





First floristic study on epiphyllous bryophytes of the state Terengganu, Peninsular Malaysia

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Abstract

A floristic exploration was carried out of the epiphyllous bryophytes in Mount Tebu Forest Reserve, in the state of Terengganu, Peninsular Malaysia. Epiphyllous liverworts are reported for the first time from Terengganu. A total of 54 species from 18 genera and seven families of epiphyllous bryophytes were discovered, and of these, 43 liverworts are newly reported from Terengganu. The largest family is represented by Lejeuneaceae, with 44 species (81%) from 12 genera, and the largest genus is *Cololejeunea*, with 15 species (28%). Most of the species (43 spp., 69%) have an Indo-Pacific distribution.

Keywords

Bryophytes, Marchantiophyta, epiphylls, biodiversity, phytogeography, Malaysia, taxonomy

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Introduction

The bryophyte diversity in Malaysia is neither completely known nor well studied but nonetheless appears to be rich with almost 2250 species and infraspecific taxa (Lee et al. 2019). The history of liverwort exploration and recent papers on Malaysian liverworts have been reviewed by Lee et al. (2018), and the first study on epiphyllous communities in Sabah has been conducted by Pócs et al. (2020). Although Malaysian bryophytes have been collected since the 19th century, many areas in Peninsular

Malaysia are still under-collected; for example, only two species of liverworts have been reported in Terengganu (Pócs and Lee 2016; Lee et al. 2018, 2019). Liverworts are undoubtedly the dominant and commonest of epiphyllous bryophytes. Epiphyllous liverworts—that is, liverworts inhabiting living leaves—usually occur and thrive well in moist, warm forests of tropical and subtropical regions (Chen and Wu 1964). They often show high levels of endemism, and their occurrence on leaves are

categorized into three types, obligate, facultative, and occasional (Pócs 1996; Jiang et al. 2018) or, alternatively, into two types, typical and facultative (Gradstein 1997), whereby typical epiphylls possess morphological adaptations to the epiphyllous habitat, whereas facultative (or accidental) epiphylls lack them. Moreover, epiphyllous liverworts are usually dominated by the members of the family Lejeuneaceae (Zhu and So 2001). They are generally sensitive of their surroundings, which qualify them as crucial indicators of climate and environmental changes (Pócs 1996; Frego 2007; Jiang et al. 2014). Thus, a minute modification on the forest structure, for example the opening up of the canopy, would significantly affect the diversity of the liverworts in that forest (Pócs 1989; Gradstein 1997; Pócs and Tóthmérész 1997).

Mount Tebu, rising to 1039 m, is the fifth highest peak in Terengganu (Fig. 1). At the base of Mount Tebu is a recreational forest, Hutan Lipur Lata Belatan, covering an area of 20 ha, out of the total approximately 25600 ha of the forest reserve. Additionally, both the mountain and recreational forests are located within Besut District and with a unique, historical landscape and natural ecosystem consisting of diverse habitats for plants, animals, and microorganisms (Abdul Rahim et al. 2014). A scientific expedition and inventory were organized in 2012 by the Forestry Department of Peninsular Malaysia which yielded a considerable amount of plant specimens as well as several extensive floristic studies (Abdul Rahim et al. 2014). The plant diversity of various groups, including mosses, ferns, trees, gingers, and palms, have been well documented as a result of the expedition. However, no study on epiphyllous bryophytes had been done in this

area. We aim to provide the first comprehensive and updated checklist of epiphyllous bryophytes of Mount Tebu Forest Reserve in Terengganu.

Study Area

Geologically, Mount Tebu is made up of igneous rocks known as Lawit Granite, while low, undulating areas to the north, east, and south of the mountain consist of metasedimentary rocks (shale, metasandstone, and metaconglomerate) (Abdul Rahim et al. 2014). The low-lying area is occupied by a recent river and coastal alluvium, which is made up of unconsolidated sand and mud. The water catchment area of Mount Tebu has been assessed as environmentally stable and of high quality. The forest is generally made up of lowland dipterocarp forest, hill dipterocarp forest, and upper hill dipterocarp forest (Fig. 2). Hence, this forest reserve contains diverse tropical flora and fauna, with valuable timber species mainly from the families Euphorbiaceae and Dipterocarpaceae contributing towards a large diversity of tree species, of which Dipterocarpaceae are dominant.

Methods

Random sample collection was carried out along the streams and available trails within the study area (Fig. 2). Any of the epiphyllous liverworts spotted on the living plants were collected including fallen leaves on the forest floor. All liverwort specimens were deposited in the Herbarium of Universiti Malaysia Terengganu (UMTP), while moss specimens were deposited in the Herbarium of Universiti Kebangsaan Malaysia (UKMB). The

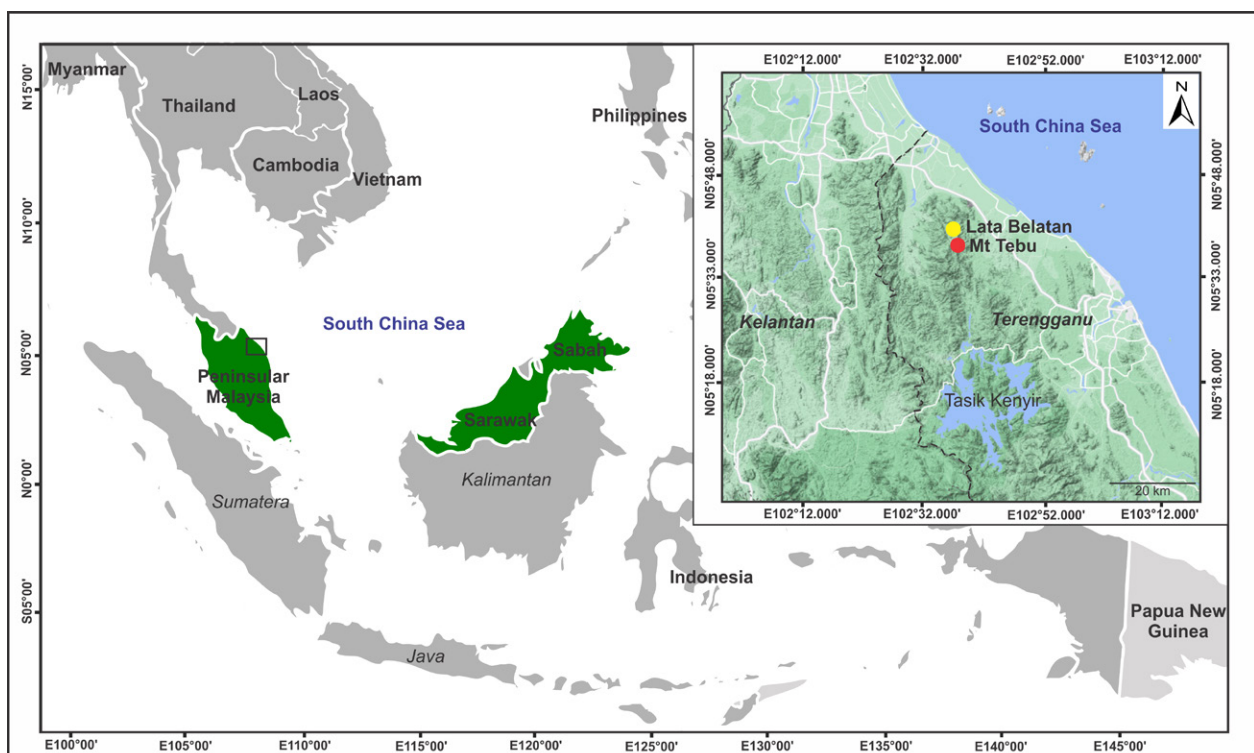


Figure 1. Map of Mount Tebu Forest Reserve including Lata Belatan in Terengganu, Malaysia.

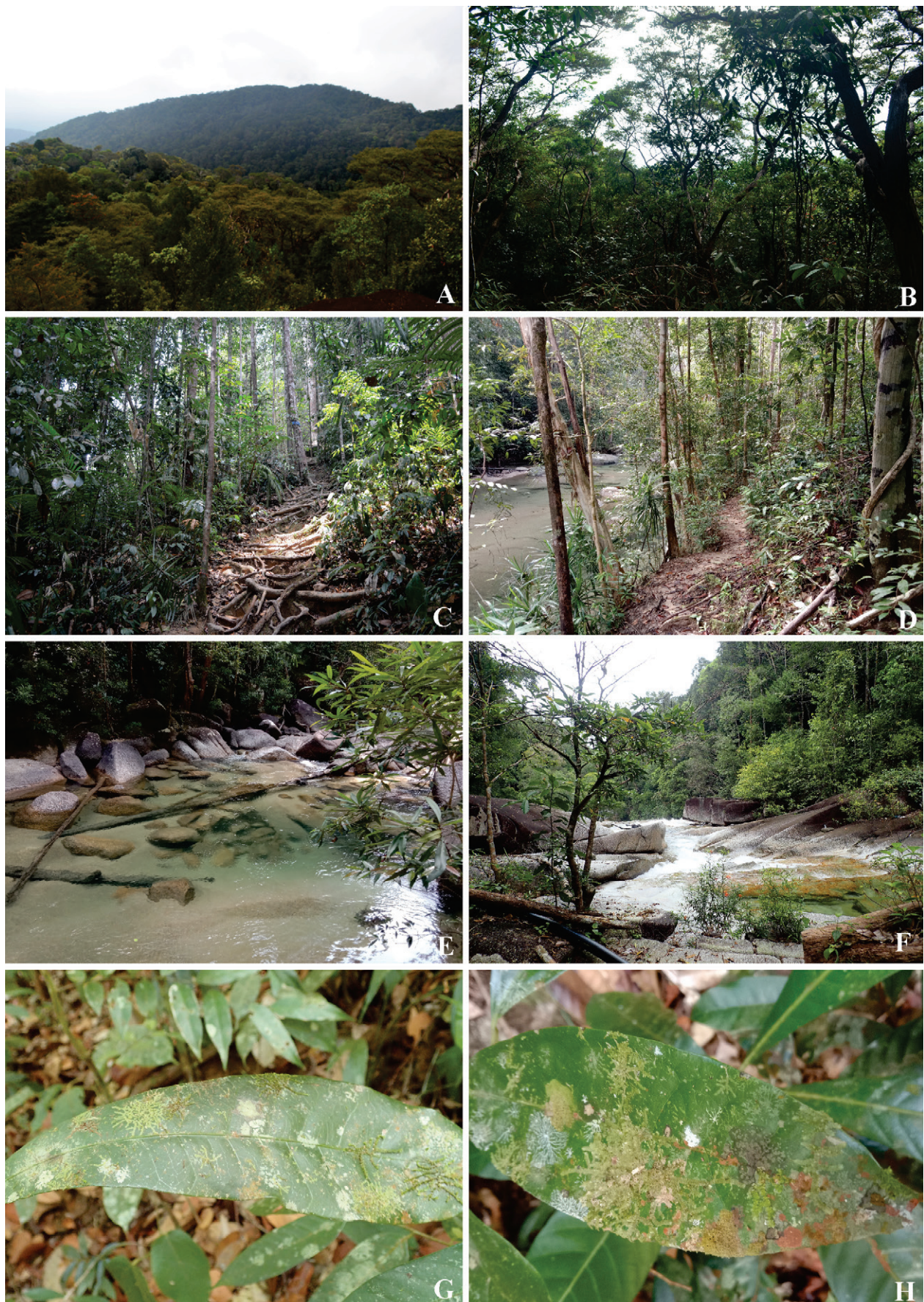


Figure 2. Habitats of epiphyllous bryophytes. **A–D.** Lowland dipterocarp forest, hill dipterocarp forest and upper hill dipterocarp forest. **E, F.** Stream areas. **G, H.** Liverworts spotted on the leaves.

Table 1. Distribution pattern of epiphyllous liverworts and mosses recorded from Mount Tebu Forest Reserve. Phytogeographical distribution, IP = Indo-Pacific; MP = Malesian-Pacific; SA= Southeast Asian; PAL = Palaeotropical; PAN = Pantropical. Distribution in Malaysia, BD= Broadly distributed; MD= Moderately distributed; RE = Restricted. State Distribution, Pn = Pulau Pinang; Kd = Kedah; Pk = Perak; Tg = Terengganu; Kl = Kelantan; Ph = Pahang; Jh = Johor; MI = Melaka; NS = Negeri Sembilan, SI = Selangor; Kul = Kuala Lumpur; Ps = Perlis; Sb = Sabah; Sr = Sarawak.

Taxon	Phytogeographical distribution	Distribution in Malaysia	State distribution
Bryophyta			
Calymperaceae			
<i>Mitthyridium constrictum</i> (Sull.) H. Rob.	SA, IP	BD	Jh, Kl, NS, Ph, Sb, SI, Sr, Tg
Daltoniaceae			
<i>Ephemeropsis tjiobodensis</i> K.I. Goebel	PAL, SA	BD	Jh, Kd, NS, Ph, Pn, Pk, Kl, Sb, SI, Sr, Tg
Sematophyllaceae			
<i>Taxithelium isocladum</i> (Bosch & Sande Lac.) Renaud & Cardot	PAL	BD	Jh, Kd, Kl, Ph, Pn, Pk, Ps, Sb, SI, Sr, Tg
Marchantiophyta			
Frullaniaceae			
<i>Frullania apiculata</i> (Reinw. et al.) Nees	PAL, IP	MD	Kd, Ph, SI, Sb, Tg
Lejeuneaceae			
<i>Caudalejeunea reniloba</i> (Gottsche) Steph.	IP	BD	Pn, Pk, Ph, SI, Jh, Sr, Sb, Tg
<i>Ceratolejeunea minor</i> Mizut.	IP	RE	Sb, Tg
<i>Ceratolejeunea singapurensis</i> (Lindenb.) Schiffn.	SA, IP	RE	Sr, Tg
<i>Cheilelejeunea ceylanica</i> (Gottsche) R.M. Schust. & Kachroo	IP	BD	Kd, Pn, Ph, NS, Sr, Sb, Tg
<i>Cheilelejeunea trapezia</i> (Nees) Kachroo & R.M. Schust.	IP	BD	Kd, Pn, Ph, Jh, Sr, Sb, Tg
<i>Cheilelejeunea trifaria</i> (Reinw. et al.) Mizut.	PAN	RE	Pk, Sb, Tg
<i>Cololejeunea appressa</i> (A. Evans) Benedix.	IP	RE	Sb, Tg
<i>Cololejeunea aequabilis</i> (Sande Lac.) Schiffn.	IP	MD	Jh, Sr, Sb, Tg
<i>Cololejeunea equalbi</i> Tixier.	IP	RE	Sb, Tg
<i>Cololejeunea falcata</i> (Horik.) Benedix	PAL, IP	MD	Kd, Pn, Ph, Sb, Tg
<i>Cololejeunea floccosa</i> (Lehm. & Lindenb.) Schiffn.	PAL, IP	BD	Kd, Pn, Pk, Ph, NS, MI, Sr, Sb, Tg
<i>Cololejeunea inflata</i> Steph.	IP	MD	Kd, Ph, MI, Sr, Sb, Tg
<i>Cololejeunea inflectens</i> (Mitt.) Benedix	PAL, IP	MD	Kd, Ph, Jh, Sr, Sb, Tg
<i>Cololejeunea lanciloba</i> Steph.	PAL, IP	MD	Pn, Ph, Jh, Sb, Tg
<i>Cololejeunea metzgeriopsis</i> (K.I. Goebel) Gradst. et al.	IP	MD	Ph, Pk, Sb, Tg
<i>Cololejeunea ocelloides</i> (Horik.) Mizut.	IP	MD	Pk, Ph, MI, Sb, Tg
<i>Cololejeunea planissima</i> (Mitt.) Abeyw.	IP	MD	Pn, Pk, Jh, Sb, Tg
<i>Cololejeunea schmidtii</i> Steph.	IP	RE	Sb, Tg
<i>Cololejeunea sigmoidea</i> Jovet-Ast & Tixier	IP	MD	Pn, Ph, Sb, Tg
<i>Cololejeunea stephanii</i> Schiffn. ex Benedix	IP	BD	Kd, Pk, Ph, Jh, Sr, Sb, Tg
<i>Cololejeunea verrucosa</i> Steph.	IP	MD	MI, Jh, Sb, Tg
<i>Colura acroloba</i> (Prantl) Jovet-Ast	IP	BD	Ph, SI, Kul, NS, MI, Jh, Sr, Sb, Tg
<i>Colura ari</i> (Steph.) Steph.	IP	RE	Sb, Tg
<i>Colura conica</i> (Sande Lac.) K.I. Goebel	IP	MD	Pn, NS, MI, Sr, Sb, Tg
<i>Colura corynophora</i> (Nees et al.) Trevis	IP	MD	Pn, NS, Jh, Sr, Sb, Tg
<i>Colura inuii</i> Horik.	IP	RE	Tg
<i>Drepanolejeunea dactylophora</i> (Gottsche et al.) J.B. Jack & Steph	IP	MD	MI, Sr, Sb, Tg
<i>Drepanolejeunea levicornua</i> Steph.	IP	MD	Ph, SI, Sr, Tg
<i>Drepanolejeunea longicornua</i> (Herzog) Mizut.	MP	MD	Pn, Sr, Sb, Tg
<i>Drepanolejeunea pentadactyla</i> (Mont.) Steph.	IP	BD	Kd, Ph, SI, MI, Jh, Sr, Sb, Tg
<i>Drepanolejeunea spicata</i> (Steph.) Grolle & R.L. Zhu	IP	MD	Ph, Sr, Sb, Tg
<i>Drepanolejeunea ternatensis</i> (Gottsche) Schiffn.	IP	RE	Sb, Sr
<i>Drepanolejeunea thwaitesiana</i> (Mitt.) Steph.	IP	MD	Kd, Ph, SI, Sb, Tg
<i>Lejeunea micholitzii</i> Mizut.	MP	BD	Kd, Kl, Ph, SI, NS, Sr, Sb, Tg
<i>Lejeunea adpressa</i> Nees	PAN	BD	Ps, Kd, Pn, Pk, Ph, SI, Kl, NS, Jh, Sr, Sb
<i>Lepidolejeunea bidentula</i> (Steph.) R.M. Schust.	IP	BD	Pn, Ph, SI, NS, Jh, Sr, Sb, Tg
<i>Leptolejeunea amphiphthalma</i> Zwickel	IP	RE	Kd, Sb, Tg
<i>Leptolejeunea subacuta</i> A. Evans	IP	BD	Pk, Ph, NS, MI, Jh, Sb, Tg
<i>Leptolejeunea epiphylla</i> (Mitt.) Steph.	PAL	BD	Kd, Pn, Ph, SI, NS, MI, Sb, Tg
<i>Leptolejeunea maculata</i> (Mitt.) Schiffn.	PAL	BD	Kd, Pk, Ph, NS, Jh, Sr, Sb, Tg
<i>Leptolejeunea vitrea</i> (Nees) Schiffn.	IP	BD	Kd, Pn, Pk, Ph, NS, Jh, Sr, Sb, Tg
<i>Metalejeunea cucullata</i> (Reinw. et al.) Grolle	PAN	MD	Kd, Ph, NS, Sr, Sb, Tg
<i>Microlejeunea punctiformis</i> (Taylor) Steph.	IP	RE	Kl, Sb, Tg
<i>Tuyamaella molischii</i> (Schiffn.) S. Hatt.	IP	RE	Kd, Tg
Radulaceae			
<i>Radula acuminata</i> Steph.	IP	MD	SI, NS, Sb, Tg
<i>Radula assamica</i> Steph.	IP	RE	Ph, SI, Tg
<i>Radula grandilobula</i> Promma & Chantanaor.	SA	RE	Tg
<i>Radula nymannii</i> Steph.	IP	RE	Ph, Sb, Tg
<i>Radula tjiobodensis</i> K.I. Goebel	IP	MD	Pn, Ph, Sb, Tg

distribution pattern of epiphyllous bryophytes in Malaysian states was adopted from de Oliveira et al. (2018), of which species are categorized as broadly distributed, moderately distributed, and restricted. We categorized epiphyllous bryophytes occurring in 1–3 Malaysian states as restricted, while species occurring in 4–6 states and seven or more as moderately and broadly distributed, respectively.

Results

We identified 54 species of bryophytes from 18 genera and seven families from the study area; 51 species are liverworts and three are mosses (Table 1). Overall, the most speciose family is Lejeuneaceae with 44 species (81%) in 12 genera, and the dominant genus is

Cololejeunea (Spruce) Steph. with 15 species (28 %), followed by *Drepanolejeunea* (Spruce) Steph. with seven species; *Colura* (Dumort.) Dumort. and *Radula* Dumort. each have five species. Only three species of mosses were found: *Ephemeropsis tjobodensis* K.I. Goebel, *Mitthyridium constrictum* (Sull.) H. Rob., and *Taxithelium isocladum* (Bosch & Sande Lac.) Renauld & Cardot.

Most of the species recorded in this study are moderately distributed (39%) and only 16 species (30%) are broadly distributed (Fig. 3). Moreover, five distribution patterns are recognized, Indo-Pacific, Malesian-Pacific, Southeast Asian, Palaeotropical, and Panropical. Most of species (43 spp., 69%) had an Indo-Pacific distribution pattern, followed by Palaeotropical species (10 spp., 16%). Species with a Malesian-Pacific distribution were the fewest (2 spp., 3%) (Fig. 4). Out of 51 liverwort species, 43 are newly recorded from Terengganu, while the remaining eight species have already been reported by Sarimi et al. (in press). Brief characteristics of these new records are provided in alphabetical order and selected species are illustrated (Figs. 5–8).

Caudalejeunea reniloba (Gottsche) Steph.

Figure 5A

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 952 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1915.

Identification. This species is recognized by the dentate margins of leaf lobes, underleaves, female bracts, and bracteoles, the strongly involute free margin of leaf lobules, the 2–4 teeth in the leaf lobules, the dentate

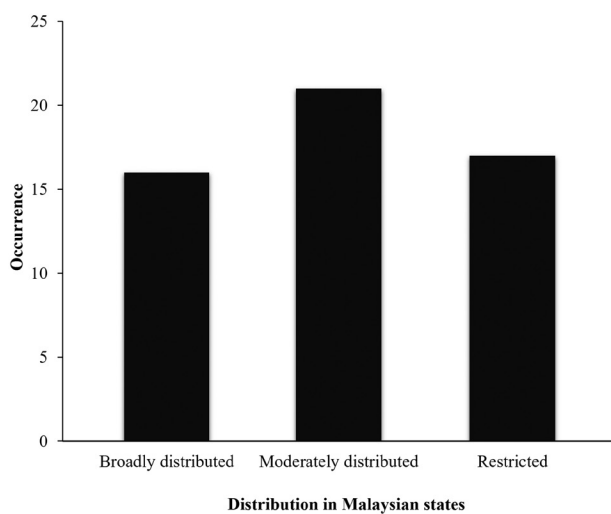


Figure 3. Distribution pattern of species in Malaysian states.

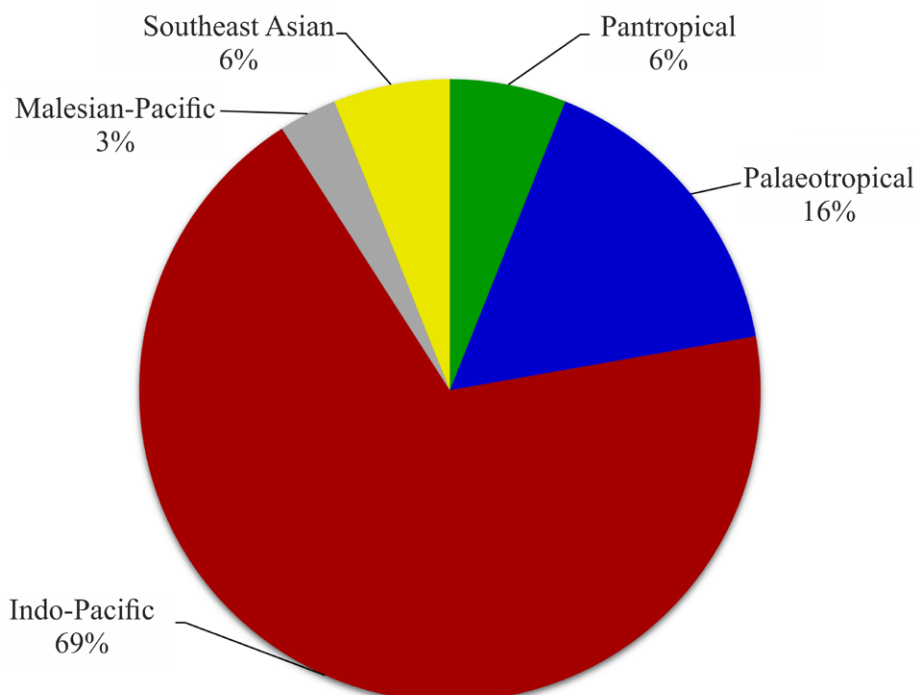


Figure 4. Distribution types of epiphyllous bryophytes recorded from Mount Tebu Forest Reserve, Terengganu.



Figure 5. Epiphyllous liverworts and their habit. **A.** *Caudalejeunea reniloba*. **B.** *Cheilolejeunea trapezia*. **C.** *Colura acroloba*. **D.** *Drepanolejeunea dactylophora*. **E.** *Drepanolejeunea spicata*. **F.** *Drepanolejeunea thwaitesiana*. **G.** *Leptolejeunea amphiphthalma*. **H.** *Leptolejeunea vitrea*.

wings of perianth keels, and the circinate gemmiferous branches with large underleaves.

Distribution. A broadly distributed Indo-Pacific species (Zhu and So 2001; Lee et al. 2013; Shu et al. 2017; Pócs and Kovács 2019; Söderström et al. 2020; Bardat et al. 2021).

***Cheilelejeunea ceylanica* (Gottsche) R.M. Schust. & Kachroo**

Figure 6B

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 937 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1937.

Identification. Diagnostic characteristics are the long, 4–7 cells, and curved second tooth of leaf lobules, the intercalary male bracts, and the well-developed trigones of the leaf cells.

Distribution. An Indo-Pacific species distributed from Asia to Australia and the Fiji Islands (Zhu and So 2001; Söderström et al. 2011; Lee et al. 2013; Shu et al. 2017).

***Cheilelejeunea trapezia* (Nees) Kachroo & R.M. Schust.**

Figure 5B

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 952 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1915.

Identification. Leaf lobes ovate to oblong, and leaf lobules large, oblong to rectangular, of which the second tooth usually distinct but short, curved at apex.

Distribution. An Indo-Pacific species, broadly distributed in Asia, Australia, and the Pacific islands (Zhu and So 2001; Lee et al. 2013; Singh and Singh 2016; Shu et al. 2017; Söderström et al. 2011, 2020).

***Cheilelejeunea trifaria* (Reinw., Blume & Nees) Mizut.**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1989.

Identification. This species is recognized by the rounded apex of the leaf lobes, distinct second tooth of the leaf lobules, and large cordate underleaves, 4–6 times as wide as the stem.

Distribution. Pantropic (Zhu and So 2001; Söderström et al. 2011; Lee et al. 2013; Shu et al. 2017).

***Cololejeunea aequabilis* (Sande Lac.) Schiffn.**

Figure 6C

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19102.

Identification. Plants brownish; leaves distant to

contiguous or slightly imbricate, asymmetrically ovate with rounded apices. Leaf lobules inflated, with first tooth bicellular and second tooth unicellular and obtuse. Hyaline papilla is ental, at the base of the first tooth. Perianth with elongated auriculate wings.

Distribution. A Southeast Asian-Pacific species (Pócs and Piippo 2011; Lee et al. 2013; Shu et al. 2017).

***Cololejeunea falcata* (Horik.) Benedix**

Figure 6D

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1999.

Identification. This species is characterized by the falcate-ovate leaf lobes with entire or slightly denticulate margins and rounded apices. The leaf lobe vitta is made up of either single or often double to triple lines, 5 or 6 cells long.

Distribution. A pantropical species (Pócs and Piippo 2011; Lee et al. 2013; Pócs et al. 2014; Shu et al. 2017).

***Cololejeunea floccosa* (Lehm. & Lindenb.) Schiffn.**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 940 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee.; UMTF 1958.

Identification. This species is distinguished by having the leaf lobules with a curved first tooth at apex and the vitta composed of 1 or 2 rows of ocelli. The keels of leaf lobules are papillose at the apex but smooth at the base.

Distribution. Palaeotropical species (Zhu and So 2001; Lee et al. 2013; Pócs 2016; Shu et al. 2017; Söderström et al. 2020).

***Cololejeunea inflata* Steph.**

Figure 6E

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 884 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1962.

Identification. This plant is easily identified by its hyaline marginal cells and vitta on leaf lobes, median leaf cells with short cylindrical papillae, and the presence of 2 teeth on leaf lobules (the first erect-spreading and 2 cells long; the second is slightly curved and 1 or 2 cells).

Distribution. An Indo-Pacific species (Zhu and So 2001; Lee et al. 2013; Pócs 2016; Shu et al. 2017; Söderström et al. 2020).

***Cololejeunea inflectens* (Mitt.) Benedix**

Figure 6F

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19101.

Identification. Diagnostic characteristics are the ovate

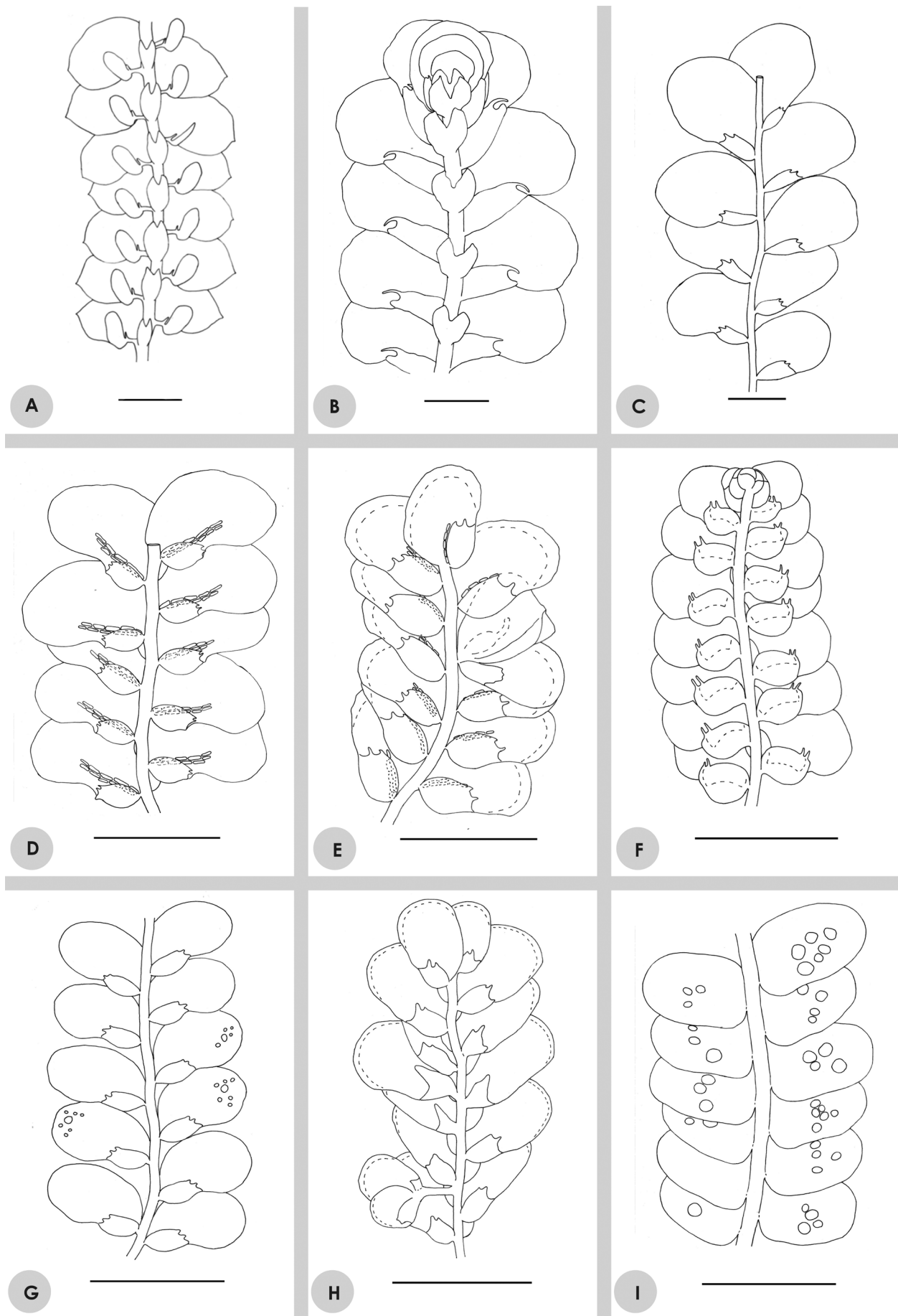


Figure 6. Epiphyllous liverworts from Mount Tebu Forest Reserve. **A.** *Frullania apiculata*. **B.** *Cheilolejeunea ceylanica*. **C.** *Cololejeunea aequabilis*. **D.** *Cololejeunea falcata*. **E.** *Cololejeunea inflata*. **F.** *Cololejeunea inflectens*. **G.** *Cololejeunea obliqua*. **H.** *Cololejeunea planissima*. **I.** *Cololejeunea sigmoidea*. Scale bars: A, B = 250 μ m; C–E = 500 μ m; F–H = 1250 μ m; I = 550 μ m.

and inflated leaf lobules with strongly involute free margin.

Distribution. A palaeotropical species (Zhu 1995; Lee et al. 2013; Pócs 2016; Shu et al. 2017).

***Cololejeunea lanciloba* Steph.**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.418'N, 102°35.932'E; alt. 308 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1972.

Identification. Distinguishing features are the asymmetrically ovate leaf lobes, the hyaline cells throughout the margin of leaf lobes, the narrowly ligulate leaf lobules with one side tooth, the finely segmented oil bodies, and the absence of ocelli and vitta. Gradstein (2011, 2021) considers *C. lanciloba* to be a possible synonym of *C. planissima*.

Distribution. Palaeotropical species (Zhu and So 2001; Lee et al. 2013; Shu et al. 2017; Pócs and Kovács 2019; Söderström et al. 2020).

***Cololejeunea metzgeriopsis* (K.I.Goebel) Gradst., R.Wilson, Ilk.-Borg. & Heinrichs**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°36.383'N, 102°36.189'E; alt. 780 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1967.

Identification. The finger-like projections on the dorsal surface of thallus cell and the minute leafy branches produced at the apex of the thallus, and the densely ciliate margin of thallus are unique and striking features of *C. metzgeriopsis*.

Distribution. An Indo-Pacific species, widely distributed from Southeast Asia to Papua New Guinea, New Caledonia, and the Fiji Islands (Grolle and Piippo 1984; Gradstein et al. 2006; Söderström et al. 2011).

***Cololejeunea obliqua* (Nees & Mont.) Schiffn.**

Figure 6G

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF19109.

Identification. The obovate and papillose perianth with 4 short keels (which never form auriculate wings), unicellular stylus, papillose leaf cells, and crenulate margins of leaf lobes are characteristic.

Distribution. A pantropical species (Grolle 1995; Zhu and So 2001; Pócs and Piippo 2011; Lee et al. 2013; Shu et al. 2017).

***Cololejeunea ocelloides* (Horik.) Mizut.**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.491'N, 102°36.668'E; alt. 1006 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1908.

Identification. This species is characterized by leaf

lobules large, almost half the length of leaf lobes, unicellular stylus, distinct vitta, and the smooth keel of leaf lobules.

Distribution. An Indo-Pacific species and well distributed from Asia to Australia and New Guinea (Zhu and So 2001; Lee et al. 2013; Shu et al. 2017).

***Cololejeunea planissima* (Mitt.) Abeyw.**

Figure 6H

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.418'N, 102°35.932'E; alt. 308 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1968.

Identification. Similar to *C. lanciloba*, this species differs by the broadly lanceolate to triangular leaf lobules and the absence of hyaline cells on the ventral leaf lobe margins.

Distribution. A widely distributed Indo-Pacific species (Zhu and So 2001; Pócs and Piippo 2011; Lee et al. 2013; Shu et al. 2017; Söderström et al. 2020).

***Cololejeunea sigmoidea* Jovet-Ast & Tixier**

Figure 6I

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 940 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1952.

Identification. Diagnostic features are the strongly reduced leaf lobules, the linear-flexuous marginal leaf cells, and the numerous discoid gemmae on ventral surface of leaf lobes.

Distribution. An Indo-Pacific species distributed from Southeast Asia to China, Japan, and Papua New Guinea (Zhu and So 1998; Pócs and Piippo 2011; Lee et al. 2013; Shu et al. 2017).

***Cololejeunea stephanii* Schiffn. ex Benedix**

Figure 7A

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.491'N, 102°36.668'E; alt. 1006 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1907.

Identification. *Cololejeunea stephanii* is differentiated by the hyaline marginal cells of leaf lobes, the curved first tooth of leaf lobules, the distinct vitta, and the unicellular stylus.

Distribution. An Indo-Pacific species (Zhu 1995; Lee et al. 2013; Pócs and Piippo 2011).

***Cololejeunea verrucosa* Steph.**

Figure 7B

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 980 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1926.

Identification. This species is characterized by the stellate papillae on leaf lobe cells, the vitta 3 or 4 cells long,

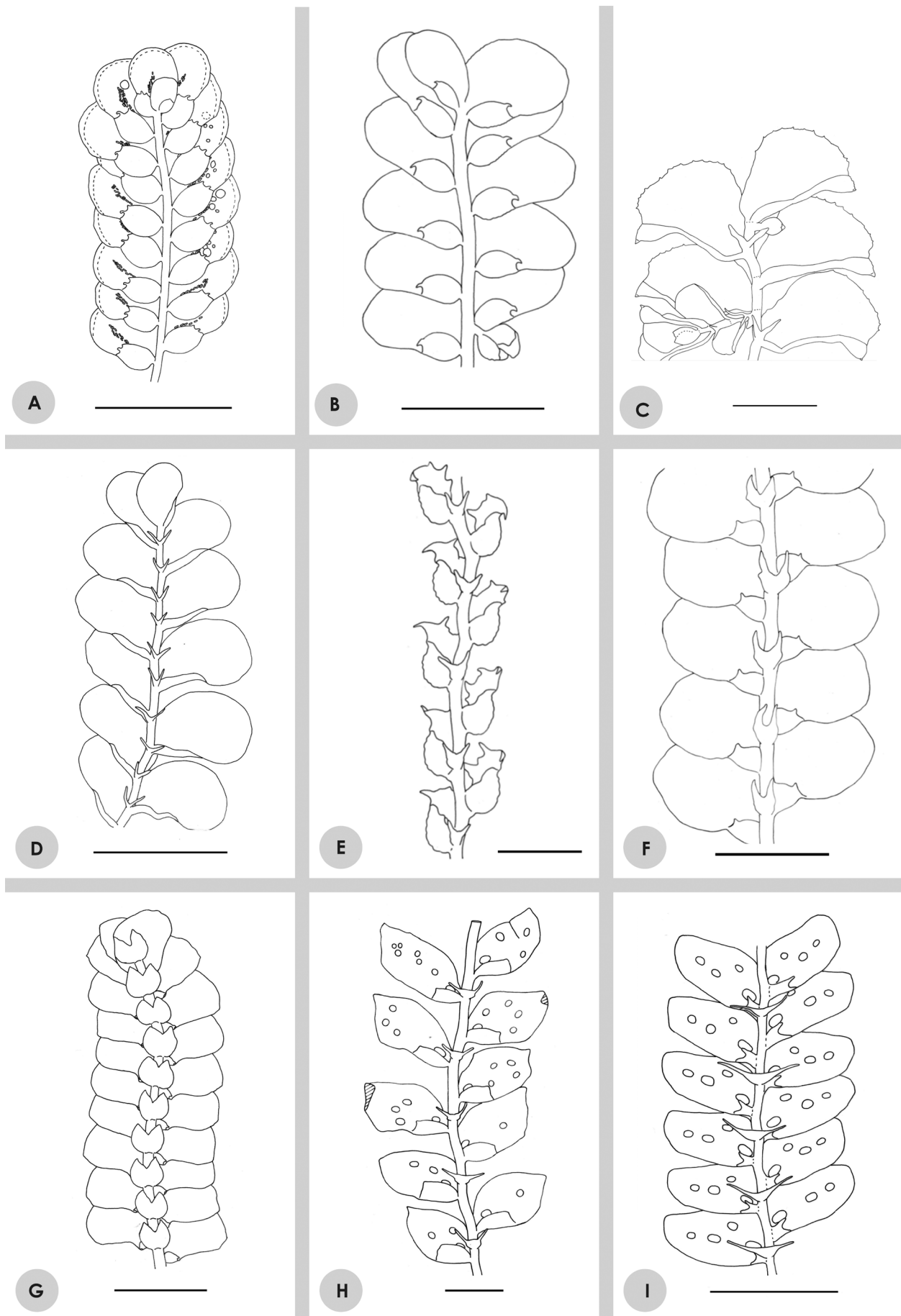


Figure 7. Epiphyllous liverworts from Mount Tebu Forest Reserve. **A.** *Cololejeunea stephanii*. **B.** *Cololejeunea verrucosa*. **C.** *Colura conica*. **D.** *Colura corynophora*. **E.** *Drepanolejeunea pentadactyla*. **F.** *Lejeunea micholitzii*. **G.** *Lepidolejeunea bidentula*. **H.** *Leptolejeunea subacuta*. **I.** *Leptolejeunea epiphylla*. Scale bars: A, C, D, G = 1250 μ m; B, F, I = 500 μ m; E = 250 μ m; H = 200 μ m.

the curved first tooth of leaf lobules, and the papillose perianths.

Distribution. An Indo-Pacific species, distributed in Asia, Australia, and the Pacific islands (Miller et al. 1983; Zhu 1995; Zhu and So 2001; Lee et al. 2013; Pócs 2016; Shu et al. 2017; Söderström et al. 2020).

***Colura acroloba* (Prantl) Jovet-Ast**

Figure 5C

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.491'N, 102°36.668'E; alt. 1006 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1905.

Identification. This species is recognized by its autoicy, leaf lobes with entire margin, rounded sac at the apex, and the valve consists of 10–20 median cells and circled by 14–20 hyaline marginal cells.

Distribution. An Indo-Pacific species from India to China, Australia, New Caledonia, and the Fiji Islands (Zhu and So 2001; Pócs et al. 2011; Lee et al. 2013; Pócs 2016; Shu et al. 2017).

***Colura conica* (Sande Lac.) K.I. Goebel**

Figure 7C

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19154.

Identification. The serrate margin of leaf lobes, acute sac at the apex and distinct hinge of the valve are characteristic.

Distribution. An Indo-Pacific species distributed from Indonesia and China to the Pacific islands (Zhu and So 2001; Pócs and Eggers 2007; Lee et al. 2013; Shu et al. 2017; Pócs and Kovács 2019; Söderström et al. 2020).

***Colura corynophora* (Nees, Lindenb. & Gottsche) Trevis.**

Figure 7D

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19103.

Identification. This species is easily differentiated from other *Colura* species by the predominantly non-saccate leaf lobules and the slender, wide base of the underleaves.

Distribution. An Indo-Pacific species from Southeast Asia, China to the Mariana Islands and Fiji (Zhu and So 2001; Pócs and Eggers 2007; Lee et al. 2013; Shu et al. 2017).

***Drepanolejeunea dactylophora* (Gottsche, Lindenb. & Nees) J.B. Jack & Steph.**

Figure 5D

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19103.

Identification. Easily recognized by its densely toothed margins of leaf lobes and obovate perianths with densely toothed (2–4 celled) keels.

Distribution. An Indo-Pacific species, from Asia to Australia and to the Caroline and Fiji Islands (Miller et al. 1983; Zhu and So 2001; Söderström et al. 2011; Lee et al. 2013; Shu et al. 2017).

***Drepanolejeunea levicornua* Steph.**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1933.

Identification. Distinguishing characters are the asymmetrical leaf lobes, the mamilliose perianths with 5 horn-like keels, the short lobes of underleaves, the leaf lobes without median ocelli, and the absence of gynoeical innovation.

Distribution. An Indo-Malesian species distributed from China, Indonesia, Thailand, Malaysia, and Papua New Guinea (Mizutani 1990; Zhu and So 2001; Lee et al. 2013).

***Drepanolejeunea longicornua* (Herzog) Mizut.**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19153.

Identification. The obliquely ovate leaf lobes with 2–10 scattered ocelli and without basal ocellus, and the perianths with 3–5 distinct wings are characteristic features of this species.

Distribution. A Malesian species distributed in Malaysia, Indonesia, and Papua New Guinea (Mizutani 1990; Lee et al. 2013).

***Drepanolejeunea pentadactyla* (Mont.) Steph.**

Figure 7E

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 940 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1953.

Identification. Similar to *D. dactylophora* but differentiated by the sparingly toothed leaf margins (usually 1–5 teeth), the weakly arched to straight ventral margin with the keel, and the perianths with less toothed keels.

Distribution. A palaeotropic species (Zhu and So 2001; Lai et al. 2008; Lee et al. 2013; Singh and Singh 2016; Shu et al. 2017; Pócs and Kovács 2019).

***Drepanolejeunea spicata* (Steph.) Grolle & R.L. Zhu**

Figure 5E

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19103

Identification. This species is easily separated from

other *Drepanolejeunea* species by the 5 long, tubular, horn-like keels of the perianths, falcate leaf lobes, 2 moniliate basal ocelli on the leaf lobes, and the horizontally spreading underleaf lobes, each 6–10 cells long.

Distribution. A common Indo-Malesian species distributed in Cambodia, China, India, Indonesia, Japan, Laos, Malaysia, Thailand, and Vietnam (Zhu et al. 1999; Lai et al. 2008; Lee et al. 2013; Shu et al. 2017; Söderström et al. 2020).

***Drepanolejeunea ternatensis* (Gottsche) Schiffn.**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 920 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1945.

Identification. This species is characterized by the strongly caducous leaves, falcate leaf lobes, crenulate to denticulate margin of leaf lobes, papillose keel, and constricted apex of leaf lobules.

Distribution. A broadly distributed Indo-Pacific species, from India to China to Australia, Papua New Guinea, and the Fiji Islands (Zhu and So 2001; Söderström et al. 2011; Lee et al. 2013; Singh and Singh 2016).

***Drepanolejeunea thwaitesiana* (Mitt.) Steph.**

Figure 5F

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 69 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19112

Identification. The numerous ocelli scattered in all parts of the plant except male bracts and perianths, the dentate dorsal margin of leaf lobes, and the obovate to obtriangular perianths with 3–5 wings are features that distinguish this species.

Distribution. An Indo-Malesian species widely distributed from Ceylon to New Guinea (Mizutani 1990; Lai et al. 2008; Lee et al. 2013; Singh and Singh 2016; Shu et al. 2017).

***Frullania apiculata* (Reinw., Blume & Nees) Nees**

Figure 6A

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 105 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19198.

Identification. This species is characterized by the apiculate apex of leaf lobes, the absence of moniliate ocelli, and the filiform, uniseriate, stylus 3–5 cells long.

Distribution. A paleotropic species, widely distributed in the tropical regions of Africa, Asia, Australia, and the Pacific islands (Zhu and So 2001; Söderström et al. 2011, 2020; Shu et al. 2017).

***Lejeunea adpressa* Nees**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E;

alt. 952 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1914.

Identification. A common species, recognized by the obovate perianths with 5 sharp keels, distant underleaves with lanceolate, divergent lobes, the smooth cuticle of leaf cells, the autoicy, and the glistening-botryoidal, *Calyptogeia*-type oil bodies.

Distribution. A pantropical distribution, known from tropical America, Africa, Asia, Australia, and the Pacific islands (Söderström et al. 2011; Lee 2013; Lee and Gradstein 2013; Shu et al. 2017; Gradstein 2021).

***Lejeunea micholitzii* Mizut.**

Figure 7F

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 69 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19151.

Identification. This species is recognized by the reniform, deeply bifid underleaves with acute lobes, the well-developed trigones and conspicuous intermediate thickenings, and the obovate perianths.

Distribution. A Malesian-Pacific species known from Sri Lanka to the Philippines and the Fiji Islands (Lee 2013; Lee and Gradstein 2013; Söderström et al. 2011; Shu et al. 2017).

***Lepidolejeunea bidentula* (Steph.) R.M. Schust.**

Figure 7G

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19204.

Identification. *Lepidolejeunea bidentula* is easily recognized by the numerous and scattered ocelli in the leaf lobes, underleaves, female bracts and bracteoles, the ocelli about as large as the leaf cells, the shallowly bifid underleaves, and the marginal rhizoids on the leaf margins.

Distribution. An Indo-Pacific species distributed from India to China, Papua New Guinea, and the Pacific islands (Zhu and So 2001; Lai et al. 2008; Söderström et al. 2011; Lee et al. 2013; Shu et al. 2017).

***Leptolejeunea amphiophthalmia* Zwickel**

Figure 5G

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19120.

Identification. The presence of scattered ocelli in the leaf lobes, lobules and underleaves, and the smooth cuticle of leaf cells are characteristic. When dry, the colorless ocelli turn to dark-reddish color, which is unique for this species and not known from any other member of the genus *Leptolejeunea*.

Distribution. A Southeast Asian species, distributed

from Indo-China to Borneo, New Guinea, and the Ryukyu Archipelago (Mizutani 1978; Yang and Lin 2008; Lee et al. 2013).

***Leptolejeunea subacuta* A.Evans**

Figure 7H

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 69 m; 19.IV.2019; S. Sarimi, E. Pesiú & G.E. Lee leg.; UMTF 19209.

Identification. *Leptolejeunea subacuta* is recognized by the obtuse to subacute leaf apices, the presence of one large basal ocellus, and the homogeneous oil bodies, 3–10 per leaf cell. This species is similar to *L. balansae*, but the latter differs in having the elliptic leaf lobes with three ocelli in a broken row, finely segmented oil bodies, and the presence of gemmae on dorsal surfaces of the leaf lobes.

Distribution. An Indo-Pacific species widely distributed in Asia and the Fiji Islands (Zhu and So 2001; Söderström et al. 2011, 2020; Lee et al. 2013; Shu et al. 2017; all as *L. elliptica*).

***Leptolejeunea epiphylla* (Mitt.) Steph.**

Fig. 7I

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 69 m; 19.IV.2019; S. Sarimi, E. Pesiú & G.E. Lee leg.; UMTF 19125.

Identification. Characteristic features are the truncate apex of leaf lobes, the strongly reduced leaf lobules, and the linear underleaf lobes which are usually 3–4 cells long and 1 cell wide throughout.

Distribution. A paleotropical species distributed from Africa to China, Papua New Guinea, and the Fiji Islands (Zhu and So 2001; Söderström et al. 2011, 2020; Lee et al. 2013; Shu et al. 2017).

***Leptolejeunea maculata* (Mitt.) Schiffn.**

Figure 8A

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiú & G.E. Lee leg.; UMTF 19118.

Identification. This species is recognized by its oblong leaf lobes, serrate margins of leaf lobes, large trigones, distinct intermediate thickenings (2–4 per cell), and 1–5 scattered ocelli in the leaf lobes.

Distribution. A paleotropic species (Zhu and So 2001; Söderström et al. 2011; Lee et al. 2013; Shu et al. 2017).

***Leptolejeunea vitrea* (Nees) Schiffn.**

Figure 5H

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiú & G.E. Lee leg.; UMTF 19116.

Identification. *Leptolejeunea vitrea* is often confused with *L. maculata*, but the former differs by having one large basal ocellus at the base of leaf lobes.

Distribution. An Indo-Pacific species distributed from Southeast Asia to China and the Pacific islands (Lai et al. 2008; Lee et al. 2013; Shu et al. 2017; Söderström et al. 2020).

***Metalejeunea cucullata* (Reinw., Blume & Nees)**

Grolle

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 65 m; 19.IV.2019; S. Sarimi, E. Pesiú & G.E. Lee leg.; UMTF 19151.

Identification. This species is characterised by its minute size, obovate-oblong leaf lobes, the crenulate keel of leaf lobules, the small, distant underleaves, and the pycnolejunoid innovations.

Distribution. A pantropical species (Zhu and So 2001; Lai et al. 2008; Söderström et al. 2011, 2020; Lee et al. 2013; Singh and Singh 2016; Shu et al. 2017; Pócs and Kovács 2019).

***Microlejeunea punctiformis* (Taylor) Steph.**

Figure 8B

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiú & G.E. Lee leg.; UMTF 19175.

Identification. This species is recognised by the small plant with thin stems (3 medullary cells in stem cross-section), the 1 or 2 basal ocelli on leaf lobes, the presence of male bracteoles throughout androecial shoot, and the winged keel of female bracts.

Distribution. An Indo-Pacific species distributed from Bhutan to China, Japan, and Australia (Zhu and So 2001 as *Lejeunea punctiformis*; Pócs and Lee 2016; Singh and Singh 2016; Shu et al. 2017).

***Radula acuminata* Steph.**

Figure 8D

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°35.809'N, 102°36.375'E; alt. 940 m; 19.IV.2019; S. Sarimi, E. Pesiú & G.E. Lee leg.; UMTF 1951

Identification. This is a common species, easily recognizable by the falcate-ovate leaf lobes with narrowly rounded apices, the triangular-ligulate leaf lobules, and the presence of discoid gemmae on ventral surface of leaf lobes.

Distribution. An Indo-Pacific species distributed from Nepal to China to the Philippines, Papua New Guinea, and the Fiji Islands (Zhu and So 2001; Söderström et al. 2011, 2020; Promma and Chantanaorrapint 2015; Singh and Singh 2016; Shu et al. 2017; Pócs and Kovács 2019).

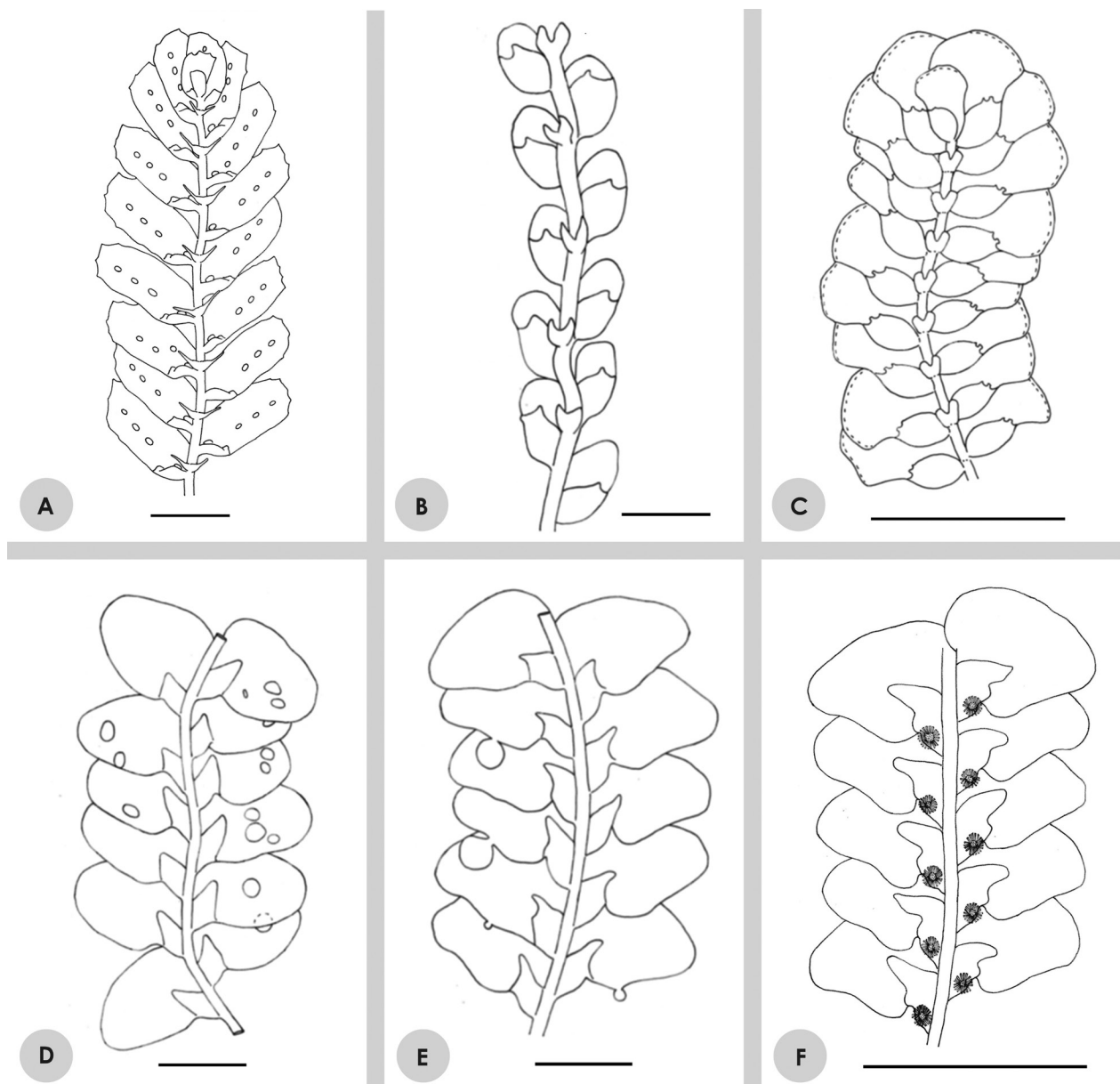


Figure 8. Epiphyllous liverworts from Mount Tebu Forest Reserve. **A.** *Leptolejeunea maculata*. **B.** *Microlejeunea punctiformis*. **C.** *Tuyamaella molischii*. **D.** *Radula acuminata*. **E.** *Radula assamica*. **F.** *Radula nymannii*. Scale bars: A, D, E = 500 μ m; B = 200 μ m; C, F = 1250 μ m.

***Radula assamica* Steph.**

Figure 8E

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1989.

Identification. Distinguishing characters are the falcate leaves with obtuse to rounded apices, the discoid gemmae developed at ventral margin of leaf lobes, and the triangular-ligulate leaf lobules.

Distribution. An Indo-Pacific species (Zhu and So 2001; Lai et al. 2008; Promma and Chantanaorrapint 2015; Shu et al. 2017).

***Radula nymannii* Steph.**

Figure 8F

Material examined. MALAYSIA – Terengganu • Besut,

Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E; alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19208.

Identification. This species is recognized by the inflated leaf lobules with the apices conspicuously elongated and abruptly turning away from the stem, numerous fasciculate rhizoids arising in the middle of leaf lobules, and the presence of discoid gemmae on ventral margin of leaf lobes.

Distribution. An Indo-Pacific species distributed from Southeast Asia to China, Papua New Guinea, New Caledonia, and Micronesia (Söderström et al. 2011; Promma and Chantanaorrapint 2015; Shu et al. 2017).

***Radula tjibodensis* K.I. Goebel**

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°37.832'N, 102°35.774'E;

alt. 89 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 19108

Identification. Characteristics of this species are the quadrate to subquadrate leaf lobules, discoid gemmae on the dorsal margin of leaf lobes, and thin-walled leaf cells with indistinct trigones.

Distribution. An Indo-Pacific species distributed from India to China, Papua New Guinea, New Caledonia, and the Fiji Islands (Zhu and So 2001; Lai et al. 2008; Söderström et al. 2011; Promma and Chantanaorrapint 2015; Shu et al. 2017).

***Tuyamaella molischii* (Schiffn.) S. Hatt.**

Figure 8C

Material examined. MALAYSIA – Terengganu • Besut, Mount Tebu Forest Reserve; 05°36.383'N, 102°36.189'E; alt. 780 m; 19.IV.2019; S. Sarimi, E. Pesiu & G.E. Lee leg.; UMTF 1967.

Identification. This species is characterized by the hyaline marginal cells of leaf lobes, the obcordate underleaves with obtuse apices, and the leaf lobules with 2 teeth and the hyaline papilla on the inner surface of first tooth.

Distribution. An Indo-Pacific species distributed from Southeast Asia to China, Japan, and the Pacific islands (Zhu and So 2001; Lee et al. 2013; Shu et al. 2017).

Discussion

Our study establishes the first checklist of epiphyllous bryophytes in Mount Tebu Forest Reserve. Forty-three species are newly recorded from Terengganu. The high number of epiphyllous liverwort species recorded in this area are indicative that the forest is still intact, with constant moisture and high humidity, which are favorable for epiphylls. However, the center of epiphyllous diversity on Peninsular Malaysia is in Pahang, where many areas are well explored compared to other states. Reasons for this possibly include safe and good road infrastructure in some of the highlands and montane forests in Pahang (e.g., Cameron Highlands, Genting Highlands, and Fraser's Hill), making these areas well accessible, while Terengganu is highly under-collected and bryologically little known (Lee et al. 2019).

Generally, epiphyllous mosses are much fewer than epiphyllous liverworts (Gradstein 1997). In our study, we found that the diversity of epiphyllous moss species is extremely lower than that of liverworts; 51 species of liverworts were collected but only three mosses were found. Similarly, in a rainforest on Bioko Island, Guinea, 55 epiphyllous liverworts were reported and only two mosses were found (Müller and Pócs 2007), and in El Salvador, 66 species of liverworts were recorded but only 12 mosses were found (Winkler 1967). The moss *Ephemeropsis tjobodensis* is thus far considered to be an obligate epiphyll, while *Taxithelium isocladum* and *Mitthyridium constrictum* are more facultative species that often grow

on twigs and tree trunks. Occasionally, *T. isocladum* is observed to grow on twigs and then spread to the leaf, indicating that some epiphyllous mosses are apparently struggling to colonize the leaf surface. Most of the liverwort species are firmly appressed onto the leaf surfaces (e.g., *Cololejeunea* and *Leptolejeunea* spp.). This flattened habit is an adaptation for gaining ample moisture from the surroundings and for maintaining moisture for a long period and preventing the rapid loss of water (Zhu and So 2001). Therefore, the success of many epiphyllous liverworts compared to mosses may reflect the fact that the liverworts have leaves in two rows supporting their establishment on the leaf while such characteristic is not seen in mosses.

Lejeuneaceae are known to form dense coverage on leaves in the rainforest and are the dominant members of epiphyllous bryophyte flora (Cornelissen and Gradstein 1990; Piippo 1994; Gradstein et al. 2006). Thus, the greatest number of epiphyllous species in Mount Tebu Forest Reserve, as expected, is in the family Lejeuneaceae. Possible adaptations of Lejeuneaceae are the protonematal spores which can germinate quickly, flattened habit and numerous rhizoids facilitating the attachment of the gametophyte onto the leaf, specialized lobule (or water sacs) with the water-holding function for maintaining the moisture levels, and asexual reproduction (Glime and Pócs 2018). According to Pócs (1996), the center of diversity for epiphyllous liverworts is different depending on the genera: for example, *Cololejeunea* species have the highest diversity in the Malesian archipelago, but *Ceratolejeunea* is more diverse in the Neotropics. Almost all the species in this study are Indo-Pacific in their distribution, while nine are palaeotropical (*Frullania apiculata*, *Cololejeunea falcata*, *C. floccosa*, *C. inflectens*, *C. lanciloba*, *Leptolejeunea epiphylla*, *L. maculata*, *Ephemeropsis tjobodensis*, and *Taxithelium isocladum*), and four species are pantropical (*Cheilolejeunea trifaria*, *Cololejeunea obliqua*, *Lejeunea adpressa*, and *Metalejeunea cucullata*). Moreover, *Radula grandilobula*, *Ceratolejeunea singaporensis*, *Ephemeropsis tjobodensis*, and *Taxithelium isocladum* are of Southeast Asian distribution while two are Malesian-Pacific species, *Drepanolejeunea longicornua* and *Lejeunea micholitzii*.

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Authors' Contributions

Conceptualization: GEL. Data curation: EP, SS, AS, CWK, GEL. Funding acquisition: NN. Investigation: EP, GEL. Methodology: EP, SS. Writing – original draft: EP, GEL. Writing – review and editing: MG, NN, TP.

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