Diversity of Microbes and Cryptogams

Bryophyta

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Date of submission: *May 11, 2006*
Version: **English**

Significant Key words: **Bryophyta, Hepaticopsida (Liverworts), Anthocerotopsida (Hornworts), , Bryopsida (Mosses).**

Contents

Introduction

Bryophytes are “Avascular Archegoniate Cryptogams” which constitute a large group of highly diversified plants.

Systematic position in the plant kingdom

The plant kingdom has been classified variously from time to time. The early systems of classification were mostly artificial in which the plants were grouped for the sake of convenience based on (observable) evident characters. Carolus Linnaeus (1753) classified the plants into 24 classes by using only one character, “the number and morphological arrangement of the stamens. He recognized the class Cryptogamia, and placed all the flowerless (stamenless) plants – Algae, Fungi, Bryophytes and Pteridophytes in this class. This artificial system of classification is also known as sexual system of classification (see Naik 2000).

Subsequently “Bernard de Jussieu” (1699-1777), a contemporary worker of Linnaeus, proposed another, somewhat improved classification in the Book “Genera Plantarum” (1789) published by his nephew, Antonie Laurent. This may be marked as beginning of the “Natural system of classification”. In this system, the plants were classified into three groups – Acotyledons, Dicotyledons and Monocotyledons. About 100 orders were recognized with 14 classes for flowering plants and a solitary class for the cryptogams. Acotyledons (Cryptogams) include mosses along with Algae and Fungi (see Naik 2000).

“Augustin Pyramus de Candoll” (1778-1841) further developed the system of classification propsed by ‘de Jeussie” in the book “Theorie Elementarie de la Botanique” (1813) in which principles of classification were outlined. He introduced the term ‘Taxonomy’ to designate the theory of plant classification. His monumental work “Prodrums Systematis Naturalis Regni Vegetabilis” was published in 17 volumes (1824 – 1873). According to his system of classification, the plant kingdom was divided into two divisions I. Vasculares (plants with vascular bundles and cotyledons) and II. Cellulares (plants without vascular bundles and cotyledons). The “Cellulare” includes Mosses and Liverworts along with Algae, Fungi and Lichens (see Naik 2000, Sivarajan 1991).

Endlicher (1836) divided the plant kingdom into **Thallophyta** and **Cormophyta**. The name Cormophyta was given due to the definite solid ‘Cormus’ – type of plant body. While Engler (1886) suggested that the plant kingdom should be divided into two groups **Thallophyta** and **Embryophyta** as zygote develops into a multicellular embryo.

Eichler (1880, 1883) gave another phylogenetic system of classification and divided the plant kingdom into two main groups. I. **Cryptogamae or Cryptogamia** (Cryptogams - non-flowering plants) and II. **Phanerogamae or Phanerogamia** (Phanerogams - flowering plants). 1. Cryptogams (Greek word- Kryptos = concealed, gamos = marriage) i.e. Hidden marriage or Hidden wedded). 2. Phanerogams (Phaneros = evident, gamos = marriage) i.e. Evident marriage or Open wedded. The cryptogamic portion of the plant kingdom was divided into three divisions: **Thallophyta, Bryophyta** and **Pteridophyta** while phanerogamic portion was divided into two divisions: **Gymnosperms** (naked ovule or seed) and **Angiosperms** (covered ovule or seed).

Subsequently, Adolf Engler (1892, 1892a) in his “Syllabus der Pflanzenfamilien” divided the plant kingdom into **Thallophyta** and **Embryophyta**. The Embryophyta was further classified into two groups – (i) **Embryophyta Asiphonogama** (Bryophyta and Pteridophyta) and (ii) **Embryophyta Siphonogama (Spermatophyta).**

In the early twentieth century, it was suggested that the Pteridophytes and Spermatophytes are the vascular plants and they form a distinct group within Embryophyta, which should be named as **Trachaeophyta** (parallel to Bryophyta). While the name **Archegoniatae** was proposed to include Bryophyta, Pteridophyta and Gymnosperms as all these three are having archegonia (female sex organ).

Tippo (1942) divided the plant kingdom into two subkingdoms (i) **Thallophyta** and (ii) **Embryophyta,** which were further divided into Phylum (Phyla). But according to the International Code of Botanical Nomenclature (ICBN), the term ‘phyla’ is not appropriate for the group of plants and it should be changed to the ‘divisions’. However, Tippo divided Embryophyta into **Bryophyta** and **Trachaeophyta.** He also suggested an alternative name **Atracheata** to Bryophyta.

Takhtazan (1953) gave another term – **Telemophyta** in place of Embryophyta on the basis of 'Telome theory' and placed Bryophyta along with the **Trachaeophyta** considering that the Bryophytes are the reduced forms of Trachaeophytes.

Bold (1956, 1957) recognized two divisions (i) **Hepaticophyta** and (ii) **Bryophyta.** While Cronquest, Takhtazan and Zimmerman (1966) recognized two subkingdoms (i) **Thallobionta** (Thallophytes) and (ii) **Embryobionta** (Cormophytes or Telomophytes), the latter one with the divisions: Rhyniophyta (Psilophytales), Bryophyta, Psilophyta (Psilotales) and other Trachaeophytes.

In the present day of taxonomy, the terms – 'Cryptogamia', 'Phanerogamia' and 'Archegoniatae' are more or less obsolete now. However, Bryophyta, Pteridophyta, Gymnosperms and Angiosperms still have their definite entity.

Alternation of generations

Hofmeister (1851) for the first time investigated alternation of generations in Bryophytes and indicated that the Bryophytes and Pteridophytes share certain common features like multicellular gametangia, true alternation of generation of dissimilar generations, warranting their consideration as one large group, generally called as 'Archegoniatae'. According to him, the Archegoniatae shows two well-marked and distinct generations (Gametophyte and Sporophyte), which follow one after the other in alternate manner. The gametophyte is sexual phase in the life-cycle which produces gametes in the sex organs while sporophyte is asexual phase in the life-cycle which produces spores in the spore bearing organ – sporogonium/sporangium (Plate I).

Till 1894, the actual position of the chromosome number in two different generations was not known. The duplication and the reduction in the chromosome number in connection with the alternation of generation was later on recognized by Strassburger (1894) who ascertained that in a life-cycle there is not only an alternation between two different morphological forms but there is also an alternation in the level of ploidy – the gametophyte with single set of chromosomes and the sporophyte with double set of chromosome. The gametophytic and sporophytic generation rotates in between the two processes – 'Syngamy' and 'Meiosis'. The gametophytic phase intervenes between meiosis to syngamy while sporophytic phase intervenes between syngamy to meiosis (See Plate I).

Life cycle pattern (in Bryophytes)

Bryophytes show sharply defined heteromorphic alternation of generations in which the gametophytic phase and the sporophytic phase are entirely different in their morphology as well as in function. The main plant body is gametophyte, which produces antherozoids and eggs in antheridia and archegonia respectively. After fertilization (syngamy) the zygote is formed which develops into the sporophyte. The sporophyte is generally differentiated into foot, seta and capsule. Spores are produced in the capsule after meiosis. The spore is the first cell/stage of the haploid/gametophytic generation, which ends at the egg till it is unfertilized. The zygote/fertilized egg is the first cell/stage of the diploid/sporophytic generation and it remains till the reduction division (meiosis) takes place in the sporogenous tissue. The spore mother cell represents the last stage of the sporophytic generation.

Affinities with Algae and Pteridophytes

Bryophytes stand at a higher level than the algae as they (Bryophytes) are more complexed in morphology but at a lower level than the Pteridophytes as Pteridophytes are more complexed than the Bryophytes. Hence, in the plant kingdom Bryophytes have been placed in between Algae and Pteridophytes. On the one hand, they share some common features with the algae [specially (chlorophyceae)-green algae] and on the other hand with Pteridophytes. The similarities with the algae are in the nature of photosynthetic pigment (chlorophyll), cell wall component, photosynthetic product (reserve food-starch) and the flagella. Besides, water is necessary for the sexual reproduction (process of fertilization) in both the groups. However, they (Bryophytes) differ prominently in having multicellular sex organs - (Antheridia and Archegonia) which are protected by the sterile jacket while in the algae, the sex organs (Antheridia and Oogonia) are unicellular which are not jacketed. With Pteridophytes, the Bryophytes share the common life-cycle pattern of heteromorphic alternation of generations and the multicellular, jacketed sex organs – Antheridia and Archegonia. Besides, the zygote and embryo (embryonic sporophyte) is permanently retained within the archegonium in both the groups. However, they differ mainly in the vascular tissue. Bryophytes lack typical vascular tissue while the pteriodophytes have well developed vascular system having xylem and phloem.

Apart from this, in Bryophytes the main plant body is the gametophyte (either being leafy or thalloid) and the sporophyte is attached as well as dependent on the gametophyte. The sporophytic phase is never free living and independent. The sporophyte is differentiated into foot, seta and capsule and it has a limited growth. While in the Pteridophytes, the main plant body is the sporophyte, which is of course attached to the gametophyte initially for a short period in the life - cycle but it is fully independent at maturity. The sporophyte is differentiated into well developed root, stem and leaves. They are perennial and have unlimited growth.

General characters

Bryophytes, “Liliputians of Plant Kingdom” are essentially small plants ranging from few millimeters to few centimeters. This is the only plant group, which exhibits a remarkable range of morphological diversity not found in any other group of the plant kingdom. With the exception of few aquatic forms, they are truly first land inhabiting plants. They represent a phase in the evolution when the plants have migrated from water to land but they seem to be incompletely adapted to the land habit, as they still require water for the process of fertilization in completing their life - cycle. The ciliate antherozoids have to swim in the film of water for the act of fertilization. Their complete dependence on water for successful fertilization imposes serious restriction on their distribution. They are mainly confined to moist and humid places and are also described as “Amphibians of Plant Kingdom”.

Habitat

Bryophytes are basically shade loving land plants, capable of growing on moist soil. They form small, vivid, green patches on the floor in all possible shades of green. Sometimes they form cushion, extensive mats or a thin or thick blanket cover on the tree trunk, tree branches and even sometimes on the leaf surface also.

Gametophyte

The Bryophytes generally form a natural group where the main plant body is a gametophyte. It is a conspicuous, long-lived, prominent and independent phase in the life cycle as compared to that of sporophyte. Due to presence of chloroplast, it is nutritionally self- sufficient. The gametophyte, although small, yet are highly diversified and well developed. The plant body is either undifferentiated (thalloid forms) or differentiated (leafy forms) into definite axis and leaves. In the leafy form, the stem (axis) and leaves are entirely different from true vascular plants (Trachaeophytes) as they belong to gametophytic phase whereas in the vascular plants they are the parts of the sporophyte. In fact, in Bryophytes, the axis and leaves are caulidia (central axial column) and phillidia (lateral appendages) but for the sake of convinience the terms axis (stem) and leaves are commonly used. The true roots are entirely absent in Bryophytes. The functions of roots, the attachment of the plant to the substratum and the absorption of water and minerals, are mainly performed by simple hair like structures called as rhizoids. The rhizoids are generally unicellular, simple (smooth walled) in hornworts; simple, tuberculate or sinuate in liverworts or multicellular, oblique septate in mosses.

Reproduction

The sex organs are always dorsal in position in the thalloid forms while in the leafy forms they are terminal/apical on the leafy axis. Some times male sex organs may be axillary in position as in most of the leafy liverworts.

Antheridia

The male reproductive organ – antheridia have a short or long stalk and spherical to elongated or clavate to cylindrical antheridial body. The androgonial cells /androcytes/ antherozoid mother cells are protected by a single layer of sterile jacket. Each of the androcyte gives rise to a single ciliated motile antherozoid.

Archegonia

The female reproductive organ is the archegonium, which is more or less flask shaped. The swollen basal portion of archegonium is called as venter and somewhat narrow, slender, elongated upper portion is called as neck. The archegonium consists of an axial row of number of neck canal cells, a ventral canal cell and a single, large egg, which are surrounded by sterile jacket.

Fertilization

The mature antheridium dehisces and releases antherozoids. They swim in the film of water and reach to the neck of the arehegonium. At the time of fertilization the neck canal cells disintegrate. The antherozoid swims upto the archegonial venter passing through the neck and fertilizes the egg.

Embryo

The fertilized egg starts dividing immediately after the fertilization without undergoing any resting period and remains inside the archegonial wall. It develops into a multicellular embryo, which differentiates into the sporophyte. Simultaneously, the cells of the archegonial venter actively divide to form a protective covering around the developing sporophyte and it is called as calyptra.

Sporophyte

The sporophyte consists of foot, seta and capsule. The foot is parenchymatous, conical structure, which remains embedded in the gametophytic tissue and derives nourishment for the developing sporophyte. Seta is the stalk, which holds the capsule. This may be of variable length. The capsule is the main fertile portion of the sporophytic generation. It has 1-many layered capsule wall enclosing archesporium. The archesporial cells get differentiated into spore mother cells only in mosses or both the spore mother cells and the elater mother cells in liverworts and hornworts. The spore mother cells, after meiotic division, form spore tetrads having haploid spores. The elater mother cells form elaters, which are sterile and help in the dispersal of spores. The Bryophytes are homosporous. All the spores are of same size. Under suitable conditions, the spore germinates to form new gametophyte either directly (as in liverworts and hornworts) or a distinct phase intervenes which is called as protonema (as in mosses). The buds develop on the protonema to form new gametophytes.

Classification

History

Braun (1864) for the first time introduced the name 'Bryophyta' but at that time Algae, Fungi, Lichen and mosses were also included in this group. Schimper (1879) placed Bryophyta at the level of division and since then it occupies the same rank till date.

The classification, proposed by different botanists, has no common agreement regarding the number of classes in the division Bryophyta. Eichler (1883) for the first time included two groups Hepaticae and Musci and since then it becomes a tradition to divide Bryophyta into, at least, these two classes. Some bryologists placed liverworts and hornworts (Anthocerotes) in a single class while others placed them into two different classes. Usually all mosses were placed in a single class separately since very beginning by all the workers. Engler (1892) divided the class Hepaticae into three orders: Marchantiales, Jungermanniales and Anthocerotales. This pattern of classification of Bryophyta and Hepaticae was followed by a number of botanists viz.: Fritsch (1929), Wettstein (1933-55), Bower (1935), and Evans (1939). While a number of botanists: Howe (1899), Campbell (1918, 1940), Smith (1938, 1955), Takhtajan (1953), Schuster (1953, 1958) realized that Anthocerotales should attain the level of class equivalent to the Hepaticae and Musci. They divided the Bryophyta into three classes: Hepaticae, Anthocerotae and Musci, after raising the order Anthocerotales upto the class level due to many characters which are remarkably different. This system of classification is more natural, placing liverworts, hornworts and mosses in three different classes: Hepaticae, Anthocerotae and Musci respectively. However, Verdoorn (1932) still recognized Hepaticales, Anthocerotales as two sub-classes of Hepaticae.

Rothmaler (1951) changed the name of classes from Hepaticae to Hepaticopsida, Anthocerotae to Anthoceropsida and Musci to Bryopsida. This nomenclature is considered more scientific as this is also in accordance with the recommendations of "International Code of Botanical Nomenclature" (i.e. the correct word ending of class is – **opsida** and the sub-class is – **idae**). Regarding the class – Anthoceropsida, Proskauer (1957) suggested that the name (Anthoceropsida) should be changed to Anthocerotopsida as the stem of the "misbegotten name *Anthoceros* is Anthocerot – rather than Anthocer – " (See Parihar 1959). However, Schuster (1953, 1966, 1979, 1984, 1984a, 1984b and Udar 1976,1976a) still recognized the class 'Hepaticae' in place of 'Hepaticopsida' giving reason that it is a "recommendation" only and thus not a binding.

Bryophyta has been divided into three classes:

1. Hepaticopsida (Hepaticae – liverworts)
2. Anthocerotopsida (Anthocerotae – Hornworts)
3. Bryopsida (Musci – Mosses)

Hepaticopsida

Study on the 'Hepatics' started a long time ago in 'Pre-Linnaean' period. But 'Hepaticology' as a Science is essentially "Post-Linnaean". 'Hepatica' is a latin word meaning 'liver' and this name was given to those plants which have liver-shaped bodies (thus they are commonly called as 'liverworts'). In the medieval times there was a great belief in the "Doctrine of Signature". According to this belief, the God would mark or sign each plant in some or the other way to indicate its medicinal value. The resemblance of a "plant" and an "organ" indicates the cure of any ailment or disease of that particular organ in that particular plant. The 'Hepatics' were supposed to be good for liver ailments.

The class Hepaticopsida is mainly characterized by dorsiventrally flattened gametophytes, which may be thalloid, either simple (homogenous) or internally differentiated (heterogenous – composed of various tissue) or leafy – differentiated into axis and leaves. The sex organs are always dorsal in position and are formed by superficial cell of dorsal surface of thallus (exogenous in origin). Some times they are terminal also as in leafy forms. The sporophyte has distinct foot, seta and capsule. The seta is massive, short at younger stage. It elongates only after the maturation of the capsule. The sporogenous tissue is endothecial in origin. The sporophytes are determinate in growth.

The class Hepaticopsida includes a large number of plants probably 6500-7000 valid taxa belonging to about 328 genera and 70 families (Schuster, 1984a).

Classification

The class Hepaticopsida has been classified variously. It was the nineteenth century when the hornworts were also placed along with the liverworts in Hepaticae (Endlicher 1841; Eichler, 1883; Engler 1892; Schiffner, 1893-95; Wettstein, 1903-1908, 1911; Verdoorn 1932; Evans 1939). Among the early system of classification, Endlicher (1841) gave the first systematic classification based on morphological characters and divided Hepaticae in the following 5 groups:

Class - Hepaticae

Ordo – I	Ricciaceae (*Riccia, Corsinia* and *Sphaerocarpos*)
Ordo – II	Anthocerotae (*Anthoceros, Monoclea* and *Calobryum*)
Ordo – III	Targioniaceae (*Targionia* and *Cyathodium*)
Ordo – IV	Marchantiaceae (± Marchantiinae)
Ordo – V	Jungermanniaceae (Frondosae, Jubuleae, Ptilideae, Mastigophoreae, Trichomanoideae, Geocalycaceae, Jungermannideae, Gymnomitreae)

Schiffner (1893-95) recognized three orders in the class:

CLASS – HEPATICAE

Order –	*I.*	*Marchantiales (Ricciaceae, Corsiniaceae, Marchantiaceae)*
	II.	Jungermanniales (Sphaerocarpaceae, Metzgeriaceae)
	III.	Anthocerotales (Anthocerotaceae)

While Wettstein (1903-1908, 1911) classified Hepaticae as follows:

Class – Hepaticae

Order – I.	Jungermanniales (Haplomitriaceae,Acrogynaceae (Jungermanniaceae), Anacrogynaceae (Metzgeriaceae and Sphaerocarpaceae)
Order – II.	Marchantiales (Marchantiaceae, Ricciaceae)
Order – III.	Anthocerotales (Anthocerotaceae)

Verdoorn (1932) recognized two subclasses first and then the orders:

Subclass – 1. Hepaticales
- Order – 1. Jungermanniales acrogynae
- 2. Jungermanniales anacrogynae
- 3. Sphaerocarpales
- 4. Marchantiales

Subclass – 2. Anthocerotales

While Evans (1939) recognized 4 orders in the following sequence:

Order – 1. Jungermanniales
2. Marchantiales
3. Sphaerocarpales
4. Anthocerotales

In this conventional treatment, basically 3-(4-5) groups/orders were recognized, which were placed in different sequence by various workers according to their view following progressive or retrogressive theory of evolution.

However, Cavers (1910-11) divided Bryophytes somewhat differently into 10 orders eliminating the tradition of classifying Bryophyta division first into the classes and then into the orders. The 10 orders are like this:

1. Sphaerocarpales
2. Marchantiales (Monocleaceae)
3. Jungermanniales (Calobryaceae)
4. Anthocerotales
5. Sphagnales
6. Andreaeales
7. Tetraphidales
8. Polytrichales
9. Buxbaumiales
10. Eu-bryales

Out of these (first 3 orders are for liverworts, next one is for hornworts and subsequent six orders are for mosses. But this system was not followed widely later on.

Since the beginning of twentieth century, the trend of classification was slightly changed and the Hornworts were kept in a separate class-Anthocerotae. In this pattern of classification Smith (1938) classified Hepaticae into four orders:

1. Sphaerocarpales – Sphaerocarpaceae, Riellaceae
2. Marchantiales – Ricciaceae, Corsiniaceae, Targioniaceae, Monocleaceae, Marchantiaceae
3. Jungermanniales – Suborder – Metzgerineae, Suborder - Jungermannineae
4. Calobryales

Schuster (1953) also considered Anthocerotae as a separate class and divided Bryophyta into three classes:

Class I. Anthocerotae – (Order – Anthocerotales)

Class II. Hepaticae –
- Subclass I – Jungermanniae (Orders: Calobryales, Jungermanniales, Metzgeriales)
- Subclass II – Marchantiae (Order: Monocleales, Naiaditales, Sphaerocarpales, Marchantiales)

Class III. Musci –
- Subclass I – Andreaeobrya
- Subclass II – Sphagnobrya
- Subclass III – Eubrya

Schuster (1966, 1979, 1984) revised the classification but the basic pattern remained more or less same (See Table I).

Table I

Schuster (1966)	Schuster (1979)	Schuster (1984)
Class – Hepaticae	**Class** - Hepaticae (Hepaticopsida)	**Class** – Hepaticae
Subclass – Jungermanniae	**Subclass** – Jungermannidae	**Subclass** – Jungermannidae
Orders: 1. Takakiales	**Orders**: 1. Calobryales	**Orders:** 1. Calobryales
2. Calobryales	2. Jungermanniales	**Suborder** – Takakiinae
3. Jungermanniales	3. Treubiales	**Suborder** – Calobryinae
4. Metzgeriales	4. Metzgeriales	2. Metzgeriales
Subclass – Marchantiae	**Subclass** – Marchantiidae	3. Treubiales
5. Sphaerocarpales	5. Monocleales	4. Jungermanniales
6. Monocleales	6. Sphaerocarpales	**Subclass** – Marchantiidae
7. Marchantiales	7. Marchantiales	5. Sphaerocarpales
		6. Monocleales
		7. Marchantiales

Grolle (1972, 1983) proposed the following classification including the order Anthocerotales within Hepaticae (See Table II).

Table II

Grolle (1972)	**Grolle (1983; See Bapna & Kachroo, 2000)**
Orders	**Orders**
1. Anthocerotales	**1. Anthocerotales**
2. Marchantiales	**2. Takakiales**
3. Metzgeriales	**3. Calobryales**
4. Calobryales	**4. Jungermanniales**
5. Jungermanniales	**5. Metzgeriales**
	6. Monocleales
	7. Sphaerocarpales
	8. Marchantiales

At one time, the monotypic order – Takakiales was included in class Hepaticopsida (Hepaticae) and it was placed before the order Calobryales (see Table I and II). But after the discovery of male plants and the sporophytes, *Takakia*, which was earlier considered as a liverwort, turned out to be a moss and now it has a new systematic position in Andreaeopsida as proposed by Smith and Davison (1993).

In the recent trend of classification the class Hepaticopsida has been divided into six orders (See Rashid 1998):

1. Calobryales (Moss like Hepatics)
2. Jungermanniales (Scale Moss Hepatics)
3. Metzgeriales (Multiform thallose Hepatics)
4. Monocleales (Giant thallose Hepatics)
5. Sphaerocarpales (Bottle Hepatics)
6. Marchantiales (Chambered Hepatics)

Three genera *Frullania*, *Pellia* and *Marchantia* belonging to three different orders Jungermanniales, Metzgeriales and Marchantiales respectively, have been discussed here in detail to represent the diversity of the group. All these forms are commonly found and can be easily available for teaching the students of under graduate level for their clearcut understanding.

Calobryales D.H. Campbell ex Schuster (1966) ex Hamlin (1972)

The order is mainly characterized by the heterotrichous nature of the plant (Fig. 2: 1,2). The gametophyte is differentiated into prostrate growing rhizomatous axis and erect growing aerial axis (stem). The aerial branches are radially symmetrical with three vertical rows of leaves, which are spirally arranged and transversely inserted on the axis. All the leaves are alike in shape and size. Sometimes one row may be relatively smaller. The leaves are generally unistratose but sometime may be bistratose at the base (Fig. 2: 4). They are without midrib. The rhizoids are totally absent. The plant body is densely covered with copious amount of mucilage produced by number of mucilage papillae (2-3 celled) present on the axis. The growth of the axis takes place by a pyramid like apical cell having three cutting faces. The stem is internally differentiated into outer cortical and inner meduallary regions. The cortical cells are large parenchymatous filled with starch grains. The meduallry cells are comparatively smaller. The sex organs are present on somewhat flattened apical portion of the axis where the leaves are closely arranged and they are larger in size also. The plants are dioecious. They may be acrogynous (Calobryum) or anacrogynous (Haplomitrium). Antheridia have short stalk and somewhat spherical to ovoid antheridial body (Fig. 2: 5,6). Archegonia have long, twisted neck with 4 rows of cells in the jacket enclosing 16-20 neck canal cells and slightly wider arehegonial venter which has bistratose jacket at maturity (Fig. 2: 7,8). The ontogeny of both the sex organs is same at the early stages (Fig. 1. A1-6; E1-7). The sporophyte has distinct foot, long massive seta and cylindrical capsule (Fig. 2: 3,9). The capsule has unistratose jacket except the apical portion of the capsule. The cells have longitudinally oriented ring like thickening. The spores are small and elaters are long tapered. The capsule dehisces into 4 valves.

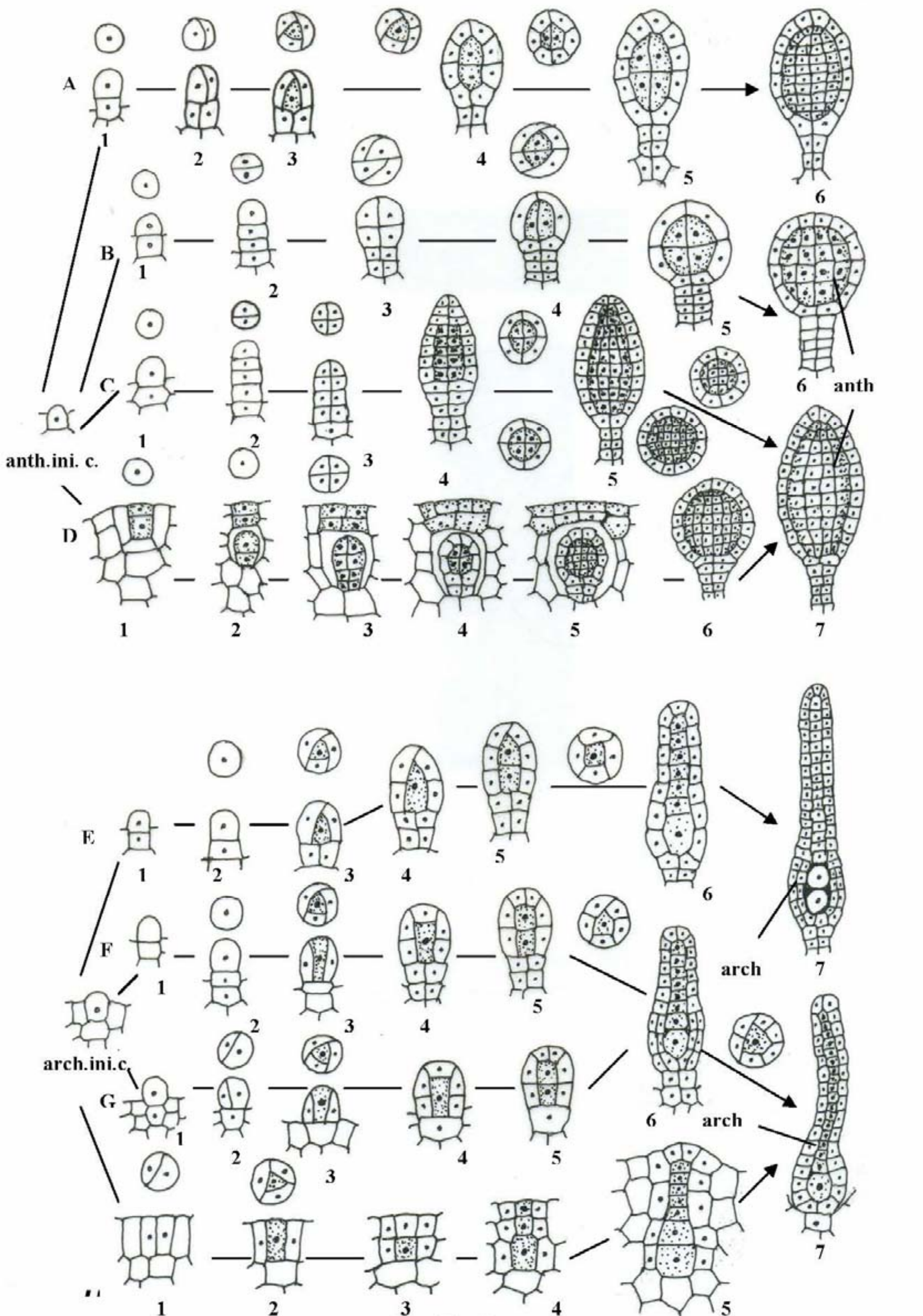

Fig.1

Fig. 1. Development of sex organs (schematic representation); A-D, Antheridial development; A:1-6. Calobryales, B:1-6. Jungermanniidae (Jungermanniales, Metzgeriales), C:1-7. Marchatiidae (Machantiales, Monocleales); D:1-7. Anthocerotae E-F. Archegonial development; E:1-7. Calobryales, F:1-7. Jungermanniidae (Jungermanniales, Metzgeriales), G:1-7. Marchatiidae (Machantiales, Monocleales), H:1-7. Anthocerotae. (anth. ini. c. – antheridial initial cell, anth – antheridium, arch. ini. c. – archegonial intial cell, arch – archegonium). Figures drawn at the top are the cross-section & at the bottom are longisection of identical stages. (After Schuster)

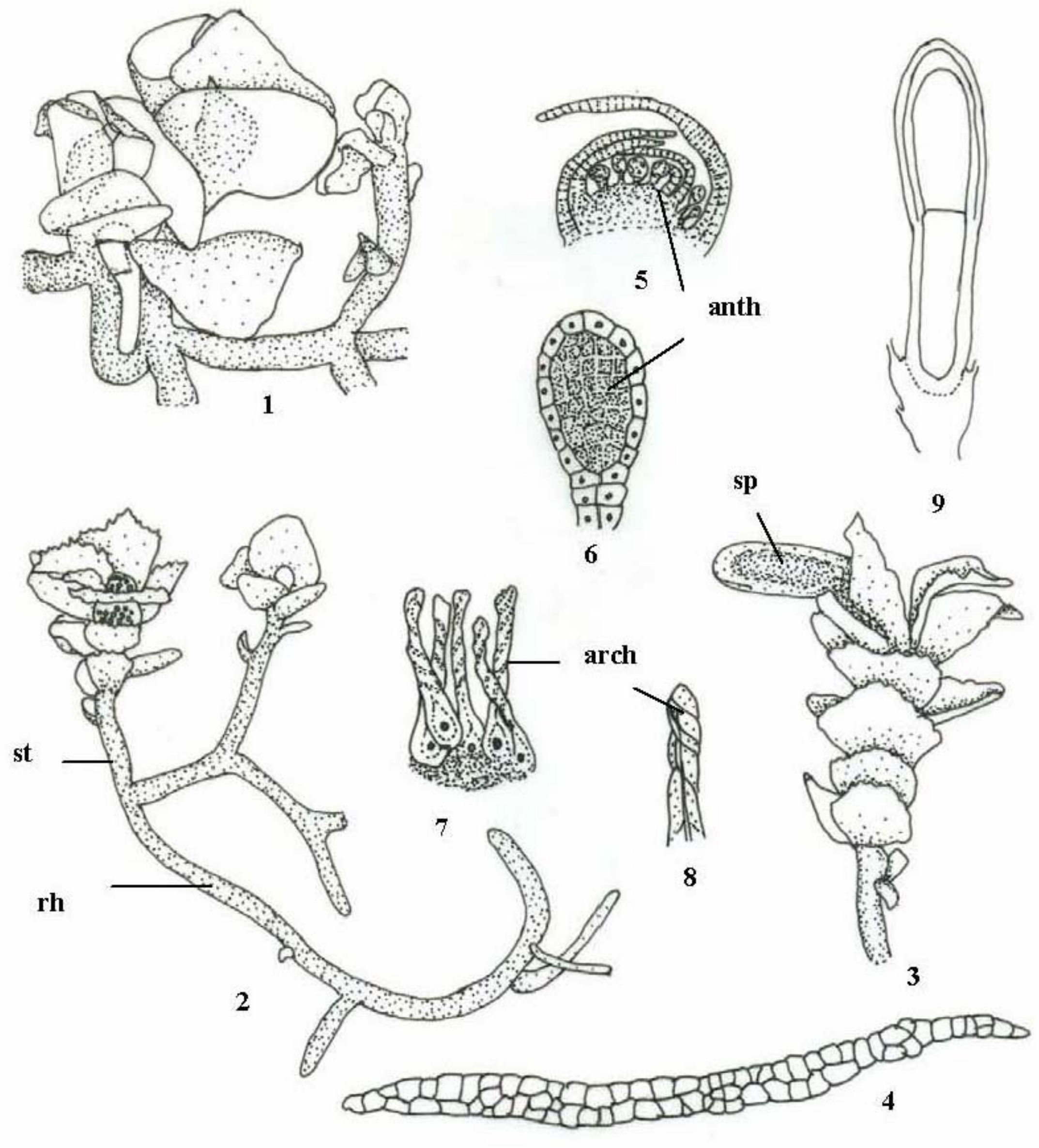

Fig. 2. ***Calobryum*** 1. A plant showing heterotrichous habit, 2. A male plant, 3. A femal plant with young sporophyte, 4. Cross – section of leaf at base, 5. Antheridial group at apex, 6. A single antheridium, 7. Archegonial group, 8. Twisted neck of the archegonium, 9. Vertical longitudinal section of young sporophyte. (rh – rhizomatous axis, st – stem, sp – sporophyte, anth – antheridia, arch – archegonium). Figs. 1, 5-9 *C. indicum* (After Udar & Chandra), Figs. 2-4 *C. dentatum* (After Kumar & Udar

The order Calobryales is phylogenetically very important as it shows combination of both primitive and advance characters. It seems to be originated from same evolutionary line from which Jungermanniales has originated but they have been segregated from that line very early. That is why it has been often, placed along with Jungermanniales by earlier workers. However, the distinctive features of the group like ontogeny of antheridium, structure of archegonium (with 4 rows of cells in neck portion), single layered capsule wall with annular thickening, copious amount of mucilage, heterotrichous nature of plant, absence of rhizoids and acrogynous as well as anacrogynous condition justify the placement of this group at the order level.

The order Calobryales includes a single family Haplomitriaceae and two genera: Calobryum Nees, Haplomitrium Nees with 10 – 12 species. In India, the order in represented by both the genera and six species: Calobryum with three species: C. dentatum, C. blumei, C. indicum and Haplomitrium with three species: H. hookeri, H. kashyapii and H. grollei (Srivastava, 1998).

2. Jungermanniales Limpr. (in Cohn 1876)

This order is most important in having large number of leafy liverworts, which exhibit the great extent of morphological diversity as well as the habitat diversity. This single order itself only constitutes about 85% of the total Hepatics (Schuster 1984a). This group may be considered as most successful as the plants grow on variety of habitats as corticolous, foliicolous, rupicolous, saxicolous, terricolous populations. Some of the members are aquatic also like *Jungermannia vulcanifolia, Scapania undulata*. The order includes exclusively leafy gametophytes. It is mainly characterized by the plant body, which is differentiated into axis and the leaves. They are usually bilaterally symmetrical and sometimes radially symmetrical in some primitive forms. The leaves may be arranged in 2-3 rows showing isophylly or anisophylly. In isophyllous condition all the three rows of leaves are alike as in some primitive forms whereas in anisophyllous forms, two rows of dorsolateral leaves are large and alike. The third ventral row has smaller leaves, which are generally called as underleaf/ventral leaf or amphigastrium. The leaves are subtransverse-obliquely attached to the axis showing overlapping among them. The arrangement of the leaves on the axis may be succubous or incubous. The leaves are always unistratose and are without mid rib. The leaf-cells may be thin walled or thick walled forming trigones of diverse forms at the corners. The rhizoids are simple, smooth walled and they are present throughout the ventral surface of the axis or confined to the base of underleaf in group/fascicle. The growth of the axis takes place by tetrahedral apical cell with three cutting faces giving the radial symmetry in some primitive forms and bilateral symmetry in the advanced forms where the one (ventral) segment is reduced or vestigial. The axis in simple internally, differentiated into cortical and medullary cells.

The plants may be unisexual (dioecious) in primitive taxa while generally bisexual (monoecious) in advanced taxa. The development of both the sex organs is entirely different since beginning (Fig. 1. B.1-6; F.1-6). Antheridia are usually globose, axillary in position and are protected by male bracts. Archegonia are always terminal (acrogynous) occurring singly or in groups. They are protected by a definite structure, formed by the fusion of perichaetial leaves, called as perianth. Archegonial neck has five vertical rows. Sporophyte has distinct foot, seta and capsule. The capsule has multilayered [2-8(10)] capsule wall, large number of small spores and elongated elaters which may be fixed to the capsule wall sometimes. The capsule dehisces into distinct 4 valves.

At present the order has 39 families and 263 genera (Schuster, 1984a). In India, the group is represented by 13 families, 65 genera and 520 species (Srivastava, 1998). The genus *Frullania* has been taken as representative of this group of leafy liverworts.

Frullania

- *Habitat and Distribution*

  The genus, *Frullania*, generally grows on moist rocks as well as on the trees in the form of corticolous (bark surface) and foliicolous (leaf surface) populations. They form dense cushion of plants, which are dark brown, reddish – brown or black in colour. They are widely distributed in tropical and temperate regions. The epiphyllous species are quite common in tropical rain forests. The genus is representated by 58 taxa in India, which grow abundantly in south India, eastern and western Himalayas (Parihar *et al* 1994).

- *Gametophyte*

  The plants of *Frullania* are dorsiventral and pinnately branched. They are differentiated into axis and leaves (Fig.3: 1). The leaves are present in three rows. Two rows of large dorsolateral leaves and one row of small ventral leaf, also termed as underleaf or amphigastrium (Fig.3: 3-6). The dorsolateral leaves are complicate bilobed with the dorsal lobe large called as leaf-lobe and the ventral lobe small, modified in to a sac like structure called as leaf-lobule (Fig.3: 3-6). The leaves are incubously arranged on the axis in which the anterior end of the older leaf covers the posterior end of the young leaf when the plant is observed from dorsal side (Fig.3: 2). The branching of the axis is *Frullania* – type where the branch is subtended by a leaf having dorsal lobe only. The ventral leaf-lobule is absent as the ventral portion of the lateral segment of the apical cell is used up in the formation of lateral branch (Fig.3: 2).

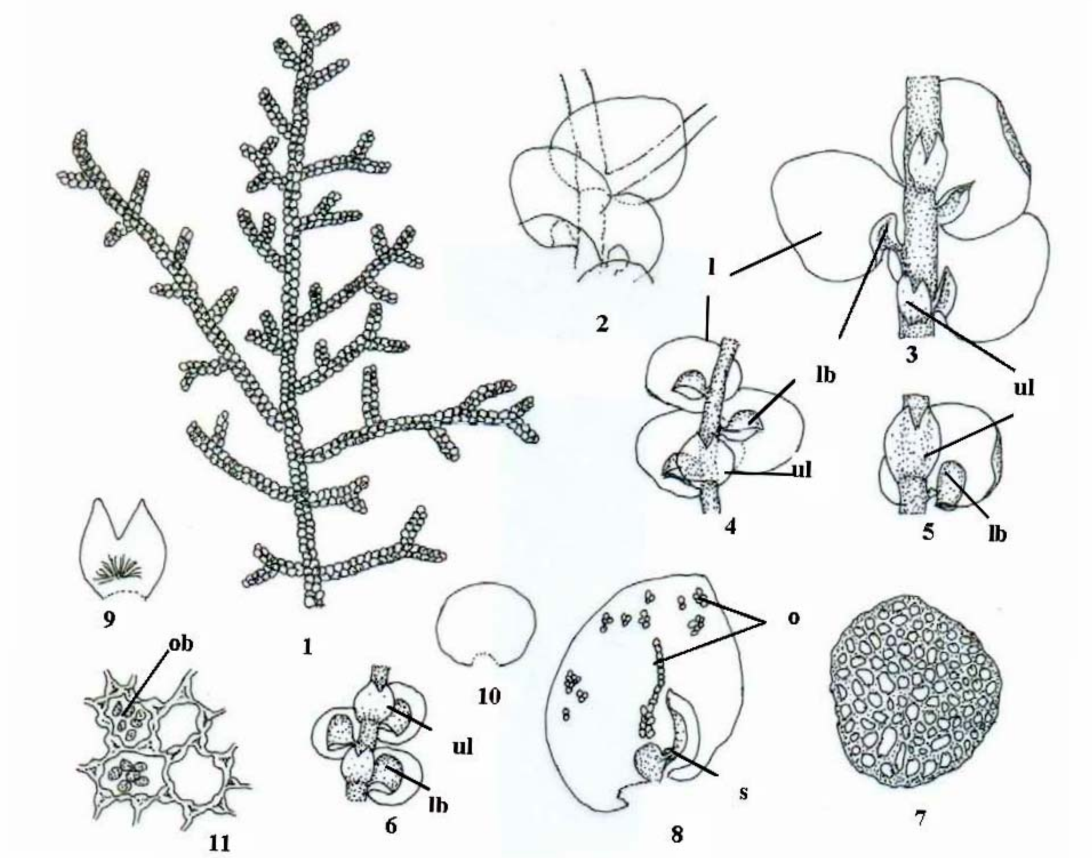

Fig.3

Fig. 3. ***Frullania*** 1. A plant showing pinnate branching and incubous arrangement of the leaves (dorsal view), 2. A portion of plant showing *Frullania* – type branching (dorsal view) 3-6. Portion of plants showing explanate (3), galeate (4) and saccate (5,6) leaf-lobules (ventral view), 7. Cross-section of axis, 8. A leaf with explanate leaf - lobule, ocelli and stylus, 9. A bifid underleaf (amphigastrium) with rhizoids, 10. An entire underleaf, 11. Leaf cells with oil bodies. (s – stylus, o – ocelli, ob – oil bodies, l – leaf lobe, lb – leaf lobule, ul – underleaf). Figs. 1,2,7,11 (After Udar), Figs. 3,6,8-10 (After Kamimura), Figs. 4,5 (After Schuster).

The leaves are unistratose without midrib. The leaf cells are thick walled, and the thickenings are more prominent at the corners, called as trigones (Fig.3: 11). The oil-bodies in the leaf-cells may be homogenous or granular, spherical to ovoid and few to many (2-8) in number (Fig.3: 11). These oil-bodies are present in fresh and living plants only. This is the characteristic feature of not only *Frullania* but of all the liverworts. In some species, besides the normal leaf-cells, there are few enlarged conspicuous cells in the leaf, which may be present scattered or arranged in a row. These are the ocelli (Fig.3: 8). The ventral leaf-lobule is of diverse forms and they are of three main types (i) Saccate (Fig.3: 5) (ii) Galeate (Fig.3: 4) (iii) Explanate (Fig.3: 3). The saccate leaf-lobule is club shaped or cylindrical having a narrow sac, which is open at one end. The galeate leaf-lobule is helmet shaped having a broad sac, which also opens at one end. The explanate leaf-lobule has concave face, which opens at both the ends. These leaf-lobules are helpful in retaining the water. In some species, at the junction of lobule and stem, stylus is present (Fig.3: 8). It consists of one row or several rows of cells. It may be conspicuous or indistinct.

The underleaves are of two types: (i) they may be unlobed where the apical portion is entire (Fig.3: 10) found in some species, (ii) or they may be bilobed where the apical portion is divided into two lobes (Fig.3: 9) which is found quite commonly. The size, attachment on the axis and relative width of the underleaf vary from species to species. The rhizoids are unicellular, simple, smooth walled and present at the base of underleaves (Fig.3: 9).

- *Axial anatomy*

The stem is internally differentiated into outer cortical and inner medullary region. The cortical cells are small, thick walled and brownish whereas the medullary cells are comparatively larger, thin walled and without pigmentation (Fig.3: 7).

- *Vegetative reproduction*

In *Frullania* there is no special mode of vegetative reproduction as such. However, it takes place by means of fragmentation of branches by death and decay of older portion of axis. Each separated branches (fragments) grow into new gametophyte by the apical cell. Sometimes the leaves are caducous in which the dorsal lobes are shed off and the ventral leaf-lobule remain intact to the parent axis. The detached lobes may give rise to new plants. Besides regeneration is also common, in which the leaf cells regenerate to form globose mass of cells on the leaf surface, which develops into new gametophyte (Fig.4: 37-40).

- *Sexual reproduction*

The plants may be monoecious or dioecious. In monoecious species the male and female sex organs are present on separate branches (autoecious condition).

- *Antheridia*

The antheridia are present in the axil of leaves on a short capitate or long – spikate lateral branch (Fig.4: 1). The entire lateral branch may develop into antheridial branch or the antheridial bracts are either terminal or intercalary. The leaves, subtending the antheridia are greatly modified, saccate with both the dorsal and ventral lobes, almost of equal size. These are called as male (antheridial) bracts (Fig.4: 2). The number of bracts per antheridial branch may vary. The underleaves on the antheridial branch may be present throughout or confined to the base only and are called as bracteoles. There are 1-2 antheridia per antheridial bract. A mature antheridium has spherical antheridial body and biseriate long stalk (Fig.4: 2).

- *Development of antheridium*

The antheridium is exogenous in origin, not only in Frullania but in all the liverworts. The development process also is more or less same in all Jungermanniales, Metzgeriales and Marchantiales except the position of antheridial initial cell in leafy and thalloid liverworts and the number of segments produced, which are responsible for the shape of antheridium. Superficial antheridial initial cell get differentiated in the axil of young bract. It slightly protrudes out and divides transversely forming 2-celled rudiment with outer and inner cell (Fig.1: B.1). The outer cell forms the antheridium proper and the inner cell forms the stalk. The outer cell generally divides transversely forming 4-5- celled filament, which further divides longitudinally by vertical centric walls and then by vertical eccentric (oblique) walls twice in such a way that they produce two central androgonial cells surrounded by four peripheral jacket cells (Fig.1: B. 2-4). The peripheral jacket cells divide anticlinally forming single layered jacket of antheridium while the androgonial cells divide and redivide to form spermatogenous cells, which finally get differentiated into biflagellate spermatozoids (Fig.1: 5,6).

- *Archegonia*

The archegonia are always terminal, present in groups at the apex of main axis or lateral branch. The number of archegonia may vary 2-12. They are enclosed in a sac like covering called as perianth (Fig.4: 3,4). Archegonia have swollen ventrer and long, narrow neck with five rows of cells. The perianth is somewhat wider in the middle portion and is narrower towards the apex and the base. It opens at the apex by a narrow, tubular opening forming a prominent beak. The perianth surface may be smooth or has minute tubercles, which are more prominent on the keels. The perianth is formed by the fusion of three leaves hence it is generally trigonous with prominent folds, also called as keels/plicae. It is more or less flat on the dorsal side and angled on the ventral and lateral sides (Fig.4: 5). The perianth is supported by 2-4 pairs of bracts and bracteoles, which are modified leaves and underleaves respectively. The female bract has larger bract lobe and smaller bract lobule, which is different from leaf lobule and is not saccate (Fig.4: 6,7). The bracteole is more or less similar to underleaf but it is larger in size (Fig.4: 8). The margins of the bracts and bracteoles may be dentate or smooth, entire as found in vegetative leaves and underleaves. In case of ocellate species of Frullania, bracts also have occelli.

- *Development of archegonium*

Like antheridium, the development of archegonium is also similar in all the liverworts except the number of cells in neck portion both in peripheral region (5 or 6 vertical rows) and axial regions (number of neck canal cells). Further the position of archegonial initial cell also differs in leafy and thalloid liverworts but in both the cases they are superficial and hence exogenous in origin. The archegonial initial cell first divides transversely forming 2-celled rudiment with outer bulging cell, which forms proper archegonium and the inner cell, which forms the base (Fig.1: F.1,2). The archegonial mother cell divides by three oblique walls in such a way that they produce an axial cell surrounded by three peripheral cells (Fig.1: F.3). Two larger cells, out of three peripheral cells divide by vertical wall producing 5 rows of cells, which further divides transversely forming jacket of archegonium. The neck has fixed 5 vertical rows of cells while in venter portion the number is not constant. The axial cell first divides to form outer primary cover cell and inner central cell. The primary cover cell divides twice vertically intersecting each other, thus forming 4 cover cells. The central cell divides to form primary canal cell and primary venter cell. The primary canal cell divides transversely to produce variable number of neck canal cells while the primary venter cell divides to form a ventral canal cell and an egg (Fig.1: F.4-6).

- *Fertilization*

The inflated perianth, bracts and bracteoles help in retaining the moisture around the sex organs, which is necessary for the movement of spermatozoids released from mature antheridia. The spermatozoids reach to the archegonial neck and fertilization takes place.

- *Sporophyte*

The sporophyte has distinct foot, seta and capsule, which remain inside the perianth at younger stage (Fig.4: 23). The foot is flattened with more or less elongated cells, which are haustorial in nature. The seta is massive short and broad, which is not sharply demarcated from the capsule. The capsule is spherical with 2-layered capsule wall, spores and elaters. The cells of the outer layer of the capsule wall has nodulose thickening at the corners while the cells of inner layer has sheet like irregular thickening (Fig.4: 24,25). The spores are more or less spherical, globose or oblong. The spore has two layers - exine and intine. The exine surface is variously sculptured with minute papilla, spines tubercles or verrucae (Fig.4: 27). The elaters are elongated, trumpet shaped (broader at one end) with single spiral thickening band and are fixed to the capsule wall at both the ends (Fig.4: 23,28).

- *Development of sporophyte*

The zygote first divides transversely forming the outer epibasal cell and inner hypobasal cell (Fig.4: 11). The epibasal cell further divides transversely while the hypobasal cell divides vertically forming a 3-tiered embryo, which develops into the capsule, seta and foot starting from the apical tier (Fig.4: 11). The basal cells (lower tier) divide vertically forming number of elongated cells of the foot. The middle cells (middle tier) divide both vertically and transversely giving rise to seta as well as lower portion of the capsule. The apical cells (upper tier) divide periclinally and get differentiated into outer amphithecium and inner endothecium (Fig.4: 14-18). The amphethecium further divides both periclinally and anticlinally thus producing an arched structure with two-layered capsule wall of half spherical capsule (Fig.4: 20). The thickening develops later on in the cells of both layers. The inner, four endothecial cells divide vertically only and the cells thus produced are longer in the middle portion of the capsule and are shorter towards the periphery (Fig.4: 19, 20). They further differentiate very characteristically into alternate sterile and fertile cells in a regular manner (Fig.4: 21). The sterile cells are relatively narrow and called as elater mother cells. They simply elongate, and remain attached to the apical and basal portion of the capsule. Later on thickening develops in the form of single spiral (Fig.4: 28). The fertile cells first divide mitotically and form vertical rows of spore mother cells, which further divide meiotically forming the spore tetrads (Fig.4: 21,22). Simultaneously the cells of archegonial venter divide actively forming the calyptra within the perianth.

- *Dehiscence of the capsule*

At the maturity, seta elongates, pushing the capsule outside the calyptra and perianth. Due to loss of moisture in the cells of the outer layer of the capsule wall, the cells shrink more rapidly than the inner layer and thus tension is built up causing the rupturing of capsule wall into four valves (Fig.4: 9,26). These valves get stretched backwardly and the fixed elaters are snatched with the force to get detached from the base and the spores get dispersed with jerk to greater distances.

- *Spore germination*

The spores of Frullania germinate in situ. They start germinating within the capsule and the phenomenon is also termed as 'precocious' germination. The exposure does not rupture. The spore first divides by a transverse wall (Fig.4: 29,30). Then the upper cell divides by a vertical wall (Fig.4: 31). Further divisions take place in all the three planes resulting into a multicellular globose 40-50 celled sporeling withing the stretched spore coat (Fig.4: 32,33). After dispersal from the capsule and getting suitable substratum, the sporeling develops rhizoids from one end and leafy shoot from another end (Fig.4: 34,35). The first formed leaves are ovate to oblong about 2-4 celled broad at base. The underleaves are also ovate and narrow. The young (juvenile) leaves are strongly inflated and saccate (Fig.4: 36).

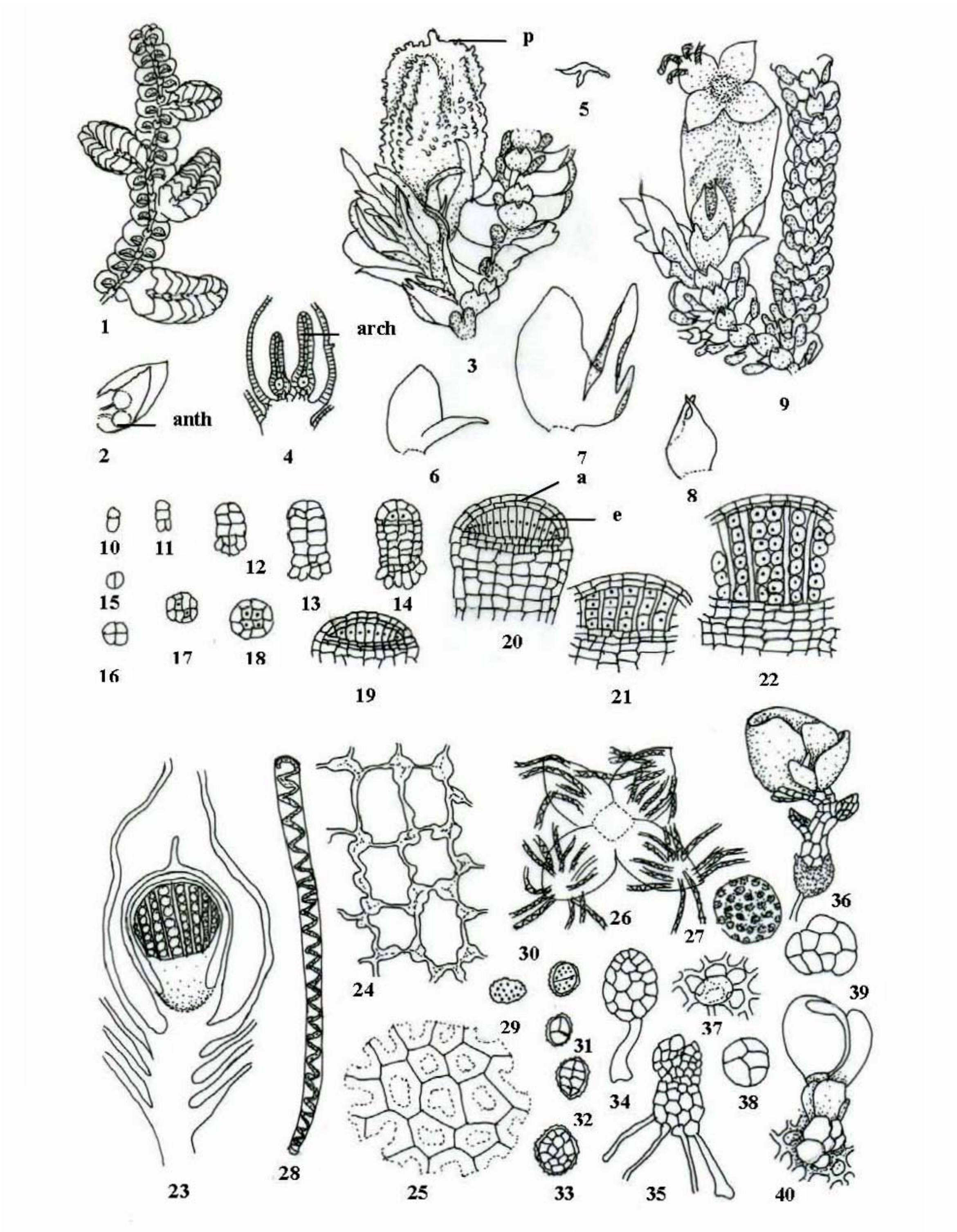

Fig.4

Fig. 4. *Frullania*

1. A plant with antheridial branches, 2. Antheridial (male) bract with two antherida, 3. A plant with perianth and female bracts, 4. Archegonia, 5. Cross-section of perianth, 6,7. Female bracts, 8. Female bracteole, 9. A portion of plant with dehisced capsule (Sporophyte), 10-22. Stages in the development of sporophyte, 23. Vertical longitudinal section through sporophyte. 24. Capsule wall (outer layer), 25. Capsule wall (inner layer), 26. Dehisced capsule with fixed elaters, 27. Spore, 28. Elater, 29-36. Stages in spore germination, 37-40. Stages in regeneration from leaf cells. (a – amphithecium, e – endothecium, p – perianth, anth – antheridium, arch – archegonium). Figs. 1, 23-28 (After Udar), Figs. 2,4,10-22 (After Cavers), Figs. 3,5-9 (After Kamimura), Figs. 29-35 (After Hofmeister), Fig. 36 (After Goebel), Figs. 37-40 (After Fulford).

3. Metzgeriales Schuster ex Schjakov

This order is important in having a large number of plants, which are very simple in both the morphology and anatomy. Besides, they show anacrogynous condition. The order includes both the morphoforms, primarily thallose being undifferentiated but some members are leafy (foliose) also which are differentiated into axis and leaf like lateral lobes. The plants are strictly dorsiventral in position. Rhizoids are simple and scattered on the ventral surface of the plant. In leafy forms, the leaves are longitudinally inserted. The apical cell is with 2-(4) cutting faces. In some forms it may be tetrahedral. The conducting strand is well defined in some members like Pallavicinia, while some other members are devoid of conducting strand as in case of Pellia, Riccardia and Fossombronia. The plants may be monoecious or dioecious. The sex organs are dorsal in position (never axillary) and are present in acropetal manner. Antheridia are usually globose and arehegonia have 5 rows of cells in neck portion. The sporophyte has distinct foot, seta and spherical to elongated capsule. The capsule has two - layered capsule wall, numerous small spores and elongated elaters. Besides, short stumpy elaters and fixed sterile cells are also present. These sterile cells are called as elaterophores, which may be basal in case of Pellia while it is apical in Metzgeria and Riccardia. The dehiscence of the capsule is bivalved (Pallavicinia) or 4 valved (Pellia).

Grolle (1972) recognized 8 families in the order: 1. Aneuraceae, 2. Balasiaceae, 3. Codoniaceae, 4. Hymenophytaceae, 5. Metzgeriaceae, 6. Pelliaceae, 7. Phyllothalliaceae and 8. Treubiaceae, while Schuster (1984) recognized 12 families and 28 genera : 1. Fossombroniaceae, 2. Pelliaceae, 3. Allisoniaceae, 4. Phyllothalliaceae, 5. Pallaviciniaceae, 6. Sandoethallaceae, 7. Makinoaceae, 8. Blasiaceae, 9. Aneuraceae, 10. Vendiemeniaceae, 11. Metzgeriaceae and 12. Hymenophytaceae. At Present, the order includes 13 families (including Treubiaceae) and 30 genera (including Treubia and Apotreubia). In India, the order is represented by 7 families, 12 genera and 58 taxa (Srivastava, 1998). The genus Pellia has been taken as representative of this order.

Pellia

- *Habitat and Distribution*

  Pellia usually prefers to grow in moist and shady places near the streams, springs, on moist soil or rocks, under the shade of trees. Occasionally, the genus has been found growing under very humid conditions as under dripping or flowing water. In that case, the plants are usually sterile, green and show more pronounced vegetative growth. While the plants, growing in exposed sites under intense light and drier conditions, are fertile and develop brown pigmentation in thalli. The genus Pellia is widely distributed in temperate regions. In India, the genus is represented by two species: P. epiphylla and P. endivaefolia. Pellia epiphylla is found growing luxuriantly in eastern Himalayas while P. endivaefolia has been found in western Himalayas forming the extensive mats (Srivastava, 1998).

- *Gametophyte*

  The plants are thin, dorsiventral, dichotomously branched thallus, which generally form green large patches over the substratum. The thallus has distinct broad mid rib and the wings, which have either entire or wavy margins (Fig. 5: 1,2). The apical portion of the thallus is notched in which the growing point (apical cell) is located. The club - shaped mucilage hairs (papillae) are present in the apical notch on ventral side of the thallus, which bent over the apical cell to protect the growing point. Ventral scales are totally absent in the genus and the rhizoids are simple, unicellular, smooth walled, present on the ventral surface of the thallus along the mid rib.

- *Thallus anatomy*

  The thallus is very simple internally without any tissue differentiation. It has upper and lower epidermis made up of smaller cell. In between all the cells are alike, thin walled and parenchymatous (Fig. 5: 5-7). The thallus is about 8-16 cells thick in the middle portion and gradually becomes thin towards the margins, which are one cell layer thick. The upper epidermal cells have numerous chloroplasts as compared to the lower epidermal and thallus cells. Generally all the thallus cells are densely filled with starch grains. In case of P. epiphylla and P. neesiana, some fibrous cells with thickening bands are also present in the thallus which are absent in Pellia endivaefolia (Fig. 5: 6, 7).

- *Apical growth of the thallus*

The apical growth of the thallus takes place by means of an apical cell. In P. endivaefolia the apical cell is cuneate (wedge shaped) with four cutting faces: one dorsal, one ventral and two lateral (Fig. 6: 38) while in P. epiphylla the apical cell is lenticular, cylindric which has a posterior convex and two lateral cutting faces (Fig. 6: 37).

- *Vegetative reproduction*

In Pellia, the adventitious shoots are common which develop from superficial cells. When they get detached from parent plants, they form new independent thalli. In P. endivaefolia, the apex of thallus often repeatedly dichotomously branched forming a dense mat of small lobes (Fig. 5: 3). Each lobe is a sort of miniature thalli with its own growing point. When it gets detached from the parent thallus, it develops into a new thallus. Fragmentation may also serve for vegetative reproduction.

- *Sexual reproduction*

The plants may be monoecious or dioecious. Pellia epiphylla is monoecious and protandrous in which the antheridia are present just behind the archegonial group (Fig. 5: 2). Pellia endivaefolia and P. neesiana are dioecious (Fig. 5: 4).

- *Antheridia*

The antheridia are present embedded in thallus tissue (antheridial chamber) on the dorsal side in 2-4 rows along the mid rib (Fig. 5: 2,4). The antheridial chambers are somewhat raised from thallus surface and have an apical opening (Fig. 6: 10). Generally there is single antheridium per antheridial chamber but sometime two antheridia may be present in a single antheridial chamber (Fig. 6: 10). A mature antheridium has spherical antheridial body and a short slender stalk.

- *Development of antheridium*

The antheridial initial cell becomes evident as a small papillate protrusion near the apical cell (Fig. 6: 1). It divides transversely (Fig. 6: 2). The outer cell projects out and divide both transversely and vertically (Fig. 6: 3). The upper cell forms the antheridium proper and the lower cell forms the stalk. Now the upper cell divides twice by oblique vertical walls, which intersect each other forming two central androgonial cells and four peripheral jacket cells (Fig. 6: 5-9; Fig. 1: B.1-6). The jacket cells divide anticlinally to form the single layered jacket of the antheridium. The androgonial cells divide in various planes to form numerous, small, cubical spermatogenous cells which give rise to spermatozoids having spirally coiled body with 2 long flagella at the anterior end. Simultaneously, the thallus cells adjacent to developing antheridia grow up around the antheridium forming antheridial chamber.

- *Archegonia*

The archegonia are present in groups on dosal surface of the thallus associated with mucilage hairs. They lie horizontally with their necks directed towards the apex and are protected by involucre which is flap like in P. epiphylla while it is tubular in P. endivaefolia and cylindrical in P. neesiana. The archegonium has long neck and somewhat dilated venter, which is not sharply demarcated. The jacket of neck region consists of 5 vertical rows of cells. The axial row has apical cover cells, 6-9 neck canal cells, a ventral canal cell and an egg (Fig. 6: 16-18).

- *Development of archegonium*

The archegonia develop from the segments produced by the apical cell near growing point. They are not formed very regularly in acropetal manner. Any cell may become archegonial initial cell. Hence the young and old archegonia are intermixed. The archegonia develop in usual manner. The archegonial initial cell divides transversely into outer and inner cells. The outer cell somewhat projects out and again divides into two cells (Fig. 6: 11,12). The outer cell divides by three vertical ecentric oblique walls in such a way that a central axial cell and three peripheral cells are produced

(Fig. 1: F.3). The axial cell divides transversely into primary cover cell producing cover cells and central cell, which divides to form 6-9 neck canal cells, ventral canal cell and egg (Fig. 6: 13-16, Fig. 1: F.3-6). Out of three peripheral cells, only two cells divide vertically to form 5 vertical rows of cells, which further divide transversely to form the jacket of neck portion. The jacket wall in venter portion has variable numbers of cells which become two layered also. Simultaneously with the development of archegonia, the thallus tissue grows upward to protect the archegonia. This outgrowth of the thallus is called involucre, which are of various shapes.

- *Fertilization*

At maturity, the antheridium ruptures when it comes in contact with water releasing the androcytes. They spread in the film of water and reach to the archegonial involucre where spermatozoids emerge out from androcytes and fertilization takes place.

- *Sporophyte*

The sporophyte consists of foot, seta and capsule (Fig. 6: 25). The foot is conical in shape with all the cells parenchymatous. The edges are somewhat extended forming a collar around the base of seta. The seta is massive and consists of several longitudinal rows of cells arranged regularly. At younger stage the seta is short but at the maturity elongates rapidly by the elongation of cells (Fig. 5: 8,9). The capsule is spherical with 2-3 layered capsule wall, spores, elaters and basal elaterophores (Fig. 6: 24). The cells of outer layer of capsule wall are polygonal with nodular thickening at the corners as well as intermediate nodular thickening (Fig. 5: 12). The cells of inner layer of capsule wall are somewhat narrow, elongated with semiannular thickening bands (Fig. 5: 13). In P. endivaefolia the inner layer is lacking in thickening. There are 4 distinct longitudinal lines of dehiscence (Fig. 5: 9,10). The spores are somewhat globose-oblong, unicellular at young stage but later on they become multicellular at the time of dispersal (Fig. 5: 14). The elaters are long, slender with 2-3- spiral thickening bands (Fig. 5: 15). Besides spores and free elaters, basal elaterophores are also present in the center of the capsule (Fig. 5: 11, Fig. 6: 24,25).

- *Development of sporophyte* (Fig. 6: 19 – 28)

The zygote first divides to transversely forming upper epibasal cell and lower hypobasal cell (Fig. 6: 19,20). The hypobasal cell forms the haustorium (Fig. 6: 22,23), which is one celled or it may divide once or twice occasionally. The epibasal cell forms the entire sporophyte. It divides first transversely and then vertically resulting into 4-cells and subsequently into group of cells (Fig. 6: 21,22). The lower cells divide and redivide to form foot and seta, while the upper cells get differentiated into outer amphithecium and inner endothecium by periclinal division (Fig. 6: 23). The amphithecium further divides periclinally and anticlinally forming 2-3 layered capsule wall. Later on thickening develops in the cells except along the four vertical lines, which indicate the line of dehiscence. The endothecium forms the archesposium, which repeatedly divides and produce mass of cells. Some of the cells at the base of the capsule get differentiated into basal eleterophore. Rest of the cells form sporogenous tissue, which further differentiates into spore mother cell and elater mother cell. The spore mother cells become conspicuously 4-lobed in tetrahedral manner and after meiotic division form haploid spores (Fig. 6: 26). The elater mother cells elongate and develop 2-3- spiral thickening bands in their walls (Fig. 5: 15; Fig. 6: 27). In the meantime calyptra develops from archegonial venter.

- *Dehiscence of the capsule*

At the maturity the seta elongates enormously carrying the capsule outside the calyptra and involucre (Fig. 5: 8). The elongation of the cells is often upto 40 times of their length and during the process the starch in converted to sugar, which increases the osmotic concentration of the cells. As a result water is rapidly absorbed causing cell elongation. When the mature capsule in exposed to air, due to loss of moisture in the wall cells, the capsule dehisces into 4 distinct valves through line of dehiscence upto the base. At later stages these valves get deflexed, hanging down exposing the basal elaterophores (Fig. 5: 11). Hygroscopic movement of the elaters and elaterophores help in loosening the spore mass as well as in the dispersal of spores to some distances.

- *Spore germination*

In the genus Pellia also, the spores germinate in situ (precociously) within the capsule and at the time of dispersal they are multicellular. During the process (germination) the spore divides transversely forming first 2-celled and then 4-celled filamentous sporeling (Fig. 6: 29-31). After that it divides vertically and becomes multicellular (Fig. 6: 32,33). The spore coat remains intact. At this multicellular stage, spores get dispersed. It further divides by vertical divisions in the central region and oblique divisions in the apical region thus forming a wedge shaped apical cell, which is broader towards the apex and narrow at the base (Fig. 6: 34,35). Meantime the rhizoid develops as an outgrowth from basal cell (Fig. 6: 34-36). Further growth takes place by the apical cell and the young thallus develops.

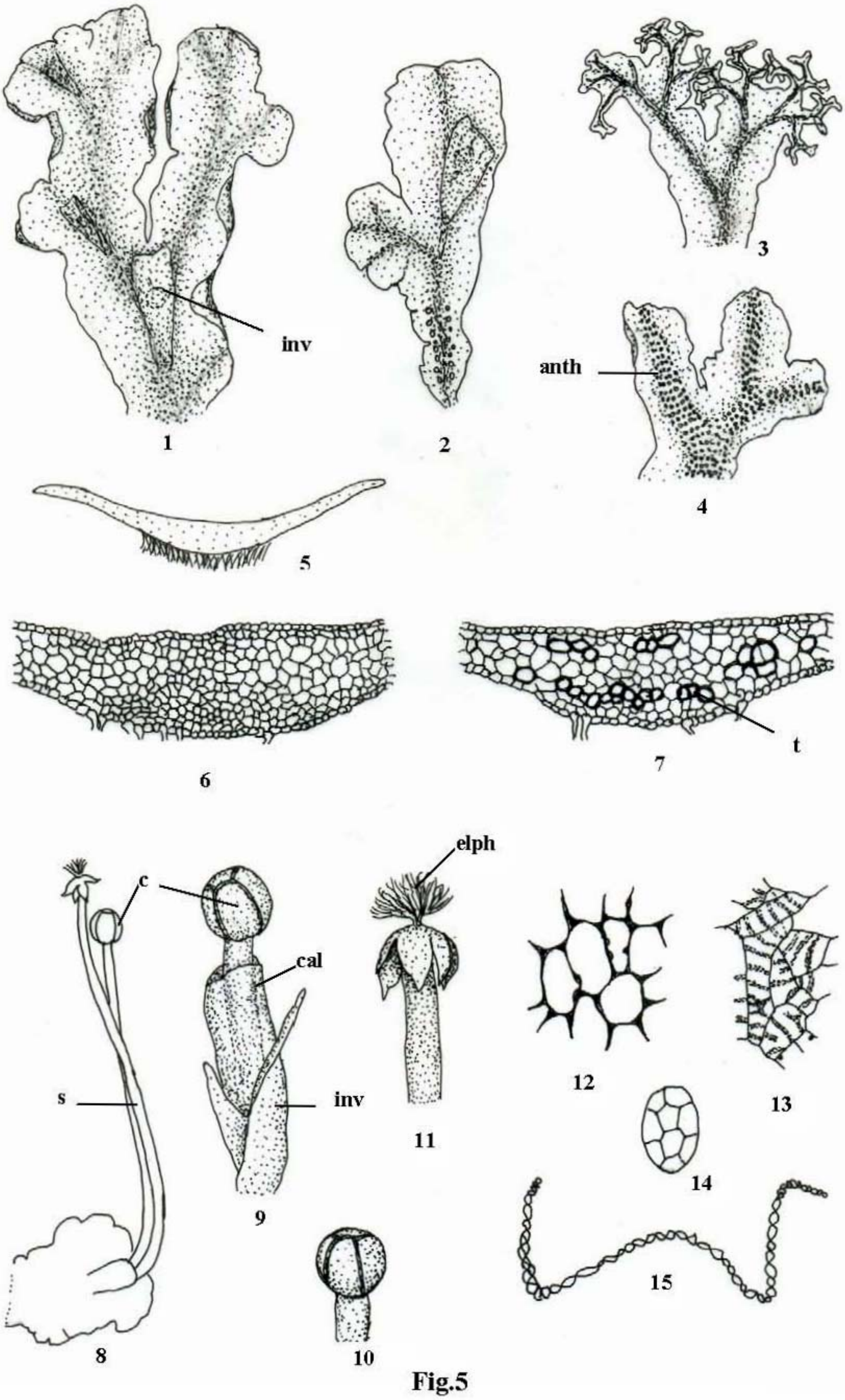

Fig. 5. ***Pellia*** 1. A Thallus with involucres, 2. A thallus with involucre and antheridia, 3. A thallus showing repeated dichotomies at apex, 4. A male thallus showing antheridia. 5. Cross-section of thallus (diagrammatic), 6. Cellular details (A portion), *P. endivaefoliia,* 7. Cellular details (A portion), *P. epiphylla,* 8. A thallus with two mature sporophytes, 9. A portion of involucre with sporophyte emerging out from calyptra, 10. Mature capsule showing line of dehiscence, 11. Dehisced capsule with basal elaterophore, 12. Capsule wall (outer layer), 13. Capsule wall (inner layer), 14. Spore (multicellular), 15. Elater. (inv – involucre, anth – antheridial chamber, t – thickening band, elph – elaterophore, cal – calyptra, s – seta, c – capsule). Figs. 1,2,7-15 *Pellia epiphylla*, Figs. 3-6 *Pellia endivaefolia*, Figs. 1-7, 9-15 (After Udar). Fig. 8 (After Proskaur).

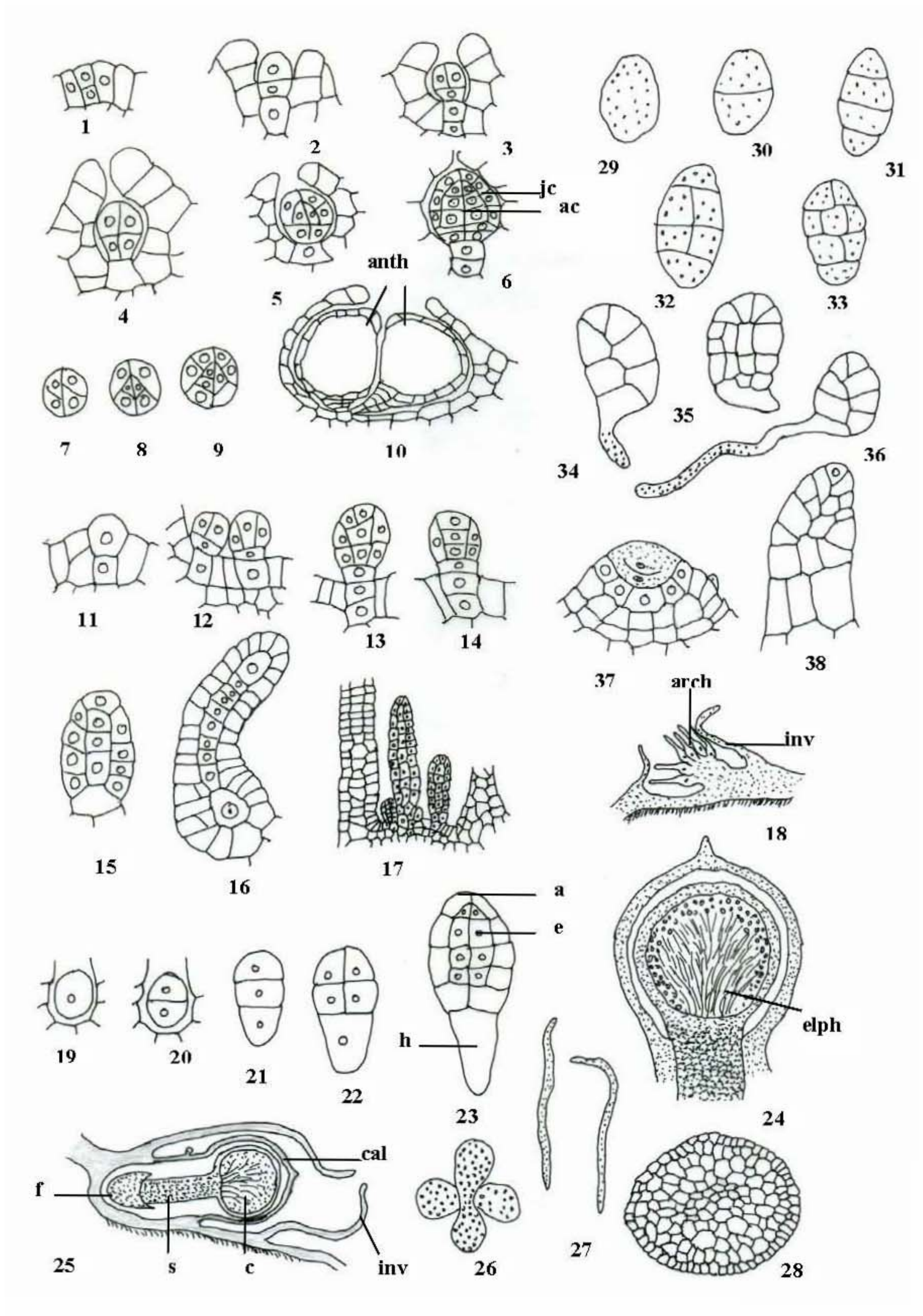

Fig.6

Fig. 6. *Pellia*1-10. Stages in antheridial development, 11-18. Stages in archegonial development, 19-24. Stages in sporophyte development, 25. Vertical longitudinal section through involucre and sporophyte, 26. Spore tetrad, 27. Young elaters, 28. Cross-section of seta, 29-36. Stages in spore germination, 37. Apical cell in *Pellia epiphylla*, 38. Apical cell in *P. endivaefolia*. (jc – jacket cells, ac – androgonial cells, anth – antheridium, arch – archegonium, inv – involucre, c – capsule, s – seta, f – foot, cal – calyptra, a – amphithecium, e – endothecium, h – haustorium, elph – elaterophore,). Figs. 1-17, 29-36 (After Hutchinson), Figs. 18, 28 (After Udar), Figs. 1-17, 29-33, 37 *Pellia epiphylla*, Figs. 18-28, 34-36, 38 *Pellia endivaefolia.*

4. Monocleales Schuster

This order is interestingly monotypic with single family Monocleaceae and single genus Monoclea, with its two species: M. gottschei and M. forsteri. The order is mainly characterized by extremely large, pure green, translucent thalloid gametophyte, which shows many features common to order Metzgeriales. Internally the thallus is very simple and undifferentiated. The rhizoids are simple, smooth walled. The sex organs are present on dorsal surface of the thallus. Antheridia are embedded in the thallus tissue (Fig. 7: 7). The archegonium is protected by flap like involucre and is anacrogynous (Fig. 7: 8). The sporophyte has well defined foot, elongated seta and cylindrical or elongated capsule. The capsule dehisces through single lateral slit.

Regarding the phylogenetic position of the group, there was a controversy among the workers. Evans (1939) placed it in Metzgeriales while Smith (1938) placed it in Marchantiales. The group is unique in having combination of characters, which resemble with different orders in one or the other characters - like one celled thick capsule wall (Marchantiales), anacrogynous position of sporophyte with much elongated seta (Metzgeriales), long necked archegonium (Calobryales) etc. Schuster (1953, 1963, 1966) discussed its systematic position at a length with the opinion that the group should be placed in separate order and thus he recognized the order Monocleales under the subclass Marchantiidae. In India the order is not represented.

5. Sphaerocarpales Cavers

The order is unique in having very delicate, translucent, green gametophytes, which are generally short lived. The plant body has central thick midrib portion and lateral wing portion which is thin and unistratose. The growth of plant takes place by the apical cell with 4 cutting faces. The plants are strictly dioceious. Sex organs are present on dorsal surface of thallus in acropetal manner and protected by bottle shaped involucre (Fig. 7: 1-3). Archegonial neck has six rows of cells. The sporophyte has small bulbous foot. The seta is very short (abbreviated), which never elongates even after the maturity. Hence, the sporophyte remains enclosed within the involucre. The capsule is small, spherical with single layered delicate capsule wall. The spores are large, permanently remain attached in tetrad form and are viable for longer period. Elaters are absent however some sterile nurse cells are present. The capsule is cleistocarpous and the spores are released after the decaying of capsule wall and the surrounding tissue.

In the order Sphaerocarpales, the vegetative structure is similar to Metzgeriales but the development and structure of the sex organs is similar to Marchantiales. Due to this combination of characters along with very peculiar features, the presence of globose flask shaped involucre around each sex organs, this group has been placed separately at order level otherwise it was earlier placed in Jungermanniales.

The order includes two families, three genera and 12-14 species (Schuster, 1984a). The family Riellaceae with single genus Riella Mont. (Fig. 7: 4-6) and Sphaerocarpaceae with two genera Sphaerocarpos (Mich.) Boehm (Fig.76: 1-3) and Geothallus Campb. In India the order is represented by single genus - Riella with two species R. affinis (=R. vishwanathii; see Pande et al., 1954; Proskaur, 1955, Fig. 7: 6) and R. cossoniana (Patel, 1977, 1977a).

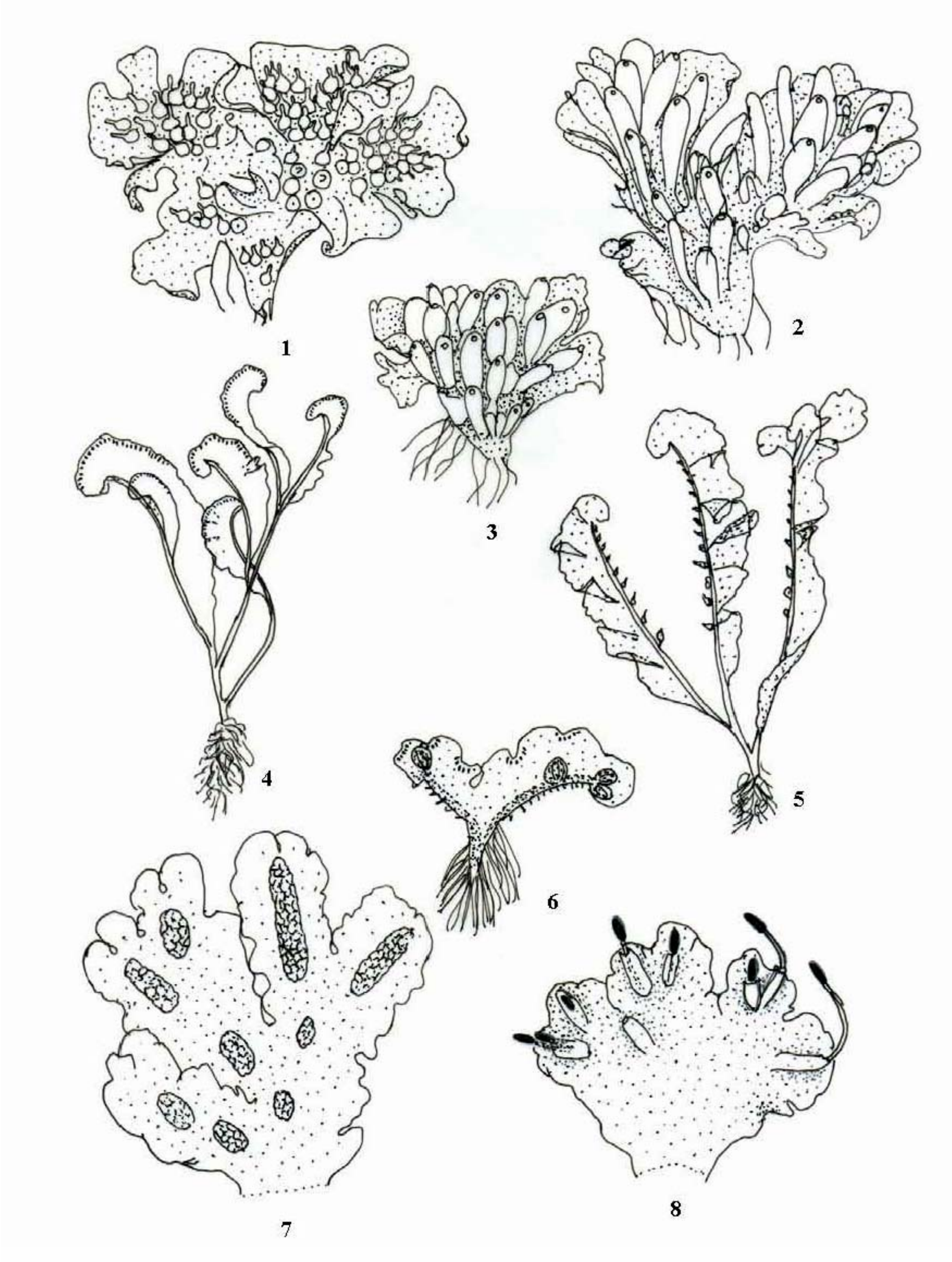

Fig.7

Fig. 7. ***Sphaerocarpous*** **1-3,** ***Riella*** **4-6,** ***Monoclea*** **7,8**
1. *Sphaerocarpous texanus* - male plant, 2,3. *Sphaerocarpous texanus* - female plants, 4. *Riella americana*, - male plant, 5. *Riella americana* - female plant, 6. *Riella affinis* (*R. vishwanathii*), 7. *Monoclea gottschei* - male plant 8. *Monoclea forsteri* - female plant. Figs. 1-3 (After Allen), Figs. 4,5 (After Studhalter), Figs. 6 (After Pande *et al*.), Figs.7,8 (After Schuster).

6. Marchantiales Limpr.

The order Marchantiales is the largest order of thalloid forms only. Many of them are remarkably physiological draught resistant and have evolved many anatomical devices to check the water loss. This is the only group in the liverworts, which are basically adapted to grow in exposed sites with intense light. The plant body is dorsiventrally flattened and dichotomously branched thallus, which is attached to the substratum by means of simple and tuberculate rhizoids. The presence of ventral scales is a unique feature of this order. The thallus is internally differentiated into upper assimilatory zone and lower storage zone. The sex organs are always present on a specialized receptacle, which may be stalked or sessile. Archegonial neck has six rows of cells. The sporophyte is determinate in growth having well marked foot, short seta and the capsule. The seta has lost the ability to elongate. In extreme cases foot and seta is absent also (Riccia). The capsule has unistratose capsule wall, number of small to large spores of diverse sporoderm patterns and elongated elaters.

The order Marchantiales has been divided into 13 families and 29 genera (Schuster 1984a). The 13 families are - 1. Cleveaceae, 2. Aytoniaceae (Rebouliaceae), 3. Lunulariaceae, 4. Conocephalaceae, 5. Exormothecaceae, 6. Marchantiaceae, 7. Monoselaniaceae, 8. Targioniaceae, 9. Cyathodiaceae, 10. Carrpaceae (Monocarpaceae), 11. Corsiniaceae, 12. Oxymitraceae, 13. Ricciaceae. In India the order is represented by 10 families and 21 genera. The genus Marchantia has been taken as the representative of the group.

Marchantia

- *Habitat and Distribution*

  Marchantia – the type genus of the order Marchantiales, is a terrestrial form usually grows in moist and shady places. It is widely distributed all over the world. About 11 species have been validly recorded from India. These are M. emarginata (M. palmata), M. assamica, M. paleacea (M. nepalensis), M. subintegra, M. polymorpha, M. robusta (M. indica, M. kashyapii), M. linearis, M. pandei, M. papillata subsp. grossibarba, M. hartlessiana and M. gemminata. The genus is represented in all the four major Bryogeographical regions of India but they show maximum distribution in Himalayas. The genus shows dense growth in hilly areas. However, Marchantia paleacea and M. polymorpha are found in plains also.

- *Gametophyte*

  The plants are large, dorsiventral, dichotomously branched thallus. A mature thallus may attain a length of 2-10 cm. They form very large green patches over the substratum (Fig. 8: 1). The thallus has a distinct midrib, which is marked by a shallow groove on the dorsal surface of the thallus and is projected on the ventral side. Often the mid rib portion forms a distinct blue streak as in case of *M. paleacea*. The apex of the thallus is notched in which the growing point is located. The dorsal surface of the thallus has distinct polygonal areas, which have a distinct central pore (Fig. 8: 2). They are smaller in the apical regions while they are larger in basal portion. The ventral surface of the thallus has rhizoids and ventral scales (Fig. 8: 3). The rhizoids are of two types: simple and tuberculate. (i) The simple rhizoids are smooth walled (Fig. 8: 9) and generally present all over the ventral surface in between the ventral scales. They mainly help in the attachment of the thallus to the substratum. (ii) Tuberculate rhizoids are comparatively narrow and have small tubercles or peg like projections in the walls (Fig. 8: 10). They generally form dense tuft along the midrib and can absorb sufficient amount of water through capillaries thus mainly help in the absorption. However, the distribution of rhizoids is not so particular and both the types of rhizoids may be intermixed. The ventral scales are multicellular, unistratose membranous structure. They are present in 2-3 rows on both the sides of midrib (Fig. 8: 3). They may be termed as marginal, laminar and median starting from the margin. There are two types of ventral scales: marginal unappendaged (Fig. 8: 11) and median appendaged (Fig. 8: 12,13). The appendaged scales have three main parts: (i) an apical appendage (ii) a short constricted neck and (iii) a prominent basal decurrent body through which it is attached to the thallus from apex towards the base. The margin of the scales has many mucilage papillae. The oil cells are present, scattered in between the cells. The ventral scales are mainly protective in function and help in retaining the moisture. The appendages of the appandaged scales bend over the thallus apex and protect the growing point.

- *Thallus anatomy*

The thallus is internally differentiated into upper, narrow assimilatory (photosynthetic) zone and lower, broad storage zone (Fig. 8: 14). The assimilatory zone consists of air chambers, pores and assimilatory filaments. Air chambers are present in a single row. They are well defined and partitioned by unistratose septa. Each chamber opens out side by a central pore, present in the roof of chamber formed by the upper epidermis. These epidermal pores are not simple but very characteristics barrel shaped. The half of barrel is projected outside above the epidermis and other half of the barrel is projected inside the air chamber (Fig. 8: 14). The opening (pore) is bounded by number of cells, which are present in concentric rings. These pores on the outerside (observed from dorsal surface) are more or less rounded – oval (Fig. 8: 4) while on the innerside they may be rounded, angular (Fig. 8: 5), stellate (Fig. 8: 7,8) or cruciate (Fig. 8: 6) depending upon the arrangement of the cells, whether they are evenly placed, superimposed or projected. At the base of the air chambers number of assimilatory filaments are present which may be branched or unbranched. The cells of the filament are chlorophyllous densely packed with the chloroplasts (Fig. 8: 15). Just beneath the assimilatory zone, the storage zone is present. It consists of all the thin walled parenchymatous cells, which are packed with the starch grains. Besides some of the cells are filled with the oil, while some other, are filled with mucilage, called as oil cells and mucilage cells respectively. In some species, mucilage canals are also present. They are elongated tubes, filled with the mucilage, and are lined by distinctly demarcated cells. They are mostly present in mature thalli and generally traverse in midrib portion. Besides, some thick walled cells – scleroids, are also present, scattered in between the thallus cells. The outermost layer on lower side of the thallus forms lower epidermis. Some of cells get elongated and develop into rhizoids. Ventral scales are also attached to it, which appear as a uniseriate, filament of beaded cells, in the section of thallus.

- *Growth of the thallus*

The growth of a mature thallus takes place by a group of apical cells present in the apical notch. In the young gametophyte developing from sporeling, there is a single, 2-sided apical cell, which divides to form group of marginal meristem.

- *Vegetative/asexual reproduction*

In *Marchantia*, vegetative reproduction may take place by death and decay of the older thallus portion due to which apical thallus lobes get separated and develop into individual thalli. This mode of fragmentation is quite common. Sometimes adventitious branches develop from ventral surface of thallus or any other part like stalk and disc of archegoniophore (Kashyap, 1919, see also Parihar 1959) which get detached from parent thallus and develop into independent thalli. In this genus *Marchantia*, the most specialized method is the formation of characteristic asexual reproductive bodies called as gemmae. They are produced in a cup like structure (Fig. 8: 16,17). These gemma cups develop near the growing point and have number of gemmae attached to the base of the cups associated with numerous small, clavate, mucilage papillae (Fig. 8: 26). The margins of the cups may be smooth, dentate or frilled depending upon the different species. A mature gemma has unicellular stalk and multicellular biconvex discoid body (Fig. 8: 24). It has two lateral notches in which the growting point is located. Due to these notches it takes a shape of the number '8'. Both the growing points are opposite to each other and have a single marginal row of apical cells. All the cells of gemmae are chlorophyllous having number of chloroplast. Some of the marginal cells are colourless, devoid of chloroplasts called as rhizoidal cells, which form rhizoid at the time of gemma germination. Some of the cells are filled with oil, called as oil – cells.

- *Development of gemma and gemma cups*

At the beginning, the gemma cups appear as a circular area near the apex of the thallus. The epidermal cell of this area protrudes out as an outgrowth in the form of papilla. It acts as gemma initial and divides transversely forming basal cell, stalk cell and primary gemma cell. The stalk cell does not divide further and forms a short, single celled stalk of gemma. The primary gemma cell divides transversely producing a 4-5 celled filament, which further divides in both the vertical and horizontal planes forming multicellular gemmae (Fig. 8: 18 – 24)). Initially, the gemmae are unistratose but later on by periclinal division, they become thick in the center forming typical discoid gemmae (Fig. 8: 25). Meantime the thallus tissue grow upward all around forming a hollow cup. Mucilage papillae also develop from the inner wall of the cup.

- *Gemma dispersal and germination*

The mucilage papillae secrets the mucilage, which absorbs moisture and swells up causing the gemmae to break as their stalks are slender. The detached gemmae are dispersed by splashing of rain drops or washed away by rain water. Under suitable conditions, when gemma falls on the soil, it starts germinating. The rhizoidal cells, which are in contact with the soil, develop into the rhizoids and absorb water. Soon the apical cells become active and two young thalli start developing in opposite direction. Gradually the central part of the gemma disintegrates. Two young thalli become separated and develop into new independent thalloid gametophyte.

- *Sexual reproduction*

The genus *Marchantia* is strictly dioecious. Both the sex organs, antheridia and archegonia develop on a specialized stalked receptacle called as antheridiophore and archegoniophore respectively.

- *Antheridiophore*

Antheridiophores are always terminal and present at the apices of the thallus (Fig. 9: 1). The apical growing point is utilized in their formation, so that the further growth of the thallus is checked. An antheridiophore has an elongated stalk and a terminal flat, lobed disc (Fig. 9: 2). The number of lobes may vary from 2-10. The antheridia are embedded in the disc (lobes) inside the antheridial chambers on the dorsal side (Fig. 9: 3). The antheridial chambers are present alternate with the air chambers, which are same as found in thallus, having assimilatory filaments and barrel shaped pores. Each antheridial chamber, normally, has single antheridium with short multicellular stalk and more or less ovate – elongated antheridial body. In some species, mucilaginous filaments may arise from the inner wall of antheridial chamber. These mucilaginous cells help in retaining the moisture in the chambers. The antheridia develop in acropetal manner. The older antheridia are present in the center of the disc while the younger ones are near the apex of the lobes.

- *Archegoniophore*

The archegoniophores are also terminal and always present at the apices of the thallus (Fig. 9: 13). In this case also the growth of thallus is checked as the growing point is consumed in the formation of archegoniophore. An archegoniophore has elongated stalk and lobed disc of various forms depending upon the species. In *M. polymorpha* the disc has finger like sterile lobes hanging down giving an umbrella like appearance to archegoniophore (See Udar, 1976; Bischler 1989). The archegonia are superficial and present on fertile lobes of the discs. They also develop in acropetal manner. The young archegonia are present towards the apex of lobes and older archegonia are present in the center of the discs. At initial stage these archegonia are dorsal in position but with the growth, subsequent to fertilization, the lobes get curved downwardly pushing the archegonia towards the lower side of the disc (Fig. 9: 14-17). The archegonia, which were dorsal in position as well as in origin, now become inverted and ventral in position (only). Each archegonium has a long neck and swollen venter with number of neck canal cells, a ventral canal cell and an egg (Fig. 9: 29). The neck portion has 6 vertical rows in the jacket (Fig. 9: 27). Each archegonium is enclosed in a protective covering called as perigynium while each archegonial group on the lobe is protected by another pendent covering, called as perichaetium. It is unistratose with free, laciniate, fringed margin having filamentous projections (Fig. 9: 30). The upper (dorsal) portion of the disc and sterile lobes have distinct (i) assimilatory zone with air chambers, barrel shaped pores as well as assimilatory filaments and (ii) storage zone with parenchymatous cells having starch grains, and oil cells like the thallus.

- *Stalk of antheridiophore/Archegoniophore*

The stalk of both the male and female receptacle is same in the structure. It is small at young stage but till maturity it attains a considerable height and becomes erect. Internally it is differentiated into assimilatory and storage zones, like the thallus. Towards the morphological dorsal side (the side in continuation with the dorsal surface of the thallus), the stalk has assimilatory zone with reduced air chambers, barrel shaped pores and lesser number of assimilatory filaments. This assimilatory zone may be highly reduced to even absent in some species. Adjacent to the assimilatory zone, storage zone is present having thin walled parenchymatous cells. In the central region the cells are narrow, elongated which help in conduction and appear smaller in cross section. Towards the morphologically ventral side (the side in continuation with the ventral surface of the thallus), there are two cavities or furrows, present on lateral sides. These are called as rhizoidal furrows. The rhizoids and scales are present in these cavities (Fig. 9: 29).

- *Development of Antheridiophore/Archegoniophore*

The initial stages in the development of antheridial and archegonial discs are same. The growing point, located in the apical notch, divides and redivides dichotomously resulting into many- lobed structure with its own growing point. In antheridial disc, a number of antheridia are produced embedded in the disc while in archegonial disc a number of archegonia are produced on the surface of the disc. Both the sex organs develop in acropetal manner. With the growth, stalk develops at base of the disc, which later on elongates considerably carrying the disc upward.

All these structures – stalk and the discs (male and female) as well as gemma cups are the modified thallus tissue to bear the sex organs and gemmae.

- *Development of antheridium*

The development of antheridium is more or less similar as found in other liverworts. The antheridial initial appears near the growing apex of the lobe of the antheridial disc. It becomes evident somewhat in a conical form and remains embedded in the lobe tissue (Fig. 9: 4). It divides transversely forming 2- celled rudiment with lower stalk cell and upper antheridial cell (Fig. 9: 5). The stalk cell divides in regular manner both transversely and vertically forming a short multicellular stalk. The upper antheridial cell first divides in transverse plane forming 2-4- celled filament, which further divides both vertically as well as periclinally differentiating into outer primary jacket cells and inner primary androgonial cells (Fig. 9: 6-9). The primary jacket cells divide anticlinally forming single layered jacket of antheridium. The primary androgonial cells divide repeatedly producing large number of androgonial cells which, at last, divide diagonally forming two triangular androcytes from each androgonial cell (Fig. 9: 10-12, see also Fig. 1: C.1-7). Later on, androcytes differentiate into coiled, biflagellate spermatozoids. Simultaneously, the adjacent cells of lobe divide and encircle the developing antheridia. Thus mature antheridium remains embedded in antheridial chamber.

- *Development of archegonium*

The archegonial development is also similar to other liverworts. However, it differs in the number of cells in the vertical rows of archegonial neck region. The archegonial initial makes it appearance as a projection (papillate outgrowth) on the lobe of archegonial disc (Fig. 9: 18). It divides into upper and lower cell. The upper cell divides thrice vertically by oblique walls, which intersect each other resulting into an axial and three peripheral cells (Fig. 9: 19,20). Now, each of the three peripheral cells divides vertically resulting into six rows of cells forming the jacket of neck, which is a characteristic feature of the order Marchantiales (Fig. 9: 27). Now axial cell divides to form four cover cells, 4-6 neck canal cells, a ventral canal cell and an egg (Fig.9: 21-26,29, see also G. 1-7). After fertilization, these archegonia become shifted on the lower side of the disc. New archegonia may develop at this stage but on the ventral side and remain inverted.

- *Fertilization*

After the maturity of antheridium, if water falls on the disc, it finds its way to antheridial chamber. The jacket cells of the antheridium ruptures when they come in contact with water releasing androcytes in a long smoke like column. The androcytes spread on the water surface and antherozoids get liberated vary soon. According to Strassburger (1869) when the water drops fall over the surface, they spread the antherozoids to longer distance upto 2 feet by splashing of water drops. The water drops containing antherozoids, fall over the archegonial disc, which may flow over the edges reaching to the archegonial neck and fertilization takes place.

- *Sporophyte*

The mature sporophyte has distinct foot, seta and capsule (Fig. 10: 25). The foot is broad somewhat conical in shape and anchors the sporophyte in the tissue of archegonial disc and derive nourishment for developing sporophyte. The seta is short massive, which elongates at maturity. The capsule is more or less spherical to oval in shaped with single layered capsule wall, spores and elaters. The cells of the capsule wall have thickening bands in the form of stripes (Fig. 10: 26). The spores are very small and numerous (Fig. 10: 23). They may be polar or cryptopolar. The polar spores are globose, without triradiate mark and with two spore coats (exine and intine) while the cryptopolar spores are somewhat tetrahedral in shape (not globose) with indistinct triradiate mark and three spore coats – exine, intine and perinium or perisporium. The elaters are long narrow, pointed at both the ends having 2-3 spiral thickning bands (Fig. 10: 24).

- *Development of sporophyte*

The zygote first divides by transverse or somewhat oblique wall forming upper and lower cell (Fig. 10: 1,2,6-8). The next division may be at right angle to the first division resulting into a quadrant embryo (e.g. *M. polymorpha* - Durand, 1908, and *M. domingensis*, - Anderson 1929, see Fig. 10: 3,4,9,10) or the next division may be parallel to the first division resulting into filamentous (3-celled)) embryo (e.g. *M. chenopoda* - Mc Naught, 1929, (Fig. 10: 5)). In case of *M. polymorpha* the upper cells (facing downward as archegonia are inverted in position) develop into capsule and lower cells develop into seta and foot (Fig. 10: 3). In case of *M. domingensis* the upper cells form the capsule and part of seta while the lower cells form the part of seta and foot (Fig. 10: 4). In 3- celled filamentous embryo of *M. chenopoda*, the upper cell forms capsule, middle cell forms seta and lower cell forms foot (Fig. 10: 5). With these developments, the cells of the archegonial venter start dividing periclinally forming multilayered calyptra around the developing sporophyte. The cells adjacent to venter also divide to form single layered membranous perigynium around the venter.

Now the cells of the embryo divide in various planes forming more or less a globular multicellular structure (Fig. 10: 13). The terminal portion becomes somewhat broader than the inner portion and becomes distinct to form capsule. Now periclinal divisions takes place and it gets differentiated into outer amphithecium and inner endothecium (Fig. 10: 11-14). The amphithecium forms the single layered capsule wall in which thickening bands develop at maturity. The cells of the endothecium repeatedly divide forming numerous sporogenous cells (Fig. 10: 15). These cells elongate, separate from each other and get differentiated into (i) broader fertile cells and (ii) narrow elongated sterile cells (Fig. 10: 16). The fertile cells have dense cytoplasm and prominent nuclei. They divide repeatedly by transverse divisions producing number of daughter cells, which are arranged usually in one row sometimes in two rows within the parent cell wall (Fig. 10: 21). These are spore mother cells. During the process, after nuclear division clevage starts in the protoplast from peripheral region, which gradually deepens and the parent cell divides into two cells, each having its own wall. The cell wall of each generation is clearly visible in the fertile cell (Fig. 10: 17-20). In *M. palmata* (now *M. emarginata*) and *M. domingensis* eight spore mother cells are produced while in *M. polymorpha* 32 spore mother cells are produced. Subsequently parent cell wall disintegrates and spore mother cells become free, which divide meiotically to form spore tetrads (Fig. 10: 22). The sterile cells are elater mother cells, which do not divide further, simply elongate to form long tapering elaters (Fig. 10: 24). The cytoplasm gradually disappears and 2-3 spiral thickening bands develop in their inner wall. The elaters are hygroscopic in nature and help in spore dispersal.

In *Marchantia*, the spore mother cells and elaters mother cells do not belong to same generation and the difference is of many generations. As a result very large number of spores are produced in comparison to lesser number of elaters. For e.g. in *M. polymorpha* the ratio between the spore mother cell to elater mother cell in 32:1, hence ratio between spores and elaters is 128:1.

- *Dehiscence of the capsule*

At maturity, the seta elongates pushing the capsule out through the calyptra, perigynium and perichaetium. Now the capsule gets exposed to drier environment. Due to loss of moisture in the cells of the capsule wall, the capsule splits irregularly into 6-8 valves (Fig. 11: 1-4). The spores fall down as capsule (archegonia/sporophyte) is inverted. Coiling and uncoiling of elaters further fascilitates the spore dispersal by loosing the spore mass. The falling spores are carried away by wind current.

- *Spore germination*

Under suitable condition, the spores germinate. The spore first divides into two cells (Fig. 10: 27). One of the cells elongates to form germ rhizoid, while the other cell, which has dense chloroplasts, divides to form 2-3- celled filament (Fig. 10: 28-32). Now the cells of filament divide in other planes forming a group of cells (Fig. 10: 33-36). The cellular structure (sporeling) thus produced may be branched or unbranched. Gradually the cells are added to the developing gametophyte and a row of marginal meristematic cells appear towards the apex. By the activity of these cells, thallus grows further. In some cases, at early stage a 2-sided apical cell is formed which cuts off number of cells. Finally it divides into group of apical initial cells, which lie in the apical notch produced at the apex of the thallus.

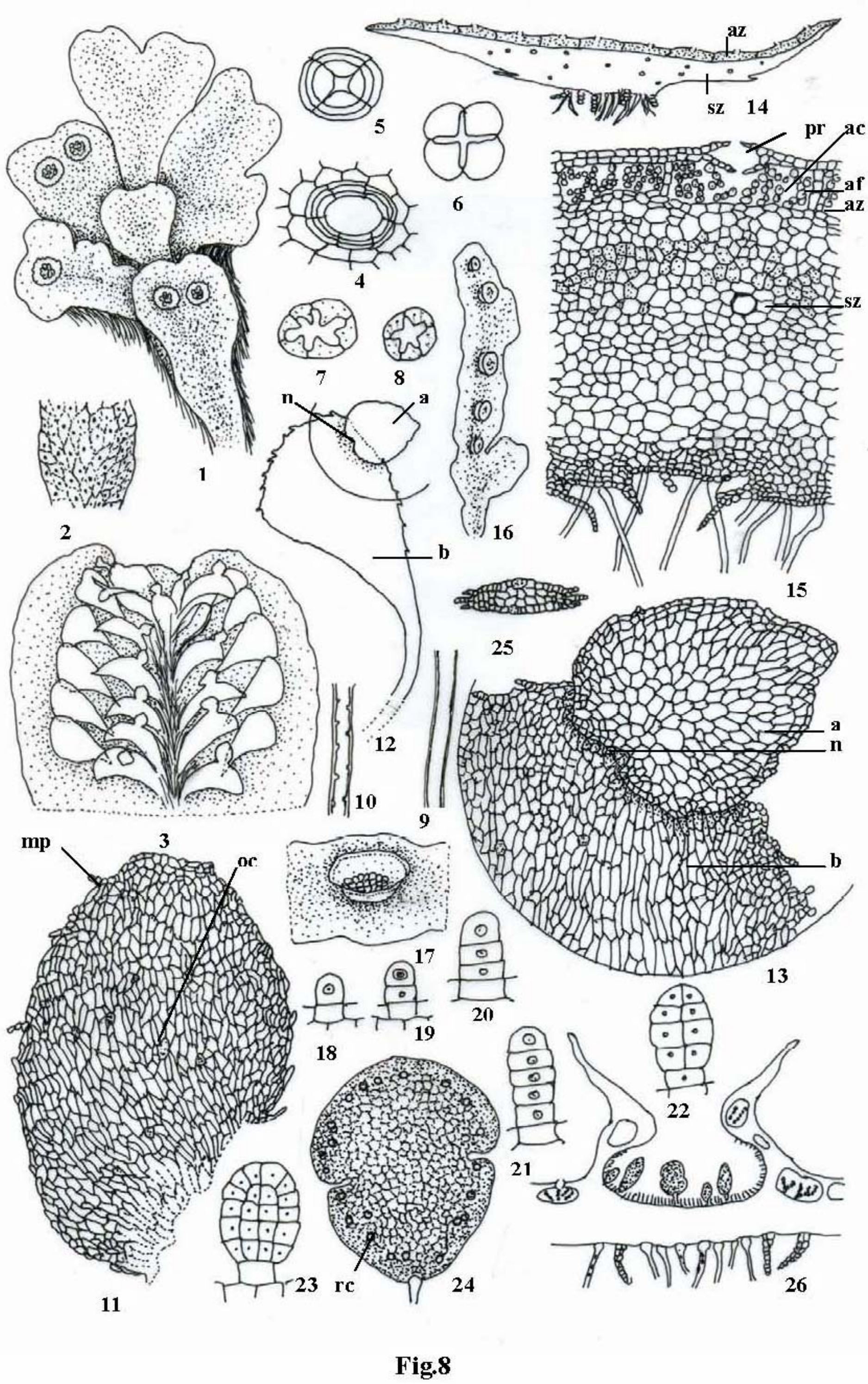

Fig.8

Fig. 8. ***Marchantia***

1. Habit, 2. A portion of thallus showing polygonal areas (dorsal view), 3. A portion of thallus showing rhizoids and ventral scales (ventral view), 4. Circular pore (outer view), 5. Angular pore (inner view), 6. Cruciate pore (inner view), 7,8. Stellate pores, 9. Simple rhizoid, 10. Tuberculate rhizoid, 11. An unappendaged scale, 12. An appendaged scale, 13. A portion of appendaged scale enlarged (cellular), 14. Cross-section of thallus (diagrammatic), 15. A portion of thallus showing assimilatory zone and storage zone (cellular), 16. A thallus with gemma cups, 17. A gemma cup (enlarged), 18-23. Development of gemma, 24. A mature gemma, 25. Cross-section of mature gemma, 26. V.T.S. of thallus through gemma cup. (az – assimilatory zone, sz – storage zone, pr – pore, ac – air chamber, af – assimilatory filament, a – appendage, n – neck, b – body, oc – oil cell, mp – mucilage papillae). Figs. 2-6, 11-17, 24, 26 (After Udar), Figs. 7,8. (After Bischler), Figs. 18-23 (After Parihar), Fig. 25. (After Kny).

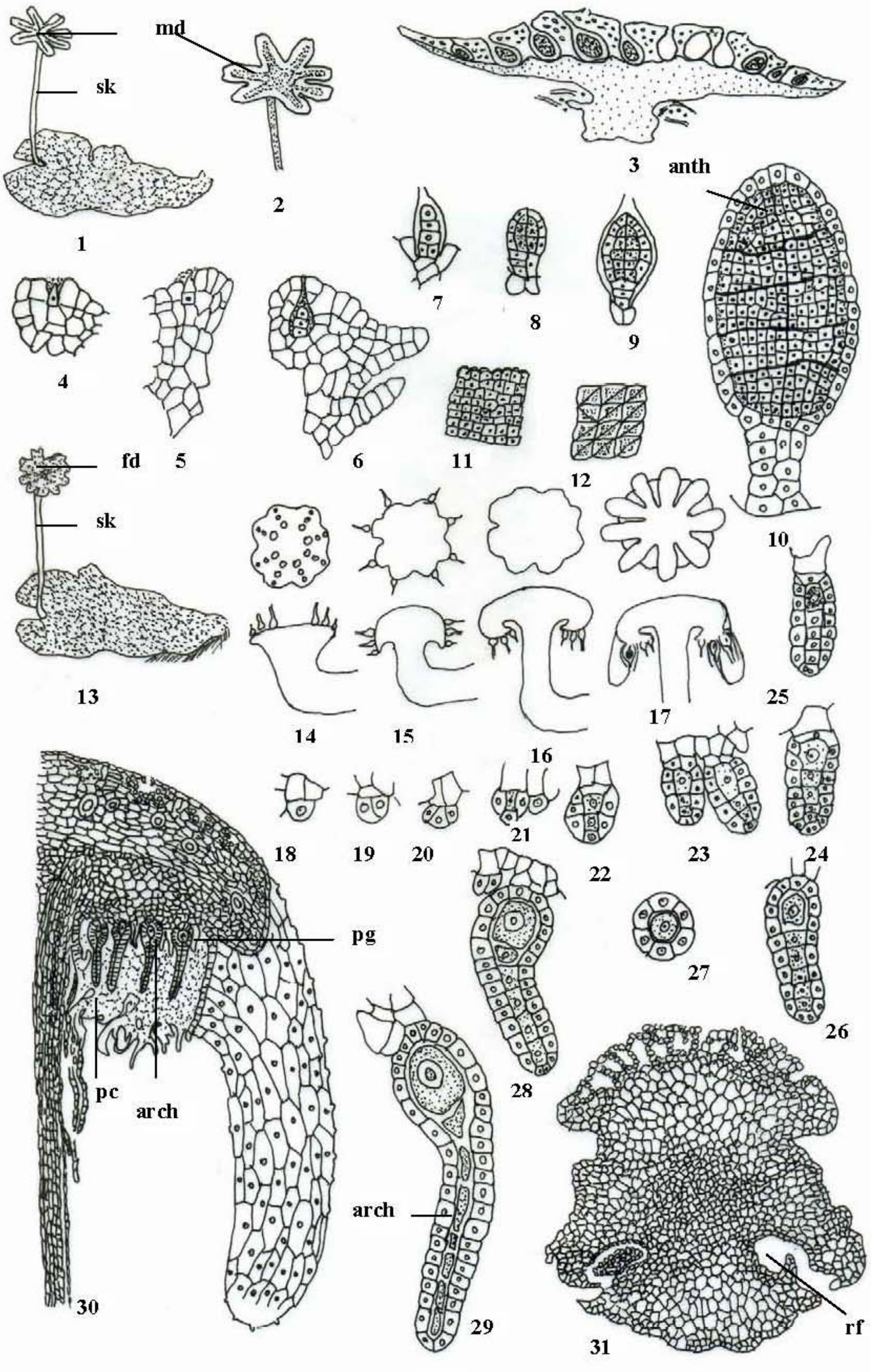

Fig. 9. ***Marchantia:*** 1. A male thallus, 2. A portion of antheridiophore (stalk & disc), 3. Vertical section through antheridial disc, 4-12. Stages in antheridial development, 13. A female thallus with archegoniophore (stalk and disc). 14-17. Stages in development of archegonial disc, 18-29. Stages in archegonial development, 30. Vertical section through archegonial disc, 31. Cross-section of the stalk of fertile disc. (sk – stalk, md – male disc, anth – antheridium, fd – female disc, arch – archegonium, pc – perihaetium, pg – perigynium, rf – rhizoidal furrow). Figs. 1-3, 13, 31 (After Udar), Figs. 4-12, 18-29 (After Durand), Figs 14-17 (After Smith), Fig. 30 (After Kny).

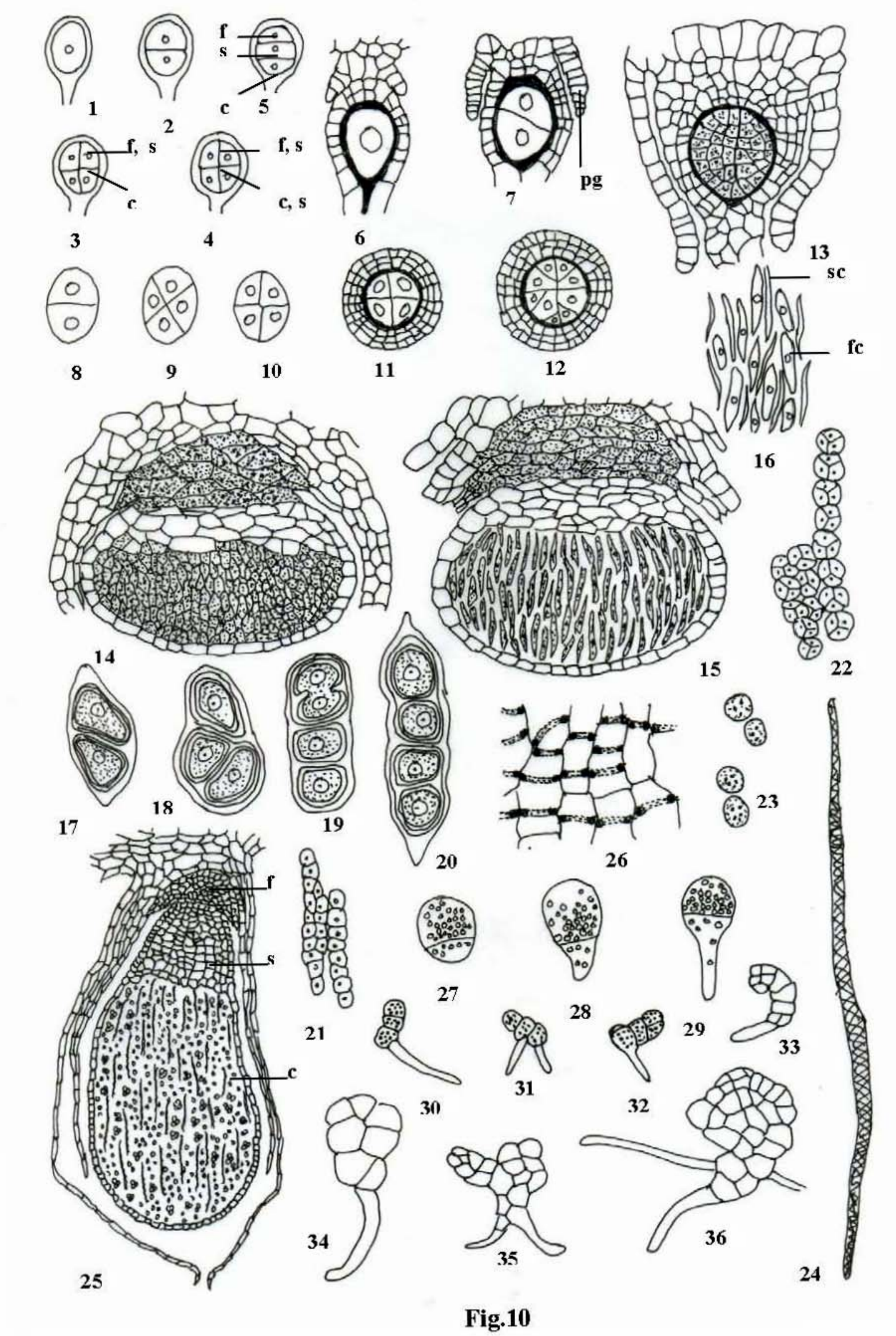

Fig. 10. ***Marchantia***

1-5. Initial stages in the development of sporophyte (schematic representation), 1. Zygote, 2. Transverse division of zyote, 3. Quandrant embryo of *M. polymorpha*, 4. Quadrant embryo of *M. domingensis*, 5. Filamentous embryo of *M. chenopoda*, 6-22. Stages in the development of sporophyte, 23. Spores, 24. Elater, 25. Vertical section of female disc passing through mature sporophyte, 26. Capsule wall, 27-36. Stages in spore germiantion. (f – foot, s – seta, c – capsule, fc – fertile cell, sc – sterile cell, pg – perigynium). Figs. 1-5, 17-20, 23, 24,26 (After Udar), Figs. 6-16, 21, 22 (After Durand), Fig. 25. (After Smith), Figs. 27-34 (After Inoue), Figs. 35, 36 (After O’Hanlon).

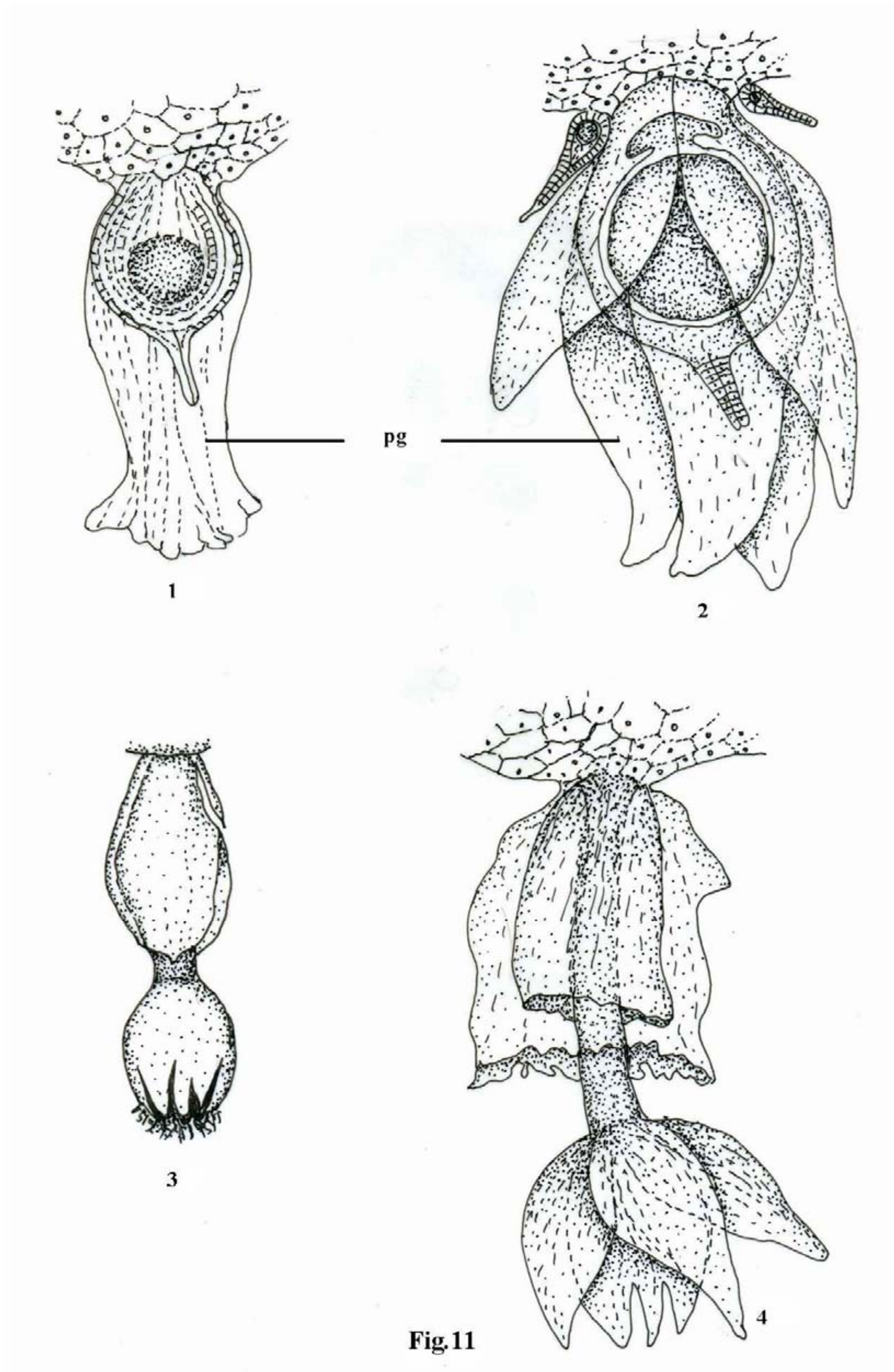

Fig. 11. *Marchantia*
1, 2 Developing sporophyte within the calyptra and perigynium, 1. Young stage, 2. Advanced stage, 3, 4. Mature dehisced sporophyte outside the calyptra and perigynium due to elongation of seta. (pg – perigynium). Figs. 1, 2, 4 (After Udar), Fig. 3 (After Smith).

Anthocerotopsida

The class Anthocerotopsida is a small group of plants in which the gametophyte is rather simple, however, sporophyte is comparatively complex and horn like or needle like. Hence members of this group are commonly called as ‘Hornworts’. The plants are dorsiventral, lobed thallus without any internal tissue differentiation. The thallus may be compact or spongy. Air chambers and pores are absent. Rhizoids are smooth walled. The ventral scales are totally lacking. The epidermal cells usually have single, large, plate like chloroplast with conspicuous pyrenoid bodies. Distinct *Nostoc* chambers and mucilage chambers are also present inside the thallus. The sex organs are embedded in the gametophytic tissue. Antheridia are present in groups or singly within the androecial chamber. They are endogenous in origin formed by the hypodermal cell on the dorsal side of the thallus (Fig. 1: D.1-7). The archegonia are exogenous in origin formed by outer cell but they remain embedded in thallus tissue with six rows of cells in the neck portion (Fig. 1: H.1-7). The sporophyte is differentiated into capsule and foot only. Seta is absent. The capsule is cylindrical ‘horn’ like and is not determinate in growth. The basal portion of the capsule is meristematic. It continues to grow and adds to the upper portion of the capsule. Capsule wall is multistratose 4-6 layered, chlorophyllous with or without stomata. The sporogenous tissue is amphithecial in origin. The entire endothecium forms the central sterile portion-columella. Sometimes the columella may be absent as in some species of *Notothylas*.

The class Anthocerotopsida (=Anthocerotae) distinctly differs from class Hepaticopsida in many features like (1) the presence of only thallose gametophytes (2) the presence of large chloroplasts with pyrenoid bodies, (3) embedded sex organs (4) endogenous origin of antheridium (5) indeterminate growth of the sporophyte (6) presence of meristematic zone at the base of capsule, (7) absence of seta (8) presence of 1-4 celled elaters (pseudoelaters) along with the spores which are amphithecial in origin (9) presence of stomata on the capsule wall. Besides above features, the sporophyte in this group is partially independent due to presence of stomata, chlorophyll (chloroplasts) and columella. Further it shows symbiotic relationship with blue green alga. Due to these distinctive features this group, which was earlier placed in Hepaticae as Anthocerotales at order level, has been raised to the class level.

Earlier only single family Anthocerotaceae and single order Anthocerotales was recognized in the class Anthocerotae (Muller, 1940) but later on two families Anthocerotaceae and Nothylaceae have been recognized (Reimer, 1954; Proskaur, 1960, Schuster 1984b). Bharadwaj (1981), however, recognized three families: Anthocerotaceae, Phaeocerotaceae and Notothylaceae. Hassel de Menendez (1986) introduced fourth family Leiosporocerotaceae to place the new genus *Leiosporoceros* (see also Hassel de Menendez, 1988). Recently, Stotler and Stotler (2005) proposed revised classification of Anthocerotophyta, recognizing the group as phylum and divided it into two classes, three orders and four families. Class (i) - Leiosporocerotopsida with order – Leiosporocerotales (one family – Leiosporocerotaceae), and Class (ii) - Anthocerotopsida with orders (a) Anthocerotales (one family - Anthocerotaceae) and (b) Notothyladales (two families - Notothyladaceae and Dendrocerotaceae).

The type genus *Anthoceros* was established by Micheli (1729), which was adopted by Linnaeus (1753). Then in subsequent years more taxa were introduced. Chronologically these are: (2) *Notothylas* (Sullivant, 1845), (3) *Dendroceros* (Nees, 1946), (4) *Megaceros* (Campbell, 1907), (5) *Aspiromitus* (Stephani, 1916), (6) *Phaeoceros* (Proskauer, 1951), (7) *Folioceros* (Bhardwaj, 1971), (8) *Leiosporoceros* (Hassel de Menendez, 1986), (9) *Sphaerosporoceros* (Hassel de Menendez, 1986), (10) *Mesoceros* (Pippo, 1993), (11) *Hattorioceros* (Hasegawa, 1994) and (12) *Nothoceros* (Hasegawa, 1994).

At present the group includes eleven genera. The family (I) Leiosporocerotaceae with (1) *Leiosporoceros* (II) Anthocerotaceae with (2) *Anthoceros*, (3) *Folioceros*, (4) *Sphaerosporoceros* (III) Notothyladaceae with (5) *Notothylas,* (6) *Hattorioceros*, (7) *Mesoceros*, (8) *Phaeoceros*, and (IV) Dendrocerotaceae with (9) *Dendroceros*, (10) *Megaceros*, (11) *Nothoceros.*

In India the group is representated by 5 genera: *Anthoceros, Folioceros, Phaeoceros, Megaceros, Notothylas* along with 38 taxa (Asthana and Srivastava, 1991; Asthana and Nath, 1993; Singh, 2003).

Anthoceros

- *Habitat and Distribution*

The genus *Anthoceras* is widely distributed in both the tropical and temperate regions. They usually grow in moist and shady places. About 200 species have been reported all over the world. In India the genus is represented by 9 species (Asthana and Srivastava 1991). Among these, *A. crispulus, A.*

erectus and *A. bharadwajii* are commonly found in all the major bryogeographical regions of the country viz.: eastern Himalayas, western Himalayas and south India. *A. angustus* and *A. punctatus* are distributed in eastern and western Himalayas. *A. alpinus* is confined to western Himalayas, *A. pandei* to eastern Himalayas, while *A. subtilis* and *A. macrosporus* are confined to south India.

- *Gametophyte*

The plants are thalloid, small dark green dorsiventrally flattened and variously lobed, which are spongy in texture. Sometimes they form distinct rosettes as in *Anthoceros crispulus* (Fig. 13: 1). In *Anthoceros erectus* the plants are erect, cylindrical in basal portion which become broad (fan out) in apical portion (Fig. 12: 8,9) while in some other species they form a large patch of overlapping thalli which are long and pinnately branched (Fig. 12: 1,2,6). In *A. angustus* (*A. gemmulosus*), the thallus has number of marginal subsessile, subspherical spongy bodies called as gemmae, which help in vegetative reproduction.

The dorsal surface of the thallus may be smooth (*A. erectus*, *A. punctatus*) or has many flat, leaf-like, lobed, radially oriented, lamellae, which give velvety appearance to the plants (*A. crispulus* Fig. 12: 6). The margins of the thallus are generally incised or lobed. Thallus is thick in the center and gradually becomes thin towards the margin. Midrib is totally lacking. The thallus has distinct bluish-green, opaque, more or less rounded to elongated, endogenous bodies inhabiting blue green alga – *Nostoc* called as Nostoc colonies/Nostoc auricles (Fig. 12: 3). Besides number of mucilage canals are also present inside, which run obliquely (Fig. 13: 4). The epidermal cells of the dorsal side of the thallus usually have 1, rarely 2 chloroplasts with central minute, distinct pyrenoid bodies (Fig. 12: 7,12, Fig. 13: 2,3). The chloroplast may be discoid, spherical (*A. angustus*) or with irregularly projected margins reaching upto the cell wall (*A. erectus* Fig. 12: 12). On the ventral surface of the thallus there are many rhizoids, which are unicellular and smooth-walled. Tuberculate rhizoids and ventral scales are totally absent.

- *Thallus anatomy*

The thallus is internally very simple, without any tissue differentiation. It is spongy due to 1-3 layers of mucilage chambers, which are separated by unistratose septa and are filled with muciliage hence called as mucilage chambers/canals. All the cells are alike, parenchymatous. The epidermal cells may be somewhat smaller and distinct from rest of the thallus cells. Some of the mucilagenous cavities are filled with Nostoc alga.

- *Growth of the thallus*

Regarding the apical growth, there is a controversy whether it takes place by a single apical cell or by a group of cells. According to Campbell (1918) the apical growth of the thallus takes place by a single apical cell which has 4 cutting faces – one dorsal, one ventral and two on lateral sides while Leitgeb (1879) as well as Mehra and Handoo (1953) reported that the apical growth takes place by a group of marginal apical cells which are meristematic. In each case the segments produced on the lateral sides add to the width of the thallus while the dorsal and ventral segments add to the thickness of the thallus. Each of the dorsal and ventral segments further divides into outer and inner cells. The inner cells, derived from both the dorsal and ventral segments form the central tissue of the thallus while the outer cells, on the dorsal side form the upper epidermis and sex organs whereas that outer cell on ventral side form lower epidermis and rhizoids.

The mucilage chambers present in the thallus are mainly schizogenous cavities, which appear first as a small, intercellular spaces near the growing point by the partial separation of the cells. With the growth, these cavities expand obliquely upward forming superimposed chambers in the middle portion of the thallus, which later on becomes filled with mucilage secreted by surrounding cells. The Nostoc filaments enter in these cavities and form endogenous Nostoc colonies in the Nostoc chambers.

- *Vegetative reproduction*

In some species like A. angustus (A. gemmulosus) definite spongy bodies develop on the thallus margins, which help in vegetative reproduction (Fig. 12: 2-5). In some other species, during unfavourable condition, tubers are produced which have outer few corky layers to protect the inner tissue with reserve food. These tubers help in facing prolonged period of drought. They regenerate readily on availability of moisture in favourable condition. While in A. personii and A. fusiformis, the whole thallus die off during summer except the growting point along with adjacent tissue. This remaining apical portion of thallus continues to grow into a new thallus when the conditions become favourable. Besides fragmentation of thallus lobes may also serve vegetative reproduction but it is not common.

- *Sexual reproduction*

Anthoceros shows both the monoecious as well as dioecious sexuality. Some species like A. fusiformis, A. crispulus and A. punctatus are monoecious and protandrous while some other species like A. angustus and A. erectus are dioecious. Both the sex organs are present on the dorsal surface embedded in the thallus tissue behind the apical growing region.

- *Antheridia*

Antheridia are generally present in groups enclosed in a chamber, which forms discrete dorsal areas on the thallus (Fig. 12: 1,8,9). These are androecia, which are usually present along the median line in acropetal manner. They are somewhat raised from thallus surface with central opening forming hemispherical elevations on the thallus or they appears as scooped areas as in case of A. erectus. Inside the androecial chamber antheridia are present in variable numbers at different stages of development (Fig. 13: 16). The number may vary upto 30 in A. angustus, 22 in A. erectus and 7 in A. crispulus. A mature antheridium has multicellular stalk with four rows of cells and a club shaped, clavate or cylindrical, orange coloured antheridial body (Fig. 13: 17). The jacket is unistratose and the cells are arranged in four tiers. The cells of lower three tiers are rectangular and elongated. Among these, the cells of lower most tier are smallest and are comparatively narrow towards the base. The cells of upper tier are triangular with their narrow end towards the apex. At the time of maturity these cells get separated and partially deflexed due to longitudinal thickening band present in jacket cells releasing the spermatozoids. Generally there is a continuous release of spermatozoids for a longer period of time as there is continuous production of antheridia in androecial chamber, which probably result into large number of sporophytes production in the genus Anthoceros.

- *Development of Antheridium/Androecium*

The androecium develops from the dorsal segment of the apical cell. A dorsal superficial cell near the growing point become active but does not protrude out in the form of papilla from thallus surface. It divides transversely forming outer wall initial cell and inner antheridial initial cell (Fig. 13: 9). Subsequently these two cells get separated from each other and the space, thus developed in between the cells, becomes filled with mucilage. The wall initial cell divides by periclinal and then anticlinal divisions forming two- layered wall of the androecium (Fig. 13: 16). The antheridial initial cell divides by two vertical divisions, which intersect each other froming four primary antheridial initial cells (Fig. 13: 18-20). Each of the 4 cells divides transversely forming upper and lower cells first and then probably lower cell further divides ultimately resulting into 3-celled filaments (Fig. 13: 10-13, 21). The outer cell is the antheridial initial cell, the middle cell is the stalk cell and the inner most cell is the basal cell forming basal cushion (Bharadwaj, 1958). As there are 4 antheridial initial cells, hence four antheridia develop in an androecium initially. Subsequently more secondary antheridia are produced from the base of older antheridia by budding. The free end of the basal cell divides by an oblique wall forming a triangular lateral segment or bud (Fig. 13: 22). It takes the dorsal position on the parent basal cell due to its lateral growth and acts as antheridial initial cell for secondary antheridium (Fig. 13: 23). The laterally extended basal cell further produces the bud and gets separated from primary basal cell by vertical walls. This process is repeated again and again in all primary basal cells resulting into a ‘basal cushion’ formed by primary as well as secondary basal cells and number of antheridia attached on it (Fig. 13: 15,23-26). Among these the older (Primary) antheridia are present in the middle of androecium, which are surrounded by the younger (Secondary) antheridia all around. The number of antheridia per androecial chamber depends upon the meristematic activity of basal cell. If the activity remains for longer period, a large number of antheridia are produced (A. angustus), otherwise less number of antheridia develop where the activity is for short period (A. crispulus).

- *Archegonia*

Archegonia are present completely embedded in the thallus tissue in acropetal manner. A mature archegonium has 2-4 cover cells, 4-6 neck canal cells, a ventral canal cells and an egg (Fig.13: 30,31). The jacket of archegonium has 6 rows of cells in neck portion (Fig. 13: 32) but in lower (venter) portion they are not arranged in six rows. As the archegonia are completely embedded in the thallus tissue, the jacket cells merge with the lateral thallus cells and are not distinct. Generally it is difficult to locate the archegonium in the thallus from external surface, but the presence of distinct broad mucilage mound clearly indicate the presence of archegonium at the site (Fig. 13: 36).

- *Development of Archegonium*

The archegonia also develop from dorsal segment of the apical cell. The archegonial initial cell becomes evident due to its dense cytoplasmic contents as compared to the adjacent cells (Fig. 13: 27). The initial cell divides transversely into outer primary archegonial cell and inner primary stalk cell as in A. crispulus and A. angustus while in A. erectus the archegonial initial cell directly acts as primary archegonial cell without any division. The primary archegonial cell divides by three vertical walls, which intersect each other forming outer three peripheral cells enclosing inner axial cell (Fig. 13: 28). The axial cell divides transversely into (i) outer and (ii) inner cells. The (i) outer cell further divides transversely forming primary cover cell towards outerside and primary neck canal cell towards inner side (Fig. 13: 29). The primary cover cell divides once or twice forming 2-4 cover cells (Fig. 13: 30) while primary neck canal cell divides transversely to produce 4-6 neck canal cells. The (ii) inner cell is the primary ventral cell, which also divides transversely forming ventral canal cell and egg (Fig. 13: 30). The three peripheral cells first divide vertically into 6 peripheral cells (Fig. 13: 32), which subsequently divide transversely forming the jacket of the archegonium but they are indistinguishable from thallus cells.

- *Fertilization*

At the time of fertilization the cover cells of the archegonium are thrown off. The neck canal cells and the ventral canal cell gets disintegrated forming a mucilaginous mass and the egg remains present inside mucilage filled cavity (Fig. 13: 31). This mucilagenous mass remains in continuation with the mucilage mound present on the thallus surface at the apex of archegonium (Fig. 13: 36). The spermatozoids released from mature antheridium get trapped in this mucilage mound and reach to the egg through neck where the syngamy takes place.

- *Sporophyte*

The mature sporophyte consists of foot and cylindrical capsule (Fig. 14: 21). Seta is totally lacking. In its place, in between the foot and capsule, meristematic zone is present which continuously adds to the capsule tissue. The foot is deeply embedded in the thallus tissue and derives nourishment as the cells are in close contact with thallus cells. It is expanded and bulbous. The outer superficial lining layer has palisade like cells with dense content. They are haustorial in nature. The inner cells are parenchymatous, vacuolated and are not regularly arranged. The capsule is elongated, cylindrical, smooth, slender and erect. It has three distinct parts. Starting from the outerside, there is multilayered capsule wall, then there is the archesporium (Sporogenous tissue) and in the center, columella is present. The capsule wall is 4-6 layered and amphithecial in origin. The outer most layer has thick walled elongated cells. The functional stomata are present which are longitudinally arranged on the capsule (Fig. 14: 25). The stomata are linear with stomatal pore and two elongated guard cells. The chloroplasts are presents in the cells of the capsule wall. The epidermal layer has 2-4 shallow grooves, which are the marking of line of dehiscence but the capsule dehisces into two valves along two lines only. Inner to the capsule wall, sporogenous tissue is present. It is also amphithecial in origin. Generally, the archesporium is single layered as in A. crispulus and A. erectus but it may be 2-3 layered as in A. angustus (= A. gemmulosus).

In the apical portion of the capsule the archesporium arches over the columella and becomes massive having several layers of cells (Fig. 14: 8-11). The young archesporial cells, at the base of the capsule, are cubical with dense cell contents. At little height, near the middle portion of the capsule, these cells get differentiated into large spherical spore mother cells and narrow elliptical elater mother cells which remain obliquely arranged in alternate manner (Fig. 14: 13). Just above this portion near the apical region, this set arrangement get disturbed having spores and elaters/pseudoelaters. Spores are more or less spherical, tetrahedral in shape with distinct triradiate mark. The sporoderm pattern may be reticulate, reticuloid, spinate, papillate, or often with unsculptured stripes, adjacent to the triradiate mark (Fig. 14: 14, 15 17,18). The elaters are elongated, 4- celled, compound structure, homologous to the spore tetrad. They often break into one, two or three celled pieces and termed as pseudoelaters (Fig. 14: 16,19). Columella is the central sterile column which in endothecial in origin. It is present from base to the apex of the capsule and is composed of 16 rows of cells arranged in a solid square (Fig. 14: 20). Often the rows may be increase upto 36 or 49 as observed in A. angustus.

At the base of the capsule, the meristematic zone is present. Due to its position in between the foot and seta, this zone is often regarded as reduced seta. However, it is entirely different from seta. This intercalary meristem is a characteristic feature of Hornworts. Its continuous activitiy for a longer period results into an enlongated needle shaped capsule in Anthoceros.

- *Development of sporophyte*

After syngamy, the fertilized egg increases in size filling the entire archegonial venter. Usually it divides vertically (Fig. 13: 38) but in case of *Anthoceros crispulus* the first division is transverse (Fig. 13: 39). The second division takes place at right angle to the first division forming 4-celled embryo (Fig. 13: 40) in which the cells are arranged in 2-tiers. The cells may be of equal or unequal size. Then it divides vertically forming 8-celled-octant embryo (Fig.13: 41). The cells of the upper and lower tiers may remain undivided (as *A. erectus*) where the lower tier forms foot and upper tier forms the capsule (Fig. 13: 42-44). Sometimes one tier may divide transversely forming 3-tiered and 12-celled embryo as in *A. angustus*. Where the lowest tier forms foot, and upper two tiers form capsule (Fig. 13: 45-47). In case of *Anthoceros crispulus*, both the tiers divide transversly forming 4-tiered and 16-celled embryo in which lower two tiers form the foot and the upper two tiers develop into the capsule (Fig. 13: 48- 50). The cells of lower tier, in foot region, divides obliquely forming the elongated outwardly curved cells of the foot which later on get differentiated into outer palisade layer and inner parenchymatous cells (Fig. 14: 8-21).

The capsular region of embryo divides periclinally forming the outer amphithecium and inner endothecium (Fig. 14: 4). The amphithecial region further undergoes periclinal division thus forming outer amphithecium (sterile layer) and inner amphithecium (fertile layer). (i) The outer amphithecium divides both periclinally and anticlinally forming multilayered capsule wall (ii) The inner amphithecium forms the archesporium which get differentiates into spore mother cells and elater mothers cells first and then into spores and elaters (Fig. 14: 7-13). (iii) The entire endothecium develops into the columella, which has 4 rows of cells at early stage of development but later on at maturity has 16 rows of cells (Fig. 14: 10-20).

- *Involucre*

During the whole process of development of sporophyte, a protective covering develops around the sporophyte. This protective sheath is called as the involucre, which develops from sterile jacket of arechegonium as well as thallus cells. The involucre encloses the developing sporophyte completely. As the sporophyte elongates, the involucre ruptures in the apical region and its broken part remain attached at the apex of the capsule, which falls off later on. The lower ruptured portion of the involucre forms a collar around the base of the sporophyte and helps in retaining the moisture (Fig. 14: 21).

- *Dehiscence of the capsule*

The maturation of the capsule starts from the apex, which become dark due to black coloured spores and proceeds downwardly. Due to loss of moisture the capsule dehisces into two valves through the line of dehiscence present in shallow depression on opposite sides of the capsule. Initially it may dehisce through single line only and then along the other line also (Fig. 14: 22,23). The valves remain attached at the tip exposing the columella when the line of dehiscence is short, not up to the apex. But when it is present upto the apex, the valves get separated, become strap-shaped and twisted in dry condition releasing the spores with little force. The further dispersal of spores to greater distances is facilitated by air current.

- *Spore germination*

The spores may germinate immediately without undergoing rest period (*A. erectus* and *A. punctatus*) or it may rest for certain period as in *A. fusiformis*. During germination the spores absorb moisture and swell up. The exine surface ruptures along the triradiate mark and the intine protrudes out in the form of germ tube (Fig. 14: 26). It divides transversely near the tip and the 3-celled filament is produced (Fig. 14: 27,28). The outer 2-cells then divide twice vertically with the walls at right angle to each other producing an octant at the tip (Fig. 14: 29, 30). The terminal four apical cells further develop into young sporeling (Fig. 14: 30,31). The spore coat remains attached at the base of sporeling. By the activity of multicellular marginal meristem the young thallus develops (Fig. 13: 32). The first rhizoid develops rather late in direct continuation with the cell (Fig. 14: 31).

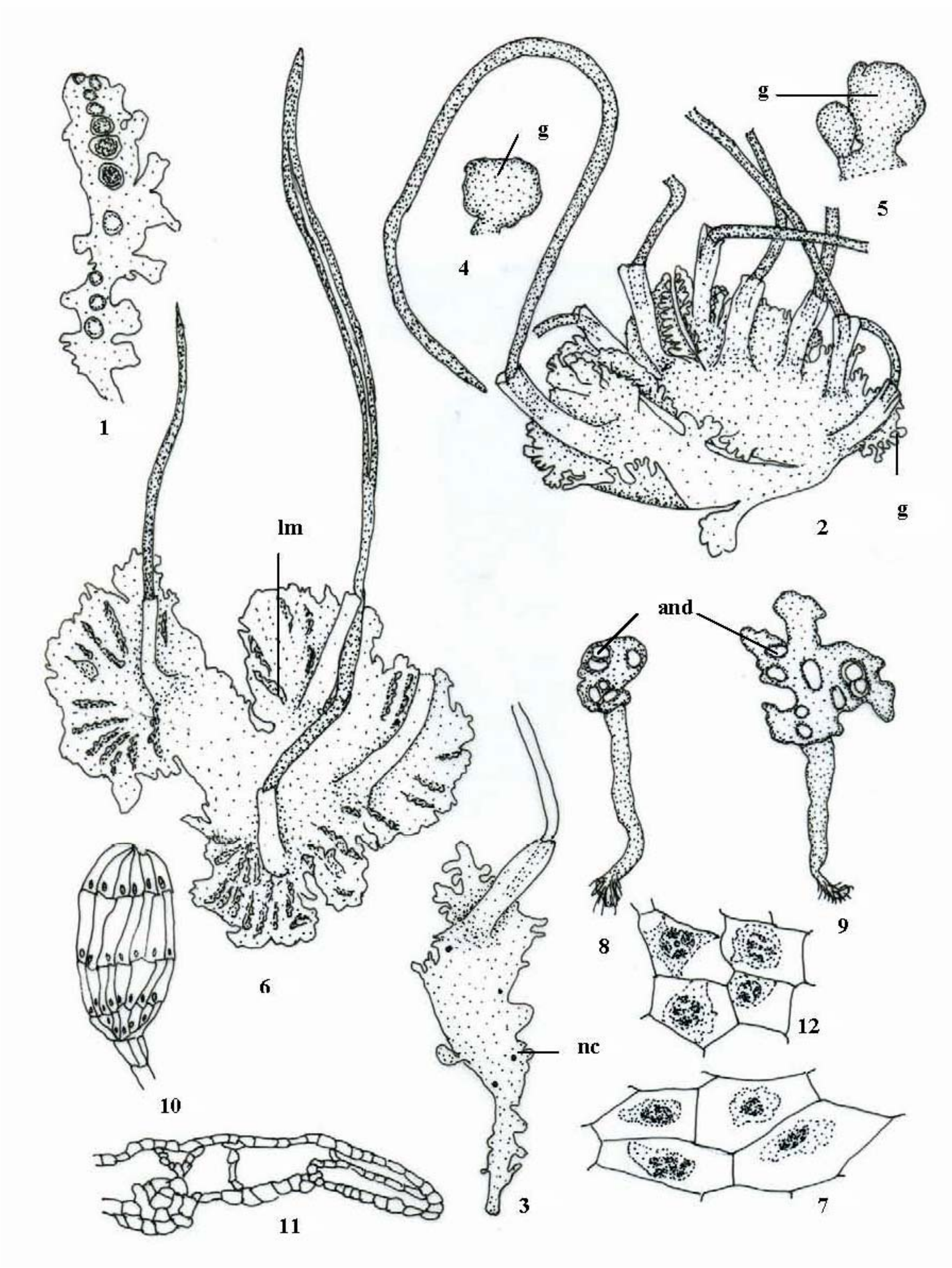

Fig. 12. *Anthoceros*
1. Male thallus, 2,3. Female thalli with marginal gemmae. 4,5. Gemmae, 6. Female thallus with crispate / lamellate dorsal surface, 7. Chloroplast in the thallus cells, 8, 9. Male thalli with cylindrical stalk, 10. Atheridium, 11. Cross-section of thallus (a portion), 12. Chloroplast in the thallus cells. (and – androecium, g – gemmae, lm – lamellae, nc – nostoc chamber). Figs. 1-12: (After Asthana & Srivastava). Figs.1-5. *A. angustus*, Figs. 6,7. *A. erectus*, Figs. 8-12. *A crispulus.*

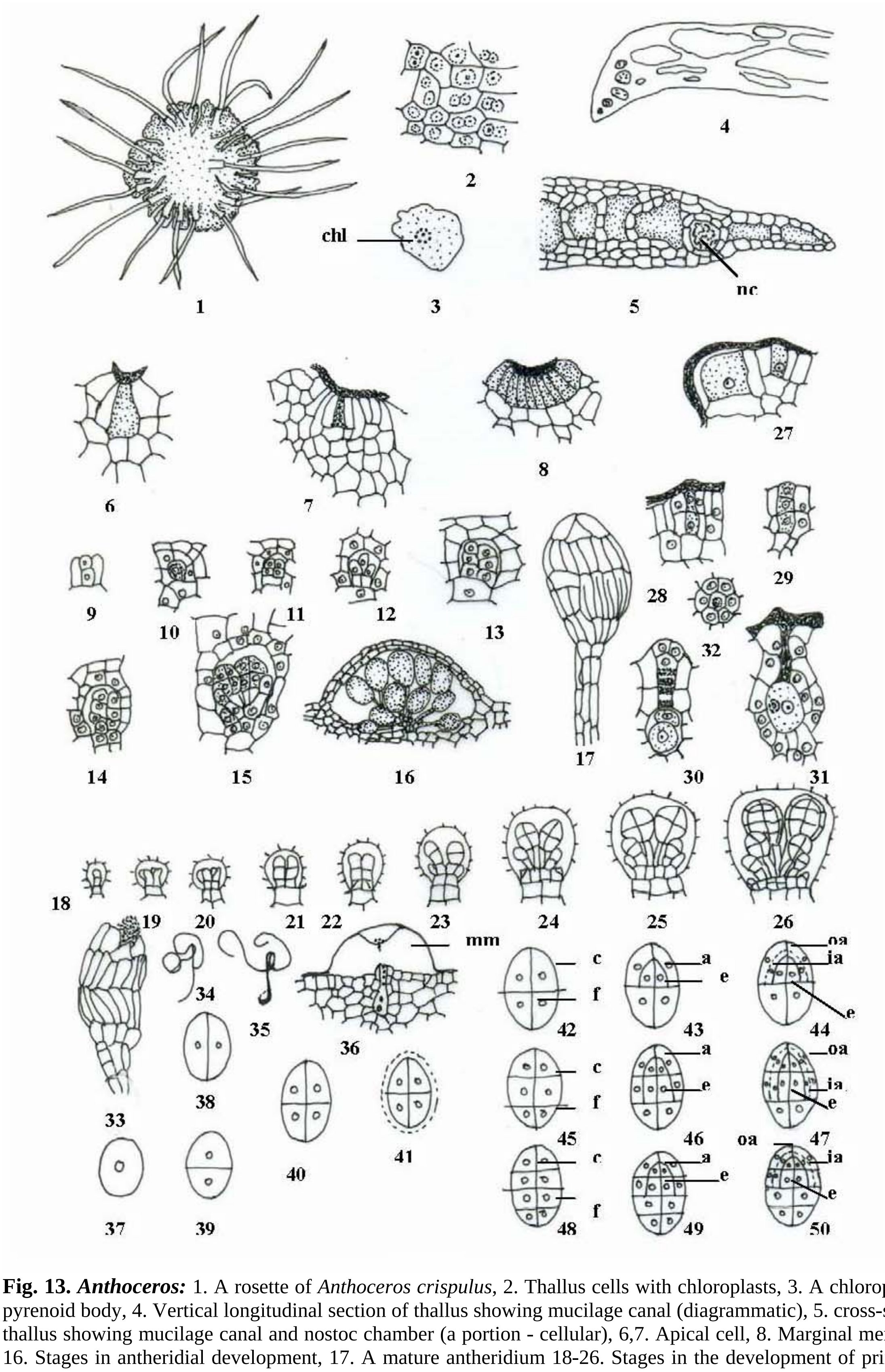

Fig. 13. *Anthoceros:* 1. A rosette of *Anthoceros crispulus*, 2. Thallus cells with chloroplasts, 3. A chloroplast with pyrenoid body, 4. Vertical longitudinal section of thallus showing mucilage canal (diagrammatic), 5. cross-section of thallus showing mucilage canal and nostoc chamber (a portion - cellular), 6,7. Apical cell, 8. Marginal meristem, 9-16. Stages in antheridial development, 17. A mature antheridium 18-26. Stages in the development of primary and secondary antheridia (schematic representation), 27-32. Stages in archegonial development, 33. Dehiscing antheridium, 34, 35. Spermatozoids, 36. An archegonium with protruted neck and mucilage mound, 37-50. Stages in sporophyte development (schematic representation), 37-41. Common initial stages, 42-44. Stages in *A. erectus*, 45-47. Stages in *A. angustus* (*A. gemmulosus*), 48-50. Stages in *A. crispulus*. (chl – chloroplast, nc – nostoc chamber, f – foot, c – capsule, a – amphithecium, oa – outer amphithecium, ia – inner amphithecium, e – endothecium, mm – mucilage mound). Figs. 1-4, 9-16, 18-32 (After Bharadwaj), Figs. 5, 37-50 (After Udar), Figs. 6-7 (After Campbell), Fig. 8 (After Mehra and Handoo), Figs. 17, 33-36 (After Proskaur).

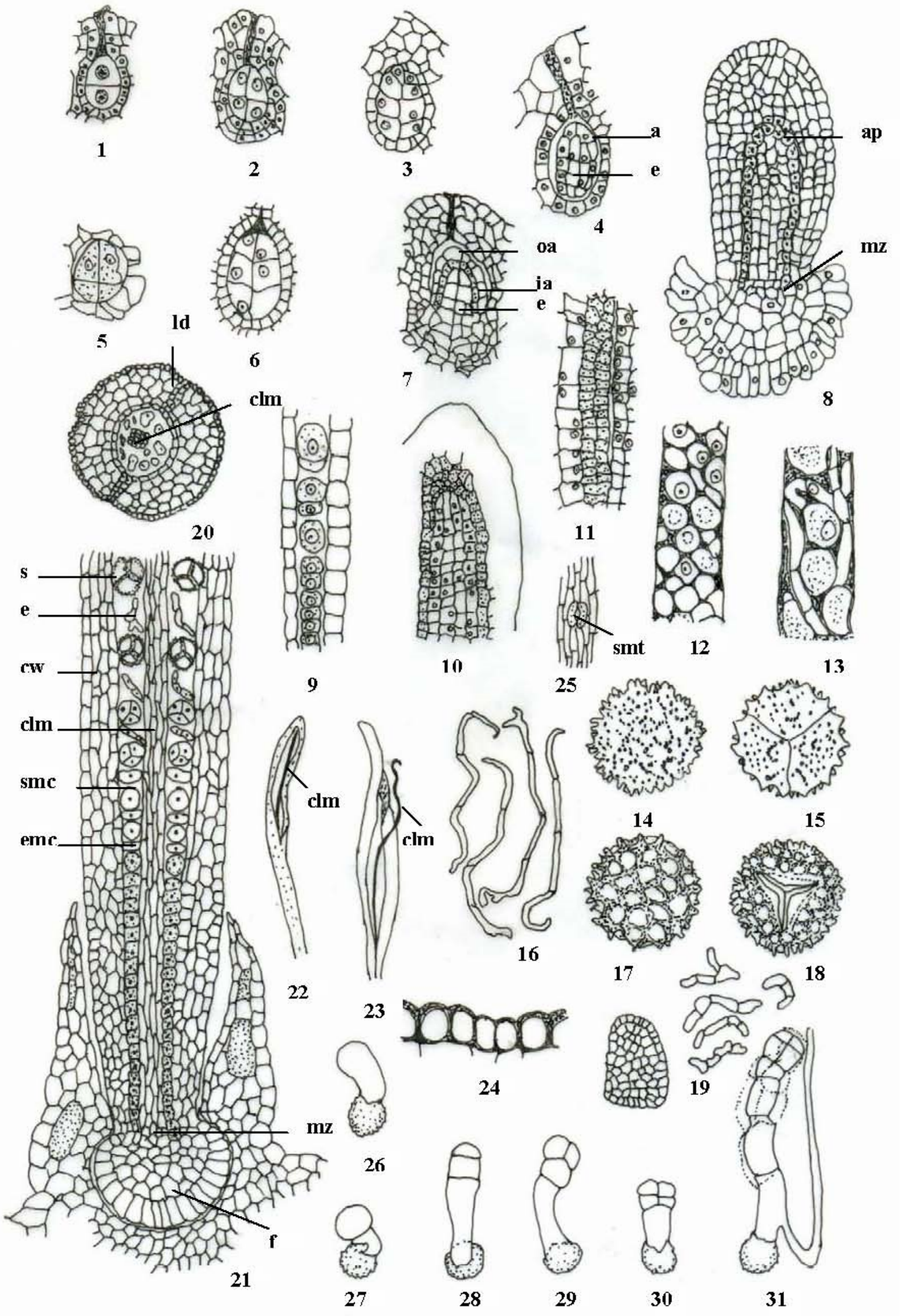

Fig. 14. ***Anthoceros:*** 1-13. Stages in sporophyte development, 14, 15. Spores of *A. angustus*, (14) in distal view, (15) in proximal view, 16. Elaters (*A. angustus*), 17, 18. Spores (*A. erectus*), (17) in distal view, (18) in proximal view, 19. Elaters (*A. erectus*), 20. Cross-section of sporophyte, 21. Longitudinal section of sporophyte, 22, 23. Dehiscence of capsule, 24. Outer layer of capsule wall, 25. Capsule wall with stomata, 26-32. Stages in spore germination. (a – amphithecium, e – endothecium, oa – outer amphithecium, ia – inner amphithecium, mz – meristematic zone, ap – archesporium, smt – stomata, s – spore, e – elater, cw – capsule wall, smc – spore mother cell, emc – elater mother cell, clm – columella, f – foot, ld – line of dehiscence). Figs. 1-4, 6 - 20, 22-25 (After Bharadwaj), Fig. 5. (After Mehra & Handoo), Fig. 21 (After Udar), Figs. 26-32 (After Mehra & Kachro

Bryopsida

The class Bryopsida (Musci) has acquired a separate, independent status, parallel to the class Hepaticopsida (Hepaticae) since very beginning. This group is mainly characterized by exclusively leafy gametophytes. Generally they are erect growing (acrocarpous) while some others are prostrate growing (pleurocarpous). Some epiphytic forms may be hanging or pendulous (see Schofield and Hebant 1984). They are differentiated into axis and spirally arranged leaves. The leaves are usually with distinct midrib being multistratose in midrib portion and unistratose in wing portion. The rhizoids are multicellular and obliquely septate. The sex organs are always terminal, present in groups. They are exogenous and develop by means of an apical cell. They are associated with multicelullar uniseriate paraphysis and are protected by perigonial (male bracts) or perichaetial (female bracts) leaves. Antheridia are stalked with clavate to elongated cylindrical antheridial body. Archegonia are also stalked with long neck. Peristome is an important feature of the moss capsule and helps in spore dispersal. Besides, protonema – a short intervening phase is present in between the spore and adult gametophyte). The sporophyte is of determinate growth and partially independent due to presence of chloroplasts and stomata in the capsule wall. It (sporophyte) consists of foot, seta and capsule. Foot is embedded in the apical gametophytic axis. Seta is much elongated, stout, rigid and elongates before the maturation of the capsule. The capsule is generally cylindrical – elongated with outermost multilayered capsule wall, the central sterile column – columella, and in between the spore sac, which has spores only. Elaters are totally absent. The sporogenous tissue is endothecial in origin. The capsule has a distinct operculum, which gets removed at maturity. At the mouth of the capsule there is a fringe of peristome teeth (Arthrodontous or Nematodontous type), which help in the dispersal of spores. The moss spores, after germination form a short distinct phase – protonema first. On the protonema, buds are produced which develop into adult gametophytes. Thus a single spore gives rise to number of gametophytes. This is one of the main reasons why mosses are more dominant than the liverworts and hornworts where a single spore gives rise to a single, adult gametophyte in both the liverworts and hornworts. Bryopsida includes a large number of mosses, which are variously classified by giving importance to one or the other characters (see Edwards 1984, Vitt 1984).

A. One group of systematists like Bridel (1819, 1826-27), Nees *et al*. (1823) and Schimper (1855) gave importance to the position of archegonia/sporophyte and classified the mosses into two main groups.
   (1) Acrocarpi (Erect plants with apical sporophyte on main axis).
   (2) Pleurocarpi (Prostrate plants with apical sporophyte on lateral branch).

B. While Muller (1848-51) recognized dehiscence of the capsule of prime importance and classified the mosses into three main groups.
   (1) Schistocarpi (longitudinal dehiscence of capsule into valves)
   (2) Cleistocarpi (Capsule without operculum and peristome)
   (3) Stegocarpi (Capsule with definite operculum and peristome)

C. Some other systematists like Mitten (1859), Philibirt (1884-1890), Fleischer (1904-23, 1920), Cavers (1910-11), Brotherus (1924-25), Dixon (1932) recognized peristome feature as primary character and divided mosses into two major groups.
   (1) Arthodonti/Arthodonteae (Articulate, thin peristome formed by a portion of fused cell plates)
   (2) Nematodonti/Nematodonteae (thick solid peristome formed by concentric layers of whole cells)

The group Arthodonteae was further classified into two groups:
   (1) Haplolepideae (single ring of peristome)
   (2) Diplolepideae (double ring of peristome)

This view, of classifying mosses on the basis of peristome feature, is widely accepted and is still followed. All the earlier workers divided the mosses into three groups either at the order level (Bower, 1935; Wettestein, 1933-35; Campbell, 1940) or at the subclass level (Fleischer, 1904-23; Brotherus, 1924-25; Dixon, 1932).

1. Sphagnales/ Sphagnidae
2. Andreaeales/ Andreaeidae
3. Bryales/ Bryidae

However, Cavers (1910-1911) recognized six orders to include mosses without dividing bryophytes into classes (Hepaticae, Anthocerotae and Musci).

1. Sphagnales
2. Andreaeales
3. Tetraphidales
4. Polytrichales
5. Buxbaumiales
6. Eubryales

Smith (1938, 1955) recognized three subclasses with the names:

1. Sphagnobrya
2. Andreaeobrya
3. Eubrya

Simultaneously Engler *et al*. (1954) and Reimer (1954) recognized 5-sub-classes.

1. Sphagnidae
2. Andreaeidae
3. Bryidae
4. Buxbaumiidae
5. Polytrichidae

While Richardson (1981) recognized three major groups:

1. Sphagnopsida (Peat Moss)
2. Andreaeopsida (Granite Moss)
3. Bryopsida (True Moss) with 3 subclasses
    - i. Polytrichideae
    - ii. Buxbaumiideae
    - iii. Eubryideae

Vitt (1984) divided Bryopsida into three main subclasses:

1. Subclass – Sphagnidae
    - I. Sphagnales
        - i. Sphagnaceae
            - *Sphagnum*
2. Subclass – Andreaeidae
    - I. Andreaeales
        - i. Andreaeaceae
            - *Andreaea*
        - ii. Andreaeobryaceae
            - *Andreaeobryum*
3. Subclass – Bryidae
    - I. Polytrichales
        - i. Polytrichaceae (21 genera)
            - *Pogonatum*
            - *Polytrichum*
            - *Dawsonia*
    - II. Tetraphidales
        - i. Tetraphidaceae
            - *Tetraphis*
            - *Tetradontium*
        - ii. Colomniaceae
            - *Colomnium*

III. Bryales (15 suborders, 85 families and 765 genera)

The suborders are:

1. Archidineae
2. Funariineae – *Funaria*
3. Splachnineae
4. Orthotrichineae
5. Bryineae
6. Hypnineae
7. Leucodontineae
8. Hookeriineae
9. Buxboumiineae – *Buxbaumia*
10. Encalyptineae
11. Pottineae
12. Dicranineae
13. Fissidentineae
14. Seligeriineae
15. Grimmineae

During the period of 1951-1993, the genus *Takakia* remained a controversial genus regarding its systematic position whether it is an interesting liverwort or an interesting moss, as vegetative plants with only archegonia were known at that time (Grolle, 1963). However, after the discovery of antheridia and sporophyte (Smith, 1990; Smith and Davison, 1993; Schuster, 1997; Higuchi and Zhang, 1998) the genus turned out to be a moss due to its moss like antheridia and the sporophyte. Smith and Davison (1993) proposed new systematic position of the taxon in Andreaeopsida along with *Andreaea* and *Andreaeobryum.*

Division – Andreaeopsida
- Subclass – 1. Andreaeidae
  - Order – Andreaeales
    - Fam. – Andreaeaceae
      - *Andreaea*
- Subclass – 2. Takakiidae
  - Order – 1. Takakiales
    - Fam. – Takakiaceae
      - *Takakia*
  - Order – 2. Andreaeobryales
    - Fam. – Andreaeobryaceae
      - *Andreaeobryum*

Thus, at present there are 7 orders [Sphagnales, Andreaeales, Takakiales, Andreaeobryales, Polytrichales, Tetraphidales and Bryales] 92 families and 793 genera in Bryopsida (Moss). In India the class is represented by 1576 taxa belonging to 5 orders 57 families and 338 genera (Lal 2005).

Sphagnales

The group is a monotypic in the subclass – Sphagnidae with single order Sphagnales, single family Sphagnaceae and single genus *Sphagnum*. In India the genus is representated by 22 species (Lal, 2005).

Sphagnum is an aquatic moss and commonly called as ‘Bog Moss’ / ‘Peat Moss’ / ‘Moss Cotton’. The genus is remarkably unique in having some features common to liverworts (Hepaticae), some features common to hornworts (Anthocerotae) and some features common to Mosses (Musci). Besides it has some peculiar features of its own which make the genus – synthetic and occupies an independent status upto to the level of subclass – Sphagnidae.

The plants have leafy organization, which is differentiated into axis and spirally arranged leaves (moss character). At the apex, there is a cluster of short, stout ‘comal’ branches forming a compact head. Lateral branches show unique feature in being axillary and develop at certain intervals. They are of two types: (i) pendent and (ii) divergent (Fig. 15: 1,2). The leaves are unistratose, without mid rib having dimorphic leaf-cells (hyaline and chlorophyllous) arranged in a regular reticulate pattern. The chlorophyllous cells are small, linear elongated with numerous discoid chloroplasts. The hyaline cells are large polygonal, without chlorophost. They also have distinct pores and thickening bands (Fig. 15: 7,8). The rhizoids are totally absent in adult gametophyte while present in protonemal phase (Fig. 16: 32 - 34). The growth of the axis takes place by means of an apical cell with three cutting faces. The axis in internally differentiated into cortex and medulla. Depending upon the species, the cortex may be single or multilayered, with or without pores and thickening bands. The medullary region may have only thick walled cells or further differentiated into outer thick walled and inner thin walled cells (Fig. 14: 3 - 6). In some species, like *S. molluscum*, few enlarged, flask shaped, modified cells are present in the cortex, which are called as 'Retort Cell' (Fig. 15: 5,6). Vegetatively, the plants reproduce by death and decay of older portion of plants, resulting into separation of lateral branches, which develop into new plant. Sex organs are present on special branches. Antheridial branch is short, spindle shaped (Fig. 15: 1). Antheridia are present in the axil of male bracts /perigonial leaves (Fig. 15: 9). They have long stalk with 2 – 4 rows of cells and spherical antheridial body with single layered jacket and number of androcytes (Fig. 15: 15). At maturity, antheridium dehisces into number of lobes, which become revoluted releasing the androcytes – a feature resembles to the liverwort - *Porella* (Fig. 15: 16). Antheridia develop from 2- sided apical cell (Fig. 15: 10 - 15). The archegonial branch is short bud like having large, bright green conspicuous perichaetial leaves with 1-3 archegonia (Fig. 15: 1,3). Among these, there is single primary archegonium developing from apical cell and other two are secondary archegonia, which are not developed from the apical cell but from the segments produced by the apical cell (Fig. 15: 21). The segments divide transversely forming a filament, which develop into secondary archegonia (Fig. 15: 17-30). The sporophyte has bulbous foot and spherical capsule only (Fig. 16: 17). Seta is absent but pseudopodium is present (Fig. 15: 2; Fig.16: 1). It is a leaf less extension of the gametophytic axis to raise the capsule. The capsule has multilayered capsule wall with rudimentary stomata, dome shaped arehesporium which arches over the central columella (Fig. 16: 17 -20). The archesporium is amphithecial in origin while columella is endothecial in origin – a feature common to hornworts (Fig. 16: 2 – 17). Distinct annulus is present which demarcates the operculum from the capsular region. Peristome is absent. The dehiscence of the capsule is somewhat special through 'Gun shot Mechanism' or 'Air Gun Mechanism' in which the operculum is thrown off with jerk (Fig. 16: 21 – 24). Spores are tetrahedral in shape with distinct triradiate mark. It germinates to form exosporic thalloid protonema, which further may develop into secondary protonema and buds giving rise to new gametophyte (Fig. 16: 25 - 34).

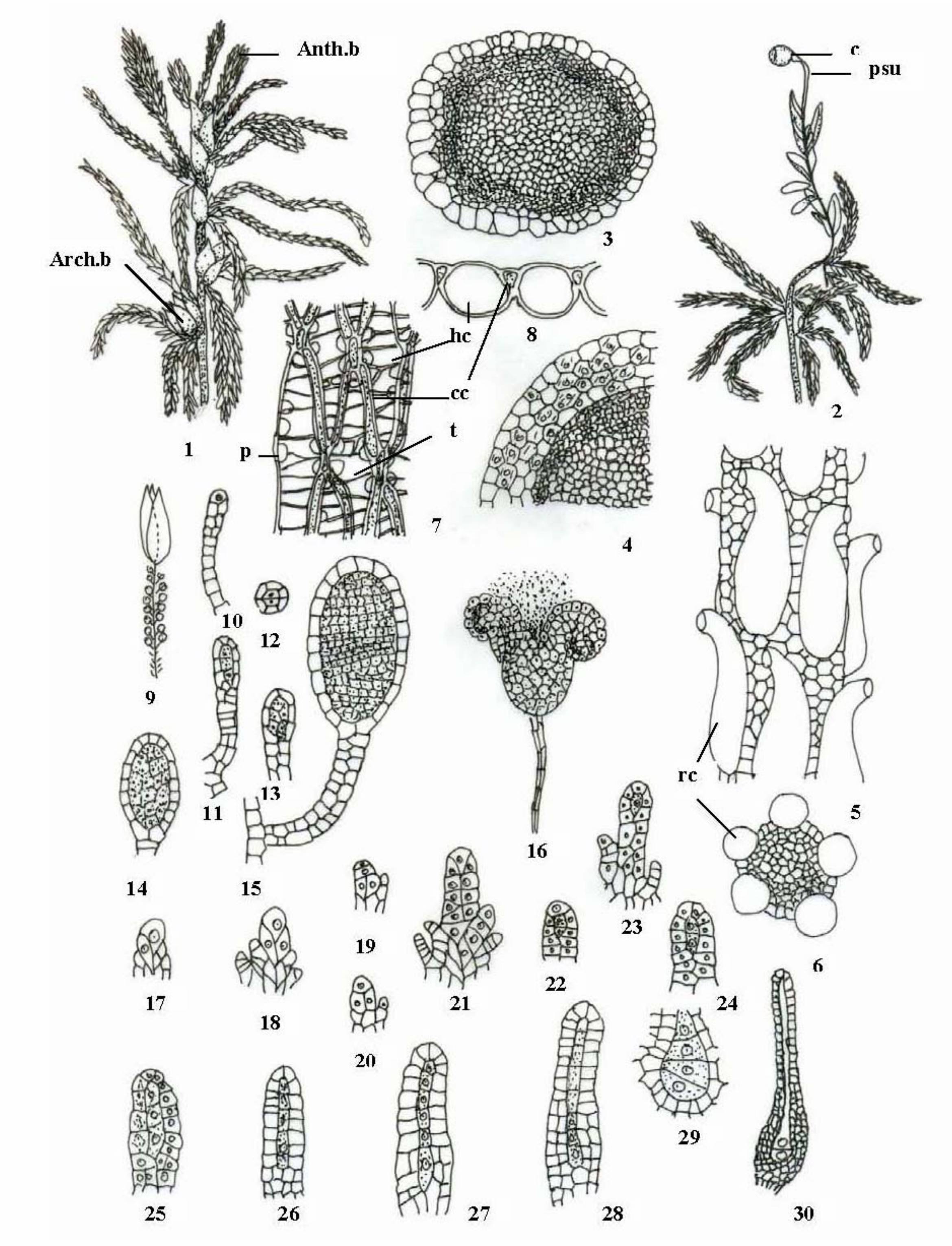

Fig. 15. ***Sphagnum***
1. A portion of plant showing antheridial and archegonial branches, 2. A portion of plant with mature capsule and elongated pseudopodium, 3,4 Cross-sections of axis, 5. A portion of axis showing retort cells, 6. Cross-section of axis with retort cell, 7. Leal cells showing chlorophyllous and hyaline cell, 8. Cross – section of leaf, 9. A male branch (antheridial bracts removed), 10-15. Stages in antheridial development, 16. Dehisced antheridium, 17-30. Stages in archegonial development. (anth. b – antheridial branch, arch. b – archegonial branch, psu – pseudopodium, c – capsule, cc – chlorophyllous cells, hc – hyaline cells, p – pore, t – thickening band, rc – retort cell). Figs. 1, 9, 16 (After Schimper), Fig. 2 (After Udar), Figs. 3-8 (After Cavers), Figs. 10-15, 20, 23 (After Smith), Figs. 17-19, 21, 22, 24-30 (After Bryan).

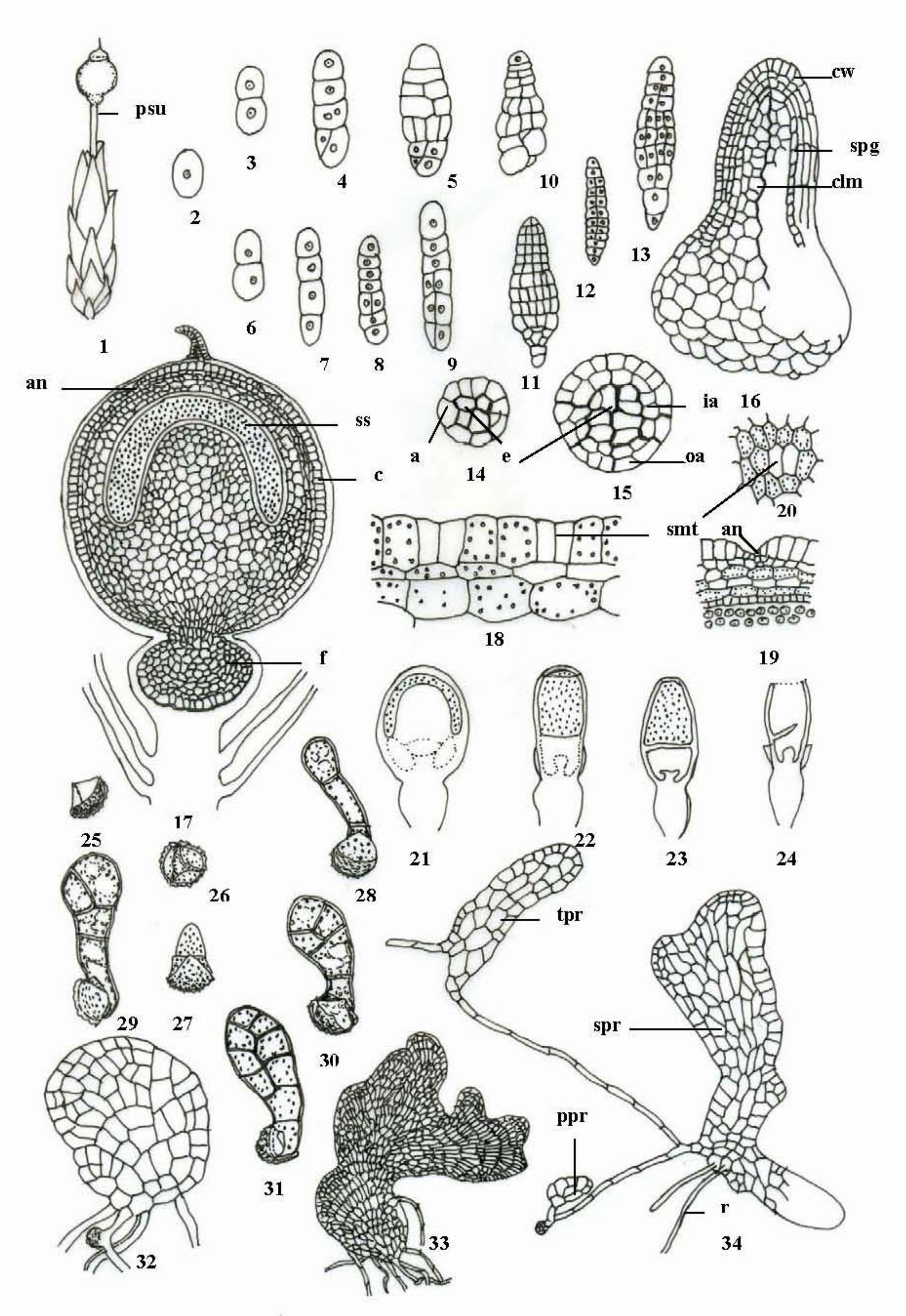

Fig. 16. ***Sphagnum:*** 1. A female branch with sporophyte 2-16. Stages in sporophyte development, 17. Longitudinal section of capsule, 18, 19. Cross-sections of capsule wall showing stomata and annulus respectively, 20. Capsule wall in surface view showing stomata, 21-24. Dehiscence of the capsule, 25. Spore, 26-32. Stages in spore germination, 33. An irregularly lobed thalloid protonema, 34. Formation of secondary and tertiary protonema. (psu – pseudopodium, c – capsule, f – foot, a – amphithecium, oa – outer amphithecium, ia – inner amphithecium, e – endothecium, ss – spore sac, r – rhizoids, ppr – primary protonema, spr – secondary protonema, tpr – tertiary protonema, smt – stomata, an – annulus, cw – capsule wall, spg – sporogenous tissue, clm - columella). Fig. 1 (After Schimper), Figs. 2,3,6-13 (After Bryan), Figs. 4,5,14-16 (After Waldner), Figs. 17-20 (After Cavers), Figs. 21-24 (After Nawaschin), Figs. 25-33 (After Muller), Fig. 34 (After Noguchi).

Andreaeales

The order Andreaeales also is a monotypic group in the subclass Andreaeidae having single family Andreaeaceae and single genus *Andreaea*. Previously *Andreaeobryum* was also placed in this group but Smith and Davison have separated the genus and placed it in Andreaobryales within the subclass Takakiidae. The genus *Andreaea* is a high altitude plant (Moss) growing on fairely exposed, dry, silicious rocks, called as ‘Granite Moss’. Six species of this genus are known from India (Lal, 2005).

The plants are dark brown in colour. They are differentiated into axis and spirally arranged leaves, which may be with or without midrib (Fig. 17: 1-3). The midrib portion in multistratose while wing portion is unistratose. Rhizoids are unique in being multicellular, cylindrical or flat, plate like which penetrate into the rock crevices or stick to the rock surface. The stem is simple internally with outer, more or less thick walled cortex and comparatively thin walled medulla with somewhat larger cells (Fig. 17: 4). Plants are mostly monoecious. Antheridia are grouped, terminal in position having a short stalk and elongated club shape antheridial body associated with multicellular, uniseriate paraphysis (Fig. 17: 5). Archegonia are typical moss like having a short stalk, swollen venter and long neck (Fig. 17: 6,9). Both the sex organs develop through the apical cell. The sporophyte has more or less ovoid capsule and swollen foot (Fig. 17: 1,7 – 9, 21). Seta is absent but pseudopodium is present (Fig. 17: 7). The capsule has multilayered capsule wall, dome shaped archesporium which arches over columella (Fig. 17: 21). Archesporium as well as columella both are endothecial in origin (Fig. 17: 10 - 20). Annulus, operculum and peristome are absent. The dehiscence of the capsule takes place through four longitudinal lines forming four distinct valves but these valves remain attached at apex and base forming four slits (Fig. 17: 1,7,8). The spores have two spore coats and divide to form multicellular globose structure within the stretched exospore called as endosporic thalloid protonema (Fig. 17: 22-26). The exospore ruptures and it develops into a filamentous structure (Fig. 17: 27-30). The buds appear on these filament which give rise to new gametophyte (Fig. 17: 31).

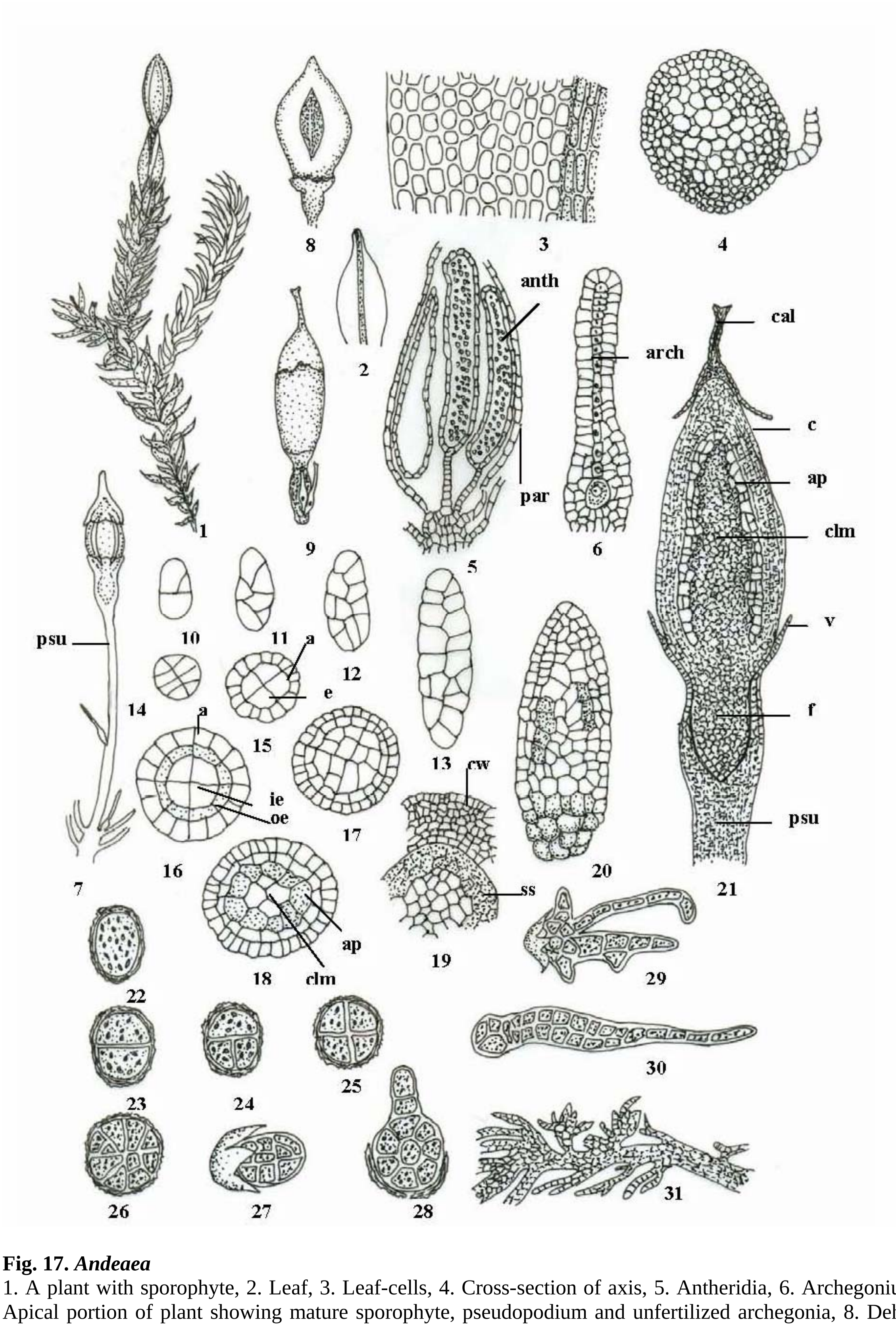

Fig. 17. ***Andeaea***
1. A plant with sporophyte, 2. Leaf, 3. Leaf-cells, 4. Cross-section of axis, 5. Antheridia, 6. Archegonium, 7. Apical portion of plant showing mature sporophyte, pseudopodium and unfertilized archegonia, 8. Dehisced capsule, 9. A mature sporophyte with unfertilized archegonia, 10-20. Stages in sporophyte development, 21. Longitudinal section of sporophyte 22-31. Stages in spore germination. (anth – antheridia, arch – archegonia, par – paraphysis, psu – pseudopodium, clm – columella, c – capsule, f – foot, cal - calyptra, ap – archesporium, v – vaginula, a – amphithecium, e – endothecium, oe - outer endothecium, ie – inner endothecium, ss – spore sac, cw - capsule wall). Figs. 1, 8, 9 (After Bryolog. Europ), Figs. 2-4 (After Vohra & Wadhwa), Figs. 5, 6 (After Smith), Figs. 7 (After Cavers), Figs. 10-20 (After Waldner, Muller Berol & Cavers), Fig. 21. (After Kuhne), Figs. 22-31 (After Kuhne & Berggren).

Takakiales

It is also a monotypic group having single family Takakiaceae and single genus *Takakia*. The genus is characterized by heterotrichous nature of plants, which are differentiated into prostrate growing rhizomatous axis and erect growing aerial axis or shoot (Fig. 18: 1). Both the shoots are densely covered with mucilage papillae (Fig. 18: 6,7). The leaves are present in three rows, which are spirally arranged (Fig. 18: 2,8). These leaves (phyllids) are cylindrical, with 2-4 finger like lobes (Fig. 18: 3,4). Rhizoids are absent. Antheridia are terminal and present in groups. Archegonia are also present in group either terminal or on stem surface. They are stalked with long neck. The sporophyte has distinct foot, elongated seta and ovate-elongated capsule, with multilayered capsule wall, dome shaped archesporium and central columella (Fig. 17: 8,9). Operculum, annulus and peristome are absent. The outermost layer of the capsule wall has characteristic thickning in the cell due to which cell lumen becomes more or less flask shaped (Fig. 18: 13,14). Dehiscence of the capsule takes place through single longitudinal line (slit), which is dextrosely oriented and the cells are without thickening (Fig. 18: 1,10-15). The spores are tetrahedral in shape with distinct triradiate mark (Fig. 18: 16).

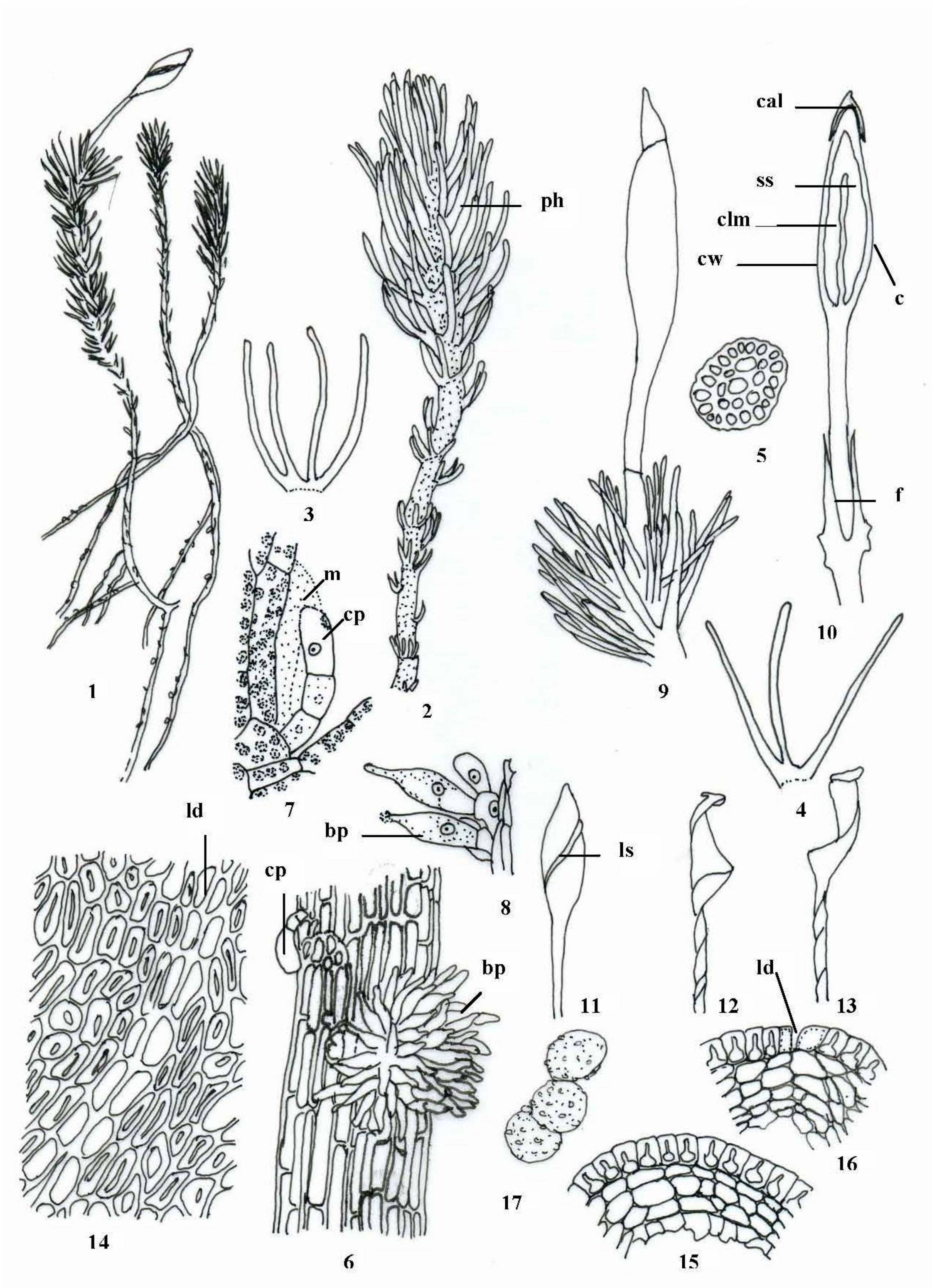

Fig. 18. ***Takakia:*** 1. A plant showing rhizome and aerial axis, 2. A portion enlarged showing phyllids (leaves). 3,4. Leaves (phyllids). 5. cross – section of axis, 6. A portion of axis showing beaked and clavate mucilage papillae, 7. Clavate mucilage papillae, 8. Beaked mucilage papillae, 9. Apical portion of plant showing sporophyte, 10. Longitudinal section of sporophyte, 11 – 13. Dehiscence of capsule, 14. Capsule wall (surface view), 15,16. Cross-section of capsule wall, 17. Spores. (m – mucilage, cp – clavate mucilage papillae, bp – beaked mucilage papillae, ph – phyllids (leaves), cw – capsule wall, clm – columella, ss – spore sac, ls – longitudinal slit, ld – line of dehiscence, cal - calyptra). Figs. 1,2,8 – 16 (After Higuchi & Zhang), Figs. 3 – 5 (After Schuster), Figs. 6,7 (After Proskauer).

Polytrichales

The order Polytrichales is mainly characterized by erect growing, robust (giant sized) plants which are differentiated into axis, spirally arranged leaves and multicellular, branched, oblique septate rhizoids. The leaves have a sheathing base and upper limb portion along with distinct midrib and lateral wings. The vertical photosynthetic lamellae are usually present on the leaf surface. Stem is highly differentiated internally with specialized hydroid and leptoids cells (Fig. 19: 15). The sporophyte has distinct foot, long, rigid seta and erect, elongated capsule. The capsule has distinct operculum and nematodontous type of peristome having 32-64 solid teeth, which remain attached to the membranous covering epiphragm. Calyptra is usually hairy. The archesporium is present all around the columella and endothecial in origin. The protonema is filamentous. The order has single family Polytrichaceae and 21 genera. Among these, Pogonatum, Polytrichum, Dawsonia are large sized mosses. Pogo*natum* is quite common while *Polytrichum* is quite rare in Indian territories. However, *Dawsonia* is not represented in India. The genus *Pogonatum* has been discussed in detail as a representative of this group.

Pogonatum

- *Habitat and Distribution*

  Pogonatum is a large genus with about 200 species all over the world. In India about 35 species have been reported (Gangulee and Kar, 1995, Lal, 2005). It grows extensively in the Himalayas as well as in hills of south India in between the altitude of 3000-8000 feet on damp soil, moist rocks, shady as well as exposed places. The plants usually grow over large area forming pure population.

- *Gametophyte*

  The plants are robust, erect, and differentiated into stem, leaves and rhizoids. The basal portion of the stem is rhizomatous region, which is stout, stiff and densely covered with fluffy growth of rhizoids (Fig. 19: 1,2). The rhizoids are much elongated, branched, multicellular, oblique septate and thick walled (Fig. 19: 3). The bunch of rhizoids, often form a twisted string, which help in capillary conduction of water. The apical portion of axis can be differentiated into (i) non leafy region (a short portion of axis adjacent to rhizomatous region without any lateral appendages) (ii) scale leafy region (a portion just above the non leafy region with small reduced yellow scale leaves) and (iii) leafy region (the apical portion of axis with well developed normal, green leaves (Fig. 19: 1). The leaves are spirally arranged on the axis with distinct midrib and dentate (serrated) margins (Fig. 19: 7,8). They are rather stiff and spread out from the axis. They have two distinct regions (i) a broad thin, yellowish or lighter coloured sheathing base and (ii) a terminal, erect spreading, green-dark coloured, brownish limb region (Fig. 19: 4-6). On the upper surface (adaxial) of the leaves, there are number of vertical, photosynthetic lamellae which are confined to midrib portion only. They appear as longitudinal striations, which run parallel from base to apex on limb region (Fig. 19: 5).

- *Axial anatomy*

  The axial anatomy slightly differs from rhizomatous region to apical leafy region in both the outline and internal structure. The rhizome is more or less circular in outline. The outer most layer-epidermis is rather indistinct due to the presence of rhizoids, which densely cover the surface. The cortex is multilayered with 2-3 or more layers of cells. The inner most layer of the cortex has conspicuously enlarged cells which separates the central cylinder from the cortex. The cortical region is interrupted by three radial strands, which are placed at equal distance giving radial symmetry to the axis. These radial strands have outer thick walled hypodermal cells adjacent to epidermis and inner thin walled cells. The rhizoids are dense at the point of these radial strands. The central cylinder is distinctly 3-lobed with the alternate, raised (ridges) and depressed areas (furrow). These depressed areas form concavities where the radial strands are present. In these concavities of central cylinder, at the base of the radial strands, group of specialized cells are present which are known as leptoid cells. The central cylinder consists of numerous thick walled cells called as steroids along with few scattered isolated groups of 2-3 cells having outer thick walls, called as hydroid. The hydroids cells are specialized for water conduction, while leptoids cells – for the food conduction. The steroids are mainly for mechanical support (Fig. 19: 13).

The aerial portion of the axis is more or less triangular in shape. The outer most layer epidermis is well defined in the lowermost non-leafy region while it is irregular due to the presence of scale leaves and green leaves in apical regions. The cortex is broad with outer thick walled, dark coloured (brownish) smaller cells, present in 2-3 layers and inner thin walled, light coloured, larger, compactly arranged parenchymatous cells. The innermost layer of cortex has normal cells (not enlarged as in rhizomatous region) and radial strands are also absent. All the cells of the cortex are filled with starch grains. The non- leafy portion of the axis has no leaf traces in cortical region while they are present in leafy portion. In the scale leafy region, there are usually three leaf traces while in the apical region there are number of leaf traces as there are more number of spirally arranged leaves present densely. The leaf traces arise from central cylinder and go to the leaves. They have few hydroid cells surrounded by leptoid cells. Inner to the cortex, the central cylinder has hydroids, which can be differentiated into two distinct zones. The central hydrom having groups of 2-4 hydroids cells and peripheral hydrom having a sheath of thin walled cells – called as Hydrom sheath / Hydrom mantle. Outer to this, a distinct layer of starch sheath in present and then the leptoids cells are present forming the leptom mantle. Besides steroids are also present which gradually becomes less in the apical portion (Fig. 19: 14).

- *Leaf anatomy*

The sheath is unistratose with thin walled cells in the broad wing portion, while multistratose with thick walled cells in the narrow midrib portion. The limb region is multistratose in midrib portion, which gradually becomes thin towards the margin and the wing portion is unistratose (Fig. 19: 9,10). The lowermost layer on abaxial side forms the thick walled lower epidermis. Just above this layer, there are few layers of first thick walled cells and then thin walled parenchymatous cells. In between, there are few thick walled cells present in isolated groups. The uppermost layer is distinct in having comparatively larger cells on which 30-70 vertical photosynthetic lamellae are present. These lamellae are separated by narrow air spaces, which help in gaseous exchange as well as in retaining the water through capillaries to keep the leaves moist (Fig. 19: 10-12). In the cross-section, these lamellae appear as uniseriate filaments of 4-5 cells, which are densely filled with chloroplasts. The terminal cell of the filament differs from rest of cells. They are of diverse form being smooth, mamillate, beakd or forked depending upon the species. They are generally devoid of chloroplasts and form upper epidermis of the leaf.

- Apical growth

The apical growth takes place by means of tetrahedral apical cells with three cutting faces, which produce segments on three sides producing leaves. As these segments are produced in spiral manner hence the leaves are spirally arranged on the axis.

- *Vegetative reproduction*

The plants of *Pogonatum* are usually perennial growing indefinitely. New branches proliferate from parent axis, which get detached and develop into new independent gametophyte.

- *Sexual reproduction*

The plants are dioecious. Both the sex organs develop on separate plants forming perigonium (antheridial head) and perichaetium (archegonial head).

- *Antheridia*

Antheridia are terminal in position. They are present in group surrounded by conspicuous enlarged red to orange coloured perigonial leaves which form a cup like structure called as perigonia or antheridial head (Fig. 19: 1). The apical cell is not utilized in the formation of antheridia. It may proliferate into vegetative axis, which may further form another antheridial head. Thus on a single plant there may be several antheridial heads/cups (Fig. 19: 16). A mature antheridium has a short stalk and club shaped, elongated antheridial body with single layered jacket and number of spermatogenic cells. The antheridial groups are associated with uniseriate paraphysis (Fig. 19: 17).

- *Development of antheridium*

The development of antheridium takes place by an apical cell, which is a characteristic feature of moss in contrast to liverworts and hornworts. The antheridial initial cell first divides to form lower stalk cell and upper antheridial mother cell. The stalk cell does not divide much and develops into a short stalk. The antheridial mother cell divides by two oblique walls which intersect each other, thus producing an apical cell with two cutting faces (Fig. 20: 1-3). It produces 13-15 segments on both the sides and then looses its activity (Fig. 20: 4). Except one or two lower segments, all the apical segments further divide in a characteristic manner to produce elongated club shaped antheridial body (Fig. 20: 5-6,14). Each of the segments first divides vertically into 2 unequal cells. The larger cell further divides vertically resulting into the formation of 3-cells in a row (Fig. 20: 10). The middle cell then divides by third vertical wall, which meets the previous two vertical walls thus producing a single spermatogenic cell surrounded by three peripheral cells (Fig. 20: 11). From both the segments, a total of six peripheral cells and two spermatogenic cells of semicircular shape are produced. Spermatogenic cell may divide vertically forming 4 spermatogenic cells initially which further divide in all the planes very regularly forming numerous spermatogenic cells with their original boundary of parent cells till the maturity (Fig. 20: 12-14). The peripheral cells divide radially and transversely forming single layered jacket. In *P. microstomum* the apical segments divide somewhat differently. Both the segments divide by first vertical wall and then by second vertical wall in such a way that both the walls intersect producing two central spermatogenic and four peripheral cells (Fig. 20: 7-9). Further divisions are same. Simultaneously with antheridial initials, paraphysis initials are also produced, which divide transversely producing uniseriate paraphysis.

- *Archegonia*

Archegonia are also terminal in position. They are present in a group of 3-6 archegonia, which are surrounded by perichaetial leaves (Fig. 20: 18,19). The apical cell is used up in the formation of archegonium thus the further growth of plant is checked. However, lateral bud may develop into lateral branch. A mature archegonium is stalked having a long neck with six vertical rows of cells and swollen venter. The axial row has variable number of neck canal cells, a ventral canal cell and an egg. The archegonial group is also associated with uniseriate paraphysis as found in antheridial group.

- *Development of archegonium*

In the development of archegonial group, it is not certain whether the first /or last /or any other archegonium is formed by the apical cell of female shoot but it is utilized sooner or later. The archegonial initial cell appears as a papillate outgrowth then divides transversely into lower stalk cell and upper arehegonial mother cell (Fig. 20: 15,16). The stalk cell divides repeatedly in several planes to form a multicellular prominent stalk (Stalked archegonium is a characteristic feature of mosses). The upper archegonial mother cell divides by three oblique walls in such a way to produce a tetrahedral apical cell with three cutting faces (Fig. 20: 17-18). The apical cell is broader at free end and pointed, narrow below at inner face and produces three segments on lateral sides (Fig. 20: 17,18,22). They divide in several planes to form 2-3 layered thick wall of the archegonial venter (Fig. 20: 25). The apical cell may cut off some segments or directly divides by a transverse wall forming outer cell and central cell (Fig. 20: 19). The outer cell cuts off segments from its four cutting faces producing three rows of peripheral neck cells and a single central row of neck canal cells (Fig. 20: 20). Each of the peripheral cells divides radially forming six rows of cells in neck region which further divide transversely many time resulting into a long neck with more number of cells in jacket than the neck canal cells (Fig. 20: 21-25). With these changes, the central cell comes to the base of archegonium and divides transversely into a ventral canal cell and an egg (Fig. 20: 20). The terminal apical cell remains as the cover cell. Simultaneously paraphysis initials develop into uniseriate filamentous paraphysis.

- *Fertilization*

When the mature antheridia are flooded with water, they burst out releasing the spermatozoids, which swim in the film of water reaching to the archegonia. The neck canal cells and ventral canal cell disintegrate leaving a free passage. The mouth of the archegonium opens by splitting of vertical rows of neck cells and antherozoids move towards the egg and fertilization takes place.

- *Sporophyte*

The sporophyte consists of foot, seta and capsule. The **foot** is small multicellular, anchor shaped, deeply penetrated into the gametophytic tissue (Fig. 20: 35). The **seta** is elongated and rigid. Internally, it is more or less similar to the stem. It has outer cortical region, which may have only thin walled cells or is differentiated into outer thick walled cells and inner thin walled cells with air spaces (Fig. 22: 4). The central cylinder has hydrom (hydroids) surrounded by leptom (Leptoid and parenchyma cells).

The **capsule** is more or less elongated with three main regions: (i) lower - apophysis region (ii) middle - theca region and (iii) apical - opercular region (Fig. 21: 7). The apophysis region is the sterile basal portion of the capsule, which is present in continuation with the seta. It is not very prominent in this genus (*Pogonatum*). The middle theca region is the main fertile portion of the capsule having multilayered capsule wall followed by archesporium which is present all around the central columella (Fig. 21: 6,7; Fig.22: 5,6). The opercular region is the apical portion of the capsule, which has a cap like lid or operculum (Fig. 21: 1,2,5). At the mouth of the capsule, there is a thin, membranous, disc like covering which is called as epiphragm (Fig. 21: 3). At the rim of mouth, there is a fringe of peristomial teeth, which are usually 32 in number (Fig. 21: 4). The teeth are solid composed of number of cells with central straight cells bounded by 'U' shaped (curved) cells on both the sides (Fig. 21: 8). The tip of teeth rolls over the epiphragm.

- *Internal structure of the capsule*

In the apophysis region, the capsule wall in 3-4 layered followed by loosely arranged chlorophyllous cells. The central conducting region has somewhat elongated cells, which are in continuation with the columella towards the apical side and with the central cylinder of seta on lower side. Stomata are absent in *Pogonatum* while they are present in *Polytrichum*.

In the theca/capsular region, the wall is many layered with the outermost epidermal layers having thick walled cells. The spore sac is present in between the columella and capsule wall, which is jointed by means of trabeculae. Thus starting from the outerside, multilayered capsule wall is followed by outer trabeculae, spore sac, inner trabeculae and then the columella. The columella is in continuation with the apophysis on lower side and with the epiphragm on upper side (Fig. 22: 5,6).

- *Development of sporophyte*

The zygote first divides transversely into outer epibasal and inner hypobasal cells (Fig. 20: 26). The apical cell is organized in both the segments having 2 cutting faces (Fig. 22: 27). Now these apical cells produce segments resulting into an elongated cylindrical embryo (Fig. 20: 28). The hypobasal segments develop into anchor shaped foot (Fig. 20: 35), while the epibasal segments develop into capsule and seta. The segments produced by the apical cell of epibasal half divide vertically producing four rows of cells, which further divide (i) either periclinally producing outer amphithecium and inner endothecium. (ii) /or by 2 vertical intersecting walls to produce eight peripheral amphithecial cells and 4 central endothecial cells (Fig. 20: 29-31). Each of the amphithecial cell divides radially (anticlinally) resulting into 16 amphithecial cells enclosing four endothecial cells (Fig. 20: 31). Further divisions occur in very mathematical manner. The amphithecium divides periclinally and anticlinally forming seven layers of cells. While the endothecium divides in several planes forming multicellular endothecium but the boundaries of original four endothecial cells remain as such till maturity (Fig. 20: 33). Out of seven layers of amphithecium, outer most three layers form the capsule wall, next two layers form outer trabeculae, and inner two layers form the outer wall of the spore sac (Fig. 20: 34). The outermost layer of endothecium differentiates into archesporium, next two layers form the inner wall of the spore sac and then next two layers form the inner trabeculae. Central portion of the endothecium, which is squarish, differentiates into columella. At early stages, the spore sac is also squarish but later on it becomes 4-lobed at maturity (Fig. 21: 6; Fig. 22: 5). In the apical portion of capsule the epiphragm develops from endothecial cells hence remain in continuation with columella. The persistome develops from concentric layers of amphithecium except the outermost layer. The cell forming peristome divides by curved walls, which remain attached with the curved walls of adjacent cells thus producing group of cells having alternate raised and depressed areas (see Fig. 21: 14-17). Soon the parent cell wall disintegrates and teeth become free (Fig. 21: 8,18). Simultaneously cells of archegonial venter actively divide to form calyptra. The superficial cells become papillate and elongate to form dense hairy outgrowth on calyptra. The hairy calyptra is the characteristic feature of the genus *Pogonatum* and *Polytrichum*. The calyptra ruptures from base with the elongation of developing sporophyte, and remains as a cap at the apex of the capsule.

- *Dehiscence of the capsule*

When the mature capsule dries up in dry weather, the operculum gets detached. The epiphragm also dries up and shrinks resulting into narrow openings in between the teeth. The spores get dispersed by hygroscopic movement of peristomial teeth and by the movement (swaying) of capsule with the help of seta.

- *Spore germination*

The spores have thick exospore and thin endospore. They absorb moisture and swell up causing the rupturing of exospore at one or several points. The endospore comes out as germ tube, which elongates and develops into a branched, filamentous protonema. Some of the filaments turn upward and become green while others grow down and remain colourless forming rhizoids. The buds soon develop on green filaments, which further develop into erect leafy gametophyte by the activity of apical cell (Fig. 21: 19-24).

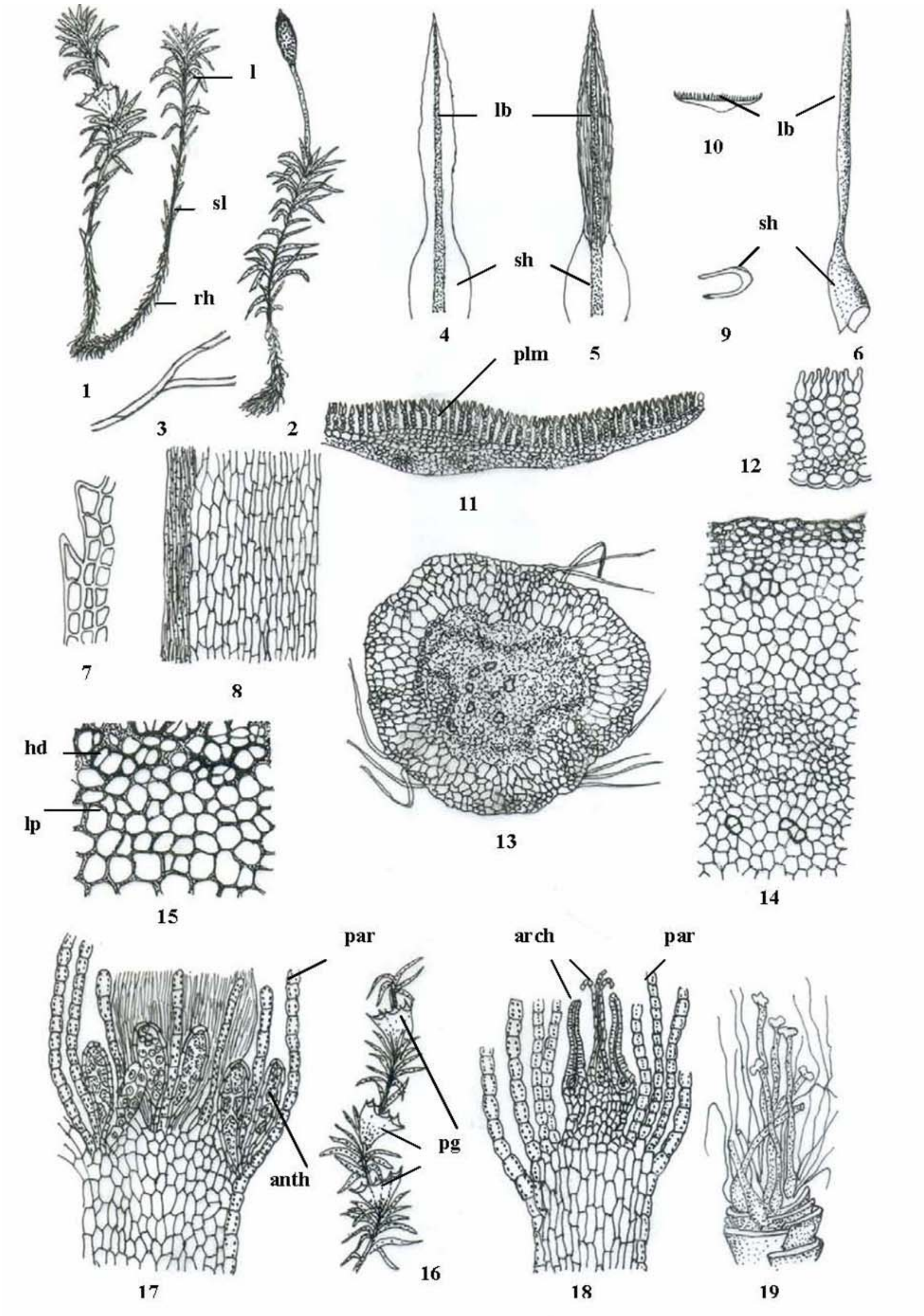

Fig. 19. ***Pogonatum***
1. Male plant, 2. Female plant with sporophyte, 3. Rhizoid (oblique septate), 4. A leaf (abaxial view), 5. A leaf (adaxial view showing photosynthetic lamellae), 6. A leaf (lateral view), 7. Marginal leaf-cells, 8. Basal leaf cells, 9. Cross-section of leaf through sheath region, 10. Cross-section of leaf through limb region (diagrammatic), 11. Same enlarged (cellular), 12. A portion of section showing photosynthetic lamellae with terminal beaked cells, 13. Cross-section of rhizome, 14. Cross-sectio of stem (a portion), 15. Hydroid cells, 16. A plant with 3 antheridial heads (perigonia), 17. Longitudinal section of shoot apex showing antheridia and paraphysis, 18. Longitudinal section of shoot apex showing archegonia, 19. Shoot apex showing archegonial group (perichaetial leaves dissected). (l - leaf, sl - scale leaf, rh - rhizome, lb - limb, sh - sheath, plm - photosyntehtic lamellae, hd -hydroid, lp - leptoid, par - paraphysis, anth - antheridia, arch - archegonia, pg - perigonia). Figs. 1,2,4-6, 9-11, 13, 19 (After Udar), Figs. 7,8, 12, 14, 17,18 (After Gangulee & Kar), Fig. 15 (After Esau *et al.*), Fig. 16 (After Schimper).

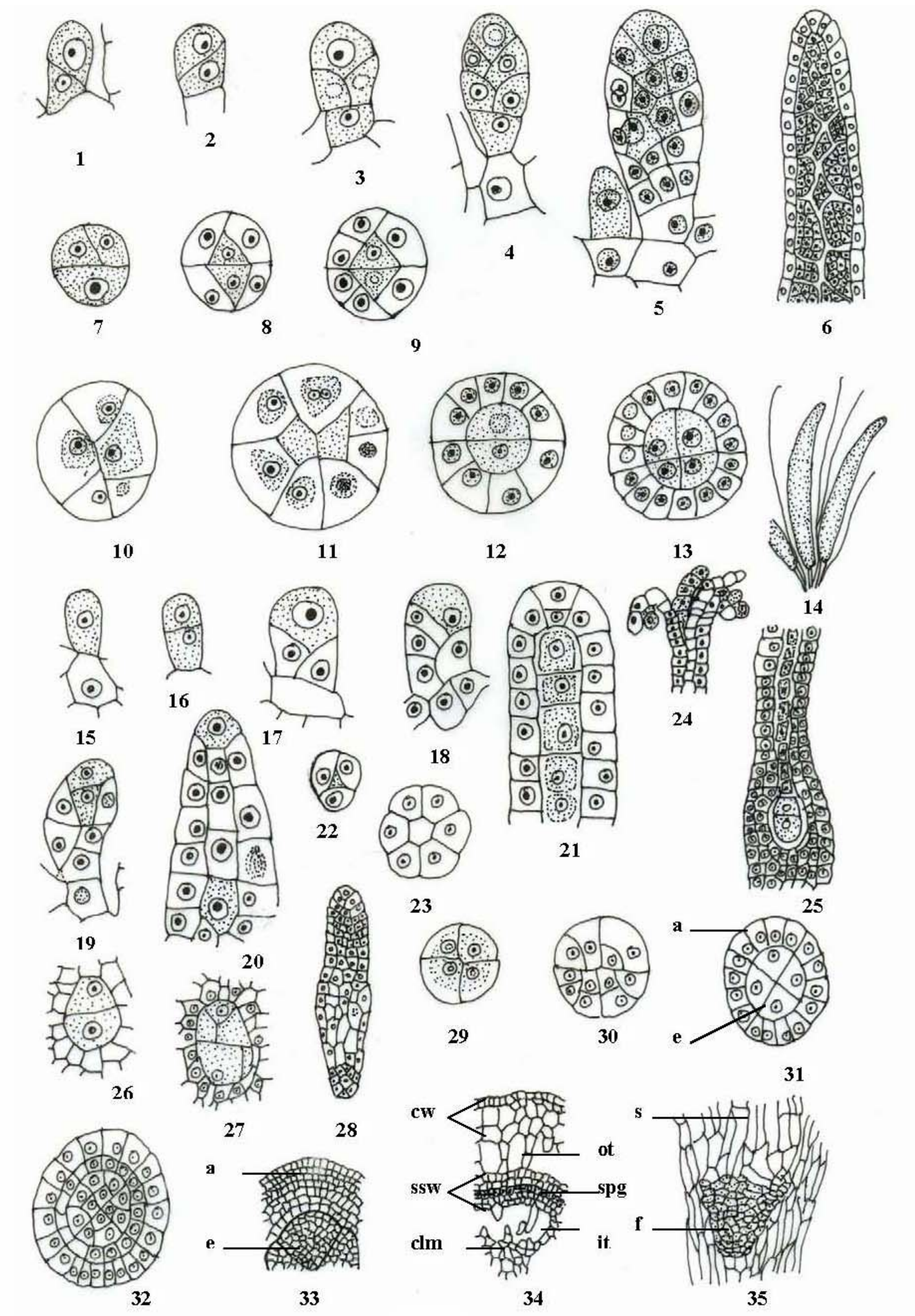

Fig. 20. ***Pogonatum:*** 1-13. Stages in Antheridial development, 14. Antheridia with paraphysis, 15-25. Stages in archegonial development, 26-35. Stages in sporophyte development. (a – amphithecium, e – endothecium, cw – capsule wall, ssw – spore sac wall, clm – columella, s – seta, f – foot, ot – outer trabeculae, it – inner trabaculae, spg – sporogenous tissue). Figs. 1-35 (After Chopra & Sharma).

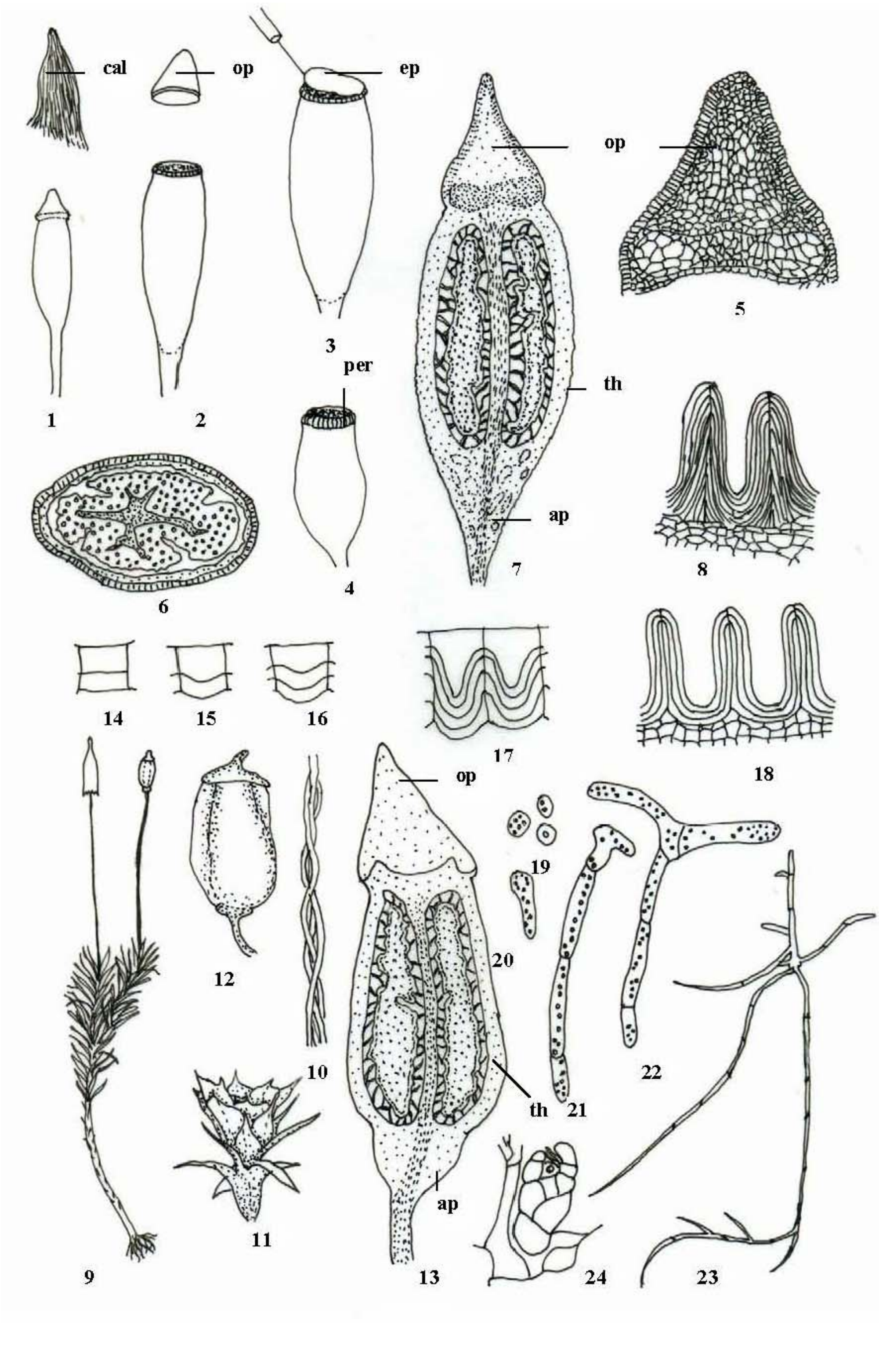

Fig. 21. ***Pogonatum*** **1-8,** ***Polytrichum*** **9-23:** 1. A capsule (hairy calyptra removed), 2. Capsule (operculum removed), 3. Capsule showing removal of epiphragm, 4. Capsule with peristomial teeth at the mouth, 5. Longitudinal section of sporophyte (opercular region), 6. Cross - section of capsule, 7. Longitudinal section of capsule (diagrammatic), 8. Peristome teeth, 9. Female plant with mature sporophyte, 10. Rhizoid bunch. 11. Antheridial cup, 12. A mature capsule, 13. Longitudinal section of capsule (diagrammatic), 14-18. Stages in the development of peristome teeth, 19. Spores, 20-24 Stages in spore germination. (cal - calyptra, op - operculum, ep - epiphragm, th - theca, ap - apophysis, per - peristome). Figs. 1-3 (After Udar), Figs. 4, 6, 12 (After Gangulee & Kar), Figs. 5, 8, (After Chopra & Sharma), Figs. 7, 13 (After Wettstein), Fig. 9 (After Parihar), Fig. 10,11 (After Schimper) Figs. 14-18 (After Goebel), Figs. 19-24 (After Wigglesworth).

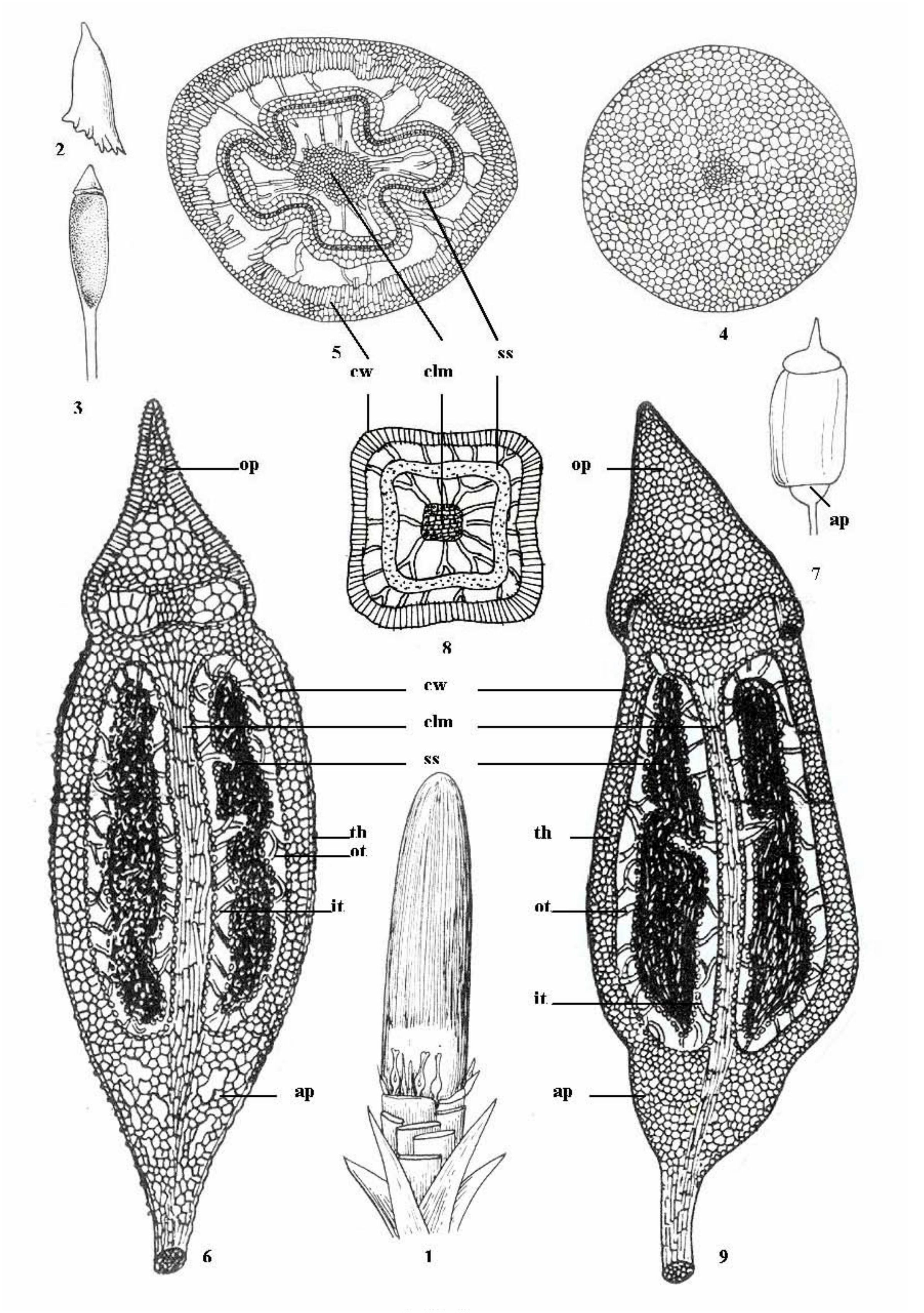

Fig. 22. *Pogonatum* 1-6, *Polytrichum* 7-9
1. Shoot Apex showing young developing sporophyte within the hairy calyptra and unfertilized archegonia, 2. Calyptra, 3. A capsule, 4. Cross-section of seta, 5. Cross-section of capsule, 6. Longitudinal section of capsule, 7. A capsule (with distinct apophysis), 8. Cross- section of capsule, 9. Longitudinal section of capsule. (op – operculum, th – theca, ap – apophysis, cw – capsule wall, ss – spore sac, clm – columella, ot – outer trabeculae, it – inner trabeculae, Figs. 1, 4, 5 (After Udar), Figs. 2,3 (After Rashid), Fig. 6,9 (After Wettstein), Fig. 7,8 (After Parihar).

Polytrichum

Polytrichum and *Pogonatum* are two very closely related genera of the family polytrichaceae. Their distinctive features are not sufficiently stable. Dixon did not recognize *Pogonatum* as a separate genus but placed it (*Pogonatum*) within the genus *Polytrichum*. However, the genus (*Pogonatum*) is internationally recognized. Osada (1965) studied Japanese Polytrichaceae and pointed out some distinctive features of these two genera. The gametophytes of both the genera are more or less similar in overall morphology but they can be distinguished on the basis of their leaves. In *Pogonatum*, the leaves are crispate in dry condition and the leaf teeth are multicellular while in *Polytrichum*, the leaves are not crispate in dry condition and the leaf teeth are unicellular. The sporophytes (capsule) in both the genera, however, distinctly differ. In *Pogonatum*, the body of the capsule is smooth, without ridges and is more or less circular in cross-section while in *Polytrichum*, the body of the capsule is angled with 4-6 distinct ridges and is somewhat squarrish in cross-section (Fig. 22: 2-9). The stomata are absent in *Pogonatum* and are present in *Polytrichum*. The apophysis region is distinct in *Polytrichum* while it is indistinct in *Pogonatum* The outermost layer of capsule wall is mamillose in *Pogonatum* and is smooth in *Polytrichum*. Beside, the number of peristomial teeth also differs, being 32 in *Pogonatum* and 64 in *Polytrichum*.

Tetraphidales

It includes single family Tetraphidaceae and the genus *Tetraphis* (*Georgia*). It is not represented in India. The genus is mainly characterized by the capsule with a definite operculum and nematodontous type of peristome teeth, which are four in number (Fig. 23: 1-4).

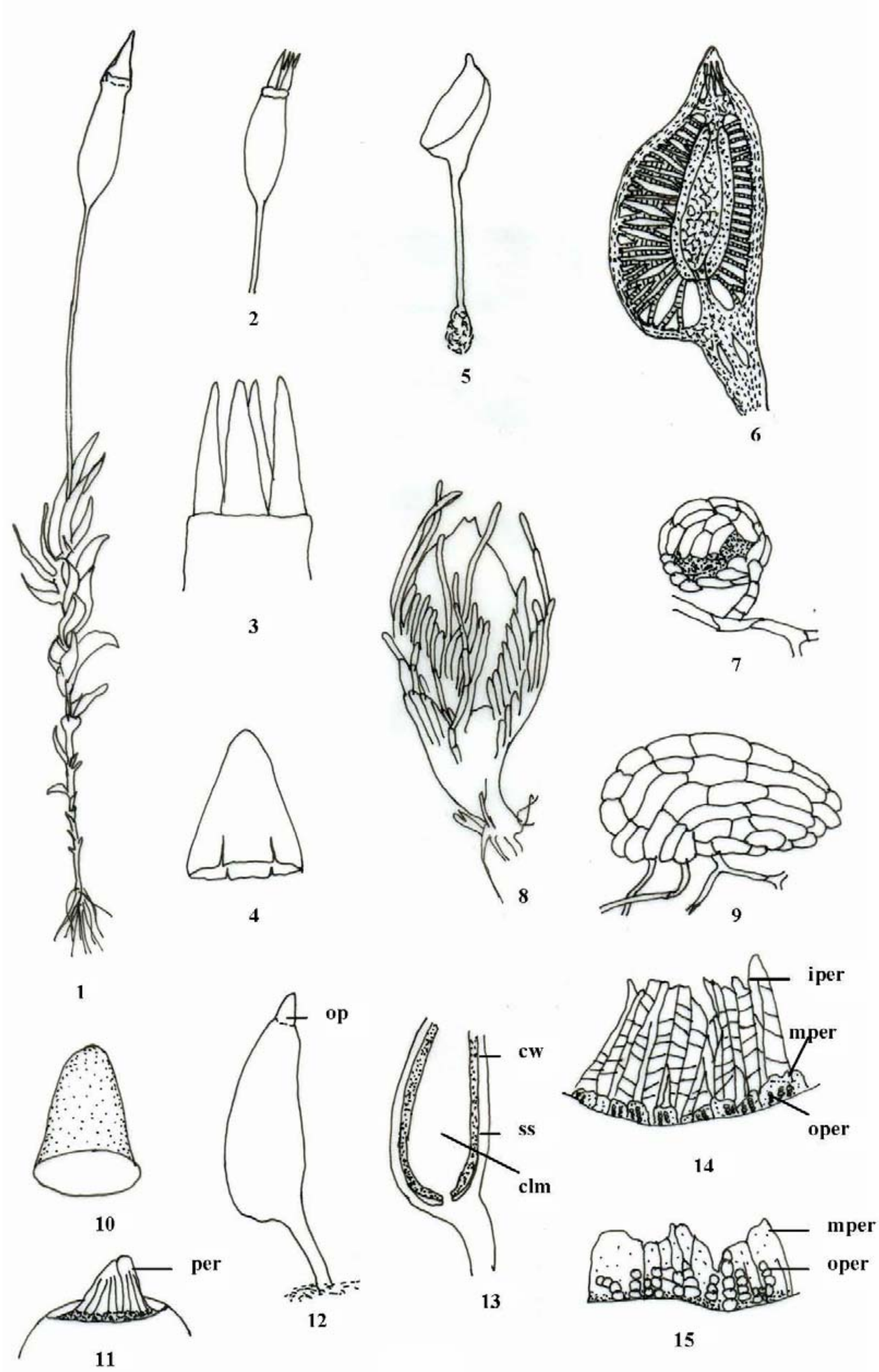

Fig. 23. *Tetraphis* 1-4, *Baxbaumia* 5 –15.: 1. A plant with sporophyte, 2. Capsule with 4 peristome teeth, 3. Same (enlarged), 4. Operculum, 5-8. *Buxbaumia aphylla,* 5. Sporophyte, 6. Longitudinal section of asymmetrical capsule, 7. Male gametophyte, 8. Female gametophyte, 9-15. *B. himalayensis*, 9. Male gametophyte, 10. Operculum, 11. Capsule apex showing peristome, 12. Sporophyte, 13. Longitudinal section of capsule, 14. Peristome teeth with outer, middle and inner ring of peristome, 15. Outer and middle peristome (enlarged). (op - operculum, cw - capsule wall, clm - columella, ss - spore sac, per - peristome, iper - inner peristome, mper - middle peristome, oper - outer peristome). Figs. 1, 2 (After Schofield), Figs. 3, 4 (After Cavers), Figs. 5,6 (After Limpricht), Figs. 7,8 (After Janzen), Figs. 9-15 (After Udar, Srivastava & Kumar).

Bryales

It includes large number of true mosses which are mainly characterized by small to large sized, erect to prostrate growing plants, differentiated into axis and 2-many rows of spirally arranged leaves with or without mid rib. Rhizoids are multicellular and oblique septate. The sporophyte has distinct foot, elongated rigid cylindrical capsule with a definite operculum and arthodontous type of peristome, present in 2-3 rings. The archesporium is present all around the columela and is endothecial in origin. The protonema is filamentous. The group has been divided into 15 suborders, 85 subfamiles and 765 genera (Vitt, 1984).

The genus *Funaria* and *Buxbaumia* have been discussed in detail to represent this group.

Buxbaumia

Buxbaumia is an interesting moss, which has small, microscopic gametophyte and large conspicuous dorsiventrally flattened sporophyte commonly called as ‘Bug Moss’. It is generally found in temperate regions. *Buxbaumia himalayensis* has been reported from India (Udar *et al*., 1971).

The gametophyte is highly reduced. The male plant is represented by a single, unistratose perigonial leaf / male bract which encloses a single antheridium with short stalk and spherical antheridial body (Fig. 23: 7,9). Female plant is also highly reduced to have 3-4 small, unistratose perichaetial leaves having 1-2 archegonia (Fig. 23: 8). The sporophyte is well differentiated into foot, seta and capsule. Foot is bulbous and embedded in tuberous tissue. Seta is short and pigmented with rough or papillose surface. The capsule is somewhat ovoid and obliquely oriented with conical operculum, flattened, asymmetrical theca and prominent expanded apophysis (Fig. 23: 5,10,12). The wall of the capsule is multistratose with stomata confined to apophysis. Spore sac is present all around the columella. Trabeculae and air spaces are present in between the capsule wall and spore sac (Fig. 23: 6,13). The peristome is more complexed, double and is formed by 3-6 concentric layers of amphithecial layers. The outer peristomial teeth (exostome) are formed by 1-4 series of slender short teeth while the inner ring of peristome (endostome) is long, thin, membranous forming 16 - (32) plicate cone like structure (Fig. 23: 11,14,15). Both the peristomes are formed by thickened cell walls only, not of entire cell groups as found in the case of Polytrichales and Tetraphidales. Besides, in *B. aphylla* the exostome is missing while in *B. himalayensis* the peristome is present in three layers. Due to their peristome feature, the genus *Buxbaumia* was variously placed earlier:

1. Either separately as Buxbaumiidae in between Bryidae and Polytrichidae (Reimer, 1954).
2. Or in Amphodontei in between the Arthodontei and Archidontei (Fleischer, 1904, 1920, 1923).
3. Or in Bryales within the Bryidae, separated from Polytrichales and Tetrahidales (Vitt, 1984).

Funaria

- *Habitat and Distribution*

  Funaria is a cosmopolitan genus, widely distributed in temperate and tropical regions of the world. It is commonly found growing on moist rocks, soils or on the walls. *Funaria hygrometrica* is a very common species growing extensively in the hills of various parts of the country. It is also called as bonfire/postfire species as it is a pioneer, agent, which first appears in colonization at the burnt sites rich in ash and nutrient contents.

- *Gametophyte*

  The plants are small, erect growing and differentiated into axis and spirally arranged leaves (Fig.24: 1-4). The leaves are small, sparsely arranged at the base while large, crowded at the apex, forming rosette. They are simple, ovate - elongated, broad at base and pointed at apex, with smooth margins and distinct mid rib (Fig.24: 6,7). The rhizoids are present at base of the axis. They are multicellular, oblique septate, brown and form a tangled mass.

- *Axial & leaf anatomy*

The axis shows very simple internal organization. It has an outer single layered epidermis, followed by 3-5 layered cortex with thick walled cells in mature plants enclosing central conducting region with narrow elongated cells (Fig.24: 8,9). In the apical portion of axis, the leaf traces are present which end blindly in the cortex. The leaf has well defined narrow, multistratose mid rib with thin walled narrow cells surrounded by a sheath of thick walled cells. The lateral wings are broad, unistratose with thin walled, elongated, rectangular to rhomboidal cells with numerous discoid chloroplasts. The marginal cells are somewhat projected near the apex giving an appearance of dentate margin (Fig. 24: 6).

- *Apical growth*

The apical growth of the axis takes place by a definite apical cell with three cutting faces giving the radial symmetry to the axis with the three rows of leaves corresponding to three cutting faces.

- *Vegetative reproduction*

Usually plants propogate vegetatively by the separation of branches from parent axis. Besides, multicellular, brown, bud like structure called as gemmae may develop on rhizoidal branches of protonema, which are the means of vegetative propogation.

- *Sexual reproduction*

The plants are monoecious (autoecious) and protandrous. Both the sex organs develop on separate branches of same plant. The antheridia develop first on the main axis. Later on side branches develops which are more vigourous, and bear archegonia. These female shoot are higher and dominant than the male shoot.

- *Antheridia*

The antheridia are present in groups at the apex of shoot (Fig.24: 10). They are surrounded by conspicuous perigonial leaves and are associated with chlorophyllous, multicellular uniseriate, filamentous paraphysis with terminal swollen cell. A mature antheridium has multicellular stalk and elongated cylindrical antheridial body with single layered jacket and numerous androcytes.

- *Archegonia*

The archegonia are also present in groups at the apex on archegonial shoot associated with uniseriate paraphysis (Fig.24: 11). A mature archegonium is stalked and flask shaped with narrow elongated neck and swollen archegonial venter (Fig.24: 12). The jacket in neck portion is unistratose with six vertical rows of cells while it is bistratose in archegonial venter. The axial row has 6-many neck canal cell, a ventral canal cell and an egg. The development is typical moss like through an apical cell as in case of *Pogonatum*.

- *Fertilization*

Fertilization takes place in usual manner. The mature antheridium dehisces when it comes in contact with water, releasing antherozoids. The cover cell, neck canal cells and ventral canal cell of archegonium disintegrate creating the passage. The spermatozoids swim chemotactically and fertilize the egg.

- *Sporophyte*

The sporophyte has a small foot (embedded into gametophytic axis), an elongated, rigid, brown seta and a pear shaped, dark brown coloured, somewhat asymmetrical, curved capsule (Fig.24: 1,4,14). The capsule has three distinct parts: (i) basal apophysis (ii) middle theca and (iii) apical opercular region. (i) The apophysis is distinct with outer most epidermal layer along with stomata followed by spongy chlorophyllous tissue with air spaces. In the center thin walled elongated cells are present which are devoid of chloroplasts. (ii) The theca portion has 2-3 layered capsule wall without stomata followed by large air spaces traversed by elongated trabeculae and then there is spore sac, which has 3 layered wall on outerside and single layered wall on innerside. In the center columella is present which has thin walled parenchymatous cells. (iii) The opercular region is separated from the theca by a distinct constriction where 2-3 layers of radially elongated cells are present forming the rim. Annulus is present just above the rim having 5-6 layers of cells with elongated uppermost cells, which help in the separation of operculum (Fig.24: 15). At the capsule mouth, (edge of the rim) peristome is present, which is arthodontous type having two rings of sixteen peristome teeth. The outer ring (exostome) has 16 large, brown coloured teeth with transverse thickening band. The inner ring also has 16 thin, delicate, pale or colourless teeth.

- *Dehiscence of capsule*

Due to loss of moisture in dry weather, the delicate thin walled annulus acts as weak point and the operculum get removed exposing hygroscopic peristome, which help in spore dispersal.

- *Spore germination*

Under suitable conditions, the exospore (spore coat) rupture at one or two points producing the germ tubes which elongate and develop into branched filamentous protonema. Some erect branches become green due to chloroplasts and called chloronomea while other growing on substratum and develop rhizoids. Buds develop on protonemal filaments, which further develop into new gametophyte by the activity of apical cell.

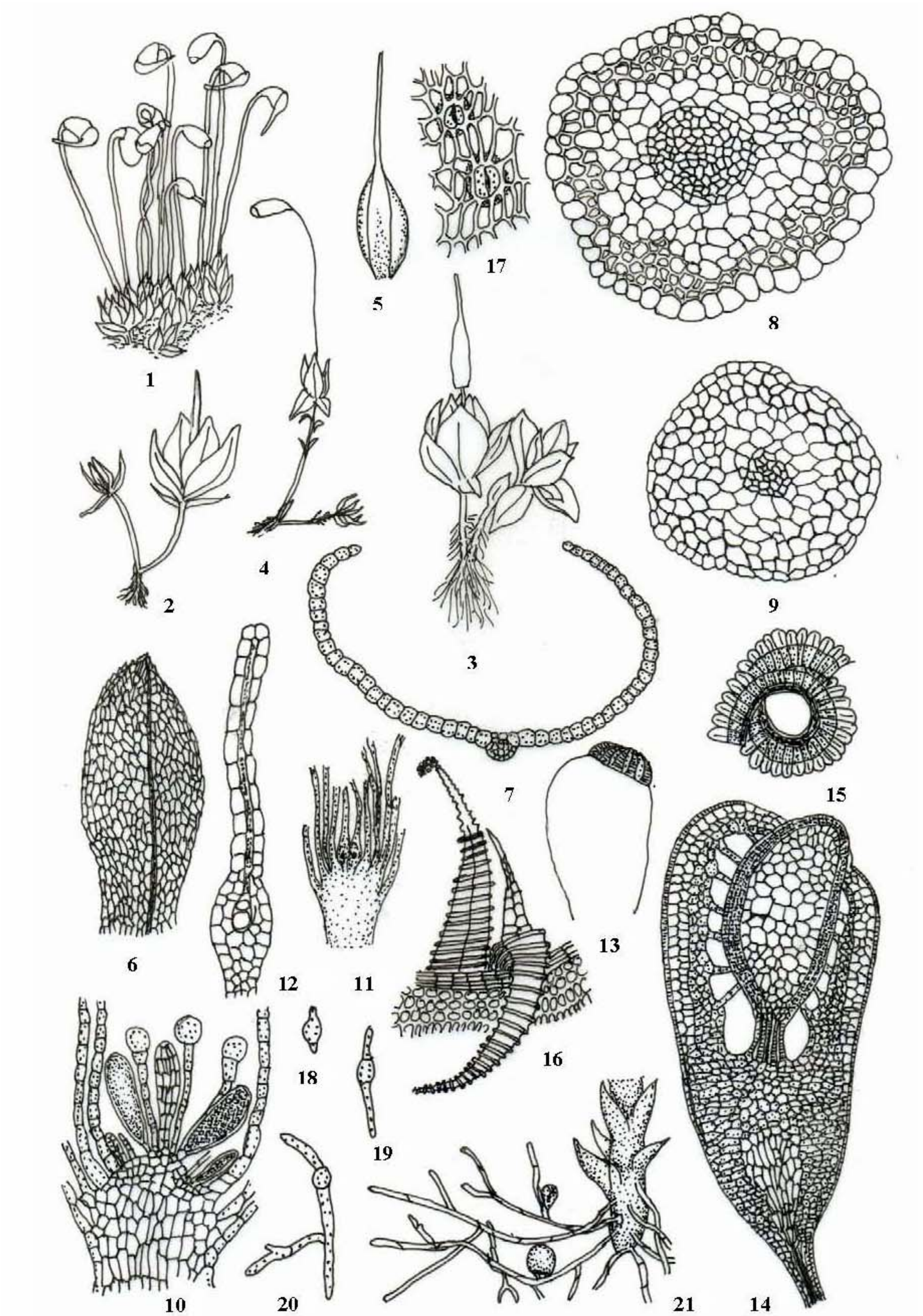

Fig. 24. *Funaria*

1. Habit, 2. A plant with male and female branch, 3. A plant with young developing sporophyte, 4. A plant with mature sporophyte, 5. Calyptra, 6. A leaf, 7. Cross-section of leaf, 8. Cross-section of axis (apical region), 9. Cross-section of axis (basal region), 10. Shoot apex showing antheridia and paraphysis, 11. Shoot apex showing archegonia and paraphysis, 12. An archegonium, 13. Capsule, 14. Longitudinal section of capsule, 15. Annulus, 16. Peristome teeth, 17. Capsule wall showing stomata, 18-21 Stages in spore germination. Figs. 1,2,4-9,13,15,17 (After Udar), Fig. 3 (After Watson), Fig. 10 (After Smith), Figs. 11, 12 (After Sachs), Fig. 14 (After Haberlandt), Fig. 16 (Welch), Figs. 18-21 (After Luerssen).

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