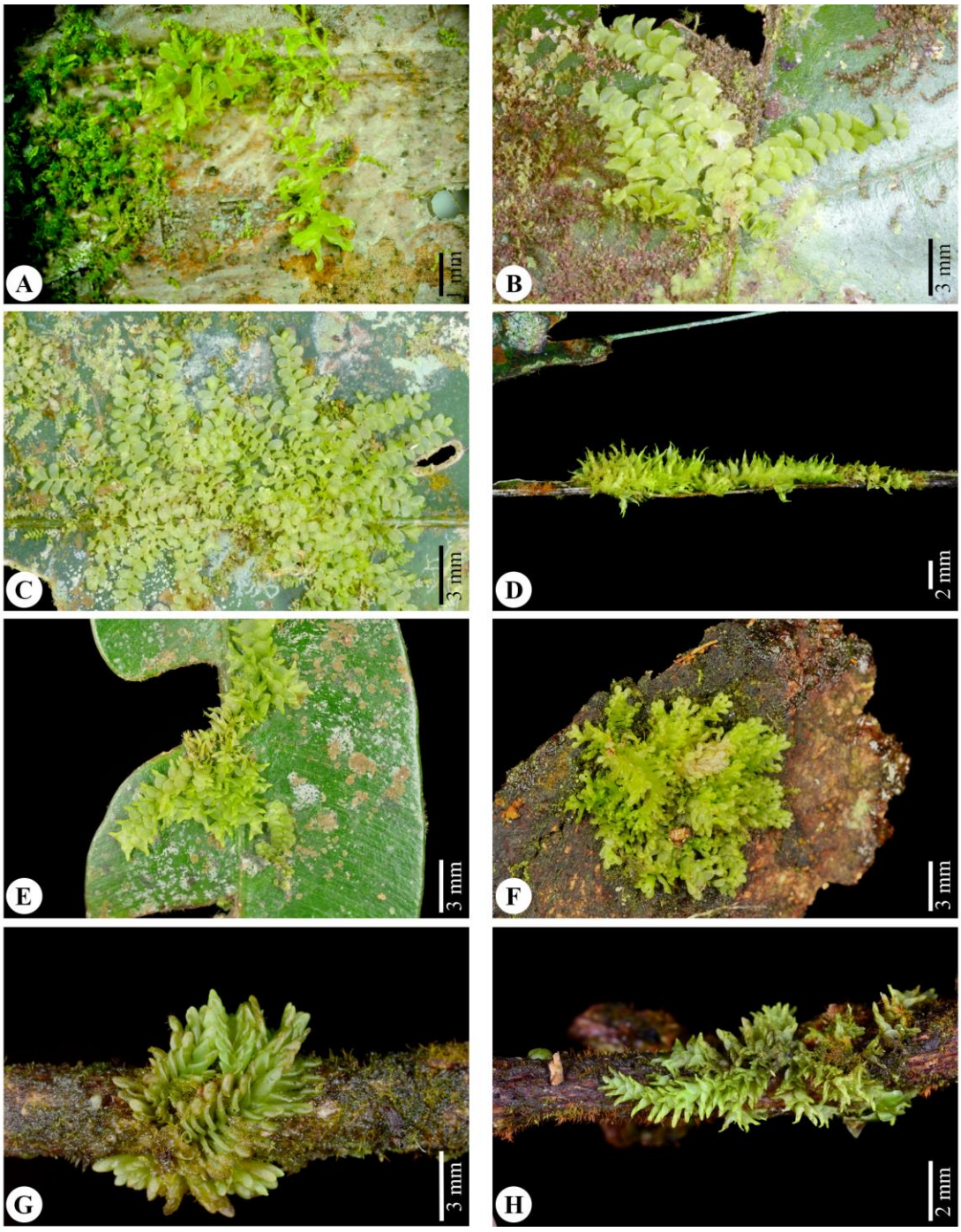

Fig. 2.1 Habitats and habits: A–E. Epiphylls, A. *Colura bisvoluta*, B. *C. conica*, C. *C. corynophora*, D. *C. pluridentata*, E. *C. verdoornii*. F–H. Epiphytes, F. *C. hemisphaerica*, G. *C. karstenii*, H. *C. valida*.

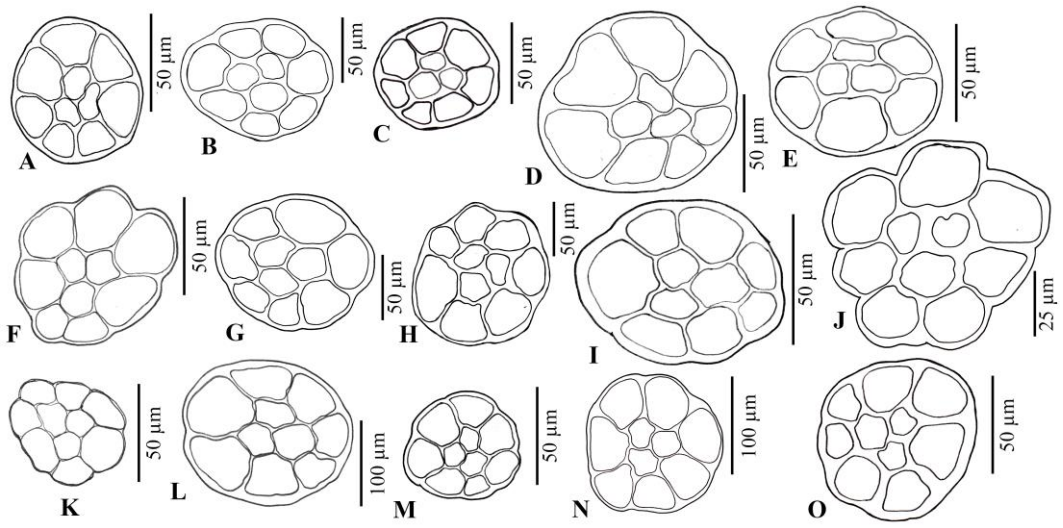

Fig. 2.2 Stems in transection showing 7 cortical and 3 medullary cells: A. *Colura acroloba*, B. *C. ari*, C. *C. bisvoluta*, D. *C. clementis* Grolle, E. *C. corynophora*, F. *C. cristata*, G. *C. denticulata*, H. *C. hemisphaerica*, I. *C. junghuhniana*, J. *C. karstenii*, K. *C. medusa*, L. *C. meijeri*, M. *C. sigmoidea*, N. *C. valida*, O. *C. verdoornii*.

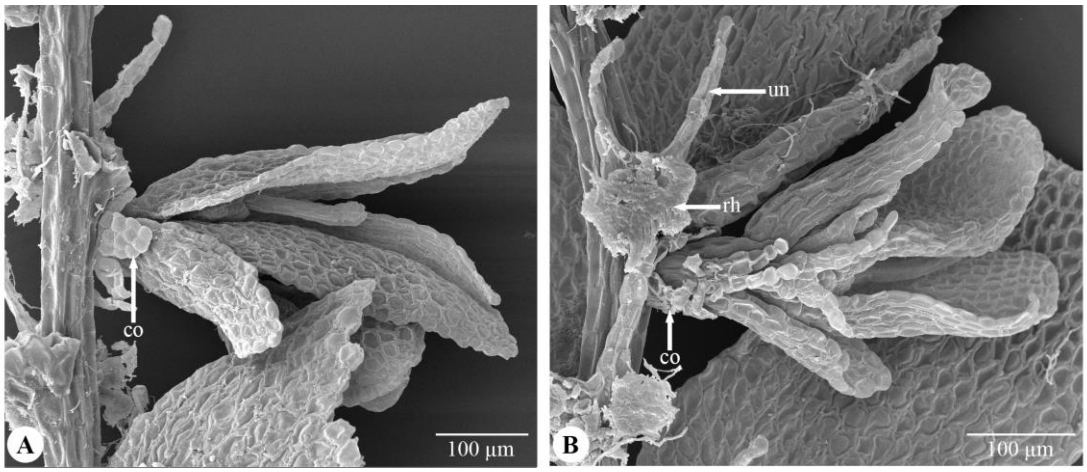

Fig. 2.3 Branching of *Colura acroloba* under Scanning Electron Microscope (SEM) investigation showing lateral branch surrounded by collar (co): A. Dorsal view, B. Ventral view (rh = rhizoid, un = underleaf).

Lateral leaves

The lateral leaves in the genus are incubous insertion (Fig. 2.4) like other genera in Lejeuneaceae. Leaf arrangements are variable in contiguous or remote to

imbricate. The mature leaf is divided into a dorsal lobe and a lobule. Leaf lobes vary in sizes and shapes. The dorsal margins of leaf lobe are entire (Fig. 2.5B, 5D & E, 5G, 5I & J), crenulate (Fig. 2.5C), denticulate to dentate (Fig. 2.5A, 5H, 5K–P) and they may be flat to undulate; nonetheless, the dorsal margins are revolute in *C. bisvoluta* and *C. karstenii* (Fig. 2.5F). Leaf lobules mostly form tubular portions at base and enlarge to be strongly inflated sacs at their tip. Leaf lobule usually fuses with leaf lobe forming a ridge cells (Fig. 2.6A & B) which are very distinct when tear the lobule out. Two leaf-types based on the presence/absence of lobule sac are proposed here as saccate and non-saccate leaves. On the other hand, lobules of non-saccate leaves are not formed tubular portions that differ from saccate leaves. Most *Colura* species have uniform lateral leaves with lobule sacs (saccate leaves) (Fig. 2.4A–C), but some species produce dimorphic lateral leaves consisting of saccate and non-saccate leaves on the same stem (Fig. 2.4D & E). Lobule sacs are variable in sizes and shapes and always have a pore in each sac.

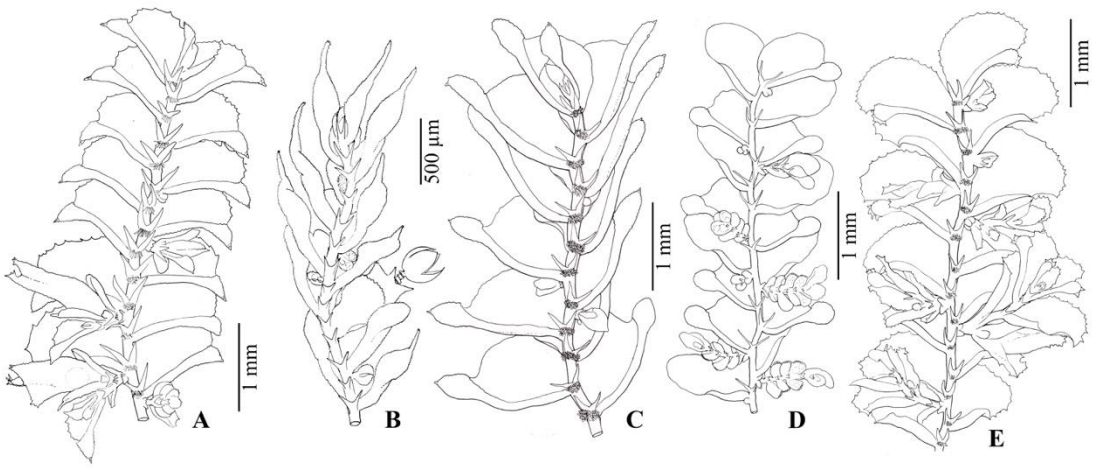

Fig. 2.4 Portions of plants in ventral view showing uniform lateral leaves (A–C) and dimorphic lateral leaves (D & E) with saccate and non-saccate leaves, A. *Colura ari*, B. *C. junghuhniana*, C. *C. verdoornii*, D. *C. corynophora*, E. *C. denticulata*.

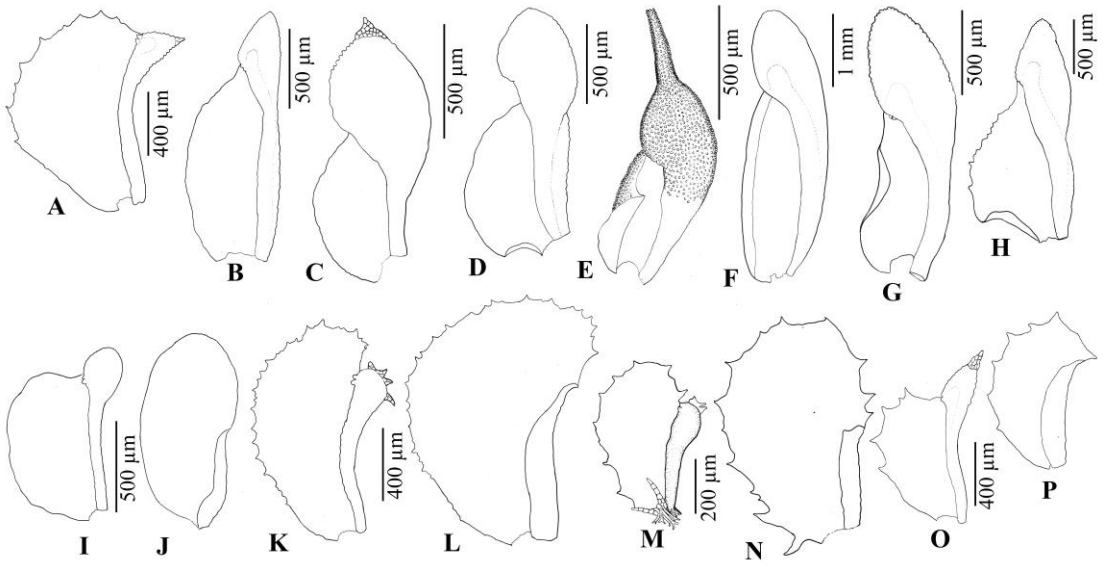

Fig. 2.5 Lateral leaves, ventral view: A–G. Uniform lateral leaves, A. *C. ari*, B. *C. clementis*, C. *C. cristata*, D. *C. hemisphaerica*, E. *C. junghuhniana*, F. *C. karstenii*, G. *C. meijeri*, H. *C. pallida*; I–P. Dimorphic lateral leaves, I & J. *C. corynophora*, K & L. *C. denticulata*, M & N. *C. imperfecta*, O & P. *C. palawanensis*.

Valves and valve frames

Valve is a door-like structure located inside the lobule sac (Fig. 2.6C & D). Valves are usually subtended by valve frames for covering the sac pore. Valves are composed of two types of cells: hyaline marginal and median chlorophyllose cells. The hyaline marginal cells are always colorless due to the lack of chloroplasts, but the median cells are green and obviously distinguished by having chloroplasts and thick-cell walls. However, the basal cells of hyaline margin may be found short and horizontally elongated; some types of valve have two elongated basal hyaline cells which lie on the left- and right-hand sides of each valve, and the elongated basal hyaline cells of some valve types can be connate to form a hyaline bordered. The hinge cells are green cells of fused-lobule, arranged near the base of each valve. Hyaline papillae are always present near the base of valve in saccate leaf (Fig. 2.6D, 7A–N). Hyaline papillae are spherical to bulbous.

According to Jovet-Ast (1953), the valve type is the important character for classification and identification within the genus *Colura*. In this work, four valve types were classified as following:

1. Type *a*: this type is characterised by the absence of hinge and basal median cells or not differentiated. Moreover, the basal hyaline marginal cells can be similar to the upper hyaline marginal cells (Fig. 2.7C & D). This type is found in *C. acroloba*, *C. corynophora*, *C. corniantha*, *C. galeata* Jovet-Ast, and *C. ornata*, or clearly distinct (Fig. 2.7A & B) in *C. bisvoluta* and *C. karstenii*.

2. Type *b*: this valve type is distinguished by a basal median cell of valve directly adnate to an upper hinge cell, and two elongated basal hyaline marginal cells also present. The basal hyaline marginal cells usually differ from the upper ones and are separated by basal median and hinge cells (Fig. 2.7E–H). This valve type is found in a few species, namely *C. cristata*, *C. hemisphaerica*, *C. meijeri*, *C. sigmoidea*, *C. valida*, and *C. verdoornii*.

3. Type *c*: this type is characterised by the basal median cells of valve not directly adnate to hinge cells but separated by hyaline bordered cells, hyaline bordered consisting of 2 rectangular cells, the presence of 3–5 hinge cells and 1–2 basal median cells (Fig. 2.7I–L). This type presents in most species found in Malesian region such as *C. ari*, *C. brevistyla*, *C. clementis*, *C. herzogii*, *C. pallida*, and *C. pluridentata*.

4. Type *d*: this type differs from the others by the basal median cells of valve not directly adnate to hinge cells, the presence of hyaline bordered cells, the hyaline bordered has only one linear cell, and the presence of 2 superimposed hinge cells and 2 basal median cells (Fig. 2.7M & N). This type is presented in the generic type, *C. calyptrifolia*, and a few others, namely *C. junghuhniana* and *C. tenuicornis*.

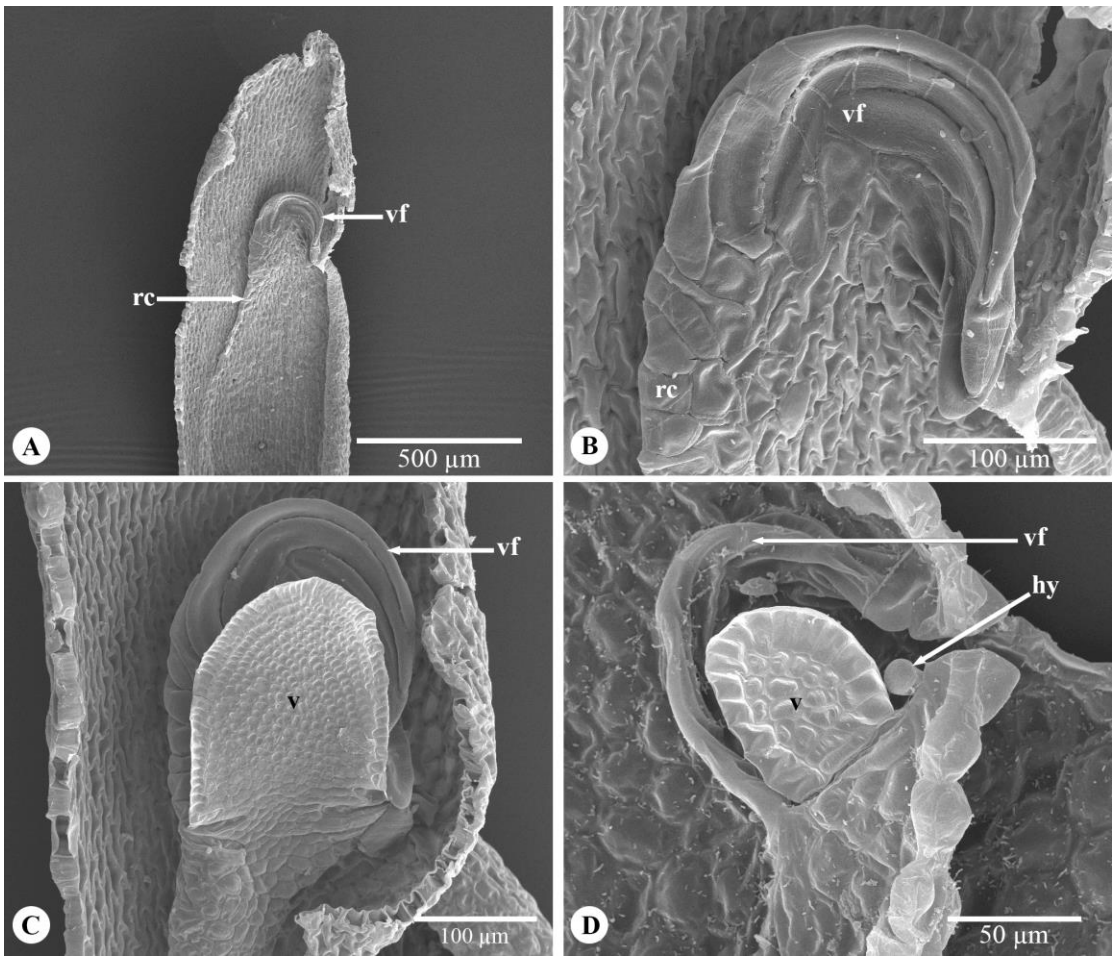

Fig. 2.6 Valves and valve frames of genus *Colura* investigating by SEM: A–C. *C. karstenii*, A. Teared leaf showing valve frame (vf) produced from ridge cells (rc), B. valve frame in high magnification, C. valve, simple-type, and its valve frame. D. *C. conica*, showing valve, complex-type, with valve frame and hyaline papilla cell (hy).

Valve frame is a semicircular (Fig. 2.8A & B) to hook-like structure (Fig. 2.8C & D) producing from protruded ridge cells that usually fit for subtending the valve. Cell walls of valve frame cells are smooth normally, but they can be nodulose in *C. karstenii* (Fig. 2.8A & B) and *C. denticulata* (Fig. 2.8C & D). However, valve frames are reduced in some species, such as *C. acroloba* (Fig. 2.8E & F), *C. corynophora*, *C. corniantha* and *C. inflata*.

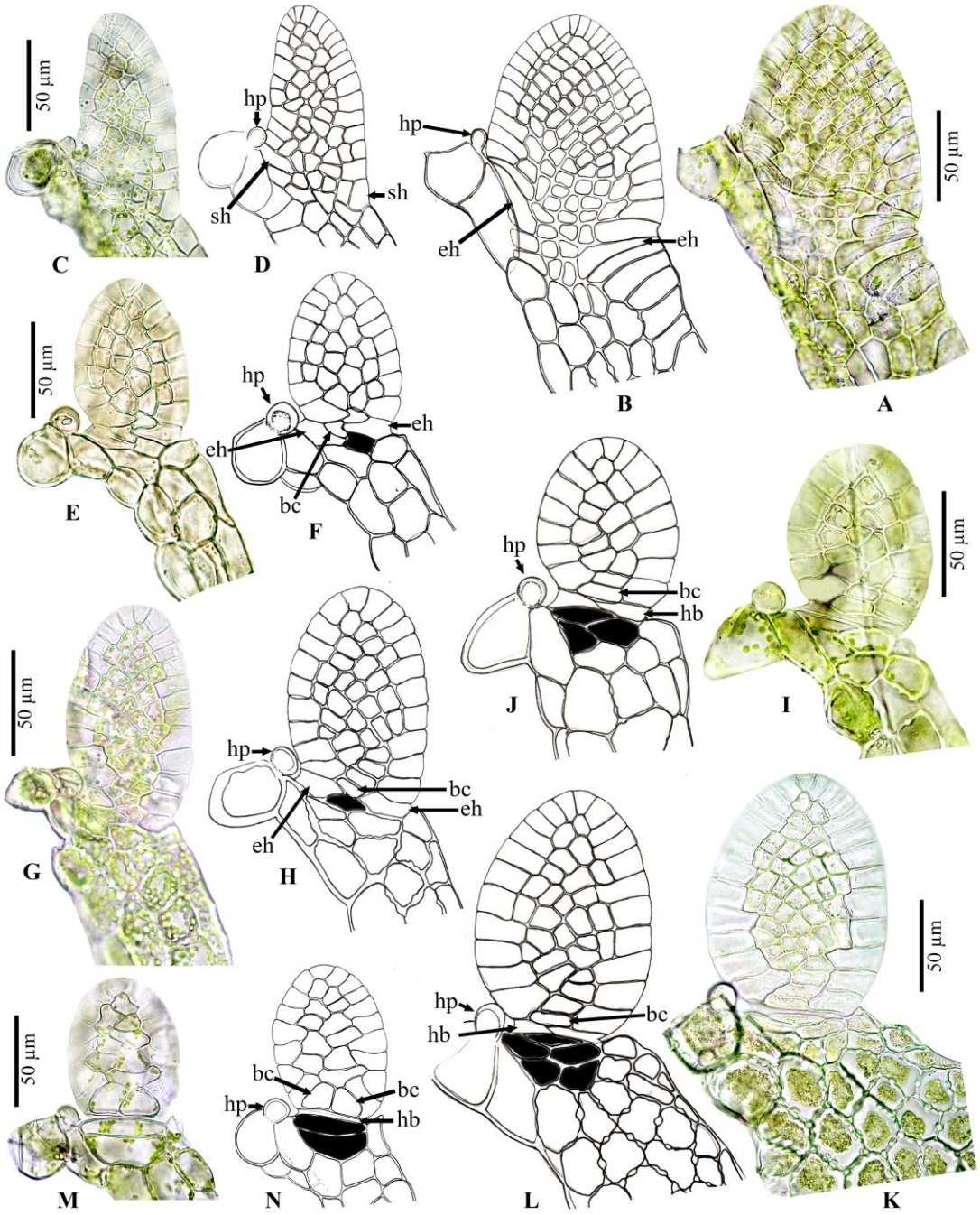

Fig. 2.7 Valve types: Type *a*; A & B. *C. bisvoluta*, C & D. *C. corniantha*. Type *b*; E & F. *C. sigmoidea*, G & H. *C. verdoornii*. Type *c*; I & J. *C. ari*, K & L. *C. hemisphaerica*. Type *d*; M & N. *C. tenuicornis*. (bc = basal median cell, hb = hyaline bordered, eh = elongated basal hyaline, hp = hyaline papilla, sh = shorted basal hyaline, dark cell is hinge cell).

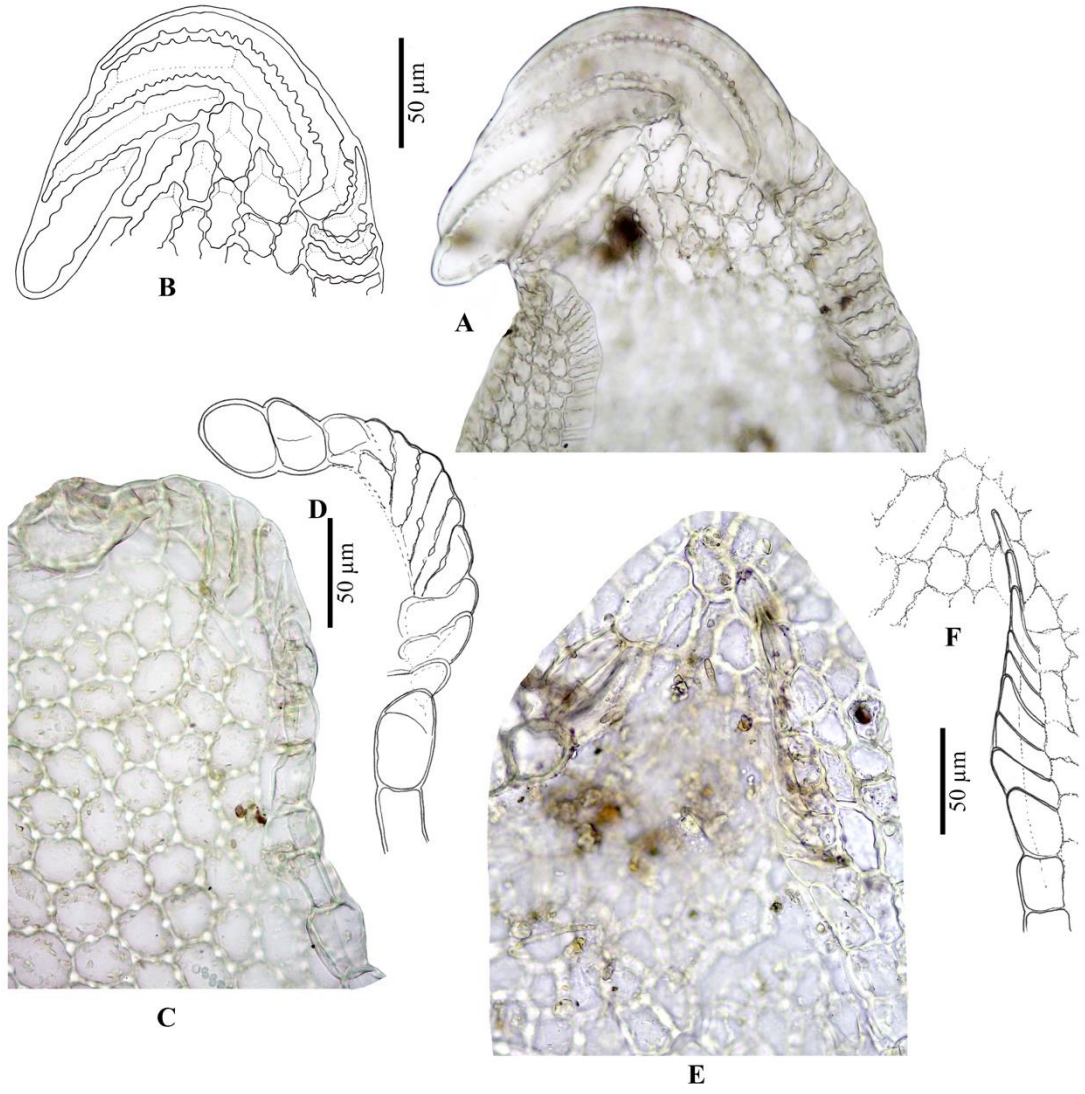

Fig. 2.8 Valve frames: A & B. Semicircular shape, *C. karstenii*. C & D. Hook-like shape, *C. denticulata*. E & F. Reduced valve frame, *C. acroloba*.

Leaf cells and oil bodies

Leaf lobe cells are varying in size and shape. They may be isodiametric, subquadrate, quadrate, rectangular, or hexagonal. The median cells of leaf lobe are mostly rectangular, but they can also be isodiametric, subquadrate, and hexagonal. The basal cells are generally rectangular to hexagonal, and occasionally isodiametric to subquadrate. Cell walls are thin and colorless bearing trigone and intermediate thickening (Fig. 2.9D–G). In some species, nevertheless, the trigone and intermediate thickening are normally absent, i.e., *C. calyptrifolia* (Fig. 2.9A), *C. medusa* (Fig.

2.9B) and *C. tenuicornis* (Fig. 2.9C). The cuticle is smooth in all species. The leaf lobe surfaces of *Colura* species are generally mamilose (Fig. 2.10A–C). However, the papillose projections on the dorsal surface of leaf lobe are found in *C. junghuhniana* (Fig. 2.10D & E), *C. medusa*, and *C. maxima* Jovet-Ast.

Oil bodies present in all cells of leaves and stems, except in the hyaline cells. Based on the investigation, two types of oil bodies were found: homogenous (Fig. 2.11A & B) and compound (Fig. 2.11C–H). Oil bodies of *Colura* are colorless or grayish ellipsoid in shape. The numbers of oil bodies are ranging from 10 to numerous per cell. Ocelli are lacking in this genus.

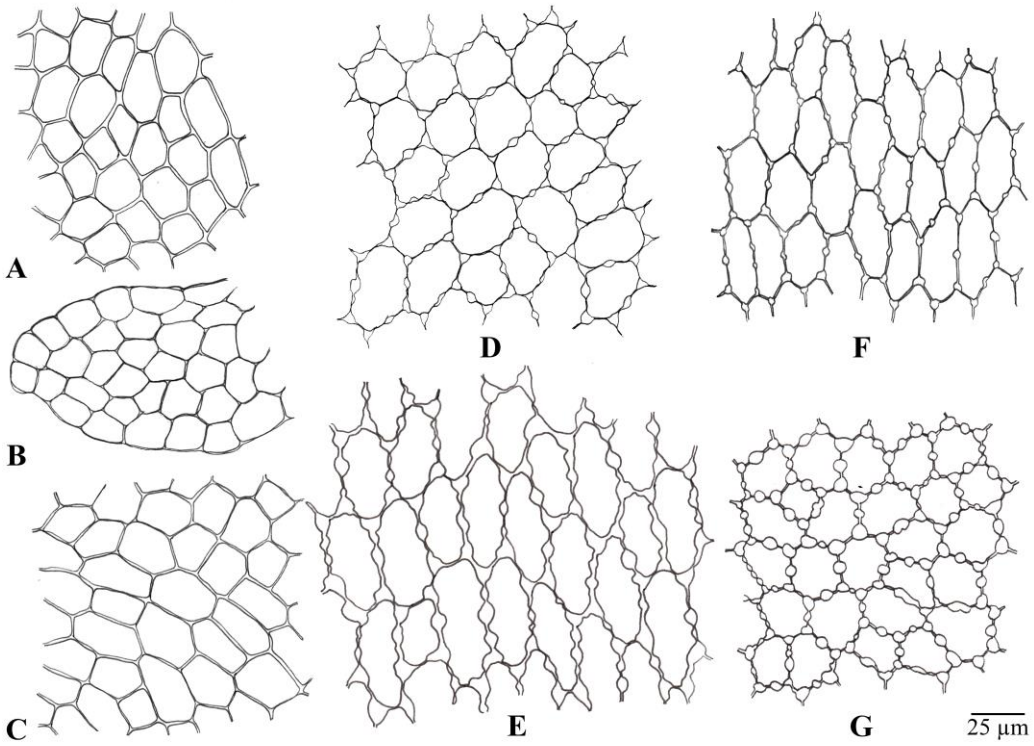

Fig. 2.9 Leaf cells: A–C. Cells without trigone and intermediate thickening, A. *Colura calyptrifolia*, B. *C. medusa,* C. *C. tenuicornis*. D–G. Cells with distinct trigone and intermediate thickening, D. *C. corniantha,* E. *C. karstenii*, F. *C. pluridentata,* G. *C. verdoornii*.

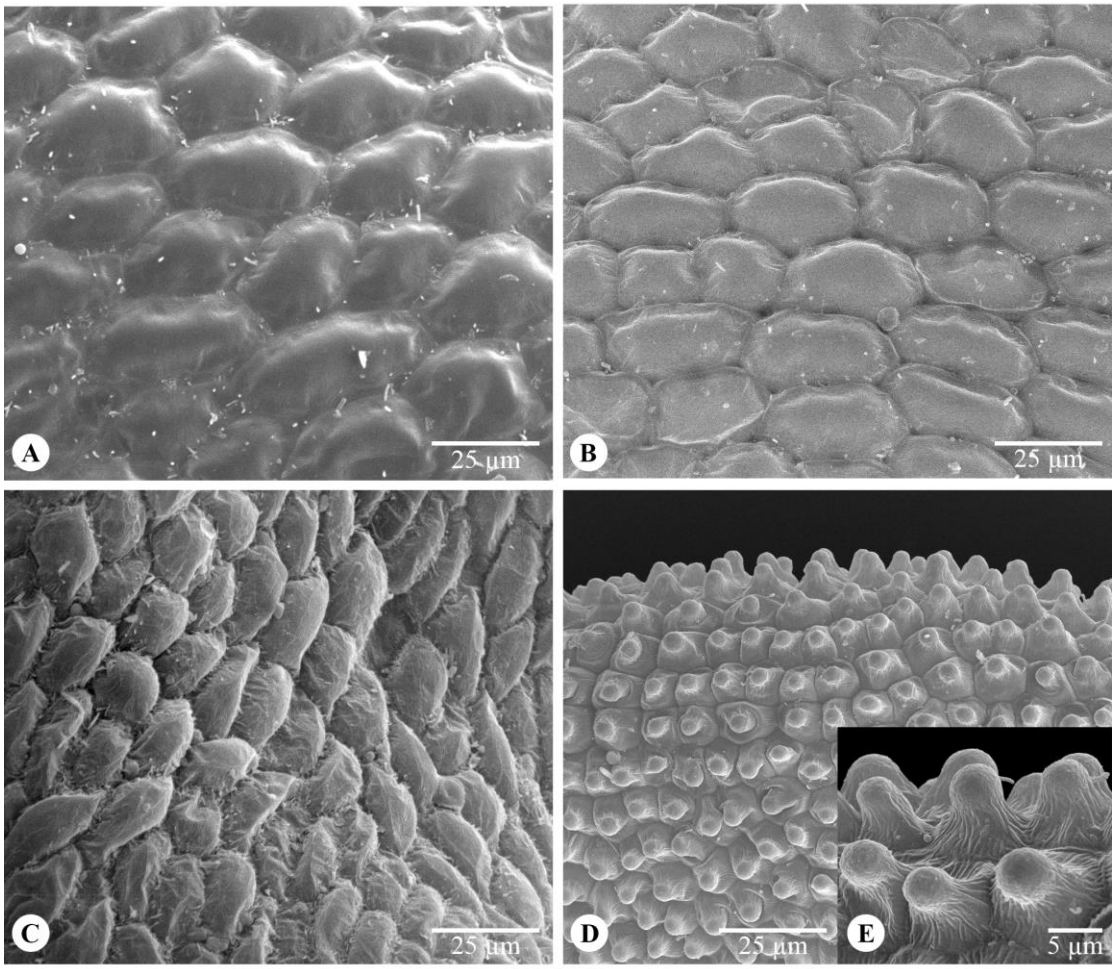

Fig. 2.10 Leaf cell surface under the SEM technique showing smooth cuticle: A–C. Mamillose cells, A. *C. conica*, B. *C. imperfecta*, *C. tenuicornis*. D & E. Papillose cells of *C. junghuhniana*, D. 1000× magnification, E. 5000× magnification.

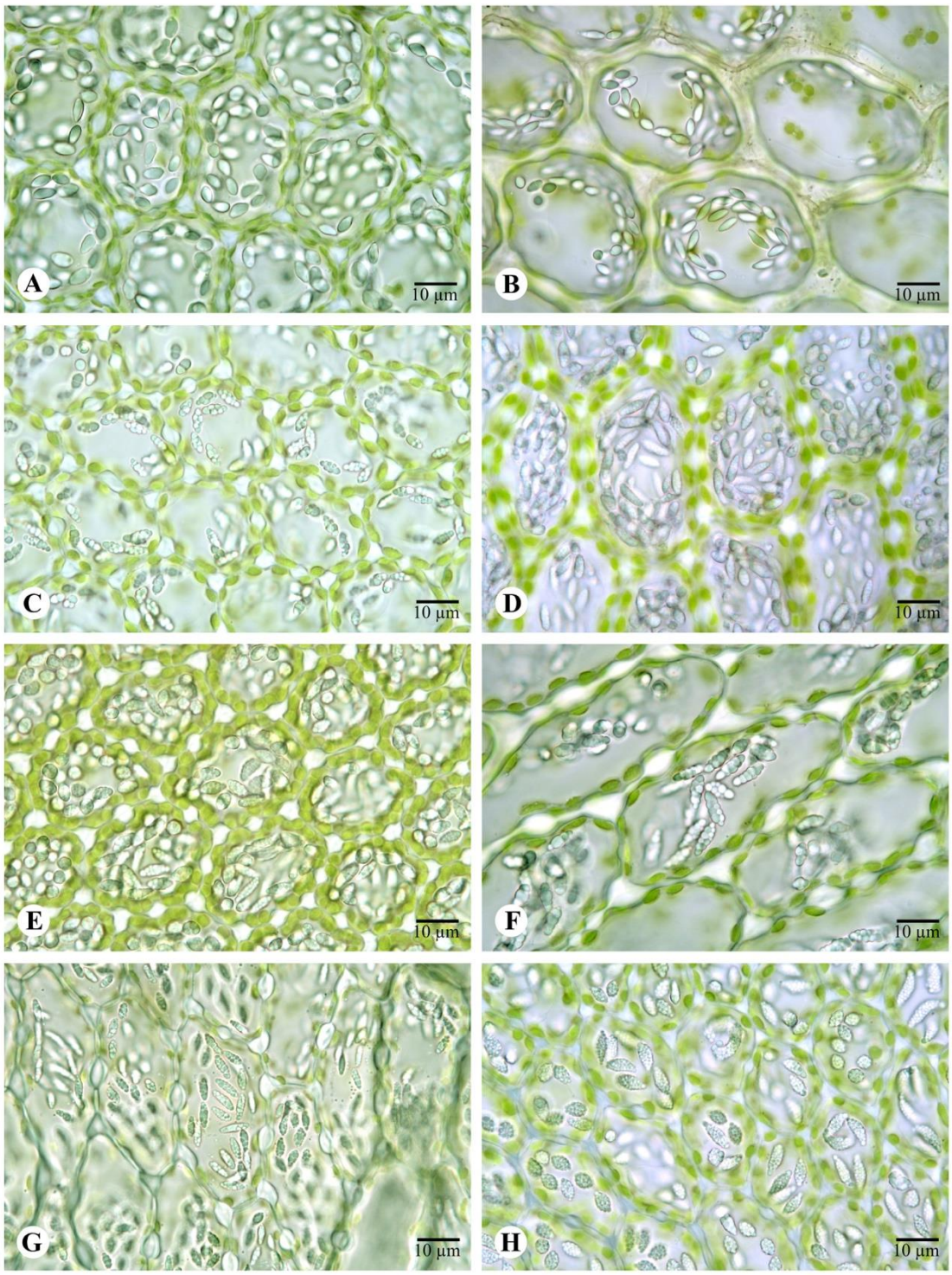

Fig. 2.11 Oil bodies of *Colura* species: A & B. Homogenous oil bodies, A. *C. hemisphaerica*, B. *C. valida*. C–H. Compound oil bodies, C. *C. acroloba*, D. *C. conica*, E. *C. corynophora*, F. *C. karstenii*, G. *C. pluridentata*, H. *C. speciosa*.

Underleaves

The underleaves or amphigastria in genus *Colura* are strongly bilobed. Moreover, the presence of one underleaf per one lateral leaf is a specific character which differs from the most genera in Lejeuneaceae (except for *Diplasiolejeunea* and *Macrocolura*). The sinus of underleaf is obtuse to acute. The underleaf lobes are roughly classified into two groups: 1) triangular to lanceolate lobe with 4–15(–22) cells long and (2–)4–9(–11) cells wide at base, e.g., *C. bisvoluta* (Fig. 2.12A), *C. hemispaherica* (Fig. 2.12B), *C. karstenii*, and *C. pallida* (Fig. 2.12D); and 2) filiform lobe with 4–8(–10) cells long and (1–)2–4 cells wide at base, e.g., *C. acroloba* (Fig. 2.12E), *C. corniantha* (Fig. 2.12F), *C. inflata* (Fig. 2.12G), and *C. palawanensis* (Fig. 2.12H). The latter type is recognized by having unseriate lobes. The vast majority of underleaf type in Malesian *Colura* is symmetrically triangular to lanceolate, except in *C. medusa* (Fig. 2.12C), which has asymmetrical underleaf.

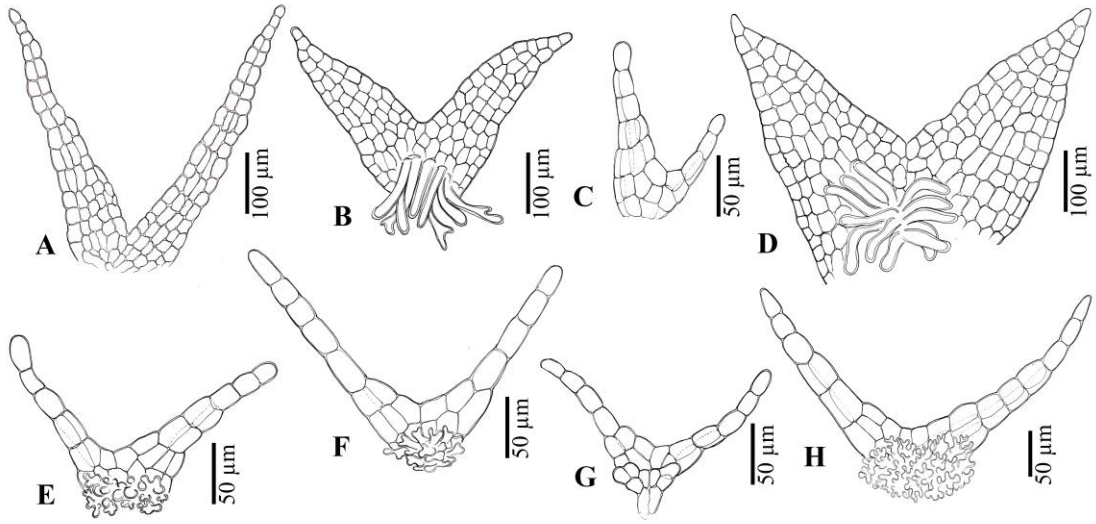

Fig. 2.12 The variation of underleaves in the genus *Colura*: A–D. Triangular to lanceolate lobe, A. *C. bisvoluta*, B. *C. hemisphaerica*, C. *C. medusa*, D. *C. pallida*. E–H. Filiform lobe, E. *C. acroloba*, F. *C. corniantha*, G. *C. inflata*, H. *C. palawanensis*.

Sexuality

In this study, three sexuality patterns were observed: autoicous (e.g., *C. ari*, *C. bisvoluta*, *C. imperfecta*, *C. inflata*, *C. jughuniana*, *C. tenuicornis*), dioicous (e.g, *C. crenulata*, *C. karstenii*, *C. meijeri*, *C. pluridenatata*, *C. sigmoidea*, *C. verdoornii*), and heteroicous was found in only one species, *C. acroloba*.

Androecia

The androecia are terminal or intermediate on main stems and lateral branches (Fig. 2.13A), consisting of 1–10(–20) pairs of male bracts. Male bracts are usually imbricate. The bract lobes are semi-circular, and their free margin are entire to crenulate (Fig. 2.14A); nonetheless, strongly dentate present in free margin of *C. imperfecta* (Fig. 2.14C) and *C. palawanensis* (Fig. 2.14G). The bract lobules are semi-circular to oblong, smaller than or as large as bract lobe. Apical keels of male bract are consistently crenulate with 1(–3) rows of projecting cells, but apical keels are sharply papillae in *C. junghuhniana* (Fig. 2.14F). The free margins of bract lobules are entire. There are two antheridia per male bracts. Male bracteoles vary greatly in size and shape occurring throughout the androecium (Fig. 2.13B, 14B, 14D, 14F, 14H).

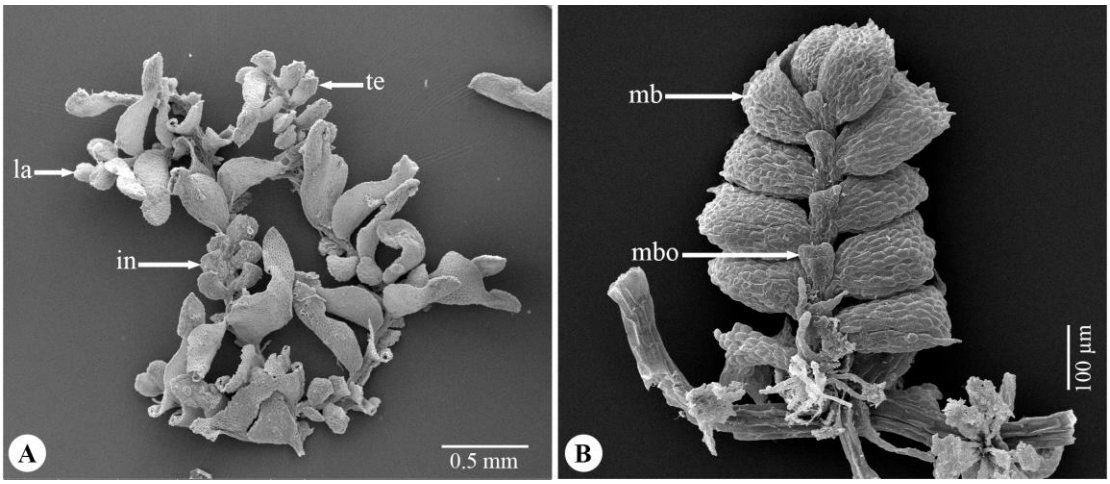

Fig. 2.13 Androecia of *Colura* species: A. Portion of *C. verdoornii* showing terminal (te), lateral (la) and intermediate (in) androecia. B. Androecium of *C. imperfecta* shows male bracts (mb) and male bracteoles (mbo) which present throughout the androecium.

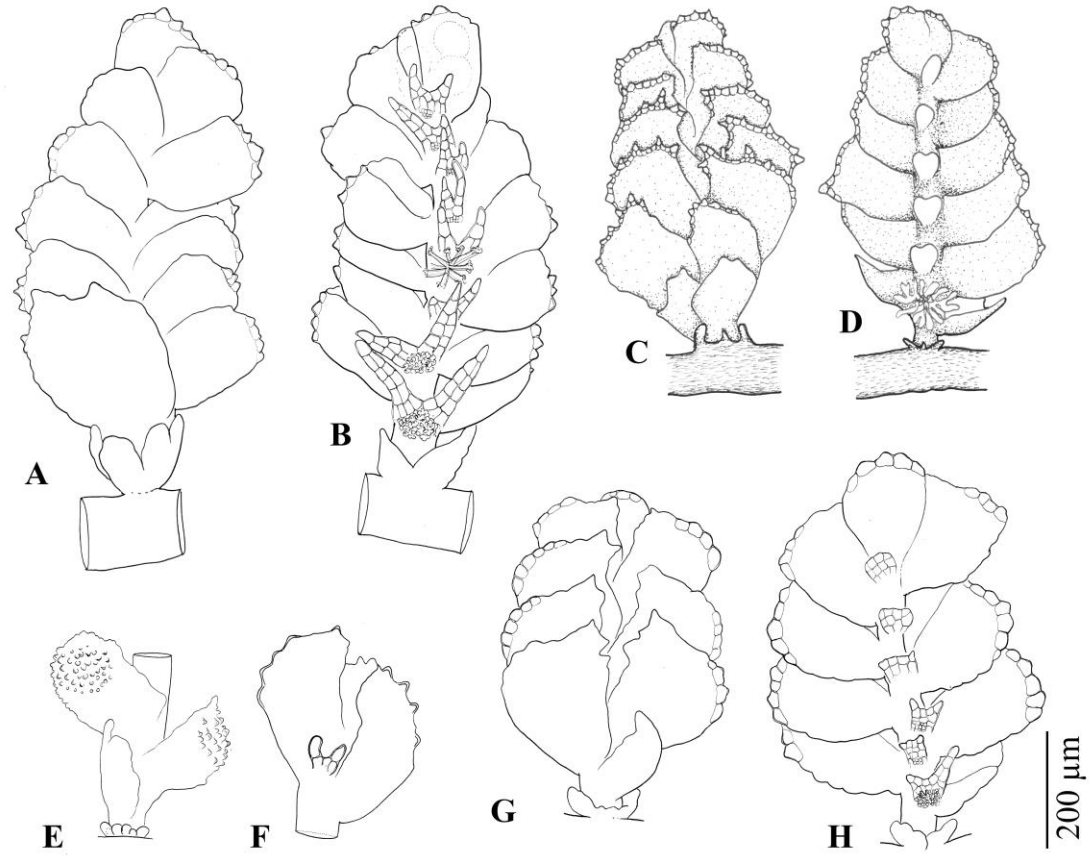

Fig. 2.14 The variations of the androecia: A & B. *C. ari*, A. dorsal view showing denticulate free margin of bract lobes, B. ventral view showing strongly bilobed bracteoles. C & D. *C. imperfecta*, C. dorsal view showing dentate free margin of bract lobe, D. ventral view showing cordate to round bracteoles. E & F. *C. junghuhniana*, E. dorsal view presenting dense papillae, F. ventral view presenting papillose apical keel. G & H. *C. palawanensis*, G. dorsal view displaying dentate free margin of bract lobe, H. ventral view displaying bilobed to subquadrate bracteole.

Gynoecia

The gynoecia of this genus are terminally produced on lateral branches with 1(–2) pycnolejeunoid innovation branches. The gynoecia are athecal branches and consist of two female bracts and one female bracteole. Female bract lobes are exceedingly various in size and shape, but female bract lobules are narrowly oblong. Female bract apexes are obtuse to acute and their margins are entire, crenulate to dentate. Only one archegonium occurs in each gynoecium. After fertilization, perianth will develope to protect a young sporophyte. The perianths of Malesian *Colura* are

various in shape being obtriangular, urceolate, oblanceolate, obovate, or elliptic with 3–5 keels (Fig. 2.15). The perianth keels are usually inflated but are swollen in *C. corniantha* and *C. inflata* (Fig. 2.15E). The keels are short ridge (Fig. 2.15A, 15C), extended triangular (Fig. 2.15G, 15I), or horn-like (Fig. 2.15K). The perianth and keel surface are regularly entire or mamillose, but the papillae are dense on perianth and keel surfaces of *C. junghuhniana* (Fig. 2.15G). Perianth beaks are normally short with 1–3(–6) cells long (Fig. 2.15B, 15D, 15F, 15H, 15J, 15L).

Sporophytes

The development of sporophyte is inside the calyptra (Fig. 2.16A) and sporangium will be protruded out by elongated seta cells when mature and in high humidity condition (Fig. 2.16B). Elongated setae are vertically articulate with 8–9 cells in length (Fig. 2.17C, 17G); nonetheless, seta can be found longer in *C. hemisphaerica* (Fig. 2.17D), *C. junghuhniana* (Fig. 2.17E), and *C. karstenii* (Fig. 2.17F). Seta in transverse section consist of 12 outer cells and 4 inner cells (Fig. 2.17A). The number of cell ring of foot in surface view is 3 transversal cell rings. Normally, the mature capsules are spherical and dark-brown to blackish. The capsules split into 4 valves and remain fused at their base.

The capsule walls have 2–3 hyaline cell thickenings. Outer wall cells can be roughly divided into 3 zones *viz*. marginal cells, upper part cells, and lower hinge cells (Fig. 2.17H–J). The shapes of hinge vary from broadly quadrate (Fig. 2.17H), butterfly-shape (Fig. 2.17I), and rectangular (Fig. 2.17J). Inner walls show 2 zones, i.e. upper and lower part. Cells at upper part are usually small and nodulous, but lower part cells reveal two distinct types, nodular median and smooth marginal cells.

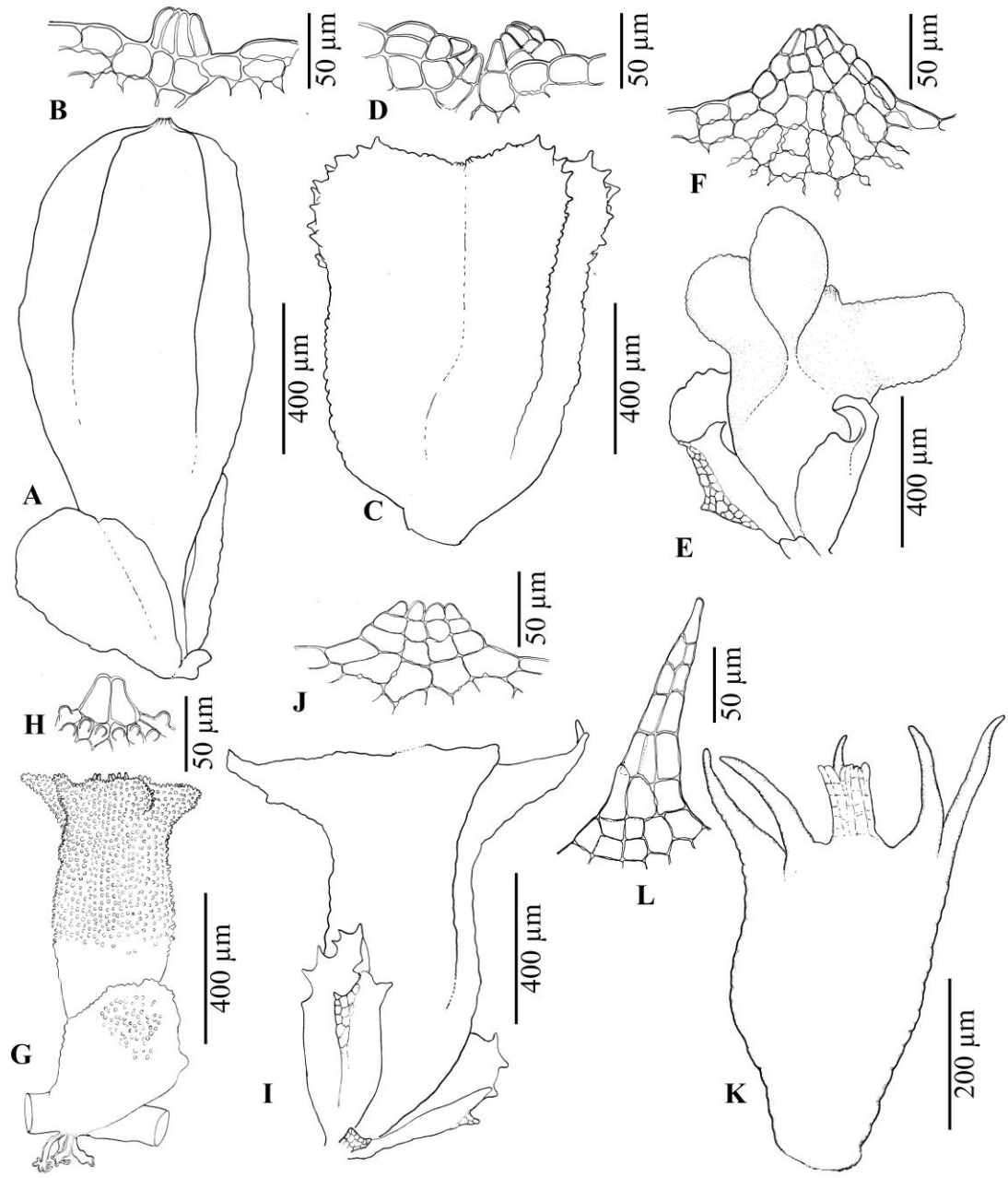

Fig. 2.15 The variations of perianths and beaks: A & B. *C. hemisphaerica*, C & D. *C. denticulata*, E & F. *C. inflata*, G & H. *C. junghuhniana*, I & J. *C. apiculata*, K & L. *C. medusa*.

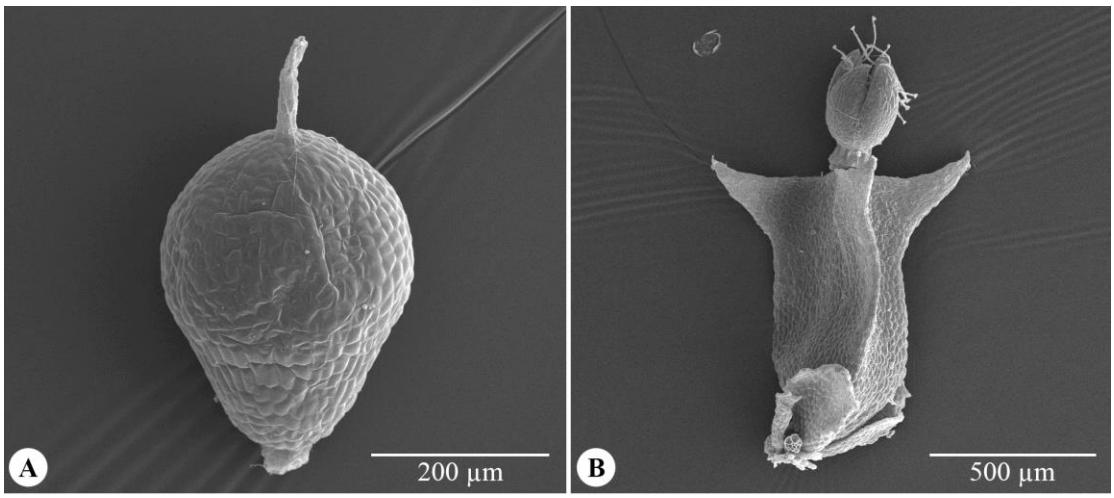

Fig. 2.16 Sporangia of *Colura apiculata*: A. Young sporophyte enclosed by calyptra. B. Mature sporophyte extended outside the 3-keels perianth.

The elaters are colorless to yellowish and can be grouped into 2 types: marginal and additional elaters. The marginal elaters had been divided into upper and lower marginal elater based on their position and morphology (Sangrattanaprasert *et al*. 2017, 2018). The number and arrangement of elaters are identical in opposite valves. Each valve contains 4 or 5 upper marginal elaters, 2 or no lower marginal elaters, and one additional elater (Fig. 2.18A). The upper marginal elaters are linear with irregular to annular thickening and attach to upper half of valve at only one end; the other is free (Fig. 2.18B & C). The lower marginal elaters are oblong to linear with irregular to annular thickening (Fig. 2.18C). Moreover, the lower marginal elaters are attached to valve both at ends. The additional elaters present along the middle of each valve (Fig. 2.18D & E). The thickenings of additional elaters are generally smooth, but they can be irregular in some species.

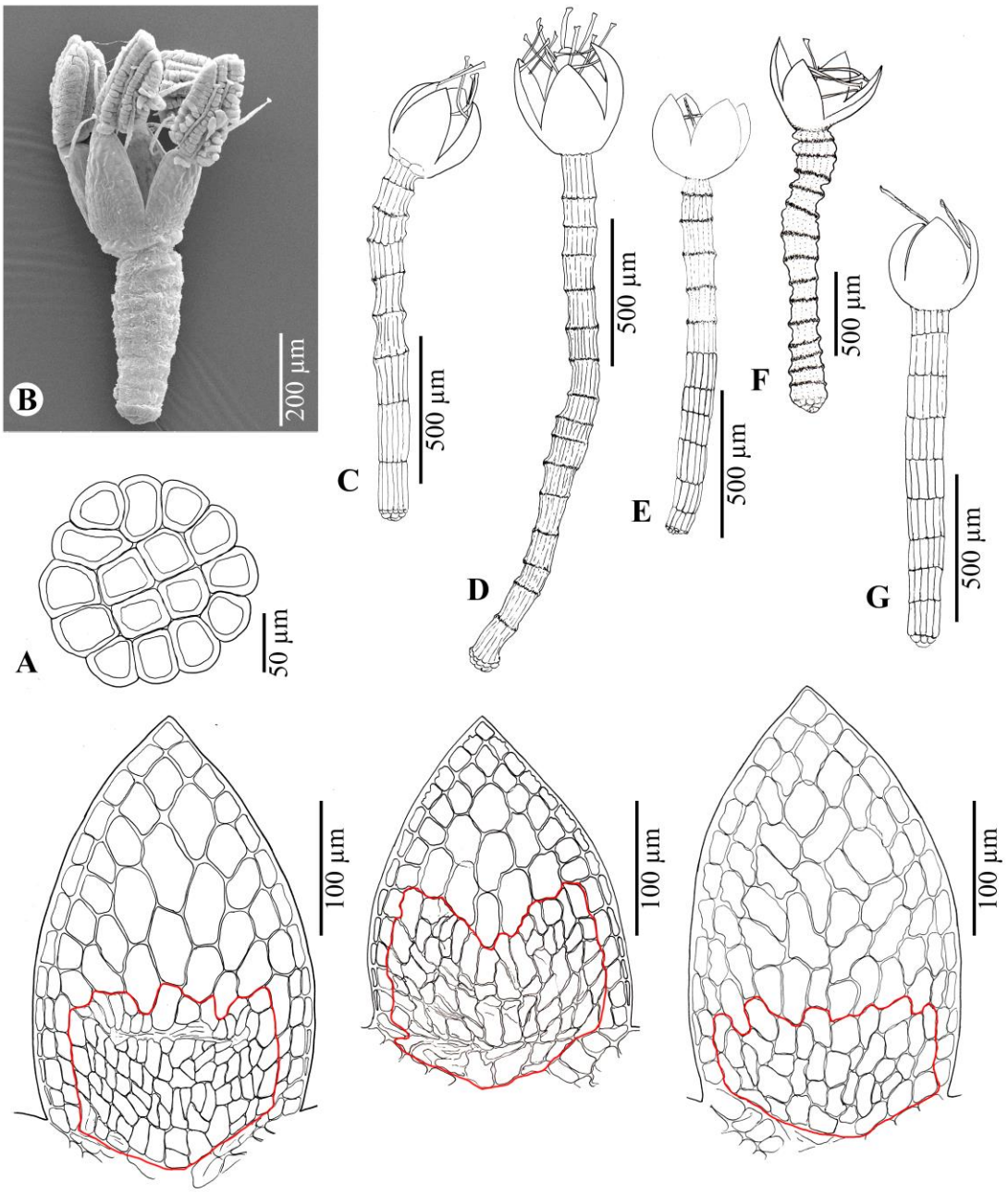

Fig. 2.17 The mature sporophytes of genus *Colura* varying in number of seta cell in length: A. The seta in transection showing 12 outer and 4 inner cells. B. Mature sporophyte of *C. conica* under SEM. C–G. The variation of seta cell length, C. *C. ari* (9 cells), D. *C. hemisphaerica* (16 cells), E. *C. junghuhniana* (12 cells), F. *C. karstenii* (14 cells), G. *C. ornata* (9 cells). H–J. Outer wall cells of sporangial valves displaying marginal cells, upper part cells, and lower hinge cells (in red line), H. valve of *C. ari* showing broadly quadrate hinge, I. valve of *C. cristata* showing butterfly-shape hinge, J. valve of *C. hemisphaerica* showing rectangular hinge.

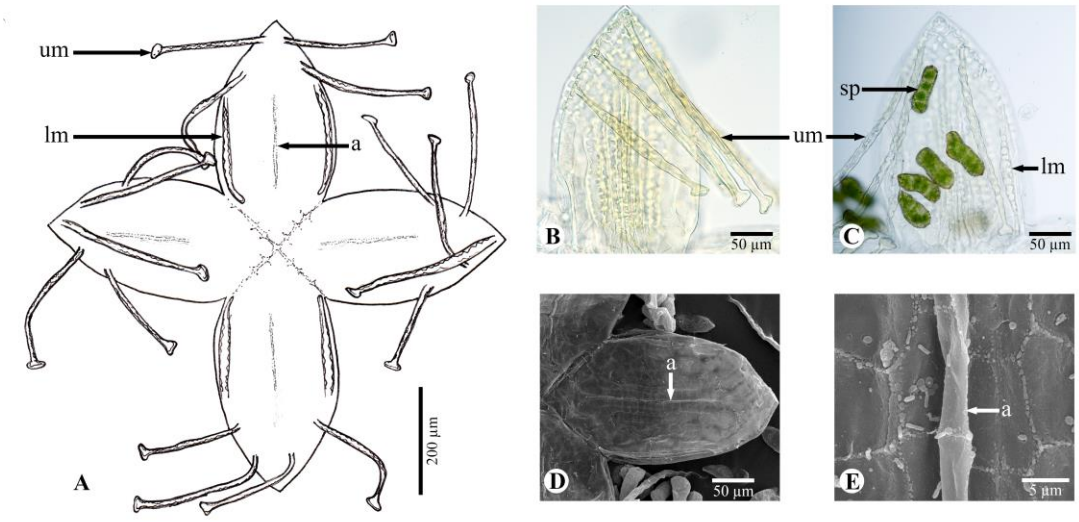

Fig. 2.18 Elaters of the sporangium in genus *Colura*: A. Sporangial valves of *C. meijeri* showing upper marginal (um), lower marginal (lm) elaters which present in 1+2+2 (left & right) and 2+2+2 (top & bottom) patterns and an additional elater (a) present at the middle part of each valve. B & C. Sporangial valves of *C. verdoornii* under the compound microscope presenting the yellowish to colorless elaters and pale green spores (sp). D & E. Sporangial vale of *C. speciosa* under SEM showing additional elater, D. 450× magnification, E. 5000× magnification.

The mature spores are irregularly oblong and pale green. They undergo precocious germination inside the capsule before dehiscence. Thus, the mature spores often show the multicellular endosporic germination. There are two distinct types of spore ornamentation: 1) papillate found in *C. junghuhniana* and *C. tenuicornis* (Fig. 2.19A & B), and 2) irregularly lamellate presenting in most of the remaining species (Fig. 2.19C & D). Generally, the rosettes of *Colura* spores are rarely known, but in the present study, the rosettes are observed in *C. tenuicornis* (Fig. 2.19A & B). According to this investigation, the sporelings are found in some species i.e. *C. acroloba*, *C. conica*, *C. crenulata*, *C. cristata*, *C. hemisphaerica*, *C. karstenii*, and *C. valida*. All the sporelings are *Lejeunea*-type which include typically 8(–10) divided cells.

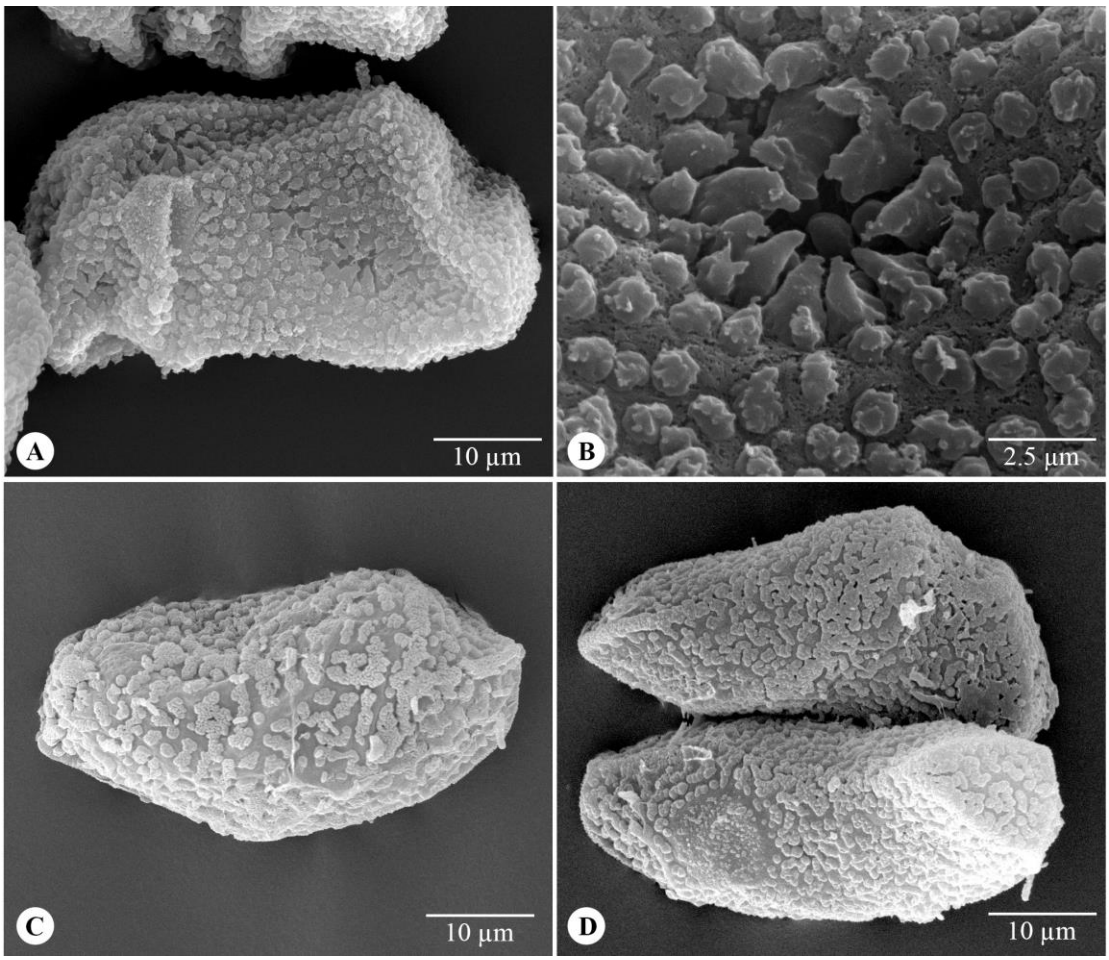

Fig. 2.19 Spore ornamentations of the genus *Colura*: A & B. *C. tenuicornis*, A. papillated spores with rosettes, B. rosette in high magnification. C & D. *C. apiculata* & *C. speciosa*, irregular lamellae spores without rosette.

Asexual reproduction

The multicellular discoid gemmae are a typical type of asexual reproductive structure in this genus. They are originated from leaf lobe and/or lobule sac cells parallelly (Fig. 2.20A–C). The gemma initial cells develop outside their broken cell walls (Fig. 2.20B). They enlarge and divide anticlinally into two equal cells. Then, each cell perpendicularly divide again to form four unequal cells, 2 large and 2 small cells. Then, the mother cells undergo a series of regular divisions until there are 24–34 isodiametric cells (Fig. 2.20D). The gemmae usually found occurring on lobule sac

and leaf lobe surface; some of them, however, may be found on dorsal lobes of female bracts (*C. meijeri* and *C. sigmoidea*) and perianth keels (*C. crenulata*).

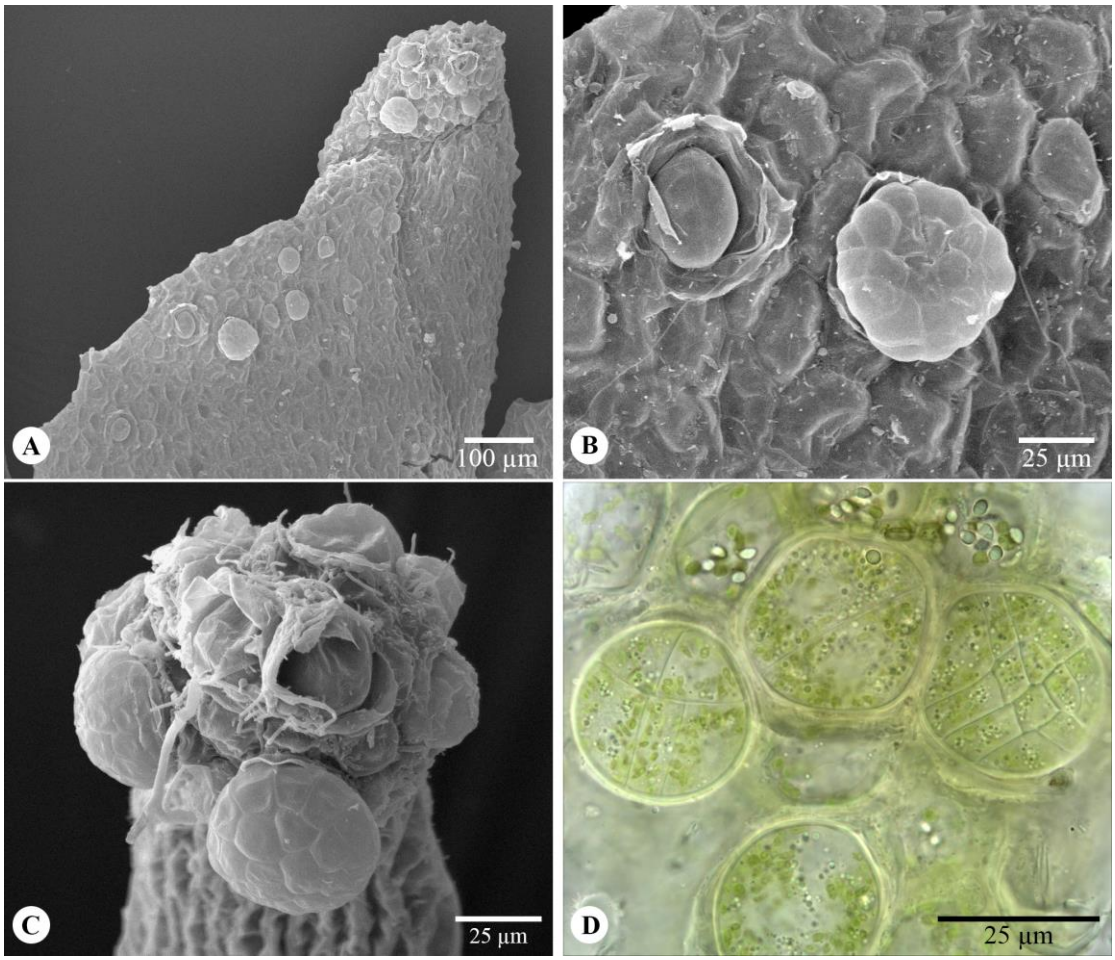

Fig. 2.20 Gemmae of genus *Colura*: A & B. Gemmae of *C. conica* occurring on leaf lobe and lobule sac (SEM), A. low magnification, B. high magnification showing gemma initial cell (left) and discoid gemma (right). C & D. Gemmae of *C. pluridentata* occurring at sac apex, C. high magnification showing dense gemma production (SEM), D. Cell divisions of gemma initial cells investigated by compound microscope.

2.4 Discussions

From the present study, some populations of some dimorphic-leaf species, such as *C. corynophora*, *C. inflata* and *C. speciosa*, may produce more non-saccate

leaves than saccate leaves, which is rather confused with member of the genus *Diplasiolejeunea*. However, the members of the genus *Colura* can be distinguished from the *Diplasiolejeunea* by 1) narrowly oblong lobules of non-saccate leaves, 2) the presence of enlarged sac at lobule apex of saccate leaf, and 3) the absence of ocelli (Zhu & So 2001).

The lobule valve of *Colura* is an apomorphic character which sets it apart from other genera in Lejeuneaceae. However, the lobule valve can be found in genus *Pleurozia*, Pleuroziaceae (a monogeneric family), which lateral leaf also develops closed sac, where a valve is formed covering a sac pore. The valve of *Pleurozia* contains hyaline marginal and median cells as also found in the valve of *Colura*, but the former is an inversed valve. Moreover, the *Pleurozia*'s valve resembles valve of *Colura karstenii* by the large size of valve including more than 200 cells and the absence of hinge cells. The latter, however, differs from the former by having elongate basal hyaline and hyaline papilla (Fig 2.21). For phylogenetic relationship, the genus *Pleurozia* has been treated as a member within Pleuroziaceae, Metzgeriidae (simple thalloid clade) with a strongly supported, while the genus *Colura* was placed in Lejeuneaceae, Jungermanniidae (leafy clade) (Shaw & Renzagilia 2004, Wilson *et al*. 2007, Gradstein 2013). Hence, the valve character in both genera may have evolved convergently.

For this work, the investigated elater patterns of all 23 *Colura* species reveal similarity within the genus and the related genera in subtribe Cololejeuneinae by having similar patterns (only at valve margin) and number (1+2+2 or 2+2+2) of elaters (Mizutani 1961, Gradstein *et al*. 2003). Moreover, three patterns of hinge at the outer layer of sporangium wall (quadrate, butterfly-shape, and rectangular) were found in the genus, while only quadrate-shape was reported previously (Gradstein *et al*. 2003). Besides, two types of spore ornamentation found in this study is similar to spore wall sculpture of six *Colura* species reported by Jovet-Ast (1976). The irregularly lamellate type is presented in most *Colura* species, whereas papillate type is found only in *C. junghuhniana* and *C. tenuicornis*. The rosettes on spore sculpture can be found only on papillate spore. To fill the gap of knowledge, the sporophyte

characters and spore ornamentation of the remaining species and other related genera are still awaiting further studies.

The morphological and anatomical characters are the important and basic tool for taxonomic classification and identification. The examinations of more field specimens as much as possible and herbarium type specimens make it more valuable to explain which character is variant or distinctive one. Some characters, however, are too variable to delimit species boundary. Thus, molecular phylogenetics, might be needed for clarifying species delimitation.

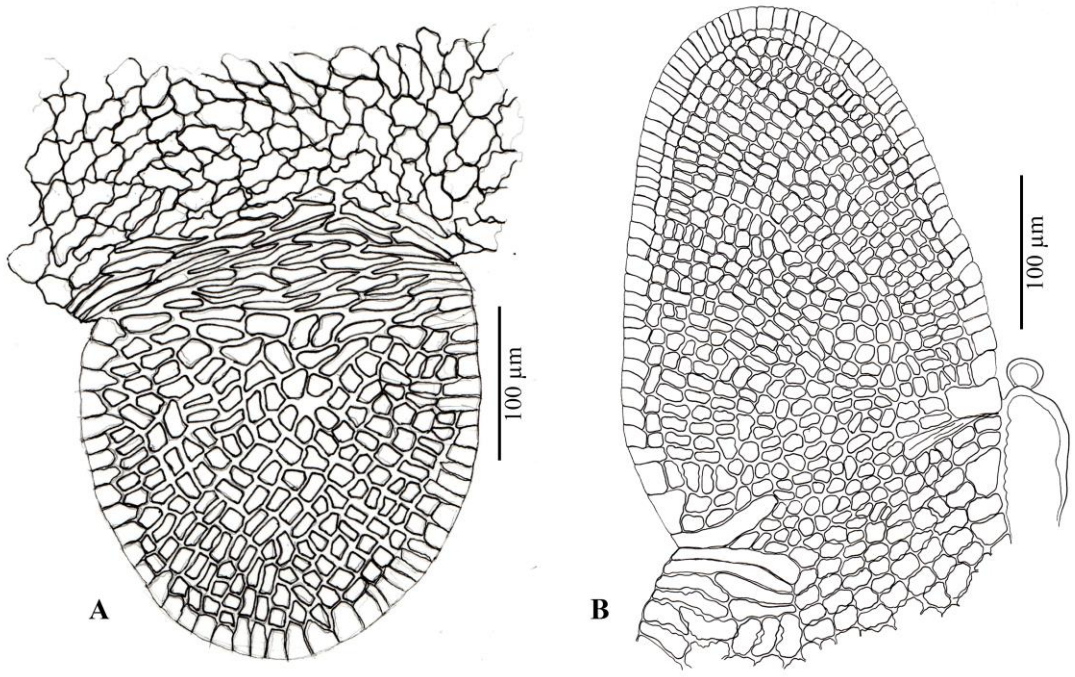

Fig. 2.21 The comparison between lobule valve of *Pleurozia* and *Colura*: A. *Pleurozia gigantea* (F.Weber) Lindb. B. *Colura karstenii*.

CHAPTER 3

MOLECULAR PHYLOGENY

3.1 Introduction

The genus *Colura* is one of the largest genera in Lejeuneaceae with 83 accepted taxa (Söderström *et al*. 2016). The molecular phylogenetic studies (Gradstein *et al*. 2006, 2013, Wilson *et al*. 2007) showed that the genus *Colura* was resolved as a monophyletic group nested within subfamily Lejeuneoideae, tribe Lejeuneeae, subtribe Cololejeuneinae; however, some phylogenetic analyses (Heinrichs *et al*. 2014a, 2014b) revealed the generic paraphyly, because the monotypic genus *Macrocolura* was nested within, though with a rather weak support. Most of the members of the genus are mainly pantropical distribution, but some species are dispersed into the subtropical and temperate zones (Jovet-Ast 1954, Pócs 1996). The highest number of species (32 spp.) of *Colura* was found in Malesian region (Jovet-Ast 1953, 1954, 1958b & 1967b, Tan & Engel 1986, Söderström *et al*. 2010, Chuah-Petiot 2011).

For the infrageneric classification, six sections of the genus were proposed by Jovet-Ast (1953), based on valve types and leaf characters, but all of them were invalidly published at that time. Since then, the valid names of all six sections were reestablished, namely sect. *Colura*, sect. *Gamolepis*, sect. *Glotta*, sect. *Harmophyllum*, sect. *Heterophyllum*, and sect. *Oidocorys* (Grolle 1965, 1969, Jovet-Ast 1983, Grolle & Zhu 2002), and two subgenera (subg. *Colura* and subg. *Glotta*) were described subsequently, based on valve features (Grolle & Zhu 2002). However, the infrageneric classification, as well as species delimitation, for this genus has always been problematic due to a high level of morphological variation and sparse samplings in the previous taxonomic studies.

Section *Heterophyllum* includes 15 species from Southeast Asia, among these 13 species occur in Malesian region (except *C. tixierii* and *C. vietnamensis* Jovet-Ast which have been also reported to occur in Indochina region (Jovet-Ast 1961, Tixier 1973, 1970)). Species of the sect. *Heterophyllum* are characterized by dimorphic leaves (having saccate and non-saccate leaves in the same stem) (Fig. 3.1A, E, I), the

absence of hinge and basal median cells of valve (Fig. 3.1C, G, K), and three perianth keels (Fig. 3.1D, H, L) (Jovet-Ast 1983). From the recent phylogenetic study, sect. *Heterophyllum* was regarded as a paraphyletic group and split into two entities, but the morphological interpretation of this issue is unresolved due to sparse samples (Heinrichs *et al*. 2012).

Moreover, *Macrocolura* was segregated from the genus *Colura* by insertion of underleaves being invertedly J-shaped, asymmetrical underleaves, and rhizoid fascicule originating at the middle of underleaves (Grolle & Zhu 2002). The genus *Macrocolura* is a monotypic genus to which only *M. sagittistipula* (Spruce) R.M.Schust. belongs, because *M. clavigera* (Gottsche *ex* Ast) R.M.Schust and *M. lyrata* have been treated as synonym of *M. sagittistipula* by Grolle & Zhu (2002). Nonetheless, many phylogenetic investigations of generic relationships within the Lejeuneaceae show that the genus *Macrocolura* has been placed sister to or nested within *Colura* clade (Wilson *et al*. 2007, Heinrichs *et al*. 2012, 2014a, 2014b). Hence, the phylogenetic relationship between *Colura* and *Macrocolura* should be reinvestigated.

Another issue with *Colura* classification is species delimitations within a species complex. *Colura inflata* was described from Sumatra, Indonesia in 1928 with very distinct characters, including dimorphic leaves, dorsal margin of leaf lobes being denticulate to weakly dentate, sac apices ending with small crest, valves with indistinct hinge cells, and strongly inflated perianth keels (Fig. 3.2G–L). Subsequently, Jovet-Ast (1961) proposed a new species from South Vietnam, *C. cornuta* Jovet-Ast, which resembles *C. inflata* by sharing the swollen perianth keels, but the former differs by having teeth at the perianth keel apices (Fig. 3.2A–F). However, *C. cornuta* was an illegitimate name because of being homonymous with the former "*Colura cornuta* (Lindenb.) Trevis.". Therefore, Grolle (1965) established a replacement name "*Colura corniantha*". Finally, *Colura siamensis* was proposed in 1967 as a new species from Thailand. This species is morphologically related to *C. inflata* and *C. corniantha* but can be distinguished by small leaf lobe of saccate leaf, leaf dorsal margin being dentate with a few teeth, and the absence of teeth at perianth keels apices (Fig. 3.2M–Q) (Jovet-Ast 1967a). These three species constitute a "*Colura inflata* complex" due to their shared morphological characters: sac apices

usually ending with a small crest, dorsal margin of leaf lobe being denticulate to dentate, and the swollen perianth keels, balloon-like shape (Fig. 3.2). The distinctions between these three species are not clear, and they were even suspected to be conspecific by their author (Jovet-Ast 1961, 1967a). However, the issue remains unresolved due to the sparse sampling and lack of molecular data.

Therefore, to clarify the infrageneric classification and species delimitation in the genus *Colura*, we collected DNA data comprising two chloroplast regions and one nuclear region from 31 *Colura* species and *Macrocolura sagittistipula*. The molecular phylogeny is reconstructed. The resulting phylogeny is then used to evaluate against the current classification and species delimitation, leading to a proper infrageneric reclassification of the genus.

3.2 Materials and methods

3.2.1 Taxon and character sampling

Material of 24 species of *Colura* collected from various locations in Thailand, Malaysia, and China were included in this study, representing five sections of the genus (*Colura*, *Gamolepis*, *Glotta*, *Harmophyllum*, and *Heterophyllum*). Members of section *Oidocorys* are not found in Malesian region, however. Thus, no new DNA sequence was generated. The sequences of *C. ornithocephala* Herzog, belonging to sect. *Oidocorys*, as well as of the remaining species of *Colura* and of *Macrocolura* were obtained from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and included in the phylogenetic analysis. The details about specimens, voucher information, and their GenBank accession numbers were listed in Table 3.1.

According to the previous study on phylogenetic relationships of genera in Lejeuneaceae, *Siphonolejeunea elegantissima* (Steph.) Grolle and *Myriocoleopsis gymnocolea* (Spruce) M.E.Reiner *et* Gradst. formed a sister relationship with *Colura* (Heinrichs *et al*. 2014b). Thus, these two species were selected as outgroups for this analysis. Their sequences were obtained from GenBank as well.

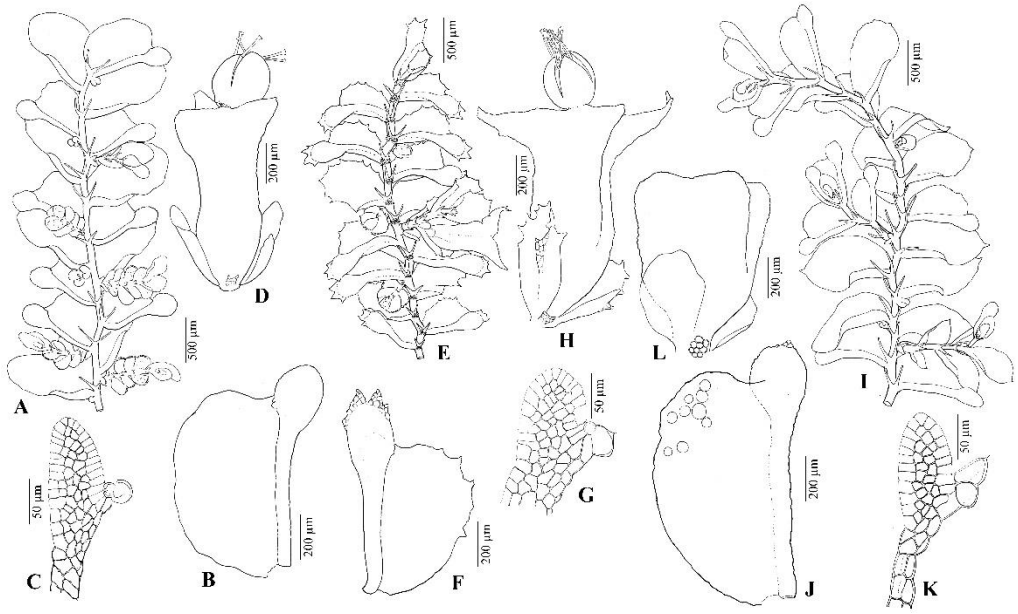

Fig. 3.1 The significant characters of *Colura* section *Heterophyllum* Jovet-Ast: A–D. *C. corynophora*. E–H. *C. apiculata*. I–L. *C. vietnamensis*; A, E, I. Portions of plant with saccate and non-saccate leaves, ventral view; B, F, J. lateral leaves; C, G, K, valves; D, H, L. Perianths with 3 keels.

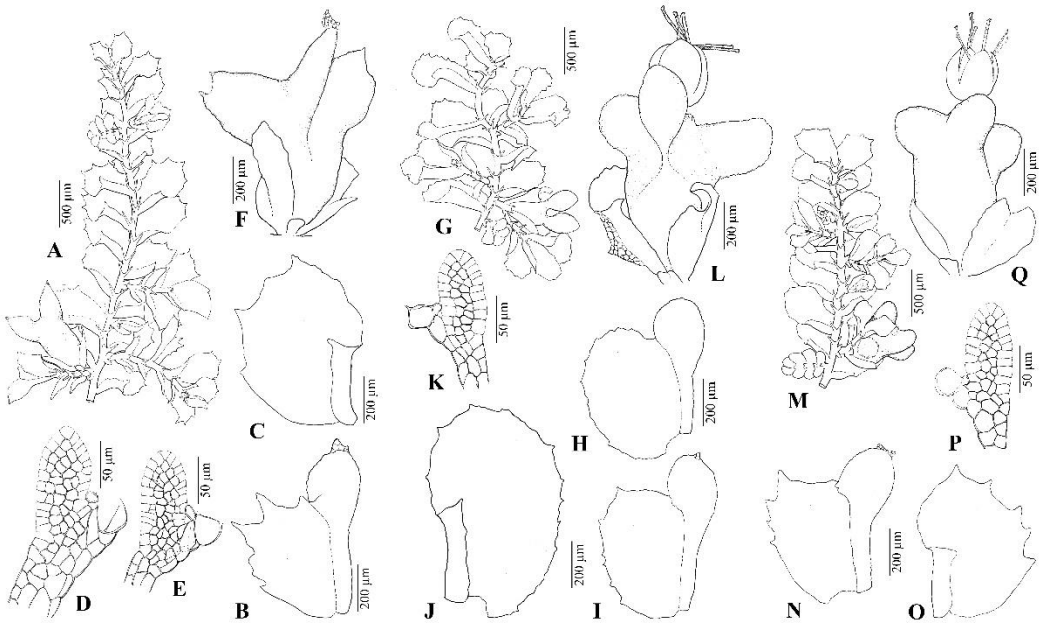

Fig. 3.2 Morphological comparison within *Colura inflata* complex: A–F. *Colura corniantha*. G–L. *C. inflata*. M–Q. *C. siamensis*; A, G, M. Portions of plants, ventral view; B, H & I, N. Saccate leaves, C, J, O. Non-saccate leaves; D & E, K, P. Valves; F, L, Q. Perianths.

3.2.2 DNA extraction, amplification, and sequencing

Total genomic DNA of 42 voucher specimens was extracted from silica-gel dried shoots using DNeasy Plant Mini Kits (Qiagen, Hilden, Germany). The extract was eluted in 100 mL AE buffer and kept at -80°C (Zhu *et al*. 2018). The primers of nrITS, *trnL–F* region, and *rbcL* gene were used for PCR amplification, following the previous work on this genus (Table 3.2). The amplification conditions of each region were carried out according to the previous publication: nrITS1–5.8S–ITS2 region from Hartmann *et al*. (2006) and *trnL–F* region and *rbcL* gene from Gradstein *et al*. (2006). The PCR products were purified and bi-directionally sequenced by Shanghai Meiji Biomedical Technology Co., Ltd., China (http://www.majorbio.com).

3.2.3 Phylogenetic analyses

All sequences of each region were aligned separately with MAFFT (Katoh *et al*. 2017) and manually adjusted in PhyDe v.0.9971 (http://www.phyde.de/index.html). Gaps approximate 50% and more were excluded from the alignments. Maximum parsimony analysis was implemented in TNT v1.5 (Goloboff & Catalano 2016). All characters were equally weighted and unordered. Incongruence among regions was evaluated by analyzing each region individually, to see if there was any significant conflict in clade support (Seelanan *et al*. 1997, Wiens 1998). Multiple most parsimonious trees were generated by a heuristic search of the combined data, with 9000 replicates of random sequence addition, saving 10 trees per replicate, and using the tree bisection and reconnection branch-swapping algorithm. Clade support was measured by bootstrap percentage (BS_{MP}). A default change probability was used. Ten thousand replicates were run, each with ten replicates of random sequence addition, saving ten trees per replicate. A clade with $BS_{MP} \geq 80\%$, 70%–89%, and 50%–69% was considered strongly, moderately, and weakly supported, respectively.

Maximum-likelihood (ML) analysis and Bayesian inference (BI) were performed, using IQ-TREE v1.6.1 (Nguyen *et al*. 2015) and MrBayes on XSEDE v.3.2.6 (Ronquist & Huelsenbeck 2003) via the CIPRES Science Gateway (Miller *et al*. 2010, http://www.phylo.org), respectively. The ML analysis was performed under partition models (Chernomor *et al*., 2016) implemented with the "-spp" command. The GTR+I+Γ, selected as a substitution model, was implemented for BI analysis.

Four chains of Markov chain Monte Carlo (MCMC) simulation were executed for 20 million generations each with trees being sampled every 1,000th generation. The initial 25% of the sampled trees were discarded as burn-ins, and a majority rule consensus tree of all remaining trees was calculated.

3.3 Results

In this work, 42 new nrITS, *trnL–F*, and *rbcL* sequences were generated (Table 3.1). The combined dataset comprised 3064 positions including 1183 from nrITS, 517 from *trnL–F*, and 1364 from *rbcL*. The strict consensus tree from maximum likelihood, maximum parsimony analyses and Bayesian inference resulted in similar tree topologies. Therefore, only the maximum likelihood tree with the ML, MP bootstrap support (BS_{ML}, BS_{MP}) and BI posterior probability (PP_{BI}) at the nodes was shown here (Fig. 3.3).

According to the tree, two main clades was recovered as maximally supported clade within the genus *Colura* (BS_{ML} = 100, BS_{MP} = 100, PP_{BI} = 1). The first clade, Clade 1, included the members of sect. *Colura* (Clade B) and *Oidocorys* (Clade C), both of which were monophyletic entities with strong support (BS_{ML} = 100, BS_{MP} = 100, PP_{BI} = 1). Besides, the *Macrocolura sagittistipula* (Clade A) was also placed as sister to those two sections with rather weak supports (BS_{ML} = 69, BS_{MP} = 51, PP_{BI} = 0.86). Another main clade, Clade 2, included the other four sections forming a well-supported clade (BS_{ML} = 100, BS_{MP} = 97, PP_{BI} = 1). The sect. *Glotta* (Clade D) was resolved as sister to the rest of the clade with the strong support. The sect. *Gamolepis*, *Harmophyllum*, and *Heterophyllum* (Clade E–G) were resolved as polyphyletic. From the results, the current two subgenera are paraphyletic, because two sections (sect. *Gamolepis* and sect. *Harmophyllum*) belonging to subg. *Colura* are nested within subg. *Glotta* (Fig. 3.3).

Table 3.1 List of taxa used in the present study, including information about locality, information and deposited herbaria of voucher specimens, as well as their GenBank Accession numbers. Sequences in bold letter were obtained from GenBank.

Taxa	CODE	Locality	Collecter	nrITS	*trnL-trnF*	*rbcL*
Colura acroloba	COLU32	Malaysia, Sabah	Zhu *et al*. 20160920-28B-1 (HSNU)	MH986157	MH991892	MH991934
C. acroloba	COLU35	Thailand, Nakhon Si Thammarat,	Sangrattanaprasert 97/14 (PSU)	MH986160	MH991895	MH991937
C. acroloba	COLU36	Thailand, Trang	Sangrattanaprasert 244/14A (PSU)	MH986161	MH991896	MH991938
C. acroloba	COLU37	Thailand, Yala	Chantanaorrapint *et al*. 2549A (PSU)	MH986162	MH991897	MH991939
C. acroloba	GENB01	Malaysia	Schäfer-Verwimp & Verwimp 18860/A (JE)	**JX470989**	**JX470977**	**JX470966**
C. apiculata	COLU16	Thailand, Yala	Sangrattanaprasert 177/14A (PSU)	MH986147	MH991882	MH991924
C. ari	COLU03	Thailand, Krung Ching, Nakhon Si Thammarat	Sangrattanaprasert 224/14A (PSU)	MH986136	MH991871	MH991913
C. ari	COLU04	Thailand, Songkhla	Sangrattanaprasert 250/14B (PSU)	MH986137	MH991872	MH991914
C. ari	COLU30	Malaysia, Sabah	Zhu *et al*. 20160916-84 (HSNU)	MH986156	MH991891	MH991933
C. ari	COLU45	Thailand, Trang	Sangrattanaprasert 237/14A (PSU)	MH986167	MH991902	MH991944
C. calyptrifolia	GENB02	Dominican Republic	Schäfer-Verwimp & Verwimp 26843 (JE)	**JX470993**	**JX470981**	**JX470970**
C. conica	COLU02	Thailand, Yala	Sahut *et al*. 2644A (PSU)	MH986135	MH991870	MH991912
C. conica	COLU05	Thailand, Trang	Sangrattanaprasert 164/14 (PSU)	MH986138	MH991873	MH991915
C. conica	COLU11	Thailand, Phangnga	Sangrattanaprasert 324/15A (PSU)	MH986142	MH991877	MH991919
C. conica	COLU40	Thailand, Nakhon Si Thammarat	Sangrattanaprasert 216/14A (PSU)	MH986164	MH991899	MH991941
C. conica	COLU46	Thailand, Surat Thani	Sangrattanaprasert 303/15 (PSU)	MH986168	MH991903	MH991945
C. corniantha	COLU06	Thailand, Phangnga	Sangrattanaprasert 318/15D (PSU)	MH986139	MH991874	MH991916
C. corniantha	COLU38	Thailand, Chumphon	Sahut *et al*. 3899D (PSU)	MH986163	MH991898	MH991940

Taxa	CODE	Locality	Collecter	nrITS	*trnL-trnF*	*rbcL*
C. corniantha	COLU48	Thailand, Nakhon Si Thammarat	Sangrattanaprasert 228/14B (PSU)	MH986170	MH991905	MH991947
C. corynophora	COLU07	Thailand, Phangnga	Sangrattanaprasert 312/15A (PSU)	MH986140	MH991875	MH991917
C. corynophora	COLU33	Malaysia, Sabah	Zhu *et al*. 20160920-28B-2 (HSNU)	MH986158	MH991893	MH991935
C. corynophora	COLU52	Malaysia, Sabah	Zhu *et al*. 20160916-88B (HSNU)	MH986174	MH991909	MH991951
C. crenulata	COLU49	Thailand, Trang	Sangrattanaprasert 120/14C (PSU)	MH986171	MH991906	MH991948
C. cristata	COLU51	Malaysia, Sabah	Zhu *et al*. 20160916-2 (HSNU)	MH986173	MH991908	MH991950
C. cylindrica	GENB03	Guadeloupe	Schaefer-Verwimp & Verwimp 22154/B (JE)	**JX470992**	**JX470980**	**JX470969**
C. cylindrica	GENB04	Panama	Schaefer-Verwimp & Verwimp 30741 (JE)	**JX470996**	**JX470984**	**JX470973**
C. digitalis	GENB13	Reunion	Schaefer-Verwimp & Verwimp 20134 (JE)	**JX471000**	**JX470988**	**-**
C. hemisphaerica	COLU10	Thailand, Nakhon Si Thammarat	Sangrattanaprasert 104/14 (PSU)	MH986141	MH991876	MH991918
C. herzogii	COLU29	Malaysia, Sabah	Zhu *et al*. 20160920-01 (HSNU)	MH986155	MH991890	MH991932
C. imperfecta	COLU12	Thailand, Songkhla	Sangrattanaprasert 300/15B (PSU)	MH986143	MH991878	MH991920
C. imperfecta	GENB05	Papua New Guinea	Streimann 41383/a (JE)	**JX470994**	**JX470982**	**JX470971**
C. inflata	GENB11	Malaysia	Schäfer-Verwimp & Verwimp 19010/A (JE)	**JX470991**	**JX470979**	**JX470968**
C. irrorata	GENB12	Ecuador	Gradstein et al. 10033A (GOET)	**DQ987279**	**AY548072**	**AY548073**
C. karstenii	COLU14	Thailand, Nakhon Si Thammarat	Zhu *et al*. 20111215-23 (HSNU)	MH986145	MH991880	MH991922
C. karstenii	COLU41	Malaysia, Sabah	Zhu *et al*. 20160915-93B (HSNU)	MH986165	MH991900	MH991942
C. meijeri	COLU15	Thailand, Nakhon Na Yok	Sangrattanaprasert 342/15B (PSU)	MH986146	MH991881	MH991923
C. ornata	COLU18	Thailand, Nakhon Si	Sangrattanaprasert 218/14C (PSU)	MH986148	MH991883	MH991925

Taxa	CODE	Locality	Collecter	nrITS	*trnL-trnF*	*rbcL*
		Thammarat				
C. ornithocephala	GENB06	Ecuador, Carchi	Schäfer-Verwimp *et al*. 24391/A (JE)	**JX470998**	**JX470986**	**JX470975**
C. ornithocephala	GENB07	Ecuador, Azuay	Schäfer-Verwimp & Nebel 32854 (JE)	**JX470997**	**JX470985**	**JX470974**
C. pallida	COLU19	Thailand, Nakhon Si Thammarat	Sangrattanaprasert 479/16 (PSU)	MH986149	MH991884	MH991926
C. pluridentata	COLU27	Thailand, Phangnga	Sangrattanaprasert 452/16 (PSU)	MH986154	MH991889	MH991931
C. pluridentata	COLU50	Malaysia, Sabah	Zhu *et al*. 20160916-112B (HSNU)	MH986172	MH991907	MH991949
C. rhynchophora	GENB14	Dominica	Schäfer-Verwimp & Verwimp 17755 (JE)	**JX470999**	**JX470987**	**JX470976**
C. siamensis	COLU13	Thailand, Yala	Sahut *et al*. 2503B (PSU)	MH986144	MH991879	MH991921
C. siamensis	COLU21	Thailand, Nakhon Ratchasima	Sangrattanaprasert 343/15 (PSU)	MH986150	MH991885	MH991927
C. siamensis	COLU47	Thailand, Trang	Sangrattanaprasert 236/14 (PSU)	MH986169	MH991904	MH991946
C. sigmoidea	COLU54	Thailand, Nakhon Si Thammarat	Sangrattanaprasert 105/14B (PSU)	MH986175	MH991910	MH991952
C. speciosa	COLU22	Thailand, Songkhla	Sangrattanaprasert 300/15E (PSU)	MH986151	MH991886	MH991928
C. tenuicornis	COLU34	Thailand, Nakhon Si Thammarat	Sangrattanaprasert 193/14 (PSU)	MH986159	MH991894	MH991936
C. tenuicornis	COLU42	China, Tibet	Zhao C.X. 20160831-2B (HSNU)	MH986166	MH991901	MH991943
C. tenuicornis	GENB08	Dominican Republic	Schäfer-Verwimp & Verwimp 27039 (JE)	**JX470990**	**JX470978**	**JX470967**
C. tenuicornis	GENB09	West Indies	Schäfer-Verwimp & Holz 22538/A (JE)	**JQ991140**	**JQ991370**	**JQ991255**
C. tortifolia	GENB10	Guadeloupe	Schäfer-Verwimp & Verwimp 22441/C (JE)	**JX470995**	**JX470983**	**JX470972**
C. valida	COLU24	Thailand, Nakhon Si Thammarat	Sangrattanaprasert 480/16 (PSU)	MH986153	MH991888	MH991930
C. verdoornii	COLU23	Thailand,	Sangrattanaprasert	MH98	MH99	MH99

Taxa	CODE	Locality	Collecter	nrITS	*trnL-trnF*	*rbcL*
		Nakhon Si thammarat	374/15 (PSU)	6152	1887	1929
C. vietnamensis	COLU01	Thailand, Nakhon Na Yok	Sangrattanaprasert 342/15 (PSU)	MH98 6134	MH99 1869	MH99 1911
Macrocolura sagittistipula	MACR01	Dominica	Schäfer-Verwimp 18014 (GOET)	**DQ98 7367**	**DQ98 7466**	**DQ98 3707**
Myriocoleopsis gymnocolea	MYRI01	Ecuador	Gradstein *et al*. 10020	**DQ98 7277**	**DQ23 8583**	**DQ23 8568**
Siphonolejeunea el egantissima	SIPH01	Australia	Pocs & Brown s.n.	**DQ98 7352**	**DQ98 7452**	**DQ98 3726**

Table 3.2 Primer sequences used for PCR amplification and sequencing.

Locus/Primer	Direction	Sequence 5′–3′	Source reference
nrITS			
Bryo18SF	Forward	GGTGAAGTTTTCGGATCGCG	Hartmann *et al*. 2006
Bryo5.8SR	Reverse	TGCGTTCTTCATCGTTGC	Hartmann *et al*. 2006
Bryo5.8SF	Forward	GACTCTCAGCAACGGATA	Hartmann *et al*. 2006
Bryo26SR	Reverse	AGATTTTCAAGCTGGGCT	Hartmann *et al*. 2006
trnL–trnF			
*trnL*Lej-F	Forward	GGTAGACGCTACGGACTT	Gradstein *et al*. 2006
trnL/*trnF*-F	Reverse	ATTTGAACTGGTGACACGAG	Taberlet *et al*. 1991
rbcL			
rbcL-1Pl-F	Forward	ATGTCACCACAAACGGAGACT AAARCAGGT	Wilson *et al*. 2004
rbcL-600-R	Reverse	CCAACGCATAAATGGTTGAG	Gradstein *et al*. 2006
rbcL-640-F	Forward	CTCAACCATTTATGCGTTGG	Gradstein *et al*. 2006
rbcL-M1390R	Reverse	CTTTCAAAYTTCACAAGCAGCAG	Lewis *et al*. 1997

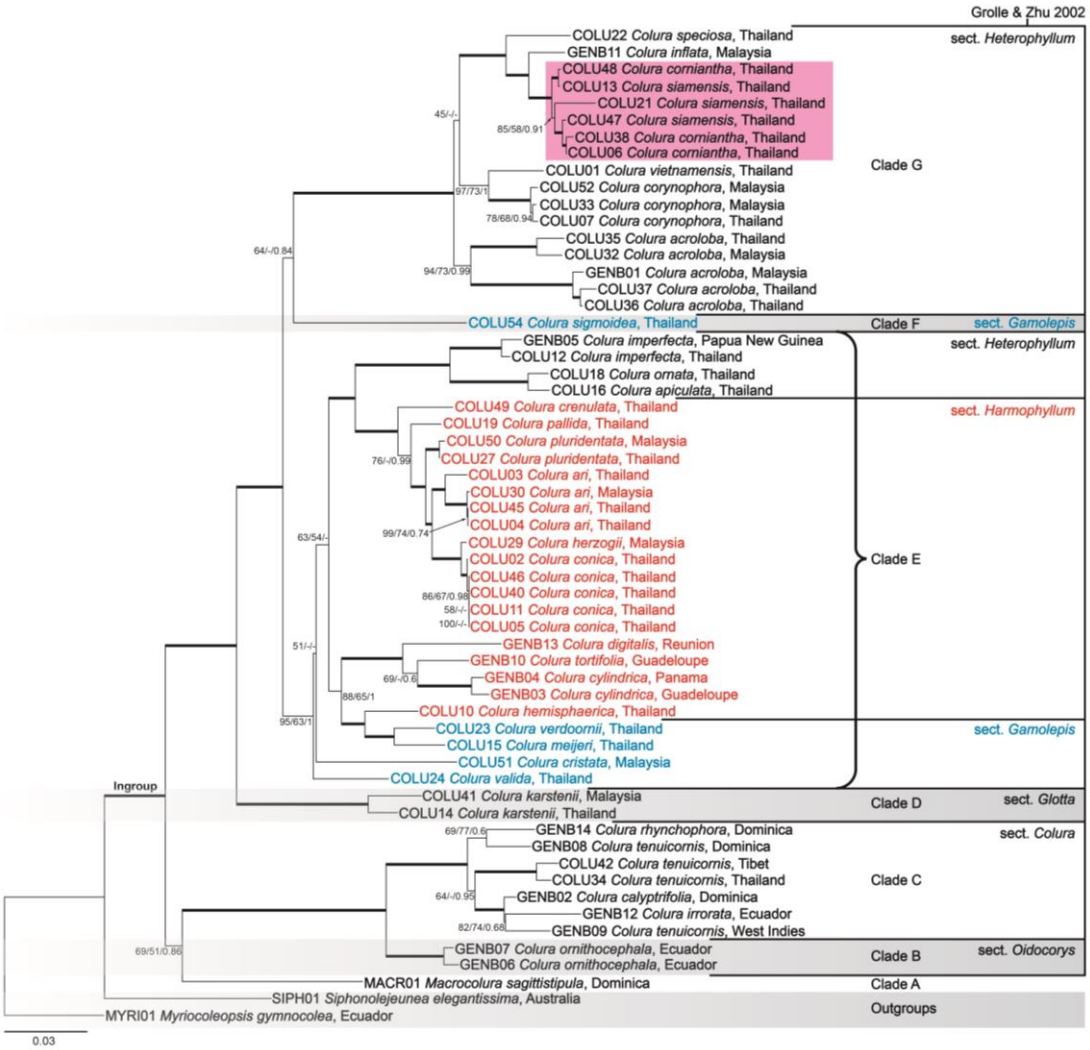

Fig. 3.3 Maximum likelihood phylogenetic reconstruction of the genus *Colura*, inferred from combined dataset (nrITS, *trnL-trnF*, and *rbcL*). Maximum likelihood bootstrap percentage (BS_{ML}), Maximum Parsimony bootstrap percentage (BS_{MP}) and Bayesian posterior probability values (PP_{BI}) are indicated on branches (BS_{ML}/BS_{MP}/ PP_{BI}). Thickened branches indicate $BS_{ML} \geq 80\%$, $BS_{MP} \geq 80\%$ and $PP_{BI} \geq 0.95$. Pink box shows a species complex of *C. corniantha* and *C. siamensis*. The previous infrageneric classification based on Grolle and Zhu (2002).

3.4 Discussions

3.4.1 Phylogenetic relationship of the infrageneric classification

This study presents the comprehensive molecular phylogeny within the genus *Colura*, with a set of taxonomic samples covering all previously described infrageneric subdivisions. The resulted topology, however, shows incongruence between morphological and phylogenetic infrageneric classification that corresponds

well with discussion of Heinrichs *et al*. (2012). The topology shows two major groups (Fig. 3.3). The first one consists of Clade B and C, which is distinctly placed sister to the *Macrocolura sagittistipula* (Clade A). Thus, the result suggests that *Macrocolura* should be retained as a member of *Colura* but may be formed a new subgenus with its apomorphies: 1) insertions of underleaves being invertedly J-shaped, 2) having asymmetrical underleaves, and 3) rhizoid fascicules originating at the middle of underleaves. However, additional voucher specimens and genomic loci will be needed to confirm its taxonomic status. Clade B consists of *C. ornithocephala* belonging to sect. *Oidocorys* and Clade C includes members of sect. *Colura*. with strong supports. The sect. *Colura* was resolved here as a monophyletic group. These two sections are also belonging to subg. *Colura*. Three major synapomorphies which unite these two sections are 1) valves with two superimposed hinge cells, 2) leaf-cell lacking intermediate thickenings and 3) perianths with 5 keels.

Another group is a core group of *Colura* including four clades (Clade D, E, F, and G). Morphological synapomorphies for these clades are 1) lobule sacs usually smaller than leaf lobe, 2) the presence of trigones and intermediate thickenings, and 3) having 3(4–5) perianth keels. From the resulted topology, Clade D, including *C. karstenii* which belongs to the sect. *Glotta*, seems to be a monophyletic group because it was separated with strong supports. Nonetheless, only specimens of *C. karstenii* (K.I.Goebel) from Thailand (COLU14) and Malaysia (COLU41) were included in this analysis. In addition, the vast majority of species belonging to sect. *Glotta* are distributed in Africa and Australia, therefore are not included in the current analysis. To confirm the monophyly of this section, a broader set of taxa from this section should be included.

Within Clade E, members of three sections were included, namely sect. *Harmophyllum* (red), sect. *Heterophyllum* (black), and sect. *Gamolepis* (blue). The only synapomorphy of these three sections is the presence of semicircular to hook-like valve frame. The sect. *Harmophyllum* are resolved as polyphyletic, according to the species in the main clade of sect. *Harmophyllum* are resolved as sister to sect. *Heterophyllum* (*imperfecta-apiculata*), while the American species belonging to sect. *Harmophyllum* (*digitalis-cylindrica*), which form a strong clade are placed sister to sect. *Gamolepis* clade (*meijeri-verdoornii*). Besides, *Colura hemisphaerica* is also

sister to the sect. *Gamolepis* with high supports (BS_{ML} = 100, BS_{MP} = 99, PP_{BI} = 1). From the present investigation, the valve characters of *C. hemisphaerica* are 1) the presence of basal median cell of valve directly adnate with an upper cell of the hinge and 2) two elongated basal hyaline marginal cells are also presented which these two features resemble more of the species in sect. *Gamolepis*. Therefore, *C. hemisphaerica* should not be the member of sect. *Harmophyllum*. According to the phylogeny, the species belonging to sect. *Gamolepis* are polyphyletic and their phylogenetic relationships within the section are still unclear. More accessions from a number of locations might resolve the taxonomic problems of this section. Although the recent new species, *C. sigmoidea* (Clade F), is recognized by its basal median cells of valve adnate to hinge cells to form a sigmoid curve in outline which resembles valves of species in sect. *Gamolepis*, the molecular phylogeny provides the weak supports (BS_{ML} = 64, BS_{MP} = -, PP_{BI} = 0.84) for the placement of the new species as sister to the rest of sect. *Heterophyllum* (Clade G) and also support this species as a distinct species within the genus *Colura*.

All vouchers of Clade G belonging to sect. *Heterophyllum* are recognized by 1) having dimorphic leaves, 2) the presence of small crest at sac apices, and 3) having reducing valve frame. The other heterophyllous species, including the type of the section (*C. imperfecta*) nested in Clade E, are distinguished from them by 1) having distinct valve frame, hook-like shape and 2) sac apices ending with a large crest with (1–)2–4 teeth. Hence, the sect. *Heterophyllum* is a polyphyletic group. According to this reconstruction, the dimorphic-leaf characters may be evolved twice in genus *Colura*. Thus, the morphological and phylogenetic analyses provide the support to split this section into two entities.

Molecular data suggested that the genus *Colura* should be divided into 2 subgenera, namely subg. *Colura* and subg. *Glotta*. The subg. *Colura* is now including only two sections, namely sect. *Colura* (Clade C) and sect. *Oidocorys* (Clade B) while subg. *Glotta* appears to include four groups: sect. *Glotta* (Clade D), unresolved Clade E and Clade F, and Clade G. The taxonomic status of *Macrocolura* (Clade A) is still unclear. To formally resolve their taxonomic statuses, the rest of *Colura* species mainly distributed in Africa and Neotropics and more loci should be included in further molecular phylogenetic analysis.

3.4.2 *Colura inflata* and related species

In this study, I used an integrative approach to investigate species boundaries within *C. inflata* complex. The resulted topology shows non-monophyletic species between *C. corniantha* and *C. siamensis*, while *C. inflata* is separated as a distinct clade (Fig. 3.3, pink box). Based on additional specimens collected from varied places along Thai-Malay Peninsula, *Colura inflata* resembles *C. corniantha* and *C. siamensis* by strongly swollen perianth keels; however, the former differs from the latter two species by non-saccate leaf apices being obtuse, entire or denticulate (Fig. 3.2J), and denticulate leaf lobe margin and teeth distributed from apex to base (Fig. 3.2H–J). Thus, the morphological and molecular evidence supports *Colura inflata* as a distinct species.

Monophyly of *C. corniantha* and *C. siamensis* was strongly supported, consistent with their shared morphological characters. Their shared morphological features vary greatly even in the same locality, indicating that the characters used to distinguish these species from each other are not constant. In other words, the presence of apical teeth on perianth keel is vary greatly on many specimens collected in this work (Fig. 3.4). According to the field surveys and herbarium collections, as well as the previous reports (Jovet-Ast 1953, Jovet-Ast 1961, Jovet-Ast 1967a), these two species were found to be overlapping in distribution ranged from South Vietnam, North East Thailand, and Thai-Malay Peninsula. Based on the presented morphological, molecular and distribution data, it is suggested that *C. corniantha* and *C. siamensis* should be conspecific. Therefore, *C. siamensis* is here reduced to synonymy with *C. corniantha*.

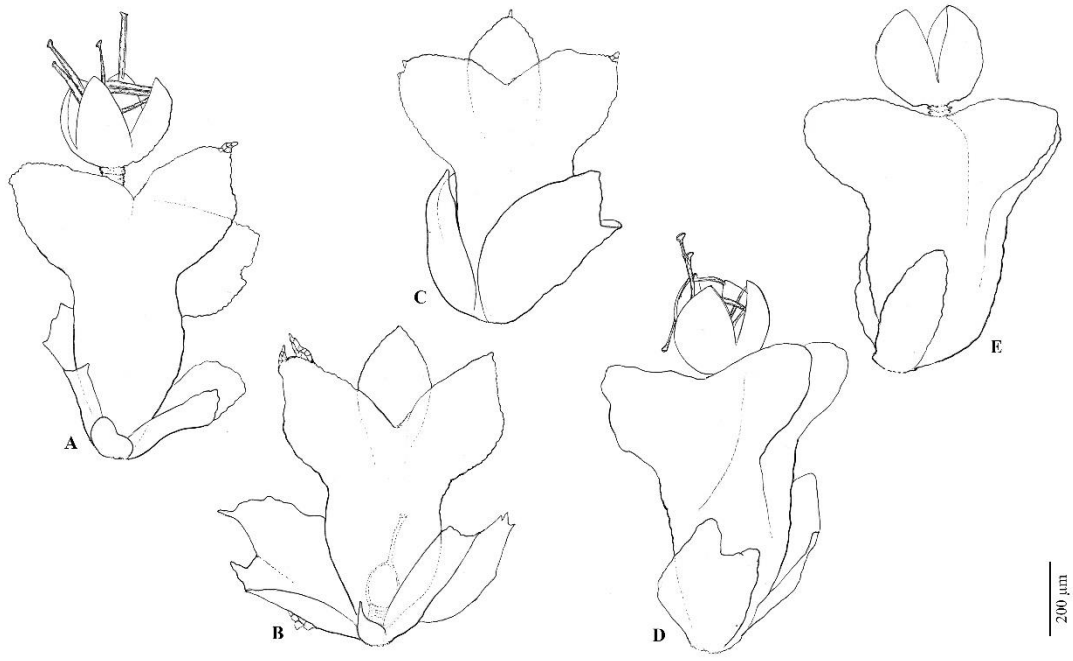

Fig. 3.4 The comparison of perianth keel apices of *Colura corniantha* and *C. siamensis* showing the presence/absence of apical teeth: A–C. *C. corniantha*; A. Krung Ching Waterfall, Nakhon Si Thammarat (COLU48); B. Heo Lom Waterfall, Chumphon (COLU38); C. Ton Deng Waterfall, Phangnga (COLU06). D & E. *C. siamensis*; D. Peninsular Botanical Garden (Thung Khai), Trang (COLU47); E. Khao Yai National Park, Nakhon Ratchasima (COLU21).

3.4.3 Cryptic species

According to the resulted topology, *Colura acroloba*, a common species, was reconstructed into two groups with strong supports. The first group includes highland plants (COLU32 & 35) and the other comprises lowland vouchers (COLU36 & 37). These two groups share similar characters, such as 1) equal size of saccate and non-saccate leaves, 2) the obtuse lobe-apices of saccate leaves, and 3) elliptic sac ending with small crests; the highland plants, however, are morphologically distinguished in having obviously larger plants and monoicy, while the lowland plants are smaller in size and dioicy. Both morphological and molecular evidences suggest that *C. acroloba* seems to be cryptic species as had been observed in many genera, such as *Conocephalum*, *Frullania*, *Metzgeria*, *Pellia*, *Ptilidium* and *Diplasiolejeunea* (Dong *et al*. 2012). For further study, more specimens from various localities and more loci are needed to delimit the species boundary within this cryptic species.

CHAPTER 4

TAXONOMIC TREATMENTS

4.1 Introduction

Because of a large number of *Colura* species around the world, the taxonomic study of this genus should be conducted in the regional scale. In terms of biodiversity, Malesian region is considered to be the hottest hotspot, including Sundaland, Wallacea, and Philippines, in Southeast Asia, because around 42,620 plant species were found in this area. Amongst this, ca. 17,083 endemic plants (7.4% of global plants) were also reported in Malesia (Myers *et al*. 2000). Moreover, all these three biodiversity hotspots encompass Indo-Burma through Kangar-Pattani line (Myer *et al*. 2000). The Malesian region is lined along the Equator where tropical rain forest (including montane forests) is the main vegetative type. The tropical rain forests may harbour more bryophyte species than any other of the world's major ecosystems (Gradstein & Pócs 1989). Furthermore, tropical forests usually provide a large variety of microhabitats fit for bryophytes (Pócs 1982). Therefore, the Malesian region is one of the most interesting areas for bryophyte examination.

Thirty species of *Colura* have been previously reported in Malesian region (Sande Lacoste 1864, Stephani 1916, Jovet-Ast 1953, 1954, 1958b, 1967a, 1967b, 1976, Grolle 1965, Reed & Robinson 1967, Tixier 1970, 1973). However, new records and new species of *Colura* in Malesia and adjacent area are discovered continuously (Pócs & Eggers 2007, Pócs *et al*. 2011, Chantanaorapint & Pócs 2014, Pócs 2013, Pócs & Lee 2016, Sangrattanaprasert *et al*. 2017, 2018, 2019). It supports that this region is a major area for investigation the diversity of this genus. Furthermore, the critical explorations of *Colura* species in unexplored areas are necessary, and more new species and new records are expected. Hence, the present study aims to revise the genus *Colura* in Malesia taxonomically, based on field collections and herbarium specimen examination.

4.2 Materials and Methods

This revision is performed based on plant materials approximate 1,200 specimens from both field collections and herbarium specimens from the following herbaria: BCU, BKF, BM, BO, CMU, E, EGR, HSNU, JE, KLU, L, MO, PC, and SING (herbarium code following Thiers 2018). In addition, the habitat, ecology, and phytogeography are noted. Description of the genus, key to species, as well as descriptions, habitat, ecological data, and distribution of each species are also provided.

Plant length and width were measured when the plants were completely rehydrated (Fig. 4.1A). Shoot width was sized as the width between the opposite leaf apices (Fig. 4.1A). The stem width was examined by both measuring the distance of diameter and counting number of cortical and medullary cells in transection. The cortical and medullary cells were also sized. Cell length was defined as the greatest distance between opposite of the middle of cell walls and cell width was measured perpendicularly to length. Leaf arrangement was observed, and leaf insertion angle was measured as the angle from the line of lobular margin to the vertical line formed by stem (Fig. 4.1A). For the saccate leaves, leaf length was measured as the distance from the base to lobule sac apex; lobule sacs and leaf lobes were also sized in length and width (Fig. 4.1B). For the non-saccate leaves, leaf length was measured from the base to apex of leaf lobe and leaf width was sized perpendicularly to length from dorsal margin to ventral margin of leaf lobe; lobule length and width were also measured (Fig. 4.1C). Leaf lobe cells from three regions, namely marginal, median, and basal cells were measured in length and width like the cells of stem. Oil body numbers were counted per cell and each of them was measured in length and width as well. Valve patterns were observed, and valve length was sized from the base of basal hyaline to apical hyaline cells; the width of valves is the widest distance from side to side (Fig. 4.1D). Valve frame width is the distance edge to edge (Fig. 4.1E). Hyaline papillae were sized the distance of diameter (Fig. 4.1D). Underleaf lobes are triangular, lanceolate or filiform in shape; thus, their length was measured from the base to apex of lobe and lobe width is the widest distance of lobe base (Fig. 4.1F). Male/female bract lobe and lobule and bracteole were measured in both length and

width (Fig. 4.1G–J). Perianth length is the distance from the basal insertion to perianth beak, and perianth width is the greatest distance between opposite keels. The elongated keels were also measured (Fig. 4.1K). Sporangia were measured distance of diameter in mature and non-dehisced capsule. After dehiscence, sporangial valve length was sized from apex to base of valve lobe and valve width was measured from side to side at valve base (Fig. 4.1L). Elater length and width were also measured. Spores were observed at 1000× magnification for measurement and ornamentation investigation (Fig. 4.1M).

The full descriptions and line drawings of all species are provided. The key to species of *Colura* in Malesian region are constructed. Ecological data and their distributions were also provided based on literatures, herbarium labels, and the recent collections. The author names are abbreviated according to Brummitt and Powell (1992), the terminology described in this work was followed Malcolm and Malcolm (2006).

The recent specimens of *Colura* from field surveys were deposited at Prince of Songkla University Herbarium (PSU) and some duplicated specimens were housed at BKF and HSNU.

4.3 Results and discussions

Based on approximately 1,200 specimens of *Colura* investigated from either fresh field material or herbarium specimen in this present study, 34 species are recognised in Malesian region (Table 4.1). The description of genus, key to species as well as descriptions, distribution, habitat, ecological data, examined specimens, and illustrations of each species are provided.

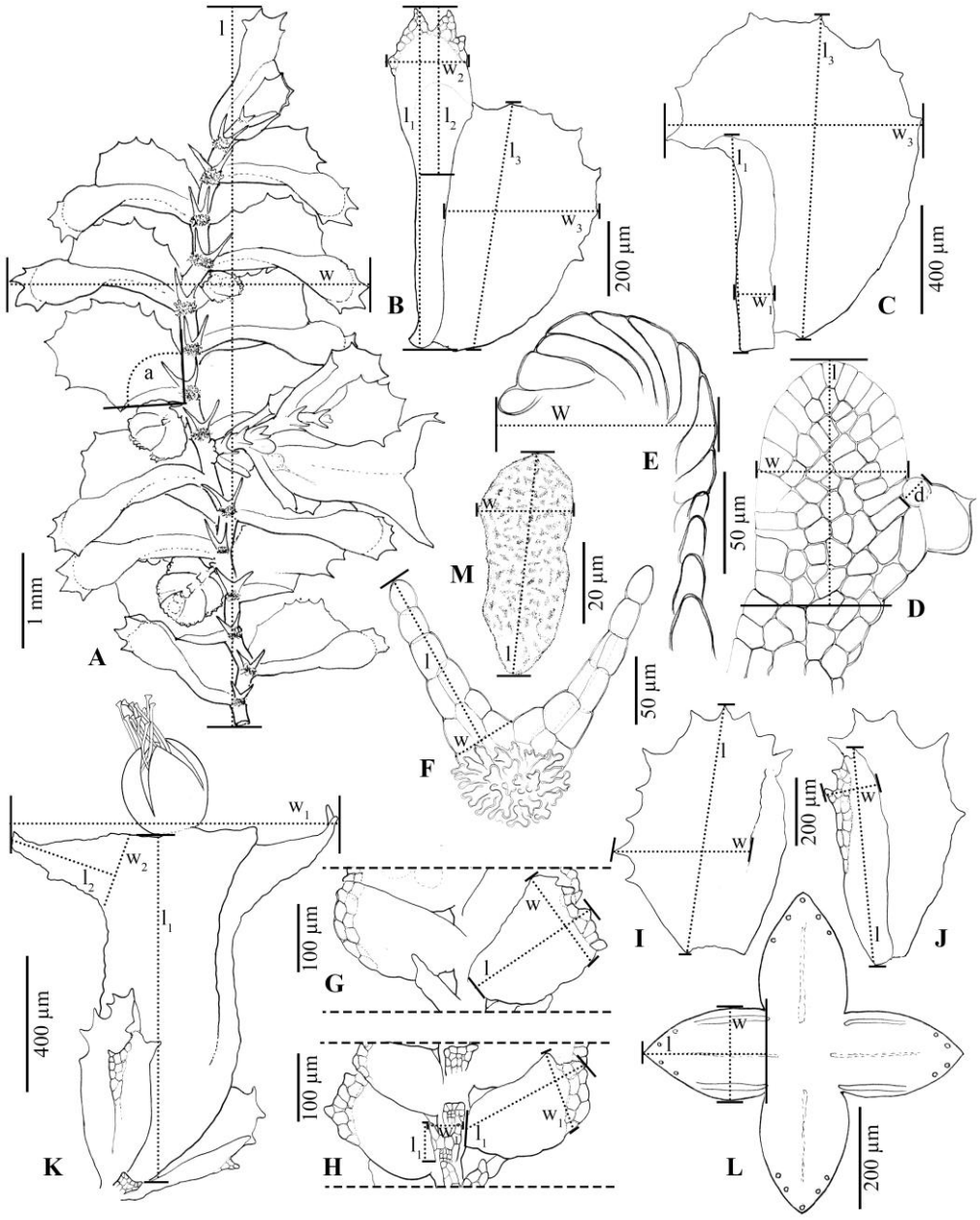

Fig. 4.1 Methods of measurement in *Colura*: A. Portion of plant, ventral view (a = leaf insertion angle, l = length, w = width). B & C. Saccate and non-saccate leaves, ventral view (l_1 = lobule length, l_2 = sac length, l_3 = lobe length, w1 = lobule width, w_2 = sac width, w_3 = lobe width). D. Valve (d = diameter of hyaline papilla, l = length, w = width). E. Valve frame (w = width). F. Underleaf (l = lobe length, w = lobe width). G. Male bracts, dorsal view (l = lobe length, w = lobe width). H. Male bracts, ventral view (l = lobule length, w = lobule width). I. Female bract, dorsal view (l = lobe length, w = lobe width). J. Female bract, ventral view (l = lobule length, w = lobule width). K. Perianth with mature sporangium (l_1 = perianth length, l_2 = keel length, w_1 = perianth width, w_2 = keel width). L. Dehisced sporangium (l = valve length, w = valve width). M. Spore (l = length, w = width).

Table 4.1 Habitats, elevations and forest types of *Colura* species recorded in Malesian region. Microhabitat: E = epiphyllous, R = ramicolous, C = corticolous. Forest type: lef = lowland evergreen forest, lmf = lower montane forest, umf = upper montane forest.

	Species name	Microhabitats			Elevations (m)	Forest types
		E	R	C		
1	*Colura acroloba* (Mont.) Jovet-Ast	✓			20–2900	lef, lmf, umf
2	*Colura apiculata* (Schiffn.) Steph.	✓			600–1000	lef, lmf
3	*Colura ari* (Steph.) Steph.	✓			37–607	lef, lmf
4	*Colura bisvoluta* Herzog *et* Jovet-Ast	✓			70–105	lef
5	*Colura brevistyla* Herzog	✓	✓		220–1800	lef, umf
6	*Colura calyptrifolia* (Hook.) Dumort.	✓	✓	✓	2078–2130	umf
7	*Colura clementis* Grolle (1965)	✓			1230–2000	lmf, umf
8	*Colura conica* (Sande Lac.) K.I.Goebel	✓	✓		10–580	lef
9	*Colura corniantha* Grolle	✓			38–1260	lef, lmf
10	*Colura corynophora* (Nees *et al*.) Trevis	✓			10–1190	lef, lmf
11	*Colura crenulata* Grolle	✓	✓		1000–2100	lmf, umf
12	*Colura cristata* Jovet-Ast	✓		✓	170–253	lef
13	*Colura denticulata* Jovet-Ast	✓			670–900	lmf
14	*Colura galeata* Jovet-Ast	✓			1200–1500	lmf
15	*Colura hemisphaerica* Jovet-Ast	✓	✓	✓	820–1750	lmf
16	*Colura herzogii* Jovet-Ast	✓			800–1645	lmf
17	*Colura imperfecta* Steph.	✓			10–500	lef
18	*Colura inflata* K.I.Goebel	✓			300–1080	lef, lmf
19	*Colura junghuhniana* (Prantl) Steph.		✓		ca. 2430	umf
20	*Colura karstenii* K.I.Goebel	✓	✓	✓	490–1460	lmf
21	*Colura maxima* Jovet-Ast			✓	ca 300	lef
22	*Colura medusa* J.Eggers *et* Pócs	✓			100–700	lef
23	*Colura meijeri* Jovet-Ast.	✓	✓	✓	1100–1400	lmf
24	*Colura mosenii* Steph.	✓			ca. 400	lef
25	*Colura ornata* K.I.Goebel	✓			100–300	lef

	Species name	Microhabitats			Elevations (m)	Forest types
		E	R	C		
26	*Colura palawanensis* Jovet-Ast	✓			80–1300	lef, lmf
27	*Colura pallida* Steph.	✓	✓	✓	930–1070	lmf
28	*Colura pluridentata* Jovet-Ast	✓	✓	✓	38–720	lef
29	*Colura sigmoidea* Sangratt. *et al*.	✓	✓		200–1705	lef, lmf
30	*Colura speciosa* Jovet-Ast	✓			100–450	lef
31	*Colura superba* (Mont.) Steph.	✓			143–945	lef, lmf
32	*Colura tenuicornis* (A.Evans) Steph.	✓	✓		779–2139	lmf, umf
33	*Colura valida* Jovet-Ast	✓	✓	✓	850–1745	lmf
34	*Colura verdoornii* Herzog *et* Jovet-Ast	✓	✓		500–1800	lef, lmf, umf

4.3.1 Taxonomic treatment

Colura (Dumort.) Dumort., Recueil Observ. Jungerm. 12. 1835.

≡ *Lejeunea* sect. *Colura* Dumort., Syll. Jungerm. Europ. 32. 1831.

= *Colurolejeunea* (Spruce) Steph., Hedwigia 30: 208. 1891.

Type: *Colura calyptrifolia* (Hook.) Dumort (≡ *Jungermannia calyptrifolia* Hook.).

Plants small to large, pale yellowish green to dull green, epiphyllous, rarely epiphytic; shoots irregularly pinnately branched, branches of the *Lejeunea*-type. *Stems* in transverse section consisting of (6–)7 cortical and (1–)3 medullary cells; cortical cells subquadrate to oblong, medullary cells subquadrate to isodiametric; ventral merophyte of stem 2 cells wide. *Rhizoids* numerous, fasciculate at base of underleaves, hyaline. *Leaves* uniform (only saccate leaf) or dimorphic (composed of saccate and non-saccate leaves), incubous, remote, contiguous to imbricate, spreading from stem at an angle of (0°–)40°–90°(–120°). *Saccate leaf lobules* narrowly tubular, flaring toward sac; lobule sacs variable in size and shape, strongly inflated, sac surface smooth, conical mamillose or strongly papillose, apices obtuse to acute or forming a long tubular beak toward the apex, entire or cristate. *Valves* variable in size and shape, composed of one circle of hyaline marginal surrounding median cells, with or without distinction of median cells and hinge cells. *Hyaline papillae* bulbous to

spherical, 10–20 μm in diameter, situated at the end of lobule beside valve. *Valve frames* outline semicircular; cell wall smooth or nodulose; valve frames reduced in some species. *Non-saccate leaf lobules* usually narrowly oblong, not fused with leaf lobe. *Leaf lobes* variable in size and shape, flattened, undulate, or revolute; dorsal margin entire, crenulate to dentate. *Lobe cells* thin wall, usually with distinct trigones and intermediate thickenings (except for *C. calyptrifolia* (Hook.) Dumort, *C. medusa* J.Egger *et* Pócs, and *C. tenuicornis* (A.Evans) Steph.); dorsal surface smooth to mamillose or strongly papillose in some species. *Cuticle* smooth on both sides. *Oil bodies* usually more than 10 to numerous per cell, ellipsoid, greyish, homogenous or compound type; the compound one finely to coarsely segmented or knobby on the surface. *Ocelli* absent. *Underleaves* distant, deeply bilobed, sinus acute to obtuse; lobe triangular, lanceolate or filiform, 3–15(–22) cells long, 1–5 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on lobule sac apices and/or leaf lobes or even on dorsal lobes of female bracts and perianth keel apices; gemma cells subquadrate to isodiametric, consisting of 24–34 cells.

Autoicous or *dioicous* (*heteroicous in C. acroloba* (Prant) Jovet-Ast). *Androecia* lateral, terminal or intermediate on main stems and lateral branches; male bracts hemispherical, inflated, apical keel crenulate with 1(–3) projecting cell row, free margin entire to crenulate or dentate, imbricate; bract lobes oblong to semicircular; bract lobules semicircular, slightly shorter than or almost as long as the lobe; antheridia 2 per bract; male bracteoles variable in size and shape, presented throughout androecium. *Gynoecia* terminal on lateral branches with 1(–2) pycnolejeunoid innovation; female bract lobes variable in size and shape; bract lobules narrowly oblong; female bracteoles bilobed or quadrangular, oblong, round to cordate. *Perianths* exserted, variable in shape and size, inflated with 3–5 keels; surface of the perianth smooth to strongly mamillose or papillose; beak (0–)1–3(–6) cells long. *Sporophytes*. *Setae* articulate, 8–9(–16) cells long, in transverse section with 12 outer cells surrounding 4 inner cells. *Capsules* spherical, black, splitting into four erect valves after dehiscence; capsule valves hyaline, wall 2–3 stratose. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper part of valve rhombic, large, thin-walled; hinge butterfly-shaped, rectangular or broadly quardrate, hinge cells rectangular to quadrate, smaller than cells of upper half, thin-walled;

marginal cells rectangular, formed by 1–2 rows. *Inner layer of capsule valve* cells in the centre rectangular, walls with nodular thickenings; marginal cells of upper half quadrate, walls nodulose, formed by 1–2 rows, marginal cells of lower half rectangular, walls smooth; basal cells subquadrate with smooth walls. *Elaters* of 2 types: marginal and additional; marginal elaters 22 per capsule, each valve contains 4 or 5 upper marginal and 2 or no lower marginal elaters; upper marginal elaters attached to upper half of valve margin by one end, hyaline to yellowish, with irregular to annular thickenings, end attached to valve margin rounded, not expanded, free end dilated; lower marginal elaters attached to valve by both end (near and parallel to basal margin), hyaline, with irregular to annular thickenings, upper end narrowly tapered, lower end obtuse; additional elaters 4 per capsule (1 per each valve), hyaline, with smooth to irregular thickenings, attached along their whole length to median part of valve, even upon dehiscence. *Spores* green, irregular oblong or elongate rectangular; spore surface covered with irregular lamellae or papillated; rosette mostly absent (excepted in *C. junghuniana* and *C. tenuicornis*); sporeling *Lejeunea*-type.

Key to species of the genus *Colura* in Malesian Region

1. Lateral leaves dimorphic, composed of sacate and non-saccate leaves. Underleaf lobes filiform to narrowly lanceolate 2
1. Lateral leaves uniform, only saccate leaves. Underleaf lobes triangular to lanceolate, rarely filiform in *Colura cristata* 12
2. Valves of lobule sacs reduced to a few cells or entirely absent ..... **17. C. imperfecta**
2. Valves of lobule sacs present, distinctly large including more than 10 cells 3
3. Valves frames well-developed, hook-like 4
3. Valves frames reduced, remaining only ridge cells of leaf lobe 7
4. Lobule sacs triangular to lanceolate; apex of lobule sac acute ending with 1 triangular tooth ..... **26. C. palawanensis**

4. Lobule sacs round, spherical or elliptic; apex of lobule sac obtuse ending with (1–)2–4 teeth 5

5. Lobule sacs obliquely round, valves small composed of 20–42 cells. Perianth shape oblong; keel short baering course teeth at keel apex ..... **13. C. denticulata**

5. Lobule sacs spherical to elliptic, valves large composed of 38–52 cells. Perianth shape obtriangular to urceolate; keel obtriangular spreading horizontally 6

6. Perianth keels strongly horizontally extended, 160–320 × 144–200 μm in size ..... **2. C. apiculata**

6. Perianth keels short horizontally extended, 120–160 × 80–160 μm in size ..... **25. C. ornata**

7. Leaf lobe margins usually entire. Lobule sac apices entire or rarely ending with small crest, consisting of 1–3 cells 8

7. Leaf lobe margins strongly dentate to crenate. Lobule sac apices ending with crest, 1–2 teeth, consisting of more than 3 cells 9

8. Lateral leaves mostly saccate. Lobe apices of saccate leaves obtuse. Lobule sacs ovate to elliptic; apices entire or ending with a small crest ..... **1. C. acroloba**

8. Laterall leaves mostly non-saccate. Lobe apices of saccate leaves truncate. Lobule sacs round to widely elliptic; apices entire ..... **10. C. corynophora**

9. Perianth keels flattened 10

9. Perianth keels strongly inflated 11

10. Margins of non-saccate leaves densely dentate. Perianth keels bearing teeth ..... **14. C. galeata**

10. Margins of non-saccate leaves crenate to loosely dentate. Perianth keels crenate ..... **30. C. speciosa**

11. Non-saccate leaf apices acute. Saccate leaf dorsal margins strongly dentate on the upper half; teeth triangular, 3–9(–22) cells. Perianth keels apices ending with teeth or entire ..... **9. C. corniantha**

11. Non-saccate leaf apices obtuse. Saccate leaf dorsal margins denticulate from base to apex; teeth 1–3 cells. Perianth keels apices entire ..... **18. C. inflata**

12. Sac apices forming thread-like tubular beak. Leaf cell walls smooth; intermediate thickenings absent 13

12. Sac apices obtuse to acute, not forming thread-like tubular beak. Leaf cell walls nodulose; intermediate thickenings distinct 16

13. Tubular beaks long, 1/2 of lobule length 14

13. Tubular beaks shorter, 1/3–1/4 of lobule length 15

14. Sac surface nearly smooth to mamillose. Underleaves symmetrical. Perianth beak short, 1 cell long ..... **32. C. tenuicornis**

14. Sac surface conical mamillose to papillose. Underleaves asymmetrical, one side larger than other one. Perianth beak very long, 5–6 cells long ..... **22. C. medusa**

15. Sac surface strongly papillose. Underleaf lobes long, 6–10 cells long ..... **19. C. junghuhniana**

15. Sac surface nearly smooth to mamillose. Underleaf lobes short, 2–4 cells long ..... **6. C. calyptrifolia**

16. Dorsal margins of leaf revolute. Valves without basal median and hinge cells, very large consisting of 75–350 cells 17

16. Dorsal margin of leaf not revolute. Valves with distinct basal median and hinge cells, smaller than above, mostly consisting of less than 70 cells (except in *C. cristata* which can be found up to 79 cells) 18

17. Lobule sacs obovate to slightly elliptical; surface strongly mamillose; valves consisting of 70–170 cells. Perianths obovate with 3 keels ..... **4. C. bisvoluta**

17. Lobule sacs ovate to slightly elliptical; surface nearly smooth to slightly mamillose; valves consisting of more than 300 cells. Perianths obdeltoid to oblong with 5 keels ..... **20. C. karstenii**

18. Leaf dorsal margin dentate 19

18. Leaf dorsal margin entire, crenulate to denticulate 24

19. Apices of lobule sac obtuse, lacking apical crest. Underleaf lobe wide, 8–22 cells long and 6–11 cells wide 20

19. Apices of lobule sacs acute, bearing apical crest. Underleaf lobe narrow, 5–13 cells long and 3–7 cells wide 21

20. Lobule sacs elliptic. Dorsal margin of leaf lobe strongly undulate ..... **27. C. pallida**

20. Lobule sacs cylindrical fusiform to lanceolate. Dorsal margin of leaf lobe flattened ..... **28. C. pluridentata**

21. Lobule falciform in outline; sac apices horizontally exerted 22

21. Lobule straight in outline; sac apices vertically exerted 23

22. Lobule sacs large, 1/3–1/2 of lobule length (rarely reduced to tiny sac). Dioicous. Perianth keels horizontally extended ..... **8. C. conica**

22. Lobule sacs small, 1/6–1/3 of lobule length. Autoicous. Perianth keels not extended ..... **3. C. ari**

23. Lobule sacs conical to broadly elliptic; apices obtuse. Perianth keel horizontally extended ..... **16. C. herzogii**

23. Lobule sacs elliptic to cylindrical fusiform; apices acute. Perianth keels short, not extended ..... **31. C. superba**

24. Leaf surface papillose ..... **21. C. maxima**

24. Leaf surface mamillose 25

25. Lobule sac length short, 1/3 of lobule length 26

25. Lobule sac length long, ≥ 1/2 of lobule length 27

26. Lobule valve oblique elliptic; basal median cell rectangular, sometime adnate to a hinge cell ..... **34. C. verdoornii**

26. Lobule valve ovate to elliptic; basal median cell triangular to dome-shape, not adnate to hinge cell ..... **7. C. clementis**

27. Apices of lobule sac ending with apical crest 28

27. Apices of lobule sac obtuse lacking apical crest 30

28. Lobule sac ovate to lanceolate; basal median cell of valve always adnate to a hinge cell forming a sigmoid curve in outline ..... **29. C. sigmoidea**

28. Lobule sac elliptic; basal median cell of valve free or adnate with a hinge cell not forming a sigmoid curve in outline 29

29. Apical crest of lobule sac huge including 7–17 cells. Lobule valve large consisting of 59–71 cells. Perianth keels not extended ..... **12. C. cristata**

29. Apical crest of lobule sac small including 1–5 cells. Lobule valve small consisting of 38–39 cells. Perianth keels horn-like, spreading horizontally ..... **11. C. crenulata**

30. Lobule sac cylindrical fusiform to lanceolate 31

30. Lobule sac elliptic to round 32

31. Leaves short, 0.9–1.1 mm in length ..... **24. C. mosenii**

31. Leaves longer, 1.6–2.1 mm in length ..... **5. C. brevistyla**

32. Lobule sacs round to widely elliptic ..... **15. C. hemisphaerica**

32. Lobule sacs elliptic 33

33. Leaf lobes as wide as lobule sacs; underleaves 8–11 cells long and 4–5 cells wide ..... **23. C. meijeri**

33. Leaf lobes ca. 2 times width of lobule sac; underleaves 12–16 cells long and 6–9 cells wide ..... **33. C. valida**

1. *Colura acroloba* (Prantl) Jovet-Ast, Rev. Bryol. Lichénol. 22: 297, 1953.

(Figs. 4.2–4.3)

≡ *Lejeunea acroloba* Prantl, Hedwigia 29: 97, 1980. **Type:** PHILIPPINES, "Manila", s.d., Collector unknown (holotype: W n.v.).

Plants pale green, 0.3–0.7 cm long; shoots 0.98–1.56 mm wide. *Stems* 40–80 µm in diameter, in transverse section consisting of 7 cortical cells (20–30 × 20–30 µm) and 3 medullary cells (12–18 × 10–16 µm). *Leaves* contiguous to imbricate, spreading from stem at 50°–80° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaves lobes* 0.72–0.8(–1.4) mm long, 0.45–0.9 mm wide; dorsal margin flattened, entire; lobules narrowly tubular, flaring toward sac, 0.68–0.78(–1.4) mm long; lobule sacs obovate to elliptic, strongly inflated, 0.2–0.22(–0.32) mm long, 0.14–0.17(–0.23) mm wide, sac surface mamillose, apex slightly acute, entire or ending in apical crest consisting of 1–3(–5) cells; valves elliptic to ovate, 94–120(–140) × 40–60 µm, composed of one circle of 20–25 hyaline marginal and 11–30 median cells without basal median cell and hinge; hyaline papillae bulbous, 12–14 µm in diameter; valve frame reduced. *Non-saccate leaves* obovate to elliptic, 0.74–0.9(–1.4) mm long, 0.48–0.52(–0.8) mm wide; apex obtuse to rounded, usually obtuse or round, entire; dorsal margin flattened, entire; lobules narrowly oblong, 0.34–0.46(–0.8) × 0.08–0.11 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells rectangular to hexagonal, 14–30(–50) × 14–26 µm; median cells hexagonal to slightly rectangular, 24–36(–50) × 16–30 µm; basal cells rectangular to hexagonal, 32–60 × 14–30 µm. *Oil bodies* 8–18 per cell, roughly segmented, ellipsoid, 2.4–7.2 × 2.4–4 µm. *Underleaves* deeply bilobed, sinus obtuse; lobe filiform, 80–180(–240) × 20–56(–80) µm, 4–6(–10) cells long, 2–4 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on leaf lobe.

Heteroicous (*autoicous* in highland and *dioicous* in lowland). *Androecia* on lateral branches; male bracts in 8–18 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular, 160–240 × 120–160 µm; bract lobules semi-circular to oblong, 140–240 × 98–140 µm; male bracteoles oblong to bilobed, 40–80 × 34–50 µm, apex obtuse or bilobed. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract oblong to elliptic,

480–656 × 144–280(–440) µm, apical keel entire to crenulate with 1 projecting cell row; bract lobules narrowly oblong, 416–544 × 72–144 µm; female bracteoles rounded to cordate, 60–110 × 50–110 µm, apex round or emarginate. *Perianths* obtriangular, 0.94–1(–1.2) mm long, 0.64–0.86 mm wide, with 3 keels; keels oblique-triangular, 184–320 × 216–280 µm, spreading horizontally, apex obtuse, crenate; beak absent or 1–2 cells long. *Sporophytes*. *Setae* 8–9 cells long. *Capsules* 224–360 µm in diameter, splitting to ± 5/6 of its length; capsule valves 220–340 × 148–220 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic to polygonal, large, thin-walled; hinge rectangular, ca. 1/2 of valve length, hinge cells rectangular to isodiametric, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half rhombic to rectangular, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular to annular thickenings, 160–280 µm long, 10–20 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 130–190 µm long, 10–16 µm wide; additional elaters hyaline, with smooth thickenings, 90–280 µm long, 4–10 µm wide. *Spores* irregular-oblong or elongate-rectangular, 44–104 × 14–36 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura acroloba* was usually found on living leaves in lowland ever green forest and can be found up to montane rain forest, ranging from sea level to 2900 m.

Distribution: Australia, China (Hainan, Taiwan), Fiji Islands, India, Indonesia, Malaysia, New Caledonia, Papua New Guinea, Philippines, Samoa, Solomon Islands, Sri Lanka, Thailand, Vietnam (Jovet-Ast 1953, Jovet-Ast 1961, Reed & Robinson 1967, Tan & Engel 1986, Thiers 1987, Zhu & So 2001, Pócs *et al*. 2011, Pócs 2013, Udar & Awasthi 1985, Yang *et al*. 2013).

Selected specimens examined: INDONESIA. East Kalimantan, Borneo, East Kutei, Peak Balikpapan terr. Beul, 600–700 m, 30 June 1952, *Meijer B1312a*, *B1308* (L); Tulus Bewai, 150 m, 3 July 1952, *Meijer B1397c* (L); 1000 m, 18 July 1952, *Meijer B2615a*, *B2621b* (L); 1200 m, 19 July 1953, *Meijer B2697b* (L). Java, s.d.,

Teysmann s.n. (L); s.d., *Zollinger 386a* (L): s.d., *Molkenboeq s.n.* (L). Nunukan, N. of Tarakan, East Borneo N. part primary forest on hill, low altitude, November 1953, *Meijer B4818, B4895* (L); Sungai Membunut Besar narrow ravine with sandstone-boulders, 100 m, November 1953, *Meijer B5115, B5125* (L); NE. Borneo bivouac 1, 20 November 1953, *Meijer B8171* (L). Sumatra, Brastagi-Tonkkeh, summit of Delangsikut, 1700 m, 19 June 1952, *Van der Wijk 1652* (L); Mt. Korinchi, 1400–1900 m, 29 July 1956, *Meijer B9037, 7700A* (L); Sumatra west coast, E. of Lubuk Sikaping, ± 900 m, 17 June 1953, *Waalkes 2031p.p.* (L); West Sumatra, Taram, E. of Pajakumbuh sandstone region of river Tjampo, 1 August 1957, *Meijer B8527p.p.* (L). MALAYSIA. Border of Pahang and Perak, Cameron Highlands, Gunung Bringchang, 04°31'05.2"N, 101°22'55.3"E, 1985–2031 m, 31 October 2013, *Pócs, Pócs, Lee & Tang 13166/DG* (EGR); Tanah Rata, 1550 m, 23 May 1997, *Verwimp & Verwimp 18860/A, 18880/A* (EGR); Parit Falls, 04°28'26.7"N, 101°23'02.0"E, 1430 m, 1 November 2013, *Pócs, Pócs, Lee & Tang 13168/AF* (EGR). Pahang, Genting Highland, along the road to Gohtong Jaya, 820 m, 9 September 2006, *Cheah & Yong 65* (EGR, KLU). Kelantan, near the Kunci Air Sungai long No.1 water intake, 05°36'05.0"N, 101°44'18.0"E, 660 m, 6 November 2013, *Pócs, Pócs, Lee & Tang 13175/L* (EGR). Selangor, Pangsun valley around the waterfall, 03°12'12.0"N, 101°50'05.8"E, 165–200 m, 26 October 2013, *Pócs, Pócs, Lee & Tang 13161/L* (EGR). PAPUA NEW GUINEA. Morobe, Busu river area Ene of Lae, 200 m, October 1969, *Johns 1L* (EGR). Southern Highland, Nothofagus pumilio stand on the S slope of Mt. Giluwe, 2300 m, 1 September 1974, *Johns 3P* (EGR); ridgearound Lavani Valley, 2900 m, 7 September 1972, *Balázs NG–14AH* (EGR). Wau, Mt. Kaindi, 2000–2300 m, April 1965, *Balogh 3a* (EGR). West Sepik, Star Mt., 2130 m, 16 May 1975, *Touw 18243F* (EGR). THAILAND. Chumphon, Phato, Heo Lom Waterfall, 09°43'47.89"N, 98°40'58.50"E, 105 m, 4 August 2014, *Chantanaorrapint & Promma 3899A* (PSU). Krabi, Khlong Thom, Sa Morakot, 07°55'45.00"N, 99°15'18.9"E, 60–70 m, 9 November 2012, *Pócs & Somadee 1227/AB* (EGR, PSU). Nakhon Nayok, Mueang Nakhon Nayok, Khao Yai National Park, Pha Trom Chai, 14°21'30.22"N, 101°22'51.60"E, 1218 m, 1 June 2015, *Sangrattanaprasert 334/15A, 335/15A, 336/15* (PSU). Nakhon Si Thammarat, Lan Saka, Khao Luang National Park, 08°33'25.22"N, 099°45'47.00"E, 457–1800 m, 24–27 June 2015,

Sangrattanaprasert 348/15A, *349/15*, *356/15A*, *376/15A* (PSU); Nopphitam, Krung Ching Waterfall, ca. 200 m, 31 October 2012, *Pócs, U–Tayanapuh & Lee 1217AF* (PSU); 10 October 2014, *Sangrattanaprasert 214/14A*, *215/14A*, *218/14A*, *223/14A* (PSU); 08°48'38.78"N, 99°44'02.32"E, 607 m, 19 May 2015, *Sangrattanaprasert 330/15A* (PSU); Phrom Khiri, Khao Luang, Yod Lom Fon Peak, 08°32'23.30"N, 099°44'12.19"E, 1537 m, 22 April 2014, *Sangrattanaprasert 97/14* (PSU); Khao Luang, the slope trail from Prom Lok Peak, 08°32'10.27"N, 099°45'27.00"E, ca. 200, 23 April 2014, *Sangrattanaprasert 105/14A* (PSU); Ron Phiboon, Khao Ramrome, 08°14'17.70"N, 99°48'19.10"E, 930–1000 m, 25 September 2013, *Sangrattanaprasert 18/13A*, *19/13A* (PSU); Thung Song, Plew Waterfall, 200 m, 28 October 2012, *Pócs & Lee 1211AF* (PSU). Phangnga, Khura Buri, Si Phang-nga National Park, Ton Deng Waterfall, 08°59'30.96"N, 98°27'56.77"E, 66 m, 3 August 2014, *Chantanaorrapint & Promma 3890A*, *3891A* (PSU); Mueang Phangnga, Sa Nang Manora Forest Park, 08°30'44.70"N, 98°32'18.9"E, 70–110 m, 31 January 2007, *Pócs & Pócs 07015/P* (EGR); Takua Thung, Raman Waterfall, 08°27'03.10"N, 98°26'55.3"E, 20–50 m, 31 January 2007, *Pócs & Pócs 07014/AM* (EGR). Phatthalung, Kong Ra, Khao Loan, 07°26'45.33"N, 99°52'31.64"E, 942 m, 28 May 2017, *Chantanaorrapint & Suwanmala 1059A*, *1061A*, *1079A*, (PSU). Phitsanulok, Nakhon Thai, Kung Han Nam, 16°59'32.40"N, 101°00'44.60"E, 1250 m, 8 December 2013, *Sangrattanaprasert 45/13*, *46/13A* (PSU). Ranong, Suk Samran, Klong-Naka Wildlife Santuary, 09°27'40.27"N, 98°30'35.86"E, 48 m, 4 August 2014, *Chantanaorrapint & Promma 3902A* (PSU). Satun, Thung Wa, Than Plew Waterfall, 07°06'43.00"N, 99°50'30.90"E, 50–100 m, 17 December 2014, *Sangrattanaprasert 257/14A*, *258/14A*, *259/14A* (PSU). Songkhla, Hat Yai, Ton Nga Chang Wildlife Sanctuary, Ton Nga Chang Waterfall, 06°56'41.82"N, 100°13'37.92"E, 420 m, 11 January 2014, *Sangrattanaprasert 48/14* (PSU); 938 m, 21 March 2014, *Chantanaorrapint & Promma 3501A* (PSU); Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 100–150 m, 16 December 2014, *Sangrattanaprasert 248/14A*, *250/14A*, *252/14A*, *254/14A*, *255/14A* (PSU); Na Thawi, Khao Nam Kang National Park, 8 March 2016, *Sangrattanaprasert 470/16A*, *471/16*, *472/16A*, *473/16* (PSU); Sadao, Ton Nga Chang Wildlife Sanctuary, Surat Thani, Phanom, Khao Sok National Park, 08°55'20.50"N, 98°31'43.70"E, 130 m, 28 February 2015, *Sangrattanaprasert 304/15A* (PSU). Trang,

Palian, Khao Chedyod, 07°19'18.80"N, 99°54'40.48"E, 1040–1070 m, 2–3 May 2014, *Sangrattanaprasert 115/14A*, *120/14A*, *127/14A*, *137/14A* (PSU); Yan Ta Khao, Peninsular Botanical Garden (Thung Khai), 07°28'01.00"N, 99°38'24.60"E, 38 m, 12 December 2014, *Sangrattanaprasert 240/14*, *241/14A* (PSU). Yala, Betong, Ban Piyamit 2, Flower Garden, 05°49'04.40"N, 101°05'59.70"E, 860 m, 14 June 2013, *Chantanaorrapint & Promma 2503A* (PSU); Ban Chulabhorn Pattana 10, 05°49'04.40"N, 101°01'50.20"E, 570 m, 15 June 2013, *Chantanaorrapint & Promma 2534A*, *2538A*, *2541A*, *2543A*, *2549A* (PSU); Than To, Wang Sai Stream, 06°00'55.66"N, 101°16'36.36"E, 300 m, 2 July 2014, *Sangrattanaprasert 173/14*, *174/14*, *177/14B* (PSU).

Taxonomic notes: The distinctive features of *Colura acroloba* are 1) dimorphic lateral leaves, 2) the saccate leaves as large as the non-saccate leaves, 3) obtuse lobe-apices of saccate leaves, and 4) ovate to elliptic sacs and often ending with small crest. This species may be confused with *C. corynophora*, particularly viewed under the hand lens. They share similar characters of dimorphic leaves, entire leaf dorsal margins, and reduced valve frames. However, *C. corynophora* differs by large and rounded lobule sacs (0.32–0.36 × 0.22–0.26 mm), obtuse and entire sac apices, and truncate lobe-apices of saccate leaves.

According to all specimens investigated in this work, show that this species is heteroicous. In other words, the lowland populations mostly produce androecia and gynoecia on separate plants (dioicy) while the highland populations produce the male and female gametoecia on the same plant (monoicy). Moreover, *C. acroloba* also shows the morphological plasticity because of the highland specimens which are usually larger than lowland plants.

2. *Colura apiculata* (Schiffn.) Steph. Sp. Hepat. 5: 936. 1916. **(Figs. 4.4–4.5)**

≡ *Colurolejeunea apiculata* Schiffn., Forschungsr. Gazelle 4(4): 36. 1890. **Type:** NEW CALEDONIA. s.d., *Balansa 3694* (holotype: G n.v.).

= *Colura leratii* (Steph.) Steph., Sp. Hepat. 5: 939. 1916. ≡ *Colurolejeunea leratii* Steph. Rev. Bryol. 35: 30, 1908. Type: NEW CALEDONIA. Col d'Amieu, February 1907, *Le Rat s.n.* (holotype: G n.v.; isotype: JE!, PC n.v.).

Plants pale green, 0.7–1.7 cm long; shoots 0.9–1.8 mm wide. *Stems* 70–100 µm in diameter, in transverse section consisting of 7 cortical cells (18–34 × 10–26 µm) and 3 medullary cells (16–20 × 14–18 µm). *Leaves* contiguous to imbricate, spreading from stem at 70°–120° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaves lobes* 0.56–0.82 mm long, 0.34–0.52 mm wide; dorsal margin flattened, dentate; teeth triangular, 1–7 cells, teeth usually distributed on upper half of lobe; lobules narrowly tubular, flaring toward sac, 0.78–1.04 mm long; lobule sacs spherical to elliptic, strongly inflated, 0.38–0.52 mm long, 0.2–0.26 mm wide, sac surface mamillose, apex obtuse, ending with apical crest (1–)2–4 tooth, consisting of 27–33 cells; valves ovate to lingulate, 94–120 × 62–80 µm, composed of one circle of 17–21 hyaline marginal and 20–32 median cells, without basal median cell and hinge; hyaline papillae bulbous, 10–14 µm in diameter; valve frame outline semi-circular to hook-like, 90–120 µm wide; cell wall entire. *Non-saccate leaves* obovate to falcate, 0.77–1.3 mm long, 0.48–0.96 mm wide; apex obtuse, dentate; dorsal margin flattened, dentate; teeth triangular, 5–9 cells, teeth distributed on upper half of lobe; lobules narrowly oblong, 0.32–0.86 × 0.08–0.16 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells subquadrate to rectangular, 18–30 × 14–30 µm; median cells rectangular to isodiametric, 22–60 × 20–30 µm; basal cells rectangular, 38–72 × 24–40 µm. *Oil bodies* 32–50 per cell, roughly segmented, ellipsoid, 4–8 × 1.5–2 µm. *Underleaves* deeply bilobed, sinus obtuse; lobe filiform to lanceolate, 120–220 × 25–60 µm, 4–6 cells long, 2–4 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 4–5 pairs, hemispherical, apical keel crenulate with 1–3 projecting cell row, crenulate to dentate to crenulate, free margin entire; bract lobes semicircular, 180–220 × 120–200 µm; bract lobules semi-circular to oblong, 200–260 × 110–130 µm; male bracteoles subquadrate to bilobed, 30–80 × 30–60 µm, apex obtuse to emarginate. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobe oblique elliptic to obovate, 512–760 × 216–400 µm, apical keel dentate with a few teeth; bract lobules narrowly oblong, 416–600 × 100–120 µm; female bracteoles rounded, subquadrate or oblique, 80–100 × 70–90 µm, apex obtuse to emarginate. *Perianths* obtriangular, 1–1.2 mm long, 0.72–1 mm wide, with 3 keels; keels oblique

triangular, 160–320 × 144–200 µm, spreading horizontally, apex acute; beak 1–3 cells long. *Sporophytes*. *Setae* 9 cells long. *Capsules* spherical, 224–256 µm in diameter, splitting to ± 5/7 of its length; capsule valves 240–280 × 168–184 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic, large, thin-walled; hinge butterfly-shaped to broadly quadrate, ca. 1/2 of valve length, hinge cells rectangular to isodiametric, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half isodiametric, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular to annular thickenings, 154–224 µm long, 8–16 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 140–164 µm long, 10–12 µm wide; additional elaters hyaline, with smooth thickenings, 190–230 µm long, 4–8 µm wide. *Spores* irregular-oblong or elongate-rectangular, 42–52 × 18–22 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura apiculata* is usually found on living leaves in lowland evergreen forests to lower montane rain forest ranging from 40 to 1000 m elevation in Peninsular Malaysia and Indonesia.

Distribution: Australia (Babinda), Fiji, India (Agumbe), Indonesia (Java), Malaysia (Sabah), New Caledonia, Thailand (Southern) (Jovet-Ast 1953, Menzel 1988, Pócs & Streimann 2006, Pócs & Eggers 2007, Chantanaorrapint & Pócs 2014, Dey & Singh 2016).

Specimens examined: INDONESIA. East Kalimantan, East Kutai, District Sumarinda, Tandjong Bangko, W. of the estuary of the river Mahakam, Marshy forest, at sea level, 30 July 1952, *Meijer B2930* (L). West Sumatra, Mt. Tandikat, Padang Panjang, 1000 m, 23 July 1955, *Meijer 8077f* (L). MALAYSIA. Kelantan, near the Kunci Air Sungai long No.1 water intake, 05°36'05"N, 101°44'18"E, 660 m, 6 November 2013, *Pócs, Pócs, Lee & Tang 13175/AC* (EGR); Gunung Basor, halfway between Dabong and Jeri towns near BKT, Gerongan village at Renyok No. 1 water intake, 05°31'38.5"N, 101°46'17.7"E, 450–680 m, 7 November 2013, *Pócs, Pócs, Lee & Tang 13179/R, 13180/P,O, 13181/E* (EGR). THAILAND. Nakhon Si

Thammarat, Nopphitam, Khao Luang National Park, Krung Ching Waterfall, 08°44'05.50"N, 99°39'34.60"E, 280 m,10 October 2014, *Sangrattanaprasert 220/14B*, *221/14B* (PSU); Nopphitam, Khao Nan National Park, 08°48'38.78"N, 99°44'02.32", 607 m, 19 May 2015, *Sangrattanaprasert 330/15C* (PSU); Thung Song, Plew Waterfall, 150 m, 28 October 2012, *Pócs & Lee 1212Q* (PSU). Phangnga, Mueang Phangnga, Sa Nang Manora Forest Park, 08°30'44.70"N, 98°32'18.9"E, 70–111 m, 31 January 2007, *Pócs & Pócs 07015/S* (EGR). Satun, Thung Wa, Than Plew Waterfall, 07°06'43.00"N, 99°50'30.90"E, 50–100 m, 17 December 2014, *Sangrattanaprasert 258/14C* (PSU). Songkhla, Sadao, Ton Nga Chang Wildlife Sanctuary, Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 100–150 m, 16 December 2014, *Sangrattanaprasert 248/14B*, *250/14D*, *251/14B*, *252/14D* (PSU). Surat Thani, Phanom, Khao Sok National Park, 08°55'20.50"N, 98°31'43.70"E, 120 m, 28 February 2015, *Sangrattanaprasert 308/15C* (PSU). Trang, Yan Ta Khao, Peninsular Botanical Garden (Thung Khai), 07°28'01.00"N, 99°38'24.60"E, 40 m. 12 December 2014, *Sangrattanaprasert 241/14B* (PSU). Yala, Than To, Wang Sai Stream, 06°00'55.66"N, 101°16'36.36"E, 300 m, 2 July 2014, *Sangrattanaprasert 177/14A* (PSU).

Taxonomic notes: Grolle (1975) considered *Colurolejeunea apiculata* Schiffn. not to be a valid name because Schiffner (1890) proposed this name under *Lejeunea* subg. *Colurolejeunea* Spruce, but Schiffner validly published this name in 1900 while *Colurolejeunea leratii* Steph. was described in 1908. Thus, *Colurolejeunea apiculata* is an earlier name than *Colurolejeunea leratii*. I agree with Jovet-Ast (1953) and Söderström *et al*. (2015) to accept *Colura apiculata* as a correct name because its priority.

3. *Colura ari* (Steph.) Steph., Sp. Hepat. 5: 936, 1916. **(Figs. 4.6–4.7)**

≡ *Colurolejeunea ari* Steph., Hedwigia 35: 73. 1896. **Type:** PHILIPPINES. Insula Mindanao, City of Dapitan, in folio vivo *Arum* sp., s.d., *Evans s.n*. (holotype: G n.v.).

= *Colura javanica* Steph., Sp. Hepat. 5: 937, 1916. Type: INDONESIA. Java, s.d., *Karsten s.n*. (holotype: G n.v.).

Plants pale green, 0.5–1 cm long; shoots 1.6–2.3 mm wide. *Stems* 90–120 µm in diameter, in transverse section consisting of 7 cortical cells (28–40 × 20–34 µm) and 3 medullary cells (28–30 × 20–24 µm). *Leaves* uniform, imbricate, spreading from stem at 60°–80° angle. *Lobes* 1.06–1.28 mm long, 0.62–0.8 mm wide; dorsal margin flatten, dentate; teeth triangular, 1–3 cells, teeth almost distributed on upper half of leaf lobe margin. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells subquadrate to rectangular, 20–50 × 14–30 µm; median cells rectangular to hexagonal, 30–70 × 20–30 µm; basal cells rectangular, 30–60 × 14–56 µm. *Oil bodies* 20–40(–50) per cell, very fine segment, ellipsoid, 3–8 × 1–2 µm. *Lobules* narrowly tubular, flaring toward sac, often falciform in outline, 1–1.5 mm long. *Lobule sacs* conical, strongly inflated, 0.4–0.8 mm long, 0.19–0.28 mm wide, apex acute, ending in apical crest consisting of 1–3(–5) cells; sac surface mamillose. *Valves* ovate to elliptic, 68–80 × 50–70 µm, composed of one circle of 13–15 hyaline marginal and 10–12 median cells with 1–2 basal median cells; hyaline bordered present consisting of 2 cells; hinge present consisting of 3 cells. *Hyaline papillae* bulbous, 12–14 µm in diameter. *Valve frames* outline semicircular, 80–90 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus acute to obtuse; lobe lanceolate, 220–360 × 52–108 µm, 8–12 cells long, 4–7 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on leaf lobe.

Autoicous. *Androecia* terminal or intermediate on main stems and lateral branches; male bracts in 3–9 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular to oblong, 140–220(–400) × 100–140(–200) µm; bract lobules semicircular to oblong, 200–248(–400) × (70–)100–160 µm; male bracteoles bilobed, 90–180(–260) × 50–110 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract elliptic to ovate, 600–800 × 280–416 µm; bract lobules narrowly oblong, 480–704 × 80–160 µm; female bracteoles rounded, apex emarginate, 100–140 × 80–180 µm. *Perianths* oblong to narrow obtriangular, 0.9–1.24 mm long, 0.4–0.8 mm wide, with 3 keels; keels short, bearing coarse teeth near its apex; surface of perianth mamillose; beak 1–2 cells long. *Sporophytes*. *Setae* ca. 9 cells long. *Capsules* 292–400 µm in diameter, splitting ± 4/5 its length; capsule valves 280–380 × 180–252 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of

upper half of valve rhombic, large, thin-walled; hinge butterfly-shaped to broadly quadrate, hinge cells rectangular to quadrate, smaller than cells of upper-half, thin-walled; marginal cells rectangular, formed by 1–2 rows. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half quadrate, walls nodulose, formed by 1–2 rows, marginal cells of lower half rectangular, walls smooth; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline to yellowish, with irregular thickenings, 170–320 µm long, 10–20 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 150–200 µm long, 12–16 µm wide; additional elaters hyaline, with smooth thickenings, 220–280 µm long, 6–12 µm wide. *Spores* irregular-oblong or elongate-rectangular, 50–76 × 20–40 µm; spore surface covered with irregular lamellae; sporeling not seen.

Habitat and ecology: *Colura ari* usually occurs on living leaves in lowland at altitude between 37 and 607 m.

Distribution: Australia, Bangladesh, Cambodia, China, Fiji, India, Indonesia, Malaysia, New Caledonia, New Hebrides, Pakistan, Papua New Guinea, Philippines, Samoa, Sri Lanka, Thailand, Vietnam (Jovet-Ast 1953, Tan & Engel 1986, Zhu & So 2001, Pócs & Podani 2015).

Selected specimens examined: INDONESIA. Borneo, East Kalimantan, East Kutai, Peak Balikpapan, Tules R., 100 m, 1–3 July 1952, *Meijer B1320b*, *B1370x*, *B1379a*, *B2847* (L); Borneo, East Kutei, Peak Balikpapan, Tulus-Bewai, 150 m, 3 July 1952, *Meijer B1397b* (L). North Kalimantan, North of Tarakan, Nunukan, East Borneo, Northern part of the Island near bivacque, November 1953, *Meijer B4819* (L). MALAYSIA. Sabah, Sandakan city, Sepagara Forest Reserve, along Kalung-Kalungan trail, 04°57'14.87"N, 118°10'18.06"E, 490 m, 15 September 2016, *Zhu, Shu & Yin 20160915-14B* (HSNU); Sandakan city, Sepagara Forest Reserve, along trail to Silam water spring, 04°58'35.60"N, 118°10'50.13"E, 240 m, 16 September 2016, *Zhu, Shu & Yin 20160916-84* (HSNU). THAILAND. Nakhon Si Thammarat, Nopphitam, Khao Luang National Park, Krung Ching Waterfall, 08°44'05.50"N, 99°39'34.60"E, 196–280 m, 10 October 2014, *Sangrattanaprasert 214/14B*, *219/14A*, *221/14A* (PSU); Khao Nan National Park, 08°48'38.78"N, 99°44'02.32"E, 607 m, 19 May 2015, *Sangrattanaprasert 330/15B* (PSU). Phangnga, Khura Buri, Si Phang-nga National

Park, Ton Deng Waterfall, 08°59'34.76"N, 98°27'57.17"E, 110–119 m, 2 March 2015, *Sangrattanaprasert 319/15A*, *325/15*(PSU). Ranong, Suk Samran, Klong-Naka Wildlife Santuary, 09°27'35.90"N, 98°30'36.80"E, 37–42 m, 1 March 2015, *Sangrattanaprasert 314/15A*, *316/15A* (PSU). Songkhla, Hat Yai, Ton Nga Chang Wildlife Sanctuary, 06°56'45.58"N, 100°13'40.68"E, 140 m, 8 October 2013, *Sangrattanaprasert 23/13A* (PSU); Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 100–150 m, 16 December 2014, *Sangrattanaprasert 249/14*, *251/14A* (PSU). Trang, Yan Ta Khao, Peninsular Botanical Garden (Thung Khai), 07°28'01.00"N, 99°38'24.60"E, 38 m, 12 December 2014, *Sangrattanaprasert 237/14A, 238/14* (PSU). Yala, Betong, Ban Chulabhorn Pattana 10, 05°49'04.40"N, 101°01'50.20"E, 570 m, 15 June 2013, *Chantanaorrapint & Promma 2554B* (PSU); Than To, Wang Sai Stream, 06°00'55.66"N, 101°16'36.36"E, 300 m, 2 July 2014, *Sangrattanaprasert 187/14B* (PSU).

Taxonomic notes: The distinctive characters of *Colura ari* are 1) the conical lobule sacs with apical crest, 2) the strongly dentate leaf lobe margins, 3) ovate to elliptic valves with 1–2 basal median cells, and 4) perianth keels not extended. This species resembles *C. conica*, but the latter differs by 1) dioicous sexuality, 2) lobule sacs usually being broadly conical, and 3) perianth keels being horizontally extended.

4. *Colura bisvoluta* Herzog *et* Jovet-Ast, Rev. Bryol. Lichénol. 22: 228. 1953.

(Figs. 4.8–4.9)

Type: INDONESIA, West Sumatra, "Lobang-Karbau" prope Fort de Kock, *Schiffner 3480* (holotype: JE!; isotype: JE!).

Plants pale green, ca. 4 mm long; shoots 1.5–2 mm wide. *Stems* 65–110 µm in diameter, in transverse section consisting of 7 cortical cells (20–40 × 20–25 µm) and 3 medullary cells (15–30 × 10–25 µm). *Leaves* uniform, imbricate to contiguous, spreading from stem at 40°–50° angle. *Lobes* 0.7–0.86 mm long, 0.32–0.5 mm wide; dorsal margin revolute, 2–3 cells wide. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells isodiametric to subquadrate, 20–30 × 10–20 µm; median cells rectangular, 20–42 × 18–20 µm; basal cells rectangular, 26–

50 × 16–36 µm. *Oil bodies* 7–12 per cell, roughly segmented, ellipsoid, 4–6 × 2 µm. *Lobules* narrowly tubular, flaring toward sac, 0.9–1.2 mm long. *Lobule sacs* obovate to slightly elliptic, strongly inflated, 0.44–0.6 mm long, 0.3–0.4 mm wide, sac surface mamillose, apex obtuse, without apical crest. *Valves* lingulate, 140–160 × 90–100 µm, composed of one circle of 25–40 hyaline marginal and 50–80 median cells without basal median cell and hinge, elongated basal hyaline present. *Hyaline papillae* bulbous, 12–16 µm in diameter. *Valve frames* outline semicircular, 100–140 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe lanceolate, 320–440 × 56–80 µm, 12–17 cells long, 4–5 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* terminal on lateral branches; male bracts in ca. 5 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular, 160–206 × 96–144 µm; bract lobules semicircular, almost as large as bract lobes, 152–176 × 120–130 µm; male bracteoles reduced, 1 or few cells. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract ovate to lanceolate, 640–680 × 150–176 µm, apical keel entire; bract lobules narrowly oblong, ca. 640 × 88–136 µm; female bracteoles composed of 2–3 cells. *Perianths* obovate, ca. 1.0 mm long, ca. 0.64 mm wide, with 3 keels; keels flat, ridge-like, entire; beak 5 cells long. *Sporophyte* not seen.

Habitat and ecology: This species grows on palm leaves in lowland rainforests near the waterfall associated with other epiphyllous liverworts such as *C. acroloba*, *Caudalejeunea reniloba* Steph., *Cololejeunea* spp., and *Leptolejeunea* sp.

Distribution: Australia (Queensland), Indonesia (West Sumatra), Malaysia (Malacca), Thailand (Jovet-Ast, 1953, Sangrattanaprasert *et al*. 2018).

Representative specimens examined: THAILAND. Chumphon, Heo Lom Waterfall, 105 m, 4 August 2014, *Chantanaorrapint & Promma 3899B* (PSU); Phangnga, Si Phang-nga National Park, Ton Deng Waterfall, 70 m, 3 August 2014, *Chantanaorrapint & Promma 3890B* (PSU), 9 October 2015, *Sangrattanaprasert 423/15* (PSU).

Taxonomic notes: *Colura bisvoluta* is morphologically similar to *C. queenslandica* B.M.Thiers, an endemic species to Australia. The latter, however, differs from the former by the transverse section of stem consisting of 6 cortical cells

and 1 medullary cell, the dorsal margin of leaf lobe being flattened, the lobe and lobule surface without conically protuberant mamillae, the smaller valve with 47–50 cells, and the perianth having 5 keels.

5. *Colura brevistyla* Herzog, Bot. Centralbl. Beih. 38(2): 331. 1921. **(Fig. 4.10)**
Type: SRI LANKA (Ceylon). 1906, *Herzog s.n.* (holotype: JE!).

Plants 0.5–1 cm long; shoots ca. 2.5 mm wide. *Stems* 70–100 µm in diameter, in transverse section consisting of 7 cortical cells (30–54 × 20–40 µm) and 3 medullary cells (30–40 × 20–24 µm). *Leaves* uniform, contiguous to imbricate, spreading from stem at 45°–90° angle. *Lobes* 1–1.4 mm long, 0.28–0.56 mm wide; dorsal margin flattened, crenulate or nearly entire in immature plant. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells subquadrate to rectangular, 20–30 × 20–30 µm; median cells rectangular, 50–60 × 18–26 µm; basal cells rectangular, 40–66 × 20–26 µm. *Oil bodies* not seen. *Lobules* narrowly tubular, flaring toward sac, 1.6–2.1 mm long. *Lobule sacs* cylindrical fusiform to lanceolate, strongly inflated, 0.64–0.8 mm long, 0.18–0.26 mm wide, apex obtuse, without apical crest; sac surface mamillose. *Valves* ovate to elliptic, 80–100 × 76–80 µm, composed of one circle of 18–21 hyaline marginal and 18–29 median cells with 1–2 basal median cells; hyaline bordered present consisting of 2 cells; hinge cell present composed of 3 cells. *Hyaline papillae* bulbous to spherical, 16–20 µm in diameter. *Valve frames* outline semicircular, 90–120 µm wide; cell wall smooth. *Underleaves* distant, deeply bilobed, sinus acute; lobe triangular to lanceolate, 320–480 × 80–160 µm, 14–18 cells long, 7–9 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on apex of lobule sac. *Androecium* and *Gynoecium* not seen.

Habitat and ecology. *Colura brevistyla* usually occurs on branches or barks (Pócs *et al*. 2011). In Singapore, *Colura brevistyla* was found growing on *Frullania nodulosa* (Reinw., Blume *et* Nees) Nees in mangrove forest.

Distribution. Fiji (Viti Levu), Malaysia (Peninsula), Mariana Island, Philippins, Singapore, Sri Lanka, Thailand, Vietnam (Pócs *et al*. 2011,

Chantanaorrapint & Pócs 2014, Pócs & Lee 2016, Sangrattanaprasert *et al* 2019b (in press)).

Specimens examined. SINGAPORE. Northwest area, Sungei Buloh Wetland Reserve, 30 November 1889, *Goodenough 1207* (SING). THAILAND. Nakhon Si Thammarat, Nopphitam, Huai Phan village, Khao Lek, 220 m, 31 October 2012, *Pócs, U–Tayanapuh & Lee 1216M* (EGR, PSU).

Taxonomic notes. The distinctive features of *Colura brevistyla* are 1) inflated lobules forming a cylindrical fusiform to lanceolate sac, 2) entire to crenulate leaf-dorsal margin, and 3) large underleaf lobes with 14–18 cells long and 7–9 cells wide at base. Moreover, leaves of this species usually erectly protrude and often produce gemmae on their leaf apices.

Colura brevistyla is morphologically similar to *C. pluridentata* Jovet-Ast. These two species share several similar characters, including underleaf form, shape of lobule sac, valve type, and other characters. *Colura pluridentata*, nevertheless, differs only by its strong teeth at dorsal margin of leaf lobe and the number of basal median cell of valve (Jovet-Ast 1953). Based on the investigation of more specimens, *Colura pluridentata* shows the variations in lobule sac length, teeth at dorsal margin of leaf, and the number of basal median cells of valve. Thus, these two species may possibly be conspecific, and the molecular phylogenetic study is necessary to clarify this.

6. *Colura calyptrifolia* (Hook.) Dumort., Recueil Observ. Jungerm. 12. 1835.

(Fig. 4.11)

≡ *Jungermannia calyptrifolia* Hook., Brit. Jungermann. 43: 1–13. 1813. ≡ *Lejeunea calyptrifolia* (Hook.) Spreng., Syst. Veg. 4(1): 234. 1827. ≡ *Colurolejeunea calyptrifolia* (Hook.) Steph. Hedwigia 29: 97. 1890. **Type:** IRELAND. neighborhood of Bantry, on stems of *Ulex nana*, s.d., *Hutchins s.n.* (holotype: BM!).

= *Colura bulbosa* Herzog, Nat. Hist. Juan Fernandez 2: 751. 1942. Type: CHILE. Juan Fernández, Masafuera, Dicksonia forest, lower slopes of Inocentes, on *Hymenophyllum* leaves, 22 February 1917, *Skottsberg & Skottsberg 103* (holotype: JE!).

Plants pale green, 1.3–1.8 mm long; shoots 1–1.5 mm wide. *Stems* 62.5–88 μm in diameter, in transverse section consisting of 7 cortical cells (30–36 × 18–26 μm) and 3 medullary cells (20–26 × 16–20 μm). *Leaves* uniform remote to contiguous, spreading from stem at 70°–90° angle. *Lobes* 0.36–0.38 mm long, 0.28–0.32 mm wide, strongly incurved; dorsal margin entire. *Lobe cells* thin-walled, trigones absent or rarely present, intermediate thickenings absent; marginal cells slightly isodiametric to rectangular, 16–34 × 14–20 μm; median cells isodiametric to rectangular, 16–40 × 12–20 μm; basal cells rectangular to hexagonal, 24–40 × 10–20 μm. *Cuticle* smooth. *Oil bodies* not seen. *Lobules* narrowly tubular, flaring toward sac, 0.8–1 mm long, *Lobule sacs* lanceolate, strongly inflated, 0.6–0.72 mm long, 0.25–0.32 mm wide, forming a long tubular beak towards the apex, beak 0.12–0.28 mm, 1/4–1/3 as long as leaf length; surface mamillose. *Valves* elliptic, 78–90 × 60–70 μm, composed of one circle of 15–17 hyaline marginal and 11–12 median cells with 2 basal median cells; hyaline bordered present consisting of 1 cell; hinge present composed of 2 superimposed cells. *Hyaline papillae* bulbous, ca. 16 μm in diameter. *Valve frames* outline semicircular, 80–90 μm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe lanceolate to triangular, 125–240 × 37–60 μm, 4–10 cells long, 2–4 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on lobule sac apex. *Androecia and gynoecia* not seen.

Habitat and ecology: The species usually occurs on living leaf and bark of trees in montane forest. However, it can be found as a lithophyte growing on a small gorge in Norway (Hassel *et al*. 2014).

Distribution: Bolivia, Chili, China (Taiwan), England, French (Manche Finistère), Ireland, Japan, Kenya, Mauritius, Norway, Portuguese Republic (Azores), Scotland, Tanzania (Jovet-Ast 1953, Gradstein *et al.* 1983, Yang *et al.* 2013, Hassel *et al*. 2014, Pócs & Váňa 2015.).

Specimens examined: MALAYSIA. Kedah, Tambunan district, Truns Madi, Forest Reserve, near starting point, 05°33'35.31"N, 116°29'54.03"E, 2078 m, 19 September 2016, *Zhu, Shu & Yin 20160919-114B* (HSNU).

Taxonomic notes: *Colura calyptrifolia* is characterised by 1) strongly inflated lobule forming a fusiform sac with a narrow beak-like prolongation tip, 1/4–1/3 as long as leaf length, 2) smooth dorsal surface of leaf lobe and lobule sac, and 3)

smooth leaf cells without trigone and intermediate thickenings. It is most morphologically similar to *C. tenuicornis*, the widely distributed pantropical species. The latter, however, differs from *C. calyptrifolia* in having a lanceolate sac like lobule; having strongly elongated beak of lobule sac, ca. 1/2 as long as leaf length; and perianth bearing strongly elongated horn-like keels.

7. *Colura clementis* Grolle, J. Hattori Bot. Lab. 28: 45. 1965. **(Fig. 4.12)**

Type: PAPUA NEW GUINEA. Morobe, Samanzing, mt. bush, 2000 m, 1938, *Clemens 9276/H-q* (holotype: B n.v.; isotype: JE!).

Plants pale green, ca. 0.6 cm long; shoots 1.2–1.9 mm wide. *Stems* 80–120 µm in diameter, in transverse section consisting of 7 cortical cells (24–50 × 20–40 µm) and 3 medullary cells (20–26 × 14–20 µm). *Leaves* uniform, contiguous to imbricate, spreading from stem at 40°–70° angle. *Lobes* 1.04–1.3 mm long, 0.48–0.64 mm wide; dorsal margin flattened, entire. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells subquadrate to rectangular, 20–34 × 12–24 µm; median cells rectangular, 30–60 × 14–24 µm; basal cells rectangular to subquadrate, 20–44 × 14–30 µm. *Oil bodies* not seen. *Lobules* narrowly tubular, flaring toward sac, 1.3–1.6 mm long. *Lobule sacs* elliptic, strongly inflated, 0.52–0.68 mm long, 0.24–0.27 mm wide, apex acute, entire or ending in apical crest consisting of ca. 3 cells; sac surface mamillose. *Valves* ovate to elliptic, 74–86 × 56–70 µm, composed of one circle of 14–15 hyaline marginal and 15–20 median cells with 1 basal median cell; hyaline bordered present consisting of 2 cells; hinge present consisting of 3 cells. *Hyaline papillae* bulbous, 16–20 µm in diameter. *Valve frames* outline semicircular, 106–140 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus acute; lobe triangular to lanceolate, 120–170 × 34–60 µm, 6–8 cells long, ca. 4 cells wide at base; margin entire. *Asexual reproduction* not seen.

Dioicous? Androecia not seen. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract lobes oblong, 760–800 × 192–248 µm; bract lobules narrowly oblong, 680–720 × 80–144 µm; female bracteoles reduced to a few cells.

Habitat and ecology: *Colura clementis* was found on living leaves in montane rain forest at altitudes of 1230–2000 m.

Distribution: Papua New Guinea (Morobe), Indonesia (Borneo) (Jovet-Ast 1967b, Pócs 2013).

Selected specimens examined: MALAYSIA. Pahang, Cameron Highlands, Parit Falls, 04°28'26.7"N, 101°23'02.0"E, 1300–1400 m, 1 November 2013, *Pócs, Pócs, Lee & Tang 13167/AX* (EGR); Fraser's Hill, 3°42'56.0"N, 101°44'11.4"E, 1230–1266 m, 8–11 April 2014, *Sangrattanaprasert 83/14D*, *84/14B* (PSU). Sabah, Ranau city, Kinabalu National Park, from Timpohon Gate to Kandis Shelter, 06°01'52.65"N, 116°33'01.64"E, 1957 m, *Zhu, Shu & Yin 20160921–70W1* (HSNU).

Taxonomic notes: the distinctive characters of *Colura clementis* are 1) acute lobule sac apex, 2) mamillose lobule sac surface, 3) entire leaf-lobe margin, and 4) valves composed of 1 basal median cell (triangular to rectangular in shape). This species is similar to *C. verdoornii* in general appearance, but the latter differs in having oblique-elliptic valve with its basal median cell adnated with hinge cell and absence of hyaline bordered cells.

8. *Colura conica* (Sande Lac.) K.I.Goebel, Ann. Jard. Bot. Buitenzorg 39: 3, 1928. **(Figs. 4.13–4.14)**

≡ *Lejeunea conica* Sande Lac., Ann. Mis. Bot. Lugduno-Batavum 1: 311. 1864. ≡ *Colurolejeunea conica* (Sande Lac.) Schiffn. Consp. Hepat. Arch. Ind.: 258. 1898. **Type:** INDONESIA. Sumatra occidentalis, in foliis *Ficus diversifoliae,* s.d., *Teysmann s.n.* (lectotype: L n.v, designated by Grolle (1966).

= *Colura acutifolia* Jovet-Ast, Rev. Bryol. Lichénol. 22: 265. 1953. Type: INDONESIA. East-Borneo (Kalimantan Timur), Gunung Beratus, along the river Tulus, hygrophilons forest, 3 July 1952, *Meijer 1937* (holotype: PC n.v., isotype: L n.v.).

Plants pale green, 0.6–1.4 cm long; shoots 2.1–3.2 mm wide. *Stems* 80–130 μm in diameter, in transverse section consisting of 7 cortical cells (24–40 × 18–36 μm) and 3 medullary cells (20–28 × 18–20 μm). *Leaves* imbricate, spreading from stem at

60°–90° angle. *Lobes* 0.96–1.62 mm long, 0.58–1.1 mm wide; dorsal margin flattened, dentate; teeth triangular, 1–3 cells, teeth almost distribute on upper half of leaf lobe margin. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells rectangular to subquadrate, 20–40(–50) × 14–26 µm; median cells rectangular to subquadrate, 26–70 × 20–38 µm; basal cells rectangular, 50–90 × 20–40 µm. *Oil bodies* 20–40(–50) per cell, fine segment, ellipsoid, 5.6–8 × 1.6–2.4 µm. *Lobules* narrowly tubular, flaring toward sac, often falciform in outline, 0.8–1.5 mm long. *Lobule sacs* broadly to tinily conical, strongly inflated, (0.24–)0.4–0.56 mm long, (0.11–)0.3–0.36 mm wide, apex obtuse, ending in apical crest consisting of 3–6 cells; sac surface strongly mamillose. *Valves* widely elliptic, 60–90 × 50–88 µm, composed of one circle of 11–15 hyaline marginal and 7–18 median cells with 1–2 basal median cells; hyaline bordered present consisting of 2 cells; hinge present consisting of 3 cells. *Hyaline papillae* bulbous, (10–)14–18 µm in diameter. *Valve frames* outline semicircular, 70–120 µm wide; cell wall smooth. *Underleaves* distant, deeply bilobed, sinus obtuse; lobe lanceolate, 220–440 × 60–80(–112) µm, 9–13 cells long, 4–6 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on leaf lobe.

Dioicous. *Androecia* terminal or intermediate on lateral branches; male bracts in 5–20 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular, 220–360 × 140–260 µm; bract lobules oblong, 220–320 × 120–180 µm; male bracteoles bilobed, 100–200 × 40–128 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract lobes elliptic to ovate, 640–1100 × 280–496 µm; bract lobules narrowly oblong, 480–860 × 80–200 µm; female bracteoles rounded to oblong, apex emarginate, 80–120 × 80–100 µm. *Perianths* obtriangular, 1.1–1.4 mm long, 0.6–1.1 mm wide, with 3 keels; keels short to extended, keel shape oblique-triangular to rectangular, 184–280(–480) × 80–200(–320) µm, spreading horizontally, bearing coarse teeth near its apex; surface of perianth mamillose; beak 2 cells long. *Sporophytes*. *Setae* 9 cells long. *Capsules* ca. 250 µm in diameter, splitting to ± 3/4 of its length; capsule valves 280–360 × 200–224 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic, large, thin- to thick-walled, wall entire to nodular thickenings; hinge broadly quadrate, hinge cells

rectangular to quadrate, smaller than cells of upper half, thin-walled; marginal cells rectangular, formed by 1–2 rows. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half quadrate, walls nodulose, formed by 1–2 rows, marginal cells of lower half rectangular, walls smooth; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline to yellowish, with irregular thickenings, 200–288 µm long, 12–20 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 160–210 µm long, 12–18 µm wide; additional elaters hyaline, with smooth thickenings, 240–280 µm long, 6–10 µm wide. *Spores* irregular-oblong or elongate-rectangular, 36–84 × 16–30 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura conica* was usually found occurring on living palm leaves in lowland rain forest.

Distribution: Australia, Cambodia, China, Indonesia, Laos, Malaysia, New Caledonia, Papua New Guinea, Philippines, Samoa, Thailand, Vietnam (Tan & engel 1986, Zhu & So 2001).

Selected specimens examined: CAMBODIA. Koh-Kong, 11°35'15"N, 103°11'29"E, 200 m, 24 December 2011, *Bakalin Cam–86–18–11A, Cam–86–17–11B* (VBGI). INDONESIA. East Kalimantan, East Kutai, Sangkulirang, 1 July 1951, *Kostermans 6030b* (L); Samarinda, East Borneo, estuary of Mahakam R., Tandjong Bangko, 0 m, 31 July 1952, *Meijer B2942* (L); East Kutai, District Sumarinda, Tandjong Bangko, East of the estuary of the river Mahakam, 0 m, 31 July 1952, *Meijer B2931a* (L); W. of the estuary of the Mahakam River, 0 m, 1 August 1952, *Meijer B3038a* (L); S. Mukum, near Sanga2 West of estuary of Mahakam-River, low, 4–5 August 1952, *Meijer B3193*, *B3188*, *B3203*, *B3247* (L). North Kalimantan, North of Tarakan, Nunukan Island, Borneo, near bivacque 1, brookvalley, 10 November 1953, *Meijer B6657* (L); N.E. Borneo. Brookbank, bivouac I, 12 November 1953, *Meijer B8155* (L); North of Tarakan, Nunukan, East Borneo, near S.Bimusan, low, December 1953, *Meijer B5188*, *B5194*, *B5148*, *B5183* (L);, November 1953, *Meijer B4759*, *B4793*, *B4802*, *B4806*, *B4855*, *B4868*, *B4899*, *B4901*, *B4909*, *B4989*, *B5007*, *B5040*, *B5067*, *B5070*, *B5104*, *B5118* (L). West Sumatra, Taram, E. of Payakumbuh, 22 August 1957, *Meijer B8422p.p.* (L). MALAYSIA. Sabah, N. Borneo, B.S. Toelit, 1 August 1912, *Amdjah s.n.* (L); North Borneo, Tawau Res., Tawau River Forest

Reserve, on riverbank, 7 July 1959, *Meijer B10006p.p*, *B10009* (L); Mt. Kinabalu, 17 July 1960, *Meijer B10208p.p.* (L); Tawau Res., Tawau River Forest Reserve, 1 September 1960, *Meijer B10685p.p.*, *B10705p.p.* (L); Sandakan Res., N. part of Dent Penninsula, Sg. Tabin area, Sulap, 24 October 1961, *Meijer B11593p.p.* (L). Sarawak, West Borneo, Kuching; Semangoh Forest Reserve, 28 February 1960, *Meijer B12394p.p.* (L); West Borneo, Kuching; Bako National Park, 15 September 1961, *Meijer B11507p.p.* (L). THAILAND. Nakhon Si Thammarat, Nopphitam, Khao Luang National Park, Krung Ching Waterfall, 08°44'05.50"N, 99°39'34.60"E, 267–280 m, 10 October 2014, *Sangrattanaprasert 215/14B*, *216/14A*, *217/14*, *218/14B*, *220/14A*, *222/14A*, *223/14B* (PSU). Phangnga, Khura Buri, Ton Kloi Waterfall, 09°20'15.50"N, 98°27'13.70"E, 57 m, 1 March 2015, *Sangrattanaprasert 311/15A* (PSU); Khura Buri, Si Phang-nga National Park, Ton Deng Waterfall, 08°59'34.76"N, 98°27'57.17"E, 119 m, 2 March 2015, *Sangrattanaprasert 319/15B*, *324/15A* (PSU). Ranong, Suk Samran, Klong-Naka Wildlife Santuary, 09°27'40.27"N, 98°30'35.86"E, 48 m, 4 August 2014, *Chantanaorrapint & Promma 3902B* (PSU); 1 March 2015, *Sangrattanaprasert 315/15* (PSU). Satun, Thung Wa, Than Plew Waterfall, 07°06'43.00"N, 99°50'30.90"E, 50–100 m, 17 December 2014, *Sangrattanaprasert 257/14B*, *258/14B* (PSU). Songkhla, Sadao, Ton Nga Chang Wildlife Santuary, Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 300 m, 23 February 2015, *Sangrattanaprasert 284/15A*, *286/15B*, *291/15A*, *292/15A*, *294/15B* (PSU). Surat Thani, Phanom, Khao Sok National Park, 08°55'20.50"N, 98°31'43.70"E, 130 m, 28 February 2015, *Sangrattanaprasert 302/15A*, *303/15*, *304/15B* (PSU). Tak, Umphang, Umphang Wildlife Sanctuary, Thi Lo Su Waterfall, 15°55'38.20"N, 98°45'13.70"E, 555 m, 18 August 2013, *Chantanaorrapint & Promma 2750A*, *2762A*, *2763A* (PSU). Trang, Palian, Chao Pa Waterfall, 07°14'23.00"N, 99°50'39.00"E, 260 m, 18 June 2014, *Sangrattanaprasert 162/14A*, *163/14*, *164/14*, *165/14A*, *167/14* (PSU). Yala, Betong, Ban Chulabhorn Pattana 10, 05°49'04.40"N, 101°01'50.20"E, 580 m, 15 June 2013, *Chantanaorrapint & Promma 2625*, *2579A* (PSU); Than To, Wang Sai Stream, 06°00'55.66"N, 101°16'36.36"E, 300 m, 2 July 2014, *Sangrattanaprasert 178/14A*, *180/14C* (PSU).

Taxonomic notes: The diagnostic characters of *C. conica* are 1) having broadly conical lobule sacs, 2) large and semicircular leaf-lobes in outline, 3) strongly

dentate leaf-lobe margins, 4) perianth keels being usually extended, and 5) very long androecia with 5–20 pairs of male bracts. This species may be confused with *C. ari*, and their differences are given under the latter species.

9. *Colura corniantha* Grolle, J. Hattori Bot. Lab. 28: 44, 1965. **(Figs. 4.15–4.16)**
≡ *Colura cornuta* Jovet-Ast, Rev. Bryol. Lichénol. 30: 11, 1961. *nom. ill*. (*non Colura cornuta* (Lindenb.) Trevis.) **Type:** VIETNAM. South Vietnam (Sud-Vietnam), Dalao, s.d., *Tixier 259* (holotype: PC n.v.).
= *Colura siamensis* Jovet-Ast, Rev. Bryol. Lichénol. 35: 139. 1967a. Type: THAILAND. Nakhon Ratchasima, Khao Yai National Park, 700 m, 20 May 1965, *Tixier 1170* (holotype: PC n.v.). ***syn. nov.***

Plants pale green, 0.5–0.7 cm long; shoots 0.8–1.3 mm wide. *Stems* 60–70 µm in diameter, in transverse section consisting of 7 cortical cells (10–30 × 10–20 µm) and 3 medullary cells (10–16 × 8–14 µm). *Leaves* imbricate, spreading from stem at 70°–90° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaf lobes* 0.32–0.6 mm long, 0.24–0.46 mm wide; dorsal margin flattened, dentate to denticulate; teeth triangular, consisting of 3–9(–22) cells, teeth almost distributed on upper half of leaf lobe; lobules narrowly tubular, flaring toward sac, 0.4–0.72 mm long; lobule sacs ovate to rounded, strongly inflated, 0.24–0.36 mm long, 0.16–0.24 mm wide, sac surface mamillose, apex obtuse, with apical crest 1(–2) teeth, rarely entire, apical crest consisting of 2–7(–17) cells; valves elliptic to lingulate, 80–130 × (26–)40–56 µm, composed of one circle of 19–27 hyaline marginal and 17–39 median cells, without basal median cell and hinge; hyaline papillae bulbous, ca. 10 µm in diameter; valve frame reduced. *Non-saccate leaves* obliquely elliptic to ovate, 0.48–0.76 mm long, 0.36–0.52 mm wide; apex acute, dentate; dorsal margin flattened, dentate to denticulate; teeth triangular, consisting of (1–)3–8 cells, teeth mostly distributed on upper half of leaf lobe; lobules narrowly oblong, 0.18–0.37 × 0.04–0.1 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells subquadrate, 14–30 × 12–26 µm; median cells subquadrate to hexagonal, 20–50 × 20–30 µm; basal cells rectangular, 30–50 × 16–34 µm. *Oil bodies* 20–40 per cell,

roughly segmented, ellipsoid, 4–7 × 1–3 µm. *Underleaves* deeply bilobed, sinus acute to obtuse; lobe filiform, (90–)120–200 × 24–44 µm, 4–8 cells long, 2–3 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 4–10 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire to crenulate; bract lobes semicircular, 150–240 × 120–200 µm; bract lobules semicircular to oblong, 170–240 × 90–130 µm; male bracteoles bilobed to oblong, 30–80(–100) × 24–50 µm, apex bilobed to obtuse. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes ovate to elliptic, 380–584 × 140–340 µm, apical keel entire; bract lobules narrowly oblong, 320–480 × 80–160 µm; female bracteoles oblong to caudate, 70–130 × 50–100 µm, apex obtuse to emarginate. *Perianths* obtriangular, 0.64–0.86(–1) mm long, 0.4–0.86 mm wide, with 3 keels; keels ellipsoid, strongly inflated, 200–280(–360) × 144–192(–240) µm, spreading horizontally, apex acute, entire or ending with 1–3 teeth; beak 1 cell long. *Sporophytes*. *Setae* 9 cells long. *Capsules* (216–)240–268 µm in diameter, splitting to ± 4/5 of its length; capsule valves 220–280 × 140–200 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper part of valve rhombic to polygonal, large, thin-walled; hinge rectangular, ca. 1/3 of valve length, hinge cells rectangular to isodiametric, thin-walled; marginal cells rectangular, form 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half rectangular, walls nodulose, form 2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular to annular thickenings, 120–232 µm long, 8–16(–20) µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 110–170 µm long, 10–14 µm wide; additional elaters hyaline, with smooth thickenings, 160–200 µm long, 4–10 µm wide. *Spores* irregular-oblong or elongate-rectangular, 44–70 × 20–30 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura corniantha* usually grows densely on living leaves in lowland ever green forest.

Distribution: Cambodia and Thailand (as *C. siamensis*), Vietnam (Jovet-Ast 1961, 1967a).

Specimens examined: THAILAND. Chumphon, Phato, Heo Lom Waterfall, 09°43'47.89"N, 98°40'58.50"E, 105 m, 4 August 2014, *Chantanaorrapint & Promma 3899D* (PSU). Nakhon Ratchasima, Pak Chong, Khao Yai National Park, Pha Kuai Mai, 14°25'45.00"N, 101°23'32.50"E, 667 m, 1 June 2015, *Sangrattanaprasert 344/15* (PSU). Nakhon Si Thammarat, Nopphitam, Khao Luang National Park, Krung Ching Waterfall, 08°44'05.50"N, 99°39'34.60"E, 280 m, 10 October 2014, *Sangrattanaprasert 228/14B* (PSU). Phangnga, Khura Buri, Si Phang-nga National Park, Ton Deng Waterfall, 08°59'30.96"N, 98°27'56.77"E, 66–119 m, 3 August 2014, *Chantanaorrapint & Promma 3891E* (PSU); 2 March 2015, *Sangrattanaprasert 318/15D, 319/15E* (PSU). Ranong, Suk Samran, Klong-Naka Wildlife Santuary, 09°27'40.27"N, 98°30'35.86"E, 48 m, 4 August 2014, *Chantanaorrapint & Promma 3902D* (PSU); 1 March 2015, *Sangrattanaprasert 316/15C* (PSU). Surat Thani, Phanom, Khao Sok National Park, 08°55'20.50"N, 98°31'43.70"E, 121 m, 28 February 2015, *Sangrattanaprasert 308/15D* (PSU).

Taxonomic notes: *Colura corniantha* is the correct name or legitimate name, since *C. cornuta* Jovet-Ast is a homonym of *Colura cornuta* (Lindenb.) Trevis. (Grolle 1965). *Colura corniantha* is morphologically similar to *C. inflata* and their distinguishing characters are discussed under the latter species.

From my investigation of many specimens of *C. corniantha* and *C. siamensis* collected from Khao Yai National Park (type locality of *C. siamensis*) to Peninsular Thailand. The morphological data reveal that these two species share several similar characters: strongly dentate dorsal margin, sac apex ending with crest, inflated perianth keels and entire keel apex or ending with teeth varying even on the same plant. Therefore, *Colura corniantha* is rather conspecific with *C. siamensis* morphologically. Moreover, the present phylogenetic results indicate that *Colura siamensis* is nested within *C. corniantha*. Hence, *C. siamensis* is here reduced to synonymy with *C. corniantha*.

10. *Colura corynophora* (Nees, Lindenb. *et* Gottsche) Trevis., Mem. Reale Ist. Lombardo Sci., Ser. 3, Cl. Sci. Mat. 4: 402, 1877. **(Figs. 4.17–4.18)**

≡ *Lejeunea corynophora* Nees, Lindenb. *et* Gottsche, Nov. Actorum Acad. Caes. Leop.-Carol. German. Nat. Cur. 19 (Suppl. 1): 474, 1843. **Type:** PHILIPPINES, "Manila", s.d., *Meyen s.n.* (holotype: G n.v.).
= *Colura trialata* (Steph.) Herzog *et* Zwickel, Ann. Bryol. 6: 118, 1933. ≡ *Leptolejeunea trialata* Steph., Sp. Hepat. 6: 398, 1923. Type: INDONESIA. Sumatra, Jambi, s.d., *Philipp s.n.* (isotype: JE!).

Plants pale green, 0.4–1 cm long; shoots 1.2–1.6 mm wide. *Stems* 66–86 µm in diameter, in transverse section consisting of 7 cortical cells (24–40 × 20–30 µm) and 3 medullary cells (18–24 × 10–18 µm). *Leaves* imbricate to contiguous, spreading from stem at 45°–90° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaves lobes* 0.58–0.8 mm long, 0.35–0.46 mm wide; dorsal margin flattened, entire; lobules narrowly tubular, flaring toward sac, 0.76–0.9 mm long; lobule sacs rounded to widely elliptic, strongly inflated, 0.32–0.36 mm long, 0.22–0.26 mm wide, sac surface mamillose, apex obtuse without apical crest; valves ovate to obliquely elliptic, 120–160 × 56–64 µm, composed of one circle of 24–30 hyaline marginal and 23–35 median cells without basal median cell and hinge; hyaline papillae bulbous, 10–16 µm in diameter; valve frame reduced. *Non-saccate leaves* elliptic, 0.98–1.1 mm long, 0.48–0.54 mm wide; apex obtuse, entire; dorsal margin flattened, entire; lobules narrowly oblong, 0.48–0.54 × 0.08–0.12 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells isodiametric to rectangular, 16–30 × 12–20 µm; median cells hexagonal to rectangular, 20–50 × 20–30 µm; basal cells rectangular, 30–66 × 20–40 µm. *Oil bodies* 11–26 per cell, roughly segmented, ellipsoid, 7–10.4 × 2–3 µm. *Underleaves* deeply bilobed, sinus obtuse; lobe filiform, 110–200 × 20–60 µm, 5–10 cells long, 2–4 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on leaf lobe.

Dioicous. *Androecia* on lateral branches; male bracts in 2–5 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular to oblong, 200–228 × 120–160 µm; bract lobules oblong to semicircular, 170–240 × 90–134 µm; male bracteoles bilobed to rounded, 44–110 × 40–54 µm, apex bilobed or obtuse. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes elliptic, 455–520 × 208–288 µm,

apical keel entire to crenulate with 1 projecting cell row; bract lobules narrowly oblong, 320–440 × 60–104 µm; female bracteoles bilobed, rounded to few cells, 40–60 × 10–56 µm, apex emarginate or obtuse. *Perianths* obtriangular, 0.76–1 mm long, 0.62–0.76 mm wide, with 3 keels; keels oblique-triangular, 200–280 × 200–240 µm, spreading horizontally, apex obtuse, crenate; beak 1–2 cells long. *Sporophytes*. *Setae* 9 cells long. *Capsules* 280–320 µm in diameter, splitting to ± 4/5 of its length; capsule valves 240–300 × 168–188 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic to polygonal, large, thin-walled; hinge slightly rectangular, ca. 1/2 of valve length, hinge cells rectangular to isodiametric, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half rectangular, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular to annular thickenings, 170–240 µm long, 14–20 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 130–164 µm long, 8–10 µm wide; additional elaters hyaline, with smooth thickenings, 200–244 µm long, 4–8 µm wide. *Spores* irregular-oblong or elongate-rectangular, 52–60 × 18–22 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura corynophora* was typically found occurring on the smooth surface of living leaves of ferns, palms, and other dicots dominantly in humid lowland ever green forest and can be also found in lower montane rain forest.

Distribution: Cambodia, China, Fiji Islands, Indonesia, Malaysia, Mariana Islands, Philippines, Papua New Guinea, Sri Lanka, Thailand, Vietnam (Jovet-Ast 1953, 1961, 1976, Tixier 1970, Tan & Engel 1986, Zhu & So 2001, Pócs & Ninh 2005, Pócs & Eggers 2007).

Selected specimens examined: CAMBODIA. Koh-Kong, 11°48'19"N, 103°30'39"E, 200–700 m, 22–24 December 2011, *Bakalin Cam-81-142-11*, *Cam-85-43-11B*, *Cam-85-43-11B*, *Cam-85-43-11B* (VBGI). INDONESIA, Balikpapan, East Bornoe, ostuary of Mahakam River Tandjong Bangko, low altitude, 1 August 1952, *Meijer B3036*, *B3065* (L). East Kalimantan, Borneo, East Kutei, Peak Balikpapan Sembon R., 100 m, 29 June 1952, *Meijer B1274a* (L); East Kutei, Peak Balikpapan

terr. Beul, 700 m, 30 June 1952, *Meijer B1308a2* (L); Sumarinda Tandjong Bangko, W. of estuary of Mahakam river, sea level, 31 July 1952, *Meijer B2921a* (L); Sumarinda S. Mukam, near Sanga, low altitude, 5 August 1952, *Meijer B3252a* (L). Nunukan, N. of Tarakan, East Borneo near S.Binusan, low altitude, December 1953, *Meijer B5187* (L); N. of Tarakan, East Borneo Northen part of the Island near bivaoque I, low altitude, November 1953, *Meijer B4710*, *B4773*, *B4830* (L); East Borneo N. part primary forest on hill, low altitude, November 1953, *Meijer B4887* (L); East Borneo inner forestsin N. part of the Island, sea leavel, November 1953, *Meijer B5004*, *B5017* (L). Sumatra, Petani, 940 m, 18 June 1952, *Van der Wijk 1582B* (L); Taram, E. of Pajakumbuh sandstoneregion of river Tjampo, 500 m, 1 August 1957, *Meijer B8527p.p.*, *B8644b*, *B9335* (L). MALAYSIA. Sabah, Sandakan, Forest Reserve, 24 October 1961, *Meijer B11593p.p.* (L). Sarawak, N. Bornoe, s.d., *Beccari 84* (L). Pahang, Genting Highland, along the road to Gohtong Jaya, roadside vegetation, 820 m, 9 September 2006, *Cheah & Yong 52*, *54* (EGR, KLU). Selangor, around Sungai gabai waterfall, near Hulu langat town, 20 km East of Kuala Lumpur, 160–200 m, 26 October 2013, *Pócs, Pócs, Lee & Tang 13160/Y*, *13161/AD*, *13163/H* (EGR). THAILAND. Krabi, Klong Thom, Sa Marakot, 65 m, 9 November 2012, *Pócs & Somadee 1227AA* (PSU). Nakhon Nayok, Khao Yai National Park, Pha Dieo Dai, 14°21'59.39"N, 101°23'20.19"E, 1190 m, 14 November 2013, *Sangrattanaprasert 29/13A*, *32/13A*, *33/13*, *34/13* (PSU). Nakhon Si Thammarat, Lan Saka, Khao Luang National Park, 08°33'25.22"N, 099°45'47.00"E, 332–457 m, 24–27 June 2015, *Sangrattanaprasert 347/15*, *351/15*, *354/15A* (PSU). Phangnga, Khura Buri, Ton Kloi Waterfall, 09°20'15.50"N, 98°27'13.70"E, 57 m, 1 March 2015, *Sangrattanaprasert 309/15*, *310/15*, *311/15B* (PSU); Si Phang-nga National Park, Ton Deng Waterfall, 08°59'34.76"N, 98°27'57.17"E, 119 m, 2 March 2015, *Sangrattanaprasert 319/15C*, *320/15A*, *323/15* (PSU). Ranong, Suk Samran, Klong-Naka Wildlife Sanctuary, 09°27'20.60"N, 98°30'17.00"E, 37 m, 1 March 2015, *Sangrattanaprasert 316/15B* (PSU). Songkhla, Hat Yai, Ton Nga Chang Wildlife Sanctuary, Ton Nga Chang Waterfall, 06°56'43.91"N, 100°13'16.43"E, 483–495 m, 11 January 2014, *Sangrattanaprasert 49/14A*, *50/14A*, *51/14B* (PSU); Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 100–150 m, 16 December 2014, *Sangrattanaprasert 250/14C*, *254/14B* (PSU). Surat Thani, Phanom, Khao Sok National Park,

08°55'20.50"N, 98°31'43.70"E, 121–130 m, 28 February 2015, *Sangrattanaprasert 304/15C*, *307/15A*, *308/15B* (PSU). Tak, Umphang, Umphang Wildlife Sanctuary, Thi lo Su Waterfall, 15°55'38.20"N, 98°45'13.70"E, 555 m, 18 August 2013, *Chantanaorrapint & Promma 2753* (PSU). Trang, Palian, Chao Pa Waterfall, 07°14'23.00"N, 99°50'39.00"E, 260 m, 18 June 2014, *Sangrattanaprasert 162/14B*, *166/14* (PSU); Yan Ta Khao, Peninsular Botanical Garden (Thung Khai), 07°28'01.00"N, 99°38'24.60"E, 38 m, 12 December 2014, *Sangrattanaprasert 235/14A*, *243/14A*, *244/14A*, *246/14* (PSU). Yala, Betong, Ban Chulabhorn Pattana 10, 05°49'04.40"N, 101°01'50.20"E, 570 m, 15 June 2013, *Chantanaorrapint & Promma 2536*, *2591*, *2592*, *2534D*, *2537A*, *2537C*, *2538B*, *2539A* (PSU); Than To, Wang Sai Stream, 06°00'55.66"N, 101°16'36.36"E, 300 m, 2 July 2014, *Sangrattanaprasert 179/14*, *180/14B*, *181/14*, *182/14*, *183/14* (PSU) VIETNAM, Hà Tĩnh, Vũ quang Nature Reserve and District, 18°17.5'N, 105°26.9'E, 100–180 m, 23 May 2002, *Pócs 02107/L* (EGR).

Taxonomic notes: *Colura corynophora* is characterised by 1) dimorphic lateral leaves, 2) having elliptic non-saccate leaves, 2) entire leaf dorsal margin, 3) round or widely elliptic lobule sacs, large in size (0.32–0.36 × 0.22–0.26 mm), and 4) lobe apices of saccate leaves being entire and truncate, rarely obtuse. *Colura corynophora* can be confused with *C. acroloba*. For the separation of the similar species, see under the taxonomic note of the latter.

11. *Colura crenulata* Grolle, J. Hattori Bot. Lab. 28: 46. 1965. **(Figs. 4.19–4.20)**

Type: PAPUA NEW GUINEA. Morobe, Yunzaing, 1500–1800 m, 1936, *Clemens 3817/H-b* (holotype: B n.v.).

Plants pale green, 0.3–1.0 cm long; shoots 1.2–2.5 mm wide. *Stems* 100–137 µm in diameter, in transverse section consisting of 7 cortical cells (37–63 × 27–48 µm) and 3 medullary cells (25–38 × 20–28 µm). *Leaves* uniform, contiguous to imbricate, spreading from stem at 0°–70° angle. *Lobes* 0.75–1.45 mm long, 0.40–0.75 mm wide; dorsal margin ± plane, entire to crenulate. *Lobe cells* thin-walled, trigones large, intermediate thickenings very distinct; marginal cells isodiametric to slightly

rectangular or subquadrate, 25–45 × 25–35 µm; median cells rectangular, isodiametric to hexagonal, 32–63 × 22–38 µm; basal cells rectangular to hexagonal, 37–63 × 20–45 µm. *Cuticle* smooth. *Oil bodies* 14–20 per cell, homogenous, ellipsoid, 4–8 × 1.6–3.2 µm. *Lobules* narrowly tubular, flaring toward sac, 1.35–2.25 mm long. *Lobule sacs* elliptic, strongly inflated, 0.6–1.9 mm long, 0.50–0.65 mm wide, sac surface conical mamillose, apex acute, ending in apical crest consisting of 1–5 cells. *Valves* elliptic, broadly ovate to slightly round, 114–144 × 94–124 µm, composed of one circle of 18–21 hyaline marginal and 20–29 median cells, with 1 basal median cell; hyaline bordered present consisting of 2 cells; hinge present consisting of 3–4 cells. *Hyaline papillae* spherical, 15–20 µm in diameter. *Valve frames* outline semicircular, ca. 182 µm wide; cell wall smooth to undulate. *Underleaves* deeply bilobed, sinus obtuse; lobe lanceolate, 150–200 × 55–115 µm, 6–7 cells long, 4–5 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on lobule sac apex and sometimes on perianth apex.

Dioicous. *Androecia* on lateral branches or intermediate on main stems and branches; male bracts in 2–7 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes oblong to semicircular, 230–300 × 160–185 µm; bract lobules semicircular, as large as bract lobes, 220–290 × 145–185 µm; male bracteoles bilobed to round, small, 100–140 × 70–130 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes oblong to elliptic, 750–900 × 250–450 µm; bract lobules narrowly oblong, 750–800 × 150–200 µm; female bracteoles obtriangular to oblong, 100–120 × 80–90 µm. *Perianths* obovate to obtriangular, 1.35–1.50 mm long, 0.45–0.75 mm wide, with 3 keels; keels oblique-triangular or horn-like, 250–300 × 170–220 µm, spreading horizontally, bearing a coarse tooth near its apex; surface of perianth strongly mamillose; beak 1–3 cells long. *Sporophytes*. *Setae* 8–9 cells long. *Capsules* 325–360 µm in diameter, splitting to ± 2/3 of its length; capsule valves 360–370 × 230–240 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic, large, thin-walled; hinge butterfly-shaped, hinge cells rectangular to quadrate, smaller than cells of upper half, thin-walled; marginal cells rectangular, formed by 1–2 rows. *Inner layer of capsule valve*

cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half quadrate, walls nodulose, formed by 1–2 rows, marginal cells of lower half rectangular, walls smooth; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline to yellowish, with irregular thickenings, 220–305 µm long, 16–20 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, ca. 200 µm long, 20 µm wide; additional elaters hyaline, with smooth thickenings, 280–310 µm long, ca. 10 µm wide. *Spores* irregular-oblong or elongate-rectangular, 54–88 × 28–35 µm; spore surface covered with irregular lamellae.

Habitat and ecology. *Colura crenulata* occurs on living leaves and twigs of shrubs and small trees in tropical lower and upper montane forest at altitudes between 1000 and 2100 m. The species was associated with other epiphyllous liverworts, such as *Ceratolejeunea belangeriana* (Gottsche) Steph., *Cheilolejeunea trapezia* (Nees) R.M.Schust. *et* Kachroo, *Drepanolejeunea* spp., and *Metalejeunea cucullata* (Reinw. *et al*.) Grolle.

Distribution. Indonesia (West Sumatra), Malaysia (Sabah), New Guinea (Morobe), Thailand (Grolle 1965, Sangrattanaprasert *et al*. 2017).

Specimen examined. INDONESIA. West Sumatra, Mt. Tandikat, ca. 1000 m, 23 July 1955, *Meijer 8077c* (L). MALAYSIA. North Borneo, Mt. Tambuyokon, c. 15 miles NE. of Kinabalu Peak, 1800–2100 m, 6 July 1961, *Meijer B 11210* (L). PAPUA NEW GUINEA. Morobe, Yunzaing, forest hill, 1800 m, 1936, *Clemens 3726/H-a*, *3776/H-b* (JE, paratype). THAILAND. Trang, Palian, Khao Chedyod, 1040–1070 m, 07°19'18.80" N, 99°54'40.48" E, 3 May 2014. *Sangrattanaprasert 115/14C, 138/14B, 140/14B* (HSNU, PSU).

Taxonomic notes. *Colura crenulata* is easily recognised by the 1) rather large plant, with leaves 0.6–1.1 mm wide, 2) large elliptic lobule sac, 3) surface of the lobule sac and perianth being strongly mamillose, 4) presence of the apical crest on lobule sac apex, and 5) entire dorsal margin of the leaf lobule.

Colura crenulata is morphologically similar to *C. conica*, *C. herzogii* Jovet-Ast, and *C. thomeensis* Pócs. The four species share many similar characteristics in underleaf form, valve character, surface lobule sac and perianth, the presense of apical crest of lobule sac, and several other characters. *Colura conica*, a common species in

tropical and subtropical Asia (Zhu & So 2001), however, is distinguished from *C. crenulata* by the dentate dorsal margin of leaf lobes, valve consisting 13–18 median cells (with 1–2 basal cells) and one circle of 14–17 hyaline marginal cells, and perianth with (3–)4(–5) keels. *Colura herzogii*, a Malesian species (Jovet-Ast 1953), differs from *C. crenulata* in having 1–2 basal median cells of vale, and the irregularly dentate of leaf dorsal margin. *Colura thomeensis*, an endemic species from Saõ Tomé Island (Pócs 2011), is separated from *C. crenulata* by the large apical crest of lobule sac consisting of 7–15 cells and small vale composed of 12–13 hyaline marginal cells and 6–8 median cells.

12. *Colura cristata* Jovet-Ast, Rev. Bryol. Lichénol. 22: 291. 1953. **(Figs. 4.21–4.22)**
Type: INDONESIA. East Kalimantan, Samarinda District, Tandjong Bankgo, West of estuary of the Mahakam river, mangrove forest, 1 August 1952, *Meijer 3010* (holotype: BO!; isotype: PC n.v.).

Plants pale green, 0.5–1 cm long; shoots 0.8–1.5 mm wide. *Stems* 64–96 µm in diameter, in transverse section consisting of 7 cortical cells (20–34 × 20–30 µm) and 3 medullary cells (14–20 × 8–16 µm). *Leaves* uniform, remote, spreading from stem at 50°–80° angle. *Lobes* 0.32–0.64 mm long, 0.18–0.32 mm wide; dorsal margin entire to crenulate. *Lobe cells* thin-walled, trigones small or absent, intermediate thickenings distinct or absent; marginal cells isodiametric to rectangular, 20–34 × 14–20 µm; median cells rectangular to isodiametric, 22–50 × 16–36 µm; basal cells rectangular to hexagonal, 30–58 × 10–30 µm. *Cuticle* smooth. *Oil bodies* 6–11 per cell, homogenous to finely segment, ellipsoid, 5–7 × 3 µm. *Lobules* narrowly tubular, flaring toward sac, 0.6–1.04 mm long. *Lobule sacs* elliptic, strongly inflated, 0.44–0.72 mm long, 0.26–0.4 mm wide, sac surface mamillose, apex acute, ending in apical crest consisting of 7–17 cells. *Valves* lingulate to elliptic, 100–130 × 76–100 µm, composed of one circle of 25–36 hyaline marginal and 31–43 median cells with 1 basal median cell, 2 elongated basal hyaline or 2 hyaline bordered cells present, hinge present with 1 cell, basal median cell adnate with hinge cell not forming a sigmoid curve in outline or not adnate. *Hyaline papillae* spherical to bulbous, 12–16 µm in diameter. *Valve frames* outline semicircular, 110–140 µm wide; cell wall smooth.

Underleaves deeply bilobed, sinus obtuse; lobes lanceolate to filiform, 160–240 × 50–92 µm, 7–11 cells long, 4–6 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* terminal or intermediate on main stems and lateral branches; male bracts in 1–5 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes elliptic to oblong, 280–320 × 160–240 µm; bract lobules semicircular, 200–272 × 96–152 µm; male bracteoles bilobed to round, 160–200 × 40–74 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes falcate to lanceolate, 464–560 × 120–224 µm, apical keel entire; bract lobules narrowly oblong, 400–440 × 64–96 µm; female bracteoles similar to underleaves, 180–200 × 84–100 µm. *Perianths* obovate, 0.8–0.94 mm long, 0.34–0.48 mm wide, with 3 keels; keels short, ridge-like; surface of the perianth strongly mamillose; beak 1 cell long. *Sporophytes*. *Setae* 9 cells long. *Capsules* ca. 240 µm in diameter, splitting to ± 2/3 of its length; capsule valves 240–280 × 156–186 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve slightly rhombic to rectangular, large, thin-walled; hinge butterfly-shaped, hinge cells rectangular to subquadrate, smaller than cells of upper, thin-walled; marginal cells rectangular, formed by 1–2 rows. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half quardrate, walls nodulose, formed by 1–2 rows, marginal cells of lower half rectangular to suquardrate, walls smooth; basal cell subquadrate with smooth wall. *Elaters*: upper marginal elaters hyaline to yellowish, with irregular thickenings, 164–212 µm long, 8–22 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 134–144 µm long, 8–14 µm wide; additional elaters hyaline, with smooth thickenings, 170–200 µm long, 4–8 µm wide. *Spores* irregular-oblong or elongate-rectangular, 36–38 × 26–30 µm; spore surface covered with irregular lamellae.

Habitat and ecology: The species occurs on living leaves and barks in lowland evergreen and mangrove forests.

Distribution: Fiji, Indonesia, Malaysia (Sabah) (Jovet-Ast 1953, Pócs & Eggers 2007, Sangrattanaprasert *et al*. 2019a).

Specimens examined: FIJI. Kadavu Island, 2 km Northeast of Tavuki village, 19°03.829–04.102′S, 178°07.771–921′E, 170–200 m, 13 & 15 September 2003, *Pócs & Pócs 03304/AA* (EGR); 19°04.097–101′S, 178°07.980–08.249′E, 15 September 2003, *Pócs & Pócs 03309/BA* (EGR). INDONESIA. East Kalimantan, Samarinda District, Tandjong Bangko, West of estuary of Mahakam river, 1 August 1952, *Meijer B.3001b.* (BO). MALAYSIA. Sabah, Sandakan city, Sepagara Forest Reserve, along trail to Silam water spring, 04°59′08.88″N 118°11′21.87″E, 253 m, *Zhu, Shu & Yin 20160916-2* (HSNU).

Taxonomic notes: *Colura cristata* is different from other species in the lobule sac ca. 1/2 of lobule length, the large triangular crest comprised of 7–17 cells at lobule sac apex, monoicous and the small size or absent of trigone and intermediate thickening of leaf cell.

13. *Colura denticulata* Jovet-Ast, Rev. Bryol. Lichénol. 23: 2. 1954.

(Figs. 4.23–4.24)

Type: INDONESIA. West Java, Tjisarua-Selatan, along Tjisarua (Tji = river), on leaves of *Araliacea*, 600 m, 6 August 1953, *Meijer 4455* (holotype: BO!; isotype PC n.v.).

= *Colura simplicior* Jovet-Ast, Cryptog. Bryol. Lichénol. 4: 213. 1983. Type: AUSTRALIA. Queensland, Atherton Shire, Danbulla State forest, former logging site, 20 years regeneration, on leaves of monocotyledon, 1976, *Catcheside 76.65*. (holotype: PC n.v.; isotype: JE!, NY n.v.).

Plants 0.55–1 cm long; shoots 1.7–2.4 mm wide. *Stems* 100–110 μm in diameter, in transverse section consisting of 7 cortical cells (24–50 × 20–34 μm) and 3 medullary cells (ca. 30 × 20–30 μm). *Leaves* imbricate, spreading from stem at 50°–80° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaves lobes* 1.1–1.3 mm long, 0.52–0.76 mm wide; dorsal margin flattened, denticulate to dentate; teeth triangular, consisting of 1–5(–7) cells, teeth almost distributed along leaf margin excepted leaf base; lobules narrowly tubular, flaring toward sac, 0.82–1 mm long; lobule sac oblique rounded, strongly inflated, 0.28–0.4 mm long, 0.19–0.23 mm wide, sac surface mamillose, apex obtuse, ending in obliquely apical crest consisting of (1–

)2–4 teeth, teeth triangular consisting of 3–8 cells; valves ovate to rounded, 70–100 × 60–70 µm, composed of one circle of 10–21 hyaline marginal and 10–21 median cells without basal median cell and hinge; hyaline papillae bulbous, ca. 14 µm in diameter; valve frame outline hook-like, 260–520 µm wide, cell wall nodulose. *Non-saccate leaves lobes* oblique elliptic, 1.3–1.35 mm long, 0.8–1 mm wide; apex obtuse, denticulate; dorsal margin flattened, denticulate to dentate; teeth triangular consisting of 1–5(–7) cells, teeth almost distributed along leaf lobes margin, excepted leaf base; lobules narrowly oblong, 0.8–0.9 × 0.14–0.17 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells isodiametric slightly rectangular, 16–34 × 14–24 µm; median cells hexagonal to slightly rectangular, 20–54 × 20–36 µm; basal cells rectangular to slightly hexagonal, 30–50 × 16–36 µm. *Oil bodies* not seen. *Underleaves* deeply bilobed, sinus obtuse; lobe narrowly lanceolate to filiform, 120–180 × 36–56 µm, 4–7 cells long, 2–3 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 4–5 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire to crenulate; bract lobes semicircular to oblong, 188–220 × 120–140 µm; bract lobules semicircular to oblong, 172–216 × 100–128 µm; male bracteoles bilobed, rounded to lanceolate, 80–330 × 90–160 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes elliptic, 720–1000 × 368–424 µm, apical keel crenulate with 1–2 projecting cell rows; bract lobules narrowly oblong, 560–840 × 140–160 µm; female bracteoles rounded to oblong, 80–330 × 90–160 µm, apex obtuse to acute. *Perianths* oblong, 1–1.4 mm long, 0.7–0.8 mm wide, with 3 keels; keels short, bearing coarse teeth at its apex; beak absent or 1–2 cells long. *Sporophytes* not seen.

Habitat and ecology: *Colura denticulata* grows densely on living leaves in lower montane rainforest.

Distribution: Australia (Queensland), Indonesia (West Java) (Jovet-Ast 1953, Jovet-Ast 1983, Thiers 1987).

Specimens examined: INDONESIA. West Sumatra, Mountain Sago near Pajakumbuh, 900 m, 23 December 1955, *Meijer B6345*. MALAYSIA. Kelantan, Gunung Basor, halfway between Dabong and Jeli towns near BKT, Gerongan village

at Renyok no.1 water intake, 05°31.642'N, 101°46.295'E, 670 m, 7 November 2013, *Pócs, Pócs, Lee & Tang 13179/AF* (EGR).

Taxonomic notes: *Colura denticulata* is rather unique and distinctive among dimorphic-leaf species by 1) the saccate leaves as large as non-saccate leaves, 2) denticulate to dentate leaf margin, 3) apical crest of lobule sac comprising (1–)2–4 teeth, 4) ovate to rounded lobule valve composing 20–42 cells, and 5) the perianth keels bearing course teeth at their apex. This species resembles *C. imperfecta* in general appearance. Nevertheless, the latter differs in having rather small saccate leaves (ca. 1/2 times of non-saccate leaves), the absent or reduced valve of lobule sac, and the nearly smooth perianth keels.

14. *Colura galeata* Jovet-Ast, Rev. Bryol. Lichénol. 35: 146. 1967b.

(Figs. 4.25–4.26)

Type: MALAYSIA. Sabah, North Borneo, Tambuyokon Mountain, ca. 15 miles NE of Kinabalu Peak, near camp 2, 6 July 1961, *Meijer B11191* (holotype: L n.v.; isotype: PC n.v.).

Plants ca. 1 cm long; shoots 1.1–1.5 mm wide. *Stems* 52–72 µm in diameter, in transverse section consisting of 7 cortical cells (20–28 × 14–24 µm) and 3 medullary cells (14–18 × 10–14 µm). *Leaves* imbricate, spreading from stem at 40°–90° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaves lobes* 0.36–0.45 mm long, 0.20–0.28 mm wide; dorsal margin flattened, dentate; teeth triangular, 1(–5) cells, teeth distributed on upper half of leaf lobes; lobules narrowly tubular, flaring toward sac, 0.54–0.64 mm long; lobule sacs rounded, strongly inflated, 0.2–0.24 mm long, 0.16–0.2 mm wide, sac surface mamillose, apex obtuse, entire or ending in apical crest consisting of 3–5 cells; valves ovate to elliptic, 110–150 × ca. 60 µm, composed of one circle of 22–26 hyaline marginal and 29–45 median cells, without basal median cell and hinge; hyaline papillae bulbous, ca. 10 µm in diameter; valve frame reduced. *Non-saccate leaves* obliquely obovate to elliptic, 0.9–1.1 mm long, 0.58–0.7 mm wide; apex obtuse, densely dentate; dorsal margin flattened to recurved, densely dentate; teeth triangular, 1–3 cells, teeth often distributed on upper half of leaf lobes; lobules narrowly oblong, 0.38–0.6 × 0.09–0.12 mm. *Lobe cells*

thin-walled, trigones large, intermediate thickenings distinct; marginal cells subquadrate to isodiametric, 16–24 × 12–20 µm; median cells hexagonal to isodiametric, 20–40 × 14–30 µm; basal cells rectangular to slightly isodiametric, 20–44 × 14–36 µm. *Oil bodies* not seen. *Underleaves* deeply bilobed, sinus obtuse; lobe narrowly lanceolate to filiform, 70–140 × 26–40 µm, 3–7 cells long, (1–)2 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 3–5 pairs, hemispherical, apical keel crenulate with 1(–2) projecting cell row, free margin entire; bract lobes semicircular, 140–200 × 110–140 µm; bract lobules semicircular, as large as bract lobes, 180–220 × 72–168 µm; male bracteoless rounded to bilobed, 40–66 × 30–50 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes ovate, 440–464 × ca. 280 µm, apical keel crenulate with 1(–2) projecting cell row; bract lobules narrowly oblong, 344–360 × 80–104 µm; female bracteoles rounded, 120–130 × 100–110 µm, apex obtuse. *Perianths* obtriangular, 0.76–0.9 mm long, 0.44–0.6 mm wide, with 3 keels; keels oblique-triangular, spreading horizontally, bearing coarse teeth at its apex; beak absent. *Sporophytes* not seen.

Habitat and ecology: *Colura galeata* was found densely on living palm leaves in lower montane forest.

Distribution: Malaysia (Sabah) (Jovet-Ast 1967b).

Specimens examined: MALAYSIA. Sabah, North Borneo, Tambuyokon Mountain, ca. 15 miles NE of Kinabalu Peak, near camp 2, 1200–1500 m, 6 July 1961, *Meijer B11190* (L, paratype).

Taxonomic notes: The distinctive features of *Colura galeata* are 1) the dimorphic leaves, 2) dentate leaf margins and teeth distributed on the upper half, teeth consist of 1–3(–5) cells, and 3) valve of lobule consisting of 51–71 cells. This species morphologically resembles *C. speciosa* in having dimorphic leaves, entire apex of lobule sac or ending with apical crest (3–5 cells), and the recurved margins of non-saccate leaf. However, the latter differs from *C. galeata*, by the smaller size of saccate and non-saccate leaves (0.26–0.36 mm long and 0.62–0.7 mm long, respectively), the valve of lobule consisting of 19–24 hyaline marginal cells and 18–24 median cells, and the presence of rounded to weakly triangular teeth at leaf margin.

15. *Colura hemisphaerica* Jovet-Ast, Rev. Bryol. Lichénol. 22: 267. 1953.

(Figs. 4.27–4.28)

Type: INDONESIA. East-Bornéo (East Kalimantan), G. Beratus, Terrace Sulau Mandau, 1000 m, 7 July 1952, *Meijer 1854* (holotype: BO!; isotype: PC n.v.).

= *Colura cymbalifera* Herzog *et* Jovet-Ast, Rev. Bryol. Lichénol. 22: 268. 1953. Type: MALAYSIA. Malakka, s.d., *Verdoorn B(7)* (holotype: JE!) ***syn. nov.***

Plants pale green, 0.5–2 cm long; shoots 1.34–3 mm wide. *Stems* 70–137.5 µm in diameter, in transverse section consisting of 7 cortical cells (20–57.5 × 12–50 µm) and 3 medullary cells (20–50 × 20–32 µm). *Leaves* uniform, imbricate, spreading from stem at 40°–80° angle. *Lobes* 0.44–1.5 mm long, 0.34–0.75 mm wide; dorsal margin flattened, entire. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells subquadrate to rectangular, 24–38 × 18–30 µm; median cells isodiametric to hexagonal, 24–58 × 16–32 µm; basal cells rectangular, 30–50 × 20–30 µm. *Oil bodies* 15–30 per cell, homogenous to very finely segment, ellipsoid, 4.8–7.2 × 2.4–4 µm. *Lobules* narrowly tubular, flaring toward sac, 0.8–1.75 mm long. *Lobule sacs* rotund to widely elliptic, strongly inflated, 0.44–0.82 mm long, 0.36–0.57 mm wide, apex obtuse, without apical crest; sac surface mamillose. *Valves* elliptic, 110–140 × 78–110 µm, composed of one circle of 20–24 hyaline marginal and 17–34 median cells with 1 basal median cell, 2 elongated basal hyaline or 2 hyaline bordered cells present, hinge present with 1 cell, basal median cell adnate with hinge cell not forming a sigmoid curve in outline or not adnate. *Hyaline papillae* bulbous, 14–20 µm in diameter. *Valve frames* outline semicircular, 130–154 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe triangular to lanceolate, 120–280 × 60–160 µm, 6–15 cells long, 3–9 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on lobule sac apex.

Dioicous. *Androecia* terminal or intermediate on main stems or on lateral branches; male bracts in 1–4 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire to crenulate; bract lobes semicircular, 200–300 × 132–208 µm; bract lobules semicircular to slightly oblong, 200–240 × 108–148 µm; male bracteoles bilobed, 140–180 × 110–160 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract lobes elliptic to

oblong, 560–744 × 224–304 µm; bract lobules narrowly oblong, 480–640 × 80–184 µm; female bracteoles quadrangular, apex emarginate, 110–160 × 70–130 µm. *Perianths* elliptic to obovate, 1–1.5 mm long, 0.52–0.57 mm wide, with 3–5 keels; keels short, ridge shape; surface of perianth weakly mamillose; beak 1 cell long. *Sporophytes*. *Setae* 16 cells long. *Capsule* ca. 240 µm in diameter, splitting to ± 2/3 of its length; capsule valves 320–400 × 200–240 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic, large, thin-walled; hinge butterfly-shaped to broadly quadrate, hinge cells rectangular to quadrate, smaller than cells of upper half, thin-walled; marginal cells rectangular, formed by 1–2 rows. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half quadrate, walls nodulose, formed by 1–2 rows, marginal cells of lower half rectangular, walls smooth; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline to yellowish, with irregular to annular thickenings, 220–280 µm long, 16–24 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 150–160 µm long, 14–16 µm wide; additional elaters hyaline, with smooth thickenings, 260–300 µm long, 6–10 µm wide. *Spores* irregular-oblong or elongate-rectangular, 44–66 × 36–40 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura hemisphaerica* was usually found growing on bark of tree trunk in montane rain forest at altitudes between 820 and 1750 m.

Distribution: Indonesia (Borneo, Java), Malaysia (as *C. cymbalifera*) (Jovet-Ast 1953).

Specimens examined: MALAYSIA. Kedah, towards the lower summit to main summit Gunung Jerai, 05°47.8'N, 100°26.1'E, 900–1150 m, 21 February 2010, *Pócs & Pócs 1008/H*, *1009/A* (EGR). Pahang, Genting Highland, Mount. Ulu Kali, vicinity of the summit area, 1750 m, 30 November 2012, *Yong & Cheah 8000* (KLU). THAILAND. Nakhon Si Thammarat, Lan Saka, Khao Luang, 1371 m, 4 July 2017, *Chantanaorrapint & Suwanmala 1620A* (PSU); Nopphitam, Khao Nan National Park, 10 August 2007, *Sukkharak & Seelanan 369A* (BCU); Phrom Khiri, Khao Luang, Prom Lok Peak, 08°32'10.27"N, 099°45'27.00"E, 1440 m, 23 April 2014, *Sangrattanaprasert 104/14* (PSU). Phatthalung, Kong Ra, Khao Loan, 07°26'45.33"N, 99°52'31.64"E, 916–1234 m, 27 May 2017, *Chantanaorrapint &*

Suwanmala 984A, *1139A* (PSU). Trang, Palian, Khao Chedyod, 07°19'18.80"N, 99°54'40.48"E, 1040–1070 m, 2 May 2014, *Sangrattanaprasert 118/14*, *120/14B* (PSU). Yala, Betong, Ban Piyamit 2, Wanwisa Waterall, 05°49'04.40"N, 101°05'59.70"E, 820 m, 14 June 2013, *Chantanaorrapint & Promma 2457C* (PSU).

Taxonomic notes: *Colura hemisphaerica*, a little-known species which was originally described based only on the type collected in Indonesia (Jovet-Ast 1953) is very closely related to *C. cymbalifera*, a Peninsular Malaysia species. The latter species was described based on a sparse specimen which differs from the former species by only small size of leaves and the number of intermediate thickenings (Jovet-Ast 1953). More specimens collected in this work, however, reveal the morphological variant. Moreover, the examination of type specimens of both species supported that they are conspecific, so we here propose *C. cymbalifera* as synonym of *C. hemisphaerica*.

Androecia, gynoecia and sporangia of this species is found and described here for the first time. The sporangium is extremely rare, and the seta includes 16 cells long which its length is distinguised from the other species, e.g., *C. crenulata* (Sangrattanaprasert *et al*. 2017). Nevertheless, the elater pattern of this species and other *Colura* species are exactly alike.

Moreover, this species may be confused with *C. meijeri*; they share similar characters such as leaf out-line shape, characters of valve, and perianth shape. However, *C. meijeri* differs by 1) having short leaf length (1.37–1.42 mm), 2) elliptic lobule sacs, 1/2 as long as leaf length, 3) elliptic to oblong perianths, with 3 keels, and 4) oblong female bracteoles with obtuse apices.

16. *Colura herzogii* Jovet-Ast, Rev. Bryol. Lichénol. 22: 261. 1953.

(Figs. 4.29–4.30)

Type: INDONESIA. West Java, Res. Priangan, G. Geger Bentang, in silvis, praecipue in decl. orient., August 1930, *Verdoorn 67* (holotype: BO n.v.).

Plants 1–1.5 cm long; shoots 1.7–2.6 mm wide. *Stems* 100–176 µm in diameter, in transverse section consisting of 7 cortical cells (22–46 × 14–38 µm) and 3 medullary cells (20–26 × 20–24 µm). *Leaves* uniform, imbricate, spreading from stem at 40°–

70° angle. *Lobes* 1.1–1.64 mm long, 0.76–1.1 mm wide; dorsal margin flattened, denticulate to dentate; teeth triangular, consisting of 1–2 cells, almost distributed on upper half of leaf lobe margin. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells rectangular to subquadrate, 24–64 × 20–30 µm; median cells rectangular to isodiametric, 30–60 × 20–34 µm; basal cells rectangular, 30–76 × 20–40 µm. *Oil bodies* not seen. *Lobules* narrowly tubular, flaring toward sac, 1.3–1.8 mm long. *Lobule sacs* broadly conical to elliptic, strongly inflated, 0.56–0.9 mm long, 0.32–0.48 mm wide, apex obtuse, ending in apical crest consisting of 1–5 cells; sac surface strongly mamillose. *Valves* widely elliptic to ovate, 90–114 × 78–104 µm, composed of one circle of 16–18 hyaline marginal and 18–24 median cells, with 2 basal median cells; hyaline bordered present consisting of 2 cells; hinge present with 3 cells. *Hyaline papillae* bulbous, 16–20 µm in diameter. *Valve frames* outline semicircular, (110–)140–150 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe lanceolate, 220–300 × 60–90 µm, 5–8 cells long, 3–4 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on leaf lobe and lobule sac surface.

Dioicous. *Androecia* terminal or intermediate on lateral branches; male bracts in 2–6 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire to crenulate; bract lobes semicircular, 240–300 × 140–220 µm; bract lobules oblong, 200–300 × 100–140 µm; antheridia 2 per bract; male bracteoles bilobed to quadrate, 60–110 × 60–120 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract lobes elliptic, 840–980 × ca. 376 µm; bract lobules narrowly oblong, 784–800 × 120–176 µm; female bracteoles obliquely quadrate, apex emarginate, ca. 110 × ca. 100 µm. *Perianths* obtriangular, ca. 1.4 mm long, ca. 0.46 mm wide, with 3 keels; keel rectangular, 400–560 × 344–400 µm, spreading horizontally, bearing coarse teeth near its apex; surface of perianth mamillose; beak 2 cells long. *Sporophytes and spores* not seen.

Habitat and ecology: *Colura herzogii* usually grows on living leaves in montane rain forest ranging from 800–1645 m elevation.

Distribution: Indonesia (Jovet-Ast 1953).

Specimens examined: INDONESIA. West Java, Tjibodas, Mountain Gedah near Pantjuranmas, 1500 m, 1 March 1953, *Meijer B3829* (BO); Tjibodas, Mountain

Gede, Hutan Pasir Sintok, 19 September 1953, *Meijer B4517* (BO); Mountain Pangerango (Pangrango), 1645 m, April 1844, *Schiffner 3485* (Paratype: JE); G. Patoeha, August 1930, *Verdoorn (60)* (BO). West Sumatra, Mountain Tandikat, Padang Panjang, 1000 m, 23 July 1955, *Meijer 8077e* (L); East Kalimantan, Borneo, East Kutei, Peak of Balikpapan terrace Berikan Bulu, 800 m, 16 July 1952, *Meijer B2319* (L).

Taxonomic notes: This species can be recognised by 1) large leaves, 1.3–1.8 mm long, 2) the large valve composed of 34–42 cells, and 3) valve frame rather wide (110–150 µm). *Colura herzogii* is morphologically similar to *C. conica* and they are distinguished by leaves and valves size and altitudinal distribution range. Hence, these two species may be conspecific and more specimens as well as molecular data of *C. herzogii* need to be examined for understanding of their status.

17. *Colura imperfecta* Steph., Sp. Hepat. 5: 938. 1916. **(Figs. 4.31–4.32)**

Type: SOLOMON ISLANDS. s.d., *Micholitz s.n.* (holotype: G n.v.).

Plants pale green, 1–2 cm long; shoots 1–1.2 mm wide. *Stems* 74–80 µm in diameter, in transverse section consisting of 7 cortical cells (20–30 × 14–26 µm) and 3 medullary cells (16–20 × 10–16 µm). *Leaves* imbricate, spreading from stem at 45°–70° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaves lobes* 0.45–0.68 mm long, 0.24–0.36 mm wide; dorsal margin flattened, dentate; teeth deeply triangular, consisting of 3–4(–12) cells, distributed regularly from apex to base of lobe; lobules narrowly tubular, flaring toward sac, 0.32–0.56 mm long; lobule sacs oblique elliptic, strongly inflated, 0.2–0.28 mm long, 0.1–0.13 mm wide, sac surface mamillose, apex obtuse, ending in obliquely apical crest 1–3 teeth, consisting of 3–5 cells in each tooth; valves reduced to a few cells or absent; *hyaline papillae* bulbous, 7.5–12.5 µm in diameter; *valve frame* outline narrowly hook-like, 50–87.5 µm wide, cell wall entire. *Non-saccate leaves* obovate, 0.9–1.1 mm long, 0.6–0.66 mm wide; apex obtuse, dentate; dorsal margin flattened, dentate; teeth deeply triangular, consisting of 3–5(–10) cells, teeth distributed regularly from apex to base of lobe; *lobules* narrowly oblong, 0.42–0.5 × 0.06–0.15 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings very distinct; marginal cells quadrate to rectangular,

16–40 × 10–20 µm; median cells isodiametric to rectangular, 14–40 × 14–30 µm; basal cells rectangular, 30–66 × 12–30 µm. *Oil bodies* 13–25 per cell, roughly segmented, ellipsoid, 4–7 × 2–3 µm. *Underleaves* deeply bilobed, sinus obtuse; lobe filiform, 140–160 × 20–30 µm, 3–4 cells long, (1–)2–3 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 5–7 pairs, hemispherical to slightly oblong, apical keel crenulate with 1 projecting cell row; bract lobes semicircular, 220–256 × 136–196 µm, free margin dentate near apex; bract lobules semicircular, 180–210 × 124–150 µm; male bracteoles rounded to bilobed, 52–66 × 52–60 µm, apex obtuse to emarginate. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes ovate to elliptic, 480–590 × 200–320 µm, apical keel dentate with a few teeth; bract lobules narrowly oblong, 425–496 × 120–160 µm; female bracteoles rounded, 100–120 × 80–120 µm, apex obtuse. *Perianths* obtriangular to slightly oblong, 0.77–0.84 mm long, 0.3–0.38 mm wide, with 3 keels; keels oblique triangular, 80–130 × 100–120 µm, spreading horizontally, apex obtuse; beak 1–2 cells long. *Sporophytes*. *Setae* 9 cells long. *Capsules* 260–290 µm in diameter, splitting to ± 2/3 of its length; capsule valves 260–290 × 188–196 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic to polygonal, large, thick-walled; hinge slightly rectangular to broadly quadrate, ca. 1/2 of valve length, hinge cells rectangular to isodiametric, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half isodiametric to rectangular, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular to annular thickenings, 180–230 µm long, 10–14 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 156–160 µm long, 14–15 µm wide; additional elaters hyaline, with smooth thickenings, 216–230 µm long, 4–6 µm wide. *Spores* irregular-oblong or elongate-rectangular, 54–60 × 22–28 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura imperfecta* was found on living leaves in lowland evergreen and coastal forests.

Distribution: Indonesia (Borneo, Java, Sumatra), Malaysia (Malay Peninsular), Papua New Guinea, Solomon Islands (Jovet-Ast 1953, Pócs 2013).

Specimens examined: INDONESIA. East Kalimantan, Sangkulirang District, 20 m, July 1951, *Kostermans 6155* (L). Sumatra, West Sumatra, Rimbo Panti Nature Reserve, 18 June 1958, *Meijer B7500* (L). PAPUA NEW GUINEA, Morobe, Central Coastal Foothills, in virgin forest of very low elevation trees in valley of small river ca. 1 km East of Etep, 06°1.5'S, 147°12.5'E, 300–500 m, 26 August 1981, *Daniel H. Norris 65856* (EGR). SOLOMON ISLANDS, Kolombangara Island, in lowland forest along ridge north of Vanga River on northwest side of island, 07°56'S, 156°58'E, 100 m, 14 August 1977, *Noris & Roberts 49255A* (EGR). THAILAND. Nakhon Si Thammarat, Nopphitam, Khao Luang National Park, Krung Ching Waterfall, 08°44'05.50''N, 99°39'34.60''E, 196–280 m, 31 October 2012, *Pócs, U-Tayanapuh & Lee 1217AE–2*, 10 October 2014, *Sangrattanaprasert 213/14*, *224/14B*, *228/14A* (PSU). Songkhla, Sadao, Ton Nga Chang Wildlife Sanctuary, Pha Dam Waterfall, 06°46'02.19''N, 100°12'46.58''E, 100–150 m, 16 December 2014, *Sangrattanaprasert 255/14B*, *300/15B* (PSU).

Taxonomic notes: The diagnostic of *Colura imperfecta* are 1) strongly teeth distributed from apex to base of leaf margin, 2) the non-saccate leaf about 2 times of the saccate once, 3) lobule sac apex covering by 1–3 teeth, and 4) the reduced lobule valve (with none or only a few cells). The previous report of *C. imperfecta* in Thailand (Pócs & Podani 2015) was based on misidentification materials; large valves present in their leaves, so those specimens are *C. ornata*. Therefore, *C. imperfecta* are new reported to Thailnad here.

18. *Colura inflata* K.I.Goebel, Ann. Jard. Bot. Buitenzorg 39: 11, 1928.

(Figs. 4.33–4.34)

Type: INDONESIA. Sumatra, Fort de Kock, 1925, *Goebel 17/a* (isotype: JE!).

Plants pale green, 0.5–1 cm long; shoots 0.8–1.5 mm wide. *Stems* 54–80 µm in diameter, in transverse section consisting of 7 cortical cells (16–26 × 14–20 µm) and 3 medullary cells (12–20 × 12–14 µm). *Leaves* imbricate, spreading from stem at 60°–90° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate*

leaves lobes 0.36–0.65 mm long, 0.31–0.48 mm wide; dorsal margin flattened, denticulate; teeth triangular, consisting of 1–3 cells, teeth distributed along leaf lobe from apex to base; lobules narrowly tubular, flaring toward sac, 0.53–0.68 mm long; lobule sacs elliptic to rounded, strongly inflated, 0.24–0.36 mm long, 0.19–0.24 mm wide, sac surface mamillose, apex obtuse, ending in apical crest consisting of 1–6 cells, rarely entire; valves elliptic to lingulate, 90–120 × 42–60 µm, composed of one circle of 17–21 hyaline marginal and 13–24 median cells without basal median cell and hinge; hyaline papillae bulbous, 8–14 µm in diameter; valve frame reduced. *Non-saccate leaves* obliquely elliptic to obovate, 0.55–0.98 mm long, 0.31–0.65 mm wide; apex obtuse, denticulate to weakly dentate; dorsal margin flattened, denticulate to dentate; teeth triangular, consisting of 1–3 cells, teeth distributed along leaf lobe from apex to base; lobules narrowly oblong, 0.32–0.56 × 0.06–0.12 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells subquadrate to rectangular, 16–30 × 10–20 µm; median cells isodiametric to rectangular, 20–50 × 18–30 µm; basal cells rectangular, 30–60 × 18–30 µm. *Oil bodies* 18–37 per cell, roughly segmented, ellipsoid, 3–8 × 1–2 µm. *Underleaves* deeply bilobed, sinus acute to obtuse; lobe filiform, 90–140 × 20–40 µm, 4–6 cells long, 2–3 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 3–7 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular, 160–220 × 120–160 µm; bract lobules semicircular to oblong, 140–200 × 100–110 µm; male bracteoles bilobed to oblong, 50–80 × 30–60 µm, apex bilobed to obtuse. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes ovate to elliptic, 360–600 × 176–400 µm, apical keel entire to dentate with 1–3 projecting cell row; bract lobules narrowly oblong, 280–440 × 88–200 µm; female bracteoles oblong to caudate, 100–160 × 80–120 µm, apex emarginate to obtuse. *Perianths* obtriangular, 0.72–0.9 mm long, 0.48–0.9 mm wide, with 3 keels; keels ellipsoid, strongly inflated, 280–360 × 240–320 µm, spreading horizontally, apex obtuse, entire; beak 1–3 cells long. *Sporophytes*. *Setae* 9 cells long. *Capsules* 280–296 µm in diameter, splitting to ± 4/5 of its length; capsule valves 260–300 × 160–200 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic to

polygonal, large, thin-walled; hinge rectangular, ca. 1/2 of valve length, hinge cells rectangular to isodiametric, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half rectangular, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular to annular thickenings, 116–252 µm long, 8–18 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 140–170 µm long, 10–14 µm wide; additional elaters hyaline, with smooth thickenings, 200–240 µm long, 6–10 µm wide. *Spores* irregular-oblong or elongate-rectangular, 36–80 × 14–24 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura inflata* was found growing amongst other epiphyllous liverwort such as *C. acroloba*, *C. ari*, *C. bisvoluta* in lowland ever green forest.

Distribution: Indonesia (Sumatra), Vietnam (South Vietnam) (Goebel 1928, Jovet-Ast 1961).

Specimens examined: MALAYSIA. Perak, Taiping, Bukit Larut (Maxwells Hill), Regenwald an de Straβe zur Sendestation, 1080 m, 27 May 1997, *Verwimp & Verwimp 19010/A* (EGR). THAILAND. Songkhla, Sadao, Ton Nga Chang Wildlife Santuary, Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 300 m, 23 February 2015, *Sangrattanaprasert 291/15C, 292/15B* (PSU).

Taxonomic notes: The distinctive features of *Colura inflata* are 1) denticulate to dentate leaf lobe margins, 2) rounded to elliptic lobule sacs, strongly inflated, 3) sac apices usually end with small apical crest consisting of 1–6 cells, 4) having reduced valve frames, and 5) ellipsoid and strongly inflated perianth keels. Nevertheless, these distinguished characters of *C. inflata* are very variable in size and shape and the species is morphologically related to *C. corniantha*, a Vietnam species. *Colura corniantha* differs from *C. inflata* by acute apices of non-saccate leaf bearing teeth, saccate leaves smaller than non-saccate leaves, the presence of strongly teeth on upper half of saccate leaf margin and having 1–3 teeth ending at perianth keel apices.

19. *Colura junghuhniana* (Prantl) Steph., Sp. Hepat. 5: 938. 1916. **(Figs. 4.35–4.36)**
≡ *Lejeunea junghuhniana* Prantl, Hedwigia 29: xvi, 1890. **Type:** INDONESIA. Java, s.d., *Junghuhn 6873* (holotype: W n.v.).

Plants pale green, ca. 3.6 mm long; shoots 0.7–0.8 mm wide. *Stems* 68–80 µm in diameter, in transverse section consisting of 7 cortical cells (20–30 × 14–30 µm) and 3 medullary cells (20–22 × 14–16 µm). *Leaves* uniform, remote to contiguous, spreading from stem at 20°–60° angle. *Lobes* 0.5–0.55 mm long, 0.4–0.5 mm wide, strongly incurved; dorsal margin entire; dorsal surface strongly papillose. *Lobe cells* thin-walled to slightly thick-walled, trigones small, intermediate thickenings absent; marginal cells slightly subquadrate, 10–30 × 14–20 µm; median cells subquadrate, 14–32 × 10–20 µm; basal cells rectangular to hexagonal, 14–50 × 14–22 µm. *Oil bodies* not seen. *Lobules* narrowly tubular, flaring toward sac, 1.22–1.38 mm long. *Lobule sacs* lanceolate, strongly inflated, 0.96–1.12 mm long, 0.34–0.4 mm wide, forming a long tubular beak towards the apex, beak 0.2–0.3 mm, ca. 1/3 as long as leaf length; dorsal surface papillose. *Valves* ovate, 80–90 × 70–75 µm, composed of one circle of 16–18 hyaline marginal and 12–16 median cells with 2 basal median cells; hyaline bordered present consisting of 1 cell; hinge present consisting of 2 superimposed cells. *Hyaline papillae* bulbous, 18–20 µm in diameter. *Valve frames* outline semicircular, ca. 150 µm wide; cell wall smooth. *Underleaves* distant, deeply bilobed, sinus obtuse; lobe lanceolate to triangular, 130–210 × 26–56 µm, 6–10 cells long, 2–4 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* terminal or intermediate on lateral branches; male bracts in 1 pair, hemispherical, apical keel papillose, free margin entire to crenulate; bract lobes semicircular, 160–200 × 100–120 µm, papillose on dorsal surface; bract lobules semicircular to oblong, 116–140 × 50–64 µm; male bracteoles bilobed, 90–110 × 24–30 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; innermost female bracts slightly rounded, bract lobes semicircular, 240–340 × ca. 140 µm, bract lobules semicircular, 300–388 × 120–172 µm, lobule rather larger than lobe; dorsal surface entire; another female bract lobes ovate, ca. 400 × 220–240 µm, bract lobules oblong, 360–380 × 130–160 µm; dorsal surface papillose; female bracteoles bilobed, 130–140 × 26–34 µm, smaller than underleaves. *Perianths*

oblaceolate to obtriangular, ca. 0.8 mm long, 0.4–0.5 mm wide, with 5 keels; keels triangular, 80–120 × 60–110 μm; perianth surface papillose on upper half; beak 1 cell long. *Sporophytes*. *Setae* 12 cells long. *Capsule* 264–280 μm in diameter, splitting to ± 2/3 of its length; capsule valves 220–240 × 160–170 μm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve, slightly rhombic, large, thick-walled; hinge slightly rectangular to butterfly-shape, ca. 1/2 of valve length, hinge cells rectangular, thin-walled; marginal cells rectangular to subquadrate, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half rectangular (to triangular), walls not nodulose, formed by 1 row, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular thickenings, 150–200 μm long, 16–20 μm wide; lower marginal elaters hyaline, with irregular thickenings, 130–140 μm long, 8–10 μm wide; additional elaters hyaline, with smooth thickenings, 190–200 μm long, 10–12 μm wide. *Spores* irregular-oblong or elongate-rectangular, 40–60 × 20–24 μm; spore surface papillated, rosette present, 0–5 per side.

Habitat and ecology: *Colura junghuhniana* occurs on twigs in montane forest at altitude about 2430 m.

Distribution: Indonesia (Java), Papua New Guinea (Simbu) (Jovet-Ast 1953, Pócs 2013).

Specimens examined: MALAYSIA. Sabah, Ranau city, Kinabalu National Park, from the Ubah Shelter to the Layang-Layang Shelter, 06°02.249'N 116°33.619'E, 2430 m, 22 September 2016, *R.-L. Zhu, L. Shu & X.-B. Yin 20160922-348* (HSNU).

Taxonomic notes: *Colura junghuhniana* is easily distinguished from other Malesian members of *Colura* by 1) the presence of strong rounded papillae on dorsal surface of leaves and perianths, 2) the lobule sacs forming a tubular beak at apex, ca. 1/3 as long as its length and 3) perianths with 5 triangular keels. The species is morphologically similar to *C. medusa* J.Eggers *et* Pócs (Melanesian species) and *C. berghenii* Jovet-Ast (African species), which also have papillae covered on leaves and perianths surface. *Colura medusa* is distinguished from *C. junghuhniana* by conical to acute papillae covered leaf surface except leaf apex beak, long leaf apex beak (1/2 as

long as leaf length) and very long perianth keels that end in 2–3 lobe cells. *Colura berghenii* differs from *C. junghuhniana* in having weak conical papillae scattered on dorsal surface of leaves, underleaf width with 4–5 cells wide at base, and perianth consisting of 5 erect keels (Jovet-Ast 1953).

20. *Colura karstenii* K.I.Goebel, Pflanzenbiol. Schilder. 2: 153. 1891.

(Figs. 4.37–4.38)

Type: INDONESIA. Amboyna island, Wawani Hali, *Karsten s.n.* (holotype: G n.v.).

Plants dull green, 1–1.5 cm long; shoots 2–5 mm wide. *Stems* 150–250 µm in diameter, in transverse section consisting of 7 cortical cells (45–75 × 34–70 µm) and 3 medullary cells (30–68 × 26–64 µm). *Leaves* uniform. imbricate, spreading from stem at 30°–60° angle. *Lobes* 2.1–3.4 mm long, 0.7–1 mm wide; dorsal margin strongly revolute. *Lobe cells* thin-walled, trigones large, intermediate thickenings very distinct; marginal cells isodiametric to subquadrate, 26–40 × 20–28 µm; median cells rectangular, 30–70 × 18–30 µm; basal cells rectangular, 44–70 × 24–34 µm. *Oil bodies* 8–18 per cell, roughly segmented, ellipsoid, 5.5–9.6 × 3–4 µm. *Lobules* narrowly tubular, flaring toward sac, 3–3.5 mm long. *Lobule sacs* deltate to slightly elliptic, strongly inflated, 1.2–1.4 mm long, 0.8–0.85 mm wide, sac surface mamillose, apex obtuse, entire. *Valves* lingulate, 440–480 × 320–336 µm, composed of one circle of 40–70 hyaline marginal and 130–275 median cells without basal median cell and hinge, elongated basal hyaline persent. *Hyaline papillae* bulbous, 20–24 µm in diameter. *Valve frames* outline semicircular, 260–520 µm wide; cell wall nodulose. *Underleaves* deeply bilobed, sinus obtuse; lobe lanceolate to acuminate, 360–640 × 64–150 µm, 12–19 cells long, 4–9 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on lobule sac.

Dioicous. *Androecia* on lateral branches; male bracts in 5–9 pairs, hemispherical, apical keel entire, free margin entire; bract lobes semicircular, 200–280 × 140–220 µm; bract lobules semicircular, 220–280 × 120–160 µm, bract lobules as large as bract lobes; male bracteoles bilobed, slightly small. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes oblong to slightly elliptic, 900–1120 × 260–360 µm, apical keel entire; bract lobules narrowly

oblong, 840–900 × 96–180 µm; female bracteoles bilobed to linear, small with a few cells. *Perianths* obovate to slightly oblong, 1.9–2 mm long, 0.6–0.7 mm wide, with 5 keels; keels short, entire; beak 3–5 cells long. *Sporophytes*. *Setae* 14 cells long. *Capsule* ca. 260 µm in diameter, splitting to ± 4/5 of its length; capsule valves 430–480 × 250–280 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper part of valve, slightly rhombic, large, thick-walled, nodulose; hinge ca. 1/5 of valve, butterfly-shaped, hinge cells subquadrate, smaller than cells of upper half, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half subquadrate, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall smooth; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular thickenings, 270–400 µm long, 20–32 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 260–280 µm long, 20–22 µm wide; additional elaters hyaline, with irregular or smooth thickenings, 340–380 µm long, 6–10 µm wide. *Spores* irregular-oblong or elongate-rectangular, 66–90 × 34–48 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura karstenii* often occurs on twigs in lower montane forest at altitude between 490 and 1460 m.

Distribution: China (Hainan), Indonesia (Amboyna Island), Laos, Malaysia (Malay Peninsula), Papua New Guinea, Thailand, Vietnam (Jovet-Ast 1953, Tixier 1962, Zhu & So 2001, Sangrattanaprasert *et al*. 2018).

Representative specimens examined: MALAYSIA. Kedah, Gunung Jerai Mountain, 05°47.8'N, 100°26.1'E, 900–1150 m, 21 February 2010, *Pócs & Pócs 1008/J*, *1009/G* (EGR); Sabah, Sandakan city, Sepagara Forest Reserve, along Kalung-Kalungan trail, 04°57'54.76"N, 118°10'22.39"E, 490 m, 15 September 2016, *Zhu, Shu & Yin 20160915-21A*. THAILAND. Loei, Phu Luang Widlife Sanctuary, trail from Talearn to Dinosaur footprints, 17°17'51.76"N, 101°31'39"E, 1280–1460 m, 19 February 2016, *He & Sukkharak 46858A* (MO); Nakhon Nayok, Khao Yai National Park, Pha Dieo Dai, 14°21'59.39"N, 101°23'20.19"E, 1190 m, 14 November 2013, *Sangrattanaprasert 30/13A*, *39/13A* (PSU), 1 June 2015, *Sangrattanaprasert 341/15* (PSU); Nakhon Si Thammarat, Khao Nan National Park, 1100 m, 10–11

August 2007, *Sukkhalak & Seelanan, 437, 369 B* (BCU), 28 February 2008, *Chantanaorrapint 08-031* (EGR); Trang, Khao Chedyod, 1040–1070 m, 2 May 2014, *Sangrattanaprasert 115/14B, 116/14A, 134/14A, 144/14* (PSU)

Taxonomic notes: This species is morphologically similar to *C. strophiolata* Jovet-Ast, which was found in Cambodia and Malaysia, but the latter is distinguished by the longer lateral leaves ca. 4.5 mm in length and the wider underleaves with 10 cells width at base (Jovet-Ast 1976). *Colura karstenii*, however, shows the variations in leaf and underleaf sizes, which may likely overlap with *C. strophiolata*. Thus, these two species may possibly be conspecific, and the molecular phylogenetic study is needed to determine the interrelationships between them.

21. *Colura maxima* Jovet-Ast., Rev. Bryol. Lichénol. 22: 284. 1953. **(Fig. 4.39)**

Type: INDONESIA. Halmahera island, Gunung Sembilan, 300 m, 25 September 1951, *Pleyte 252* (holotype: BO!).

Plants ca. 1.1 cm long; shoots 2–3 mm wide. *Stems* 150–160 µm in diameter, in transverse section consisting of 7 cortical cells (28–60 × 20–50 µm) and 3 medullary cells (30–40 × 20–30 µm); *Leaves* uniform, contiguous to imbricate, spreading from stem at 40°–60° angle. *Lobes* 1.4–1.6 mm long, 0.64–0.72 mm wide; dorsal margin flattened, entire to denticulate; dorsal surface papillose. *Lobe cells* thin-walled, trigones large, intermediate thickenings very distinct; marginal cells subquadrate, 30–50 × 20–40 µm; median cells hexagonal to rectangular, (30–)60–80 × 26–40 µm; basal cells rectangular, 40–70 × 20–40 µm. *Oil bodies* not seen. *Lobules* narrowly tubular, flaring toward sac, 1.8–2 mm long. *Lobule sacs* conical to fusiform, strongly inflated, 1–1.2 mm long, 0.4–0.44 mm wide, apex obtuse, entire; dorsal surface papillose. *Valves* ovate, 130–140 × 110–120 µm, composed of one circle of 20–21 hyaline marginal and 29–34 median cells with 1 basal median cell; hyaline bordered present consisting of 2 cells; hinge present consisting of 3 cells. *Hyaline papillae* bulbous, 16–20 µm in diameter. *Valve frames* outline semicircular, 150–160 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus acute; lobe triangular to lanceolate, 280–300 × 80–120 µm, 10–12 cells long, 5–6 cells wide at base; margin entire. *Sexual and asexual reproduction* not seen.

Habitat and ecology: *Colura maxima* was found on common tree in disturbed forest near to Mumar river in lowland forest at altitude 300 m (Jovet-Ast 1953).

Distribution: Indonesia (Halmahera island) (Jovet-Ast 1953), endemic.

Additional specimens examined: –

Taxonomic notes: This species is rather unique and very distinctive by 1) large plants, 2) conical to fusiform lobule sacs without apical crest, and 3) sac and lobe surfaces strongly papillose. *Colura maxima*, however, resembles to *C. herzogii*, but the former differs from the latter by large plant with strong papillae on lobe and sac surface, entire sac apex without crest, entire to denticulate dorsal margin, large trigones and distinct intermediate thickenings, large valve including 49–55 cells, and large underleaf lobes (10–11 cells long, 5–6 cells wide at base).

22. *Colura medusa* J.Eggers *et* Pócs, Chenia 11: 22. 2013. **(Figs. 4.40–4.41)**

T**ype:** PAPUA NEW GUINEA. Western Province, Tabubil, Dublin Creek, rain forest remnants and secondary forest, 600–700 m, 7 August 1995, *Lenz PNG 6/115 p. p. 7* (holotype: EGR n.v.; isotype: EGR!, JE n.v.).

Plants pale green, 3–5 mm long; shoots 0.4–0.56 mm wide. *Stems* 40–56 µm in diameter, in transverse section consisting of 7 cortical cells (16–26 × 12–20 µm) and 3 medullary cells (12–16 × 12–16 µm). *Leaves* uniform, remote to contiguous, spreading from stem at 45°–70° angle. *Lobes* 0.15–0.2 mm long, 0.12–0.2 mm wide, incurved; dorsal surface moderately papillose; dorsal margin entire. *Lobe cells* thin-walled, trigones and intermediate thickenings absent; marginal cells isodiametric to rectangular, 14–24 × 10–16 µm; median cells rectangular to slightly hexagonal, 14–26 × 12–18 µm; basal cells rectangular, 24–40 × 10–14 µm. *Oil bodies* not seen. *Lobules* narrowly tubular, flaring toward sac, 0.44–0.88 mm long. *Lobule sacs* lanceolate, strongly inflated, 0.36–0.8 mm long, 0.08–0.13 mm wide, sac forming a long tubular beak towards the apex, (0.16–)0.2–0.32 mm, ca. 1/2 as long as leaf length, apices usually ending with 1 peak, rarely 2 peaks; sac surface mamillose to papillose. *Valves* elliptic to lingulate, 40–56 × 30–46 µm, composed of one circle of 10–14 hyaline marginal and 7–9 median cells with 2 basal median cells; hyaline bordered present

consisting of 1 cell; hinge present consisting of 3 cells. *Hyaline papillae* bulbous, ca. 10 µm in diameter. *Valve frames* outline semicircular, ca. 70 µm wide; cell wall smooth. *Underleaves* deeply bilobed, asymmetric, sinus obtuse; lobe lanceolate, 60–160 × 14–40 µm, 4–8 cells long, 2–4 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 1–2 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire to crenulate; bract lobes semicircular, 110–150 × 60–80 µm; bract lobules semicircular, as large as bract lobes, 100–160 × 44–74 µm; male bracteoles small with a few cells. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract lobes oblong to slightly lanceolate, 260–300 × 100–128 µm; bract lobules narrowly oblong, 180–200 × 20–32 µm; female bracteoles bilobed, 86–120 × ca. 40 µm. *Perianths* oblanceolate to obtriangular, 0.62–0.68 mm long, ca. 0.26 mm wide, with 5 keels; keels horn-like, 180–360 × 40–60 µm, perianth surface mamillose to moderately papillate; beak 5–6 cells long. *Sporophytes*. *Setae* 9 cells long. *Capsules* 180–240 µm in diameter, splitting to ± 4/5 of its length; capsule valves 170–220 × 120–156 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper part of valve, slightly rhombic, large, thin-walled; hinge rectangular to butterfly-shaped, ca. 1/3 of valve length, hinge cells rectangular, thin-walled; marginal cells rectangular to subquadrate, formed by 1–2 rows. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half rectangular, walls not nodulose to nodulose, formed by 1–2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with smooth thickenings, 120–186 µm long, 6–16 µm wide; lower marginal elaters hyaline, with smooth thickenings, 100–130 µm long, 2–6 µm wide; additional elaters hyaline, with smooth thickenings, 140–194 µm long, 4–8 µm wide. *Spores* elongate-rectangular, 52–76 × 16–20 µm; spore surface covered with irregular lamellae; sporeling not seen.

Habitat and ecology: *Colura medusa* was found occuring on living leaves in lowland evergreen rain forest, particularly along the stream.

Distribution: Papua New Guinea (Tabubil) (Pócs 2013).

Specimens examined: THAILAND. Songkhla, Ton Nga Chang Wildlife Sanctuary, Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 100–150 m, 12 September 2015, *Sangrattanaprasert 398/15* (PSU). Yala, Than To, Wang Sai Stream, 06°00'55.66"N, 101°16'36.36"E, 300 m, 2 July 2014, *Sangrattanaprasert 177/14C* (PSU).

Taxonomic notes: *Colura medusa* strongly resembles *C. tenuicornis* because of the leaf shape. However, the former is different in 1) hinge cells of valve having 3 cells, 2) asymmetrical underleaves, one side longer than the other one, 3) very long perianth beaks, 5–6 cells long, 4) spores being very long and curved in shape, 5) spore ornamemtation being irregular lamella, and 6) the absence of spore rosette. Moreover, the presence of three hinge cells beneath lobule valve is related to species belonged to sect. *Harmophyllum*, so more collections and molecular data are needed clarify their phylogenetic position.

23. *Colura meijeri* Jovet-Ast, Rev. Bryol. Lichénol. 22: 290. 1953. **(Figs. 4.42–4.43)**
Type: INDONESIA. West Java, Pangerango Mountain, *Meijer 291* (holotype: BO!).

Plants dull green, 0.6–1 cm long; shoots 1.2–2.3 mm wide. *Stems* 125–138 µm in diameter, in transverse section consisting of 7 cortical cells (30–50 × 15–25 µm) and 3 medullary cells (30–38 × 20–33 µm). *Leaves* uniform, slightly imbricate, spreading from stem at 30°–60° angle. *Lobes* 0.45–0.85 mm long, 0.36–0.4 mm wide; dorsal margin near flattened, entire. *Lobe cells* thin-walled, trigones large, intermediate thickenings very distinct; marginal cells slightly rectangular or subquadrate, 30–45 × 20–30 µm; median cells hexagonal to slightly rectangular, 27–63 × 25–33 µm; basal cells slightly rectangular to hexagonal, 37–50 × 25–40 µm. *Oil bodies* numerous per cell, homogenous, ellipsoid, 3–5 × 2–3 µm. *Lobules* narrowly tubular, flaring toward sac, 1.37–1.42 mm long. *Lobule sacs* elliptic, strongly inflated, 0.8–0.97 mm long, 0.4–0.46 mm wide, sac surface mamillose, apex obtuse, without apical crest. *Valves* elliptic, 137–150 × 105–113 µm, composed of one circle of 21–25 hyaline marginal and 25–34 median cells with 1 basal median cell, 2 elongated basal hyaline present, hinge present with 1 cell, basal median cell adnate with a hinge cell not forming a sigmoid curve in outline. *Hyaline papillae* spherical to bulbous, 15–20 µm in

diameter. *Valve frames* outline semicircular, ca. 160 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe lanceolate, 225–250 × 75–100 µm, 8–11 cells long, 4–5 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on lobule sac apex and dorsal lobe of female bract.

Dioicous. *Androecia* terminal or intermediate on main stems and lateral branches; male bracts in 4–13 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular to oblong, 250–312 × 125–200 µm; bract lobules oblong to semi-circular, as large as bract lobes, 200–300 × 100–150 µm; male bracteoles bilobed, 60–124 × 90–140 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes elliptic to slightly oblong, 700–1020 × 300–370 µm, apical keel entire; bract lobules narrowly oblong, 700–900 × 40–100 µm; female bracteoles oblong, ca. 100 × 90 µm, apex obtuse. *Perianths* elliptic to oblong, 1–1.3 mm long, 0.6–0.75 mm wide, with 3 keels; keels short, ridge-like, entire; beak 1 cell long. *Sporophytes*. *Setae* 9 cells long. *Capsules* ca. 330 µm in diameter, splitting to ± 2/3 of its length; capsule valves 330–350 × 220–230 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic to slightly rectangular, large, thin-walled; hinge rectangular, hinge cells rectangular to subquadrate, smaller than cells of upper half, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half quadrate, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall smooth; basal cell subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular thickenings, 237–300 µm long, 12–20 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 190–210 µm long, 10–18 µm wide; additional elaters hyaline, with smooth to irregular thickenings, ca. 280 µm long, 10 µm wide. *Spores* irregular-oblong or elongate-rectangular, 62–68 × 32–38 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura meijeri* was found growing densely on living leaves in montane forest at 1100–1400 m elevation. This species may grow associated with other *Colura* species such as *C. acroloba* and *C. karstenii*.

Distribution: Indonesia, Japan, Thailand (Jovet-Ast 1953, Sangrattanaprasert *et al*. 2019a).

Selected specimens examined: JAPAN. Kumamoto Prefecture, Hitoyoshi, 17 August 1947, *Mayebara 703* (PC, paratype). THAILAND. Nakhon Nayok, Khao Yai National Park, Pha Dieo Dai, 14°21′59.39″N, 101°23′20.19″E, 1190–1260 m, 14 November 2013, *Sangrattanaprasert 26/13* (PSU), Pha Trom Chai, 14°21′30.22. N, 101°22′51.60″E, 1115–1220 m, 1 June 2015, *Sangrattanaprasert 333/15*, *337/15* (PSU).

Taxonomic notes: *Colura meijeri* resembles *C. valida* in having rather large lobule sac with entire and obtuse apex, flattened dorsal leaf margin, and large underleaf lobes. Nevertheless, *C. meijeri* differs from *C. valida*, by the larger valve consisting of 21–25 hyaline marginal cells and 25–34 median cells, and elliptic to oblong perianth with 3 ridge-like keels.

24. *Colura mosenii* Steph., Sp. Hepat. 5: 935. 1916. **(Fig. 4.44)**

Type: INDONESIA. Java, s.d., *Mosen s.n.* (holotype: G n.v.).

Plants pale green, 0.3–0.4 cm long; shoots 1.6–1.8 mm wide. *Stems* 90–100 µm in diameter, in transverse section consisting of 7 cortical cells (30–60 × 20–30 µm) and 3 medullary cells (20–26 × 12–22 µm). *Leaves* uniform, contiguous to imbricate, spreading from stem at 40°–70° angle. *Lobes* 0.68–0.8 mm long, 0.29–0.4 mm wide; dorsal margin flattened, entire to slightly crenulate. *Lobe cells* thin-walled, trigones large, intermediate thickening distinct; marginal cells subquadrate to quadrangular, 22–30 × 16–30 µm; median cells rectangular, 30–60 × 16–30 µm; basal cells rectangular, 40–56 × 18–30 µm. *Oil bodies* not seen. *Lobules* narrowly tubular, flaring toward sac, 1.16–1.4 mm long. *Lobule sacs* cylindrical fusiform, strongly inflated, 0.9–1.1 mm long, 0.30–0.36 mm wide, apex obtuse, entire; sac surface strongly mamillose. *Valves* ovate to elliptic, 74–86 × 70–74 µm, composed of one circle of 15–17 hyaline marginal and 13–18 median cells with 2 basal median cells; hyaline bordered present consisting of 2 cells; hinge cell 3 cells. *Hyaline papillae* bulbous, 10–14 µm in diameter. *Valve frames* outline semicircular, ca. 110 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe triangular to

lanceolate, 240–320 × 100–128 µm, 11–14 cells long, 7–8 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on apex of lobule sac. *Androecium and gynoecium* not seen.

Habitat and ecology: *Colura mosenii* was found occurring on leaves in lowland forest at altitude about 400 m.

Distribution: Indonesia (Java), Malaysia (Kelantan) (Jovet-Ast 1953, Pócs & Lee 2016).

Specimens examined: MALAYSIA. Kelantan, Gunung Basor, halfway between Dabong and Jeri towns near BKT, Gerongan village along the road to Kuala Belah, 05°31'38.5"N, 101°46'17.7"E, 400 m, 7 November 2013, *Pócs, Pócs, Lee & Tang 13183/C* (EGR).

Taxonomic notes: *Colura mosenii* may be confused with *C. brevistyla*; they share similar characters such as shape of leaves, valves, and underleaf lobes, and gemmae occurring on lobule sac apices. However, the former is distinguished from the latter by small leaves (1.16–1.4 mm long) and lobe (0.68–0.8 × 0.29–0.4 mm), sac not extended, small valve consisting of 28–35 cells, and smaller underleaf lobes (11–14 cells long).

25. *Colura ornata* K.I.Goebel, Ann. Jard. Bot. Buitenzorg 9(1): 26, 1891.

(Figs. 4.45–4.46)

≡ *Colurolejeunea ornata* (K.I.Goebel) Schiffn., Nova Acta Acad. Caes. Leop.–Carol. German. Nat. Cur. 60(2): 243. 1893a. ≡ *Colura ornata* (K.I.Goebel) Steph., Sp. Hepat. 5: 940. 1916. **Type:** INDONESIA. Java, Depok, 1889, *Karsten s.n.* (holotype: not located).

Plants pale green, 0.5–1 cm long; shoots 1.1–1.6 mm wide. *Stems* 72–100 µm in diameter, in transverse section consisting of 7 cortical cells (28–36 × 18–22 µm) and 3 medullary cells (22–26 × 16–20 µm). *Leaves* contiguous to imbricate, spreading from stem at 60°–90° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaves lobes* 0.66–0.8 mm long, 0.4–0.52 mm wide; dorsal margin flattened, dentate; teeth triangular, 1–4 cells, teeth distributed on upper half of lobe; lobules

narrowly tubular, flaring toward sac, 0.7–0.9 mm long; lobule sacs spherical to elliptic, strongly inflated, 0.24–0.4 mm long, 0.18–0.23 mm wide, sac surface mamillose, apex obtuse, ending with apical crest 2–3 teeth, teeth consisting of 14–33 cells; valves ovate, elliptic or ligulate, 80–100 × 50–66 μm, composed of one circle of 14–19 hyaline marginal and 11–28 median cells, without basal median cell and hinge; hyaline papillae bulbous, 12–14 μm in diameter; valve frame outline semi-circular to hook-like, 90–100 μm wide; cell wall entire. *Non-saccate leaves* obovate to falcate, 0.8–1 mm long, 0.52–0.76 mm wide; apex obtuse, dentate; dorsal margin flattened, dentate; teeth triangular, 1–7 cells, teeth distribute regularly from apex to base of lobe; *lobules* narrowly oblong, 0.44–0.64 × 0.07–0.12 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells rectangular to subquadrate, 10–30 × 10–20 μm; median cells rectangular to isodiametric, 20–40 × 16–26 μm; basal cells rectangular to isodiametric, 24–50 × 20–30 μm. *Oil bodies* 30–45 per cell, roughly segmented, ellipsoid, 4–8 × 1.5–2 μm. *Underleaves* deeply bilobed, sinus obtuse; lobe filiform, 90–200 × 24–60 μm, 4–8 cells long, 2–4 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 4–7 pairs, hemispherical, apical keel crenulate with 1–3 projecting cell row, crenulate to dentate; bract lobes semicircular, 180–280 × 100–160 μm, free margin entire to crenulate; bract lobules semi-circular to oblong, 180–240 × 100–120 μm; male bracteoles rounded to bilobed, 60–114 × 40–80 μm, apex obtuse to emarginate. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes oblique elliptic, 480–600 × 228–256 μm, apical keel dentate with a few teeth; bract lobules narrowly oblong, 320–440 × 60–100 μm; female bracteoles rounded, 70–130 × 70–100 μm, apex obtuse. *Perianths* obtriangular to urceolate, 0.8–1.1 mm long, 0.4–0.7 mm wide, with 3(–4) keels; keels oblique triangular, 120–160 × 88–160 μm, spreading horizontally, apex bearing coarse teeth; beak 2–3 cells long. *Sporophytes*. *Setae* 9 cells long. *Capsules* 264–296 μm in diameter, splitting to ± 3/4 of its length; capsule valves 300–320 × 180–228 μm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic, large, thin-walled; hinge butterfly-shaped, ca. 1/2 of valve length, hinge cells rectangular to isodiametric, thin-walled; marginal cells rectangular, formed by 1 row.

Inner layer of capsule valve cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half isodiametric, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with annular thickenings, 196–280 µm long, 10–14 µm wide; lower marginal elaters hyaline, with annular thickenings, 170–190 µm long, 14–16 µm wide; additional elaters hyaline, with irregular thickenings, 220–250 µm long, 6–120 µm wide. *Spores* irregular-oblong or elongate-rectangular, 50–94 × 10–30 µm; spore surface covered with irregular lamellae; sporelings *Lejeunea*-type

Habitat and ecology: *Colura ornata* was found on living leaves in lowland evergreen forests ranging between 100 and 300 m elevation.

Distribution: Australia (Atherton Tableland), Indonesia (Java), Malaysia (Peninsula and Borneo), Papua New Guinea, Philippines, Solomon Islands, Thailand, Vietnam (South Vietnam) (Jovet-Ast 1953, Tan & Engel 1986, Menzel 1988, Pócs & Streimann 2006, Pócs & Ninh 2012, Pócs 2013, Chantanaorrapint & Pócs 2014).

Specimens examined: THAILAND. Nakhon Si Thammarat, Nopphitam, Krung Ching Waterfall, 08°44'05.50"N, 99°39'34.60"E, 200 m, 31 October 2012, *Pócs, U–Tayanapuh & Lee 1217AE–1*, *1217AE*, *1217AH* (EGR, PSU); 267 m, 10 October 2014, *Sangrattanaprasert 216/14B*, *218/14C* (PSU). Yala, Than To, Wang Sai Stream, 06°00'55.66"N, 101°16'36.36"E, 300 m, 2 July 2014, *Sangrattanaprasert 177/14D* (PSU). Songkhla, Ton Nga Chang Wildlife Santuary, Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 100 m, 23 February 2015, *Sangrattanaprasert 300/15F* (PSU).

Taxonomic notes: The diagnostic features of *Colura ornata* are 1) dimorphic lateral leaves, 2) dentate leaf margin, 3) sac apex ending with large crest, usually 3 teeth, and 4) presence of valve and valve frame. *Colura ornata* morphologically resembles *C. apiculata*. They share many similar characters such as dentate leaf lobes, apical crest of lobule sac bearing with 2–3 teeth, semi-circular to hook-like valve frame, but *C. apiculata* differs only by the strongly extended perianth keels (2 times longer than that one). Therefore, their closely related morphological characters and overlapping distribution ranges show that these two species may be conspecific.

Moreover, *C. ornata* may be confused with *C. palawanensis*. The distinguishing characters are discussed under the latter species.

26. *Colura palawanensis* Jovet-Ast, Rev. Bryol. Lichénol. 22: 305. 1953.

(Figs. 4.47–4.48)

Type: PHILIPPINES. Palawan, Brooks Point (Addison Peak), February 1911, *Elmer 12665* (holotype: BO!; isotype: BM!, L!, PC n.v.).

Plants pale green, 0.7–1 cm long; shoots 1–1.8 mm wide. *Stems* 72–92 µm in diameter, in transverse section consisting of 7 cortical cells (20–40 × 16–30 µm) and 3 medullary cells (22–26 × 18–20 µm). *Leaves* contiguous to imbricate, spreading from stem at 45°–90° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaves lobes* 0.6–0.9 mm long, 0.42–0.7 mm wide; dorsal margin flattened, dentate; teeth deeply triangular, (1–)3–5(–10) cells, teeth distributed on upper half of lobe; lobules narrowly tubular, flaring toward sac, 1–1.1 mm long; lobule sacs triangular to lanceolate, strongly inflated, 0.32–0.56 mm long, 0.18–0.24 mm wide, sac surface mamillose, apex acute, ending in apical crest consisting of 7–11 cells; valves ovate to elliptic, 90–100 × 60–66 µm, composed of one circle of 18–21 hyaline marginal and 16–21 median cells, without basal median cell and hinge; hyaline papillae bulbous, 10–14 µm in diameter; valve frame outline hook-like, 100–120 µm wide; cell wall entire. *Non-saccate leaves* oblique elliptic to falcate, 0.82–1.1 mm long, 0.48–0.64 mm wide; apex obtuse, dentate; dorsal margin flattened, dentate; teeth deeply triangular, (2–)4–7(–9) cells, teeth distribute regularly from apex to base of lobe; lobules narrowly oblong, 0.6–0.72 × 0.1–0.17 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings very distinct; marginal cells subquadrate to rectangular, 14–40 × 12–22 µm; median cells rectangular, 18–60 × 16–26 µm; basal cells rectangular, 32–60 × 20–30 µm. *Oil bodies* not seen. *Underleaves* deeply bilobed, sinus obtuse; lobe filiform, 140–180 × 30–50 µm, 5–8 cells long, 2–4 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 3–7 pairs, hemispherical, apical keel crenulate with 1 projecting cell row; bract lobes semicircular, 200–260 × 148–212 µm, free margin dentate near apex; bract lobules

semicircular, 200–240 × 120–140 µm; male bracteoles rounded to bilobed, 60–80(–120) × 50–60(–90) µm, apex obtuse to emarginate. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes oblique elliptic, 440–640 × 192–320 µm, apical keel dentate with a few teeth; bract lobules narrowly oblong, 360–544 × 80–104 µm; female bracteoles rounded, 100–120 × 80–100 µm, apex obtuse to emarginate. *Perianths* obtriangular to slightly oblong, 0.76–1 mm long, 0.44–0.6 mm wide, with 3 keels; keels oblique triangular, 120–160 × 80–120 µm, spreading horizontally to erect, apex acute; beak 1–2 cells long. *Sporophytes*. *Setae* 9 cells long. *Capsules* 280–320 µm in diameter, splitting to ± 4/5 of its length; capsule valves 280–340 × 200–220 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve rhombic to polygonal, large, thick-walled; hinge butterfly-shaped, ca. 1/2 of valve length, hinge cells rectangular to isodiametric, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half isodiametric, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with smooth thickenings, 180–268 µm long, 10–18 µm wide; lower marginal elaters hyaline, with irregular thickenings, 160–190 µm long, 6–16 µm wide; additional elaters hyaline, with smooth thickenings, 240–260 µm long, 6–12 µm wide. *Spores* irregular-oblong or elongate-rectangular, 60–80 × 30–50 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura palawanensis* was found on living leaves in lowland evergreen to lower montane rain forests ranging from 80 to 1300 m elevation.

Distribution: Philippines (Palawan) (Jovet-Ast 1953).

Specimens examined: INDONESIA. Sunda Islands, East Nusa Tenggra, Flores Island, Gegend of Ruteng, 1300 m, 10 June 1938, *O. Jaag 1854* (L). THAILAND. Surat Thani, Phanom, Khao Sok National Park, 08°54'00.6"N, 98°37'13.2"E, 80–120 m, 25 January 2007, *Pócs & Pócs 07007/N* (EGR).

Taxonomic notes: *Colura palawanensis* may be confused with *C. apiculata* and *C. ornata*; particularly under the hand lens investigation. They share similar characters such as 1) dentate dorsal margin of leaf lobe, 2) sac apex ending with

apical crest, 3) having hook-like valve frame, and 4) underleaves being filiform. However, *C. palawanensis* stand out among the others in 1) having triangular to lanceolate lobule sac, 2) apical crest being only 1 tooth, consisting of 7–11 cells, 3) strongly dentate lobe margin, teeth consisting of 3–7(–10) cells, and 4) saccate leaves as large as non-saccate leaves. From the investigation of herbarium collection, I found that the duplicated type specimens of this species housed in BM and L were erroneously identified as *C. javanica* Steph. (= *C. ari* (Steph.) Steph.).

27. *Colura pallida* Steph., Sp. Hepat. 5: 941. 1916. **(Figs. 4.49–4.50)**

Type: PAPUA NEW GUINEA. Bismarck Archipelago, October 1893, *Micholitz s.n.* (holotype: G n.v.).

Plants pale green, 0.5–1.5 cm long; shoots 2–3 mm wide. *Stems* 100–190 µm in diameter, in transverse section consisting of 7 cortical cells (50–70 × 30–50 µm) and 3 medullary cells (30–60 × 20–40 µm). *Leaves* uniform, imbricate, spreading from stem at 40°–60° angle. *Lobes* (1.1–)1.3–1.7 mm long, 0.76–1.06 mm wide; dorsal margin strongly undulate, denticulate to dentate; ca. 1 cell. *Lobe cells* thin-walled, trigones large, intermediate distinct; marginal cells subquadrate to rectangular, 24–40 × 20–26 µm; median cells rectangular, 36–70 × 20–30 µm; basal cells rectangular, 40–80 × 20–40 µm. *Oil bodies* 20–40 per cell, homogenous to compound, fine segment, ellipsoid, 4.8–8 × 0.8–2 µm. *Lobules* narrowly tubular, flaring toward sac, (1.6–)1.9–2.3 mm long. *Lobule sacs* elliptic, strongly inflated, 1–1.5 mm long, 0.29–0.5 mm wide, apex obtuse, entire; sac surface mamillose. *Valves* ovate, 110–140 × 94–110 µm, composed of one circle of 20–22 hyaline marginal and 23–28 median cells with 1 basal median cell; hyaline bordered present consisting of 2 cells; hinge present consisting of 3 cells. *Hyaline papillae* bulbous, 16–20 µm in diameter. *Valve frames* outline semicircular, 130–180 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe triangular to lanceolate, (200–)320–360 × (120–)200–240 µm, 8–15 cells long, 6–11 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on apex of lobule sac.

Dioicous. *Androecia* intermediate on main stems and terminal on lateral branches; male bracts in 3–5 pairs, hemispherical, apical keel crenulate with 1

projecting cell row, free margin entire; bract lobes semicircular, 320–360 × 180–260 µm; bract lobules oblong to semicircular, 260–360 × 160–200 µm; male bracteoles bilobed, 120–160(–240) × 92–120(–200) µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract lobes elliptic to ovate, 680–860 × 320–360 µm; bract lobules narrowly oblong, 640–800 × 112–200 µm; female bracteoles rounded to oblong, 90–160 × 80–100 µm. *Perianths* oblong to oblanceolate, 1.2–1.6 mm long, 0.6–0.8 mm wide, with 3 keels; keels oblique-triangular, spreading horizontally, bearing mamillate cells at its apex; beak 1–2 cells long. *Sporophyte* not seen.

Habitat and ecology: *Colura pallida* usually occurs on twigs and living leaves in lower montane rain forest. In Thailand, this species was often found growing mixed with *C. valida* and *C. karstenii*.

Distribution: Papua New Guinea, Thailand (Jovet-Ast 1953, Pócs 2013, Chantanaorrapint & Pócs 2014).

Selected specimens examined: THAILAND. Nakhon Si Thammarat, Ron Phiboon, Khao Ramrome, 08°14'17.70"N, 99°48'19.10"E, 930–1000 m, 25 September 2013, *Sangrattanaprasert 12/13A*, *14/13 A* (PSU); 29 July 2014, *Sangrattanaprasert 196/149*, *197/14* (PSU); March 2016, *Sangrattanaprasert, 478/16*, *479/16* (PSU); Phatthalung, Kong Ra, Khao Loan, 07°26'45.33"N, 99°52'31.64"E, 984 m, 28 May 2017, *Chantanaorrapint & Suwanmala 1100A*, *1103A* (PSU). Songkhla, Hat Yai, Ton Nga Chang Wildlife Santuary, Ton Nga Chang Waterfall, 06°58'01.40"N, 100°13'20.47"E, 938 m, 21 March 2014, *Chantanaorrapint & Promma 3501B*, *3848B*, Trang, Palian, Khao Chedyod, 07°19'18.80"N, 99°54'40.48"E, 1040–1070 m, 2 May 2014, *Sangrattanaprasert 116/14B* (PSU).

Taxonomic notes: *Colura pallida* is unique and distinct from other species of sect. *Harmophyllum* Grolle in Malesian region. The diagnostic features of this species are 1) the very large leaves, 2) leaf lobe margins being strongly crenulated and undulated, and 3) having large underleaf lobes (8–15 cells long and 6–11 cells wide). However, this species may be confused with *C. valida*, the species belonged to sect. *Gamolepis*, especially under the hand lens investigation. *Colura pallida* differs by valve character and dorsal margin being undulate and denticulate.

28. *Colura pluridentata* Jovet-Ast, Rev. Bryol. Lichénol. 22: 265. 1953.

(Figs. 4.51–4.52)

Type: INDONESIA. East Kalimantan, Samarinda district, Tandjong bangko, West of the estuary of Mahakam River, 1 August 1952, *Meijer 3035* (holotype: BO!).

Plants pale green, 0.5–1 cm long; shoots ca. 2.5 mm wide. *Stems* 95–120 µm in diameter, in transverse section consisting of 7 cortical cells (44–56 × 30–50 µm) and 3 medullary cells (24–30 × 20–30 µm). *Leaves* uniform, contiguous to imbricate, spreading from stem at 40°–90° angle. *Lobes* 0.82–1.28 mm long, 0.34–0.78 mm wide; dorsal margin flattened to slightly undulate, dentate or slightly entire in immature plant; teeth triangular, 1–3 cells, teeth almost distribute on upper half of leaf lobe margin. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells isodiametric, 22–34 × 20–30 µm; median cells rectangular, 32–54 × 18–24 µm; basal cells rectangular, 40–60 × 20–30 µm. *Oil bodies* 22–32 per cell, very fine segment, ellipsoid, 4–8 × 1.5–2 µm. *Lobules* narrowly tubular, flaring toward sac, 1.34–2.1 mm long. *Lobule sacs* cylindrical fusiform to lanceolate, strongly inflated, 1–1.6 mm long, 0.28–0.36 mm wide, apex obtuse, entire; sac surface mamillose. *Valves* ovate, 80–96 × 78–88 µm, composed of one circle of ca. 18 hyaline marginal and 19–22 median cells with 1–2 basal median cells; hyaline bordered present consisting of 2 cells; hinge cell present with 3 cells. *Hyaline papillae* bulbous, 14–18 µm in diameter. *Valve frames* outline semicircular, ca. 125 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus acute; lobe triangular to lanceolate, 376–560 × (128–)144–184 µm, (11–)14–22 cells long, 7–11 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on apex of lobule sac.

Dioicous. *Androecia* terminal or intermediate on main stems and lateral branches; male bracts in 5–11 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular, 240–360 × 100–240 µm; bract lobules oblong, 190–280 × 80–120 µm; male bracteoles bilobed, 120–240 × 36–68 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract lobes oblong to ovate, 640–1000 × 200–360 µm; bract lobules narrowly oblong, 520–900 × 40–160 µm; female bracteoles rounded to obdeltoid, 100–120 × 80–114 µm. *Perianths* oblong to oblanceolate, 1.4–1.7 mm long, 0.5–0.66

mm wide, with 3 keels; keels short, crenulate; beak 1–2 cells long. *Sporophyte* not seen.

Habitat and ecology: *Colura pluridentata* usually occurs on living leaves and twigs in lowland to lower montane rain forest at altitude between 38 and 950 m.

Distribution: Fiji, India (Andaman & Nicobar Island), Indonesia (Borneo), Papua New Guinea, Seychelles, (Jovet-Ast 1953, Grolle 1978, Miller *et al*. 1983, Pócs & Eggers 2007, Pócs 2013, Dey & Singh 2016).

Selected specimens examined: INDONESIA. East Kalimantan, Borneo, East Kutai, Peak Balikpapan, Tules R., 100 m, 1 July 1952, *Meijer B1324b* (BO) MALAYSIA. Kelantan, near the Kunci Air Sungai long No.1 water intake, 05°36'05"N, 101°44'18"E, 660 m, 6 November 2013, *Pócs, Pócs, Lee & Tang 13175/AF* (EGR, PSU). THAILAND. Chumphon, Phato, Heo Lom Waterfall, 09°43'47.89"N, 98°40'58.50"E, 105 m, 4 August 2014, *Chantanaorrapint & Promma 3899C* (PSU). Nakhon Si Thammarat, Nopphitam, Huai Phan village, Khao Lek, 220 m, 31 October 2012, *Pócs, U–Tayanapuh & Lee 1216M* (PSU); Khao Luang National Park, Krung Ching Waterfall, 08°44'05.50"N, 99°39'34.60"E, 196 m, 10 October 2014, *Sangrattanaprasert 210/14A*, *221/14C*, *225/14* (PSU). Phangnga, Kapong, Hin Lad Waterfall, 08°35'11.98"N, 98°27'05.62"E, 153 m, 31 January 2016, *Sangrattanaprasert 452/16* (PSU); Khura Buri, Si Phang-nga National Park, Ton Deng Waterfall, 08°59'30.96"N, 98°27'56.77"E, 66–119 m, 3 August 2014, *Chantanaorrapint & Promma 3891D* (PSU), 2 March 2015, *Sangrattanaprasert 319/15D* (PSU); Ton Kloi Waterfall, 09°20'15.50"N, 98°27'13.70"E, 57 m, 1 March 2015, *Sangrattanaprasert 312/15B* (PSU). Ranong, Suk Samran, Klong-Naka Wildlife Santuary, 09°27'40.27"N, 98°30'35.86"E, 48 m, 4 August 2014, *Chantanaorrapint & Promma 3902C* (PSU). Satun, Thung Wa, Than Plew Waterfall, 07°06'43.00"N, 99°50'30.90"E, 50–100 m, 17 December 2014, *Sangrattanaprasert 258/14D*, *259/14B* (PSU). Songkhla, Hat Yai, Ton Nga Chang Wildlife Sanctuary, 06°56'45.58"N, 100°13'40.68"E, 140 m, 8 October 2013, *Sangrattanaprasert 23/13C* (PSU); Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 100–150 m, 16 December 2014, *Sangrattanaprasert 250/14E*, *251/14C*, *252/14E* (PSU), 23 February 2015, *Sangrattanaprasert 284/15D, 286/15C, 287/15C* (PSU). Surat Thani, Ko Pha-ngan, Khao Rha, 09°45'38.96"N, 100°01'13.96"E, 600–630 m, 3 June 2014,

Sangrattanaprasert 151/14A, *157/14*, *158/14* (PSU); Phanom, Khao Sok National Park, 08°55'20.50"N, 98°31'43.70"E, 130 m, 28 February 2015, *Sangrattanaprasert 301/15*, *304/15D* (PSU). Trang, Yan Ta Khao, Peninsular Botanical Garden (Thung Khai), 07°28'01.00"N, 99°38'24.60"E, 38 m, 12 December 2014, *Sangrattanaprasert 235/14B*, *241/14C*, *242/14* (PSU)

Taxonomic notes: *Colura pluridentata* is characterised by 1) inflated lobules forming a cylindrical fusiform to lanceolate sac, 2) having dentate leaf dorsal margin, and 3) large underleaf lobes with (11–)14–22 cells long and 7–11 cells wide at base. From this investigation especially among Thai specimens, there are variations in lobule sac length, the presence or absence of tooth at dorsal margin, and the number of basal median cells. In young portion of plants, the lobule sac length is usually shorter than the old portions, and the leaf dorsal margin is frequently entire. Moreover, the presence of two basal median cells of valve was reported as a significant character of this species (Jovet-Ast 1953), but the number of basal median cell may be found in one to two cells even in the same branch in this study.

29. *Colura sigmoidea* Sangratt., Chantanaorr. *et* R.L.Zhu, Phytotaxa 387: 43. 2019a. **(Fig. 4.53)**

Type: MALAYSIA. Pahang: Cameron highland district, Gunung Batu Brinchang, 04°30′24″N, 101°23′13.9″E, 1705 m. 15 February 2015, *Sangrattanaprasert 263/15C* (holotype: PSU!; isotypes: BKF!, HSNU!).

Plants pale green, 4–7 mm long; shoots 1–1.2 mm wide. *Stems* 55–80 µm in diameter, in transverse section consisting of 7 cortical cells (14–30 × 12–26 µm) and 3 medullary cells (12–18 × 6–10 µm). *Leaves* uniform, remote, spreading from stem at 45°–50° angle. *Lobes* 0.59–1 mm long, 0.19–0.4 mm wide; dorsal margin entire. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells subquadrate to slightly rectangular, 18–30 × 14–22 µm; median cells rectangular to subquadrate, 22–38 × 14–22 µm; basal cells rectangular, 34–50 × 16–28 µm. *Oil bodies* numerous per cell, homogenous to coarsely segmented, ellipsoid to spherical, 2–6 × 1–3 µm. *Lobules* narrowly tubular, flaring toward sac, 0.86–1.5 mm long. *Lobule sacs* ovate to lanceolate, strongly inflated, 0.44–0.8 mm long, 0.22–0.3 mm

wide, sac surface mamillose, apex acute, ending in apical crest consisting of 3–5 cells, rarely entire. *Valves* elliptic to ovate, 70–86 × 50–56 µm, composed of one circle of 17–21 hyaline marginal and 14–20 median cells with 1 basal median cell, elongated basal hyaline present with 2 cells, basal median cell adnate with a hinge cell forming a sigmoid curve in outline. *Hyaline papillae* bulbous, (12–)14(–16) µm in diameter. *Valve frames* outline semicircular, 80–115 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe lanceolate, 100–130 × 40–54 µm, 6–8 cells long, 3–4 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on lobule sac apex and leaf lobe, sometimes on dorsal lobe of female bract.

Dioicous. *Androecia* terminal or intermediate on main stems and lateral branches; male bracts in 2–11 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular, 200–320 × 136–180 µm; bract lobules semicircular, 200–320 × 120–160 µm; male bracteoles bilobed, 98–120 × 50–60 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes obovate, 440–720 × 230–250 µm, apical keel crenulate with 1 projecting cell row; bract lobules narrowly oblong, 415–624 × 80–130 µm; female bracteoles bilobed, smaller than underleaf, 100–140 × 60–66 µm. *Perianths* oblong, ca. 0.8 mm long, ca. 0.44 mm wide, with 3 keels; keels short, ridge-like, entire or bearing small tooth at keel apex; beak 2–3 cells long. *Sporophytes* not seen.

Habitat and ecology: *Colura sigmoidea* occurs on living leaves in lowland evergreen and montane forests at altitude between 200 and 1705 m. The species was associated with other epiphyllous liverworts, such as *Cololejeunea dozyana* (Sande Lacos.) Schiffn., *C. grossepapillosa* (Horik.) Kitagawa, *Colura acroloba*, *Drepanolejeunea pentadactyla* (Mont.) Steph., and *Leptolejeunea foliicola* Steph.

Distribution: *Colura sigmoidea* is known only from Thai-Malay Peninsula (Sangrattanaprasert *et al*. 2019a).

Additional specimen examined: MALAYSIA. Pahang, Raub District, Fraser's hill, 1230–1300 m, 8–11 April 2014, *Sangrattanaprasert 75/14B*, *81/14B*, *82/14B*, *83/14E* (PSU). Pahang, Cameron highland district, Gunung Batu Brinchang, 04°30′24″N, 101°23′13.9″E, 1705 m, 15 February 2015, *Sangrattanaprasert 265/15* (PSU); Tanah Rata District, rainforest near downtown, 04°28′1″N, 101°22′41″E, 1460 m, 16 February 2015, *Sangrattanaprasert 275/15A*, *277/15C* (PSU). THAILAND.

Nakhon Si Thammarat, Phrom Khiri District, slope trail from Phrom Lok Peak to Phrom Lok Waterfall, on living leaves of palm, 08°32′10.27″N, 099°45′27.00″E, ca. 200 m, 23 April 2014, *Sangrattanaprasert 105/14B.*

Taxonomic notes: The characteristics of *Colura sigmoidea* are rather small plants 1–1.2 mm wide with leaves bearing ovate to lanceolate lobule sacs, the presence of apical crest at lobule sac apex, the basal median cell of valve adnate with hinge cells to form a sigmoid curve in outline, the entire dorsal leaf margin, the presence of crenulate projecting cells at keel of female bracts, and the presence of gemmae on the dorsal side of female bracts.

Colura sigmoidea is morphologically similar to *C. cristata* and *C. verdoornii.* The three species share many characteristics in apical crest of lobule sac, lobule sac surface, valve character, and others. However, *Colura cristata* is easily separated from *C. sigmoidea* by the autoicous sexuality, the elliptic lobule sacs with large apical crest consisting of 7–17 cells, large valve composed of 24–26 hyaline marginal and 31–33 median cells, and the basal median cell of valve fused with hinge cell not forming sigmoid curve. *Colura verdoornii* differs from *C. sigmoidea* in having the elliptic-ovate lobule sac, large elliptic valve (76–100 × 54–70 µm), and basal median cell of valve fused with hinge cell not forming sigmoid curve.

30. *Colura speciosa* Jovet-Ast, Rev. Bryol. Lichénol. 22: 307. 1953. **(Figs. 4.54–4.55)**
Type: INDONESIA. East Borneo, Samarinda, Tandjong bangko, West of the estuary of the Mahakam River, marshy coastal forest, on palm leaf, 1 August 1952, *Meijer 3081* (holotype: BO!; isotype: PC n.v.).

Plants pale green, ca. 2 cm long; shoots 0.5–1 mm wide. *Stems* 56–64 µm in diameter, in transverse section consisting of 7 cortical cells (18–30 × 10–20 µm) and 3 medullary cells (8–14 × 8–14 µm). *Leaves* imbricate, spreading from stem at 60°–90° angle; dimorphic composed of saccate and non-saccate leaves. *Saccate leaves lobes* 0.35–0.48 mm long, 0.22–0.32 mm wide; dorsal margin flattened, crenate to dentate; teeth broadly triangular; lobules narrowly tubular, flaring toward sac, 0.26–0.36 mm long; lobule sacs rounded to elliptic, strongly inflated, 0.24–0.28 mm long, 0.18–0.21 mm wide, sac surface mamillose, apex obtuse, entire or ending in apical

crest consisting of 3–5 cells; valves ovate to elliptic, 100–118 × 48–54 µm, composed of one circle of 19–24 hyaline marginal and 18–24 median cells without basal median cell and hinge; hyaline papillae bulbous, ca. 10 µm in diameter; valve frame reduced. *Non-saccate leaves* obliquely elliptic to ovate, 0.62–0.7 mm long, 0.31–0.36 mm wide; apex obtuse, crenate; dorsal margin flattened to recurved, crenate to dentate; teeth broadly triangular; lobules narrowly oblong, 0.28–0.32 × 0.06–0.08 mm. *Lobe cells* thin-walled, trigones large, intermediate thickenings very distinct; marginal cells subquadrate to isodiametric, 16–22 × 14–20 µm; median cells hexagonal to slightly rectangular, 20–40 × 14–24 µm; basal cells rectangular to hexagonal, 20–44 × 14–24 µm. *Oil bodies* 3–8 per cell, roughly segmented, ellipsoid, 7–13 × 3–4 µm. *Underleaves* deeply bilobed, sinus obtuse; lobe filiform, 100–126 × 22–34 µm, 4–6 cells long, (1–)2 cells wide at base; margin entire. *Asexual reproduction* not seen.

Autoicous. *Androecia* on lateral branches; male bracts in 5–10 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular, 160–180 × 116–144 µm; bract lobules semicircular, 176–200 × 112–120 µm, bract lobules similar to bract lobes in shape but slightly larger; male bracteoles rounded to oblong, 44–52 × 36–50 µm, apex obtuse. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes ovate to elliptic, 312–400 × 160–200 µm, apical keel entire to crenulate with 1 projecting cell row; bract lobules narrowly oblong, 280–360 × 56–80 µm; female bracteoles rounded, 110–150 × 90–130 µm, apex emarginate. *Perianths* obtriangular, 0.86–1 mm long, 0.48–0.64 mm wide, with 3 keels; keels oblique-triangular, spreading horizontally, apex obtuse, crenate; beak absent. *Sporophytes*. *Setae* 8 cells long. *Capsules* 224–240 µm in diameter, splitting to ± 2/3 of its length; capsule valves 240–264 × 168–192 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper part of valve rhombic to polygonal, large, thick-walled; hinge slightly rectangular to butterfly-shape, ca. 1/4 of valve length, hinge cells rectangular to isodiametric, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half rectangular, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular

to annular thickenings, 196–232 µm long, 8–14 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 120–170 µm long, 6–14 µm wide; additional elaters hyaline, with smooth thickenings, ca. 190 µm long, ca. 6 µm wide. *Spores* irregular-oblong or elongate-rectangular, 48–52 × 24–34 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura speciosa* was found densely on living palm leaves in lowland ever green and coastal forests.

Distribution: Indonesia (Borneo), Malaysia (Jovet-Ast 1953, Pócs & Lee 2016).

Specimens examined: INDONESIA. East Borneo, Samarinda, marshy forest near the Sungai Mukum river, West of the estuary of Mahakam river, on leaves, 4 August 1952, *Meijer 3187* (BO). MALAYSIA. Kelantan, Gunung Basor, halfway between Dabong and Jeli towns near BKT, Gerongan village along the road to Kuala Belah, 05°31.642'N, 101°46.295'E, ca. 450 m, 7 November 2013, *Pócs, Pócs, Lee & Tang 13181/F* (EGR). THAILAND. Songkhla, Sadao, Ton Nga Chang Wildlife Sanctuary, Pha Dam Waterfall, 06°46'02.19"N, 100°12'46.58"E, 100–150 m, 16 December 2014, *Sangrattanaprasert 250/14G, 252/14F*, 23 February 2015, *Sangrattanaprasert 284/15E, 300/15E* (PSU).

Taxonomic notes: *Colura speciosa* is characterised by 1) the non-saccate leaf being obliquely elliptic to ovate in outline, 2) recurved lobe margins of non-saccate leaf, 3) crenate to weakly dentate margin of leaf lobe, and 4) round to elliptic lobule sac, ending with lamella crest or entire. *Colura speciosa* can be confused with *C. galeata*. For separation from the similar *C. galeata*, see there.

31. *Colura superba* (Mont.) Steph., Sp. Hepat. 5: 941. 1916. **(Figs. 4.56–4.57)**
≡ *Lejeunea superba* Mont., Ann. Sci. Nat. Bot. (sér. 3) 10: 115. 1848. **Type:** FRENCH POLYNESIA. Tahiti, s.d., *Lépine s.n.* (holotype: G n.v.).

Plants pale green, ca. 0.5 cm long; shoots 1.5–1.7 mm wide. *Stems* 60–110 µm in diameter, in transverse section consisting of 7 cortical cells (20–40 × 12–30 µm) and 3 medullary cells (12–14 × 6–14 µm). *Leaves* uniform, contiguous to imbricate, spreading from stem at 40°–70° angle. *Lobes* 0.64–1.1 mm long, 0.44–0.6 mm wide;

dorsal margin flattened, dentate; teeth triangular, 1–3 cells, teeth almost distribute on upper half of leaf lobe margin. *Lobe cells* thin-walled, trigones large, intermediate thickenings distinct; marginal cells isodiametric to rectangular, 20–40 × 16–30 μm; median cells rectangular to isodiametric, 40–70 × 20–32 μm; basal cells rectangular, 40–60 × 20–34 μm. *Oil bodies* not seen. *Lobules* narrowly tubular, flaring toward sac, 1–1.6 mm long. *Lobule sacs* elliptic to cylindrical fusiform, strongly inflated, 0.72–0.8 mm long, 0.24–0.3 mm wide, apex acute, entire or ending in apical crest consisting of 1–3 cells; sac surface mamillose. *Valves* elliptic to ovate, 76–84 × 70–74 μm, composed of one circle of 15–18 hyaline marginal and 14–17 median cells with 1–2 basal median cells; hyaline bordered present consisting of 2 cells; hinge present consisting of 3 cells. *Hyaline papillae* bulbous, 12–14 μm in diameter. *Valve frames* outline semicircular, 80–120 μm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus acute; lobe triangular to lanceolate, 200–280 × 60–70 μm, 8–10 cells long, 4–5 cells wide at base; margin entire. *Asexual reproduction* not seen.

Dioicous. *Androecia* on lateral branches; male bracts in 3–6 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes semicircular to circular, 200–240 × 160–200 μm; bract lobules oblong to semicircular, 180–260 × 100–160 μm; male bracteoles bilobed, 68–160 × 68–88 μm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract lobes oblong to elliptic, ca. 560 × 192–224 μm; bract lobules narrowly oblong, 480–520 × 80–88 μm; female bracteoles obliquely oblong, apex emarginate to oblique, ca. 170 × ca. 110 μm. *Perianths* oblong, ca. 1.2 mm long, ca. 0.5 mm wide, with 3 keels; keels short, crenulate; beak 1–2 cells long. *Sporophytes*. *Setae* 9 cells long. *Capsules* ca. 344 μm in diameter, splitting to ± 2.5/3 of its length; capsule valves 300–320 × 168–180 μm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve, slightly rhombic, large, thin-walled; hinge butterfly-shaped, ca. 1/2 of valve length, hinge cells rectangular, thin-walled; marginal cells rectangular to subquadrate, formed by 1–2 rows. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half subquadrate, walls nodulose, formed by 1–2 rows, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular

thickenings, 192–280 µm long, 10–16 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 170–180 µm long, 10–16 µm wide; additional elaters hyaline, with smooth thickenings, 200–260 µm long, 8–10 µm wide. *Spore* not seen.

Habitat and ecology: *Colura superba* was found in lowland rain forest along the stream in French Polynesia and on the summit of montane rain forest in Indonesia.

Distribution: French Polynesia (Tahiti), Indonesia (Borneo, Sumatra), Papua New Guinea, Solomon Islands (Jovet-Ast 1953, 1958b, Pócs 2013).

Specimens examined: INDONESIA. East Java, Palau Bawean Island, summit of Mountain Berar, 22 June 1954, *Hoogerwerf 238a* (L). FRENCH POLYNESIA, Tahiti s.d., *Florence 7547* (HSNU); Society Island, Island of Moorea, Westside of Opunahu Valley, above Capitage, 149.86594°W, 17.53053333°S, 143 m, 3 June 2009, *Kraichak, Mishler & Carter 232* (UC).

Taxonomic notes: *Colura superba* is characterised by 1) having elliptic to cylindrical fusiform lobule sacs and their apex being entire or ending with small lamina crest, 2) dentate dorsal margins, 3) short perianth keels and their apex being entire. According to an examination of specimens in L herbarium, this species often be confused with *C. crenulata*. The latter species, however, is distinguished by 1) having widely elliptic lobule sacs, surface being strongly mamillose, 2) entire to crenulate dorsal margin, 3) small underleaves with 6–7 cells long, 4) strongly mamillose perianth surface, and 5) having extended perianth keels.

32. *Colura tenuicornis* (A.Evans) Steph., Sp. Hepat. 5: 942. 1916. **(Figs. 4.58–4.59)**
≡ *Colurolejeunea tenuicornis* A.Evans, Trans. Connecticut Acad. Arts 10: 455. 1900. ≡ *Colura calyptrifolia* subsp. *tenuicornis* (A.Evans) Vanden Berghen, Bull. Jard. Bot. Natl. Belg. 42: 463. 1972. **Type:** HAWAII. Oahu, Nuuanu (Cooke), on leaves of fern, s.d., *Evans s.n.* (holotype: YU n.v.).
= *Colura psuedocalyptrifolia* Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 2: 289. 1934. ≡ *Colura calyptrifolia* var. *psuedocalyptrifolia* (Horik.) S.Hatt. J. Hangzhou Univ., Nat. Sci. Ed. 5: 45. 1951. Type: CHINA. Taiwan “Formosa”, Tainan, Arisan (Shin-Boku-Numanodaira), s.d., *Horikawa 9061* (holotype: HIRO n.v.).

= *Colura pungens* Herzog, Bot. Not. 101: 333. 1947. Type: COMOROS. Comoro-Insel Johanna, 1885, *Hildebrandt s.n*. (holotype: JE!; isotype: JE!).

Plants pale green, 1(–9) mm long; shoots 1(–1.4) mm wide. *Stems* 50–54(–110) µm in diameter, in transverse section consisting of 7 cortical cells (18–24(–50) × 10–20(–40) µm) and 3 medullary cells (12–14(–30) × 12–20(–26) µm). *Leaves* uniform, remote to contiguous, spreading from stem at 45°–90° angle. *Lobes* 0.3–0.4(–0.52) mm long, 0.3–0.32(–0.48) mm wide, incurved; dorsal margin entire. *Lobe cells* thin-walled, trigones and intermediate thickenings absent; marginal cells isodiametric to rectangular, 14–32(–40) × 14–22(–26) µm; median cells rectangular to slightly isodiametric, 16–40(–50) × 12–20(–28) µm; basal cells rectangular, 16–30(–44) × 10–20(–28) µm. *Oil bodies* 4–12(–20) per cell, very fine segment, ellipsoid, 3.2–6.4(–9.6) × 1.6–2.4(–4) µm. *Lobules* narrowly tubular, flaring toward sac, 0.94–1.34(–2.26) mm long. *Lobule sacs* lanceolate, strongly inflated, 0.8–1.14(–2.1) mm long, 0.19–0.28(–0.5) mm wide, sac forming a long tubular beak towards the apex, 0.32–0.6(–0.8) mm, ca. 1/2 as long as leaf length; sac surface mamillose. *Valves* elliptic to lingulate, 50–70(–132) × 40–54(–94) µm, composed of one circle of 12–14(–18) hyaline marginal and 10–11(–15) median cells with 2 basal median cells; hyaline bordered present consisting of 1 cell; hinge consisting of 2 superimposed cells. *Hyaline papillae* bulbous, 14–16(–20) µm in diameter. *Valve frames* outline semicircular, 100–130(–200) µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe lanceolate, 140–240(–360) × 30–40(–120) µm, 6–8(–15) cells long, 2–3(–6) cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on beak of lobule sac.

Autoicous. *Androecia* on lateral branches; male bracts in 3–5 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire to crenulate; bract lobes semicircular, 120–170(–200) × 60–80(–104) µm; bract lobules semicircular, as large as bract lobes, 106–110(–184) × 64–70(–96) µm; male bracteoles round to bilobed, slightly small with a few cells. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation branch; female bract lobes oblong to slightly elliptic, 232–320(–380) × 132–148(–268) µm, apex and margin crenulate; bract lobules narrowly oblong, 200–292(–380) × 46–72(–108) µm; female bracteoles

bilobed, as large as underleaves. *Perianths* oblanceolate to obtriangular, 0.48–0.86(–1.2) mm long, 0.24–0.4(–0.56) mm wide, with 5 keels; keels horn-like, 112–240(–360) × 50–90(–180) µm, entire; beak 1 cell long. *Sporophytes*. *Setae* 8–9 cells long. *Capsules* 170–216(–360) µm in diameter, splitting to ± 2/3 of its length; capsule valves 160–200(–340) × 120–144(–248) µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper part of valve, slightly rhombic, large, thick-walled; hinge butterfly-shaped, ca. 1/3 of valve length, hinge cells rectangular, thin-walled; marginal cells rectangular to subquadrate, formed by 1–2 rows. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half rectangular, walls not nodulose, formed by 1 row, marginal cells of lower half rectangular, wall not nodulose; basal cells subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular thickenings, 120–190(–320) µm long, 10–12(–20) µm wide; lower marginal elaters hyaline, with irregular thickenings, 90–106(–180) µm long, 8–10(–14) µm wide; additional elaters hyaline, with smooth thickenings, 160–164(–320) µm long, 4–6 µm wide. *Spores* irregular-oblong or elongate-rectangular, 26–57.6(–112) × 12–22.4(–56) µm; spore surface papillated, rosette present, 0–5(–12) per side.

Habitat and ecology: *Colura tenuicornis* usually occurs on living leaves and twigs in lower montane to upper montane rain forest at altitude between 799 and 2139 m.

Distribution: Anjouan, Brazil, Cameroon, China (Fujian, Guangdong, Guizhou, Hainan, Sichuan, Taiwan, Xizang, Yunnan, Zhejiang), Colombia, Comoros, Costa Rica, Ethiopia, Galapagos Islands, Guadeloupe, Hawaii, Indonesia (Borneo, Java, Sumatra), Laos, Madagascar, Malaysia (Malay Peninsula), Martinique, Papua New Guinea, Saint-Domingue, São Tomé, Tahiti (Jovet-Ast 1953; Gradstein 1986, Zhu & So 2001, Hylander, Pócs & Nemomissa 2010, Pócs 2012, 2013).

Selected specimens examined: MALAYSIA. Pahang, Fraser's Hill, 8–11 April 2014, *Sangrattanaprasert 75/14C*, *83/14B*, *86/14* (PSU). INDONESIA. Java, Cibodas Kebun Raya, 9–10 August 2015, *Sangrattanaprasert 379/15–384/15* (PSU). THAILAND. Chiang Mai, Chiang Dao, Chiang Dao Wildlife Sanctuary, 2139 m, 28 October 2017, *Chantanaorrapint & Suwanmala 2001* (PSU); Fang, Doi Pha Hom Pok National Park, 2000 m, 9 November 2016, *Chantanaorrapint & Suwanmala 589*

(PSU). Nakhon Nayok, Mueang Nakhon Nayok, Khao Yai National Park, Pha Dieo Dai, 14°21'59.39"N, 101°23'20.19"E, 1190 m, 14 November 2013, *Sangrattanaprasert 28/13B, 32/13B*; Pha Trom Chai, 14°21'30.22"N, 101°22'51.60"E, 1218 m, 1 June 2015, *Sangrattanaprasert 335/15B* (PSU). Nakhon Si Thammarat, Lan Saka, Khao Luang National Park, 08°32'51.01"N, 099°44'15.44"E, 1313 m, 24–27 June 2015, *Sangrattanaprasert 364/15A–365/15A* (PSU); Ron Phiboon, Khao Ramrome, 08°14'17.70"N, 99°48'19.10"E, 935–1000 m, 29 July 2014, *Sangrattanaprasert 190/14–193/14*, 4 November 2017, *Chantanaorrapint & Suwanmala 2090 A* (PSU). Phatthalung, Kong Ra, Khao Loan, 07°26'45.33"N, 99°52'31.64"E, 1234 m, 28 May 2017, *Chantanaorrapint & Suwanmala 1132B, 1139C* (PSU). Phitsanulok, Nakhon Thai, Kung Han Nam, 16°59'32.40"N, 101°00'44.60"E, 1250 m, 8 December 2013, *Sangrattanaprasert 42/13A, 43/13A* (PSU). Songkhla, Hat Yai, Ton Nga Chang Wildlife Santuary, Ton Nga Chang Waterfall, 06°57'42.29"N, 100°13'78.36"E, 779 m, 22–24 May 2014, *Chantanaorrapint & Promma 3848C* (PSU). Trang, Palian, Khao Chedyod, 07°19'18.80"N, 99°54'40.48"E, 1040-1070 m, 2 May 2014, *Sangrattanaprasert 108/14A, 115/14D, 116/14C* (PSU)

Taxonomic notes: The distinctive features of *C. tenuicornis* are 1) inflated lobules forming a lanceolate sac with a narrow beak-like prolongation tip, ca. 1/2 as long as leaf length, 2) the dorsal surface of leaf and lobule sac being smooth, 3) smooth leaf cells without trigone and intermediate thickenings, and 4) perianths with 5 horn-like prolongated keels. This species resembles *C. calyptrifolia*. For their differences, see under *C. calyptrifolia*.

33. *Colura valida* Jovet-Ast, Rev. Bryol. Lichénol. 30: 6. 1961. **(Figs. 4.60–4.61)**

Type: VIETNAM. Lam Dong: Blao, School of Agriculture, December 1959, *Tixier s.n.* (holotype: PC!).

Plants pale green, ca. 1 cm long; shoots 1.4–1.7 mm wide. *Stems* 90–152 µm in diameter, in transverse section consisting of 7 cortical cells (36–60 × 14–50 µm) and 3 medullary cells (30–40 × 16–32 µm). *Leaves* uniform, imbricate to remote, spreading from stem at 30°–80° angle. *Lobes* 1.04–1.4 mm long, 0.61–1.02 mm wide;

dorsal margin ±plane, entire to crenulate. *Lobe cells* thin-walled, trigones large, intermediate thickenings very distinct; marginal cells isodiametric to subquadrate, 24–50 × 20–30 µm; median cells rectangular to slightly hexagonal, 34–68 × 20–30 µm; basal cells slightly rectangular to hexagonal, 40–80 × 26–30 µm. *Oil bodies* numerous per cell, homogenous, ellipsoid, 4–8 × 1.6–2.4 µm. *Lobules* narrowly tubular, flaring toward sac, 1.42–2 mm long. *Lobule sacs* elliptic, strongly inflated, 0.7–1.1 mm long, 0.35–0.41 mm wide, sac surface mamillose, apex obtuse, without apical crest. *Valves* ovate to elliptic, 116–130 × 70–80 µm, composed of one circle of 21–24 hyaline marginal and 22–32 median cells with 1 basal median cell, 2 elongated basal hyaline or 2 hyaline bordered cells present, hinge present with 1 cell, basal median cell adnate with a hinge cell not forming a sigmoid curve in outline or not adnate. *Hyaline papillae* bulbous to spherical, 18–20 µm in diameter. *Valve frames* outline semicircular, 100–120 µm wide; cell wall smooth. *Underleaves* distant, deeply bilobed, sinus obtuse; lobe lanceolate, 360–496 × 104–168 µm, 12–16 cells long, 6–9 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on lobule sacs.

Dioicous. *Androecia* terminal on lateral branches; male bracts in 3–5 pairs, hemispherical, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes oblong to semicircular, 264–296 × 136–176 µm; bract lobules semicircular to slightly oblong, 224–280 × 128–152 µm; male bracteoles bilobed, 70–160 × 40–60 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes elliptic to slightly falcate, 720–840 × 320–400 µm, apical keel entire, rarely crenulate with 1 projecting cell row; bract lobules narrowly oblong, 640–720 × 104–144 µm; female bracteoles semicircular to slightly oblong, 60–130 × 80–100 µm, apex obtuse to emarginate. *Perianths* oblong, 1.26–1.5 mm long, 0.62–0.8 mm wide, with 3 keels; keels short, entire; beak 3 cells long. *Sporophytes*. *Setae* 8 cells long. *Capsules* 350–400 µm in diameter, splitting to ± 4/5 of its length; capsule valves 320–360 × 192–224 µm, wall 2–3 stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve slightly rhombic, large, thin-walled; hinge butterfly-shaped, hinge cells rectangular to subquadrate, smaller than cells of upper half, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with

nodular thickenings; marginal cells of upper half quadrate to slightly rectangular, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall smooth; basal cell subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular thickenings, 200–328 µm long, 14–18 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 200–250 µm long, 16–24 µm wide; additional elaters hyaline, with irregular thickenings, 230–340 µm long, 6–10 µm wide. *Spores* irregular-oblong or elongate-rectangular, 52–60 × 22–28 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura valida* occurs on branches, barks and living leaves and was found in lower montane forest at elevation 850–1745 m.

Distribution: Malaysia (Peninsula), Thailand, Vietnam (Jovet-Ast 1961, Shu *et al*. 2017, Sangrattanaprasert *et al*. 2019a).

Selected specimens examined: MALAYSIA. Pahang, Genting Highlands, 1736–1745 m, 3 March 2013, *Chantanaorrapint, Inuthai & Promma 1953* (PSU); Cameron highland, Tanah Rata, rainforest near downtown, 04°28′1″N, 101°22′41″E, 1460 m, 16 February 2015, *Sangrattanaprasert 276/15*, *277/15D* (PSU). THAILAND. Nakhon Si Thammarat, Ron Phiboon, Khao Ramrome, 08°14′17.70″N, 99°48′19.10″E, 930–1000 m, 25 September 2013, *Sangrattanaprasert 13/13*, *20/13*, *21/13B* (PSU); 29 July 2014, *Sangrattanaprasert 188/14*, *199/14B*, *200/14B* (PSU); 25 February 2015, *Sangrattanaprasert 326/15*, *327/15B* (PSU). Phatthalung, Kong Ra, Khao Loan, 850–1235 m, 27–28 May 2017, *Chantanaorrapint & Suwanmala 953*, *1139D* (PSU).

Taxonomic notes: *Colura valida* is characterised by large leaves (1.4–2.0 × 0.7–1.1 mm) without apical crest at lobule sac apex, lobule sac about 1/2 as long as lobule length, and large underleaf lobes with 12–16 cells long and 6–9 cells wide at base.

34. *Colura verdoornii* Herzog *et* Jovet-Ast, Rev. Bryol. Lichénol. 22: 288. 1953. **(Figs. 4.62–4.63)**

Type: MALAYSIA. Johore: Ophir Mountain, *Verdoorn b2* (holotype: JE!).

Plants pale green, ca. 6 mm long; shoots 2–3 mm wide. *Stems* 90–100 µm in diameter, in transverse section consisting of 7 cortical cells (24–40 × 20–30 µm) and 3 medullary cells (20–26 × 15–20 µm). *Leaves* uniform, imbricate, spreading from stem at 60°–80°(–90°) angle. *Lobes* 0.96–1.4 mm long, 0.54–0.96 mm wide; dorsal margin entire to crenulate. *Lobe cells* thin-walled, trigones large, intermediate thickenings very distinct; marginal cells subquadrate to slightly rectangular, 22–30 × 20–28 µm; median cells hexagonal to slightly rectangular, 34–40 × 26–34 µm; basal cells rectangular to hexagonal, 24–48 × 14–20 µm. *Oil bodies* 15–35 per cell, homogenous to very finely segment, ellipsoid, 3–6.4 × 2.4–3.2 µm. *Lobules* narrowly tubular, flaring toward sac, 1.3–1.8 mm long. *Lobule sacs* elliptic to ovate, strongly inflated, 0.5–0.6 mm long, 0.24–0.3 mm wide, sac surface mamillose, apex acute, ending with apical crest consisting of (1–)3–5 cells, rarely without apical crest. *Valves* elliptic, oblique at base, 76–100 × 54–70 µm, composed of one circle of 16–24 hyaline marginal and 14–27 median cells with 1 basal median cell, 2 elongated basal hyaline or 2 hyaline bordered cells present, hinge present with 1 cell, basal median cell adnate with a hinge cell not forming a sigmoid curve in outline or not adnate. *Hyaline papillae* spherical to bulbous, 12–14 µm in diameter. *Valve frames* outline semicircular, ca. 100 µm wide; cell wall smooth. *Underleaves* deeply bilobed, sinus obtuse; lobe lanceolate, 160–200 × 40–60 µm, 7–9 cells long, 3–4 cells wide at base; margin entire. *Asexual reproduction* by discoid gemmae, occurring on lobule sacs.

Dioicous. *Androecia* terminal or intermediate on main stems and lateral branches; male bracts in 3–5 pairs, hemisphere, apical keel crenulate with 1 projecting cell row, free margin entire; bract lobes oblong to semicircular, 304–400 × 160–320 µm; bract lobules oblong to semicircular, 320–344 × 160–176 µm; male bracteoles bilobed, 50–70 × 70–90 µm. *Gynoecia* terminal on lateral branches with 1 pycnolejeunoid innovation; female bract lobes obovate to oblong, 760–1000 × 320–440 µm, apical keel entire, rarely crenulate with 1 projecting cell row; bract lobules narrowly oblong, 700–800 × 40–96 µm; female bracteoles subquadrate to semicircular, ca. 100 × 80 µm, apex obtuse to emarginate. *Perianths* oblong, 1.3–1.84 mm long, 0.4–0.6 mm wide, with 3–5 keels; keels short, entire to mamillose; beak 1–2 cells long. *Sporophytes*. *Setae* 9–11 cells long. *Capsules* 320–370 µm in diameter, splitting to ± 3/4 of its length; capsule valves 344–400 × 216–240 µm; wall 2–3

stratose, hyaline. *Outer layer of capsule valve* apex formed by 1 quadrate cell; cells of upper half of valve slightly rhombic, large, thin-walled; hinge butterfly-shaped, hinge cells rectangular to subquadrate, smaller than cells of upper half, thin-walled; marginal cells rectangular, formed by 1 row. *Inner layer of capsule valve* cells in centre rectangular, walls with nodular thickenings; marginal cells of upper half quadrate to rectangular, walls nodulose, formed by 2 rows, marginal cells of lower half rectangular, wall smooth; basal cell subquadrate with smooth walls. *Elaters*: upper marginal elaters hyaline, with irregular thickenings, 256–328 µm long, 12–24 µm wide; lower marginal elaters hyaline, with irregular to annular thickenings, 186–216 µm long, 14–20 µm wide; additional elaters hyaline, with irregular thickenings, 240–304 µm long, 8–14 µm wide. *Spores* irregular-oblong or elongate-rectangular in shape, 46–100 × 26–30 µm; spore surface covered with irregular lamellae.

Habitat and ecology: *Colura verdoornii* usually grows on living leaves in lowland to montane rain forests at altitude between 500 and 1800 m; however, it is often found on twigs at the summit of the mountain.

Distribution: Indonesia, Malaysia, Thailand (Jovet-Ast, 1953, 1958, Sangrattanaprasert *et al*. 2019a).

Selected specimens examined: INDONESIA. East Kalimantan, Kutai peak of Balikpapan, 1000 m, 18 July 1952, *W. Merjer B 2618 d* (L); West Java, Cianjur regency, Cipanas District, Cibodas Botanical Garden, ca. 1275 m, 9–10 August 2015, *Sangrattanaprasert 383/15B* (PSU). MALAYSIA. Pahang, Fraser's Hill, 1400 m, 18 March 1952, *Henderson s.n.* (L), 8–11 April 2014, *Sangrattanaprasert 79/14*, *80/14B* (PSU); Genting Highland, Gohtong Jaya, road to the resort area, 820 m, 9 September 2006, *Cheah 48*, *53* (KLU). THAILAND. Nakhon Si Thammarat, Khao Nan National Park, 10–12 August 2007, *Sukkharak & Seelanan 485*, *487*, *513*, *519* (BCU); Khao Luang National Park, 08°32′31.95″ N, 099°44′13.98″E, 1682–1800 m, 20–23 April 2015, *Sangrattanaprasert 373/15* (PSU); Phatthalung, Kong Ra, Khao Loan, 07°26′45.33″N, 99°52′31.64″E, 942 m, 28 May 2017, *Chantanaorrapint & Suwanmala 1079 B, 1100B* (PSU); Songkhla, Tone Nga Chang Waterfall, 06°56′43.91″N, 100°13′16.43″E, 500 m, 4 October 2014, *Sangrattanaprasert 204/14B* (PSU), 836 m, 1 February 2015, *Sangrattanaprasert 260/15B* (PSU); Surat Thani, Ko Pha-ngan, Khao Rha, 09°45′38.96″N, 100°01′13.96″E, 600 m, 3 June 2014,

Sangrattanaprasert 151/14B (PSU); Trang, Khao Chedyod, 07°19′18.80″ N, 99°54′40.48″E, 1040–1070 m, 2 May 2014, *Sangrattanaprasert 120/14E* (PSU); Yala, Ban Chulabhorn Pattana 10, 05°49′04.40″N, 101°01′50.20″E, 570 m, 15 June 2013, *Chantanaorrapint & Promma 2549 C* (PSU).

Taxonomic note: *Colura verdoornii* shows extreme variations in leaf lobe shapes and sizes. It is easily recognised by the presence of apical crest on lobule-sac apices, small lobules sacs 1/3 as long as lobule length, and hexagonal to slightly rectangular shape of leaf cells. *Colura verdoornii* may be confused with *C. valida*, particularly viewed under the hand lens. The latter, however, differs from the former in the lack of apical crest on the apex of lobule-sac, large ovate-elliptic valves consisting of 44–56 cells, and underleaf lobes comprising of 12–16 cells long and 6–9 cells wide.

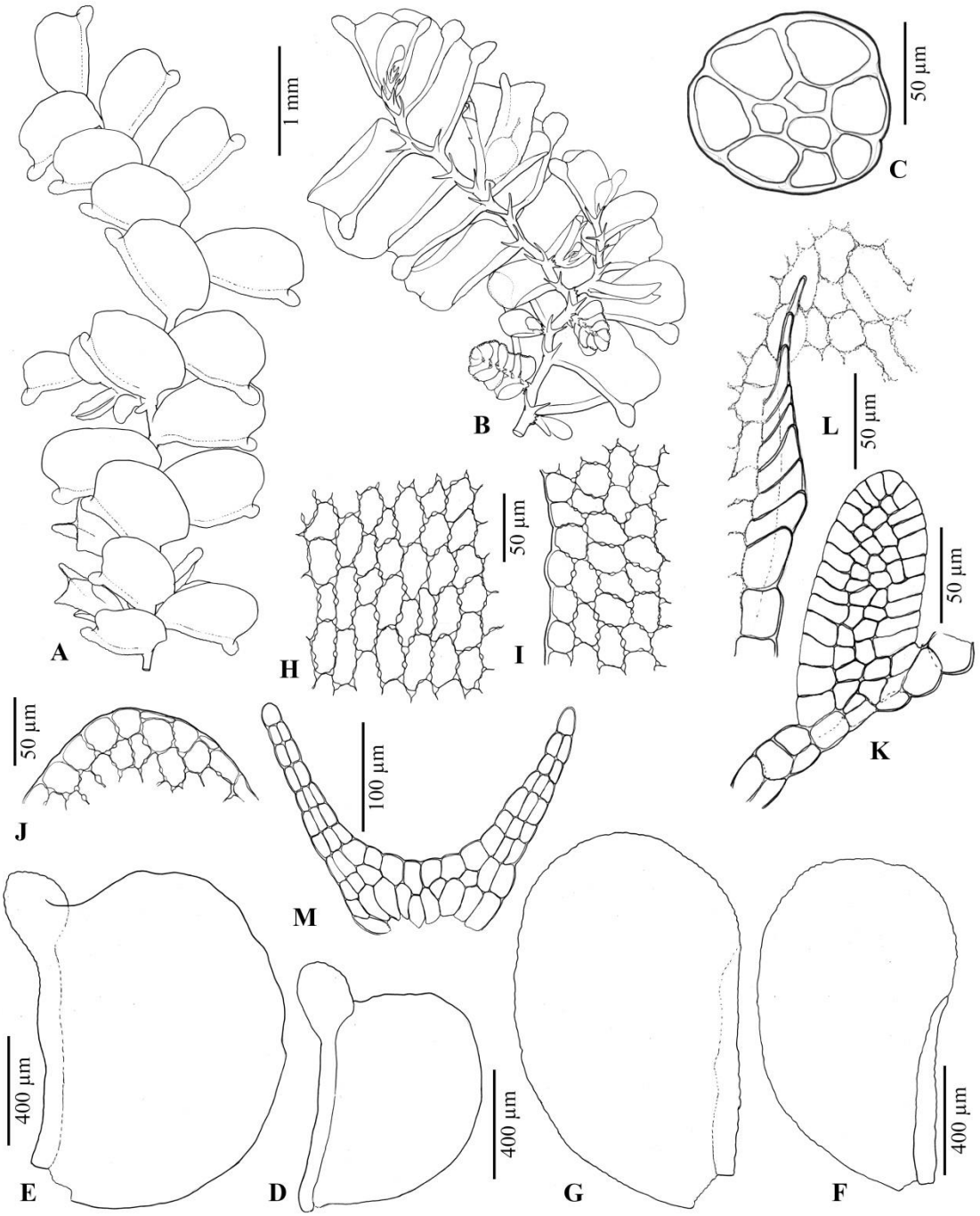

Fig. 4.2 *Colura acroloba* (Prantl) Jovet-Ast: A & B. Portions of plants with gynoecia and androecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Lobule sac apex. K. Valve of lobule. L. Valve frame. M. Underleaf. All from *Sangrattanaprasert 97/14* (PSU).

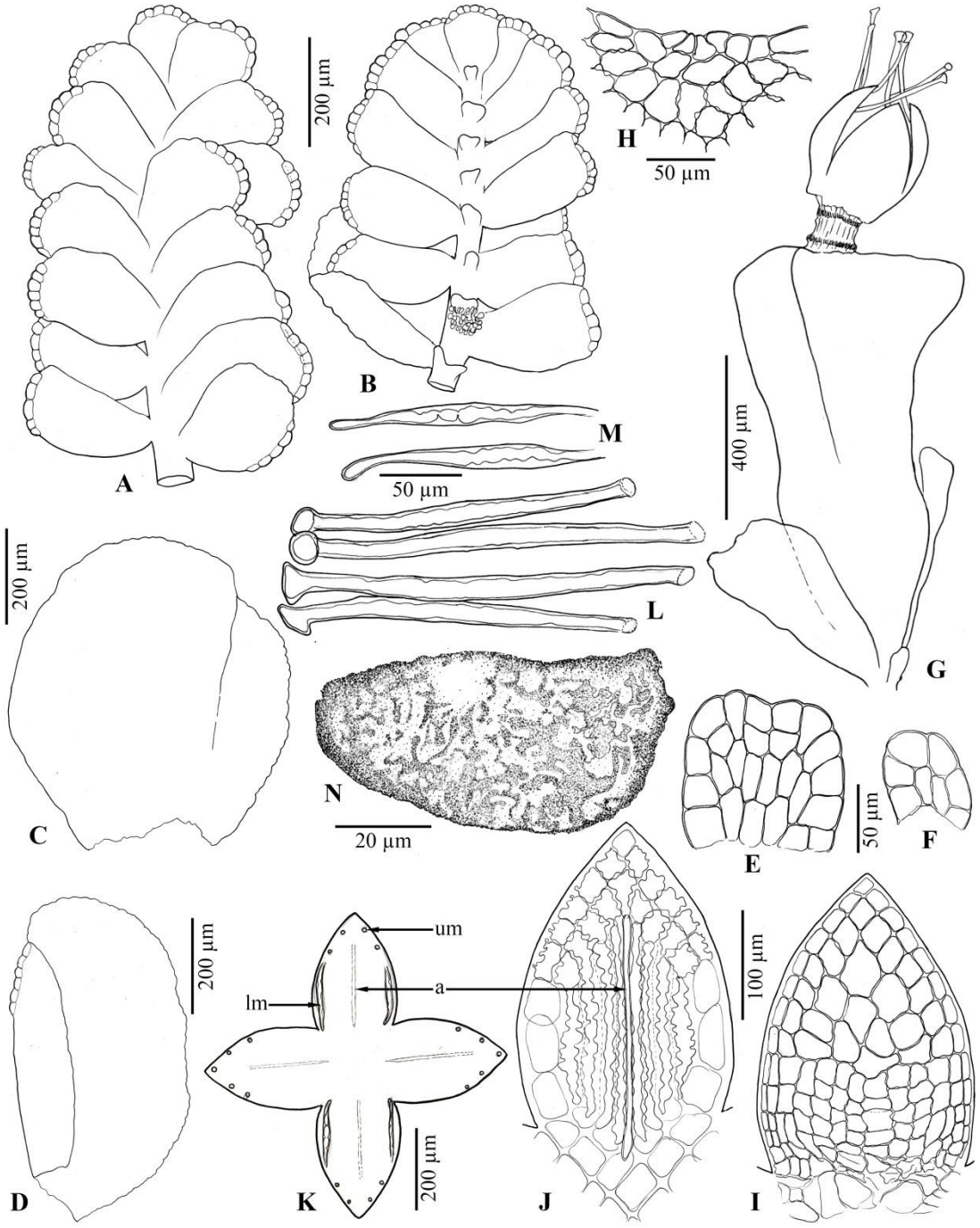

Fig. 4.3 *Colura acroloba* (Prantl) Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E & F. Female bracteoles. G. Perianth with sporophyte. H. Perianth beak. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. All from *Sangrattanaprasert 97/14* (PSU).

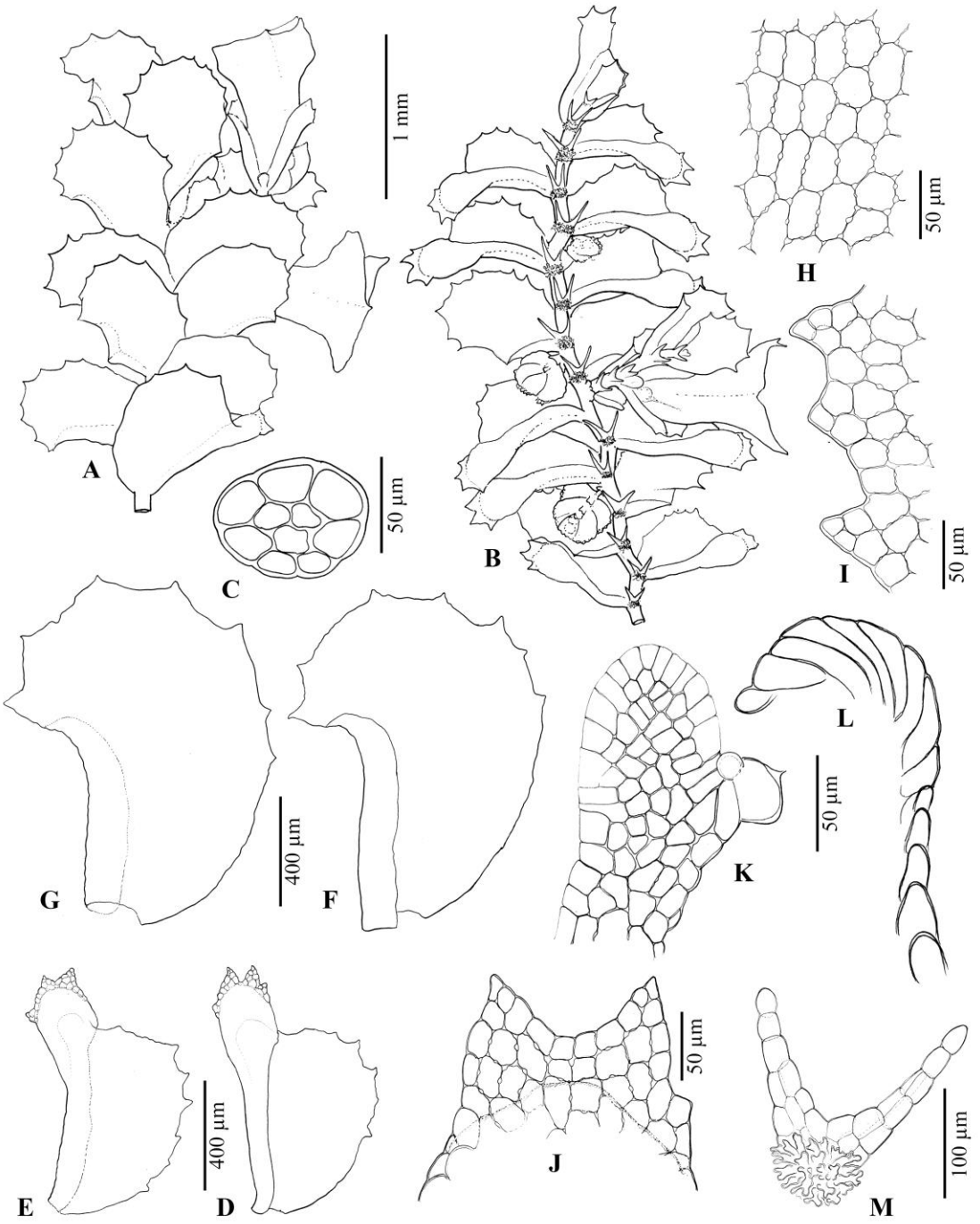

Fig. 4.4 *Colura apiculata* (Schiffn.) Steph.: A & B. Portions of plant with androecia and gynoecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Lobule sac apex. K. Valveof lobule. L. Valve frame. M. Underleaf. A. from *Meijer 8077f* (L), B–M. from *Sangrattanaprasert 241/14B* (PSU).

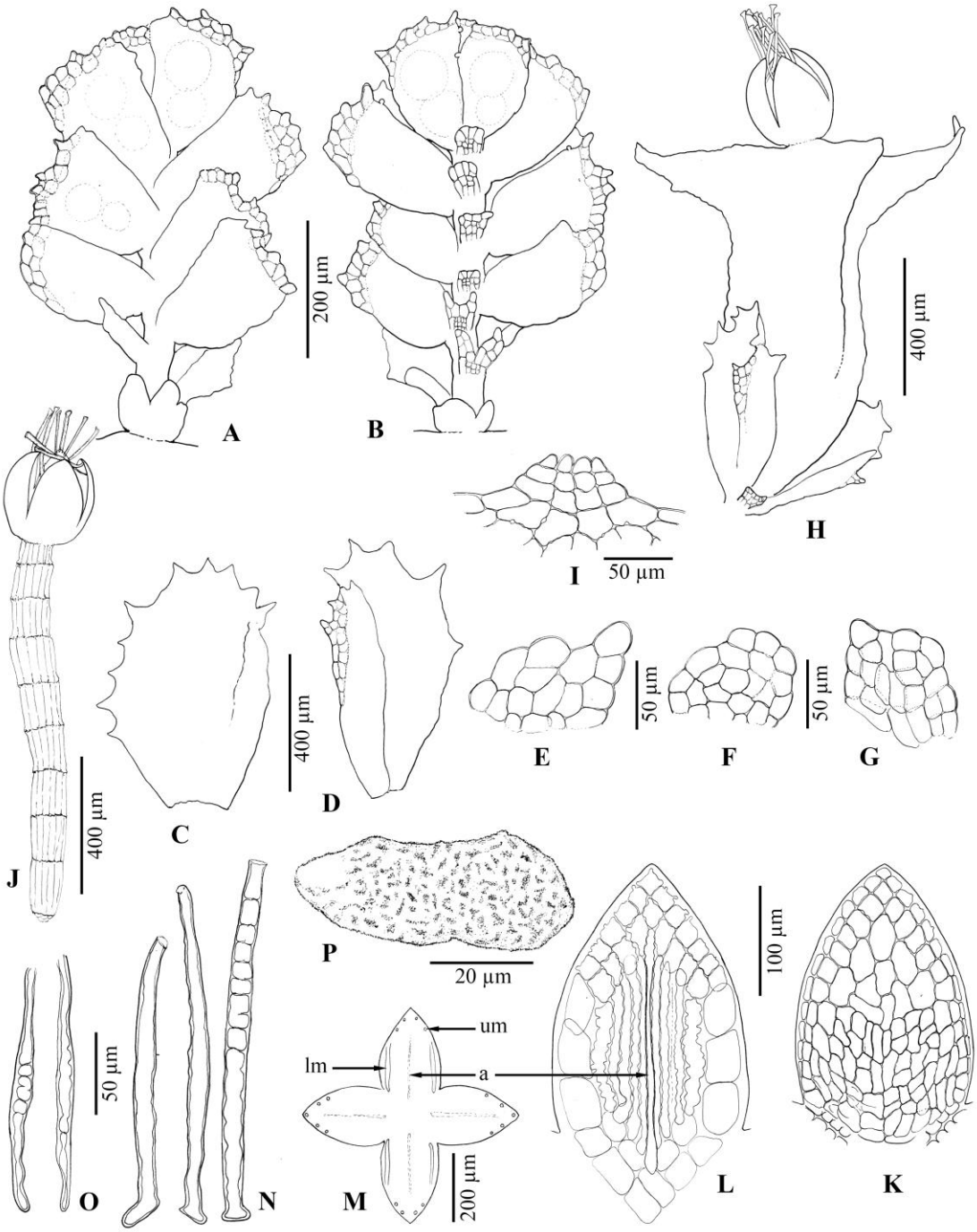

Fig. 4.5 *Colura apiculata* (Schiffn.) Steph.: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E–G. Female bracteoles. H. Perianth with bracts, bracteole, and sporophyte. I. Perianth beak. J. Mature sporophyte. K. Outer layer of capsule valve. L. Inner layer of capsule valve (a = additional elater). M. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). N. Upper marginal elaters. O. Lower marginal elaters. P. Spore. All from *Sangrattanaprasert 241/14B* (PSU).

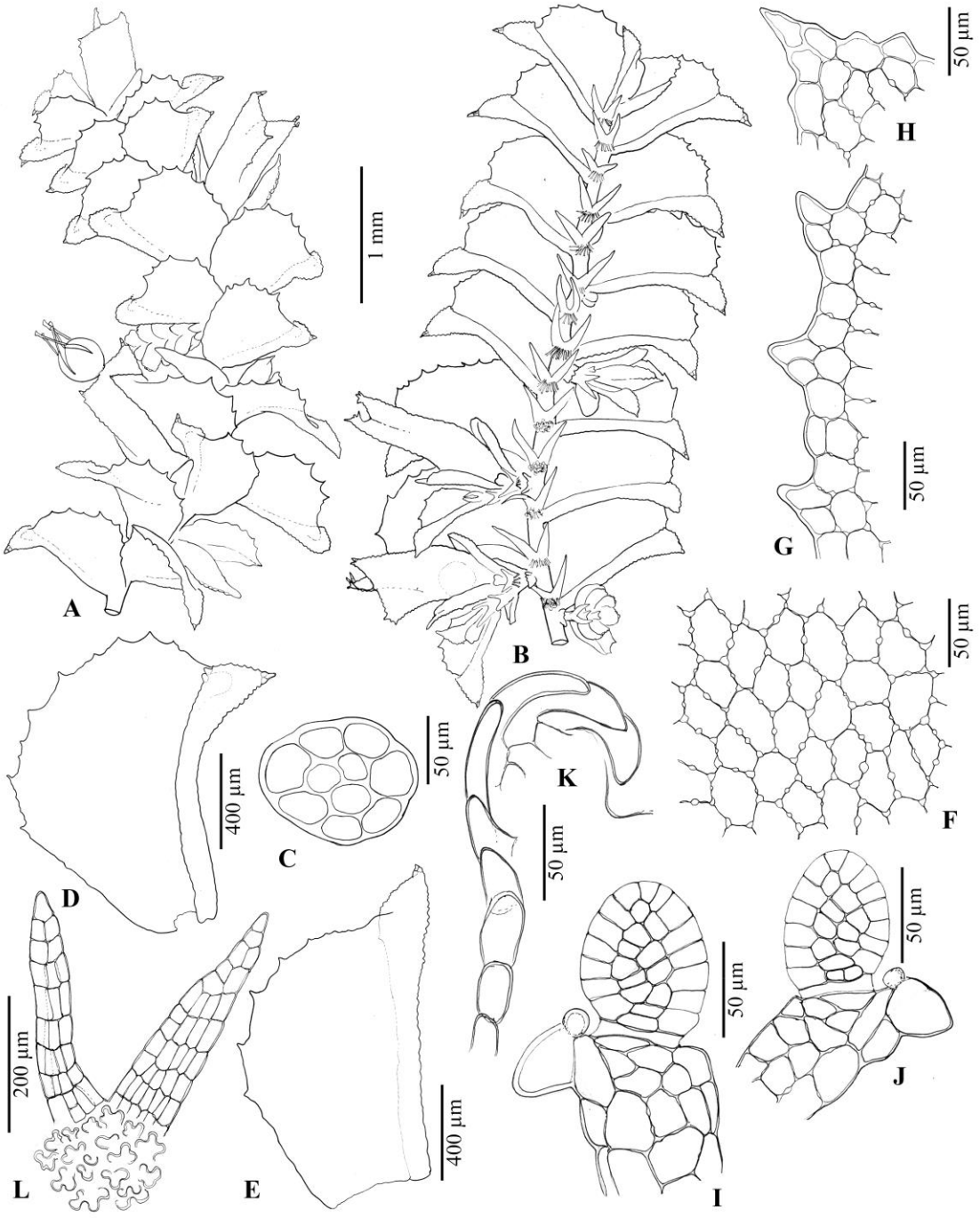

Fig. 4.6 *Colura ari* (Steph.) Steph.: A & B. Portions of plant with gynoecia and androecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I & J. Valves of lobule, I. valve with 1 basal median cell, J. valve with 2 basal median cells. K. Valve frame. L. Underleaf. All from *Sangrattanaprasert 224/14A* (PSU).

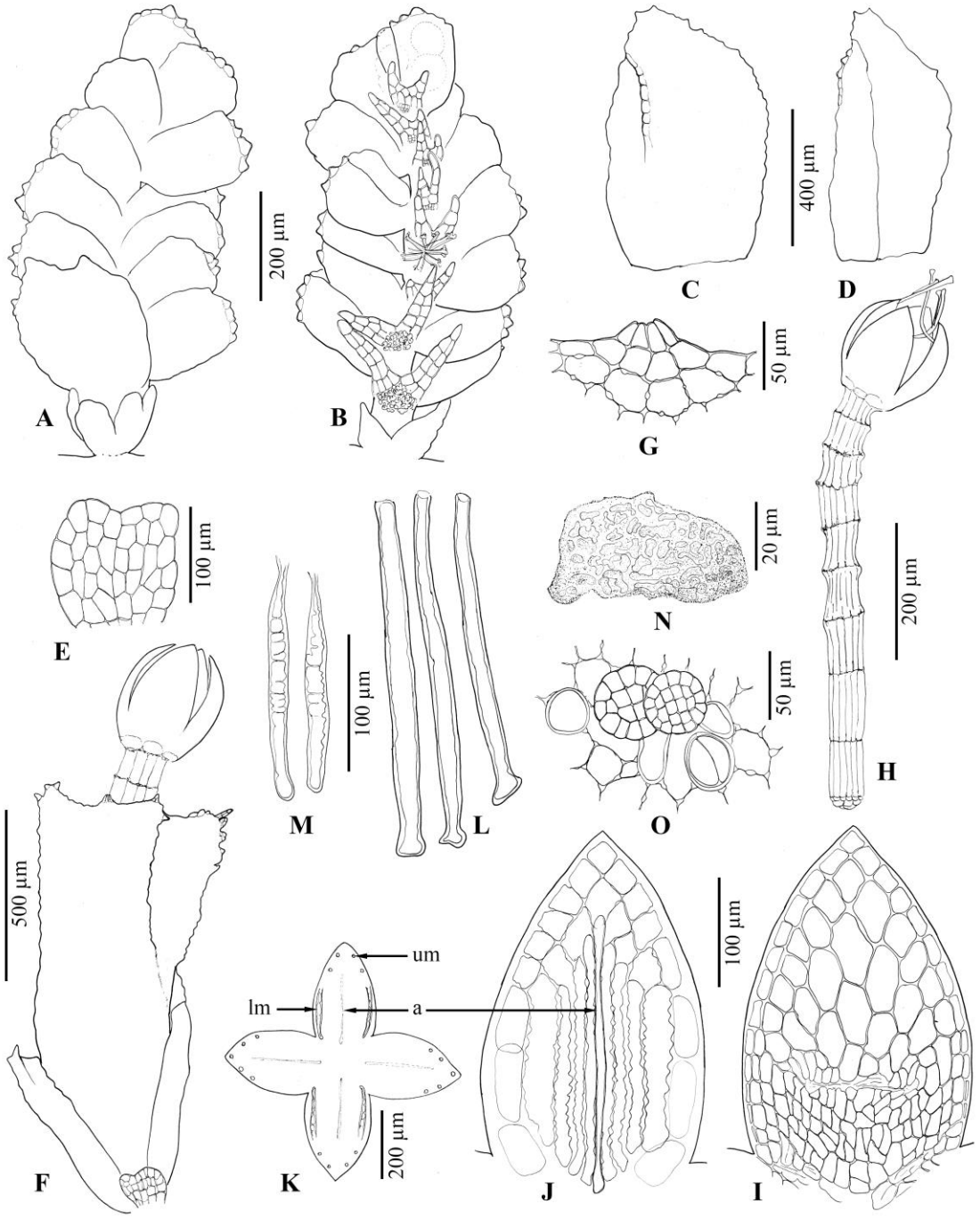

Fig. 4.7 *Colura ari* (Steph.) Steph.: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth. G. Perianth beak. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. O. Gemmae on leaf lobe. All from *Sangrattanaprasert 237/14A* (PSU).

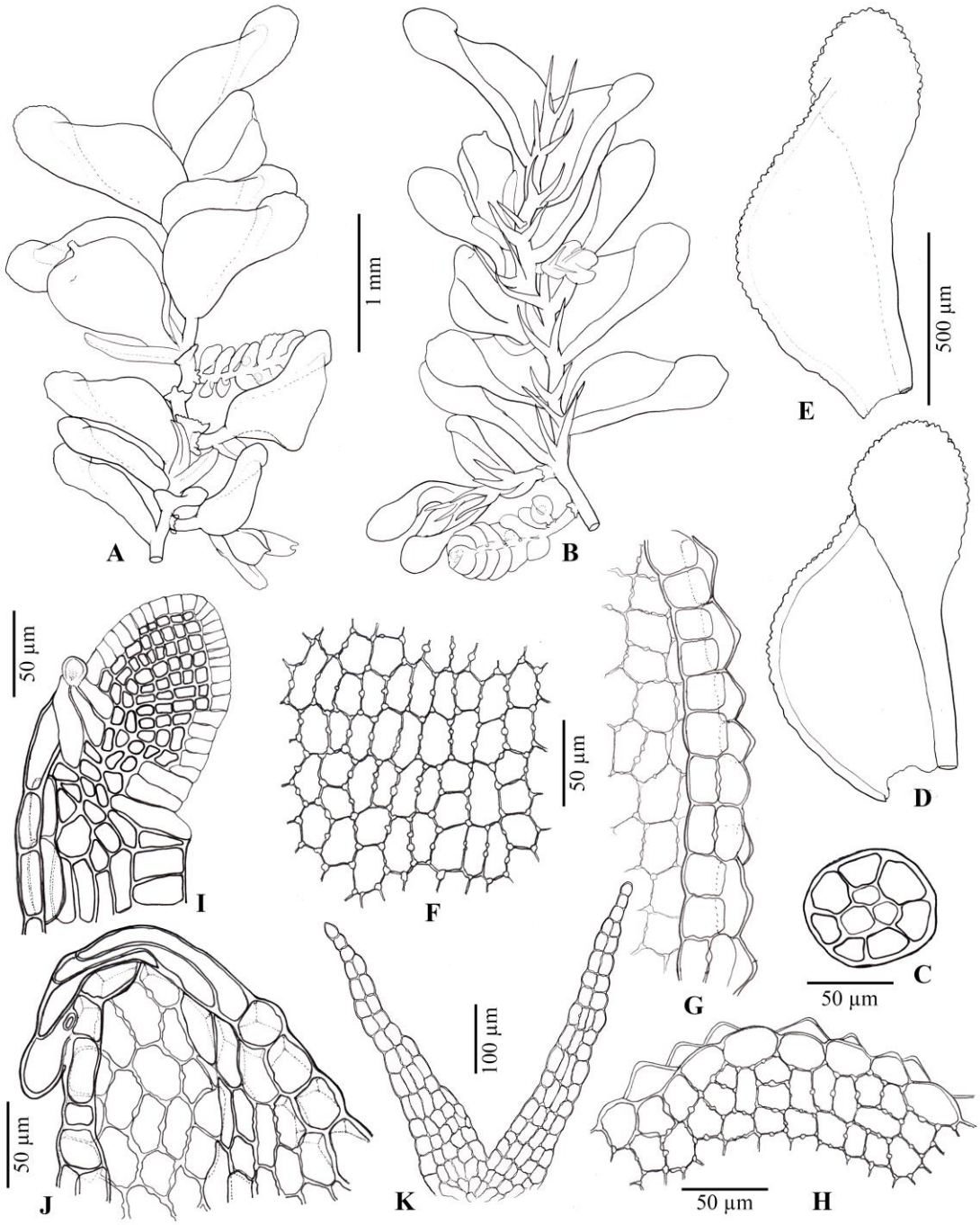

Fig. 4.8 *Colura bisvoluta* Herzog *et* Jovet-Ast: A & B. Portions of plant with androecia and gynoecia, A. dorsal view, B. ventral view; C. Stem in transverse section. D & E. Lateral leaf, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I. Valve of lobule. J. Valve frame. K. Underleaf. All from *Sangrattanaprasert 423/15B* (PSU).

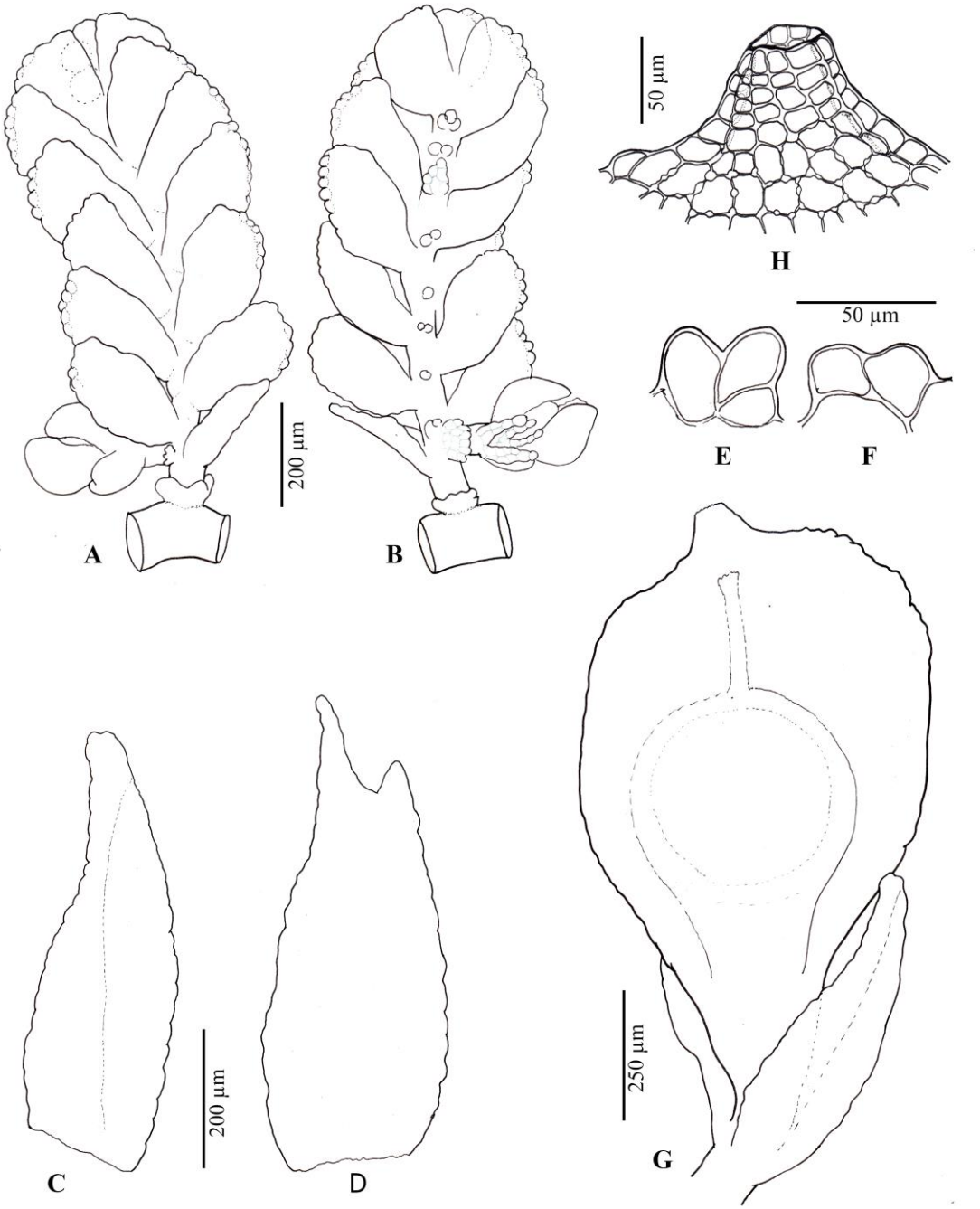

Fig. 4.9 *Colura bisvoluta* Herzog *et* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E & F. Female bracteoles. G. Perianth with young sporophyte. H. Perianth beak. All from *Sangrattanaprasert 423/15B* (PSU).

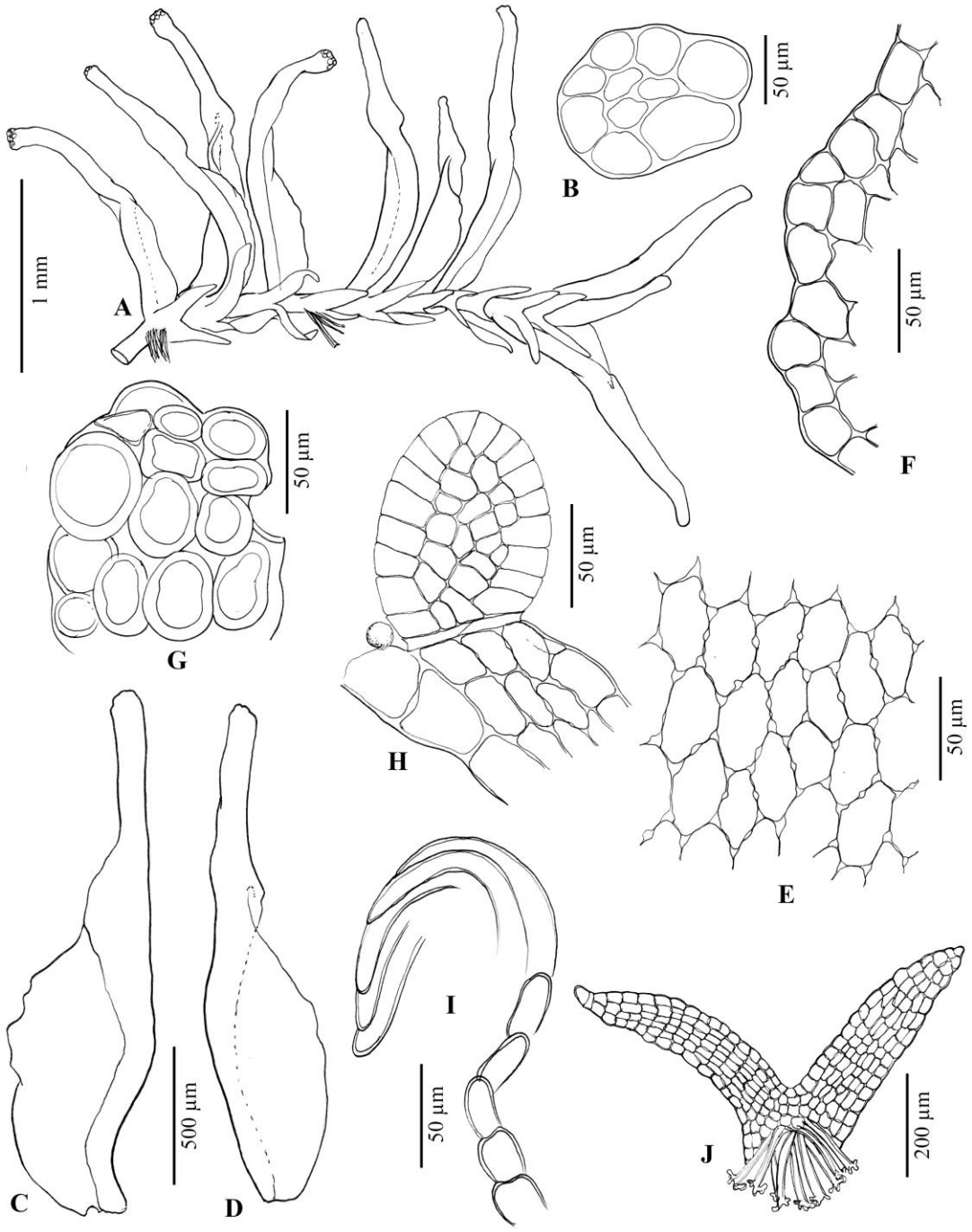

Fig. 4.10 *Colura brevistyla* Herzog: A. Portion of plant, side view. B. Stem in transverse section. C & D. Lateral leaves, C. ventral view, D. dorsal view. E & F. Leaf lobe cells, E. median cells, F. marginal cells. G. Lobule sac apex with remain cells developing gemmae. H. Valve of lobule. I. Valve frame. J. Underleaf. All from *Goodenough 1207* (SING).

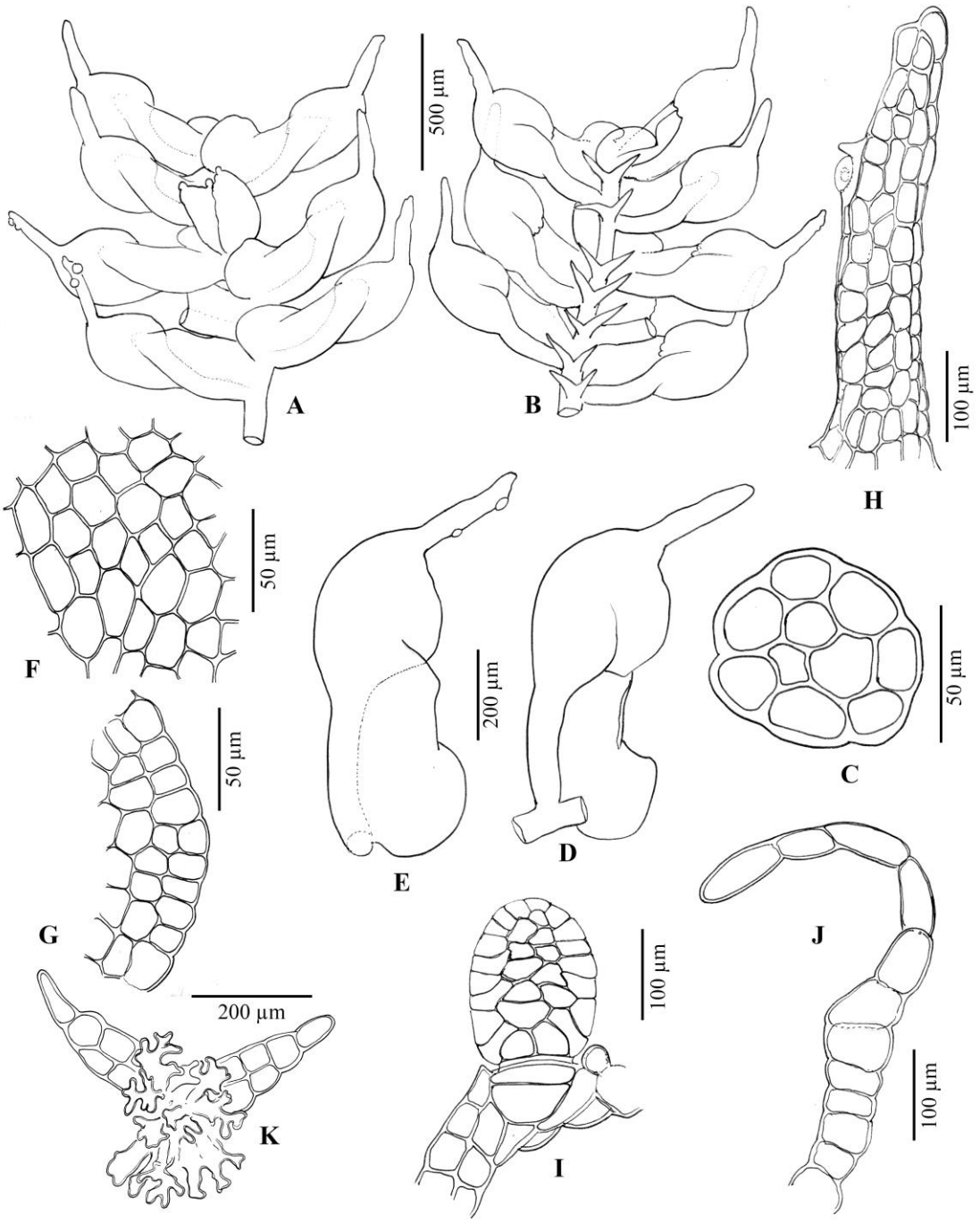

Fig. 4.11 *Colura calyptrifolia* (Hook.) Dumort.: A & B. Portions of plant, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I. Valve of lobule. J. Valve frame. K. Underleaf. All from *Zhu et al. 20160919-114B* (HSNU).

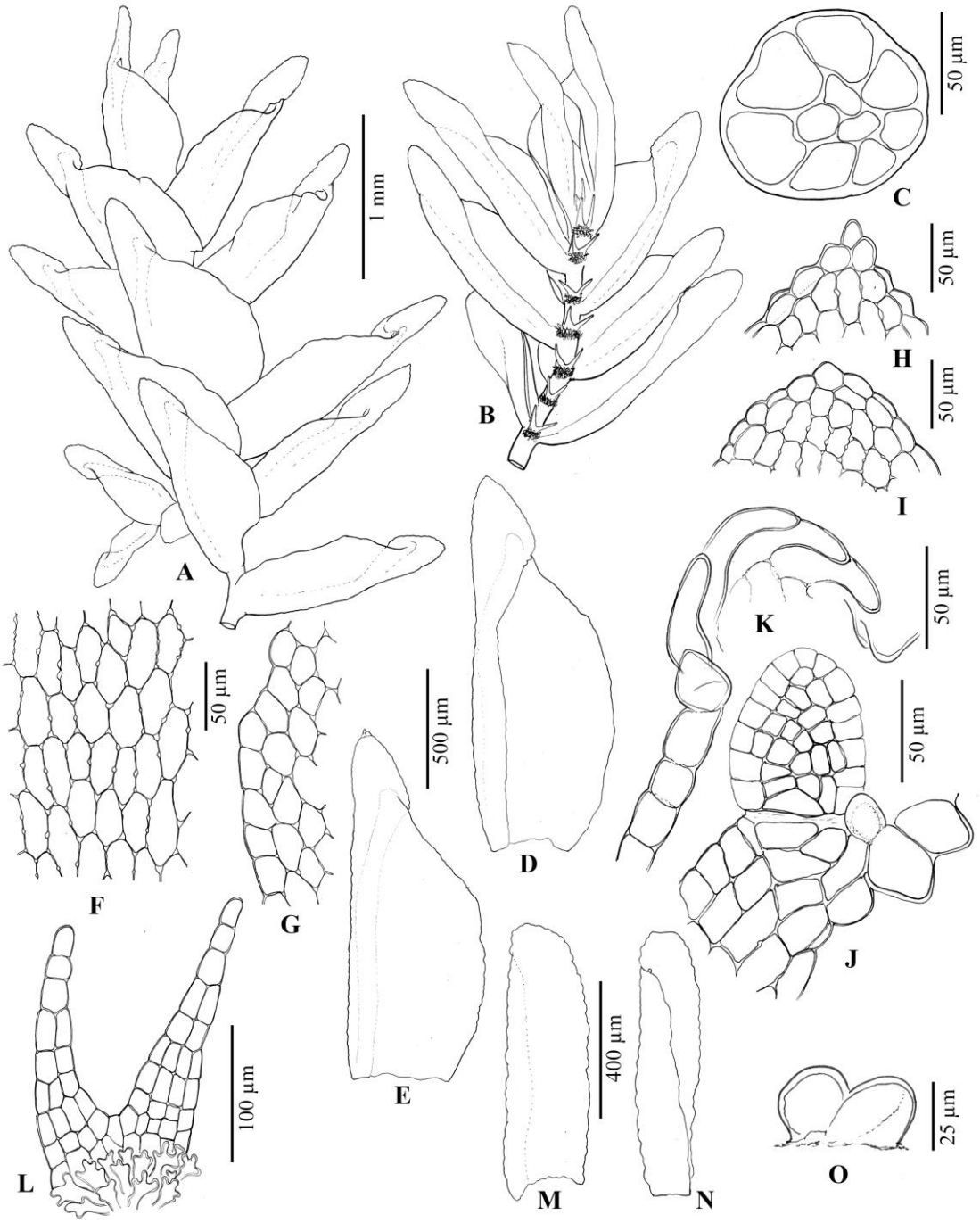

Fig. 4.12 *Colura clementis* Grolle: A & B. Portions of plant, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H & I. Lobule sac apices, H. lobule sac with crest, I. lobule sac slightly entire. J. Valve of lobule. K. Valve frame. L. Underleaf. M & N. Female bracts, M. dorsal view, N. ventral view. O. Female bracteole. All from *Sangrattanaprasert 83/14D* (PSU).

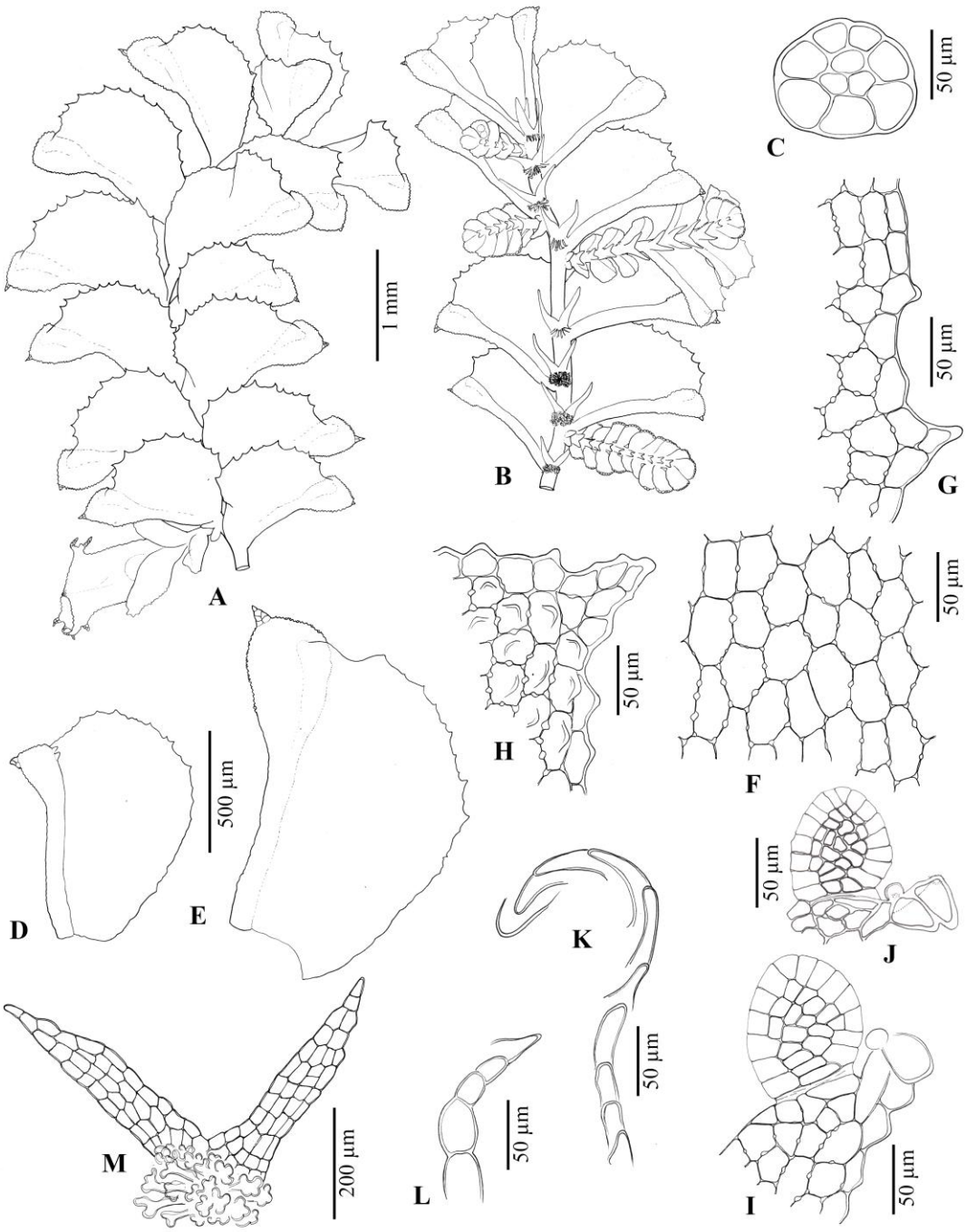

Fig. 4.13 *Colura conica* (Sande Lac.) K.I.Goebel: A. Portions of plant with gynoecia, dorsal view. B. Portion of plant with androecia, ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I & J. Valves of lobule. K & L. Valve frames. M. Underleaf. All from *Sangrattanaprasert 303/15* (PSU).

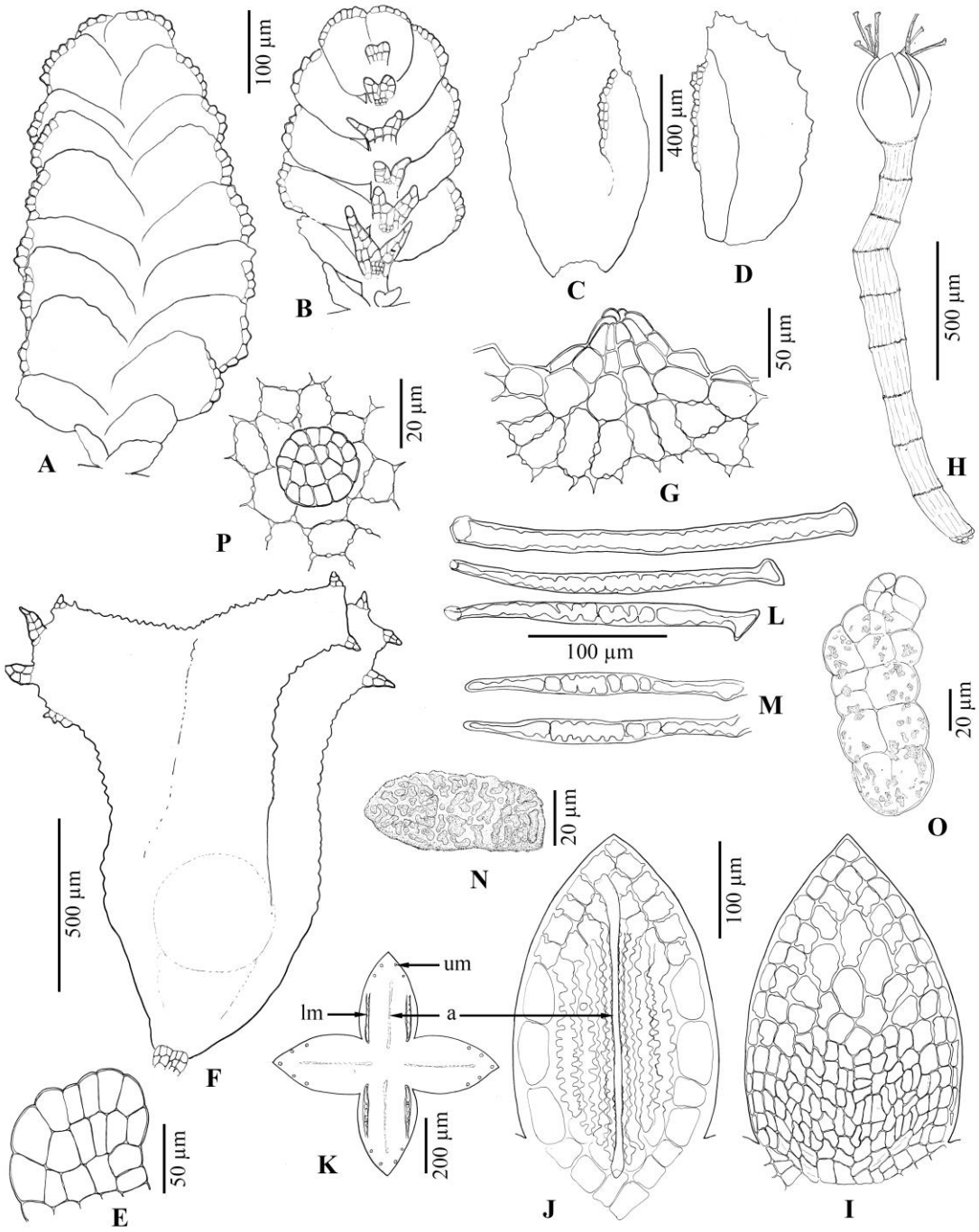

Fig. 4.14 *Colura conica* (Sande Lac.) K.I.Goebel: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth. G. Perianth beak. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. O. Sporeling. P. Gemma on leaf lobe. All from *Sangrattanaprasert 216/14A* (PSU).

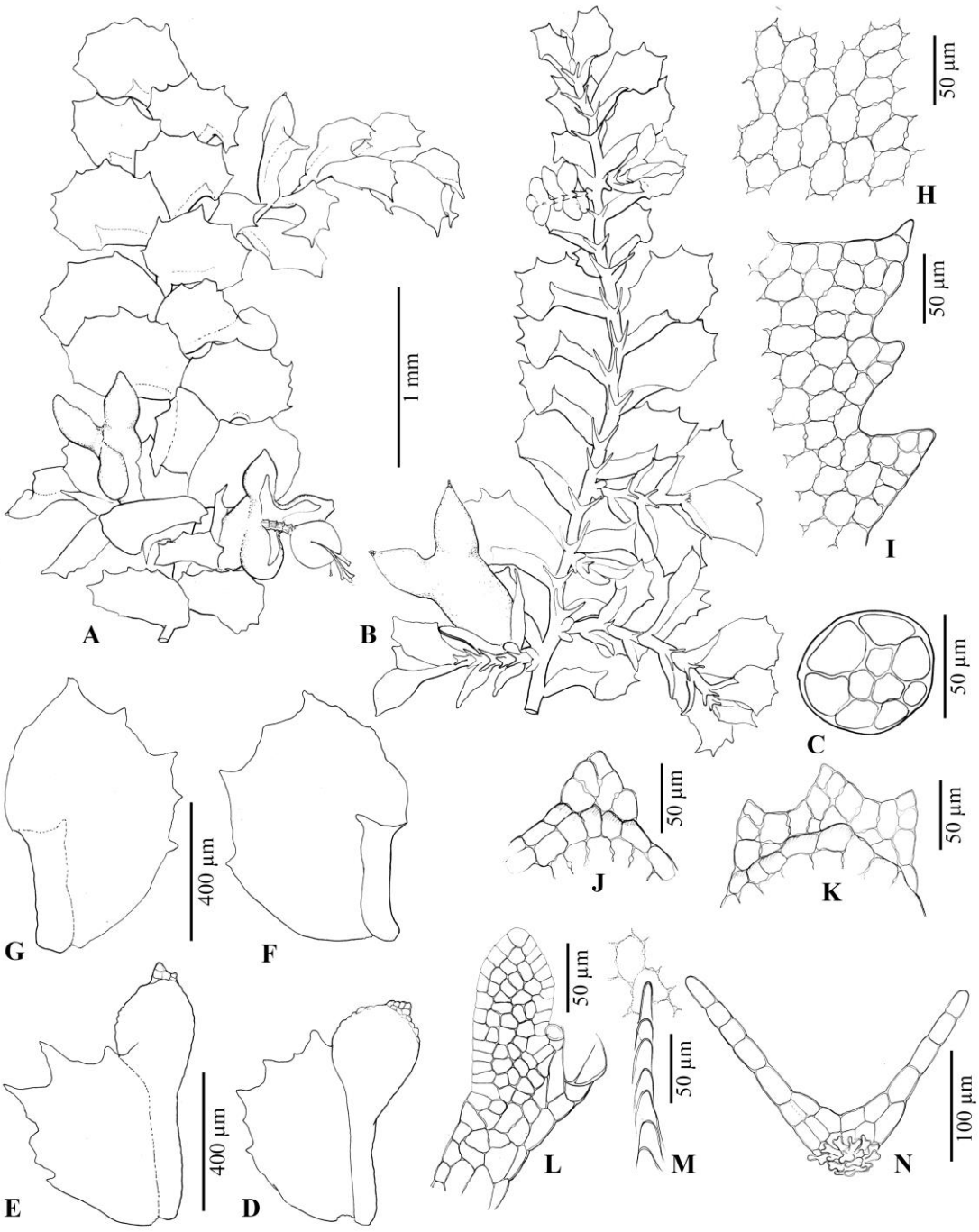

Fig. 4.15 *Colura corniantha* Grolle: A & B. Portions of plant with androecia and gynoecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J & K. Lobule sac apices with apical crests. L. Valve of lobule. M. Valve frame. N. Underleaf. All from *Chantanaorrapint & Promma 3899D* (PSU).

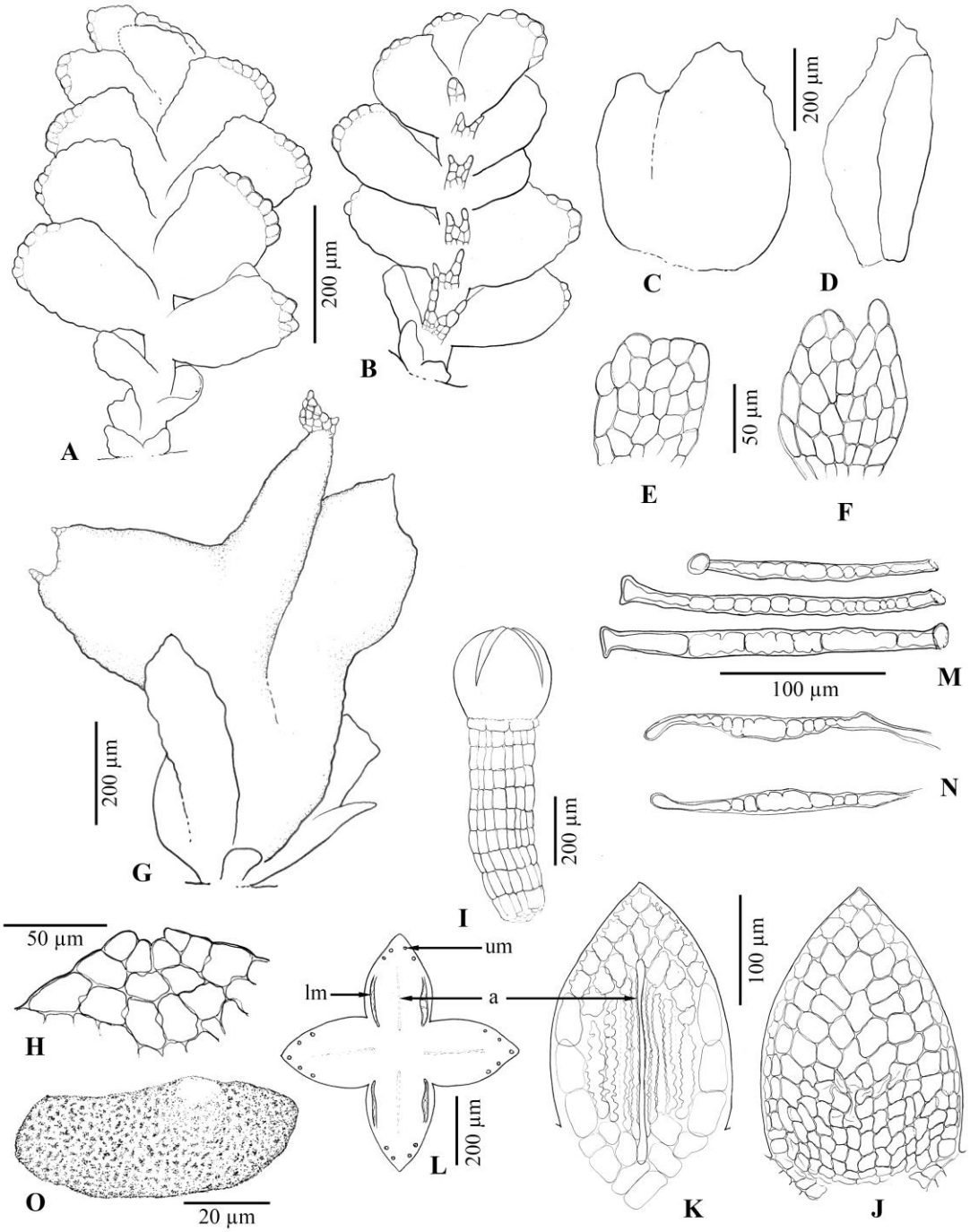

Fig. 4.16 *Colura corniantha* Grolle: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E & F. Female bracteoles. G. Perianth with bracts and bracteole. H. Perianth beak. I. Mature sporophyte. J. Outer layer of capsule valve. K. Inner layer of capsule valve (a = additional elater). L. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). M. Upper marginal elaters. N. Lower marginal elaters. O. Spore. All from *Chantanaorrapint & Promma 3899D* (PSU).

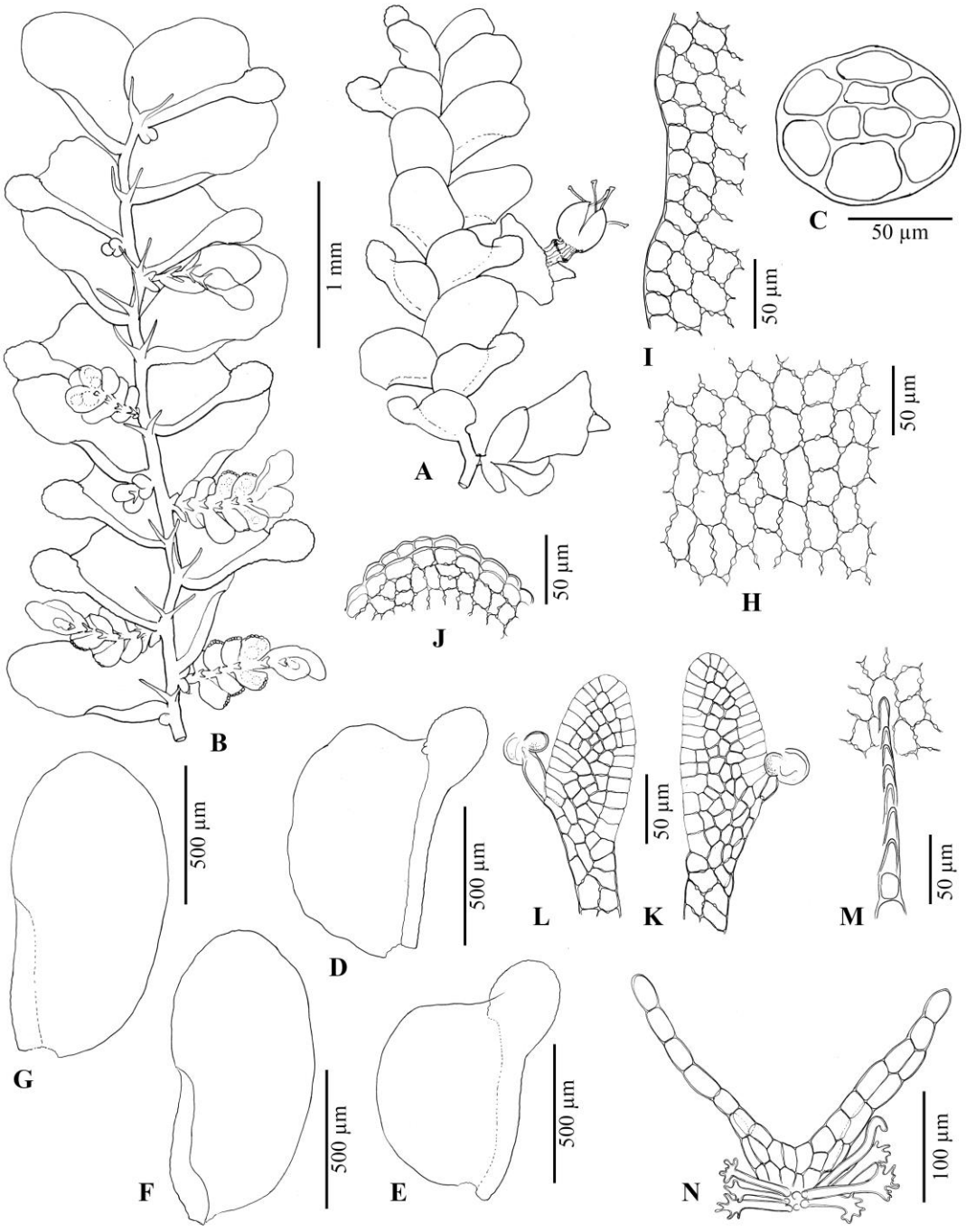

Fig. 4.17 *Colura corynophora* (Nees, Lindenb. *et* Gottsche) Trevis.: A. Portion of plant with gynoecium, dorsal view. B. Portion of plant with androecia, ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Lobule sac apex. K & L. Valves of lobule. M. Valve frame. N. Underleaf. A, C–N from *Sangrattanaprasert 312/15A* (PSU); B from *Chantanaorrapint & Promma 2534D* (PSU).

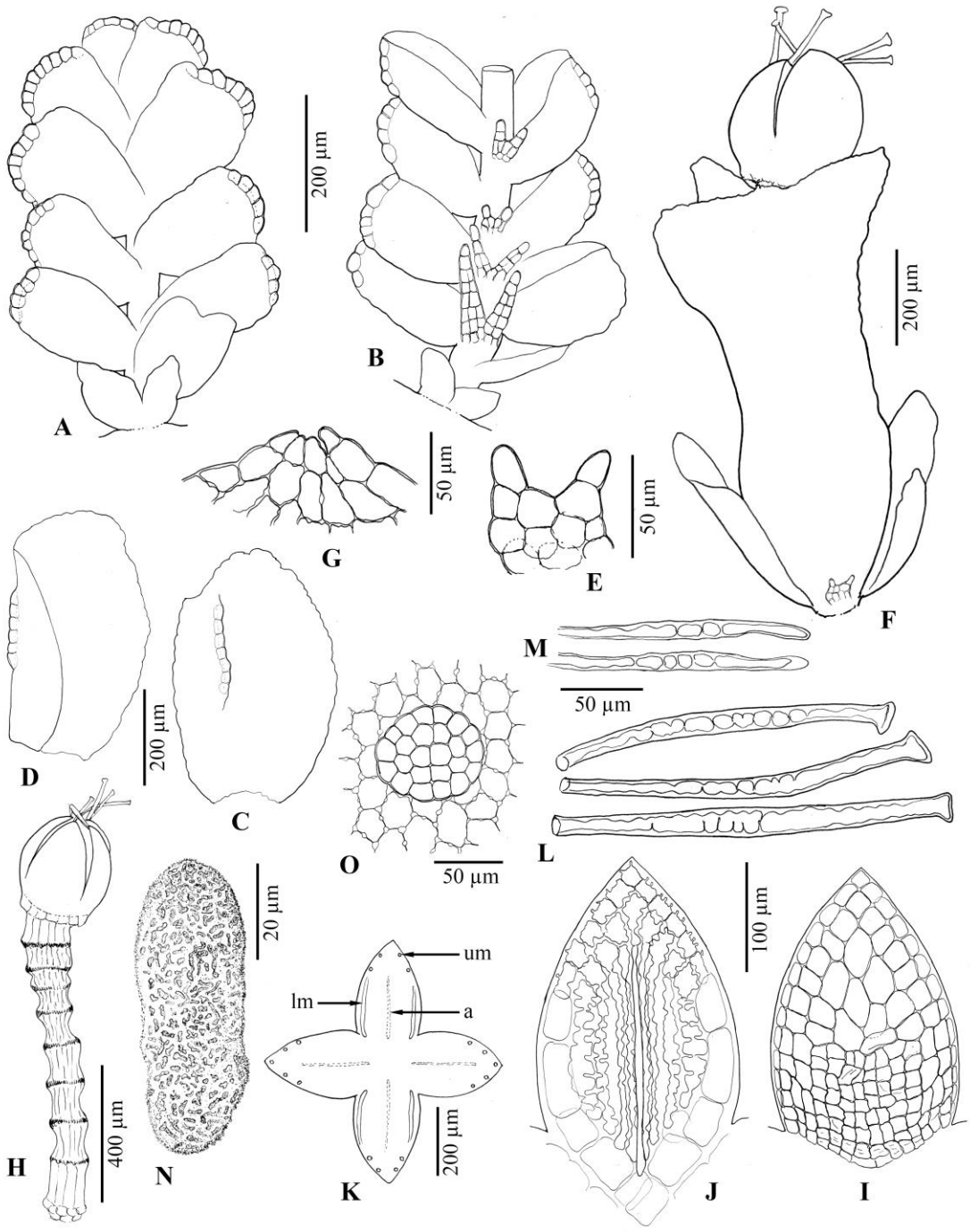

Fig. 4.18 *Colura corynophora* (Nees, Lindenb. *et* Gottsche) Trevis.: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth with sporophyte. G. Perianth beak. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. O. Gemma occurring on leaf lobe. A & B. from *Sangrattanaprasert 312/15A* (PSU), C–O. from *Chantanaorrapint & Promma 2534D* (PSU).

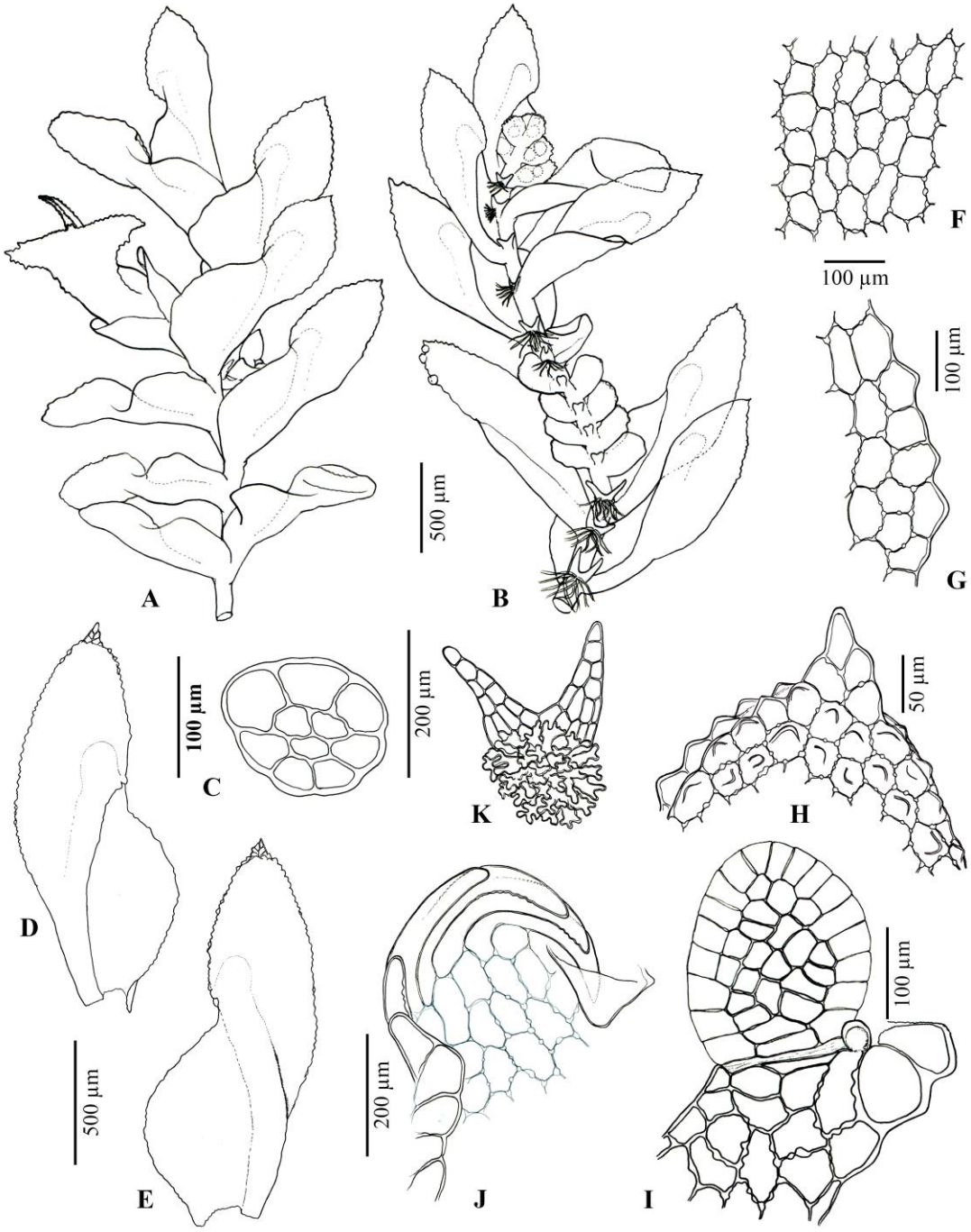

Fig. 4.19 *Colura crenulata* Grolle: A. Portion of plant with gynoecium, dorsal view. B. Portion of plant with androecia, ventral view. C. Stem in transverse section; D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Apical crest and mamillae on apex of lobule sac. I. Valve of lobule. J. Valve frame. K. Underleaf. All from *Sangrattanaprasert 138/14B* (PSU).

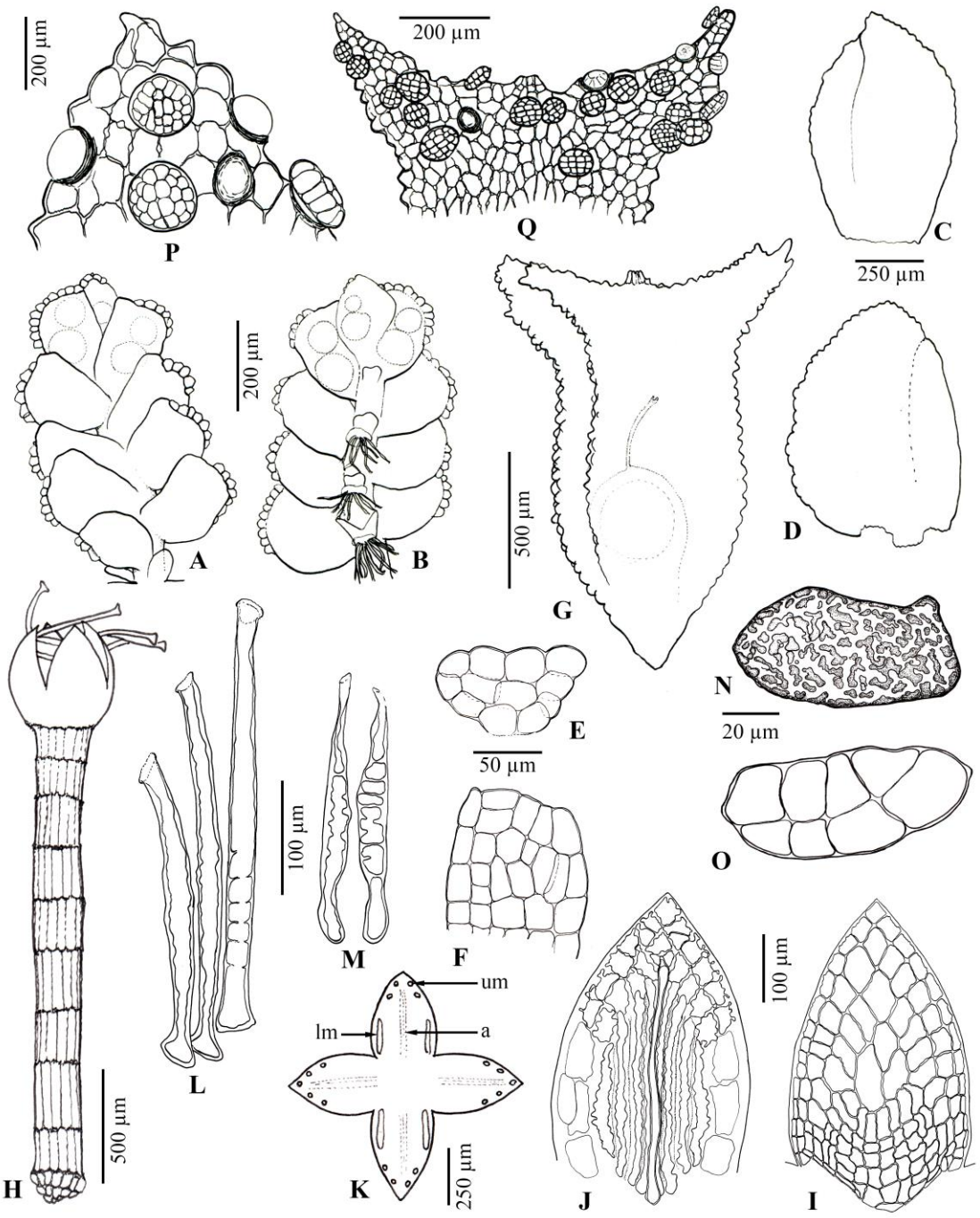

Fig. 4.20 *Colura crenulata* Grolle: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E & F. Female bractoles. G. Perianth with young sporophyte. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. O. Spore showing cylindrical protonema. P & Q. gemmae, P. occurring on lobule sac apex, Q, occurring on perianth keels. All from *Sangrattanaprasert 138/14B* (PSU).

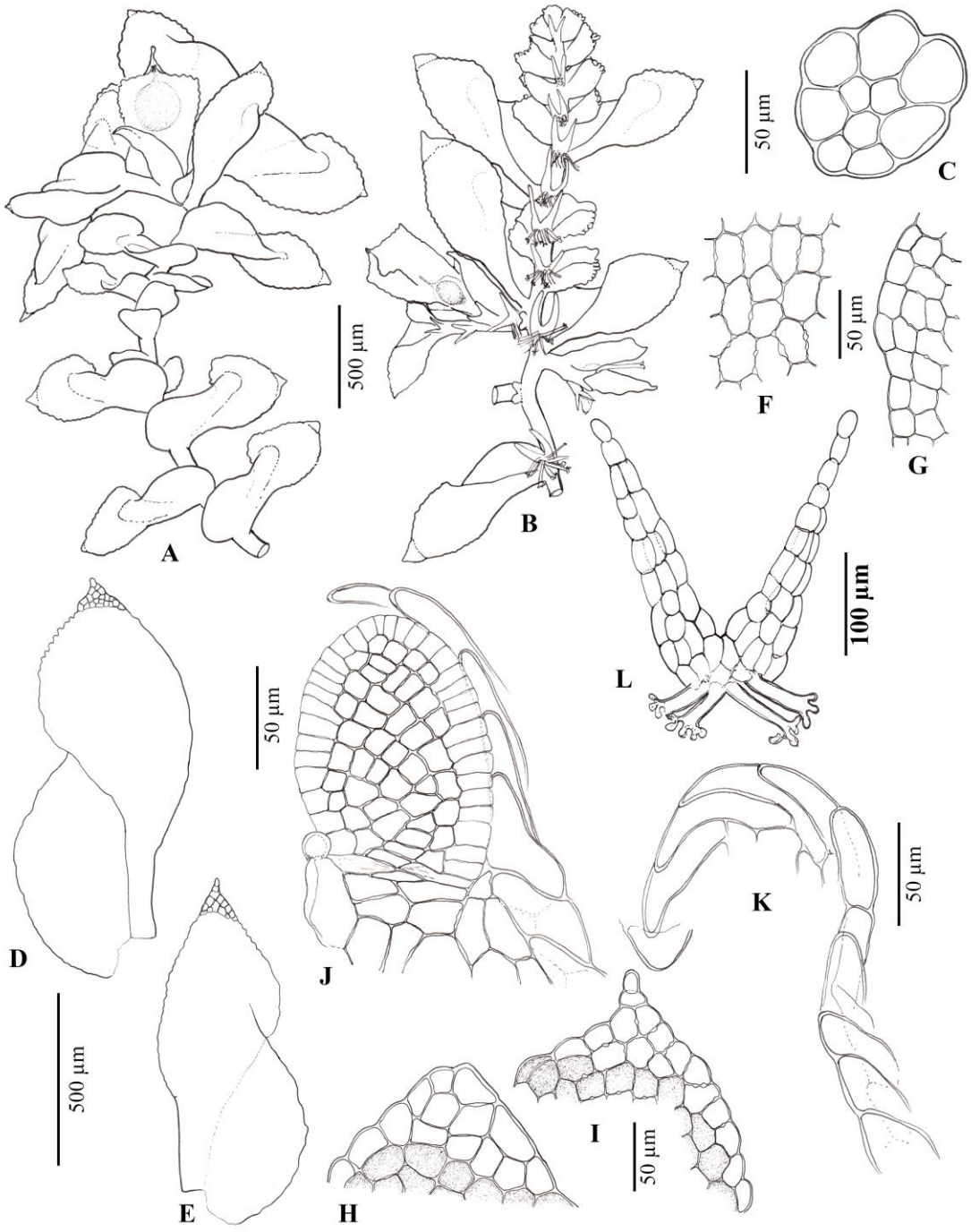

Fig. 4.21 *Colura cristata* Jovet-Ast: A & B. Portions of plant with androecia and gynoecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H & I. Crests on the apices of lobule sacs. J. Valve of lobule. K. Valve frame. L. Underleaf. All from *Zhu et al. 20160916-2* (HSNU).

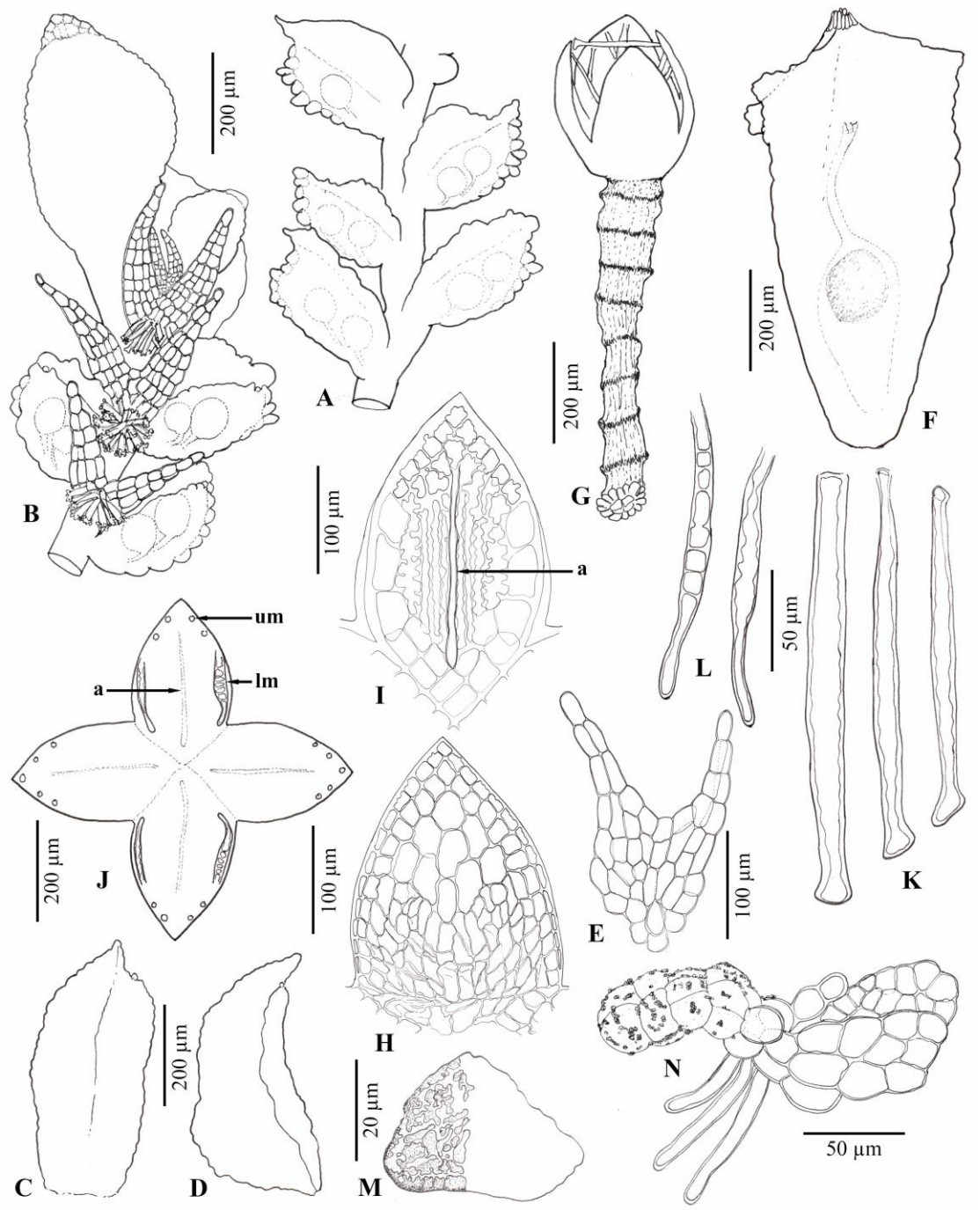

Fig. 4.22 *Colura cristata* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth with young sporophyte. G. Mature sporophyte. H. Outer layer of capsule valve. I. Inner layer of capsule valve (a = additional elater). J. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). K. Upper marginal elaters. L. Lower marginal elaters. M. Spore. N. Sporeling. All from *Zhu et al. 20160916-2* (HSNU).

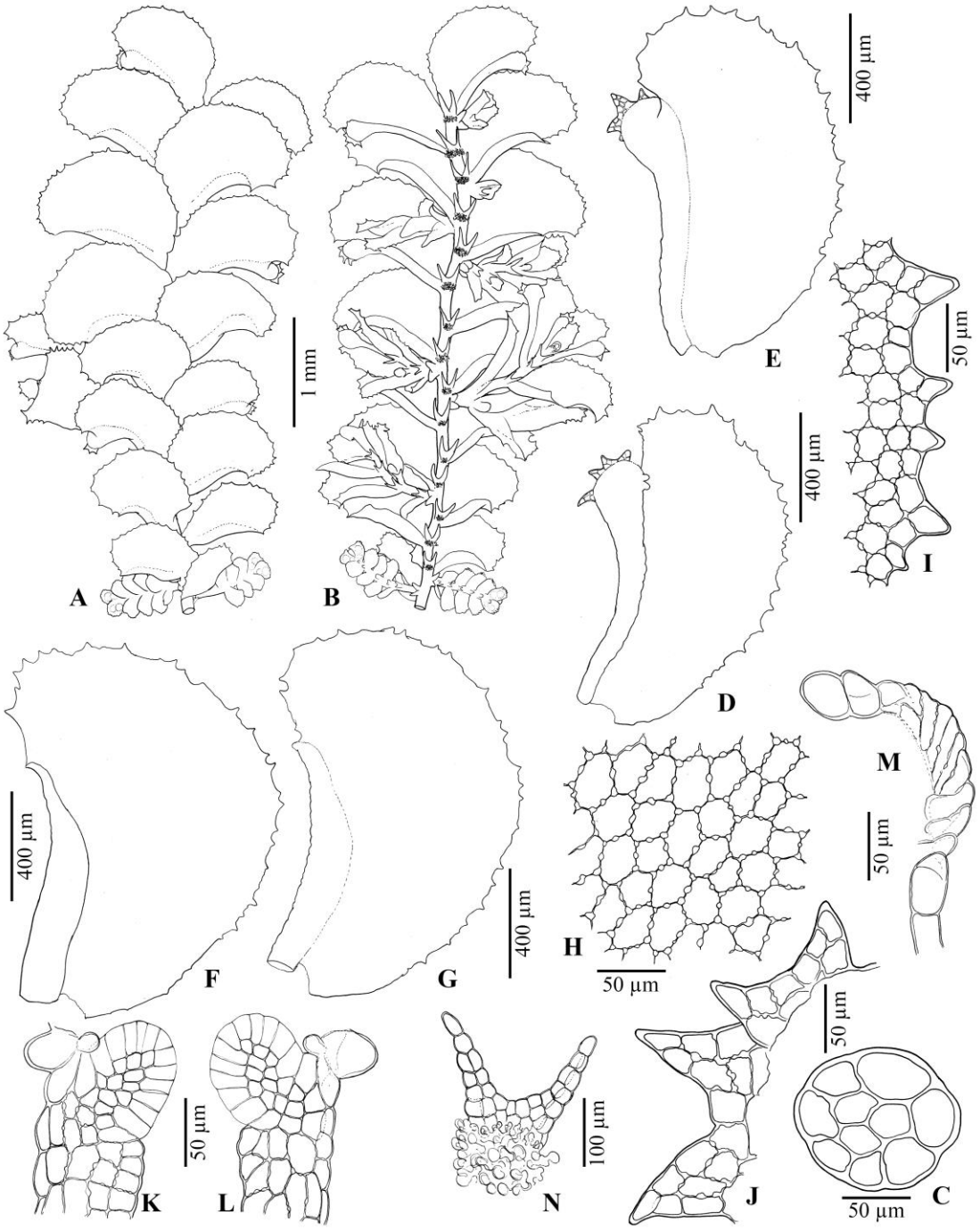

Fig. 4.23 *Colura denticulata* Jovet-Ast: A & B. Portions of plant with androecia and gynoecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Apical lamellar crest. K & L. Valves of lobule. M. Valve frame. N. Underleaf. All from *Pócs et al. 13179/AF* (EGR).

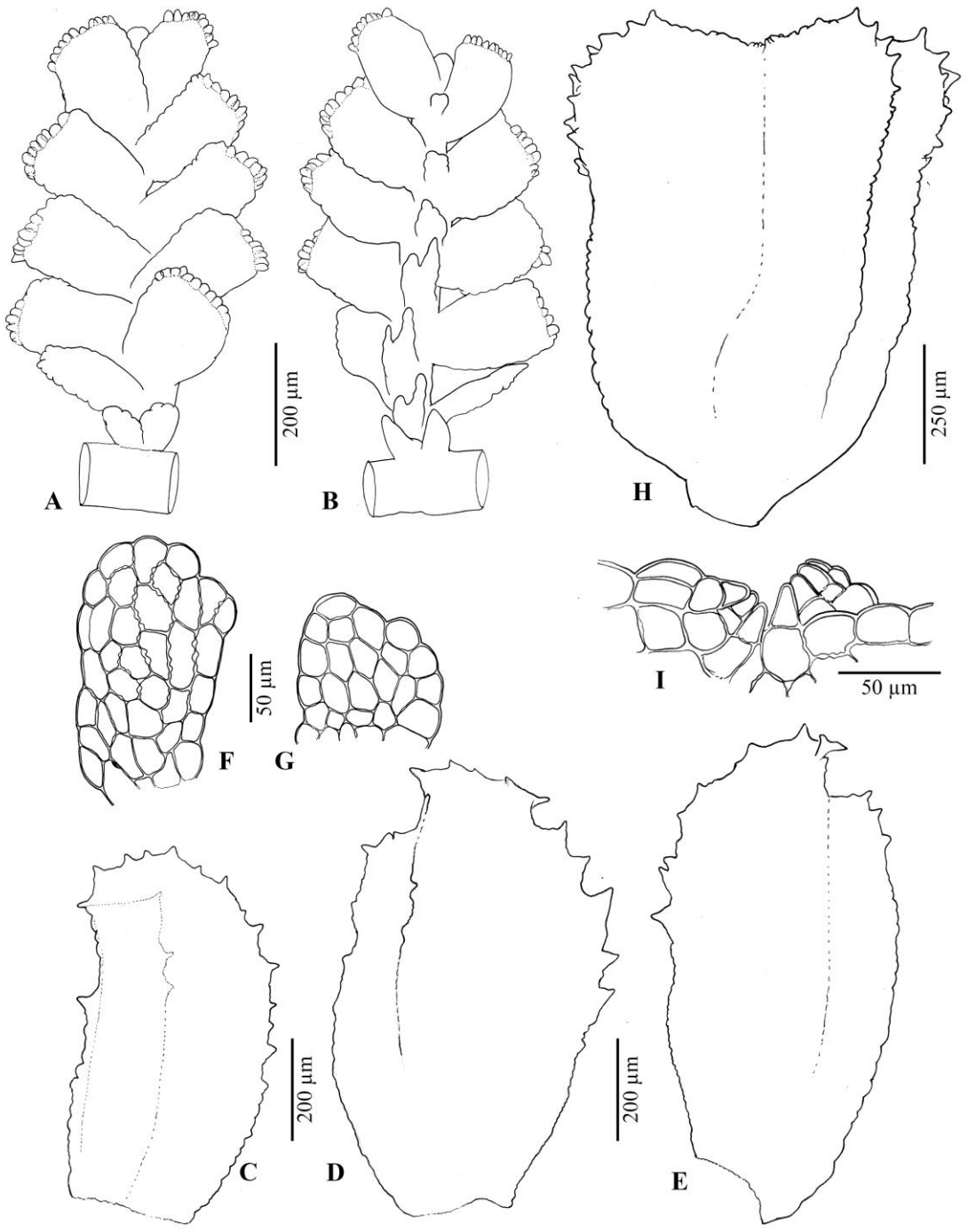

Fig. 4.24 *Colura denticulata* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C–E. Female bracts, C & D. dorsal view, E. ventral view. F & G. Female bracteoles. H. Perianth. I. Perianth beak. All from *Pócs et al.13179/AF* (EGR).

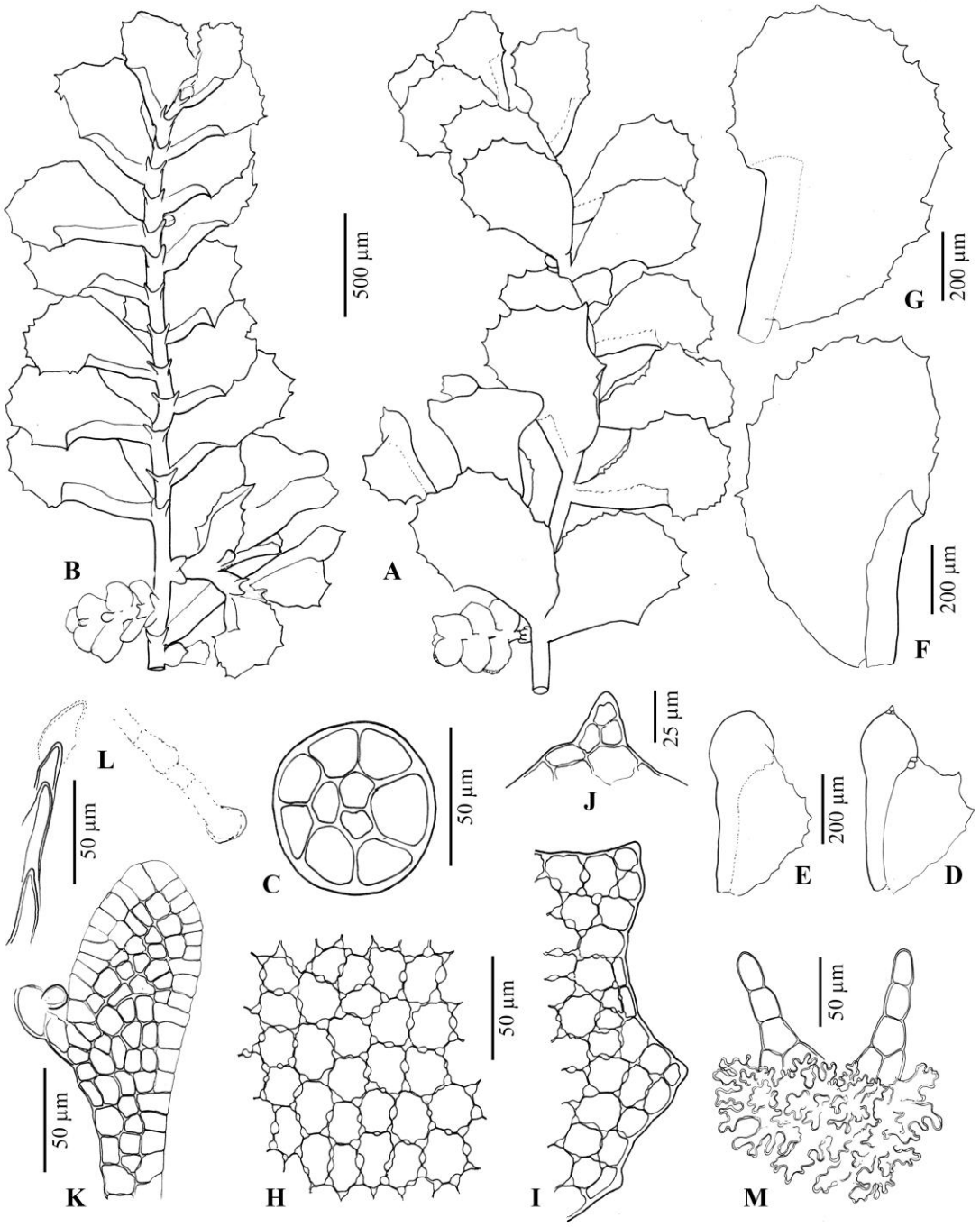

Fig. 4.25 *Colura galeata* Jovet-Ast: A & B. Portions of plant with androecia and gynoecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Lobule sac apex. K. Valve of lobule. L. Valve frame. M. Underleaf. All from *Meijer B11190* (L).

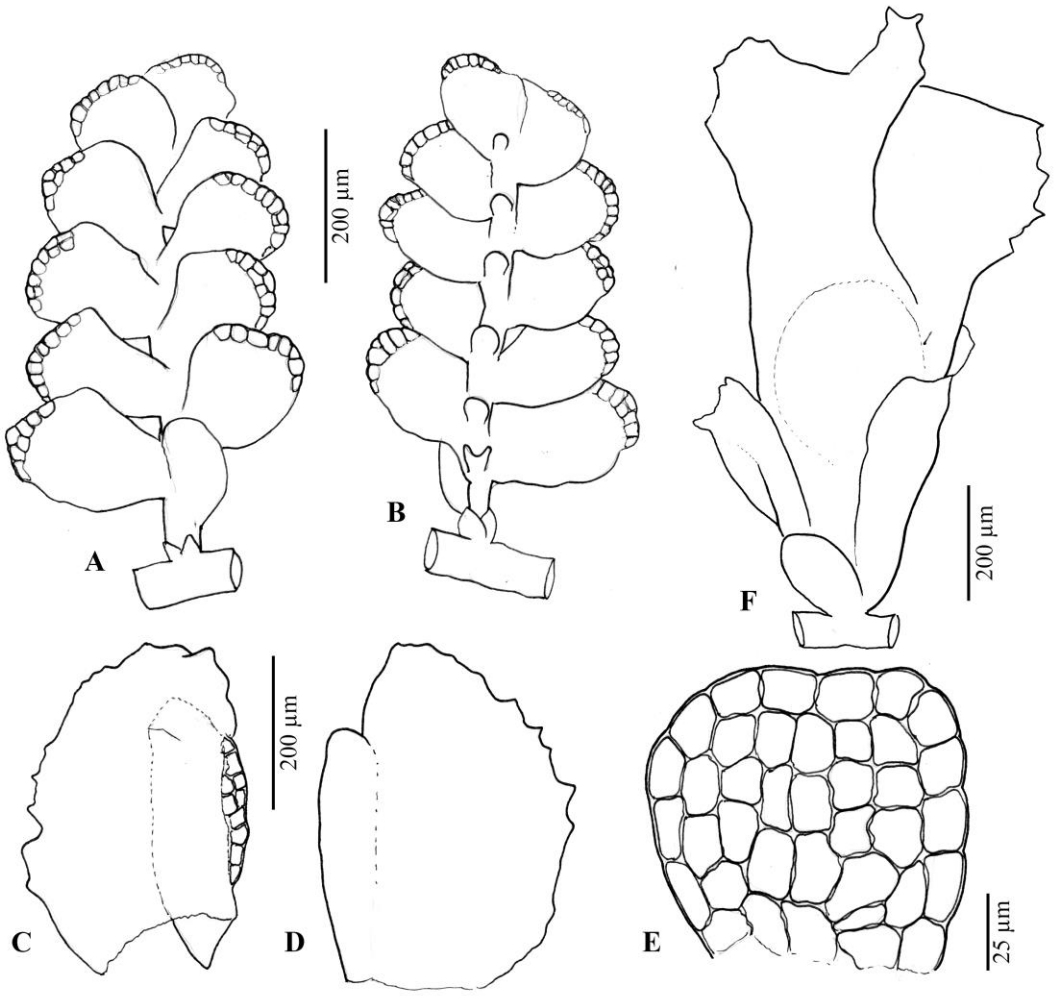

Fig. 4.26 *Colura galeata* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth with female bracts and female bracteole. All from *Meijer B11190* (L).

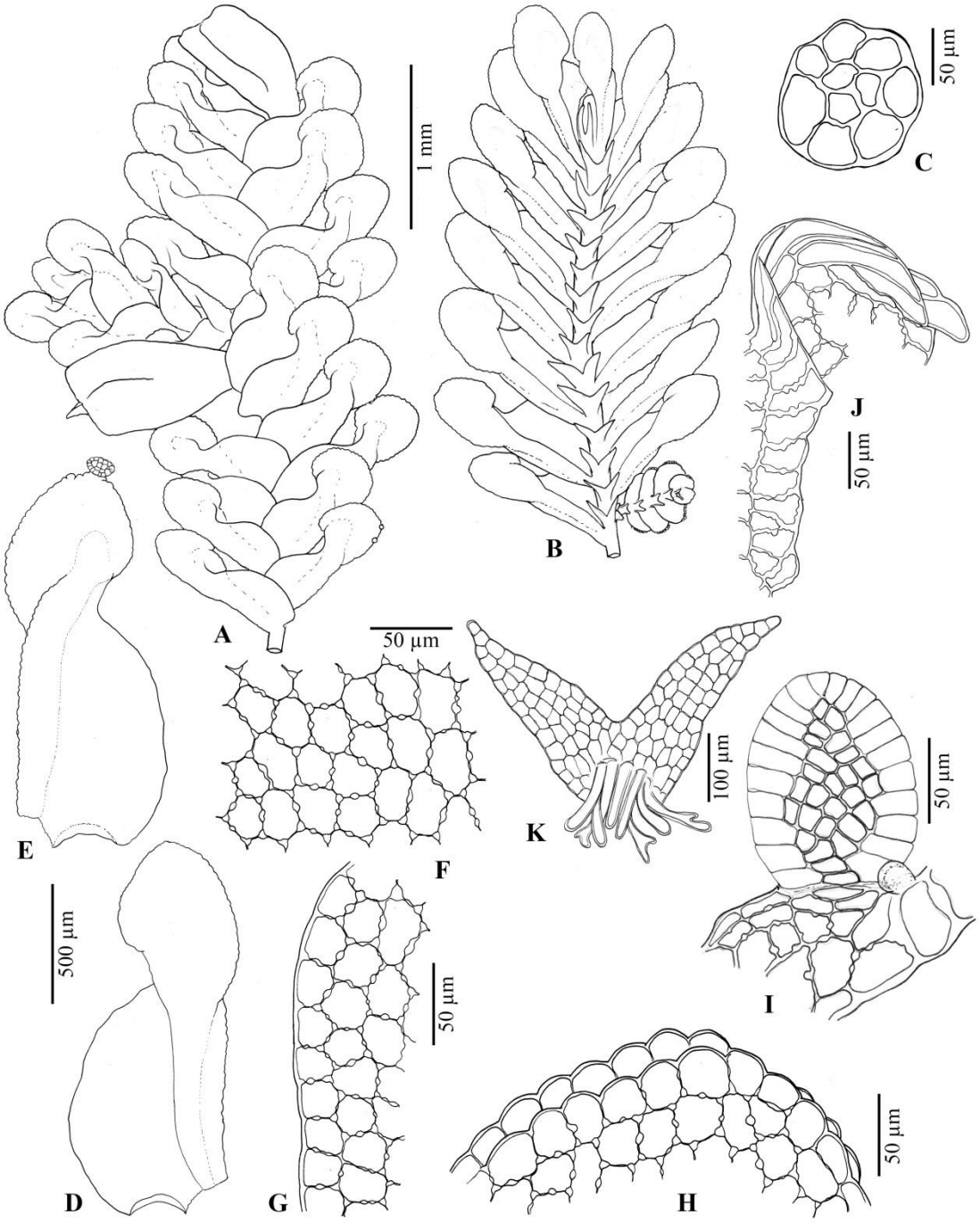

Fig. 4.27 *Colura hemisphaerica* Jovet-Ast: A. Portion of plant with gynoecia, dorsal view. B. Portion of plant with androecium, ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I. Valve of lobule. J. Valve frame. K. Underleaf. A from *Pócs & Pócs 1009/A* (EGR), B from *Chantanaorrapint & Suwanmala 1620A* (PSU), C–K from *Sangrattanaprasert 104/14* (PSU).

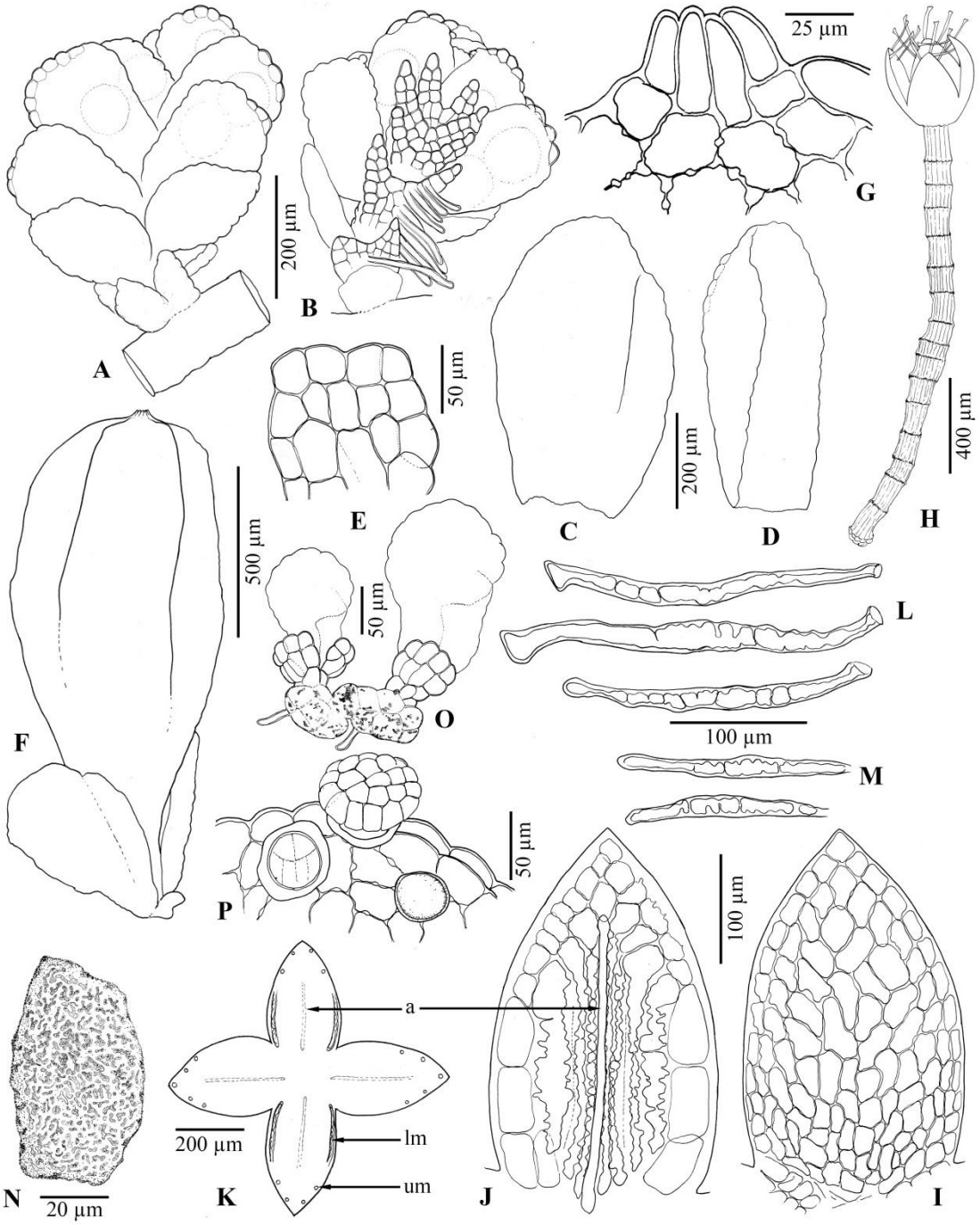

Fig. 4.28 *Colura hemisphaerica* Jovet-Ast.: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth. G. Perianth beak. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. O. Sporeling. P. Gemmae occurring on slobule sac apex. All from *Pócs & Pócs 1009/A* (EGR).

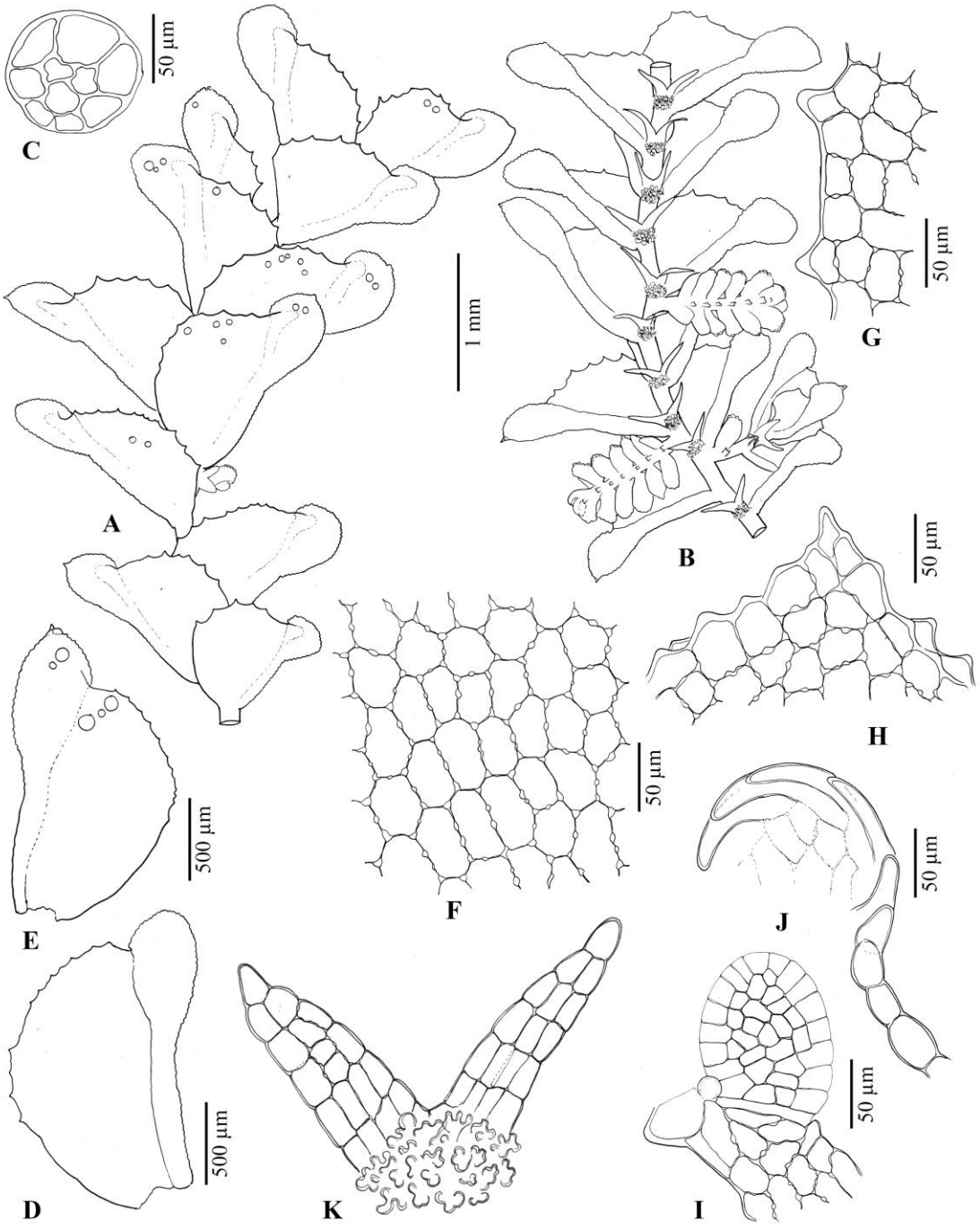

Fig. 4.29 *Colura herzogii* Jovet-Ast: A & B. Portions of plant with androecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I. Valve of lobule. J. Valve frame. K. Underleaf. All from *Meijer 8077e* (L).

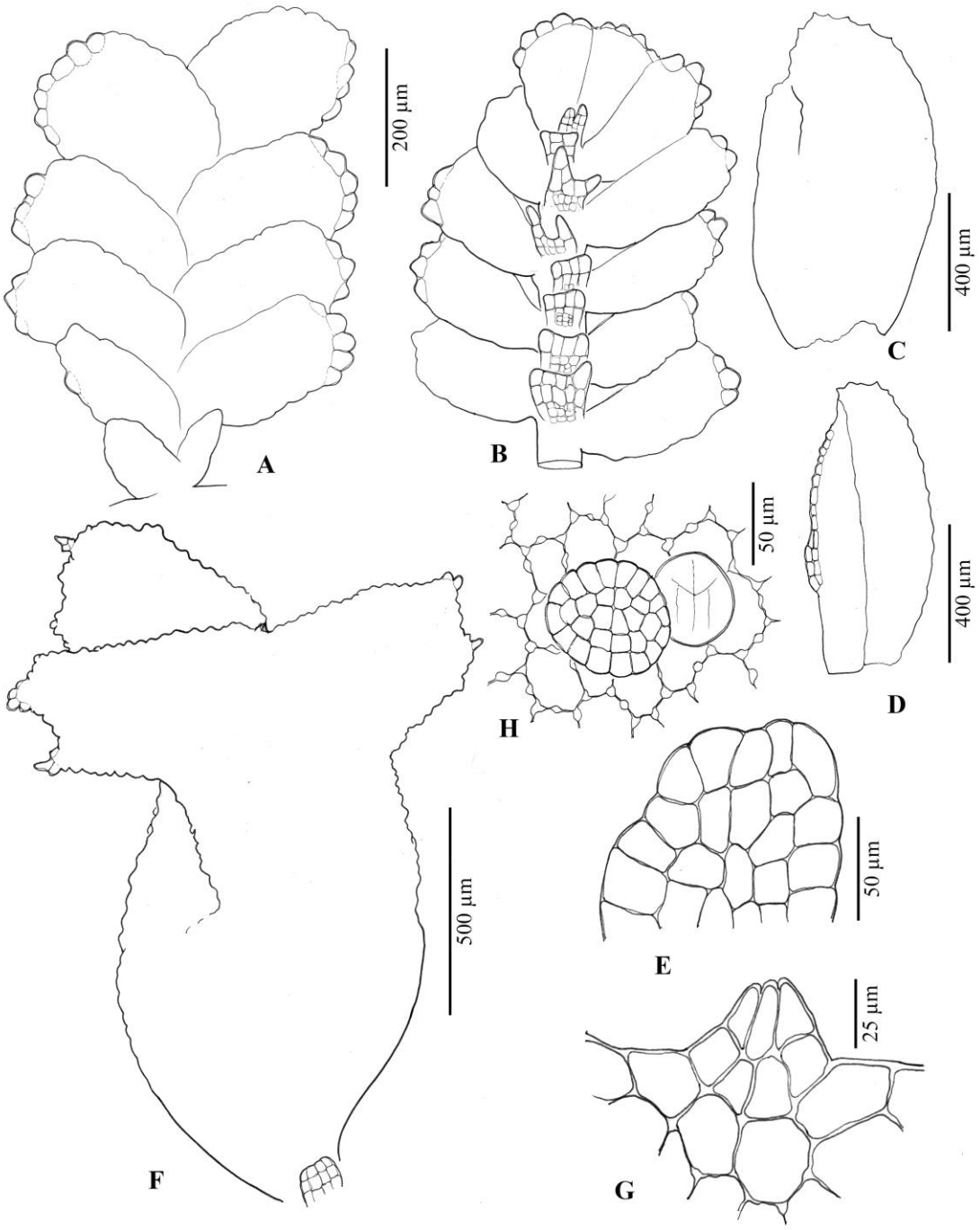

Fig. 4.30 *Colura herzogii* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth. G. Perianth beak. H. Gemmae occurring on leaf lobe. All from *Meijer 8077e* (L).

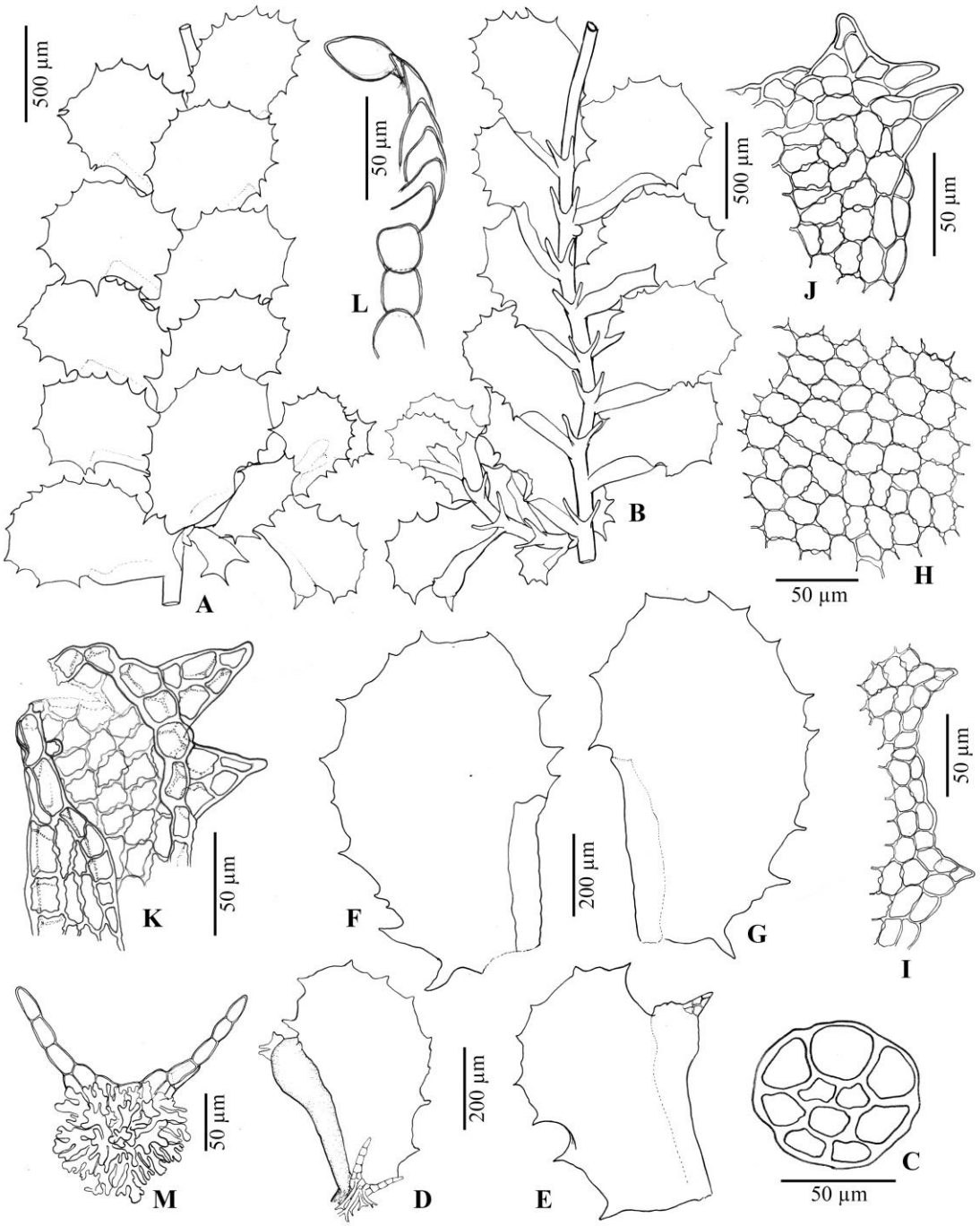

Fig. 4.31 *Colura imperfecta* Steph.: A & B. Portions of plant, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Lobule sac apex. K. Valve of lobule. L. Valve frame. M. Underleaf. All from *Sangrattanaprasert 228/14* (PSU).

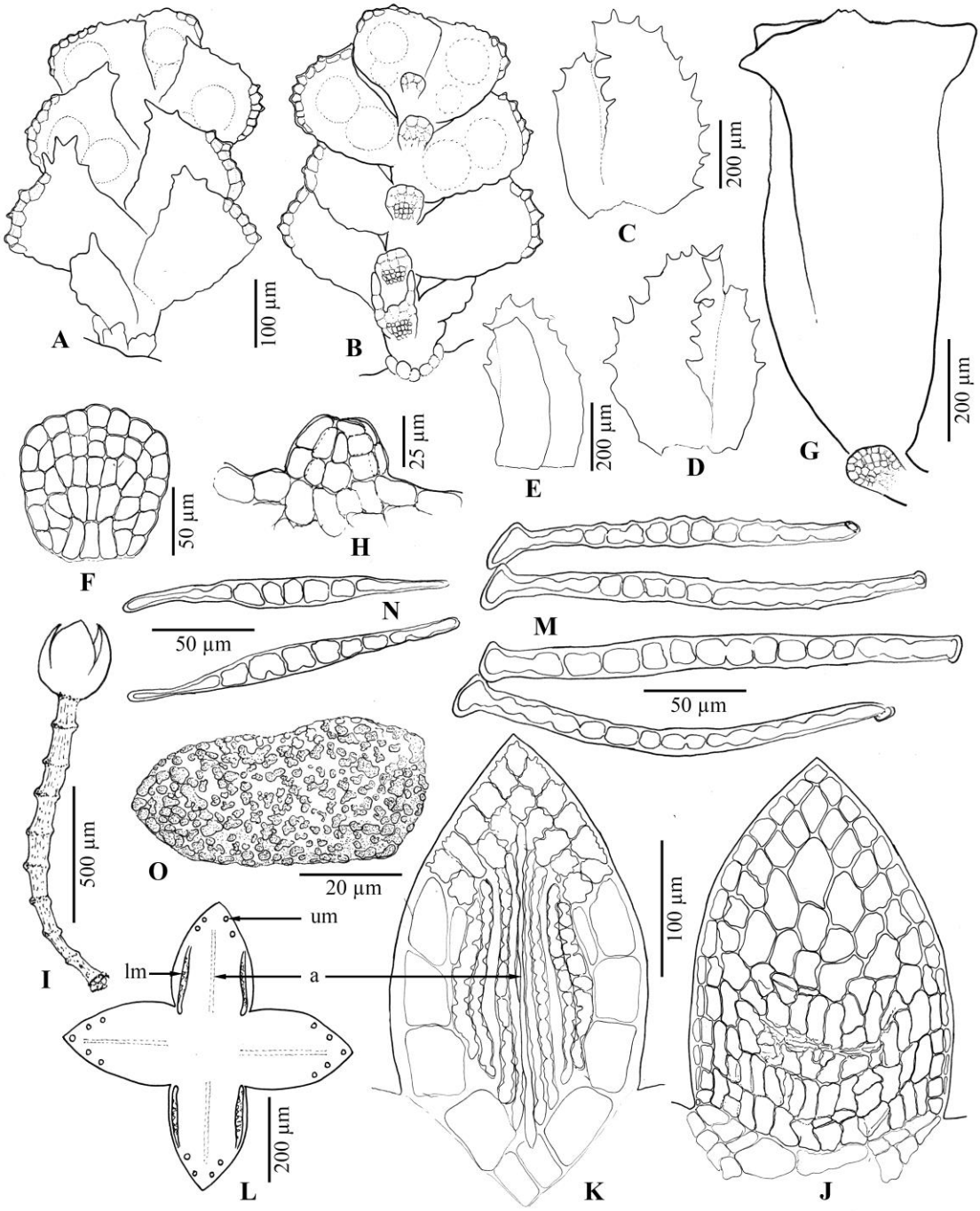

Fig. 4.32 *Colura imperfecta* Steph.: A & B. Androecia, A. dorsal view, B. ventral view. C–E. Female bracts, C & D. dorsal view, E. ventral view. F. Female bracteole. G. Perianth with bracteole. H. Perianth beak. I. Mature sporophyte. J. Outer layer of capsule valve. K. Inner layer of capsule valve (a = additional elater). L. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). M. Upper marginal elaters. N. Lower marginal elaters. O. Spore. All from *Sangrattanaprasert 228/14* (PSU).

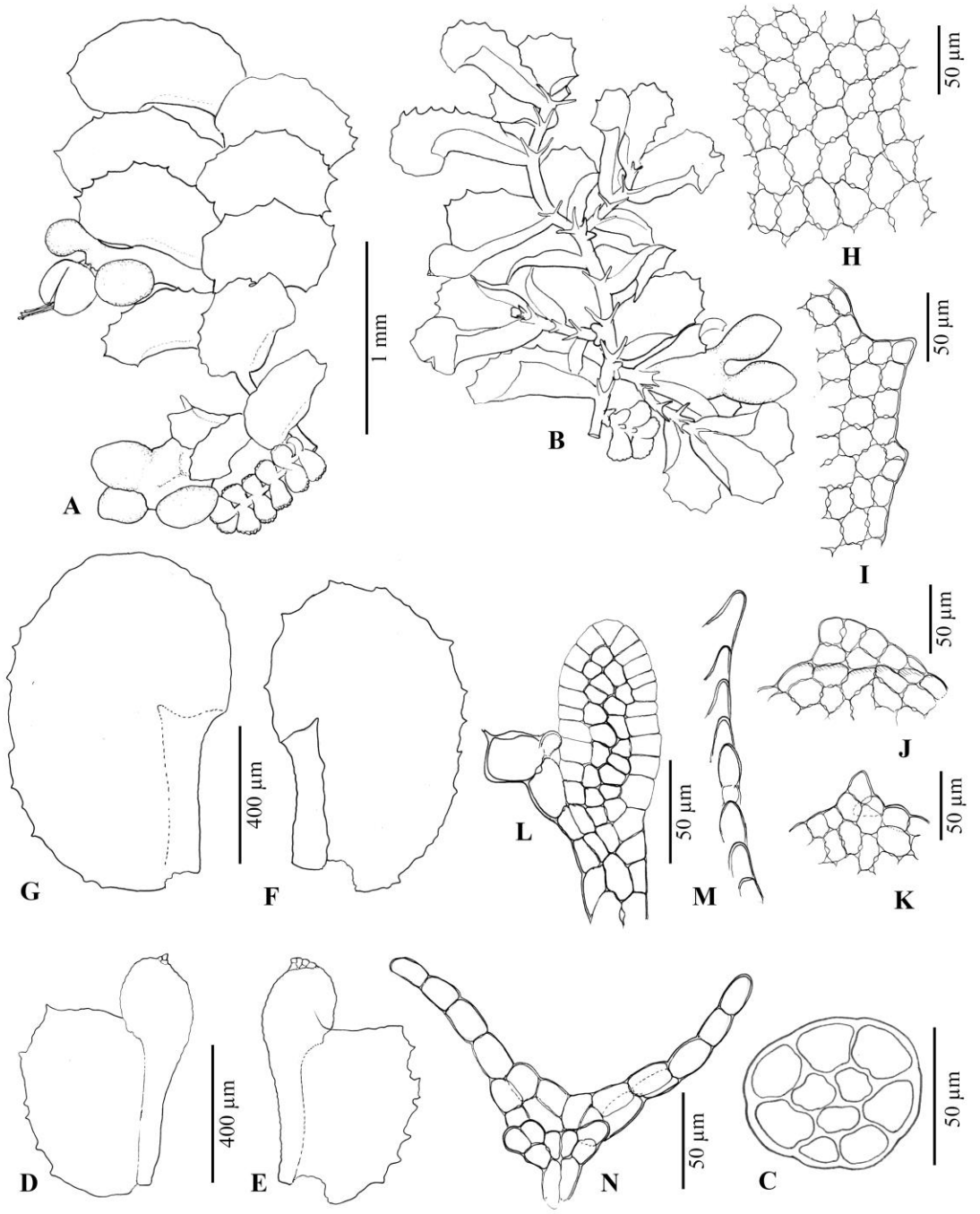

Fig. 4.33 *Colura inflata* K.I.Goebel: A & B. Portions of plant with androecia and gynoecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J & K. Lobule sac apices with apical crests. L. Valve of lobule. M. Valve frame. N. Underleaf. All from *Verwimp & Verwimp 19010/A* (EGR).

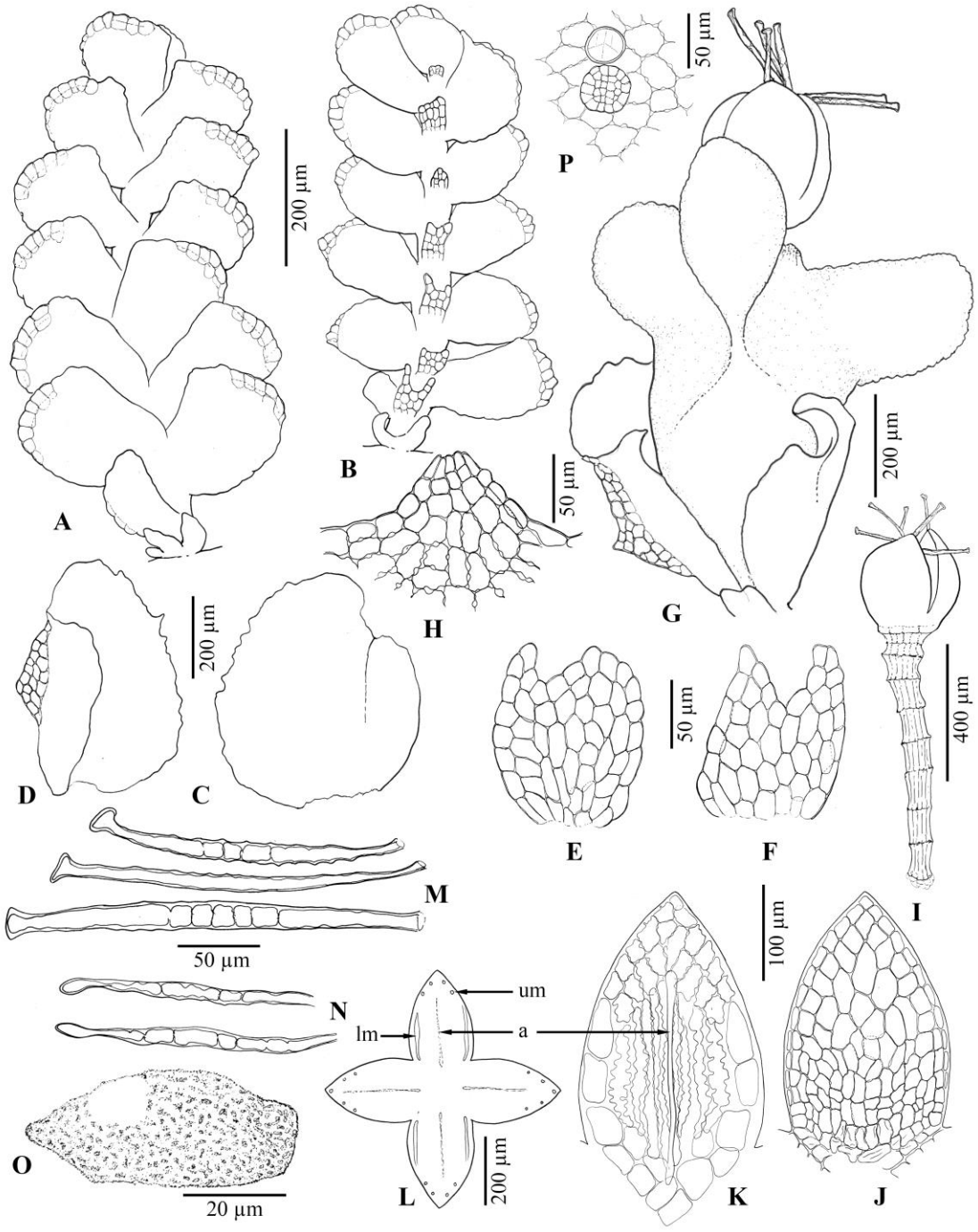

Fig. 4.34 *Colura inflata* K.I.Goebel: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E & F. Female bracteoles. G. Perianth with sporophyte. H. Perianth beak. I. Mature sporophyte. J. Outer layer of capsule valve. K. Inner layer of capsule valve (a = additional elater). L. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). M. Upper marginal elaters. N. Lower marginal elaters. O. Spore. All from *Verwimp & Verwimp 19010/A* (EGR).

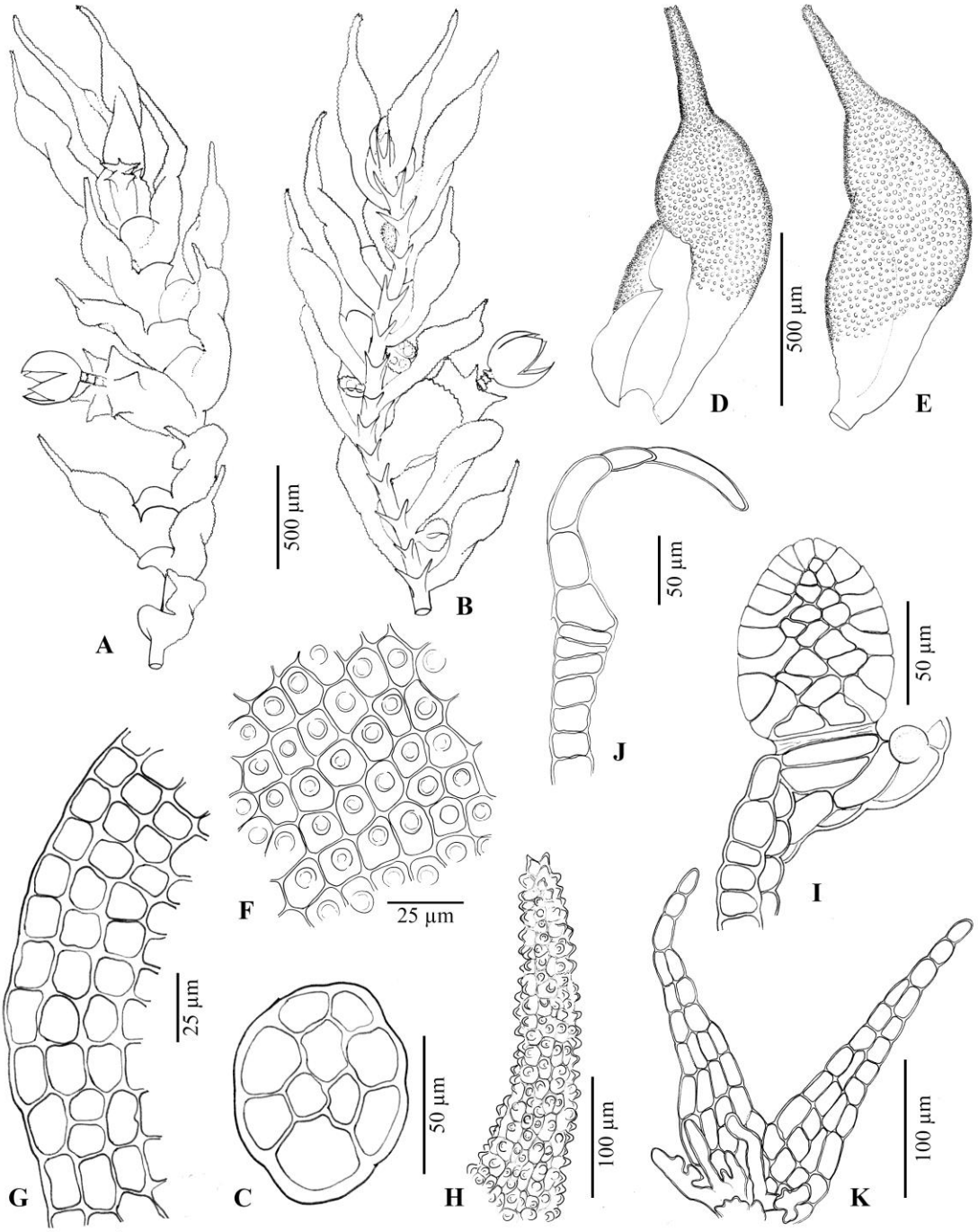

Fig. 4.35 *Colura junghuhniana* (Prantl) Steph.: A. Portion of plant with gynoecia, dorsal view. B. Portion of plant with androecia and gynoecium, ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I. Valve of lobule. J. Valve frame. K. Underleaf. All from *Zhu et al. 20160922-348* (HSNU).

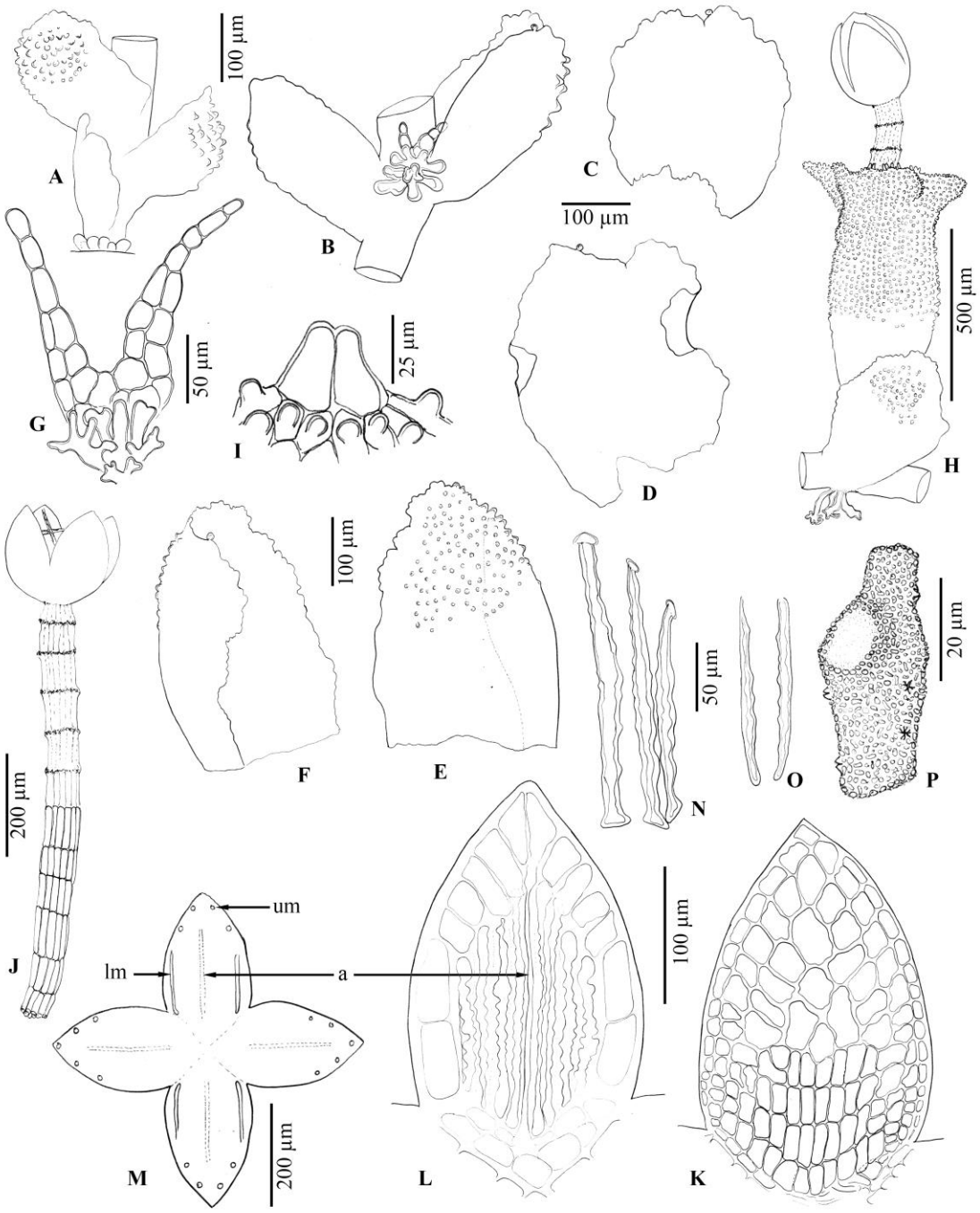

Fig. 4.36 *Colura junghuhniana* (Prantl) Steph.: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female smooth bracts, C. dorsal view, D. ventral view. E & F. Female papillose bracts, E. dorsal view, F. ventral view. G. Female bracteole. H. Perianth with sporophyte. I. Perianth beak. J. Mature sporophyte. K. Outer layer of capsule valve. L. Inner layer of capsule valve (a = additional elater). M. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). N. Upper marginal elaters. O. Lower marginal elaters. P. Spore. All from *Zhu et al. 20160922-348* (HSNU).

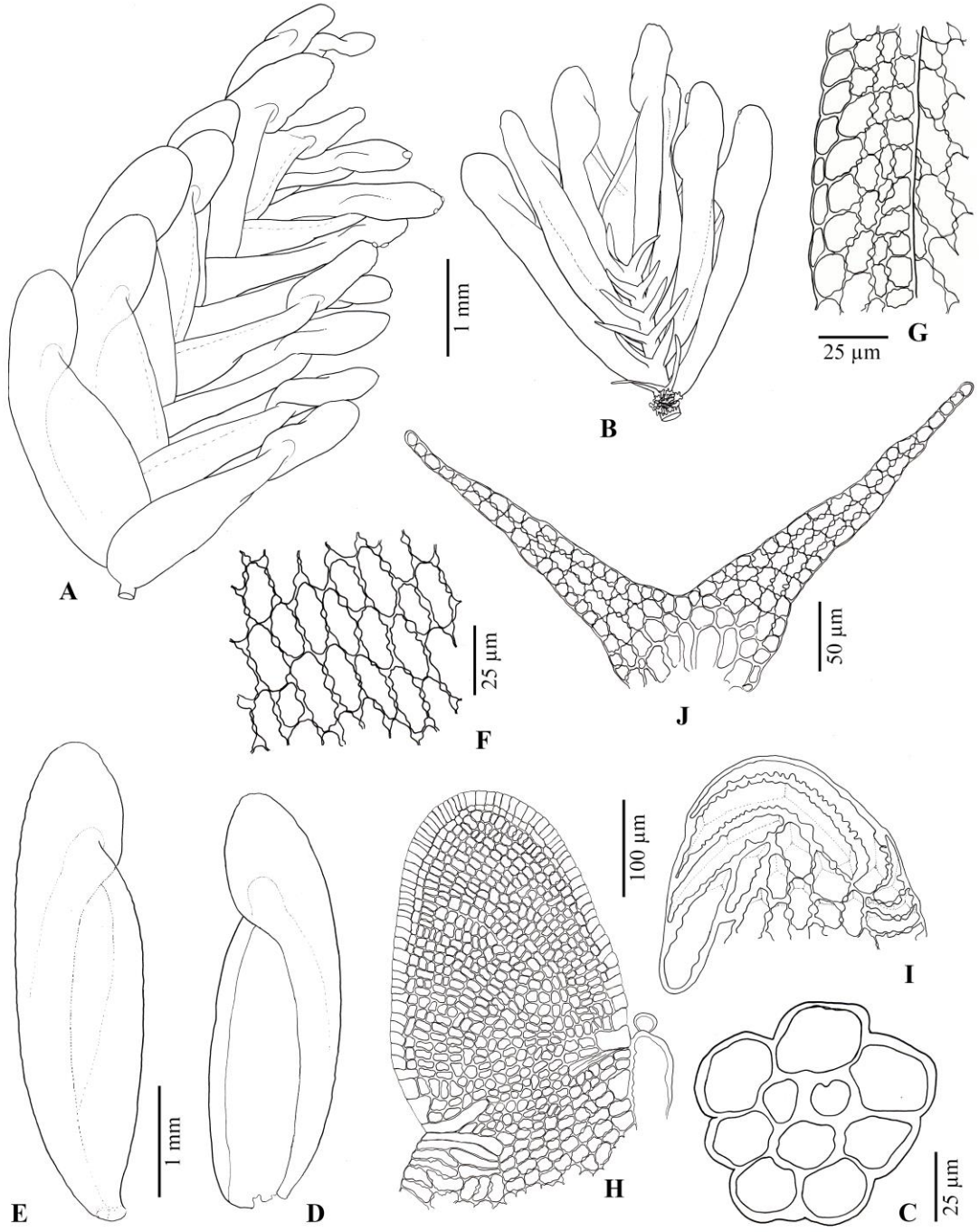

Fig. 4.37 *Colura karstenii* K.I.Goebel: A & B. Portions of plant, A. dorsal view, B. ventral view. C. Stem in transverse section. D &E. Lateral leaf, D. ventral view, E. dorsal view. F & G. Leaf lobe cells; F. median cell, G. marginal cell. H. Valve of lobule. I. Valve frame. J. Underleaf. All from *Sangrattanaprasert 116/14A* (PSU).

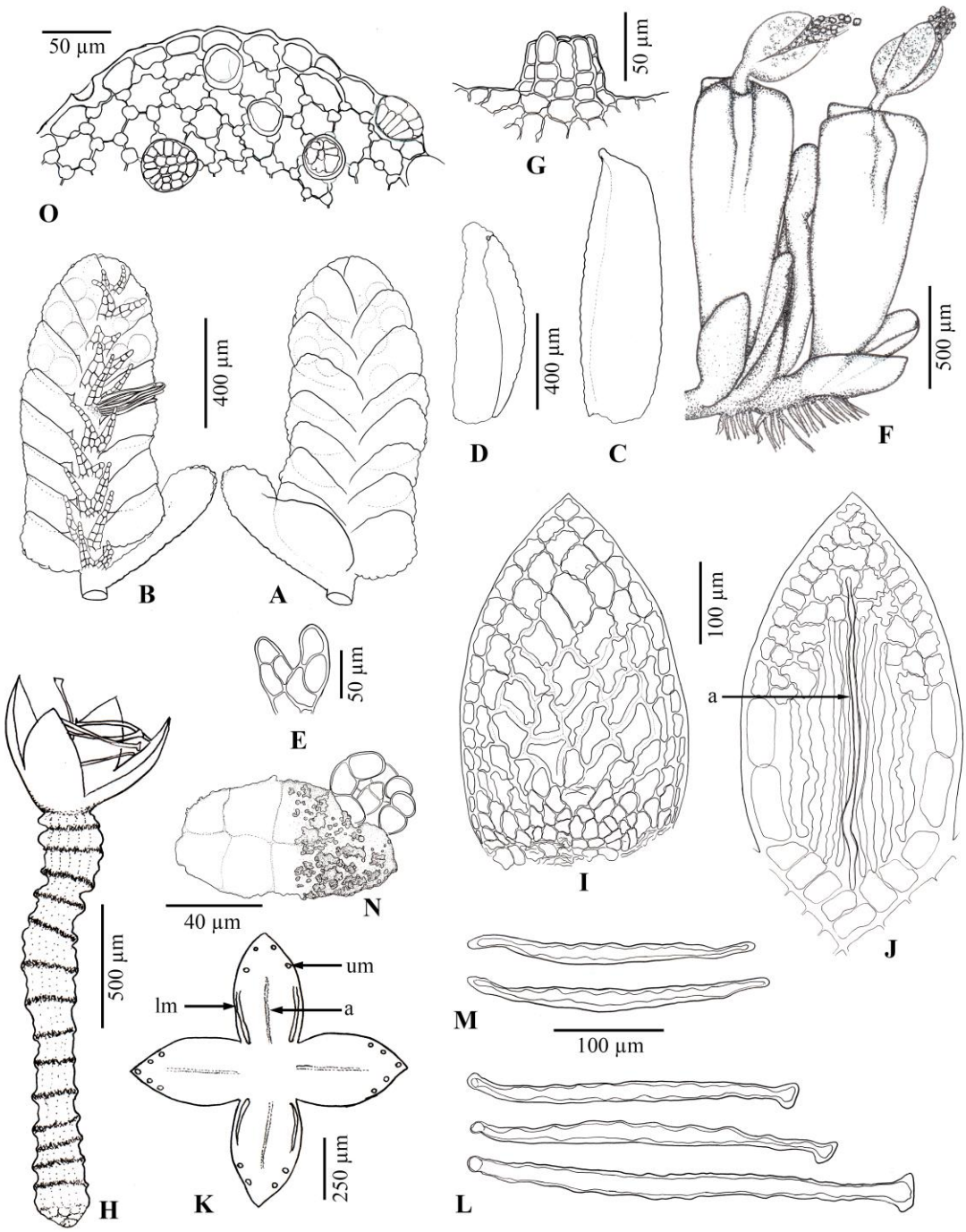

Fig. 4.38 *Colura karstenii* K.I.Goebel: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole; F. Perianths with sporophytes. G. Perianth beak. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Sporeling. O. Gemmae occurring on lobule sac surface. A & B from *Sukkharak & Seelanan 437* (BCU), C–O from *Sangrattanaprasert 116/14A* (PSU).

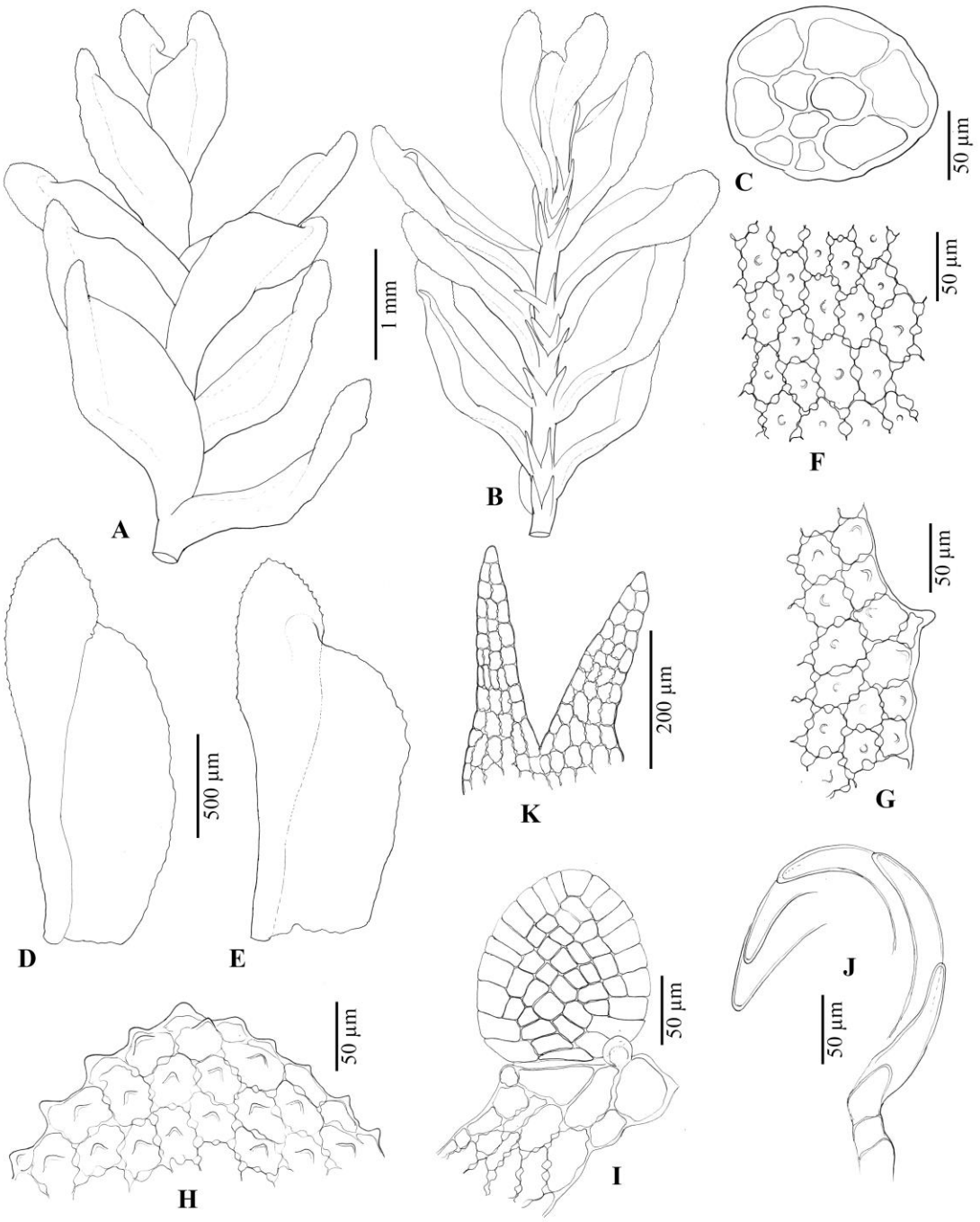

Fig. 4.39 *Colura maxima* Jovet-Ast: A & B. Portions of plant, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I. Valve of lobule. J. Valve frame. K. Underleaf. All from *Pleyte 252* (BO, holotype).

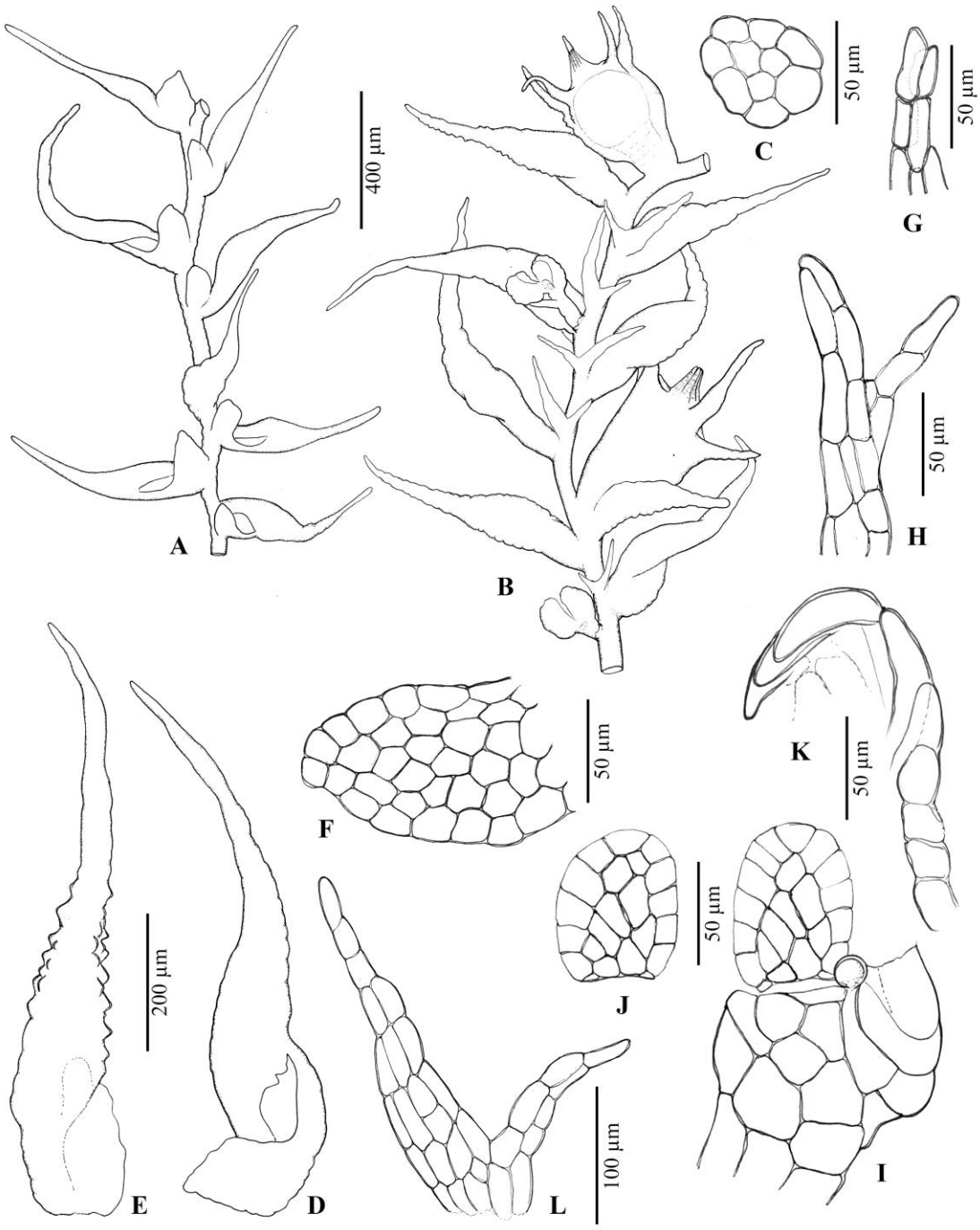

Fig. 4.40 *Colura medusa* J.Eggers *et* Pócs: A. Portion of plant, dorsal view. B. Portion of plant with androecia and gynoecia, ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F. Leaf lobe cells, showing median cells and marginal cells. G & H. Lobule sac apices, G. 1 peak, H. 2 peaks. I & J. Valves of lobule. K. Valve frame. L. Underleaf. A, C–L from *Sangrattanaprasert 398/15* (PSU); B. from *Sangrattanaprasert 177/14C* (PSU).

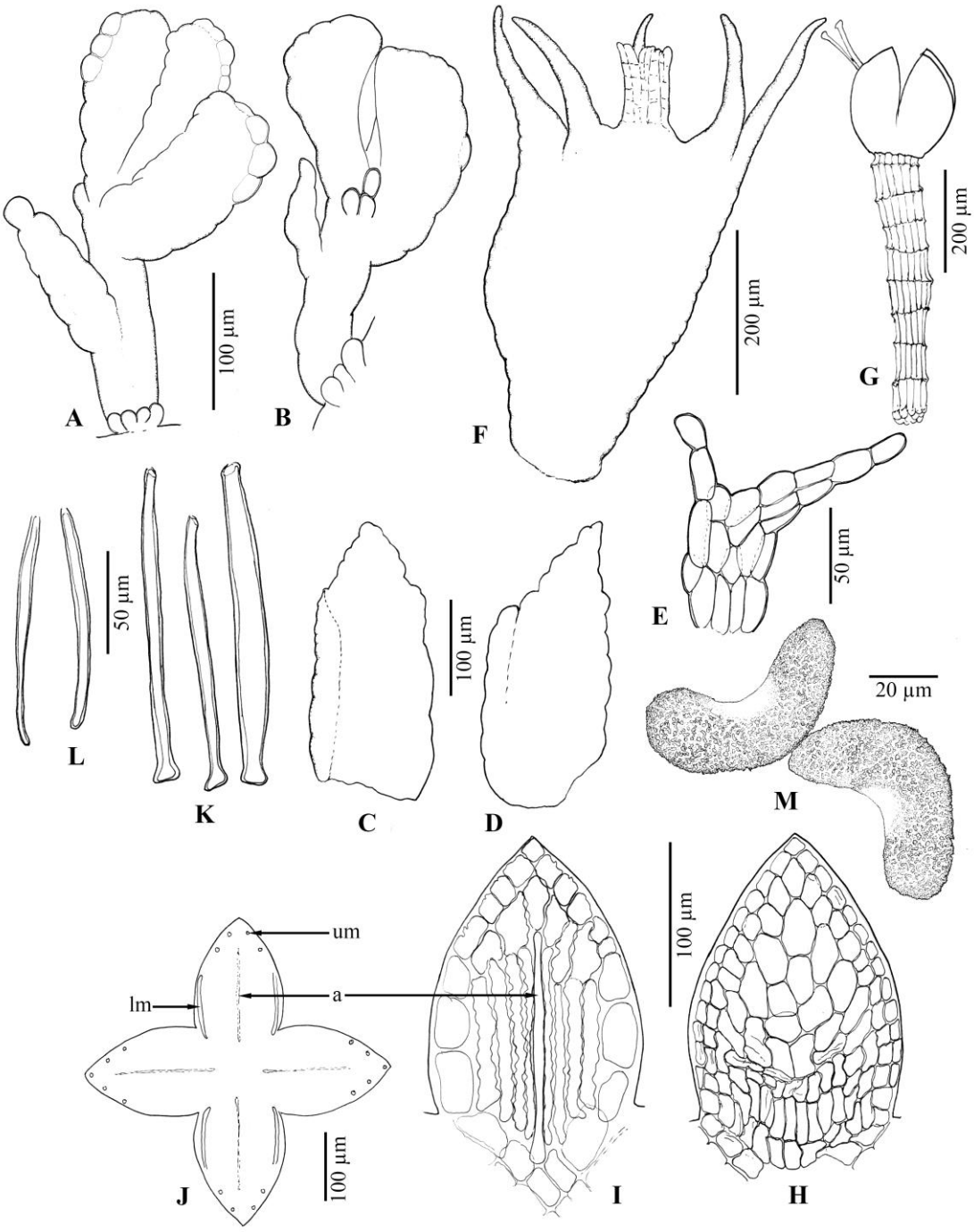

Fig. 4.41 *Colura medusa* J.Eggers *et* Pócs: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth. G. Mature sporophyte. H. Outer layer of capsule valve. I. Inner layer of capsule valve (a = additional elater). J. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). K. Upper marginal elaters. L. Lower marginal elaters. M. Spores. All from *Sangrattanaprasert 398/15* (PSU).

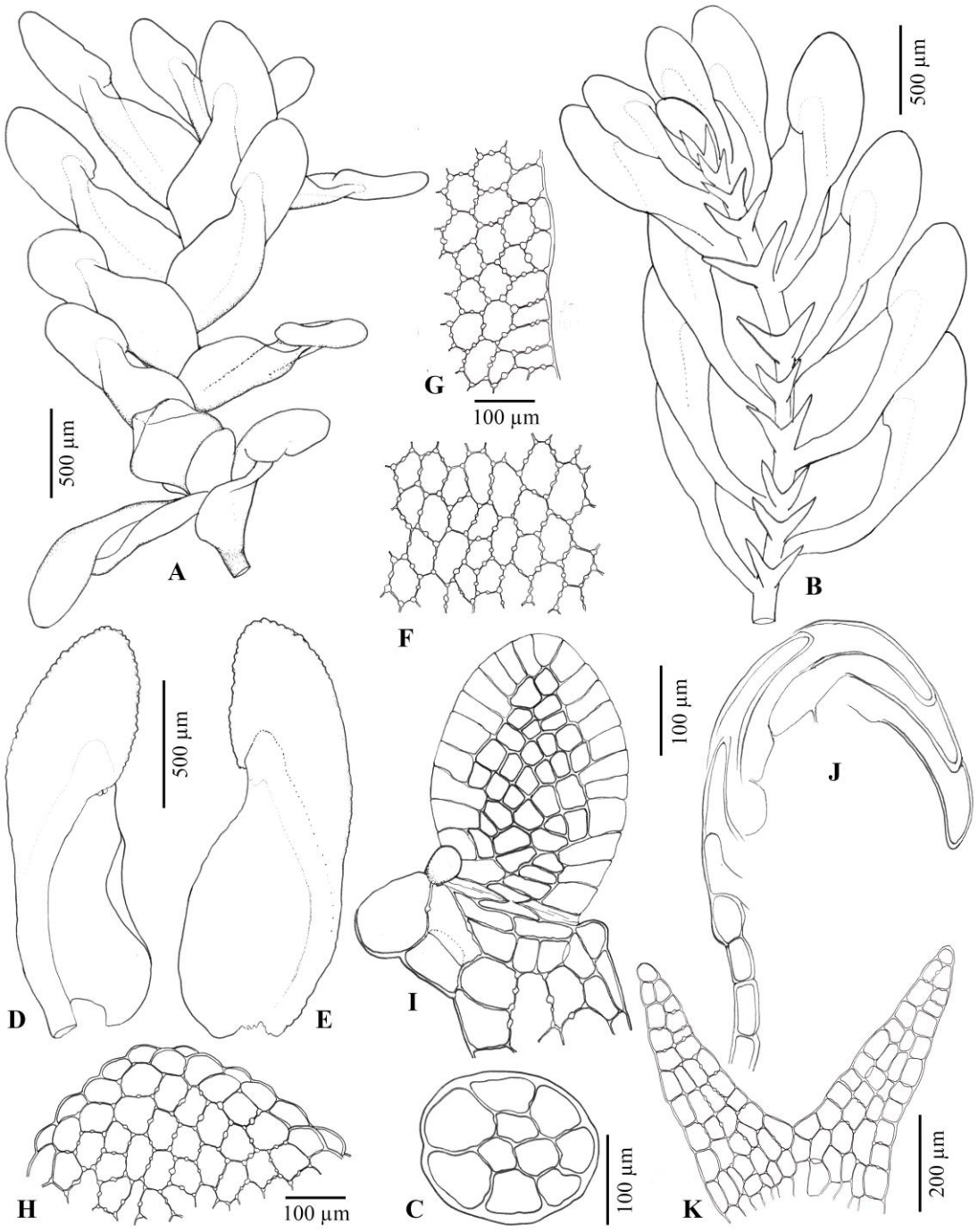

Fig. 4.42 *Colura meijeri* Jovet-Ast: A. Portion of plant with gynoecium, dorsal view. B. Portion of plant, ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I. Valve of lobule. J. Valve frame. K. Underleaf. All from *Sangrattanaprasert 26/13* (PSU).

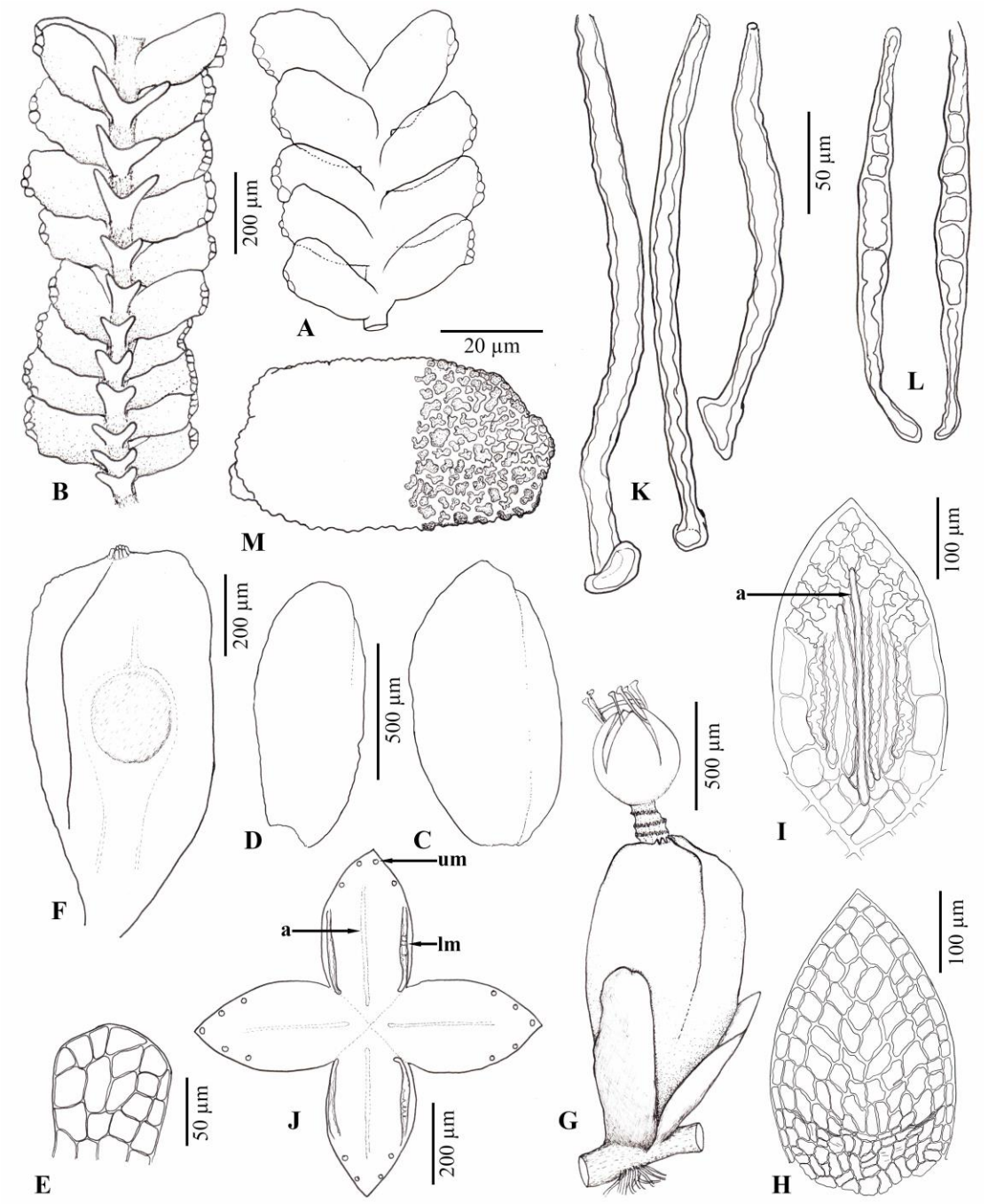

Fig. 4.43 *Colura meijeri* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth with young sporophyte. G. Mature sporophyte with gynoecium. H. Outer layer of capsule valve. I. Inner layer of capsule valve (a = additional elater). J. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). K. Upper marginal elaters. L. Lower marginal elaters. M. Spore. A–B, F–G. from *Sangrattanaprasert 26/13* (PSU), C–E, H–M. from *Sangrattanaprasert 337/15* (PSU).

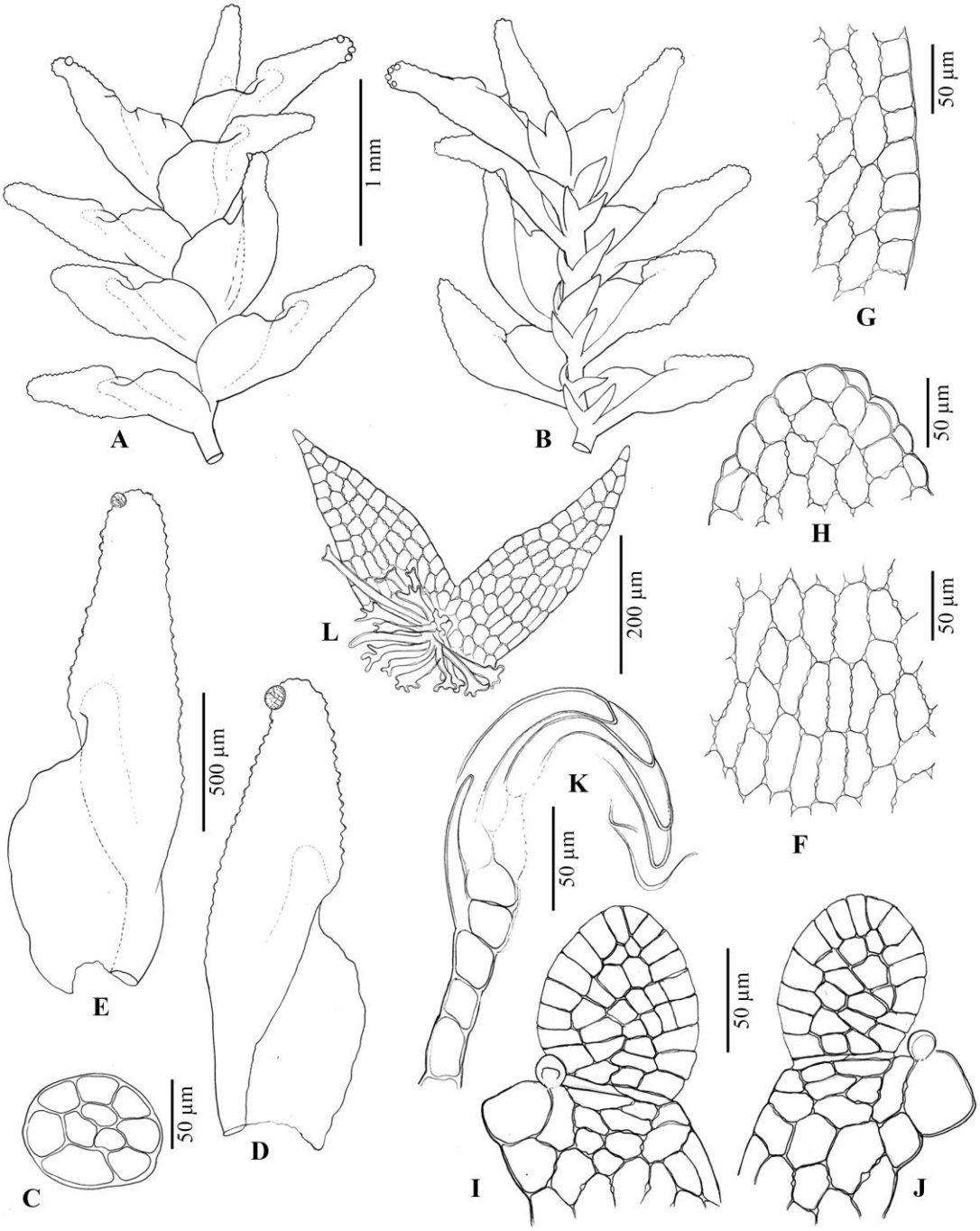

Fig. 4.44 *Colura mosenii* Steph.: A & B. Portions of plant, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I & J. Valves of lobule. K. Valve frame. L. Underleaf. All from *Pócs et al. 13183/C* (EGR).

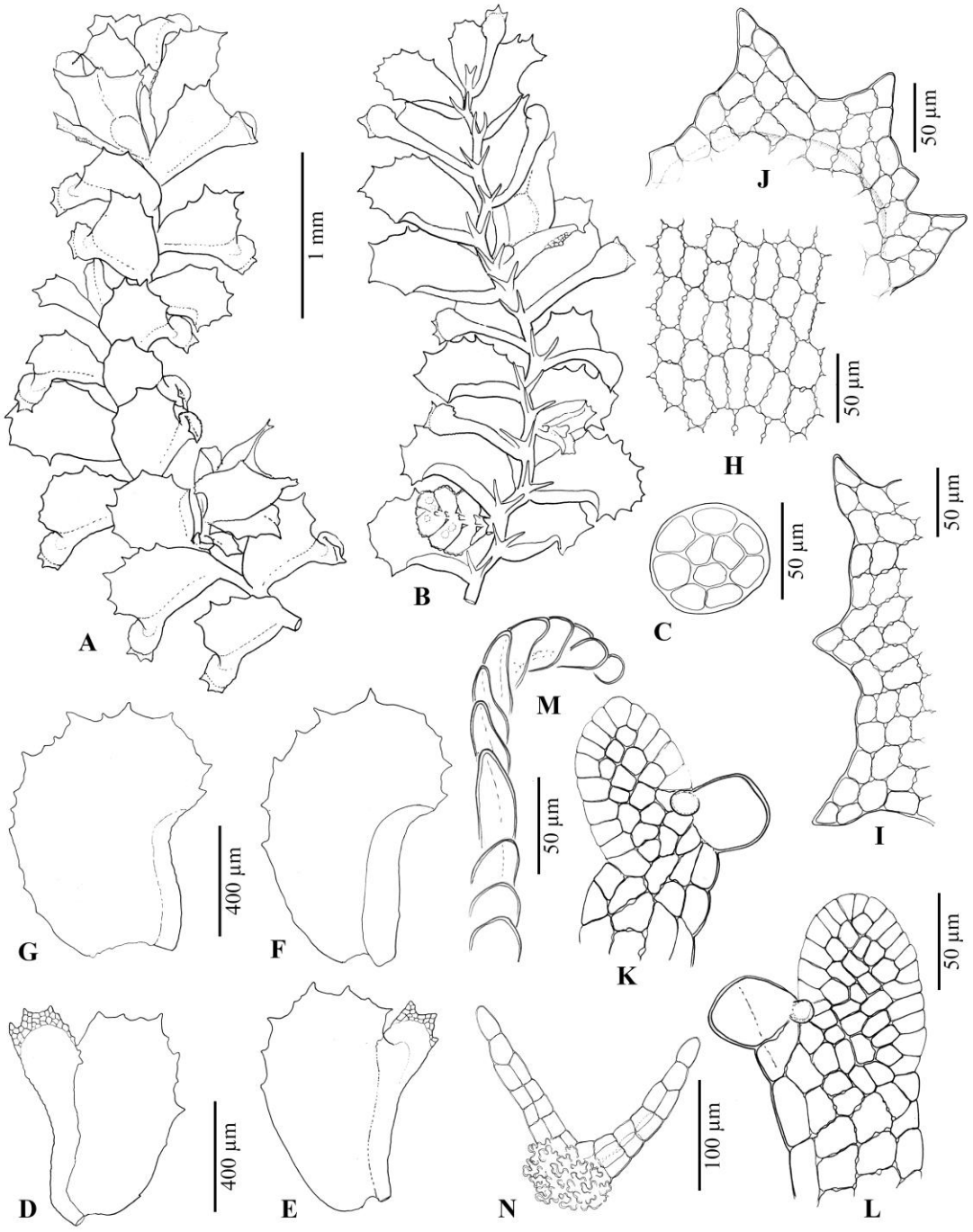

Fig. 4.45 *Colura ornata* K.I.Goebel: A & B. Portions of plant with androecia and gynoecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Lobule sac apex. K & L. Valves of lobule. M. Valve frame. N. Underleaf. All from *Pócs et al. 1217/AF* (EGR).

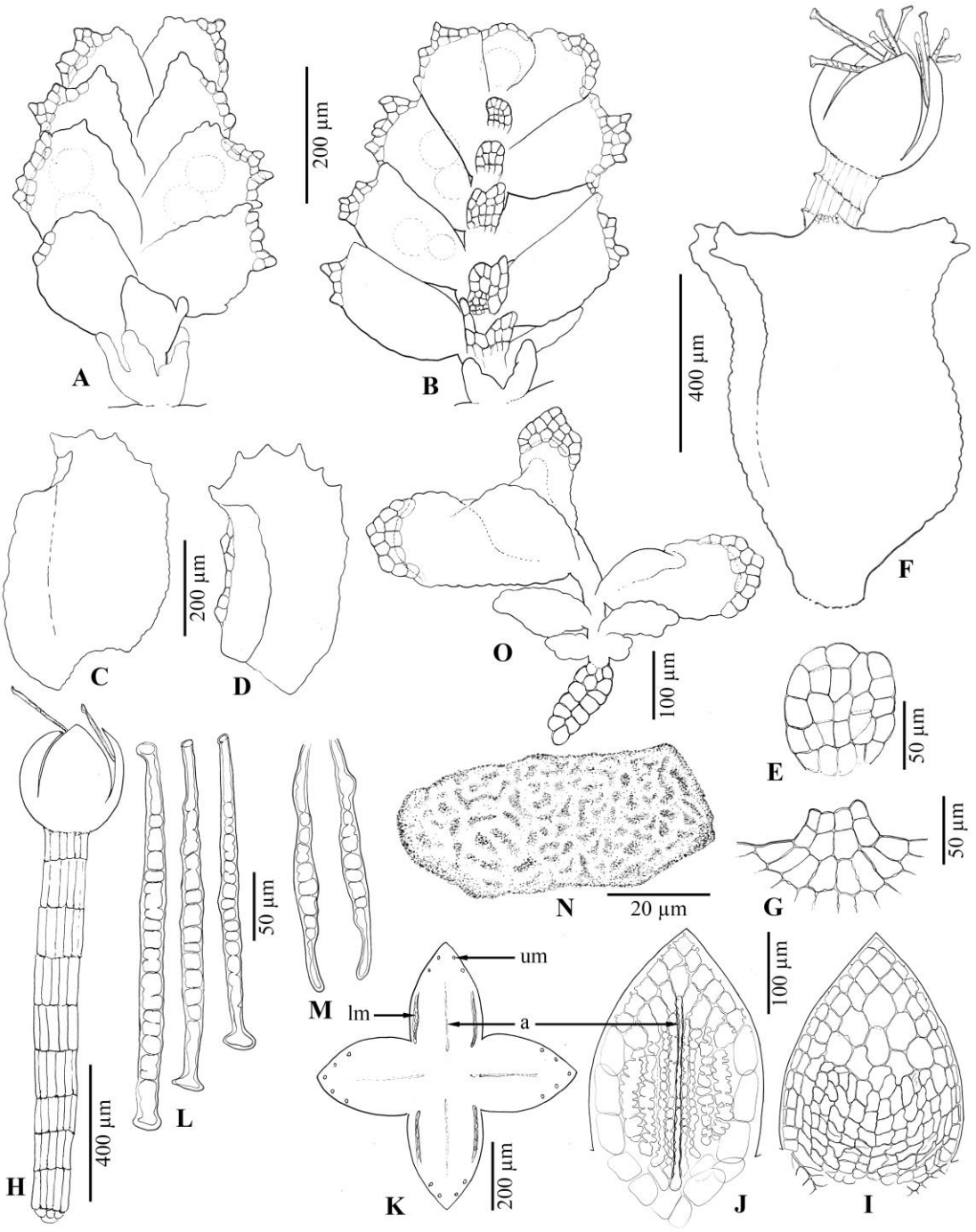

Fig. 4.46 *Colura ornata* K.I.Goebel: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth with sporophyte. G. Perianth beak. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. O. Sporeling. All from *Pócs et al. 1217/AF* (EGR).

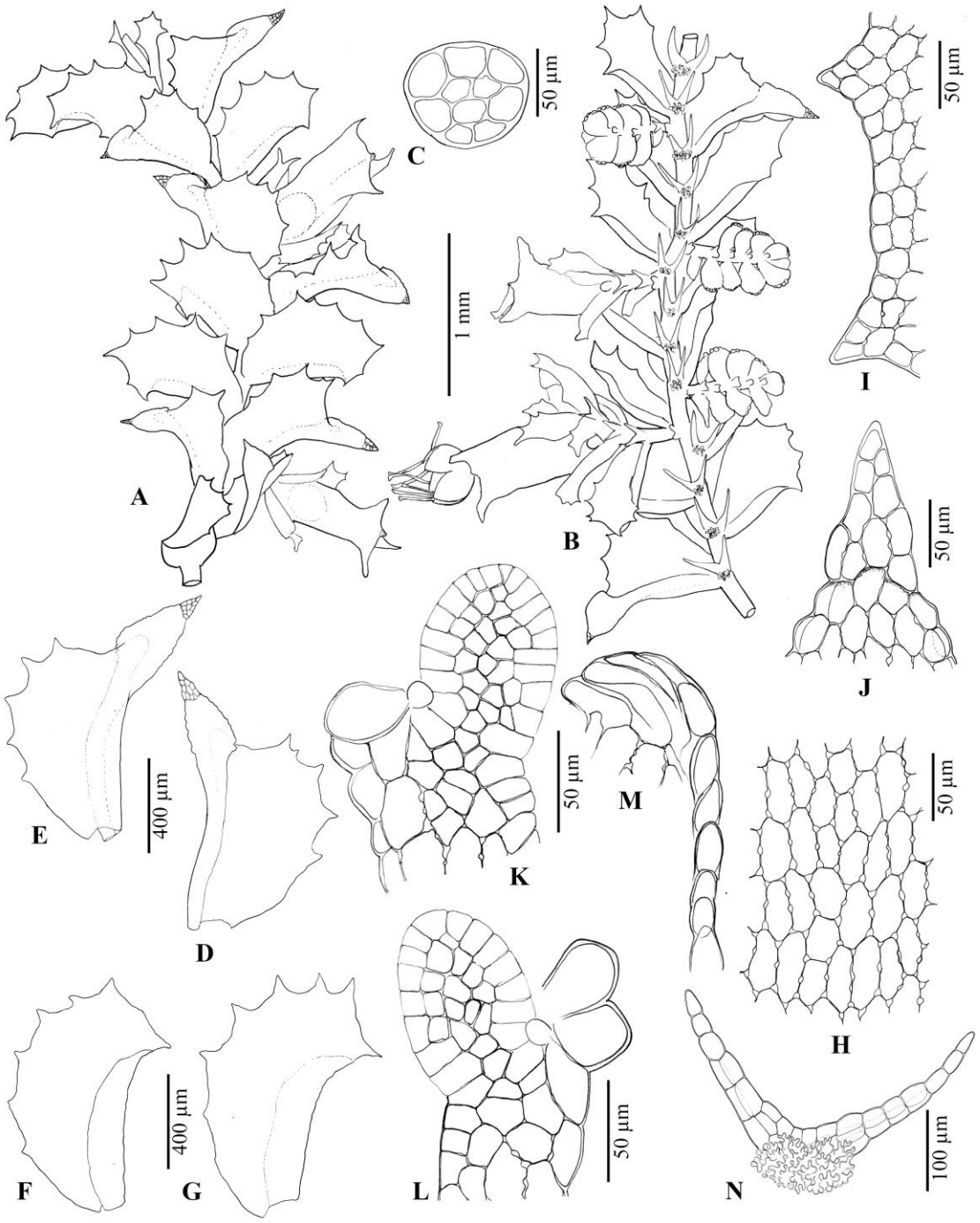

Fig. 4.47 *Colura palawanensis* Jovet-Ast: A & B. Portions of plant with androecia and gynoecia, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Lobule sac apex. K & L. Valves of lobule. M. Valve frame. N. Underleaf. All from *Elmer 12665* (L, isotype).

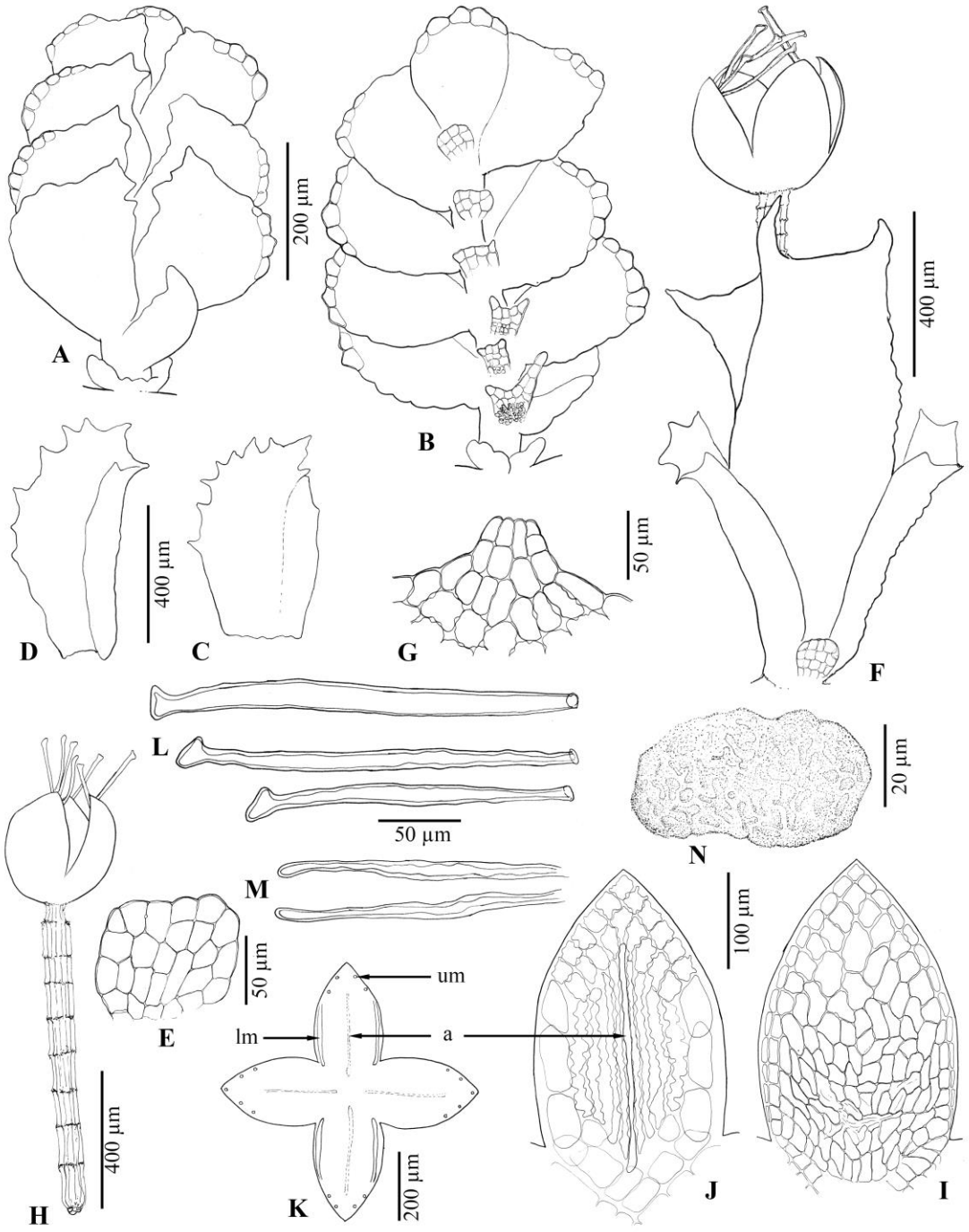

Fig. 4.48 *Colura palawanensis* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth with bract and bracteole. G. Perianth beak. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. All from *Elmer 12665* (L, isotype).

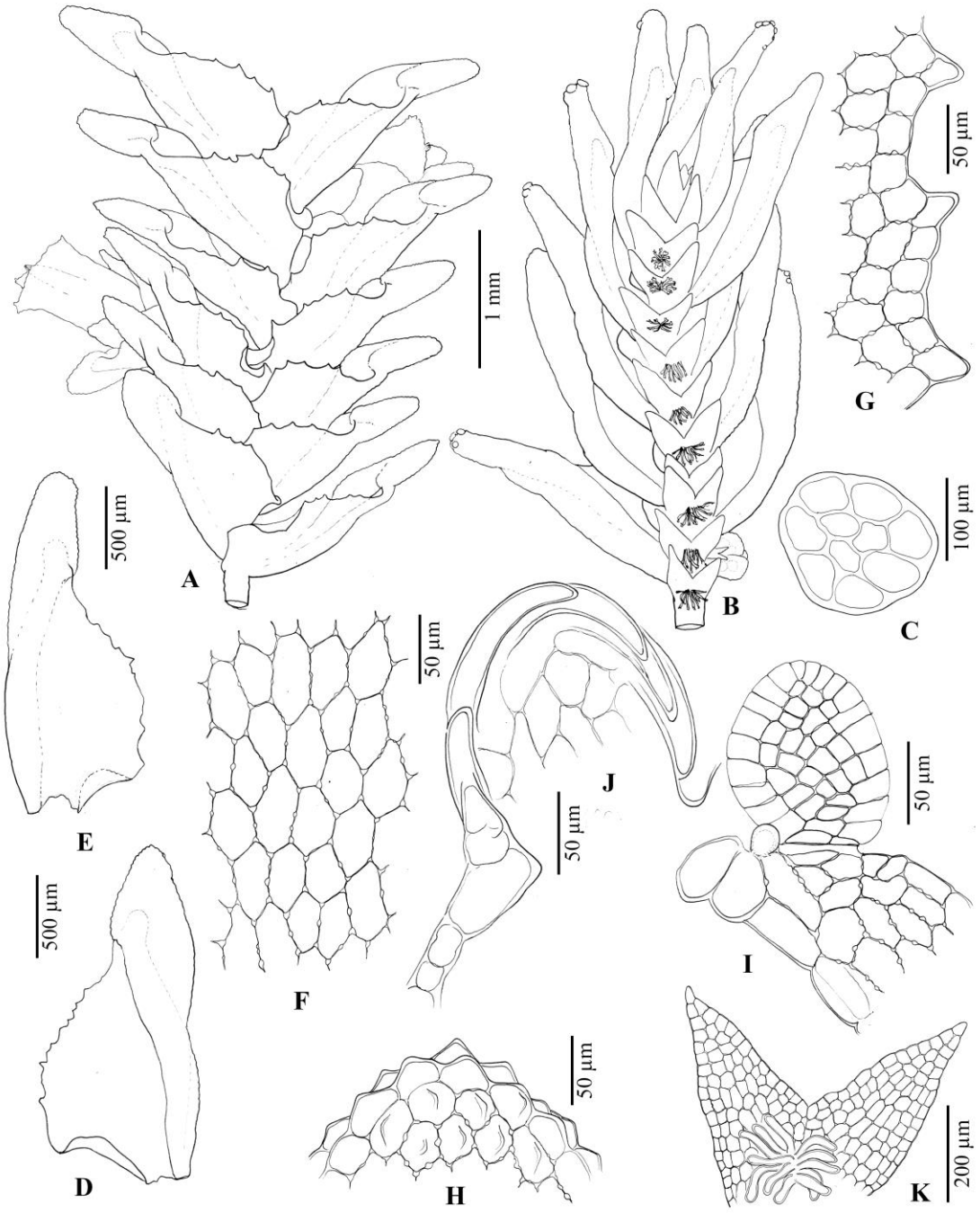

Fig. 4.49 *Colura pallida* Steph.: A. Portion of plant with gynoecia, dorsal view. B. Portion of plant with androecia, ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I. Valve of lobule. J. Valve frame. K. Underleaf. All from *Sangrattanaprasert 479/16* (PSU).

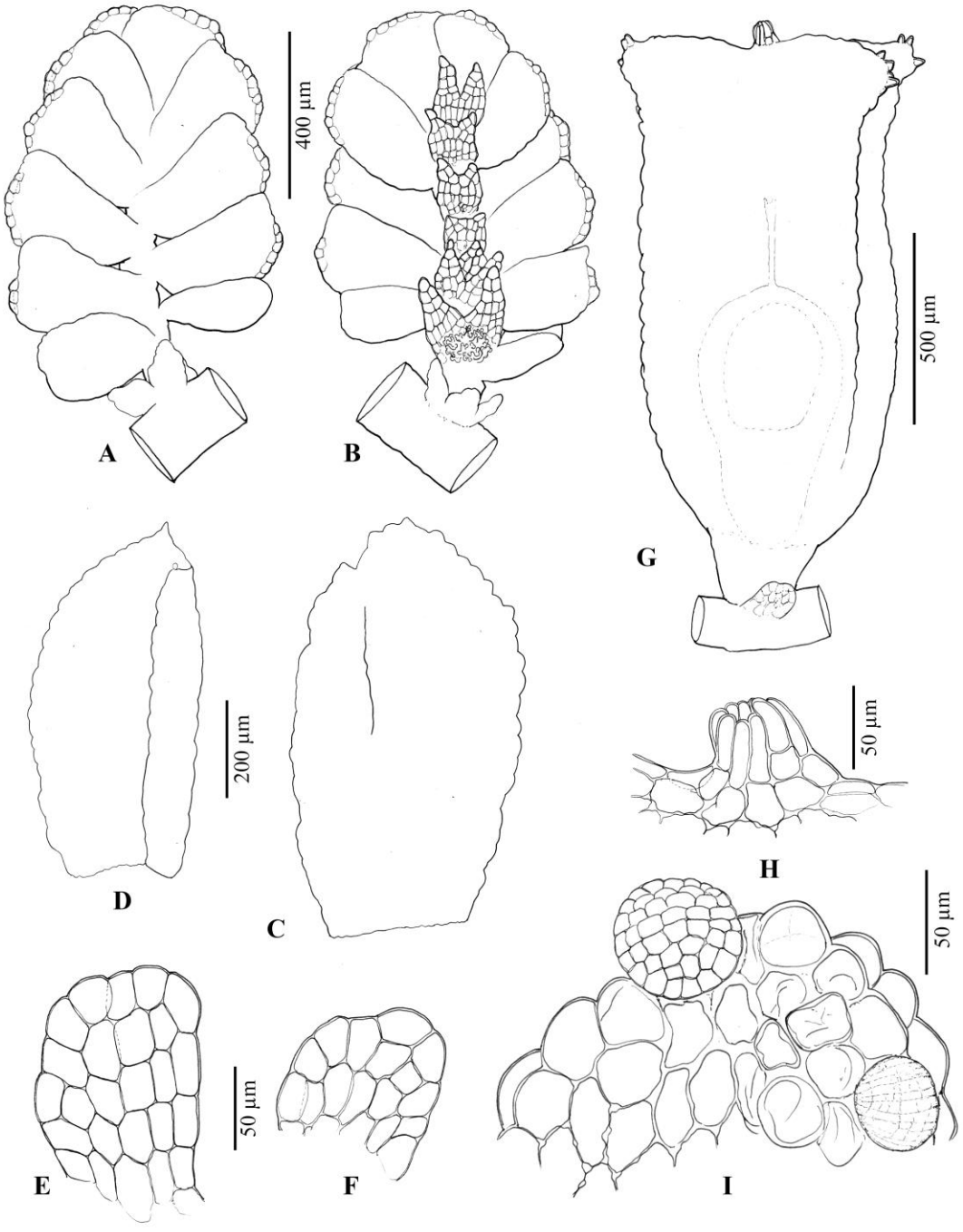

Fig. 4.50 *Colura pallida* Steph.: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E & F. Female bracteoles. G. Perianth. H. Perianth beak. I. Gemmae occurring on lobule sac apex. All from *Sangrattanaprasert 479/16* (PSU).

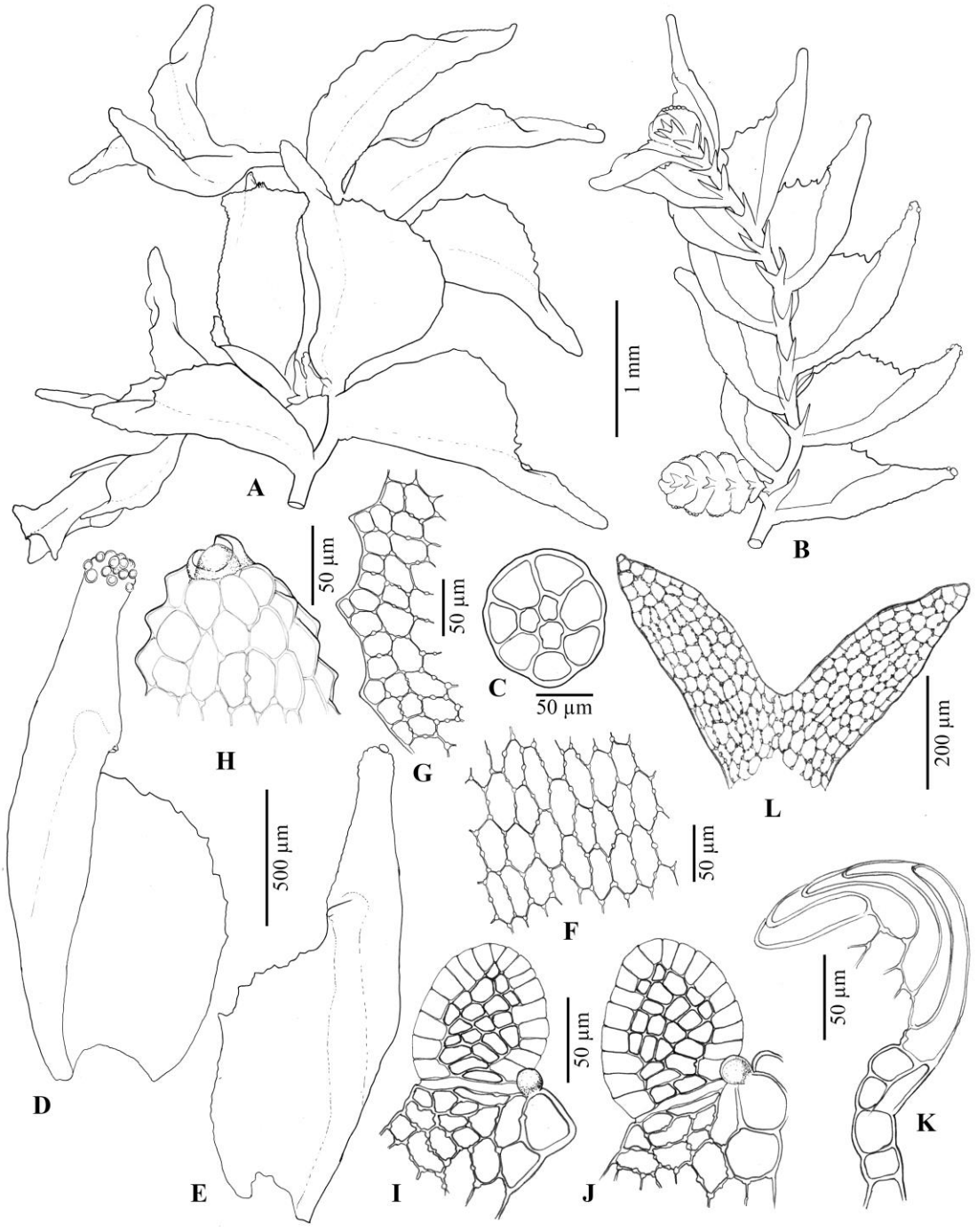

Fig. 4.51 *Colura pluridentata* Jovet-Ast: A. Portion of plant with gynoecia, dorsal view. B. Portion of plant with androecia, ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I & J. Valves of lobule, I. valve with 1 basal median cell, J. valve with 2 basal median cells. K. Valve frame. L. Underleaf. A & B. from *Sangrattanaprasert 255/14D* (PSU), C–L. from *Sangrattanaprasert 452/16* (PSU).

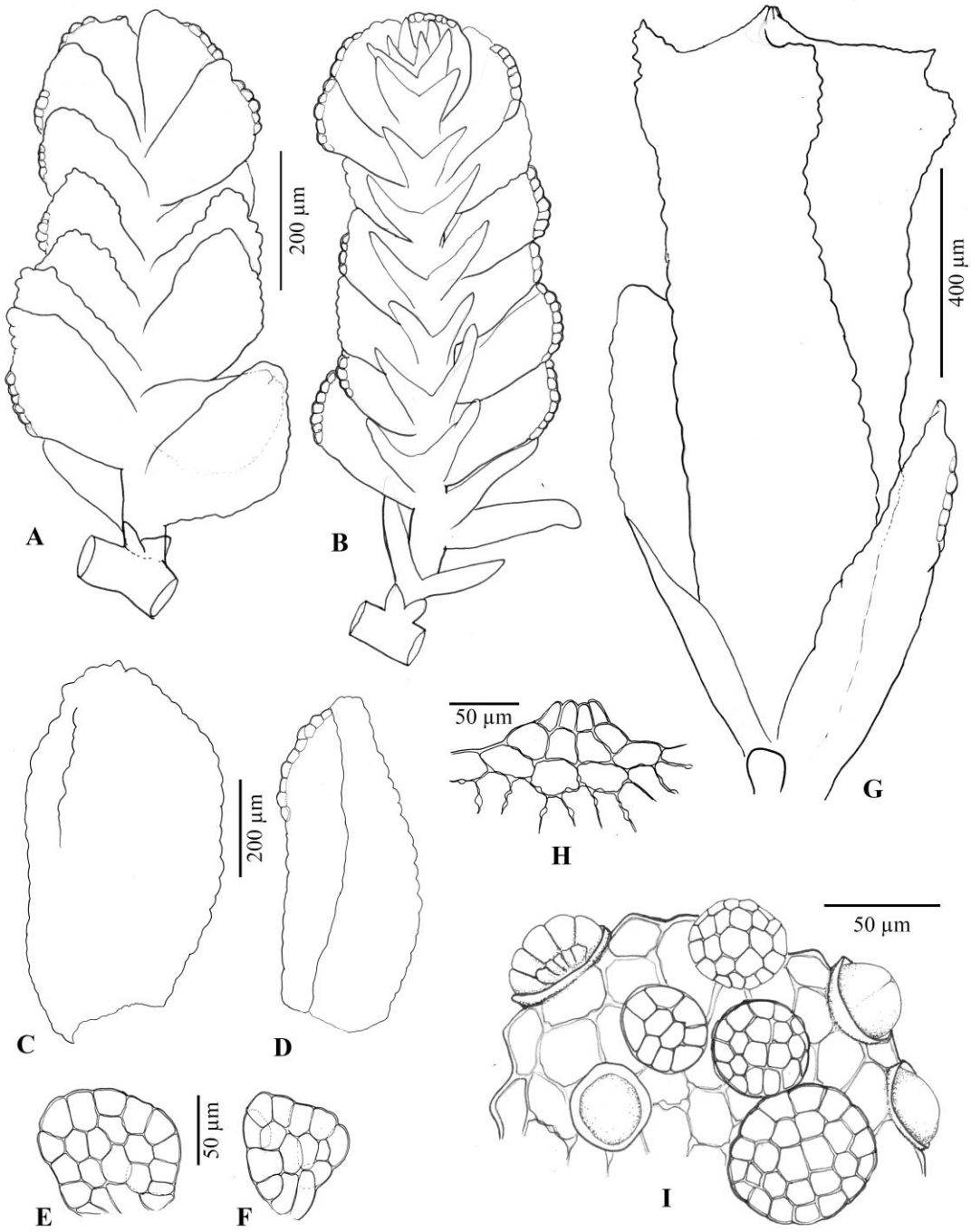

Fig. 4.52 *Colura pluridentata* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E & F. Female bracteoles. G. Perianth with female bracts and bracteole. H. Perianth beak. I. Gemmae occurring on lobule sac apex. A–H from *Sangrattanaprasert 255/14D* (PSU), I from *Sangrattanaprasert 452/16* (PSU).

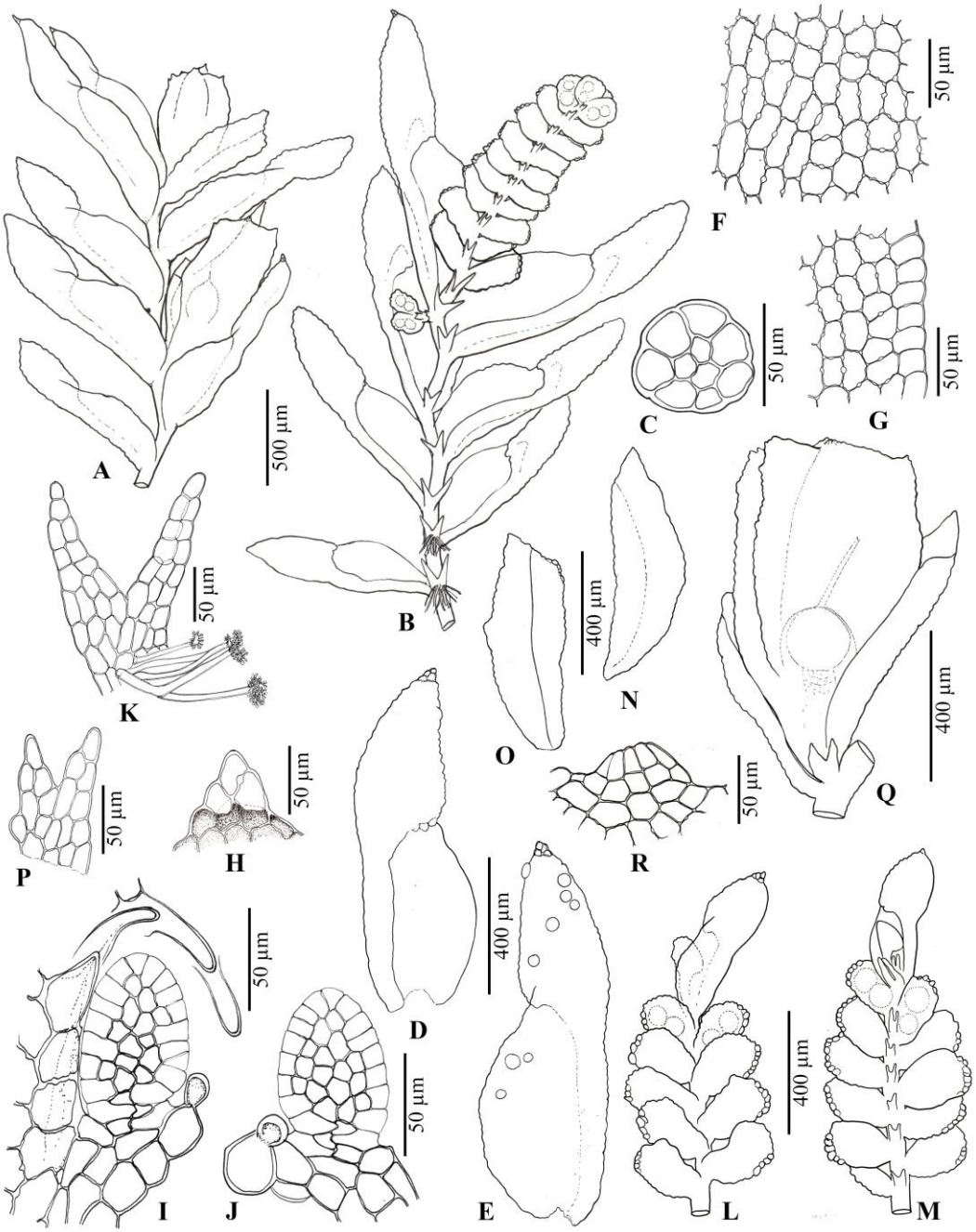

Fig. 4.53 *Colura sigmoidea* Sangratt., Chantanaorr. *et* R.L.Zhu: A. Portion of plant with gynoecia, dorsal view. B. Portion of plant with androecia, ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view with gemmae. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex with apical crest. I. Valve of lobule attracted to valve frame. J. Valve of lobule. K. Underleaf. L & M. Androecia, L. dorsal view, M. ventral view. N & O. Female bracts, N. dorsal view, O. ventral view. P. Female bracteole. Q. Perianth with bracts and bracteole. R. Perianth beak. A–B, N–R from *Sangrattanaprasert 263/15C* (PSU), C–K from *Sangrattanaprasert 105/14* (PSU), L–M from *Sangrattanaprasert 83/14E* (PSU).

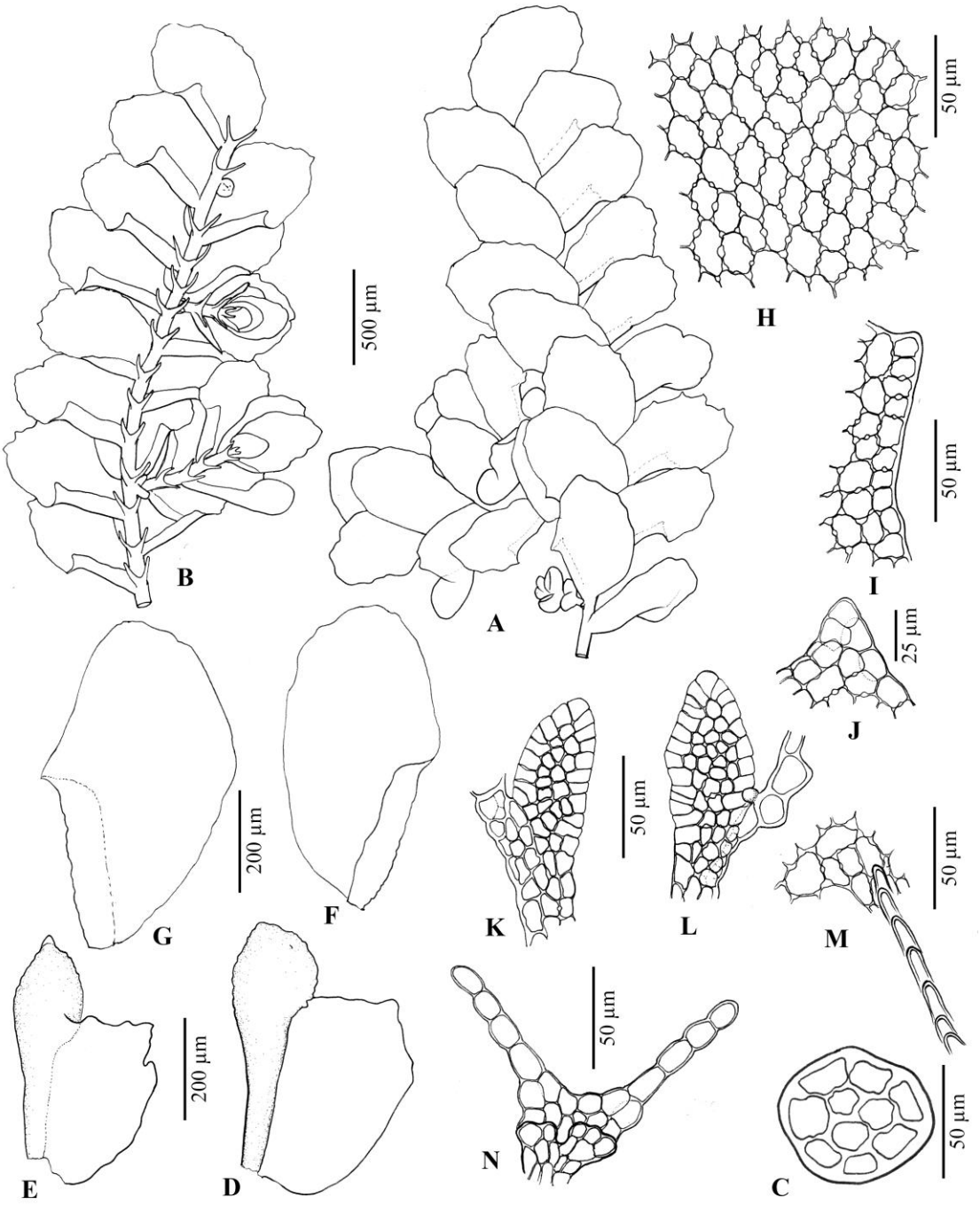

Fig. 4.54 *Colura speciosa* Jovet-Ast: A & B. Portions of plant with androecium, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Saccate leaves, D. ventral view, E. dorsal view. F & G. Non-saccate leaves, F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Lobule sac apex. K & L. Valves of lobule. M. Valve frame. N. Underleaf. All from *Sangrattanaprasert 300/15E* (PSU).

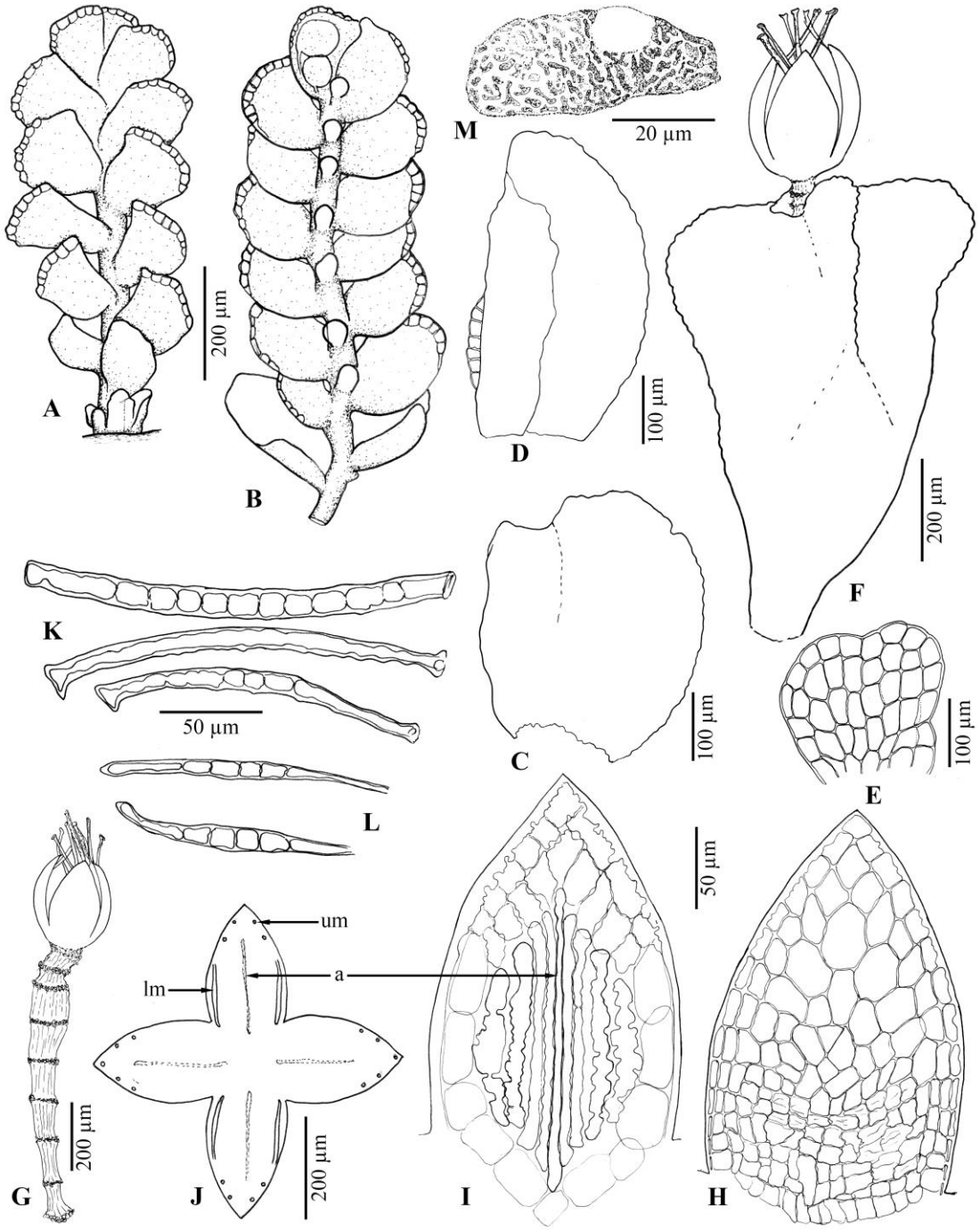

Fig. 4.55 *Colura speciosa* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth with sporophyte. G. Mature sporophyte. H. Outer layer of capsule valve. I. Inner layer of capsule valve (a = additional elater). J. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). K. Upper marginal elaters. L. Lower marginal elaters. M. Spore. All from *Sangrattanaprasert 300/15E* (PSU).

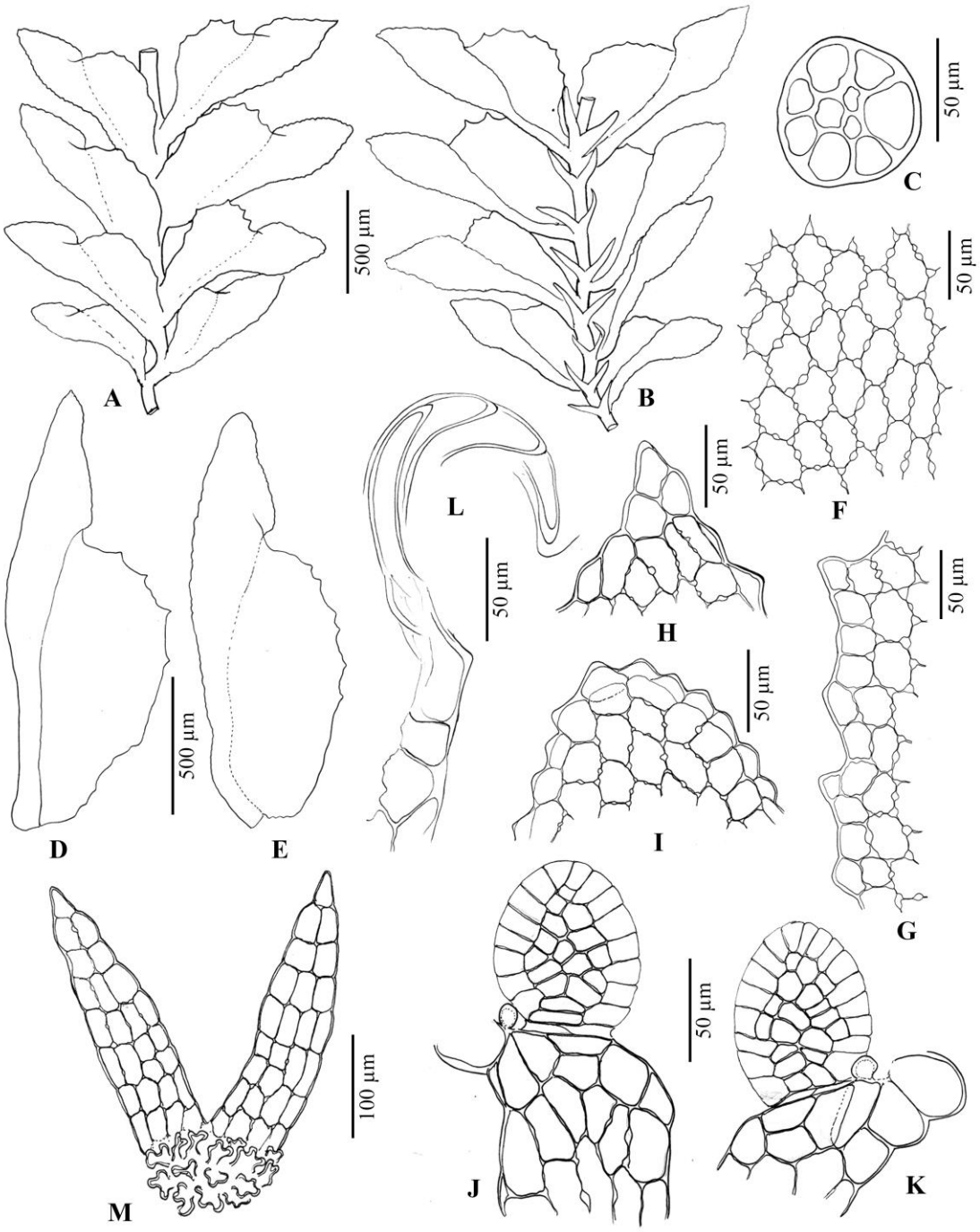

Fig. 4.56 *Colura superba* (Mont.) Steph.: A & B. Portions of plant, A. dorsal view, B. ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H & I. Lobule sac apices, H. lobule sac with apical crest, I. lobule sac entire. J & K. Valves of lobule. L. Valve frame. M. Underleaf. All from *Hoogerwerf 238a* (L).

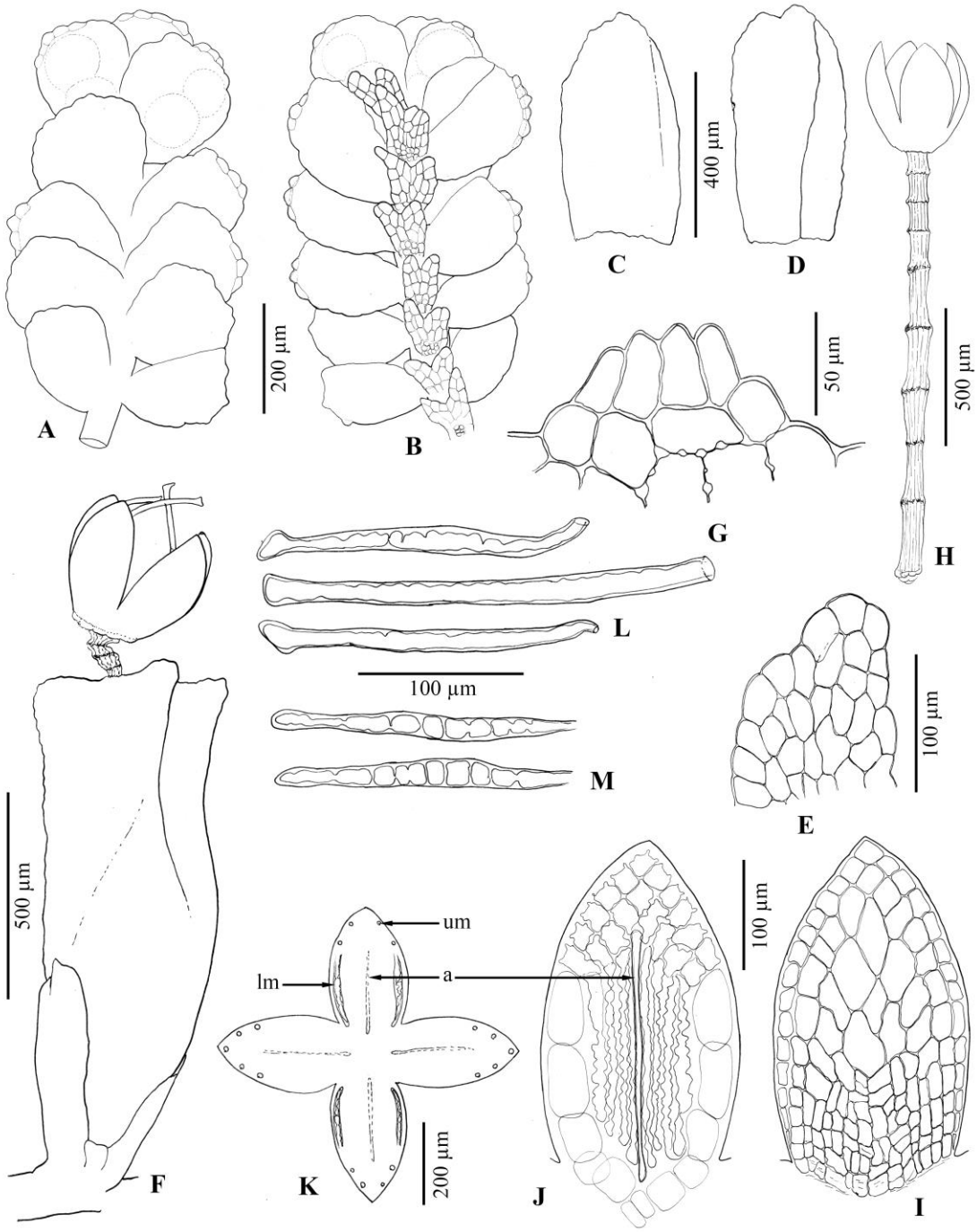

Fig. 4.57 *Colura superba* (Mont.) Steph.: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth. G. Perianth beak H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. All from *Hoogerwerf 238a* (L).

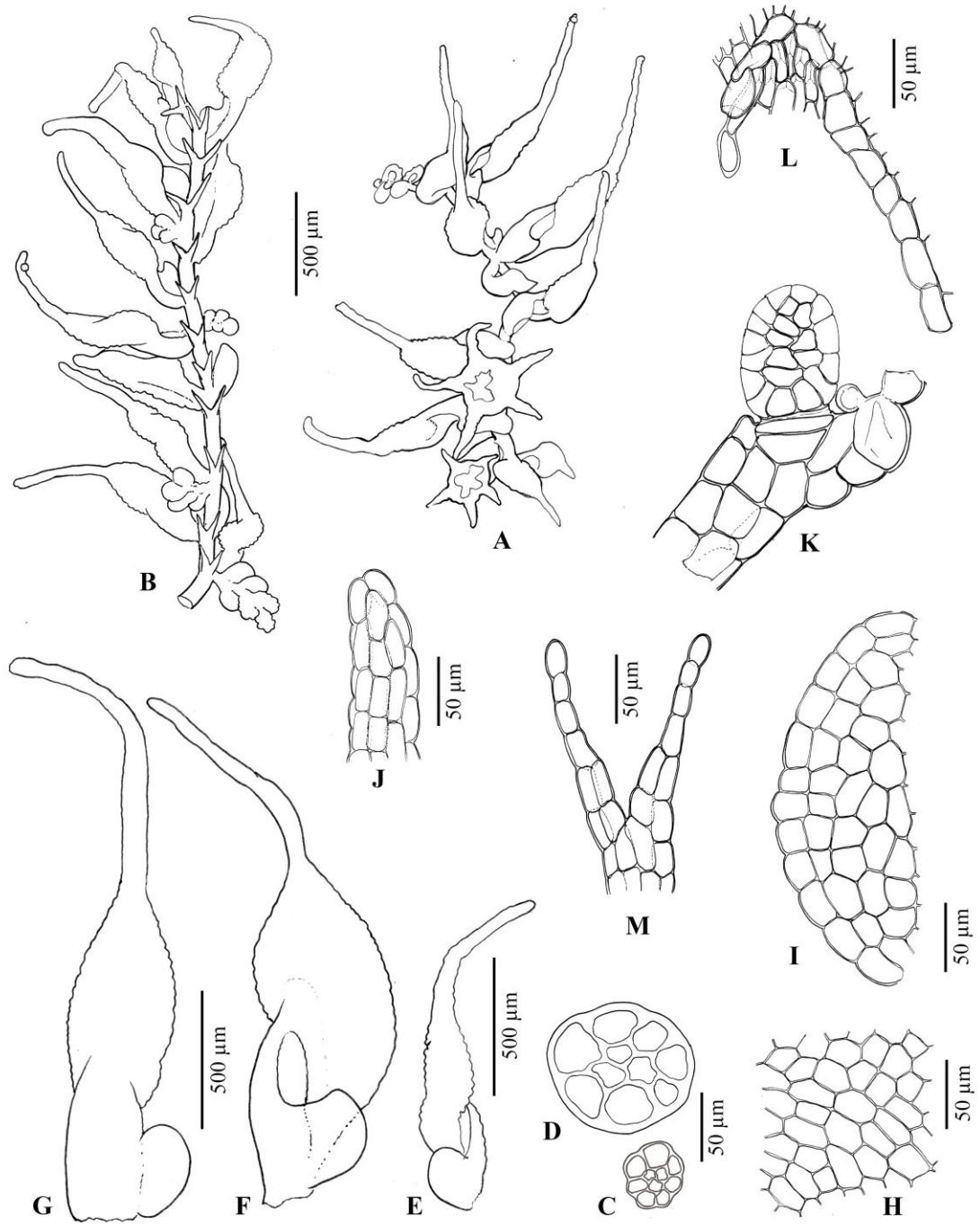

Fig. 4.58 *Colura tenuicornis* (A.Evans) Steph.: A. Portion of plant with androecia and gynoecia, dorsal view. B. Portion of plant with androecia, ventral view. C & D. Stems in transverse section. E–G. Lateral leaves, E & F. ventral view, G. dorsal view. H & I. Leaf lobe cells, H. median cells, I. marginal cells. J. Lobule sac apex. K. Valve of lobule. L. Valve frame. M. Underleaf. A–C, E, K–M. from *Chantanaorrapint & Suwanmala 2094A* (PSU), D, F–J. from *Chantanaorrapint & Suwanmala 2001* (PSU).

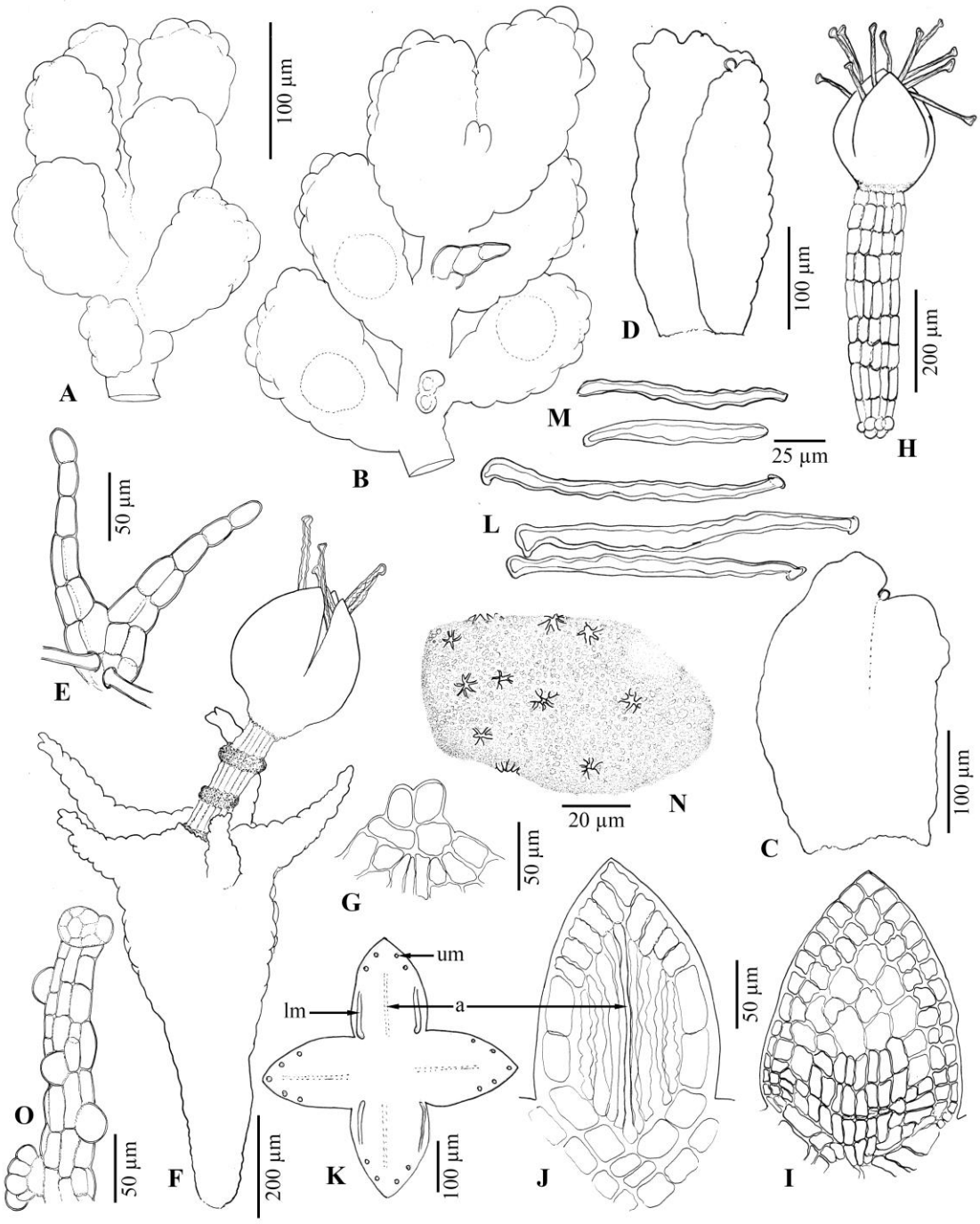

Fig. 4.59 *Colura tenuicornis* (A.Evans) Steph.: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bract, C. dorsal view, D. ventral view. E. Female bracteole. F. Perianth with sporophyte. G. Perianth beak. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. O. Gemmae on lobule sac apex. A–F, H–M, O. from *Chantanaorrapint & Suwanmala 2094A* (PSU), G, N from *Chantanaorrapint & Suwanmala 2001* (PSU).

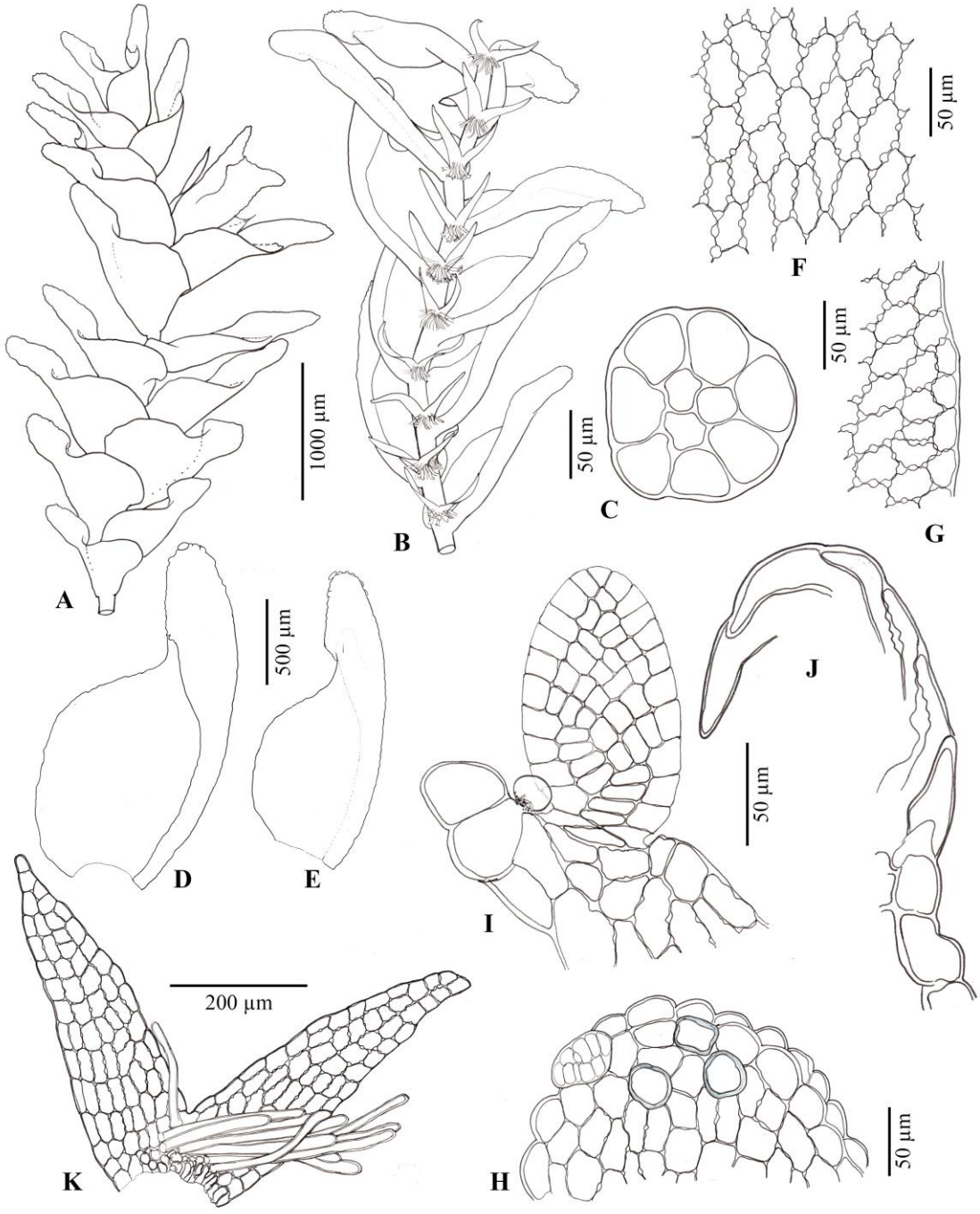

Fig. 4.60 *Colura valida* Jovet-Ast: A. Portion of plant with gynoecium, dorsal view. B. Portion of plant, ventral view. C. Stem in transverse section. D & E. Lateral leaves, D. ventral view, E. dorsal view. F & G. Leaf lobe cells, F. median cells, G. marginal cells. H. Lobule sac apex. I. Valve of lobule. J. Valve frame. K. Underleaf. A, F–G. from *Sangrattanaprasert 13/13* (PSU), B–E, H–K. from *Sangrattanaprasert 326/15* (PSU).

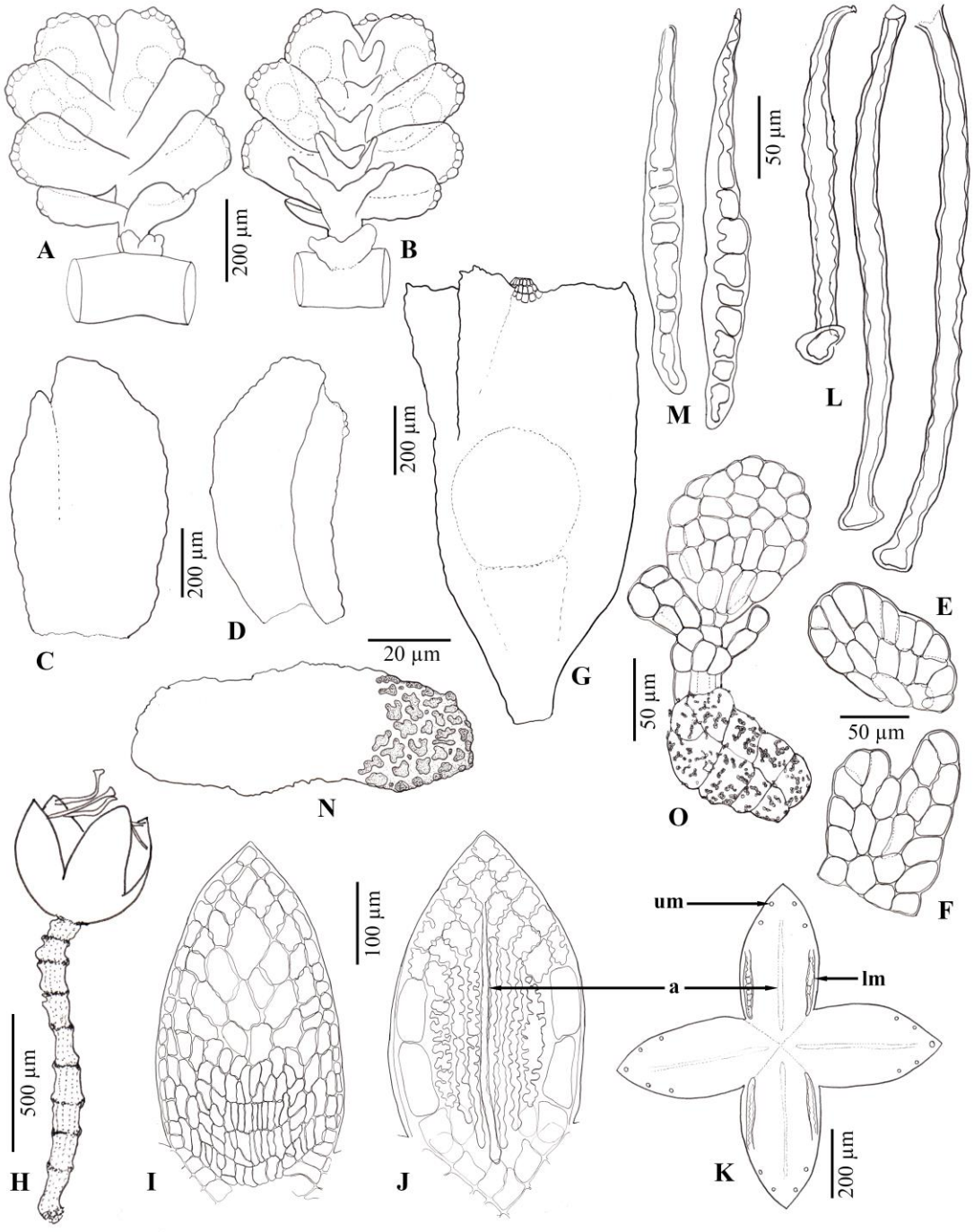

Fig. 4.61 *Colura valida* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E & F. Female bracteoles. G. Perianth with young sporophyte. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. O. Sporeling. A & B. from *Sangrattanaprasert 326/15* (PSU), C–F. from *Sangrattanaprasert 13/13* (PSU), G–O. from *Sangrattanaprasert 21/13B* (PSU).

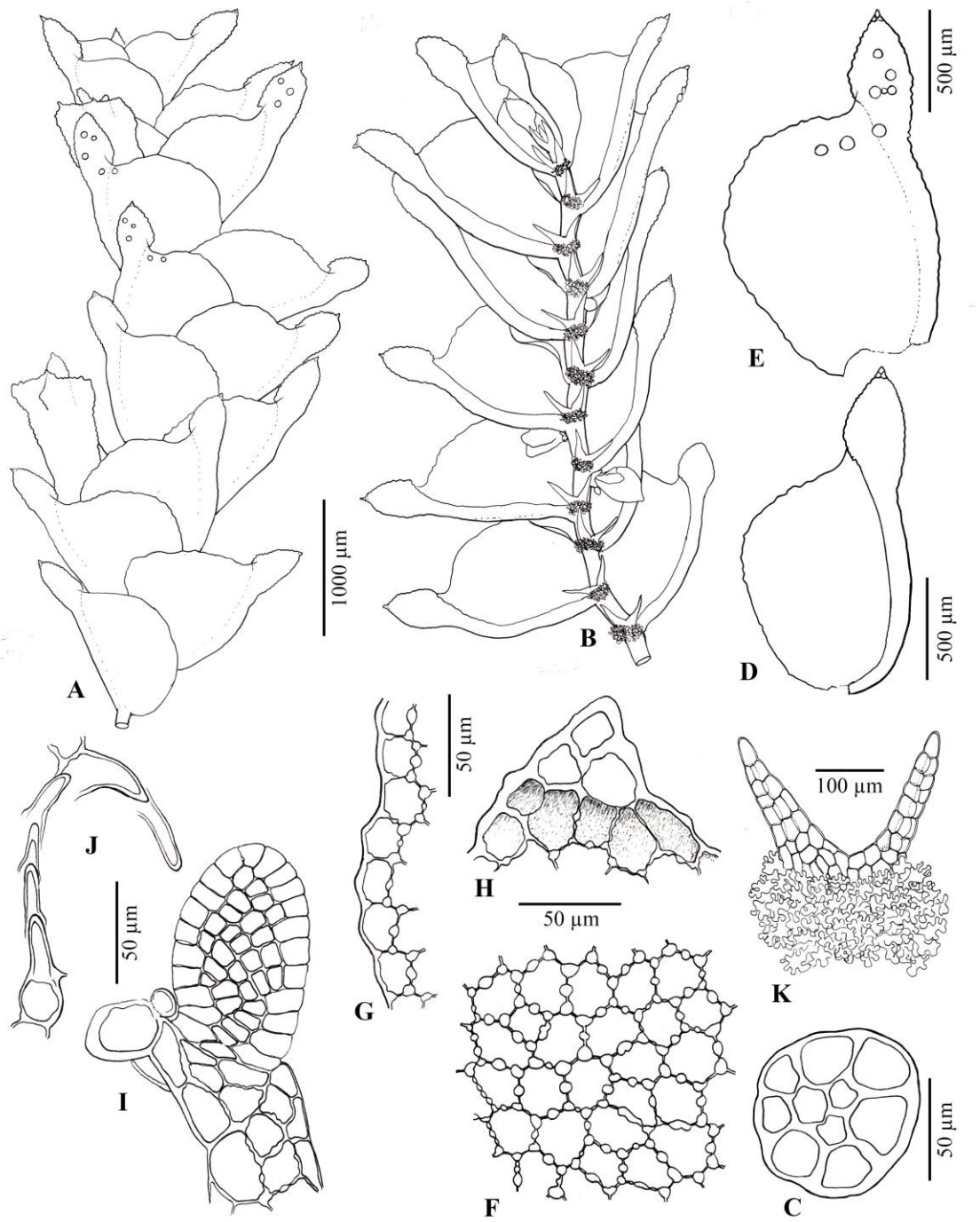

Fig. 4.62 *Colura verdoornii* Herzog *et* Jovet-Ast: A. Portion of plant with gynoecium, dorsal view. B. Portion of plant, ventral view. C. Stem in transverse section. D & E. Lateral leaf, D. ventral view, E. dorsal view. F & G. Leaf lobe cell, F. median cell, G. marginal cell. H. Lobule sac apex with apical crest. I. Valve of lobule. J. Valve frame. K. Underleaf. A & B, D & E, H–K. from *Chantanaorrapint et al. 2277A* (PSU), C, F & G. from *Sangrattanaprasert 374/15* (PSU).

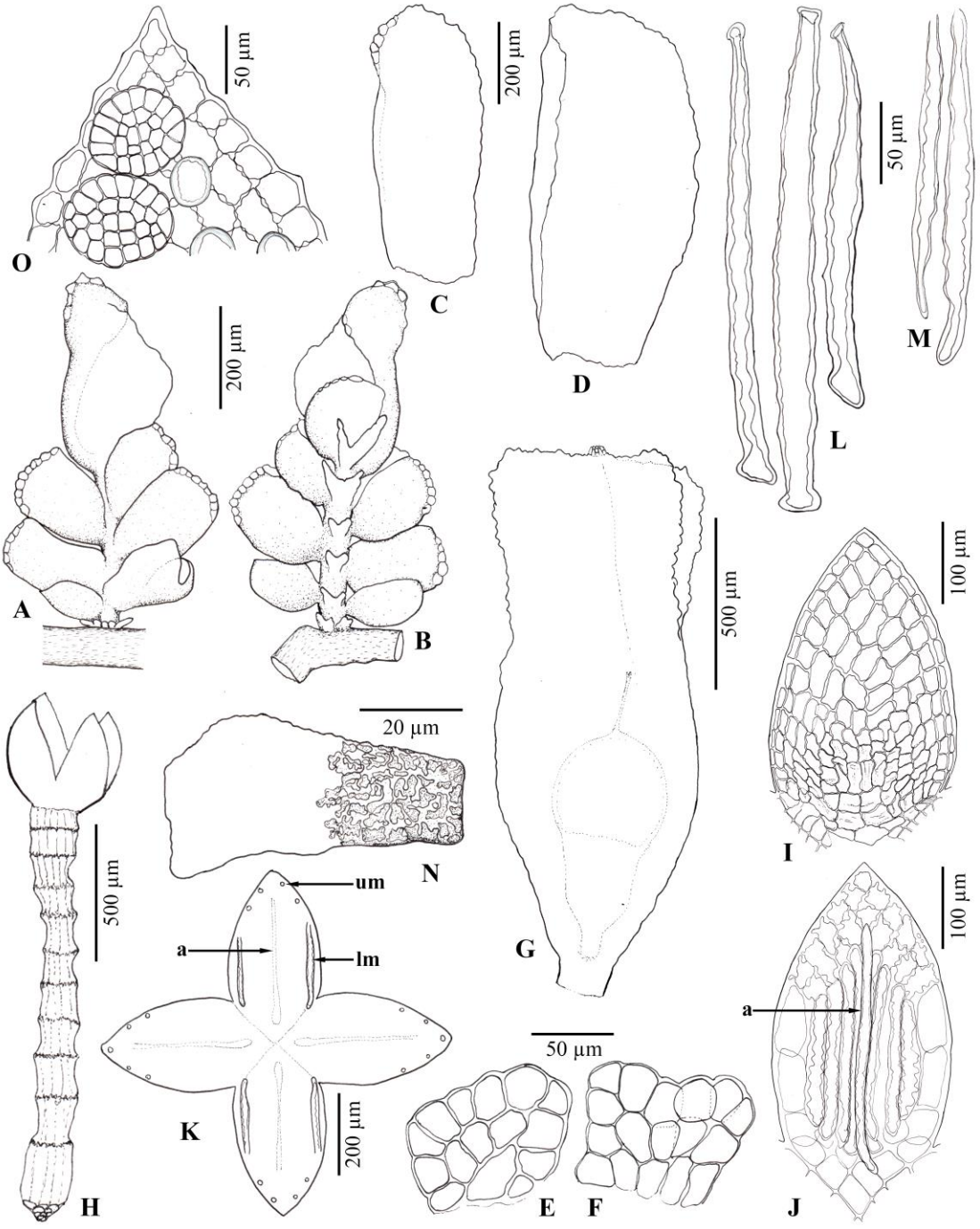

Fig. 4.63 *Colura verdoornii* Herzog *et* Jovet-Ast: A & B. Androecia, A. dorsal view, B. ventral view. C & D. Female bracts, C. dorsal view, D. ventral view. E & F. Female bracteoles. G. Perianth with young sporophyte. H. Mature sporophyte. I. Outer layer of capsule valve. J. Inner layer of capsule valve (a = additional elater). K. Scheme of elaters distribution (lm = lower marginal elater, um = upper marginal elater). L. Upper marginal elaters. M. Lower marginal elaters. N. Spore. O. Gemmae occuring on lobule sac apex. A & B. from *Sangrattanaprasert 374/15* (PSU), C–O. from *Chantanaorrapint et al. 2277A* (PSU).

4.3.2 Excluded species

Two species of *Colura* which have been recorded in Malesian region but cannot be found in this study.

1. *Colura strophiolata* Jovet-Ast, Rev. Bryol. Lichénol. 42: 917. 1976.

Type: CAMBODIA. Val d'Émeraude, Bokor, 950 m, 13 May 1967, *Tixier 2649* (holotype: PC).

Description: Jovet-Ast (1976: 918)

Illstrations: Jovet-Ast (1976: Plate IV–VI)

Colura strophiolata was known from Cambodia (*Tixier 2064*) and Peninsular Malaysia (*Tixier 5979*, *5667*, *5669*) (Jovet-Ast 1976). These type specimens were deposited at the Herbarium of the Muséum national d'Histoire Naturelle, Paris which the types are not available for loan and I do not have an opportunity to go there for type investigation. This species is morphologically related to *C. karstenii* as discussed in taxonomic note of the latter. Thus, type study and further molecular work may resolve their taxonomic status.

2. *Colura tixieri* Jovet-Ast, Rev. Bryol. Lichénol. 30: 6. 1961.

Type: VIETNAM. Lam Dong: Blao, School of Agriculture, 3 October 1957, *Tixier s.n.* (holotype: PC).

Description: Jovet-Ast (1961: 9)

Illustrations: Jovet-Ast (1961: Fig. III)

Tixier (1970) reported this species from Hot Springs, Ranong province based on his collections *Tixier 3936* and *3943*. Afterwards, the species was reported from highland evergreen forest (700 m) at Khao Yai National Park, Nakhon Ratchasima province based on the specimens of *Tixier 1180* (Tixier 1973). Unfortunately, these specimens were not available for this study. In our explorations that covered Khao Yai National Park and Thai Peninsula, *C. tixieri* cannot be found in the present study. Thus, the record of this species might be based on misidentification and should be excluded.

4.3.3 Geographical distribution of *Colura* in Malesian region

Malesian region includes three biodivertsity hotspots (Sundaland, Philippines and Wallcea) and the region is also a transition region forming a bridge between Indochina and Melanesian floras. Based on the present study, the high species number is found in Sundaland with 31 species (91.17%), Papuasia with 13 species (38.23%) and Philippines with 7 species (20.58%), respectively. Because of its highest species number, Sundaland is centre of origin of the genus *Colura*, consequently. The distribution data reveal that the species members of *Colura* are dispersed across ocean by wind or monsoon as transoceanic species.

4.3.4 Altitudinal distribution of the genus *Colura* in Malesian region

In the present study, the members of genus *Colura* were encountered in altitudinal range from sea level to 2900 msl. Almost *Colura* species (26 species) are distributed in lower montane to upper montane rain forest; some species are found occurring on broad range of elevation, from near sea level to 2900 msl, such as *C. acroloba*, *C. ari*, *C. corynophora*, *C. palawanensis*, and *C. sigmoidea*. Some of them have restricted distribution only on the montane forest, e.g., *C. calyptrifolia*, *C. clementis*, *C. crenulata*, *C. hemisphaerica*, *C. junghuhniana*, *C. karstenii*, *C. meijeri*, and *C. tenuicornis*, while some species, such as *C. bisvoluta*, *C. conica*, *C. cristata*, *C. medusa*, *C. ornata*, and *C. speciosa*, occur only in lowland evergreen forest, ranging from sea level to 700 msl.

4.3.5 Microhabitats

All voucher specimens of 34 *Colura* species were collected from living and dead leaves (epiphyllous) of various plant species, especially on palm leaves (Arecaceae), as well as from tree trunks (corticolous) and branches or twigs (ramicolous), namely *C. acroloba*, *C. brevistyla*, *C. calyptrifolia*, *C. hemisphaerica*, *C. karstenii*, *C. meijeri*, *C. pallida*, *C. pluridentata*, *C. tenuicornis*, *C. valida*, and *C. verdoornii*. The epiphytic species were usually found growing at the top of mountain

or nearby area, except for *C. pluridentata* that can be found on twig even in lowland rain forest.

4.3.6 Phytogeography

Almost *Colura* species are mainly distributed in Tropical Asia. Thirty-four species of *Colura* in this study can be divided into five phytogeographical groups based on their geographical ranges. The phytogeographic regions are determined following the World Geographical Scheme for Recording Plant Distributions of Brummitt (2001).

1. Pantropic–Subtropic and Temperate

Only two species (5.88%), (*C. calyptrifolia* and *C. tenuicornis*) are widely distributed in Pantropical, Subtropical and Temperate regions. The widespread distribution of these two species is presumably due to the very tiny plants and fast production of the sporophyte. Moreover, they also produce the gemmae at the elongated sac apices which may increase their probability of successful long-distance dispersal (Fig. 4.64A).

2. Asia Tropical and Subtropical–Australasia–Pacific

Many species are distributed from Indian subcontinent, Indochina, southern China and Japan, Malesia, Australasia and Pacific. There are 12 species (35.29%) dispersed in this region, namely *C. acroloba*, *C. ari*, *C. bisvoluta*, *C. brevistyla*, *C. conica*, *C. corynophora*, *C. denticulata*, *C. karstenii*, *C. apiculata*, *C. meijeri*, *C. ornata*, *C. pluridentata*. According to the distribution data, these species show the distribution patterns from Malesian region and Pacific distribute upwards to Indo-china, south China and Indian subcontinent and seven of them can be found extend to Australia. This phenomenon happens probably due to similarity of climate and forest type (Fig. 4.64B).

3. Malesia

This group includes the majority of the genus at 16 species (47.05%) of *Colura* distributed in Malesian region ranging from Thai-Malay Peninsula, Indonesia and Papua New Guinea. Most of them occur in lower montane to montane rain forest which is the dominant forest type in Malesian element. Moreover, these areas also provide various microhabitats that are favorable for bryophytes (Pócs 1982). Thus, it is reasonable to find the highest species number here (Fig. 4.64C).

4. Indo-china–Sumatra

The species are distributed from Indo-china, Thai-Malay Peninsula and Sumatra. This group comprises three species (8.82%): *C. corniantha*, *C. inflata*, and *C. valida*. The former two species are found occurring in lowland to lower montane rain forest, while the latter species can be growing in montane forest. Further survey in similar habitat may increase opportunities to find them (Fig. 4.65A).

5. Endemic of Maluku Islands (Indonesia)

There is only one species (3.94%), *Colura maxima*, found only once from Sembilan Mountain in Halmahera island, Indonesia (Jovet-Ast 1953), and it has never been reported in other places hitherto. Moreover, this species is characteristically large in size and has distinguished characters of large valve comprising of 49–55 cells with two distinct bordered hyaline cells and strongly papillose cells, so it cannot be overlooked (fig. 4.65C).

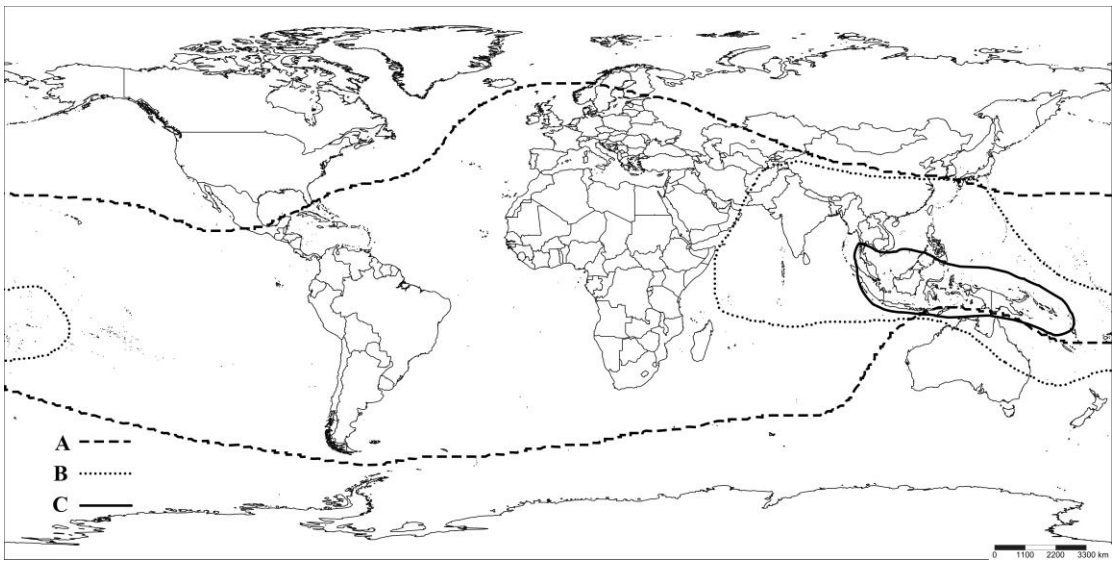

Fig. 4.64 The distribution patterns of *Colura* species in Malesia. A. Pantropic–Subtropic and Temperate. B. Asia Tropical and Subtropical–Australasia–Pacific. C. Malesia.

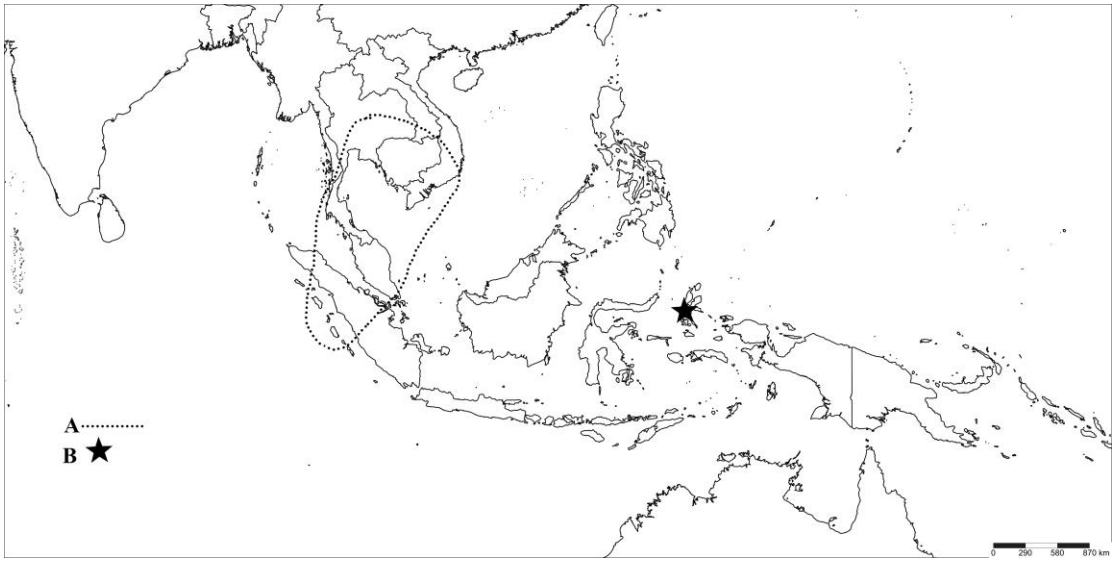

Fig. 4.65 The distribution patterns of *Colura* species in Malesia. A. Indo-china–Sumatra. B. Endemic of Maluku Islands (Indonesia).

CHAPTER 5

SUMMARY

The species of the genus *Colura* in Malesian region and adjacent areas were investigated in detail, based on fresh materials from field surveys and herbarium specimens housed in many herbaria, including BCU, BKF, BM, BO, CMU, E, EGR, HSNU, JE, KLU, L, MO, PC, and SING. The detailed descriptions of both gametophyte and sporophyte for all *Colura* species found in the present work have been provided. Oil body features cannot be observed in dried herbarium specimens. Consequently, the fresh materials are necessary for precise information in a taxonomic study. Moreover, the morphological features of sporophytes of 23 *Colura* species, most of which are investigated here for the first time, are comprehensively described. In Malesian *Colura*, three patterns of hinges of an outer layer of sporangial valves (broadly quadrate, butterfly-shape, and rectangular), as well as two types of spore ornamentation (papillate and irregular lamellate) are described. In addition, a key to species and ecological data of each taxon together with its geographical distribution are also provided.

For molecular work, 31 species of *Colura* representing all six sections (*Colura*, *Gamolepis*, *Glotta*, *Harmophyllum*, *Heterophyllum*, and *Oidocorys*) as well as *Macrocolura sagittistipula*, were analysed phylogenetically. The aligned nucleotide sequences from three markers (nrITS, *trnL-F*, and *rbcL*) of all 57 voucher specimens were combined into a single dataset of 3,064 positions and analysed via Maximum parsimony, Maximum likelihood and Bayesian inference. The phylogenetic results reveal that *M. sagittistipula* was nested within *Colura* clade with a weak support, suggesting its position as a member of the genus *Colura*. Furthermore, the subg. *Colura* comprises two sections (*Colura* and *Oidocorys*), while the subg. *Glotta* includes the remaining four sections. Section *Gamolepis*, sect. *Harmophyllum*, and sect. *Heterophyllum* are polyphyletic and their relationships were unresolved in the current study. For the *C. inflata*-complex, the molecular phylogeny confirms that *C. inflata* is a distinct species, whereas *C. corniantha* and *C. siamensis* are a conspecific.

The resulted topology also supported that *C. sigmoidea*, a recently described species, is a good species.

Based on morphological and molecular data, 34 species of *Colura* are found in Malesian region and adjacent areas. Among these, one new species, *C. sigmoidea*, is proposed from Thai-Malay Peninsula. Besides, there are four new records to Malesian region, namely *C. calyptrifolia*, *C. corniantha*, *C. medusa*, and *C. valida*. In addition, *C. cymbalifera* is now treated as a synonym of *C. hemisphaerica* as well as *C. siamensis* is here placed under the synonym of *C. corniantha*.

Suggestions for further studies

The results of the current study provide the comprehensive morphological descriptions of all *Colura* species found in the study areas. However, the sporophyte characters of some species, especially the species belonged to sect. *Oidocorys* and genus *Macrocolura* which are not found in these areas, are still waiting for comprehensive investigation. More collection from unexplored areas, furthermore, can fill the gaps in ecological and distribution data and may increase the number of species, and even new records to the area or new species may be found.

From the present molecular phylogeny, precise infrageneric relationships of the genus is not yet resolved. Thus, more loci from a larger set of additional species should be included in future molecular phylogenetic reconstructions to resolve the taxonomic classification within the genus *Colura*. Moreover, the molecular data of some morphologically related species, such as *C. brevistyla*, *C. mosenii*, and *C. pluridentata*, will be needed to confirm their taxonomic statuses, because their distinguished characters vary greatly and their distributions are overlapped within Indian Subcontinent, Malesia, and Papuasia.

REFERENCES

Ahonen, I., Muona, J. & Piippo, S. (2003) Inferring the Phylogeny of the Lejeuneaceae (Jungermanniopsida): A First Appraisal of Molecular Data. *The Bryologist* 106(2): 297–308.

Asthana, G. & Shukla, A. (2010) *Colura leratii* (Steph.) Steph. new to India. Tropical Bryology 32: 100–102.

Barthlott, W., Fischer, E., Frahm, J.-P. & Seine, R. (2000) First experimental evidence for zoophagy in the hepatic *Colura*. *Plant Biology* 2(1): 93–97.

Bonner, C.E.B. (1963) *Index Hepaticarum. Pars IV.* Ceratolejeunea *to* Cystolejeunea. Weinheim, pp. 637–926.

Brummitt, R.K. (2001) *World Geographocal Scheme for Recording Plant Distributions*. 2nd ed. Hunt Institute for Botanical Documentation Carnegie Mellon University, Pittsburgh, USA.

Brummitt, R.K. & Powell, C.E. (1992) *Authors of plant names*. A list of authors of scientific names of plants, with recommended standard forms of their names, including abbreviations. Royal Botanic Gardens Kew, London.

Chantanaorrapint, S. & Pócs, T. (2014) Southern Thailand bryophytes I, with description of *Cololejeunea ramromensis*. In: Telnov D. (ed.), *Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea. II. Rīga, the Entomological society of Latvia*, pp. 113–122.

Chernomor, O., von Haeseler, A. & Minh, B.Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65: 997–1008.

Chuah-Petiot, M.S. (2011) A checklist of hepaticae and anthocerotae of Malaysia. *Polish Botanical Journal* 56(1): 1–44.

Crandall-Stotler, B. (1972) Morphogenetic Patterns of Branch Formation in the Leafy Hepaticae: A Résumé. *The Bryologist* 75(4): 381–403.

Crandall-Stotler, B., Stotler, R.E. & Long, D.G. (2009) Phylogeny and classification of the Marchantiophyta. *Edinburgh Journal of Botany* 66(1): 155–198.

Dey, M. & Singh, D.K. (2016) Three foliicolous taxa of Lejeuneaceae (Marchantiophyta) new to India from Great Nicobar Biosphere Reserve, Andaman & Nicobar Islands. *Acta Botanica Hungarica* 58(1–2): 49–68.

Dong, S.S., Schäfer-Verwimp, A., Meinecke, P., Feldberg, K., Bombosch, A., Pócs, T., Schmidt, A.R., Reitner, J., Schneider, H. & Heinrichs, J. (2012) Tramps, narrow endemics and morphologically cryptic species in the epiphyllous

liverwort *Diplasiolejeunea*. *Molecular Phylogenetics and Evolution* 65: 582–594.

Dumortier, B.C.J. (1831). *Sylloge Jungermannidearum Europae indigenerum*. Casterman, Tournay, 113 pp.

Dumortier, B.C.J. (1835) *Recueil observation Jungermanniacées, Fascicule I.- Révision Des Genres*. Imprimerie De J.-A. Blanquart., Tournay, 27 pp.

Eggers, J. & Schäfer-Verwimp, A. (1987) Some liverworts new to Sri Lanka (Ceylon). *Journal of Bryology* 14: 531–534.

Evans, A.W. (1900) The Hawaiian Hepaticae of the tribe Jubuloideae. *Transactions of the Connecticut Academy of Arts and Sciences* 10 (8): 387–462.

Frey, W. & Stech, M. (2009) *Syllabus of Plant Families, Adolf Engler's Syllabus der Pflanzenfamilien: Part 3 Bryophytes and seedless Vascular Plant*. 13th ed. Deucherei Strauss GmbH, Mörlenbach.

Geissler, P. & Bischler, H. (1987) *Index Hepaticarum vol. 8/9.* Jungermannia *to* Lejeunites. Berlin, 310 pp.

Goebel, K.I. (1891) *Pflanzenbiologische Schilderungen. 2. Tell, VI*. Wasserpflanzen, Ewert'sche Verlagsbuchhandlung, Marburg, pp. 215–380.

Goebel, K.I. (1928) Malesische Lebermoose. *Annales du Jardin Botanique de Buitenzorg* 39: 1–116.

Goloboff, P.A. & Catalano, S.A. (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221–238.

Gottsche, C.M., Lindenberg, J.B.W. & Nees von Esenbeck, S.G. (1843) Hepaticae. (in Meyen, F.J.F., Observationes botanicas in itinere circum terram institutas). *Novorum Actorum Academia Caesareae Leopoldinae-Carolinae Germinicae Naturae Curiosorum* 19 (supp. l): 469–477.

Gradstein, S.R. (1986) The genus *Colura* in the Galapagos Islands. *Hikobia* 9: 353–356.

Gradstein, S.R. (2013) A classification of Lejeuneaceae (Marchantiophyta) based on molecular and morphological evidence. *Phytotaxa* 100(1): 6–20.

Gradstein, S.R., Cleef, A.M. & Fulford, M.H. (1977) Studies on Colombian cryptogams. IIA. Hepaticae—oil body structure an ecological distribution of selected species of tropical Andean Jungermanniales. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C* 80: 377–393.

Gradstein, S.R. & Pócs, T. (1989) *Bryophytes*. In: Lieth H. and Werger M.J.A. (eds.). Tropical Rain Forest Ecosystems. Elsevier Science Publishers, Amsterdam, The Netherlands. pp. 311–325.

Gradstein, S.R., Pócs, T. & Váňa, J. (1989) Disjunct hepaticae in Tropical America and Africa. Acta Botanica Hungarica 29(1–4): 127–171.

Gradstein, S.R., Reiner-Grehwald, M.E. & Schneider, H. (2003) A phylogenetic analysis of the genera of Lejeuneaceae (Hepaticae). *Botanical Journal of the Linnean Society* 143: 391–410.

Gradstein, S.R., Wilson, R., Ilkiu-Borges, A.L. & Heinrichs, J. (2006) Phylogenetic relationships and neotenic evolution of *Metzgeriopsis* (Lejeuneaceae) based on chloroplast DNA sequences and morphology. *Botanical Journal of the Linnean Society* 151: 293–308.

Gradstein, S.R., Zhu, R.-L., Shu, L. & Pérez, Á.J. (2018) Reinerantha foliicola, a new genus and species of Lejeuneaceae subtribe Cololejeuneinae (Marchantiophyta) from Ecuador. *Journal of Systematics and Evolution* 56: 67–75.

Grolle, R. (1965) Lebermoose aus Neuguinea. I. *Journal of the Hattori Botanical Laboratory* 28: 43–54.

Grolle, R. (1969) Hepaticae Novae Guineae Schusteranae. I. *Journal of the Hattori Botanical Laboratory* 32: 140–144.

Grolle, R. (1975) Miscellanea hepaticologica 141–150. *Journal of Bryology* 8 (4): 483–492.

Grolle, R. (1978) Die Lebermoose der Seychellen. *Wiss. Z. Friedrich-Schiller-Univ. Jena, Math.-Naturwiss. Reihe* 27: 7–17.

Grolle, R. & Zhu, R.L. (2002) On *Macrocolura* and the subdivision of *Colura* (Lejeuneaceae, Hepaticae). *Journal of the Hattori Botanical Laboratory* 92: 181–190.

Groth-Malonek, M., Heinrichs, J., Schneider, H. & Gradstein, S.R. (2004) Phylogenetic relationships in the Lejeuneaceae (Hepaticae) inferred using ITS sequences of nuclear ribosomal DNA. *Organisms, Diversity & Evolution* 4: 51–57.

Hartmann, F.A., Wilson, R., Gradstein, S.R., Schneider, H. & Heinrichs, J. (2006) Testing hypotheses on species delimitations and disjunctions in the liverwort Bryopteris (Jungermanniopsida: Lejeuneaceae). *International Journal of Plant Sciences* 167: 1205–1214.

Hassel, K., Appelgren, L., Blom, H.H., Flynn, K.M., Gaarder, G., Heegaard, E., Høitomt, T., Jordal, J.B., Lima, M., Söderström, L. & Wangen, K. (2014) *Colura calyptrifolia* a new oceanic liverwort to Norway and Scandinavia. *Lindbergia* 37: 1–5.

Heinrichs, J., Dong, S., Schäfer-Verwimp, A., Peralta, D.F., Feldberg, K., Schmidt, A.R. & Schneider, H. (2014a) Towards a monophyletic classification of

Lejeuneaceae II: subtribes Pycnolejeuneinae and Xylolejeuneinae subtr. nov., transfer of *Otolejeunea* to *Lepidolejeuninae*, and generic refinements. *Phytotaxa* 163(2): 61–76.

Heinrichs, J., Dong, S., Yu, Y., Schäfer-Verwimp, A., Pócs, T., Feldberg, K., Hentschel, J., Schmidt, A.R. & Schneider, H. (2012) A 150 year-old mystery solved: Transfer of the rheophytic endemic liverwort *Myriocolea irrorata* to *Colura*. *Phytotaxa* 66: 55–64.

Heinrichs, J., Schäfer-Verwimp, A., Czumay, A., Dong, S., Scheben, A., Feldberg, K. & Schneider, H. (2014b) Towards a monophyletic classification of Lejeuneaceae I: subtribe Leptolejeuneinae subtr. nov. *Phytotaxa* 156(3): 165–174.

Herzog, T. (1921) Die Lebermoose der 2 Freiburger Molukkenexpeditionen und einige neuen Arten der engeren Indomalaya. *Beiheft zum Botanischen Centralblatt* 38(2): 318–332.

Herzog, T. (1933) Bryophyta nova. *Annales bryologici* 6: 124–125.

Herzog, T. (1942) *Die foliosen Hepaticae der Juan Fernandez-Inseln und der Osterinsel*. In: C. Skottsberg (ed.), The Natural History of Juan Fernandez and Easter Island 2(5). Uppsala. pp. 697–752.

Hooker, W.J. (1813) *British Jungermanniae, vol. 9–15*. Longmans, London, tabs. 33–60.

Hylander, K., Pócs, T. & Nemomissa, S. (2010) Liverworts of southwest Ethiopian montane forests: ecological and biogeographical notes. *Journal of Bryology* 32(2): 92–100.

Jovet-Ast, S. (1948) Hépatiques des Antilles françaises récoltées par P. et V. Allorge en 1936. *Revue Bryologique et Lichénologique* 17: 24–34.

Jovet-Ast, S. (1953) Le genre *Colura*, Hépatiques, Lejeunéacées, Diplasiae. *Revue Bryologique et Lichénologique* 22(2/3): 206–312.

Jovet-Ast, S. (1954) Le genre *Colura*. Hepatiques, Lejeuneaceae, Diplasiae (supplement). *Revue Bryologique et Lichénologique* 23: 1–22.

Jovet-Ast, S. (1956) Deux *Colura* nouveaux de Madagascar. *Revue Bryologique et Lichénologique* 25: 272–276.

Jovet-Ast, S. (1958a) Hépatiques du Cambodge récoltées par le Professeur Roger Heim. *Revue Bryologique et Lichénologique* 27: 24–30.

Jovet-Ast, S. (1958b) Localités nouvelle de diverses espèces du genre *Colura*. *Revue Bryologique et Lichénologique* 27: 19–23.

Jovet-Ast, S. (1961) *Colura* du Sud-Vietnam (Récoltes de Pierre Tixier). *Revue Bryologique et Lichénologique* 30: 5–12.

Jovet-Ast, S. (1967a) *Colura* récoltés du Pakistan aux Philippines par Pierre Tixier. *Revue Bryologique et Lichénologique* 36: 138–142.

Jovet-Ast, S. (1967b) Compléments à l'étude des *Colura*: localités nouvelles; description d'une espèce nouvelle de Bornéo. *Revue Bryologique et Lichénologique* 36: 143–148.

Jovet-Ast, S. (1976) Compléments à la connaissance des *Colura*: espèce et localités nouvelles. *Revue Bryologique et Lichénologique* 42: 909–922.

Jovet-Ast, S. (1980) La section *Oidocorys* S. J.-A. du genre *Colura* Dum. est-elle âgée de plus de 100 millions d'années? *Cryptogamie, Bryologie et Lichénologie* 1: 277–287.

Jovet-Ast, S. (1983) *Colura* nouveaux d'origines diverses (Hépatiques, Lejeunéacées). *Cryptogamie, Bryologie et Lichénologie* 4:205–216.

Jovet-Ast, S. & Tixier, P. (1958) Hépatiques du Viet-Nam. I. *Revue Bryologique et Lichénologique* 27: 201–210.

Katoh, K., Rozewicki, J. & Yamada, K.D. (2017) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefing in Bioinformatics*: 1–7.

Kis, G. & Pócs, T. (1997) Oil body studies on African Hepaticae. *Journal of the Hattori Botanical Laboratory* 81: 175–242.

Kitagawa, N. (1969) A small collection of Hepaticae from Penang, Malaysia. *Bulletin of Nara University of Education* 18(2): 27–43.

Lai, M.J., Zhu, R.L. & Chantanaorrapint, S. (2008) Liverworts and hornworts of Thailand: an updated checklist and bryofloristic accounts. *Annales Botanici Fennici* 45: 321–341.

Lal, J. (1977) *Colura* Dum. (Hepaticae) – a genus new to Indian Flora. *Current Science* 46: 618.

Lewis, L.A., Mishler, B.D. & Vilgalys, R. (1997) Phylogenetic relationships of the liverworts (Hepaticae), a basal embryophyte lineage, inferred from nucleotide sequence data of the chloroplast gene *rbcL*. *Molecular Phylogenetic and Evolution* 7(3): 377–39.

Menzel, M. (1988) Annotated catalogue of the Hepaticae and Anthocerotae of Borneo. *Journal of the Hattori Botanical Laboratory* 65: 145–206.

Miller, H.A., Whittier, H.O. & Whittier, B.A. (1983) Prodromus Florae Hepaticarum Polynesiae. *Bryophyt. Biblioth.* 25: 1–423.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) *Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pages 1–8*. In: Proceedings

of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans.

Mizutani, M. (1961) A revision of Japanese Lejeuneaceae. *Journal of the Hattori Botanical Laboratory* 24: 115–302.

Montagne, J.F.C. (1848) Sixième centurie de plantes cellulaires exotiques nouvelles. Décades I et II. *Annales des Sciences Naturelles; Botanique (sér. 3)* 10: 106–136.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution.* 32: 268–274.

Onraedt, M. (1979) Bryophytes de Sri Lanka (Ceylan) IV. Le genre *Colura*. *Revue Bryologique et Lichénologique* 45: 443–452.

Onraedt, M. (1981) Bryophytes récoltées a Sri Lanka (Ceylan). V. *Journal of the Hattori Botanical Laboratory* 50: 191–216.

Pócs, T. (1982) *Tropical forest bryophytes*. In: Smith A.J.E. (ed.), Bryophyte Ecology. Chapman and Hall, London, pp. 59–104.

Pócs, T. (1996) Epiphyllous liverwort diversity at worldwide level and its threat and conservation. *Anales del Instituto de Biologia de la Universidad Nacional Autónoma de México, Serie Botanica* 67(1): 109–127.

Pócs, T. (2011) New or little known epiphyllous liverworts, XIV. The genus *Colura* (Lejeuneaceae) in São Tomé Island, with the description of *Colura thomeensis* sp. nov. *Bryologist* 114: 362–366.

Pócs, T. (2012) New or little known epiphyllous liverworts, XVI. A small collection from Laos. *Acta Biologica Plantarum Agriensis* 2: 5–10.

Pócs, T. (2013) The genus *Colura* (Lejeuneaceae) in New Guinea and in the neighboring areas. *Chenia* 11: 12–38.

Pócs, T. & Eggers, J. (2007) Bryophytes from the Fiji Islands, II. An account of the genus *Colura*, with a description of *C. vitiensis* sp. nov. *Polish Botanical Journal* 52(2): 81–92.

Pócs, T. & Lee, G.E. (2016) Data to the Malaysian liverwort flora, II. *Cryptogamie, Bryology* 37(1): 39–52.

Pócs, T., Luong, T.T. & Ho, B.C. (2013) New of little known epiphyllous liverworts, XVIII. records from the Bidoup-Núi Bà National Park, Vietnam, with the description of *Drepanolejeunea bidoupensis*, sp. nov. *Cryptogamie, Bryologie* 34(3): 287–298.

Pócs, T., Mizutani, M. & Piippo, S. (1994) Bryophyte Flora of the Huon Peninsula, Papua-New-Guinea LXV. Preliminary Contributions on Lejeuneaceae (Hepaticae) 1. *Annales Botanci Fennici* 31: 179–190.

Pócs, T. & Ninh, T. (2005) Contribution to the Bryoflora of Vietnam, VI. on the liverwort flora of Vu Quang Nature Reserve. *Acta Botanica Hungarica* 47(1–2): 151–171.

Pócs, T. & Ninh, T. (2012) New or little known epiphyllous liverworts, XVII. records from the Cát Tiên National Park, Southern Vietnam. *Acta Biologica Plantarum Agriensis* 2: 11–19.

Pócs, T. & Podani, J. (2015) Southern Thailand bryophytes II. Epiphylls from the Phang-Nga area. *Acta Botanica Hungarica* 57: 183–198.

Pócs, T., Sass-Gyarmati, A., Naikatini, A., Tuiwawa, M., Braggins, J., Pócs, S. & von Konrat, M. (2011) New liverwort (Marchantiophyta) records for the Fiji Islands. *Telopea* 13(3): 455–494.

Pócs, T., & Streimann, H. (2006) Contributions to the Bryoflora of Australia, I. *Tropical Bryology* 27: 19–24.

Pócs, T. & Váňa, J. (2015) East African Bryophytes XXX. New Liverwort and Hornwort Records. *Acta Biologica Plantarum Agriensis* 3: 3–21.

Prantl, K. (1890) Verzeichniss der in diesem Bande erwähnten Pflanzen (Kryptogamen). Hedwigia 29: vii–xxix.

Reed, C.F. & Robinson, H. (1967) Contribution to the bryophytes of Thailand, I. *Phytologia* 15(1): 61–70.

Ronquist, F. & Huelsenbeck, J. P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

Sande Lacoste, C.M. (1864) Hepaticae. Jungermanniae Archipelagi Indici, adiectis quibusdam speciebus Japonicis. *Annales Musei Botanici Lugduno-Batavia* 1: 287–314.

Sangrattanaprasert, J., Chantanaorrapint, S. & Zhu, R.-L. (2017) Notes on *Colura crenulata* (Lejeuneaceae, Marchantiophyta), a new record for Thailand, with a sporophyte description. *Polish Botanical Journal* 62(2): 197–202.

Sangrattanaprasert, J., Chantanaorrapint, S. & Zhu, R.-L. (2018) The genus *Colura* section *Glotta* (Lejeuneaceae, Marchantiophyta) in Thailand. *Acta Botanica Hungarica* 60(3–4): 425–435.

Sangrattanaprasert, J., Chantanaorrapint, S. & Zhu, R.-L. (2019a) The genus *Colura* section *Gamolepis* (Lejeuneaceae, Marchantiophyta) in Malesian region, with the description of *Colura sigmoidea*. *Phytotaxa* 387(1): 40–54.

Sangrattanaprasert, J., Ho, B.C., Chantanaorrapint, S. & Zhu, R.-L. (2019b) The genus *Colura* (Lejeuneaceae, Marchantiophyta) new to Singapore. *Gardens' Bulletin Singapore* 71(1): 00–00. (in press).

Schäfer-Verwimp, A. (1999) Some additions to the bryophyte flora of Dominica, West Indies. *Haussknechtia, Beiheft* 9: 317–331.

Schiffner, V. (1890) Lebermoose (Hepaticae), mit Zugrundelegung der von Dr. A.C.M. Gottsche ausgeführten Vorarbeiten. In: Naumann, F.C. (Ed.) *Die Forschungsreise S.M.S. "Gazelle" in der Jahren 1874 bis 1877 unter Kommando des Kapitän zur See Freiherrn von Schleinitz, Vol. IV*. Berlin, pp. 1–45

Schiffner, V. (1893a) Hepaticae. In: Engler, H.G.A. & Prantl, K. (eds.) *Die Natürlichen Pflanzenfamilien, Teil. I, Abt. 3*. Engelmann, Leipzig, pp. 1–144.

Schiffner, V. (1893b) Ueber exotische Hepaticae, hauptsächlich aus Java, Amboina und Brasilien, nebst einigen morphologischen und kritischen Bemerkungen über *Marchantia*. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum* 60: 220–316.

Schiffner, V. (1898) *Conspectus Hepaticarum Archipelagi Indici*. Batavia, 382 pp.

Schiffner, V. (1900) Hepaticae Masartianae Javanicae. *Hedwigia* 39: 191–208.

Schuster, R.M. (1984) *New Manual of Bryology 2*. Journal of the Hattori Botanical Laboratory, Nichinan, pp. 627–1295.

Schuster, R.M. (1992) The oil-bodies of the Hepaticae. II. Lejeuneaceae. *Journal of the Hattori Botanical Laboratory* 72: 163–359.

Schuster, R.M. (1994) Studies on Lejeuneaceae, I. *Journal of the Hattori Botanical Laboratory* 75: 211–235.

Seelanan, T., Schnabel, A. & Wendel, J.F. (1997) Congruence and consensus in the cotton tribe (Malvaceae). *Systematic Botany* 22: 259–290.

Shaw, J. & Renzaglia, K. (2004) Phylogeny and diversification of bryophytes. *American Journal of Botany* 91(10): 1557–1581.

Shu, L., Xiang, Y.-L., Cheng, X.-F., Wei, Y.-M., Wang, J., Zhang, L.-N., Li, W., Yin, X.-B., Zhang, W.-P., Zhao, C.-X., Peng, T., Do, T.V., Lu, T.N. & Zhu, R.-L. (2017) New liverwort and hornwort records for Vietnam. *Cryptogamie Bryologie* 38: 411–445.

Singh, D.K. (1996) Hepaticae (Bryophyta). In: Hajra P.K. (ed.) *A contribution to the flora of Namdapha Arunachal Pradesh. Botanical Survey of India*. New Delhi. pp. 46–67.

Singh, S.K. & Barbhuiya, H.A. (2012) A compendium to Marchantiophyta and Anthocerotophyta of Assam, India. *Archive for Bryology* 149: 1–30.

Söderström, L., Barrie, F.R., Hagborg, A., Crandall-Stotlér, B.J., Gradstein, S.R., Stotler, R.E. & Von Konrat, M. (2015) Notes on Early Land Plants Today. 73. Genera of Lejeuneaceae established in the period 1884–1893: dates of validation and implications. *Phytotaxa* 220: 143–198.

Söderström L., Hagborg, A., Von Konrat, M., Bartholomew-Began, S., Bell, D., Briscoe, L., Brown, E., Cargill, D.C., Costa, D.P., Crandall-Stotler, B.J., Cooper, E.D., Dauphin, G., Engel, J.J., Feldberg, K., Glenny, D., Gradstein, S.R., He, X., Heinrichs, J., Hentschel, J., Ilkiu-Borges, A.L., Katagiri, T., Konstantinova, N.A., Larraín, J., Long, D.G., Nebel, M., Pócs, T., Puche, F., Reiner Drehwald, E., Renner, M.A.M., Sass-Gyarmati, A., Schäfer-Verwimp, A., Segarra Moragues, J.G., Stotler, R.E., Sukkharak, P., Thiers, B.M., Uribe, J., Váňa, J., Villarreal, J.C., Wigginton, M., Zhang, L. & Zhu, R.-L. (2016) Pócs World checklist of hornworts and liverworts. *PhytoKeys* 59: 1–828.

Sprengel, C. (1827) *Systema vegetabilium. Editio decima sexta, voluminis IV, pars II*. Dieterich, Göttingen, 410 pp.

Spruce, R. (1884) Hepaticae Amazonica *et* Andinae. *Transactions and Proceedings of the Botanical Society, Edinburgh* 15: 1–308.

Stephani, F. (1890) Die Gattung *Lejeunea* im Herbarium Lindenberg 2. *Hedwigia* 29: 68–99.

Stephani, F. (1891) Hepaticae africanae. *Hedwigia* 30(5): 201–217.

Stephani, F. (1896) Hepaticarum species novae IX. *Hedwigia* 35: 73–140.

Stephani, F. (1908) Hépatiques de la Nouvelle-Calédonie et du Tonkin. *Revue Bryologique* 35: 28–35.

Stephani, F. (1916) *Species Hepaticarum 5*. Genève & Bale, pp. 849–1008.

Stephani, F. (1923) *Species Hepaticarum 6*. Genève & Bale, pp. 369–432.

Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.

Tan, B.C. & Engel, J.J. (1986) An Annotated Checklist of Philippine Hepaticae. The *Journal of the Hattori Botanical Laboratory* 60: 283–355.

Thiers, B. (1987) A Preliminary Account of *Colura* (Hepaticae, Lejeuneaceae) In Australia. *Brittonia* 39(2): 175–179.

Thiers, B. (2018) Index herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/.

Tixier, P. (1962) Bryophytes du Vietnam. Premières récoltes dans le massif de Bach-Ma. *Revue Bryologique et Lichénologique* 31: 190−203.

Tixier, P. (1970) Bryophytae Indosinicae. Bryophytes from Thai Tenasserim. *Natural History Bulletin of the Siam Society* 23: 541–559.

Tixier, P. (1973) Bryophytae Indosinicae. Liverworts collected in Thailand. *Natural History Bulletin of the Siam Society* 24: 449–456.

Tixier, P. (1975) Bryophytae Indosinicae.–XXIII. A Preliminary Contribution to the Knowledge of the Coastal Southern Bryoftora of Cambodia. *Natural History Bulletin of the Siam Society* 26: 11–24.

Trevisan de Saint-Léon, V.B.A. (1877) Schema di una nuova classificazione delle Epatiche Memorie del Reale Istituto Lombardo de Scienze e Lettere, Serie 3. *Classe di Scienze Matematiche e Naturali* 4: 383–451.

Udar, R. & Awasthi, U.S. (1985) *Colura acroloba* (Mont.) JovetAst. – new to Indian Bryoflora. *Journal of the Indian Botanical Society* 64: 284–286.

van Leeuwen, W.M. (1936) Krakatau, 1883 to 1933. Hepaticae. *Annales du Jardin botanique de Buitenzorg* 46-47: 315–322.

van Steenis, C.G.G.J. (1950) *The delimitation of Malesia and its main plant geographical divisions*. Flora Malesiana I (1): lxx–lxxv.

van Welzen, P.C., Silk, J.W.F. & Alahuhta, J. (2005) Plant distribution patterns and plate tectonics in Malesia. *Biologiske Skrifter* 55: 199–217.

Vanden Berghen, C. (1972) Hépatiques épiphylles récoltées au Burundi par J. Lewalle. *Bulletin du Jardin Botanique National de Belgique* 42: 431-494.

Wang, J., Lai, M.-J. & Zhu, R.-L. (2011) Liverworts and hornworts of Taiwan: an updated checklist and floristic accounts. *Annales Botanici Fennici* 48: 369–395.

Wiens, J.J. (1998) Combining data sets with different phylogenetic histories. *Systematic Biology* 47: 568–581.

Wilson R, Gradstein SR, Heinrichs J, Groth H, Ilkiu Borges AL, Hartmann FA. (2004) Phylogeny of Lejeuneaceae: a cladistic analysis of chloroplast gene *rbc*L sequences and morphology with preliminary comments on the mitochondrial nad4–2 spacer region. *Monographs in Systematic Botany from the Missouri Botanical Garden* 98: 189–202.

Wilson, R., Gradstein, S.R., Schneider, H. & Heinrichs, J. (2007) Unravelling the phylogeny of Lejeuneaceae (Jungermanniopsida): evidence for four main lineages. *Molecular Phylogenetics and Evolution* 43: 270–282.

Woodruff, D.S. (2010) Biogeography and conservation in Southeast Asia: how 2.7 million years of repeated environmental fluctuations affect today's pattern and the future of the remaining refugial-phase biodiversity. *Biodiversity Conservation* 19: 919–941.

Yang, L.-D., Yao, K.-Y. & Lin, S.-H. (2013) Two species of *Colura* (family Lejeuneaceae) newly recorded to Taiwan. *Taiwan Journal of Biodiversity* 15(4): 331–341.

Zhu, R.-L., Shu, L., Bastos, C.J.P. and Bôas-Bastos, S.B.V. (2018) *Yanoella* (Marchantiophyta: Lejeuneaceae), a new genus from the Brazilian Atlantic Forest. *The Bryologist* 121(3): 264–274.

Zhu, R.-L., Shu, L., Mustapeng, A.M. & Suleiman, M. (2017) Thiersianthus (Marchantiophyta: Lejeuneaceae), a new genus from lowland rainforests in Borneo. *The Bryologist* 120: 511–520.

Zhu, R.-L. & So, M.L. (2001) Epiphyllous liverworts of China. *Nova Hedwigia, Beiheft* 121: 1–418.

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List of Publications and Proceedings

Sangrattanaprasert, J., Chantanaorrapint, S. & Zhu, R.-L. (2017) Notes on *Colura crenulata* (Lejeuneaceae, Marchantiophyta), a new record for Thailand, with a sporophyte description. *Polish Botanical Journal* 62(2): 197–202.

Sangrattanaprasert, J., Chantanaorrapint, S. & Zhu, R.-L. (2018) The genus *Colura* section *Glotta* (Lejeuneaceae, Marchantiophyta) in Thailand. *Acta Botanica Hungarica* 60(3–4): 425–435.

Sangrattanaprasert, J., Chantanaorrapint, S. & Zhu, R.-L. (2019) The genus *Colura* section *Gamolepis* (Lejeuneaceae, Marchantiophyta) in Malesian region, with the description of *Colura sigmoidea*. *Phytotaxa* 387(1): 40–54.

Sangrattanaprasert, J., Ho, B.C., Chantanaorrapint, S. & Zhu, R.-L. (2019) The genus *Colura* (Lejeuneaceae, Marchantiophyta) new to Singapore. *Gardens' Bulletin Singapore* 71(1): 00–00 (in press).

Sangrattanaprasert, J., Kornochalert, S. & Chantanaorrapint, S. (2019) *Cololejeunea metzgeriopsis* (Lejeuneaceae, Marchantiophyta) a new distributional record for Thailand. *Acta Botanica Hungarica* 61(3–4): 00–00 (in press).