Liverwort genera of Thailand

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Phiangphak Sukkharak is an Associate Professor of Botany at the Department of Biology at Burapha University, Chonburi, Thailand. She completed her primary and secondary schools in Nan, where she was born in 1982. Later, she received the scholarship from the Development and Promotion of Science and Technology Talents Project (DPST) to continue her high school at Yupparaj Wittayalai School in Chiang Mai. She has been working on the Taxonomy of bryophytes, especially liverworts for more than 17 years. Her interest started during her second year of Bachelor's degree at Chiang Mai University. She submitted a proposal to the Biodiversity Research and Training program of Thailand and got the financial support to study the bryophytes of Kun Wang community forest in Chiang Mai. After that, she studied the liverworts of Khao Nan in Nakhon Si Thammarat for her master's thesis at Chulalongkorn University in Bangkok. In 2007, she met the world expert of the liverworts, Prof. Stephan Robbert Gradstein, at the World Conference of Bryology in Kuala Lumpur, Malaysia and was invited to Göttingen, Germany to conduct a monograph of the liverwort genus *Thysananthus* by using morphological, chemical, and genetic analyses for her doctoral dissertation under his guidance. However, intermediate taxa between *Thysananthus* and *Mastigolejeunea* were found. Consequently, after graduation, she continues working on *Mastigolejeunea* leading to the treatment of *Mastigolejeunea* as a subgenus of *Thysananthus* based on morphological and molecular evidences. Recently, she has been working on the revision of the liverwort genera in Thailand. The genera *Frullania, Pleurozia,* and *Metzgeria* in Thailand are revised and the Thai *Porella, Acrobulbus,* and *Syzygiella* are updated. She is also working on *Thysananthus* and *Frullania* for the Flora of Singapore project. She serves as a member of the Nomenclature Committee for Bryophytes of the International Association of Plant Taxonomists (2017-2023) and the Editorial Board of Journal of the Hattori Botanical Laboratory (2017-present). Moreover, after receiving the Young Scientist Award from the Foundation for the Promotion of Science and Technology under the Patronage of His Majesty the King in 2015 until now, she has been invited to give stimulating talks and to conduct the outreach activities for students in universities and high schools throughout Thailand to share her research experience, encourage, and motivate them into scientific careers, as well as increase their awareness of this understudied group of plants. She also was selected by the Association of the Thai Government Scholarship Student, Thailand for the Young Rising Star of Thai Government Scholarship Student Award in 2020 for her achievement and her service to the scientific and educational community.

LIVERWORT GENERA OF THAILAND

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Cover photographs

Front cover, from top to bottom: *Metzgeria furcata* (L.) Corda as a representative of thalloid liverwort showing gametophyte and sporophyte and *Anastrophyllum piligerum* (Nees) Steph. as a representative of leafy liverwort showing gametophyte and sporophyte (from Sukkharak, 2007).

Back cover, from left to right: *Bazzania tridens* (Reinw., Blume & Nees) Trevis. var. *tridens* as a representative of leafy liverwort showing incubous insertion and flagelliform branch and *Marchantia papillata* Raddi subsp. *grossibarba* (Steph.) Bischl. as a representative of thalloid liverwort showing gemma cup with gemmae on thallus (from Sukkharak, 2007, with update).

All figures are made by author.

This book has passed the evaluation by bryologists and botanists from different institutes and approval for the academic work publishing of book/ textbook by Chiang Mai University Press.

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Forword

Liverworts, (division Marchantiophyta), are any of more than 7,000 species of small non-vascular spore-producing plants. Liverworts are distributed worldwide, though they are most commonly found in the tropics area. In Thailand, liverworts have been collected and studied since 1899.

The book "Liverwort genera of Thailand" by Assoc. Prof. Dr. Phiangphak Sukkharak, Department of Biology, Faculty of Science, Burapha University, provides a synopsis on the liverwort genera of Thailand, in which 520 species in 93 genera and 39 families have been reported, representing about 7% of the world's liverwort species. The book consists of an introduction to liverworts, history of liverwort studies in Thailand, classification of liverworts in Thailand, key to genera of liverworts found in Thailand, generic descriptions, illustrations, discussion of the most important features for identification, data on the distribution and ecology, as well as the number of species worldwide and in Thailand.

As a representative of the publisher, I truly believe that this book will be useful to the worldwide academic community. It is suitable for both university students and scientists in the field, and is written based on the author's extensive research experience. The author herself has received numerous academic awards, as mentioned in her CV, guaranteeing her outstanding performance.

Professor Dr. Korakot Nganvongpanit
Editor

Preface

Liverworts of Thailand have been collected and studied since 1899. However, no identification tool has yet been published. This book provides the synopsis of liverwort genera of Thailand, in which 520 species in 93 genera and 39 families, have been reported, representing about 7% of the world's liverwort species. Of these, one genus, *Cryptolophocolea*, is newly reported for Thailand. In addition, as *Thysananthus ciliaris* (Sande Lac.) Sukkharak in Sukkharak & Gradst. is currently known only from a single population in the country, it is suggested here to be placed in the red list of Thai bryophytes. The book consists of an introduction to liverworts, history of liverwort studies in Thailand, classification of liverworts of Thailand, key to genera of liverworts found in Thailand, generic descriptions, illustrations, discussion of the important features for identification, data on the distribution and ecology as well as the numbers of species in the world and Thailand.

Phiangphak Sukkharak
Chonburi, March 2022

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Abbreviations

ca. — *circa*, approximately

cf. — *confer*, compare

et al. — *et alii*, and others

fo. — *forma*, form

l.c. — *loco citato*, as cited above

nom. cons. — *nomen conservandum*, conserved name

per. com. — personal communication

s.n. — *sine numero*, without number

subgen. — subgenus

subsp. — subspecies

syn. — synonym

var. — variety

Herbarium Acronym

Herbarium codes follow Thiers (continuously updated).

BCU — Chulalongkorn University, Bangkok, Thailand

BKF — Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand

Hb. Burapha Univ. — Herbarium of Department of Biology, Faculty of Science, Burapha University, Chonburi, Thailand

Chapter 1
INTRODUCTION TO LIVERWORTS

Liverworts or hepatics are grouped with mosses and hornworts as bryophytes, which are non-vascular, seedless, flowerless, and spore-producing land plants (Figure 1). Bryophytes have the haploid gametophyte generation as the dominant phase of the life cycle, with the sporophyte dependent on the gametophyte, whereas all vascular plants have the diploid sporophyte generation as their dominant phase. In liverworts, the gametophyte generation begins with spores which germinate into a multicellular protonema with unicellular rhizoids. Later the protonema finally differentiates into either a leafy or thalloid form. Each form produces eggs and sperm via the archegonium and antheridium, respectively. When mature, the sperm swims towards the archegonium and fertilizes the egg. This leads to a zygote which is the starting point of the sporophyte generation. As the zygote develops further, the embryo differentiates into a foot which penetrates the gametophyte together with elongation of the seta after the sporangium or capsule has differentiated and matured completely. The capsule opens by four longitudinal valves and with the help of elaters, the spores are shed (Figure 2).

Plant Kingdom

Non-vascular plants (Bryophytes)

- Phylum Marchantiophyta (Hepaticae, Liverworts)
- Phylum Bryophyta (Musci, Mosses)
- Phylum Anthocerotophyta (Hornworts)

Vascular plants (Tracheophytes)

Seedless plants

- Phylum Lycophyta
- Phylum Monilophyta

Seed plants

- Naked seed plants (Gymnosperms)
  - Phylum Coniferophyta
  - Phylum Cycadophyta
  - Phylum Ginkgophyta
  - Phylum Gnetophyta
- Flowering plants (Angiosperms)
  - Phylum Anthophyta

Figure 1. The members of plant kingdom showing the position of liverworts (Reece et al., 2014; Frey & Stech, 2009).

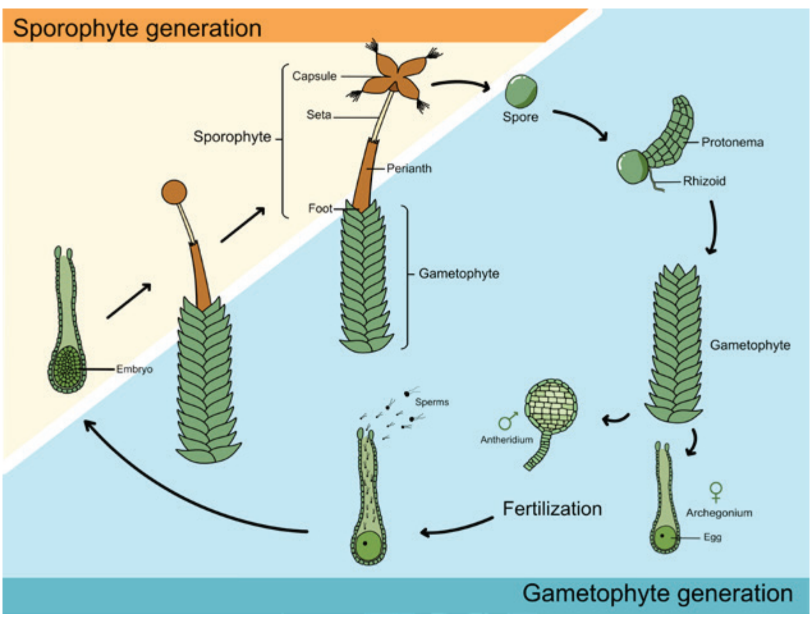

Figure 2. Life cycle of a liverwort. See text for details.

The term "liverwort" is from the Middle English *wort* meaning "plant" and "liver" referring to the first-named liverworts similar to a liver in shape. The term "hepatic" comes from the Greek *hēpatikos* meaning "liver" referring to the plant's resemblance to the organ as well. Liverworts consist of about 7,280 species in 386 genera in 87 families, with the four largest genera being *Plagiochila* (Dumort.) Dumort. (ca. 697 species), *Frullania* Raddi (ca. 576 species), *Cololejeunea* (Spruce) Steph. (ca. 405 species), and *Lejeunea* Lib. (ca. 384 species) (Söderstrom et al., 2016). The morphology of liverworts in this chapter follows Gradstein et al. (2001), Goffinet and Shaw (2009), and Vanderpoorten and Goffinet (2009). Based on their gametophyte, there are two main types of liverworts: leafy and thalloid liverworts.

LEAFY LIVERWORTS

The gametophytes are leafy, composed of a stem (caulidium or caulid, *plural* caulidia or caulids) and leaves (phyllidum or phyllid, *plural* phyllidia or phyllids). In creeping leafy liverworts, the side that contacts with the substrate is called the ventral side and the other side refers to dorsal side. In erect leafy liverworts, the term postical is used for the side bearing underleaves and the opposite side is the antical.

Rhizoids

Rhizoids are unicellular with a smooth inner wall and are scattered or in fascicles on the ventral or postical side of the stems (Figures 28A-B, F; 29E; 59K; 64J). They develop from stem epidermal cells or special cells of the underleaf base. In epiphyllous liverworts, rhizoids are grouped together to form a secondary rhizoid disc (Figures 61A, C). In *Radula* Dumort., the rhizoids are restricted to the ventral lobules. However, rhizoids are absent in some taxa. The function of rhizoids is to attach the plant to the substratum.

Stems

In leafy liverworts, the stem develops from three merophytes consisting of two lateral merophytes and ventral one. The width of the ventral merophyte is the number of the epidermal cell rows across the ventral side of the stems. It is related to the robustness of the stem and can be used for distinguishing some members of Lejeuneaceae. The stem cells in cross section are similar or differentiaed into inner medullary cells, in which a central strand can occur, and outer cortical cells, in which the outermost layer is called the epidermis (Figure 37G). According to Crandall-Stotler (1972) and Gradstein et al. (2001), there are two main types of branches: terminal (athecal or collarless) branches and intercalary (gyrothecal or sheathed) branches.

The terminal (athecal or collarless) branch is formed directly from branch initials. It diverges from the main stem at 45-60° and has no basal collar.

1. *Frullania*-type branch develops from the ventral segment-half of the lateral merophyte so it replaces the ventral half of the leaf and is associated with the half-leaf on its dorsal side. The cells of the branch fuse with those of the main stem (Figure 3A).

2. *Microlepidozia*-type branch develops from the dorsal segment-half of the lateral merophyte so it replaces the dorsal half of the leaf and is associated with the half-leaf on its ventral side. The cells of the branch fuse with those of the main stem (Figure 3B).

3. *Acromastigum*-type branch develops from the anodic segment-half of ventral merophyte so the branch develops on the ventral side of the stem and is associated with a modified half-underleaf (Figure 3C).

4. *Radula*-type branch develops from the lateral merophyte so it is associated with the unmodified leaf. The cells of the branch fuse with those of the main stem (Figure 3D).

5. *Fontinalis*-type branch develops from the second cortical cell below the leaf so it is associated with the unmodified leaf which never inserts on the branch and at a distance above the branch (Figure 3E).

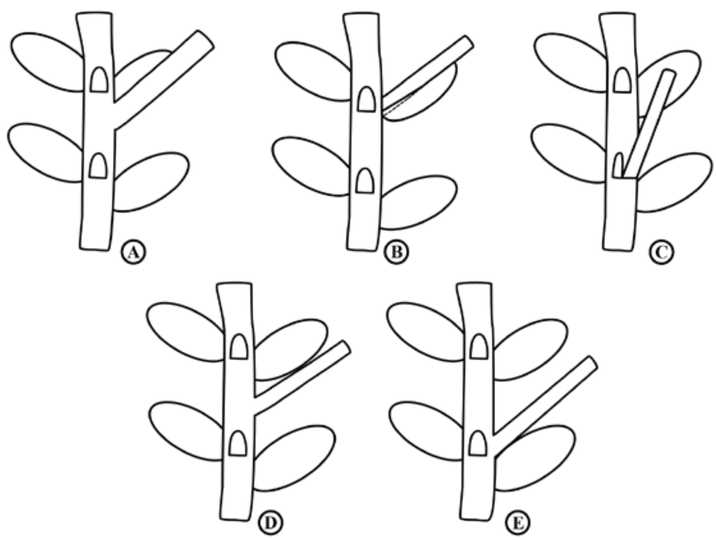

Figure 3. The terminal (athecal or collarless) branches. A. *Frullania*-type branch, ventral view. **B.** *Microlepidozia*-type branch, ventral view. **C.** *Acromastigum*-type branch, ventral view. **D.** *Radula*-type branch, ventral view. **E.** *Fontinalis*-type branch, ventral view.

The intercalary (gyrothecal or sheathed) branch is formed from superficial cells of leaf primordia. It diverges from the main stem at 90° and has a basal collar. If the branch is in the lateral leaf axil, it is called the lateral-intercalary branch but if the branch is in the underleaf axil, it is referred to as the ventral-intercalary branch.

1. *Bazzania*-type branch develops from a medullary cell in ventral merophyte with cortical cells so it occurs from the ventral side of the stem or around an unmodified underleaf with unlobed basal collar (Figure 4A).

2. *Plagiochila*-type branch develops from a medullary cell in the ventral part of a lateral merophyte with cortical cells so it occurs at the ventral side of an unmodified leaf with unlobed multilayered basal collar (Figure 4B).

3. *Bryopteris*-type branch develops from inner cells of a young basiscopic cortical cell with the outer cells so it occurs directly below an unmodified leaf with an unlobed 1 cell-layered basal collar fused with postical margins of the associated leaf (Figure 4C).

4. *Anomoclada*-type branch develops from the dorsal part of a lateral merophyte with cortical cells so it occurs on the dorsal side of the stem at an unmodified leaf with multilayered basal collar (Figure 4D).

5. *Lejeunea*-type branch develops from a basiscopic cortical cell with brace cells so it occurs directly below an unmodified leaf with lobed 1 cell-layered basal collar (Figure 4E).

6. Adventive *Radula*-type branch develops from the second cortical cell below a leaf in the differentiated region of the stem with segmentations of the branch apical cell so it occurs a short distance below an unmodified leaf with lamellae consisting basal collar (Figure 4F).

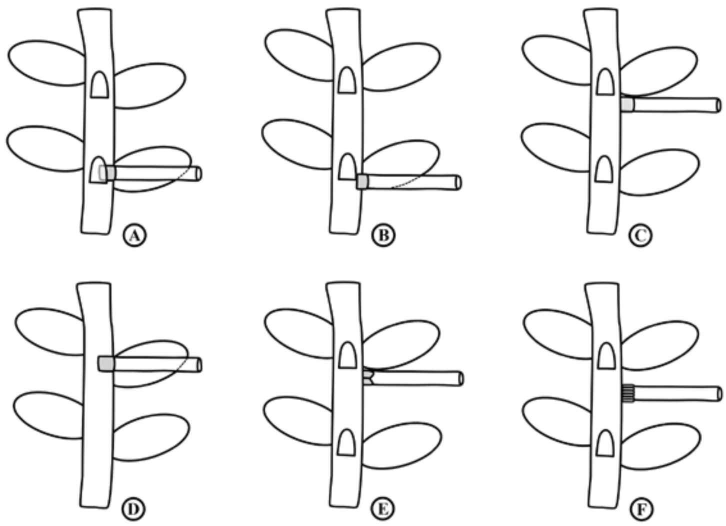

Figure 4. The intercalary (gyrothecal or sheathed) branches. A. *Bazzania*-type branch, ventral view. **B.** *Plagiochila*-type branch, ventral view. **C.** *Bryopteris*-type branch, ventral view. **D.** *Anomoclada*-type branch, dorsal view. **E.** *Lejeunea*-type branch, ventral view. **F.** Adventive *Radula*-type branch, ventral view.

Apart from an ordinary branch, there exists a flagelliform branch with its scale-like leaves (Figures 5; 30K) and a stolon, which refers to a branch without leaves. In addition, in some members of Lejeuneaceae, the innovation, in which the branch is formed below the perianth, is presented. Following Gradstein et al. (2001), two types of innovations are recognized: lejeuneoid and pycnolejeuneoid.

1. The lejeuneoid innovation refers to the type in which the basal-most position is a lateral leaf (Figure 6A).

2. The pycnolejeuneoid innovation refers to the type in which the basal-most position is an underleaf (Figure 6B).

Figure 5. Flagelliform branches in *Bazzania tridens* (Reinw., Blume & Nees) Trevis. var. *tridens*. f = flagelliform branch.

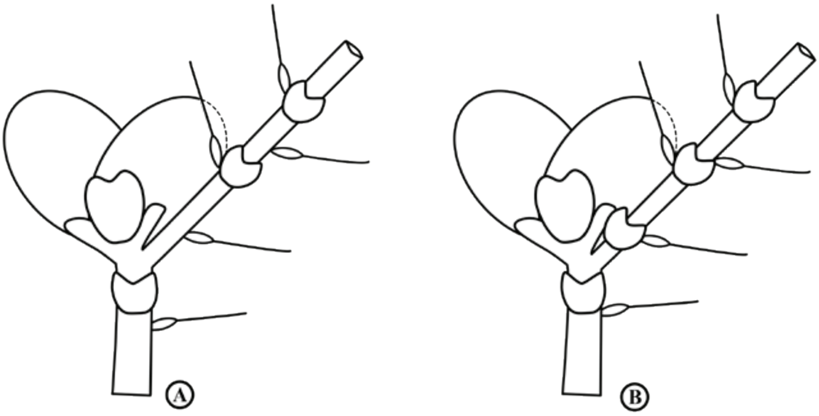

Figure 6. Innovation. A. Lejeuneoid innovation, ventral view. **B.** Pycnolejeuneoid innovation, ventral view.

Leaves

The leaves of leafy liverworts originate from two to three leaf-initial cells. Therefore, they are arranged in two to three rows: two lateral rows called lateral leaves and one ventral row called underleaves (amphigastria, *singular* amphigastrium), which maybe absent in some taxa. Underleaf bases may be free or adnate with leaves either on one side or both sides. In some genera, a stylus is recognized (Figure 59C). The insertion of underleaves is transverse but three types of insertion are recognized for lateral leaves including incubous, succubous, and transverse.

1. Incubous insertion is the leaves attach to the stem obliquely and the antical leaf margin overlaps the one immediately above (Figure 7A).

2. Succubous insertion is the leaves attach to the stem obliquely and the postical leaf margin overlaps the one immediately below (Figure 7B).

3. Transverse insertion is the leaves attach perpendicular to the stem (Figure 7C).

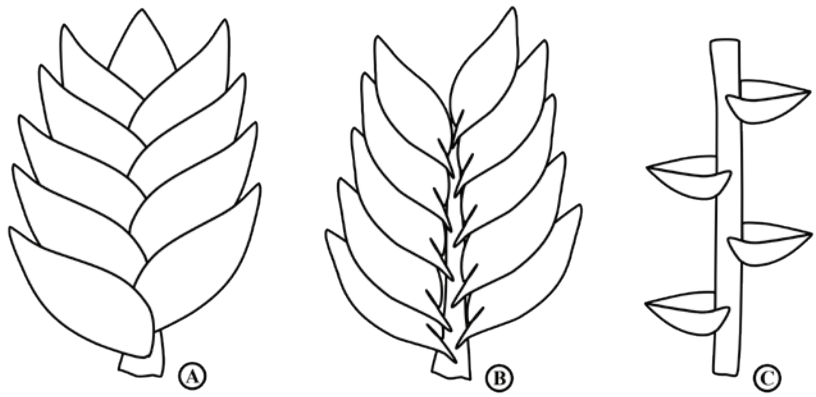

Figure 7. Leaf insertion. A. Incubous, dorsal view. **B.** Succubous insertion, dorsal view. **C.** Transverse insertion, dorsal view.

The lamina of the lateral leaf is unistratose and the midrib is absent. The cell shapes vary from isodiametric, quadrate, rectangular, pentagonal, or hexagonal. The cell walls are thin or thickened and at the corner of three adjacent cells, a trigone may be present. The cuticle can be smooth, verrucose, verruculose, or papillose (Figures 8; 24I; 27I). In some members of the leafy liverworts, a vitta (*plural*, vittae) which is a row or rows of elongated or enlarged cells, runs along the middle of the leaf lamina (Figures 9; 29G-J). The cells of the lamina have numerous chloroplasts and oil bodies which are a chemical compound-containing membrane-bound organelle (Figure 10). The secondary metabolites found in oil bodies consist of lipophilic mono-, sesqui-, and diterpenoids; aromatic compounds; flavonoids; acetogenins and lipids in a protein or carbohydrate matrix and possess several biological activities (Asakawa et al., 2013a). Although they are rich sources of secondary metabolites and possess interesting biological activities, there are approximately only 10% of liverwort species that have been studied chemically (Asakawa, 2012). According to Gradstein et al. (1977), there are four types of oil bodies including *Bazzania*-type, which is homogeneous or large up to 4 segmented globules (Figure 11A); *Massula*-type, which is homogeneous or minute up to 4 segmented globules (Figure 11B); *Calypogeia*-type, which is coarsely segmented globules (Figure 11C); *Jungermannia*-type, which is finely segmented globules (Figure 11D). In addition, ocelli, which are enlarged cells containing one or more larger-than-normal oil bodies and lack chloroplasts, occur in the leaf lamina of some leafy liverworts (Figure 12).

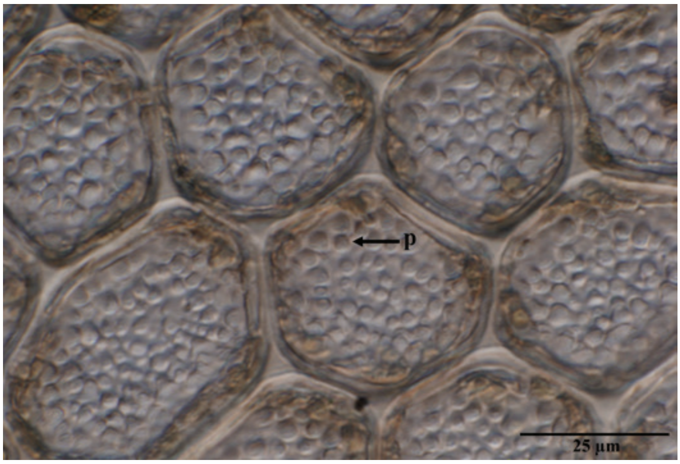

Figure 8. Papillose cuticle on the cells of *Saccogynidium muricellum* (De Not.) Grolle. p = papillose.

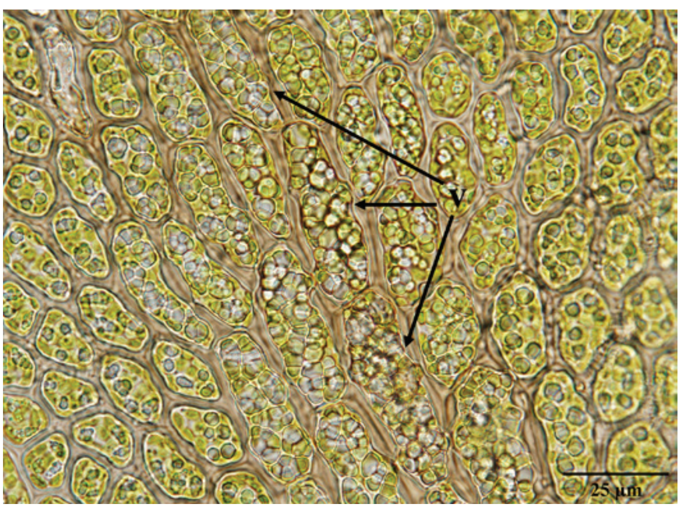

Figure 9. Vitta presenting on the lamina of *Thysananthus retusus* (Reinw., Blume & Nees) B.M.Thiers & Gradst. subsp. *retusus*. v = vittate cell.

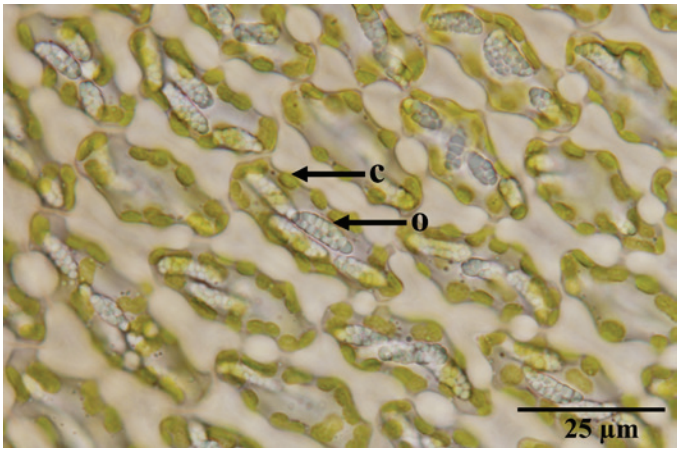

Figure 10. **Coarsely segmented globules of oil bodies and chloroplasts in cells of** ***Thysananthus convolutus*** **Lindenb. var.** ***convolutus.*** c = chloroplast, o = oil body.

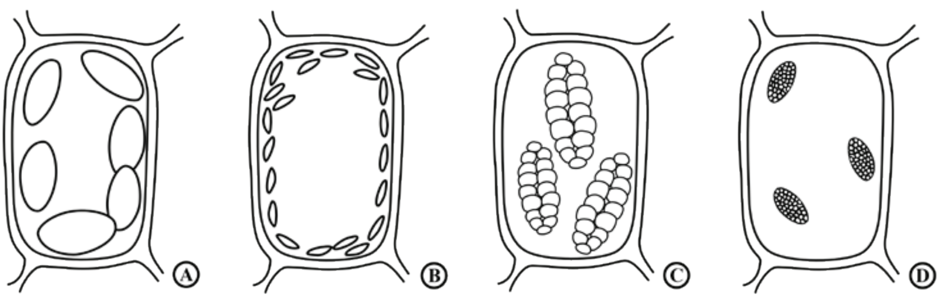

Figure 11. **Oil bodies. A.** *Bazzania*-type. **B.** *Massula*-type. **C.** *Calypogeia*-type. **D.** *Jungermannia*-type.

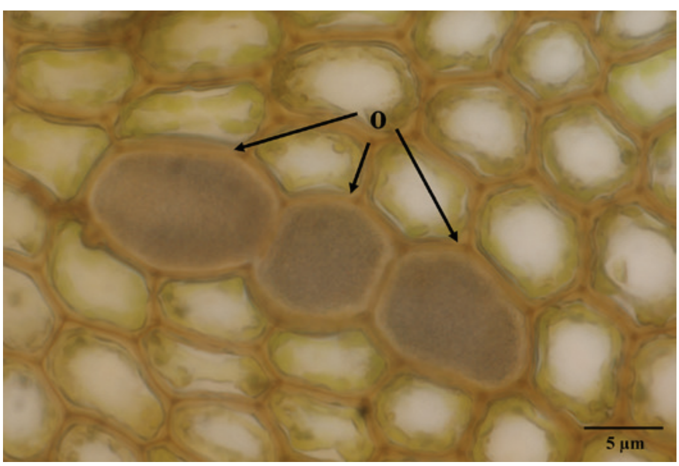

Figure 12. **Ocelli in** ***Ceratolejeunea*** **sp.** o = ocellus.

Reproductive organs

Androecia (*singular* Androecium) consist of one to several antheridia in axils of the modified leaves called bracts on the stems or branches. The antheridia are rounded or oval and adnate to the stem by a stalk. Biflagellated sperm cells swim to the egg through a film of water.

Gynoecia (*singular* Gynoecium) are composed of archegonia with surrounding modified leaves e.g. bracts (Figures 57; 68-69; 74), bracteoles (Figure 61D), perianths (Figures 14A; 20F; 21; 24A; 25; 37H-I; 39A-B, F-G; 40; 42; 55; 57; 61D; 62-63; 68-71; 72E-F; 73-74). They are located at the top of the stems. One to several flask-shaped archegonia containing an egg cell are surrounded by protective structure. After fertilization, the archegonia will develop into a calyptra protecting together with the perianths the developing sporophyte. In some members, the perianth, referring to the fused modified leaves that protect the archegonia and developing sporophyte, is absent or reduced. The perigynium, which is a tubular structure derived from stem tissue, surrounds and protects the developing sporophyte. If the perigynium is pendent, it is called a marsupium.

Distribution of gametangia is either dioicous, in which male and female sex organs are on different plants or monoicous where male and female sex organs are found on the same plant. For monoicous plants, it can be autoicous, in which male and female are in separate branches; paroicous, in which male and female are on the same branch with each sex grouped separately; or synoicous, in which male and female are on the same branch but not grouped.

Sporophyte

The sporophyte consists of a foot, a colorless and fragile seta, and spherical, ovoid, or cylindrical capsule (Figure 13). After the capsule is fully mature, the seta rapidly elongates. The capsule dehisces by four valves (Figure 14) or disintegrates and releases spores with the help of elaters which are elongated unicellular cells with spirally thickened walls (Figure 15).

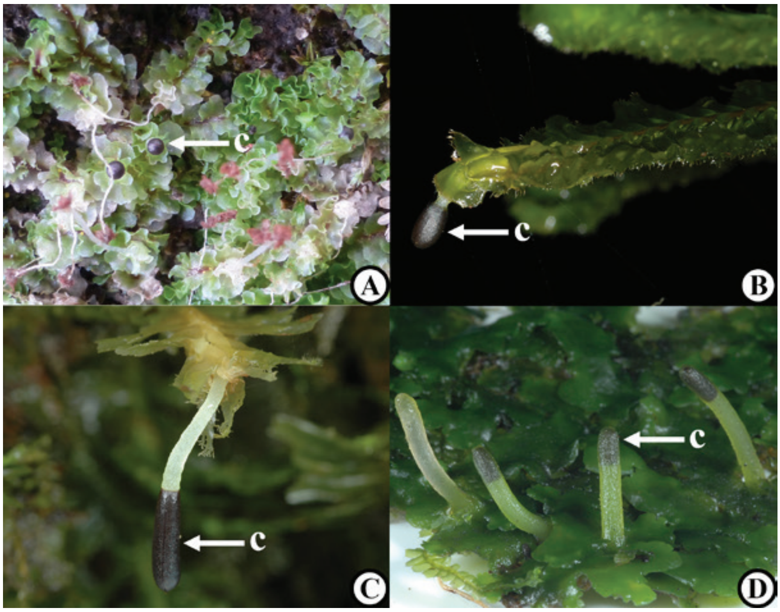

Figure 13. **Capsules. A.** Spherical in *Fossombronia pusilla* (L.) Nees. **B.** Ovoid in *Plagiochila sandei* Dozy ex Sande Lac. **C.** Cylindrical in *Schistochila blumei* (Nees) Trevis. **D.** Cylindrical within involucre of *Aneura pinguis* (L.) Dumort. c = capsule.

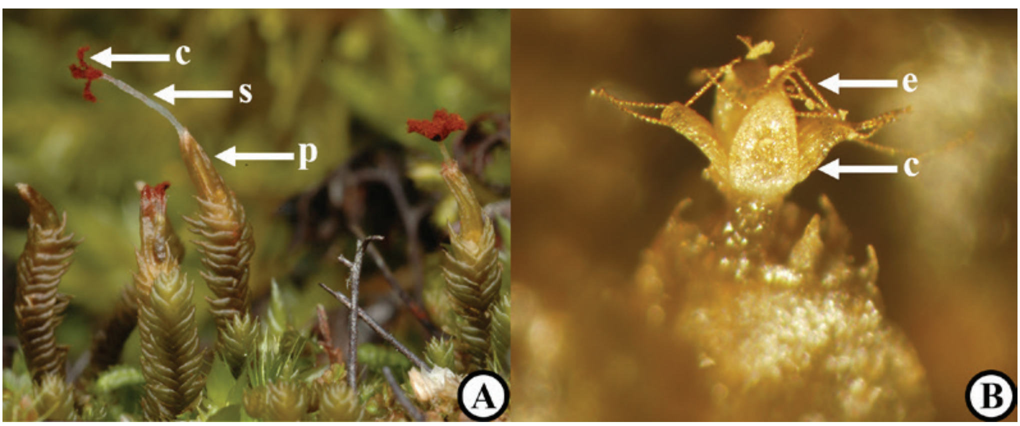

Figure 14. **Four-valve-dehiscing capsules. A.** *Anastrophyllum piligerum* (Nees) Steph. **B.** *Lopholejeunea subfusca* (Nees) Schiffn. c = capsule, e = elater, s = seta, p = perianth. (A from Sukkharak, 2007).

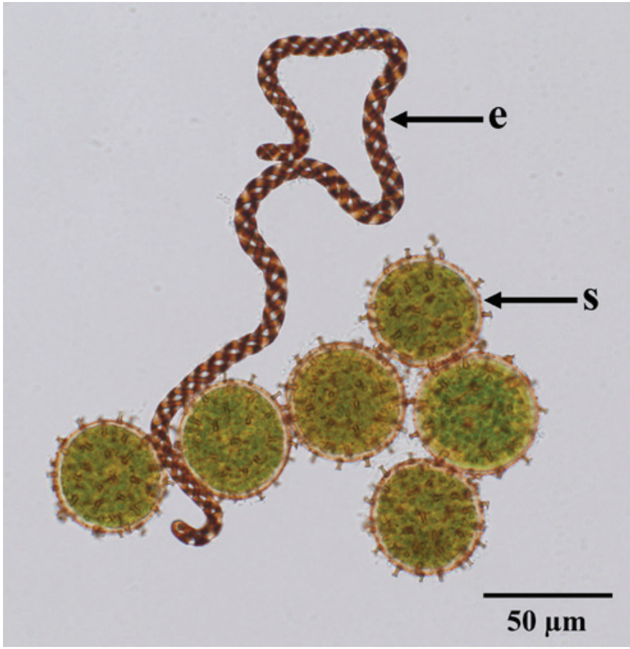

Figure 15. Spores and elater of *Radula pinnulata* Mitt. e = elater, s = spore.

Asexual reproduction

Asexual reproduction in leafy liverworts occurs through gemmae (Figure 16); caducous leaves, underleaves, or branches; fragmenting cilia or stems; regenerants from leaf margins, leaf surfaces, or dorsal side of stems; bulbils; or tubers.

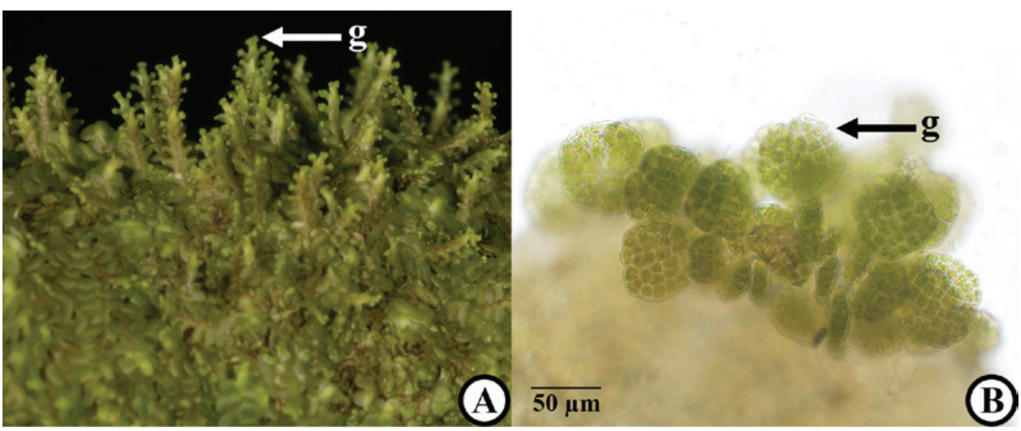

Figure 16. Gemmae. A. On leaf apices of *Radula* sp. **B.** gemmae in close-up. g = gemmae. (A from Sukkharak, 2007, with update).

THALLOID LIVERWORTS

The gametophytes are thalloid made up of ribbon-like or a flat sheet.

Rhizoid

Rhizoids are unicellular with a smooth inner wall (Figure 90E). In some complex thalloid liverworts, the tuberculate type having papillae or pegs on the inner wall also present (Figure 90F). They grow on the ventral side of thallus or from the thallus margins (in *Metzgeria* Raddi as hairs) (Figure 82A-B).

Scales

Scales, which are a colorless, purple, or blackish purple membranous structure, are present in two or more rows on the surface of ventral side, especially near the thallus apex (Figures 89E; 90C, G).

Thallus

The internal structure of the thallus is either simple or complex. For the simple thalloid group, the thallus is unistratose or multistratose along the central part and unistratose on both lateral sides (Figure 90D). In the complex thalloid group, the ventral part of the thallus is composed of hyaline tissue whereas the dorsal part consists of chlorophyllous tissue and air-chambers that open to the thallus surface by air-pores.

Reproductive organs

The spherical or ovoid antheridia are naked or surrounded by an involucre (Figure 13D) situated on the thallus surface or in antheridial chambers inside the thallus. In *Marchantia* L., antheridiophores, which are stalks with slightly lobed receptacles bearing antheridia, are present (Figure 17A).

The flask-shaped archegonia containing an egg cell are surrounded by a tubular or scale-like involucre. They are on the thallus surface or hidden inside the thallus. In *Marchantia*, archegoniophores, which are stalks with deeply lobed receptacles bearing archegonia, are present (Figure 17).

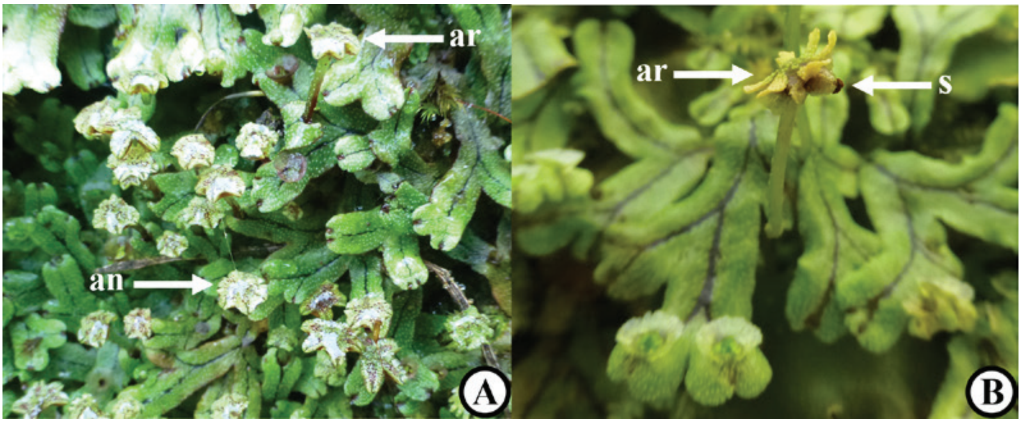

Figure 17. Antheridiophores, archegoniophores, and sporophyte of *Marchantia emarginata* Reinw., Blume & Nees subsp. *tosana* (Steph.) Bischl. **A.** Antheridiophores and archegoniophores. **B.** Sporophyte located on the receptacle of the archegoniophores. an = antheridiophore, ar = archegoniophore, s = sporophyte.

Sporophyte

The sporophyte is similar to that in the leafy liverwort. In *Marchantia*, the sporophyte is located under the receptacle of the archegoniophores (Figure 17B).

Asexual reproduction

Asexual reproduction in thalloid liverworts occurs through gemmae on the thallus surface, margins, apex (Figure 18A), or in a cup-like structure called gemma cup (Figures 18B; 89D; 92); caducous branches; or tubers.

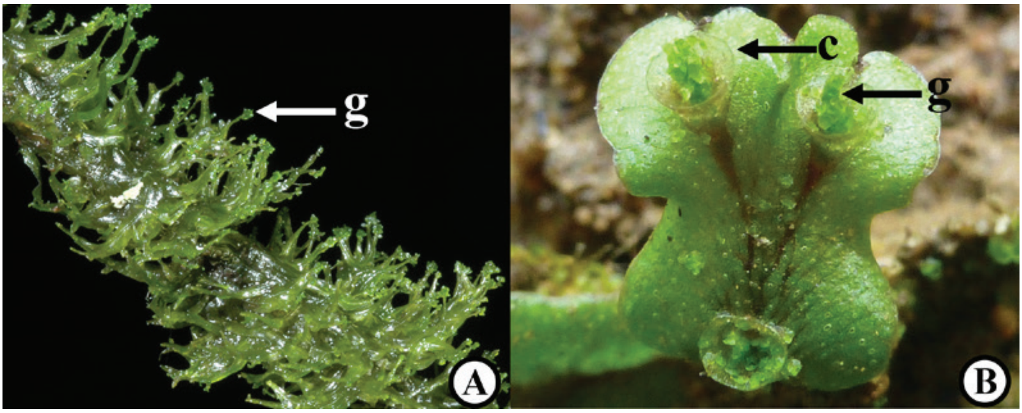

Figure 18. Gemmae. A. Occurring on the thallus apices of *Metzgeria consanguinea* Schiffn. **B.** Presenting in the gemma cups of *Marchantia papillata* Raddi subsp. *grossibarba* (Steph.) Bischl. c = gemma cup, g = gemma.

Ecology

Liverworts occur in nearly all environments, except the sea and permanently frozen areas (Vanderpoorten & Goffinet, 2009). The majority of liverworts are terrestrial including epiphytic, epiphyllous, terricolous, saxicolous plants growing on bark, branches, rotten logs, leaves, soil, rocks, many man-made substrates, or in cultivated areas (Gradstein et al., 2001; Vanderpoorten & Goffinet, 2009). Some taxa colonize aquatic environments e.g. streams, creeks, waterfalls, springs, or periodically flooded areas (Gradstein et al., 2001; Frey & Stech, 2009). *Ricciocarpos natans* (L.) Corda often float on the surface of water whereas *Riccia fluitans* L. is immersed below the water surface and some members of *Riella* are submerged and attached to the bottom (Schofield, 1985). Liverworts, like mosses and hornworts, occur in numerous micro-habitats because of the differences in ecological conditions of the substrate and environmental factors e.g. light, pH, temperature, water, nutrients, all of which provide the ecological niches in which they can grow (Hallingbäck & Hodgetts, 2000; Vanderpoorten & Goffinet, 2009). Some species are "shade epiphytes" or "understory epiphytes" growing specifically in the inner tree canopy and in the shaded and moist understory of the forest. Other species are "sun epiphytes" or "canopy epiphytes" found in the outer sections of the canopy. In addition, ecological "specialists" exhibiting a narrow vertical distribution as well as "generalists" occurring in widely vertical distributions are also present (Hallingbäck & Hodgetts, 2000; Gradstein et al., 2001, and the references therein).

Geographical Distribution

Liverworts have a broad geographical distribution that can disperse across two or more continents (Shaw, 2001). They occur from Antarctica to the Arctic region, and from Australian deserts to Amazon forests, with high diversity mainly in tropical and temperate forests (Gradstein et al., 2001; Shaw, 2001; Frey & Stech, 2009).

There are two hypotheses for the broad distribution of bryophytes: vicariance and long-distance dispersal (Vanderpoorten & Goffinet, 2009). In liverworts, like other members of bryophytes, their diaspores, such as spores or vegetative propagules such as gemmae, leaf fragments, tubers, or cells on decaying stems, can be carried some distances, especially long-distance by air currents. However, the distribution pattern of each taxon is related to the microclimatic restrictions and substratum specificity (Schofield, 1985; van Zanten & Gradstein, 1988; Glime, 2017). Vanderpoorten and Goffinet (2009) adopted the Bryofloristic classification of Schofield (1992) updated to recognized five Bryofloristic kingdoms including Holarctic, Neotropic, Paleotropic, South African, Holantarctic. The Holarctic Kingdom composes of North America, Europe, northern Africa, northern and central Asia. The Neotropics comprises Central and tropical South America while Paleotropics consists of tropical Africa and Asia. South Africa covers the temperate to sub-tropical southern Africa and Holantarctic Kingdom includes Australia and New Zealand together with temperate southern South America and Antarctica. When the distribution ranges from South America, Africa, Asia and Oceania, the term “Pantropics” is recognized.

The Importance of liverworts

Liverworts, like other members of the bryophytes, play an important role as pioneers in establishing vegetation succession and soil formation. For example, *Nardia succulenta* (A.Rich.) Spruce grows on the bare soils of a Costa Rican volcano and bridges across the boulders to form the suitable habitat for other plants (Vanderpoorten & Goffinet, 2009, and the references therein). In addition, *Marchantia berteroana* Lehm. & Lindenb. together with the mosses *Funaria hygrometrica* Hedw. and *Ceratodon purpureus* (Hedw.) Brid. have colonized Tasmanian logging coupes within the first few months after fire (Duncan & Dalton, 1982). The members of the genera *Frullania* and *Plagiochila* serve as habitat for amphibians or a material for bird nesting (Hallingbäck & Hodgetts, 2000).

With the Doctrine of Signatures theory and the folk belief, liverworts have been traditionally used for their medicinal properties. For example, *Marchantia polymorpha* L. is used for liver problems, as diuretics, healing of burns and cuts, and treating snake bites (Asakawa, 2015). *Conocephalum conicum* (L.) Dumort. was used to cure gallstones, cuts, burns, scalds, swollen tissue, and bites by poisonous snakes (Asakawa et al., 2013b). As well as *M. polymorpha*, *C. conicum* was used to heal broken bones (Asakawa, 2015). *Reboulia hemisphaerica* (L.) Raddi has been used for wounds, blotches, and bruises as well as hemostasis (Asakawa et al., 2013b). Moreover, several liverworts emit an odor or produce a hot, bitter, or sweet taste. In addition, the chemical constituents isolated from liverwort possess biological activities e.g. antibacterial activities, antithrombin activity, neuroprotective activity (Asakawa et al., 2013a).

Liverworts, especially *Marchantia polymorpha*, is commonly used in scientific research and as an experimental model plant in several interactions. *Marchantia polymorpha* genome, the first ever genome sequence of a liverwort, was first sequenced by Bowman et al. (2017) and the result shed important light on the evolution of land plants. With a reduced gene redundancy genome, a simple morphology, and having a haploid dominant phase of its life cycle, the species is suitable for genetic analysis and as a testbed for synthetic biology (Sauret-Güeto et al., 2020). *Marchantia polymorpha* is also used for autophagy studies as several cell biological tools and molecular genetic techniques have been established for it (Norizuki et al., 2019, and the references therein).