

Morphological Diversity of Complex Thalloid Liverwort Genera of Sri Lanka

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ABSTRACT

As part of a study initiated to trace the evolutionary relationships and biogeographic affinities of Sri Lankan complex thalloid liverworts, we here present the morphological diversity of Sri Lankan complex thalloid liverworts. This serves as the first detailed taxonomic study of the group in Sri Lanka. Specimens were collected from different geographical regions covering almost all topographic and climatic zones of the country. This study revealed 9 genera of complex thalloid liverworts in Sri Lanka. Based on our collections and identifications we prepared a generic key to Sri Lankan complex thalloid liverworts. Taxonomic descriptions were prepared for all identified genera.

Keywords: Liverworts, taxonomy, morphology, Sri Lanka.

INTRODUCTION

The Democratic Socialist Republic of Sri Lanka, formerly known as Ceylon, is an island in the Indian Ocean with a total land area of 65, 610 km² (Myers, 1990; Meegaskumbura *et al.*, 2002; Daskon and Binns, 2010). This relatively small island claimed by Sir Arthur C. Clark as the “*Island jewel of Indian Ocean*” lies near the southwestern tip of India and shares the same continental shelf (Weerasooriya, 1988) (Fig. 1A).

Sri Lanka is a tropical country with a diverse topography and climate. Three major climatic zones are identified based on the mean annual precipitation; wet (2500-5500 mm of rain per annum), intermediate (1900-2500 mm) and dry (<1900 mm) (Dissanayake, 1991; Zubair, 2002) (Fig. 1C). The major topographical zones distinguished by the elevation include the central highlands (1060-2420 m), the plains (270-1060 m) and the coastal belt (0 -270 m) (Vithanage, 1970) (Fig. 1B). There is a wide range of ecosystems due to this topographic and climatic heterogeneity of the country and the main types of ecosystems of Sri Lanka include forests, grasslands, aquatic, coastal and marine. These different ecosystems harbor a great variety of genera and species of plants and animals. The Western Ghats of India and Sri Lanka together form a biogeographic unit sharing a high endemism in flora and fauna and is one of the major biodiversity hotspots in the world (Myers, 1990; Meegaskumbura *et al.*, 2002; Bossuyt *et al.*, 2004). Thirty percent of Sri Lankan flowering plants are endemic to the country and nearly 75% of these occur in the Sinharaja Forest Reserve, a world

heritage site designated by UNESCO (Myers, 1990). According to floristic endemism records, ~70% of evergreen trees, 40% of lianas and 11% of mosses are endemic to the country (Gunawardene *et al.*, 2007; O’Shea, 2003). Many studies have been carried out on Sri Lankan flowering plants (Murawski *et al.*, 1994; Dayanandan *et al.*, 1999; Rubasinghe *et al.*, 2005). However, the bryophyte flora of Sri Lanka remains poorly studied. The first checklists of bryophytes of Sri Lanka were published by B. A. Abeywickrama in 1978 as compilations of a limited number of literature (Abeywickrama and Jansen, 1978 a and b; Pethiyagoda, 2011; Long and Rubasinghe, 2014; Rubasinghe and Long, 2014). Historical records on Sri Lankan bryophyte collections date back to 18th century (Rubasinghe and Long, 2014; Long and Rubasinghe, 2014; Ruklani and Rubasinghe, 2013).

Almost all the bryophyte collectors in the past were from foreign countries, and a detailed description of these collectors and their studies is given in Rubasinghe and Long (2014). A considerable percentage of bryophytes collected in the past remain in different herbaria throughout the continents and the National Herbarium of Sri Lanka contains only a few specimens (Table 1).

Although many taxonomic refinements have occurred within the past few years based on molecular phylogenetics, most of the specimens in the National Herbarium still bear older synonyms and some remain erroneously identified. There is a general scarcity of literature sources with detailed descriptions on bryophytes in Sri Lanka.

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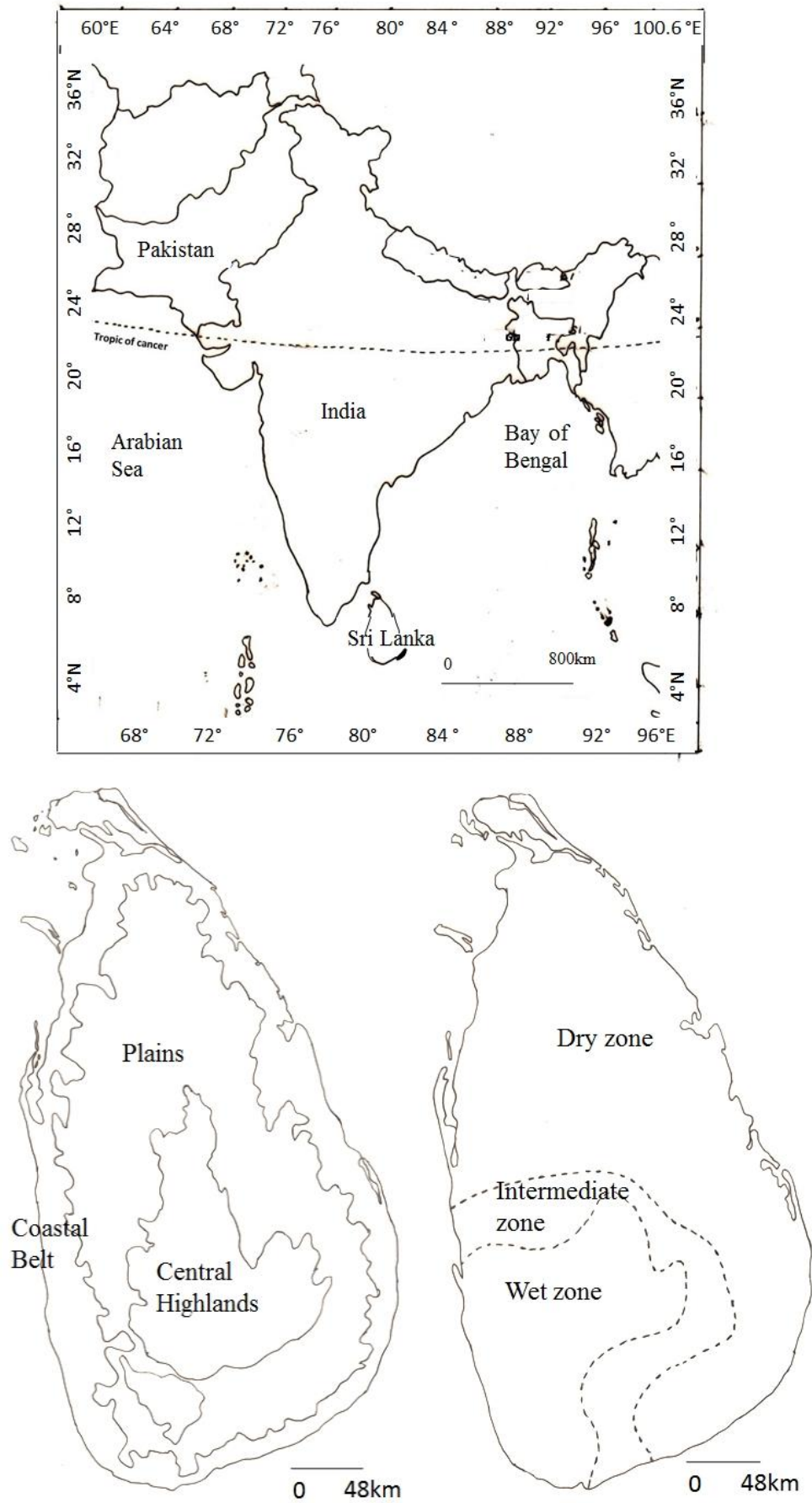


Figure 1. Maps showing (A) the geographic location, (B) topographical zones, (C) climatic zones of Sri Lanka.

The checklist of mosses of Sri Lanka was updated in 2002 by B.J. O'Shea (O'Shea, 2002). Long and Rubasinghe updated the checklist of liverworts and hornworts of Sri Lanka in 2014. However, there are no records on endemic liverworts and hornworts and these two groups of bryophytes are the least studied groups of bryophytes in Sri Lanka (Gunawardene *et al.*, 2007; Rubasinghe and Long, 2014). The liverwort checklist of Abeywickrama and Jansen (1978 a) includes 16 species of complex thalloids in 9 genera and 4 families (Abeywickrama and Jansen, 1978 a). According to the most recently updated checklist of liverworts and hornworts complex thalloids in Sri Lanka consist of 9 families; Aytoniaceae, Blasiaceae, Cyathodiaceae, Dumortieraceae, Exormothecaceae, Lunulariaceae, Marchantiaceae, Ricciaceae and Targioniaceae, 10 genera: *Plagiochasma* and *Reboulia*, *Blasia*, *Cyathodium*, *Exormotheca*, *Lunularia*, *Marchantia*, *Riccia* and *Targionia* and 17 species (Long and Rubasinghe, 2014). Classification of all the liverworts in the earliest checklist (Abeywickrama and Jansen, 1978 a) was based on Evans (1939) where *Marchantia*, *Lunularia*, *Exormotheca* and *Dumortiera* were included under the broad family Marchantiaceae and *Plagiochasma* and *Reboulia* were listed under the family Grimaldiaceae. The genus *Cyathodium* was included under the family Targioniaceae along with *Targionia*. There is no record of the genus *Blasia* in the checklist by Abeywickrama and Jansen (1978 a), although it is mentioned in Long and Rubasinghe (2014) based on the publication of Hattori in 1968 who reported a specimen of *Blasia pusilla* from Sri Lanka. Complex thalloids recorded in Abeywickrama and

Jansen (1978 a) and Abeywickrama (1959) are based mainly on the literature "*Hepaticae Indiae Orientalis*" (1860) (Hepatics of Eastern India) by W. Mitten and *Species Hepaticarum I* (1898-1925) by F. Stephani. Long and Rubasinghe (2014) compiled all the available literature reports of Sri Lankan complex thalloids up to the present. However, there is no Flora for Sri Lankan bryophytes, nor taxonomic descriptions for any of the families, genera or species.

The present study was initiated to evaluate the taxonomy, phylogeny and biogeography of the islands' liverwort and hornwort flora. As a part of this pilot study we aim to present the morphological diversity of Sri Lankan complex thalloid liverworts based on new field collections.

MATERIALS AND METHODS

Taxon sampling: A thorough literature survey was carried out to trace all past collection sites of complex thalloid liverworts in Sri Lanka. Taxon sampling was made to include all past collection sites as well as new unexplored localities within the country (Fig. 2). Fresh samples were collected along with the substrate using a penknife; wrapped in paper tissues and stored in paper packets prepared according to the Schofield (1985) method. Photographs of the fresh specimens were taken in the field at the time of collection using Nikon D3200 and Nikon D3100 digital cameras.

Table 1. Details of specimens deposited at the National Herbarium, Peradeniya, Sri Lanka.

Name as sited on the herbarium packet	Collector/Specimen number	Year of Collection	Locality
<i>Marchantia palmata</i>	A. H. G. Alston	1927	Rangala
<i>Marchantia</i> sp.	A. H. G. Alston	1925	Near Peradeniya
<i>Marchantia</i> sp.	M. Fleischer	1898	Hantana
<i>M. lecordiana</i>	M. Fleischer	1898	Peradeniya
<i>Lunularia cruciata</i>	A. H. G. Alston	1925	Hakgala
<i>Dumortiera hirsuta</i>	A. H. G. Alston	1925	Kandy
<i>Plagiochasma rupestre</i>	A. H. G. Alston	1925	Peradeniya
<i>Riccia crispatula</i>	G. Gardner	1844	Matale
<i>Riccia</i> sp.	A. H. G. Alston	1925	Peradeniya

Geo-referencing data were recorded using a Garmin Global Positioning System navigator (GPS), along with locality and habitat information, collection and collectors' details. All specimens collected were initially observed using dissecting (Hertel and Reus-Optik Kassel) and light (Eruomex, Arnhem, Holland) microscopes. Observations of detailed cellular characters were made using Olympus CX21FS1 compound microscope and Accu-scope 3025PH-BE-CS Stereomicroscope. Based on the vegetative, reproductive and spore morphological characters observed specimens were identified to their generic/specific level and a taxonomic key was

prepared for Sri Lankan complex thalloid liverwort genera. Taxonomic descriptions along with photographs were prepared for all the genera identified.

RESULTS AND DISCUSSION

A total of 84 specimens of complex thalloids were collected and identified during field excursions. These represented 9 genera of complex thalloid liverworts. A synopsis of complex thalloid liverworts collected is given in Table 2.

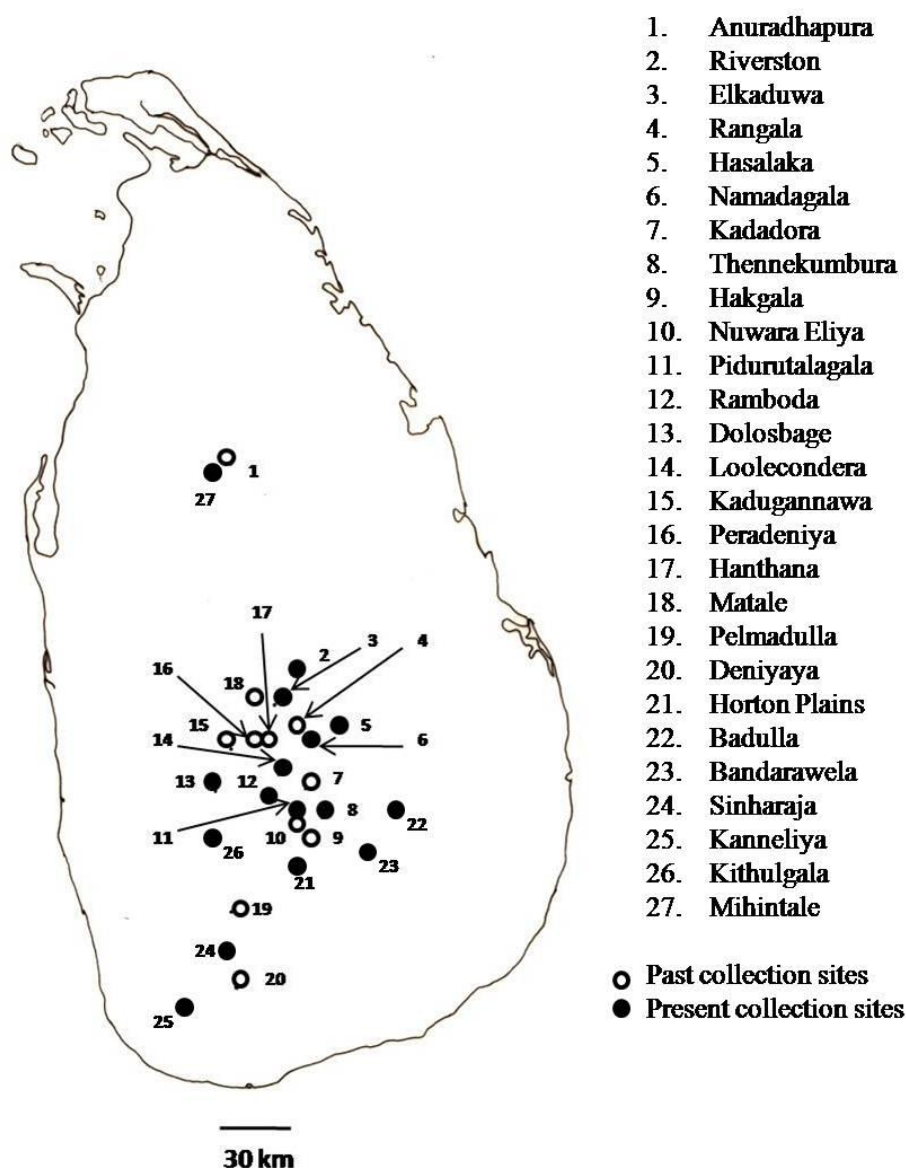


Figure 2. Map of Sri Lanka showing the taxon sampling sites.

Table 2. Synopsis of complex thalloid liverworts encountered during the present study

Order	Family	Genus	Species
Lunulariales D.G. Long	Lunulariaceae H. Klinggr	<i>Lunularia</i> Adans.	<i>L. cruciata</i> (L.) Dumort. ex Lindb.
Marchantiales Limpr.	Cyathodiaceae Stotler and Crand.-Stotl.	Cyathodium Kunze	<i>Cyathodium</i> sp.
	Marchantiaceae Lindl.	<i>Marchantia</i> L.	<i>M. paleacea</i> Bertol. <i>M. polymorpha</i> L.
	Aytoniaceae Cavers	<i>Plagiochasma</i> Lehm. and Lindenb. <i>Reboulia</i> Raddi	<i>P. rupestre</i> (G.Forst.) Steph. <i>R. hemisphaerica</i> (L.) Raddi
	Ricciaceae Rchb.	<i>Riccia</i> L.	<i>Riccia</i> sp.
	Exormothecaceae Muñ. Il. Frib. ex Grolle	<i>Exormotheca</i> Mitt.	<i>E. ceylonensis</i> Meijer
	Dumortieraceae D. G. Long	<i>Dumortiera</i> Nees	<i>D. hirsuta</i> (Sw.) Nees.
	Targioiniaceae Dumort	<i>Targionia</i> L.	<i>T. hypophylla</i> L.

Key to Sri Lankan complex thalloid liverwort genera based on gametophytic and sporophytic characters observed

1. Thallus simple, without dorsiventral differentiation; wing margins “leaf-like” with longitudinally inserted lobes; air chambers and air pores absent; ventral scales without appendages, in two rows on midrib; two types of gemmae present; rhizoids smooth; oil bodies absent or few in unspecialized cells; dioicous; antheridia arranged in two rows, partially embedded dorsally on thallus ***Blasia***
1. Thallus usually differentiated into layers, air chambers air pores present (rarely absent); ventral scales when present in 2–10 rows (sometimes absent), usually with appendages; gemmae present or absent, one type if present; rhizoids usually in one or two types, smooth and pegged, specialized oil cells usually present; monoicous or dioicous; antheridia embedded dorsally in thallus or on stalked receptacles 2
2. Archegonia scattered or loosely aggregated in a dorsal groove, a cavity or a thallus depression, or in an involucre below and beyond the thallus apex 3
2. Archegonia in well-defined cushions with several archegonial cavities, the cushions developing after fertilization into stalked archegoniophores, or archegonia initiated on ventral side of stalked archegoniophores 5
3. Archegonia and sporophytes scattered or in 2-3 rows in dorsal groove, involucre and scales lacking. Antheridia scattered or in a dorsal groove ***Riccia***
3. Archegonia and sporophytes in an involucre below and beyond thallus apex. 4
4. Thallus broadened towards the apex; margin and ventral surface of the thallus without purplish pigmentation, with tubers. Epidermal pores a simple opening among epidermal cells, without hyaline inner ring. Air chambers in 1 layer without chlorophyllose elements. Basal tissue restricted to ventral epidermis or to 1-2 cell layers. Ventral scales small, without or with filiform appendage ***Cyathodium***
4. Thallus linear; margin and ventral surface of the thallus purplish, without tubers. Epidermal pores bounded by 1-3 concentric rings of cells, with hyaline inner ring. Air chambers in 1 layer, with chlorophyllose filaments. Basal thallus tissue thick. Ventral scales large, with conspicuous, lanceolate-triangular appendage ***Targionia***
5. Epidermal pores with 1 ring of differentiated cells, with or without a hyaline inner ring; Epidermal pores strongly elevated above epidermis ***Exormotheca***
6. Epidermal pores with several concentric rings of cells and a hyaline inner ring, or compound, rarely

- vestigial or absent.6
7. Epidermal pores with 1 or several concentric rings of cells. Antheridiophores not produced; ventral scales in two rows7
6. Epidermal pores compound, absent or vestigial. Antheridiophores produced. Ventral scales in 2-6 rows 9
8. Air chambers in 1 layer, with chlorophyllose filaments. Ventral scales with a single, reniform appendage. Gemmae in crescent-shaped (semilunar shaped) gemma cups **Lunularia**
7. Air chambers in 1 or 2 without chlorophyllose filaments. Ventral scales with 1-4, ovate, lanceolate, or filiform appendages. Gemmae lacking8
9. Antheridia dorsal, terminal or on small ventral branches, in cushions or in irregular groups, scales few. Archegoniophores terminal, stalk with single rhizoid furrow. Ventral scales with 2 or 3 filiform appendages.....**Reboulia**
8. Antheridia in dorsal cushions bounded by conspicuous scales. Archegoniophores dorsal, stalk without rhizoid furrow Ventral scales with 1 or 2 ovate to lanceolate appendages**Plagiochasma**
10. Epidermal pores, and air chambers well developed, the pores compound. Ventral scales large, with 4-6 appendages, laminal scales with or without apical papillae. Bristles lacking. Cup shaped gemma cups produced**Marchantia**
9. Epidermal pores, and air chambers absent or vestigial. Ventral scales small, without marginal papillae; no laminal scales. Bristles on ventral side of thallus and male and female receptacles. Gemma cups not produced.**Dumortiera**

Taxonomic descriptions for all the specimens identified are given with relevant illustrations according to the order given in Table 2.

Family Lunulariaceae H. Klinggr

Genus *Lunularia* Adans., Familles des Plantes 2: 15. 1763.

The *gametophytic thalli* of *Lunularia* are yellowish green or green and dichotomously branched, margin often undulated (Fig. 3A). *Gemma cups* are crescent-shaped (Fig. 3B). Epidermal pores are simple and distinct with 5 - 7 cells in 3 - 5 rings. *Ventral tissue* lacks mucilage cavities. *Ventral scales* are in two rows, hyaline, lunate with a reniform appendage. *Antheridia* terminal and sessile *Archegoniophore* receptacle four-lobed, stalk without rhizoid furrows.

Lunularia is the only genus retaining under the family Lunulariaceae (Bischler-Causse *et al.*, 2005; Long, 2006; Crandall-Stotler *et al.*, 2009). The genus is so called because of the lunate shaped gemma cups (in Latin, *lunularis*= a little moon) (Bischler-Causse *et al.*, 2005; Senning, 2006). *Lunularia* is a monospecific genus with the single species *L. cruciata* (L.) Dumort. ex Lindb. and it is recorded from Sri Lanka. *Lunularia cruciata* has been collected by A. H. G. Alston (1902-1958) from Hakgala Botanic Gardens, Sri Lanka. *Lunularia* is often associated with human activities and is probably an accidental introduction from Europe.

Family Cyathodiaceae Stotler & Crand. Stotl.

Genus *Cyathodium* Kunze Novarum *et* Minus Cognitarum Stirpium Pugillus 6: 17. 1834.

Thalli of *Cyathodium* are delicate in texture, shiny yellowish green or light green, not tinged with purple, the ventral surface of thalli is whitish, and plants often form incomplete rosettes (Fig. 3C, D and E). *Epidermal pores* are simple with 5 - 7 cells in a single ring. *Ventral tissue* is reduced. Ventral scales are indistinct, hyaline, with or without appendages. *Antheridia* are embedded in the thalli. *Archegonia* are borne in archegonial cavities on the ventral surface near the thallus apex. *Sporophyte* is protected with a mostly bivalved involucre with a rim of brown pigmented cells (Fig. 3F). *Spores* are brown, granulate or baculate with an indistinct trilete scar.

The generic name was established in 1834 referring to *cyathus* which means “cup”; *kyathos* (ladle or cup) + *-odes* (similar to), i.e. similar to a cup (Bischler-Causse *et al.*, 2005; Meagher, 2008). Srivastava and Dixit (1996) treat 11 species under the genus in which the two species, *Cyathodium cavernarum* Kunze and *C. foetidissimum* Schiffn. are pantropical (Salazar Allen and Korpelainen, 2001; Allen *et al.*, 2004; Duckett and Ligrone, 2006) and 8 species are distributed in the Neotropics and Palaeotropics or Asia (Long, 1987; Allen and Korpelainen, 2006). There are two species recorded in Sri Lanka which are *C. cavernarum* and *C. smaragdinum* Schiffn. Ex Keissl (Srivastava and Dixit, 1996; Ruklani and

Rubasinghe, 2013; Long and Rubasinghe, 2014).- *Cyathodium cavernarum* is not recorded by Abeywickrama and Jansen (1978 a) although it is recorded by Long and Rubasinghe (2014). Srivastava and Dixit (1996) included records of *C. cavernarum* from a temple in Anuradhapura, Sri Lanka. There are no specimens of either two of these species in the National Herbarium (PDN).

Family Marchantiaceae Lindl.

Genus *Marchantia* L., Species Plantarum 2: 1137. 1753.

The gametophytic thalli of Marchantia species in Sri Lanka are bluish green, yellowish green, green or dark green, sometimes tinged with purple and dichotomously branching (Fig. 4A – F). Epidermal pores compound often with 4 rings of cells with 4-8 cells.



Figure 3. *Lunularia cruciata* (A) Gametophytic thallus (B) Lunate gemma cups with gemmae; *Cyathodium* sp. (C – E) Gametophytic thalli (F) Sporophytes on the ventral thallus.

Inner pore opening round, polygonal, ellipsoid or cruciate. *Ventral tissue* with or without mucilage cavities. *Rhizoids* in 2 or 3 types. *Ventral scales* in 4-6 rows. *Median scales* with a hyaline, yellow, purplish or pink appendage with or without marginal teeth. *Laminal scales* with or without apical papillae. *Archegoniophore* stalked, receptacle symmetrical or asymmetrical, shallowly or deeply divided into terete rays or 4-10 lobes, with or without a median projection (Fig. 5A – E). *Antheridiophore* stalked or sessile, receptacle peltate or palmate (Fig. 5F). *Involucres* alternate with lobes or locate underneath lobes. *Spores* polymorphic or not. *Gemma cups* are cup- shaped with entire or ciliate lobes (Fig. 5G).

Marchantia was first published in the first edition of *Species Plantarum* by Carl von Linnaeus (1707-1778) in 1753 introducing 7 species under the genus (Linnaeus, 1753; Evans, 1917): *M. polymorpha*, *M. chenopoda*, *M. cruciate* (the basionym of *Lunularia cruciata* (L.) Dumort. ex Lindb.), *M. tenella* (basionym of *Asterella tenella* (L.) P. Beauv.), *M. hemisphaerica* (basionym of *Reboulia hemisphaerica* (L.) Raddi), *M. conica* (basionym of *Conocephalum conicum* (L.) Underw.) and *M. androgyna* (basionym of *Mannia androgyna* (L.) A. Evans). Among these species only *M. polymorpha* and *M. chenopoda* remain in the genus today (Evans, 1917). There are 36 species under the genus *Marchantia* with a worldwide distribution (Bischler, 1998; Ho, 2013; Iamonico and Iberville, 2013).

The genus *Marchantia* is subdivided into subgenera and sections according to the morphological characters of both gametophyte and sporophyte

(Bischler, 1989) (Fig. 10).

Marchantia species recorded in Sri Lanka represent all the three subgenera: *M. polymorpha* (subg. *Marchantia*) (Figs. 4B and 6A), *M. paleacea* (subg. *Chlamidium*, sect. *Paleaceae*) (Fig. 4A), *M. pappeana* subsp. *robusta*, previously known as *M. robusta* (subg. *Chlamidium*, sect. *Chlamidium*), *M. papillata* (subg. *Chlamidium*, sect. *Papillatae*) and *M. acaulis* (subg. *Protomarchantia*, sect. *Protomarchantia*). Therefore, they are quite distinct from each other in morphology. *M. geminata* recorded by Abeywickrama and Jansen (1978 a) refers to *M. acaulis* as indicated in Long and Rubasinghe (2014). Both *M. amboinensis* and *M. palmata* in Abeywickrama and Jansen (1978 a) and Ruklani and Rubasinghe (2013) are synonymized under *M. emarginata* (Bischler-Causse, 1989; Long and Rubasinghe, 2014). *Marchantia linearis* in Abeywickrama and Jansen (1978 a) is a misidentification of *M. papillata* subsp. *grossibarba* (Long and Rubasinghe, 2014). The type specimen of *Marchantia robusta* was collected in Sri Lanka, however no duplicate exists in the National Herbarium, Peradeniya. According to the literature and data from the National Herbarium, Peradeniya, all records of Sri Lankan *Marchantia* species are collected from the Central Province and they belong to the collections of A. H. G. Alston (1902 - 1958), M. Fleischer (1861-1930), and F. Schmid (1811-1890). Nomenclature of most herbarium specimens has not been updated to follow the latest classifications and some of them remain as unidentified specimens. Only a limited number of specimens of the recorded species are available at the National Herbarium, Peradeniya (Table 1).

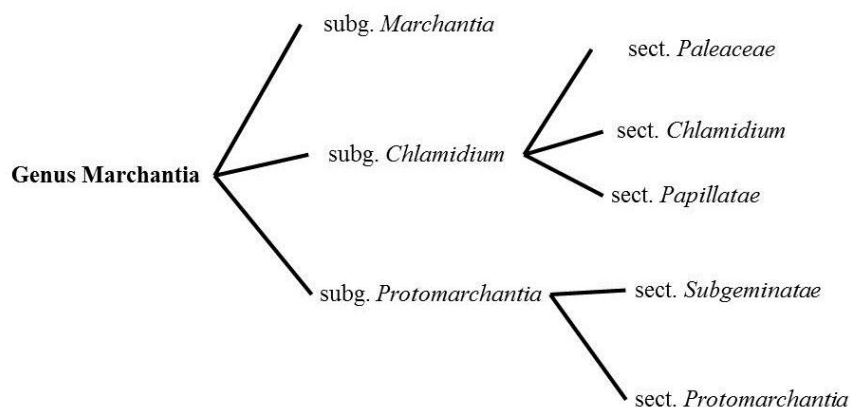


Figure 10. Classification of the genus *Marchantia* L. based on Bischler, 1989.



Figure 4. (A) Gametophytic thalli of *Marchantia paleacea*. (B) Gametophytic thalli of *M. polymorpha*. (C – F) Different gametophytic thalli morphologies of *Marchantia* sp.

Family Aytoniaceae Cavers

Genus *Plagiochasma* Lehm. & Lindenb., Novarum et Minus Cognitarum Stirpium Pugillus 4: 13. 1832.

Thallus usually grayish green to green (Fig. 6A, B and C). *Ventral surface* of the thallus often dark purplish. *Epidermal pores* simple with a single ring of 4 cells. *Ventral tissue* without mucilage cavities. *Ventral scales* in two rows with ovate to lanceolate appendages. *Appendages* light pink to hyaline, not constricted at base. *Antheridia* dorsal, in cushions along the thallus mid axis (Fig. 6D).

Archegonia dorsal, in cushions. *Archegoniophore* stalk dorsal, without rhizoid furrows. Sporophyte with globose capsules turning to brown with maturity (Figs. 6E and F). *Spores* brownish with tuberculate areoles and a distinct trilete marking.

The name *Plagiochasma* is derived from combination of two Greek terms: “*plagios*” = lateral, and “*chasma*” = opening which refers to the bilabiate involucre with lateral dehiscence (Frye and Clark, 1937; Bischler-Causse *et al.*, 2005). According to Bischler-Causse (1979) there are 30 species recognized under the genus.



Figure 5. *Marchantia* sp. (A – E) Different morphologies in female receptacles (F) A male receptacle (G) A gemma cup with gemmae.

There are two subgenera under *Plagiochasma*: *Plagiochasma* and *Micropylum* (Bischler-Causse *et al.*, 2005). Abeywickrama and Jansen (1978 a) have recorded *Plagiochasma nepalense* as the only recorded species under the genus. *Plagiochasma nepalense* (Lehm.) Steph., which was first described in Stephani (1898) is now accepted as a synonym under *Plagiochasma rupestre* (G.Forst.) Steph. (Bischler-Causse, 1979; Bapna and Kachroo, 2000). *Plagiochasma rupestre* represents the subgen. *Micropylum* and it is the only species recorded up to date in Sri Lanka (Bapna and Kachroo, 2000; Bischler-Causse *et al.*, 2005; Long

and Rubasinghe, 2014). The specimen of *Plagiochasma* collected by F. Schmid in 1954 from Mount Vernon, Central Province was determined by Sinske Hattori (1915-1992) a Japanese hepaticologist, as *P. nepalense* and a new record for Sri Lanka (Hattori, 1968). In the National herbarium of Sri Lanka all the specimens of *Plagiochasma* are referred to the synonymous genus *Aytonia* and they include the collections of A. H. G. Alston only. *Aytonia rupestris* G. Forst. was the basionym for *P. rupestre* (Stephani, 1898; Alam *et al.*, 2013).

Genus *Reboulia* Raddi, Opuscoliscientificid'una Società di professoridella Pontifical Università di Bologna 2: 357. 1818.

Thalli of *Reboulia* green to dull green in colour, tinged with purple (Fig. 7A – C). *Epidermal cells* with bulging trigones. *Epidermal pores* simple, with 5 to 8 cells in 4 or 5 rings, inner opening hexagonal pentagonal or spherical. *Air chambers* distributed thorough several layers without

chlorophyllose filaments. *Ventral tissue* without mucilage cavities. *Ventral scales* in two rows, metallic purple in colour, with oil cells and 2 or 3 filiform appendages. *Antheridia* dorsal or terminal on main or ventral branches, in cushions (Fig. 7D). *Spores* brown in colour, with distinct areoles on distal face. *Archegonia* not observed. Fresh specimens of *Reboulia* have a distinct aroma and a sweet taste when crushed.



Figure 6. *Plagiochasma rupestre* (A) A massive population (B) Thallus margins tinged with purple colour (C) Immature gematophytic thalli (D) Antheridia bound by scales (E) Archegoniophore bearing sporophytes (F) Mature archegoniophore.

The generic name is dedicated by the author to Eugen de Reboul (1781-1851), an Italian botanist from Florence (Little, 1949; Bischler-Causse *et al.*, 2005; Meagher, 2008). The only recorded species in Sri Lanka under the genus is *Reboulia hemisphaerica* (L.) Raddi, the type of the genus (Bischler, 2004; Bischler-Causse *et al.*, 2005; Long and Rubasinghe, 2014). There are herbarium specimens of *Reboulia* contributed by A. H. G. Alston in the National Herbarium. Alston's collections of *Reboulia* are recorded from Hakgala. The collection of M. Onraedt (1904-1998), who was the first to record *R. hemisphaerica* in Sri Lanka, is not present in the National Herbarium (Onraedt, 1981). However, during the present study the species was collected from several localities.

Family Ricciaceae Rchb.

Genus *Riccia* L., Species Plantarum 2: 1138. 1753.

Thalli yellowish green, bluish green or green forming rosettes or patches with or without a prominent sulcus dorsally, margin often tinged with purple both dorsally and ventrally (Fig. 7E). *Epidermal pores* not differentiated. *Ventral tissue* thick. *Ventral scales* purplish or hyaline in two rows. *Antheridia* and *archegonia* scattered. *Sporophyte* dorsally or ventrally emerging (Fig. 7F). *Spores* often brown in colour with or without a distinct trilete scar.

Riccia is the largest genus of Marchantiales comprising about 150 species (Bischler-Causse *et al.*, 2005). The generic name is dedicated to Pietro Francesco Ricci, the Italian senator and member of the Botanical Society of Florence (Kolkwitz, 1935; Crum, 1991; Bischler-Causse *et al.*, 2005). The genus *Riccia* consists of the subgenera: *Euriccia*, *Leptoriccia*, *Riccia*, *Ricciella*, *Thallocarpus*. There are 6 species recorded in Sri Lanka under *Riccia*: *R. attenuata* Pandé (subgen. *Ricciella*), *R. billardieri* Mont. & Nees (subgen. *Euriccia*), *R. crispatula* Mitt., *R. discolor* Lehm. & Lindenb. (subgen. *Euriccia*), *R. huebeneriana* Lindenb. (subgen. *Ricciella*) and *R. sorocarpa* Bisch (subgen. *Riccia*). Abeywickrama and Jansen (1978 a) record only four species under the genus; *R. crispatula*, *R. billardieri*, *R. attenuata* and *R. discolor*. The type of *R. crispatula* has been collected by the Scottish surgeon-botanist G. Gardner (1810-1849) from Matale, Sri Lanka (Martill *et al.*, 2007; Rubasinghe and Long, 2014) (Table 1).

Family Sematophyllaceae

Family Exormothecaceae Mu"ll. Frib. ex Grolle
Exormotheca Mitt., Natural History of the Azores, or Western Islands 325. 1870.

Thalli of *Exormotheca* in Sri Lanka green or

whitish green in colour (Fig. 8A, B and C). *Epidermal pores* are distinct and highly elevated. *Air chambers* contain chlorophyllose filaments. *Ventral tissue* with mucilage cavities. *Ventral scales* hyaline, without appendages. *Antheridia* are grouped and sunken in the median furrow of the thalli. *Archegonia* with 2-lobed receptacles, archegoniophore stalk with 1 rhizoid furrow (Fig. 8D and E). *Spores* brown in colour, areolate with tubercles at margin.

The name *Exormotheca* is derived from "exormos" = extruded, "theca" = capsule, referring to the short-exserted capsules (Bischler-Causse *et al.*, 2005). Willem Meijer (1923 – 2003) was the first person to record a species under *Exormotheca* in Sri Lanka. In Meijer, (1956) it is mentioned that the specimen was sent to Meijer by Prof. Abeywickrama along with some other hepatics for determination. That *Exormotheca* species had unique characters that deviate from the characters of other species mentioned in Schiffner's monograph of *Exormotheca* (Meijer, 1956). Therefore Meijer described it as a new species, *Exormotheca ceylonensis* which is the only recorded species under the genus in Sri Lanka (Fig. 8). *Exormotheca ceylonensis* is confined to the Western Ghats of India and Sri Lanka and now it is known as a threatened and rare liverwort in India (Udar and Chandra, 1964; Alam *et al.*, 2012). Prof. Abeywickrama has collected *Exormotheca* from 3 localities in Sri Lanka; Kadugannawa, Hakgala and Kadadora (Meijer, 1956). Hattori, 1968 records *E. ceylonensis* from two other localities Galagedara and Urugala (Central Province), collected by F. Schmid.

Family Dumortieraceae D. G. Long

Genus *Dumortiera* Nees, Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia Ephemeridessive Observationes Historias et Experimenta 12: 410. 1824.

Thalli of *Dumortiera* dark green in colour with bristles along the margin, dichotomously branched at the apical main thallus (Fig. 9A). *Epidermal pores* and *air chambers* absent. *Ventral tissue* without mucilage cavities. *Ventral scales* indistinct, small and hyaline, in two rows. *Antheridiophore* with disk shaped receptacles with bristles along the margin and dorsal side, concave at the middle, short stalked or sessile (Fig. 9B). *Archegoniophores* with 6-9 lobed receptacles with bristles, archegoniophore stalk with two rhizoid furrows (Fig. 9C and D). *Spores* brown in colour and tuberculate proximally.

The name *Dumortiera* was dedicated by the author to Count B. C. J. Dumortier (1797- 1878), a Belgian politician and botanist for the specimens

that had been previously determined as *Marchantia hirsuta* Sw. (Evans, 1919; Bischler-Causse *et al.*, 2005; Gledhill, 2008). There is only one recorded species in Sri Lanka under the genus and that is *Dumortiera hirsuta* (Sw.) Nees. Evans (1919) mentions that some specimens from Sri Lanka seemed to be different from *D. hirsuta* but looked like *D. irrigua* (Wilson) Nees. However

Stephani has included *D. irrigua* among the synonyms under *D. hirsuta* (Evans, 1919; Santarelli, 1958; Perold, 1993). Hattori (1968) records *Dumortiera hirsuta* var. *nepalensis* in the collection of F. Schmid from Kandy (Central Province), Deniyaya (Southern Province) and Pelmadulla (Sabaragamuwa Province).

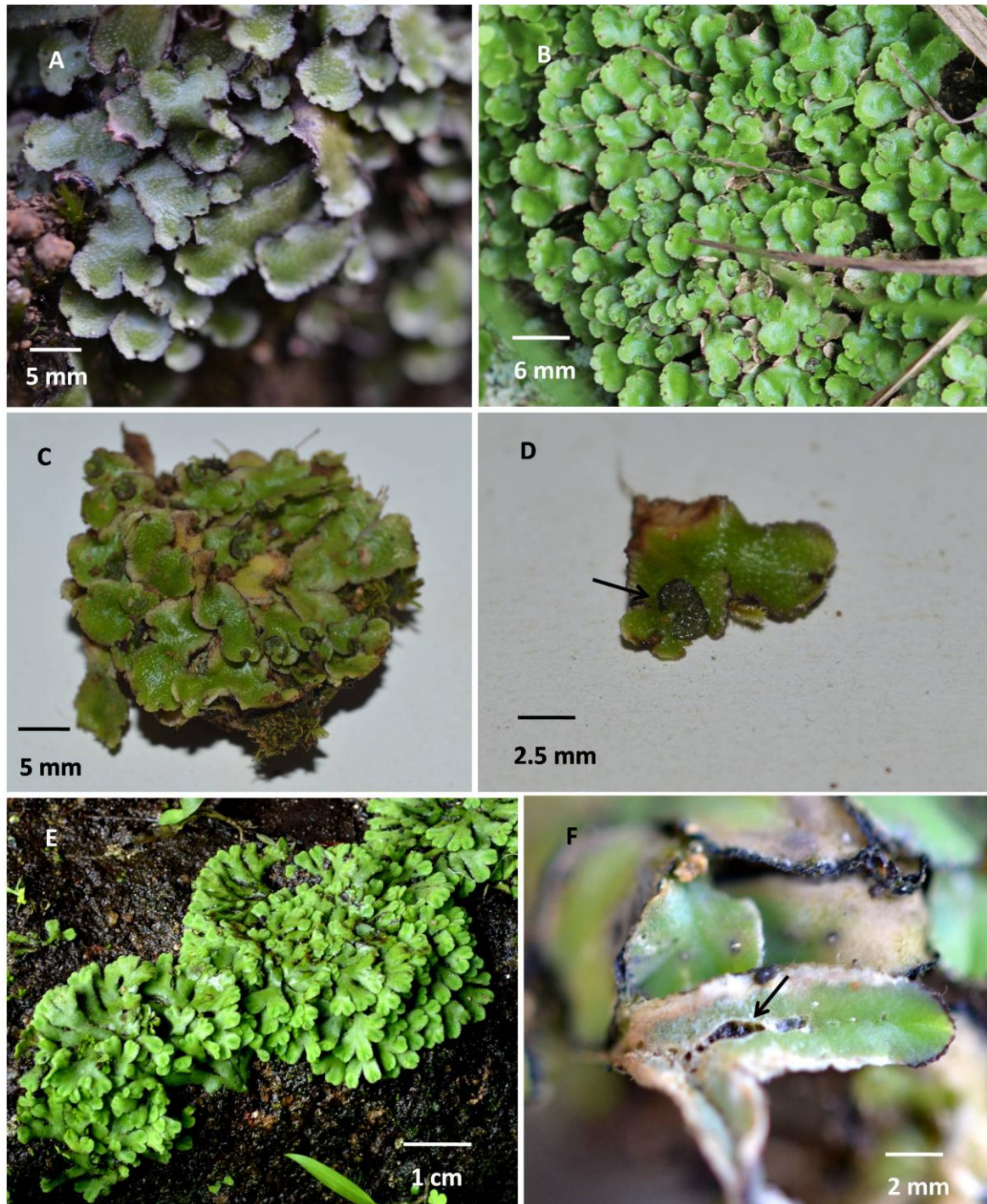


Figure 7. *Reoulia hemisphaerica* (A – C). Gametophytic thalli (D) Antheridia in cushions (E) Gametophytic thalli of *Riccia* sp. (F) Embedded sporophytes on the dorsal thalli of *Riccia* sp.

Checklists of Liverworts in Sri Lanka, 1978 and 2014 do not mention any varieties of *Dumortiera hirsuta*. But it is probable that different varieties of *D. hirsuta* to occur in the country. The existing

herbarium specimens of *Dumortiera* in the National Herbarium are collections of Alston and G. Gardner (1810-1949) from Kandy district (Table 1).

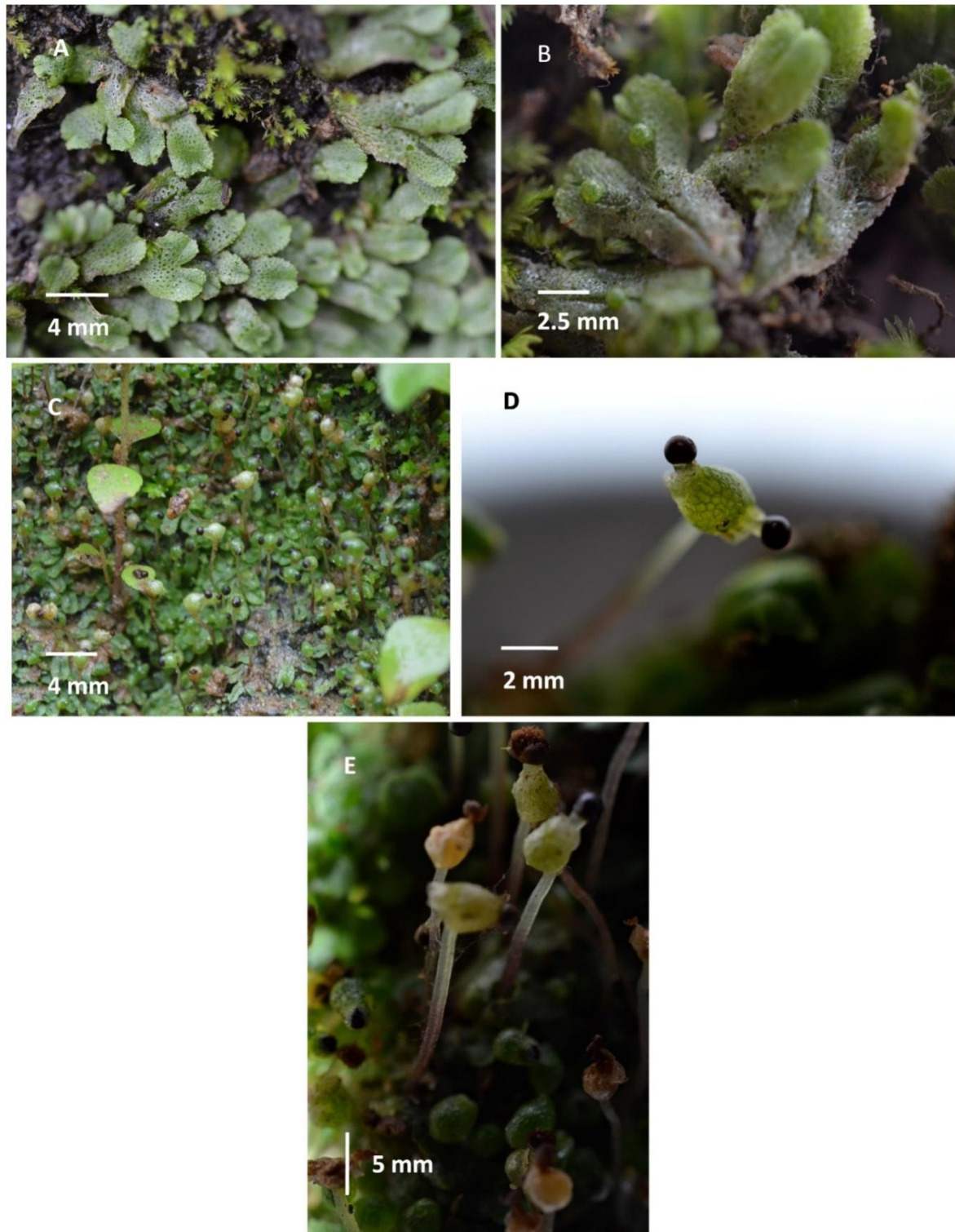


Figure 8. *Exormothea ceylonensis* (A-B) Gametophytic thalli (C) A massive sporophyte bearing population (D) Archegoniophore with two sporophytes (E) Mature sporophytes.

Family Targioniaceae Dumort.

Genus *Targionia* L. Species Plantarum 1136. 1753.

Thalli of *Targionia* is usually dull green in colour with purplish pigmentation along the margin ventrally, thalli dichotomously branched (Fig. 9E). *Epidermal pores* simple, with 6 to 8 cells in 2 to 3 rings. *Ventral scales* in two rows, dark purple and hyaline with lanceolate to ovate appendages.

Antheridia dorsal or terminal on main thallus or branches in groups. *Archegonia* and sporophytes terminal in involucre on the ventral side of thallus apex (Fig. 9F). Spores brown, with a distinct trilete marking and reticulate areoles and ridges. Generic name is dedicated to Giovanni Targioni-Tozzetti (1712-1783), Professor in Florence (Bischler-Causse *et al.*, 2005).



Figure 9. *Dumortiera hirsuta* (A) Gametophytic thalli (B) Disk shaped antheridia with bristles (C) archegoniophore with several sporophytes (D) Mature sporophytes with split capsules. *Targionia hypophylla* (E) Gametophytic thalli (F) Mussel-shaped involucre with sporophytes on the ventral side of the thallus apex.

CONCLUSIONS

Sri Lankan complex thalloid liverworts remained unexplored since 18th century where A. H. G. Alston, M. Fleischer and G. Gardner have contributed much to the only remaining collections at the National Herbarium, Peradeniya to date. With the aim to initiate research on Sri Lankan complex thalloid liverworts, field excursions were made to localities of these past recorded sites as well as new unexplored localities. Some of the older locality sites (e.g. Kadugannawa, Hakgala and Nuwara Eliya) had been destroyed due to urbanization, deforestation and removal of habitats for cultivation and construction of highways.

Complex thalloids in Sri Lanka show a high morphological diversity that they differ slightly from the taxonomic descriptions of other Asiatic taxa. During the study 8 families, 9 genera and 8 species were identified.

This study will be continued with molecular characterization and evaluation of biogeographic affinities of Sri Lankan liverworts. Threatened species and conservation sites will be proposed.

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