Structure, Reproduction and Affinities of Takakiales and Calobryales.

(Lesson Structure)

4b.0 OBJECTIVE -

This unit deals with the structure, reproduction and affinities of the two different orders Takakiales and Calobryales of Hepaticopsida (Liverworts).

4b.1 TAKAKIALES

4b.1-0 Characteristic features of the order takakiales

(i) The plant body is differentiated into small, creeping pale-yellow, leafless rhizome and erect, green, leafy 1- 1.5 cm tall shoot. These are known as the **Gametophores.**

(ii) Both the rhizome and the leafy shoots are devoid of rhizoids.

(iii) The thick, fleshly, erect, soft-textured gametophore axis bears green leaf-like appendages in a 3 - ranked phyllotaxy. The Leaf - like appendages are small fleshy, terete and isophyllous.

(iv) The leafly appendages are either undivided but more frequently 2- or 3 - 4 fid to the very base. Their leaf segments are usally called the **phyllids.**

(v) The gametophyte bears slime papillae of two types - **non-beaked type & beaked type.** Non - beaked papillae are axillary in position and beaked occurs on the stolons only.

(vi) Asexual reproduction is unknown.

(vii) The gametophytes are heterothallic. The male plant have not been discovered so far.

(viii) The archegonia on the female plants occure singly, occasionally 2 or 3 juxtaposed scattered and not in inflorescences.

(ix) The greenish archegonia are plump with a massive neck which is not very long. It consist of 6 rows of neck cells. The venter is fleshy.

(x) The haploid number of chromosome is n = 4.

Takakiales, order of Hepaticopsida, includes single family Takakiaceae.

Family - TAKAKIACEAE

The family Takakiaceae is represented by a single genus Takakia which includes two species - T. lepidozioides and T. ceratophylla. The former was discovered by Hattori and Inoue (1958) and latter by Grolle (1963)

Takakia -

4b.1- a Distribution and Habitat

T. lepidozioides was first reported from the alpine zone of Japanese Alps and also from Aleutian island and Hyperoceanic portions of British Columbia. *T.*

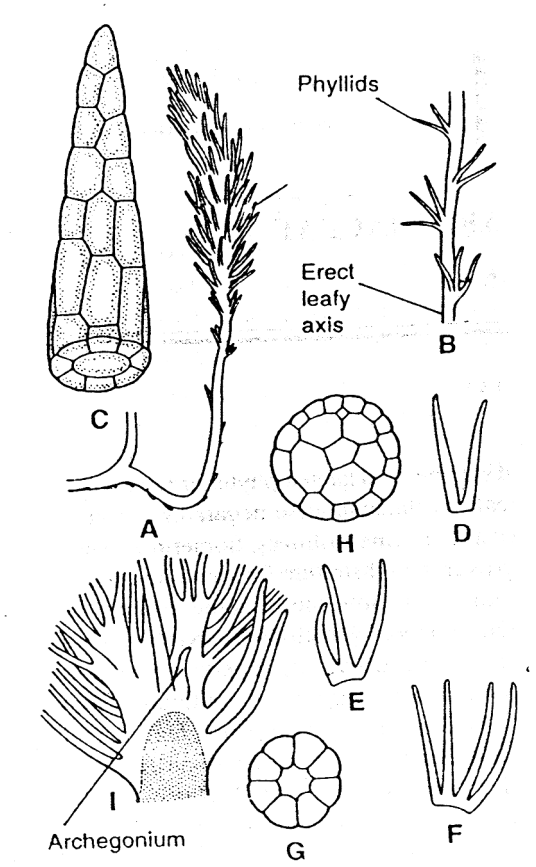

Fig. 4b.1.1 (A-1) Takakia sp. A, Rhizomatous gametophore of T. ceratophylla; B. Portion of gametophore of **T. lepidoziodies** with phyllids; C. a single undivided phyllid; D, E, F, bifid, trifid and quadrified phyllids respectively; G, T.s. Simple Phyllid; H, T.S. Phyllid of Complex construction, I. Archegonal short.

ceratopylla was reported from the pool in Sikkim in Eastern Himalayas (India). Thus both the species grow in cool, moist or wet shady places at higher altitutes. They are hygrophytes.

4B.1.B STRUCTURE :

Morphological Structure of Gametophyte -

The plant body is gametophyte which is differentiated into a cylindrical, branched, creeping, leafless, rhizome-like structure from which arise the aerial, erect, negatively geotropic radially symmetrical leafly shoots, the gametophores about 1 - 1.5 cm. tall. Sometimes a newly-formed branch from the rhizome grows horizontally for a short distance and then turns up giving rise to solitary erect leafly axis. Both the rhizome and the leafly axis are completely devoid of rhizoids. From the base of erect gemetophore (*T. lepidozioides)* may arise one or

more vertically descending leafless branches which grow downward into the substratum. These positively geotropic, leafless axis is fleshy and soft textured The leaf-like appendages borne on the erect gametophore axis are unique in form. They are isophyllous in a spiral manner from the shoot tip which grows by the activity of a 3-sided apical cell. The leaves are arranged in 3 - ranked phylotaxy. Lower down on the gametophore axis they are small and remote but higher up they become larger and continuous. The leaves are, at first, transversely inserted on the axis but with maturity become obliquely displaced. According to Schuster (1967) each leaf is forked right to the base into two three or four segments which often arise at some distance. Each leaf segment is termed as *phyllid.* The terete segments are multistratose, solid and fleshy. Each gradually tapers towards the apex ending in a short blunty and fleshy. Each gradually tapers towards the apex ending in short blunty conical cell.

Anatomy of leaf -

The leaf is 3-5 cells thick except at tip region. They gradually taper towards the apex ending in short bluntly conical cell. The cells are parenchymatous and contain chloroplasts. In a cross section above and near the middle the leaf segment of ***T. lepidozioides*** have only one big medullary cell much larger than the surrounding single-layered cortical cell. In the lower half of the leaf segment the number of medullary or axillary cell row varies from 2 to several (usually 5 rows). The central strand of medullary cells is always surrounded by a single-layered cortex of cells smaller in size.

Stem Anatomy - The transvers section of *Takakia* stem showed that it consists of two zones, outer cortical region surrounding the inner medullary region. The cortical region is 1-2 stratose thick and consists of slightly to strongly thick - walled cortical cells with brownish wall. This region is chlorophyllose. The medullary region is differentiated into a small central core of small-celled tissue constituting an ill - defined or feebly defined vestigeal central strand surrounded by thick-walled somewhat larger celled medulla. The cells of the central strand lost their protoplasmic contents and become empty. They are colourless, elongated and have delicate walls. Electron microscopic study reveals that the walls of these empty cells, especially their end wall possess many small plasmodesmata derived pores. Hebant (1975) reported the occurrence of a specialized central water conducing strand in the gametophytes of *Takakia.*

Slime Papillae - Proskauer (1942) reported the occurrence of slime papillae on the axis of Takakia . These are of two types - (i) Non - Beaked and (ii) Beaked slime Papillae.

(i) Non - Beaked slime Papillae - These occurs singly on the erect shoots in or near the leaf axils. The non - beaked slime Papillae in *T. ceratophylla* cornsists of 2-celled short filament. The lower cell functions as the stalk cell. The upper or distal cell is the mucilage secreting cell. The mucilage is secreted through its wall.

(ii) Beaked slime Papillae - These occure both on the leafly and leafless axis in small to large clusters. Each beaked slime papilla in the cluster consists of a slender, flask - shaped distal cell supported on a 2 or more - celled stalk. At maturity the distal, flask - shaped cell become beaked. The beak has an opening or aperture at its tip through which mucilage is secreted (Fig. 4b.1.2).

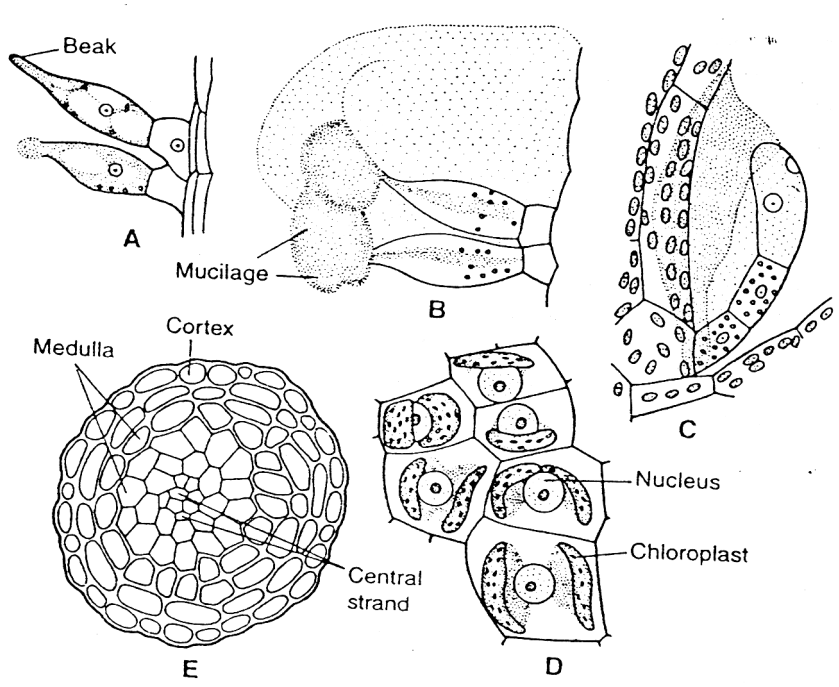

Fig. 4b.1.2 (A-E) Takakia sp. A, Immature beaked open slime papillae; C, stalked "closed" slime papillae; D, cells from the leaf primordia showing chloroplasts & nuclei; E, T.S. aerial stem.

4B.1-C REPRODUCTION

Only archegonial shoots with conspicuous pedastalled archegonia are known in Takakia. The male plants and the saprophytes have so far been found out. The archegonia occur singly or in groups of two to three on the stem apices. Neither

the archegonia have any clear relationship to the insertion of leaves nor do they involve the apical cell in their formation. The archegonium is a flask-shaped structure mounted on a stalk. It is more massive than in the Hepatics and is as large as in the mosses. The jacket of the venter is usually two layered thick. The neck is composed of six vertical rows of cell (Inoue, 1961) and not four as reported by Hattori and Mizutani (1958). The Sporophyte is unknown.

4B. 1-D AFFINITIES

Takakia is an exceedingly primitive genus, discovered almost two decades ago. It has a number of primitive features which are -

(i) The radial organization of the plant axis.

(ii) The isophyllous uniseriate to triseriate phyllids.

(iii) Mucilage hairs both on the axis and the rhizome

(iv) Total lack of rhizoids

(v) The occurrence of water conducting cells.

(vi) The massive and primitive type of archegonial structure.

(vii) The haploid chromosome number which is n = 4.

All these features show that *Takakia* an exceedingly primitivie genus and it is nearest to the ancestral stock of liverworth. Totuno. (1958) Postulated that n = 4 is the original base number of the Hepaticeae. It represent relics of a race that seems to have died out. Mehra (1969) remarked "*Takakia* is a living fossil in the Hepaticeae. The Calobryales and foliose Jungermaniales are off shoots from ancestors like Takakia but at the diploid level."

4B. 2 CALOBRYALES :

4b.2 - 0 Characteristic Features of the order Calobryales

(i) The plant body is differentiated into a basal, branched, creeping, leafless, pale, subterranean rhizome - like structure from which arise the erect gametophore. The rhizomatous plant body are features in which Calobryales differ from all other Hepaticeae except Takakiales.

(ii) The total absence of rhizoids both on the leafy axis and rhizome.

(iii) The leaves are arranged spirally in 3 vertical rows on the erect gametophore axis.

(iv) The leaves may be isophyllous or anisophyllous.

(v) The leaves are variable in form, simple, entire, unistratose but multistratose towards the base only. The flat lamina is undivided and has no midrib.

(vi) The gametophore axis bear slime papillae of non - beaked type.

(vii) Asexual reproduction is unknown.

(viii) Calobryales are sexually dimorphic and hetrothallic.

(ix) The archegonia are large with a neck composed of 4 veritcal rows of neck cells.

(x) The antheridia are ovoid body raised on long stalk composed of several superimposed tiers of 4 cells each.

(xi) The haploid number of chromosomes is n= 9.

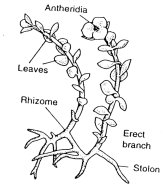

Fig. 4b.2-1a Haplomitrium sp. Male plant.

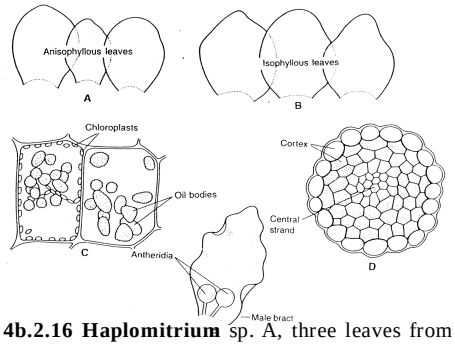

Fig. 4b.2.16 Haplomitrium sp. A, three leaves from a single cycle showing anisophelly; B. three leaves from a single cycle of **H. gibsiae** showing isophyily; C. median leaf cells with oil bodies and chloroplasts. D.t.S. stem **(H. intermedium)**; e. male bract with antheridia.

(xii) The developing sporophyte. is surrounded by a cylindrical green to yellow massive fleshy shoot calyptra. The cassule is elongated and has a unistratose capsule wall except at the tip which is bistratose.

Calobryales has single family Calobryaceae. This family includes two genera *Calobryum & Haplomitrium* which have been united by Schuster (1966) under the genus *Haplomitium.* Generic disjunction has, however, been maintained by Udar (1966).

CALOBRYUM (HAPLOMITRIUM)

4B.2-A DISTRIBUTION & HABITAT

All the species of Haplomitrium(Calobryum) are mesophytes. Some species are ***H.blumii, H. indicum, , H. giganteum. H. adinum, H. intermedium*** *etc.* They occur in India, Malaya, Japan, Philippines, New Zealand and Tropical America etc. The best known species is H. blumii.

4B.2 -B STRUCTURE

Morphological structure of Gametophyte

The plant body is gametophyte which is differentiated into creeping leafless basal, branched rhizome, from which arise the erect leafy shoot with their leaves radially disposed (known as gametophore). The gametophore is bright green or yellowih green in colour mostly 8 - 25mm tall. A newly formed branch may creep over the substratum for a time and then abruptly turns upwards, grows erect and bears the leaves. The branches are dimorphic and exogenous and intercalary in origin. The rhizome and the creeping part of the erect branch complelely lack rhizoids. The absence of rhizoids and rhizomatous gametophyte are the noteworthy features in which *Haplomitrium* (Calobryales) differs from all the Hepaticeae except Takakia. In some species of *Haplomirium (H.minioides)* one or more vertically descending leafless branches arise from the base of the erect leafy shoot, grow vertically downward and penetrate the substratum These are known as stolon or flagella.

The leaves are simple, entire, dorsiventrally flattened, soft textured and without midrib. They are radially disposed and arranged in 3 vertical rows on the erect gametophore. Schuster (1967) reported that the leaves are usually anisophyllous, occasionally isophyllous. Anisophyllous species are ***H blumii. H adinm*** and ***H. giganteum*** etc. and isophyllous species are ***H. gibbsiae, H.mnioides and H.intermedium.*** In anisophyllous species the leaves of one rank (out of three) are smaller in size.

Anatomy of Leaf - The leaves are one-layered thick (unistratose) except for the basal part which is two or four cells in thickness (multistratose). The leaves are composed of uniform parenchymatous cells containing many oil bodies per cell beside chloroplasts (Fig. 4b.2-1b).

Stem anatomy -

The transverse section of stem shows two distinct regions outer green, starch rich cortex, and inner colorless central strand. The outermost layer consists of approximately isodiametric cells with a very thin cuticle and contains more plastids, than deep lying cells. Campbell (1959) reported.

The occurrence of abundant oil drops in the cortical cells of *H. gibbsiae.* Cell organells are abundant. Some peripheral cortical cell grow into short 2-3 celled slime papillae of non beaked type with a clavate apical cell. The papillae secrete mucilage.

The central strand consist of smaller elongated leptodermis cell and is 10-15 cells in diameter. These cells contain no. cell organelles and devoid of cytoplasm resembling the hydroids of mosses. Numerous pores occur between the adjacent conducting cells. A clear continuity in size and shape exists between cortical cells and central strand cells.

Apical Growth - Growth of the stem occurs by a pyramidal apical cell with three cutting faces, one slightly narrower than the other two.

4b.2-c Reproduction: -

Asexual reproduction is unknown in the Calobryales.

Sexual Reprduction - The gametophores are dioecious. Sex organs are antheridia & archegonia produced on the expanded apex of the erect shoots of different plants.

Antheridia -- The antheridia are densely-packed in male receptacle at the apex of the main stem and resemble the gametophore of mosses. Each antheridium is sub -globose in shape and has a very long stalk.

Antheridial development in ***Calobryum blumii*** begins by a transverse division of the antheridial initial into a basal cells embedded in the thallus and an outer cell which Project above the thallus. The outer cell divides transversely into a

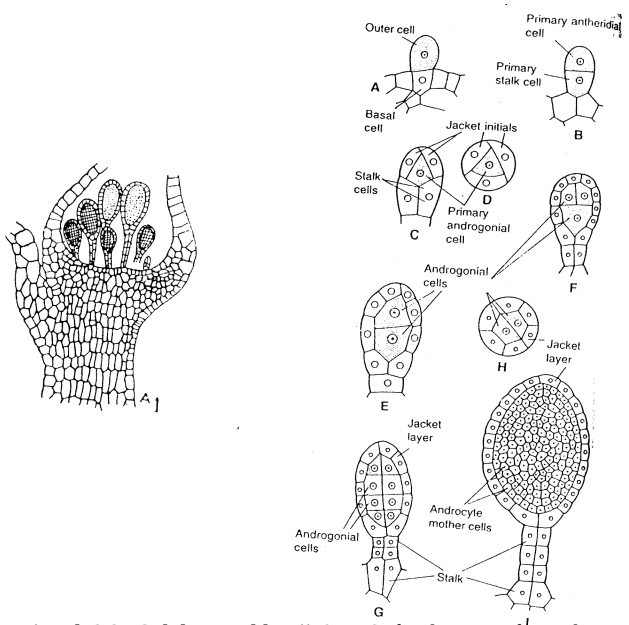

Fig. 4b.2.2: Calobryum blumii A_1 L.S. fertile apex of a male gametophyte, A-I Development of antheridium.

primary antheridial cell developing into the body of the antheridium and a primary stalk cell forming the multicelled stalk of the antheridium. Three successive vertical divisions of the primary antheridial cell result in three jacket initial enclosing a single Primary androgonial cell. The first division of the primary androgonial cell is transverse. The two daughter cells so formed divide transversely and longitudinally and finally become androcyte mother cells which by repeated mitotic divisions develop into antherozoids (Fig. 4b, 2.2).

Archegonia - The arcchegonia are borne singly at the apex of the main shoot and are usually protected by the perichaetial leaves. Female plants of *Calobryum* have the archegonia developing from about half a dozen recently formed segments cut off from the apical cell and finally the apical cell itself develops into an archegonium. The sequence of archegonial development is similar to that in an antheridium. The archegonial intial by three successive vertical divisions result in three jacket initials enclosing a primary axial cell.

The primary axial cell functions directly as central cell and by a transverse divisions form a ventral canal cell and an egg. Vertical division of only one of the three jacket initials result in an archegonial neck composed of only four rows of cell. Thus the neck of an archegonium is very long, twisted vertical row of 16-20 neck canal cells.

Towards maturity the cells of the single-layered venter wall divide periclinally

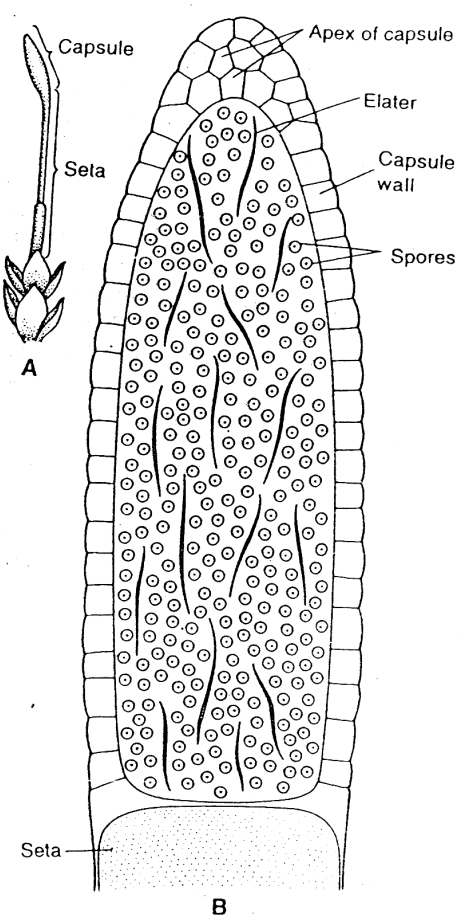

Fig. 4b.2.4: Haplomitrium sp. A. upper part of female gametophore with a terminal mature sporophyte; B.L.S. Capsule showing structure.

resulting 2-3 cells thick Venter wall. There is total lack of any leaf derived protective sheath such as the perianth around the archegonial cluster. Thus archegonia are naked (Fig. 4b.2.3).

Shoot Calyptra : -

Following fertilization, the Venter wall cells start dividing extensively, by periclinal divisions resulting in a cylindrical, fleshy green to yellowing green, brittle massive 15-17 mm long calyptra surrounding the developing sporophyte. In some species the cells near the Venter become meristematic and divide actively resulting in a massive calyptra. It is called 'Shoot Calyptra' . The sterile archegonia are elevated on the shoot calyptra.

Sporophyte :-

Sporophyte is terminal in position and surrounded by the massive shoot calyptra when young. The mature sporophyte is differentiated into the foot, the

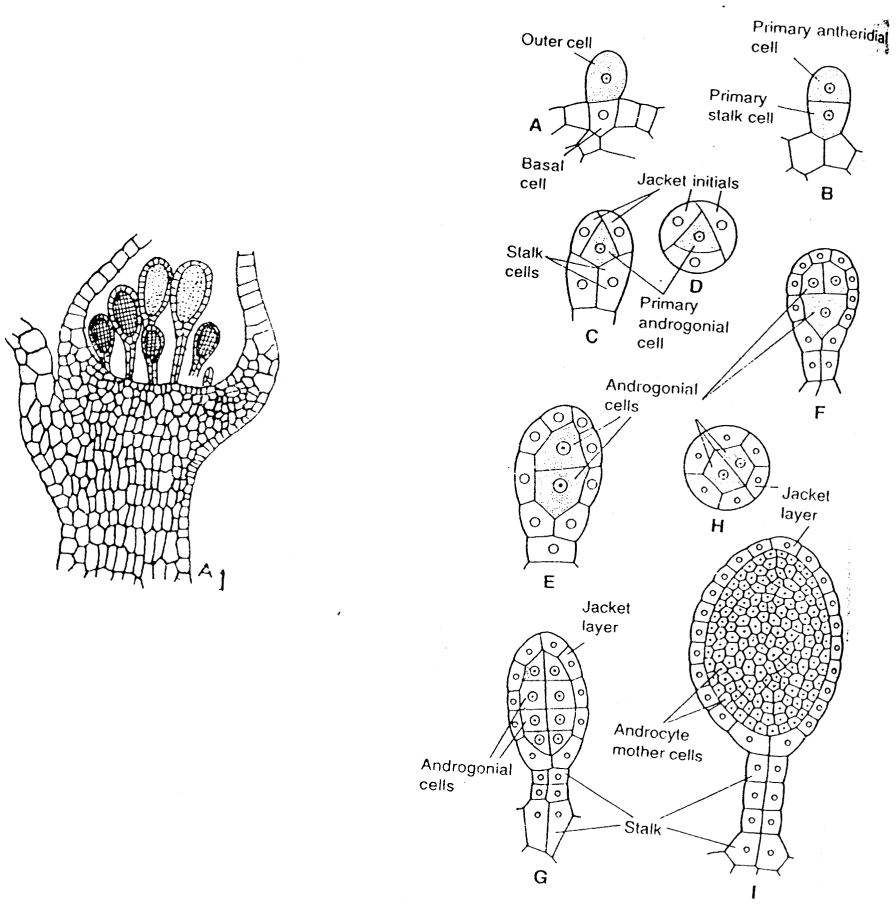

Fig. 4b.2.2: Calobryum blumii A_1 L.S. fertile apex of a male gametophyte, A-I Development of antheridium.

seta and the capsule. The seta of ***Haplomitrium*** is 25-30 mm long, massive and solid. The capsule is cylindrical 4 to 5 mm long deep-brown. The foot is acuminate in form. The capsule wall is unistratose except the tip region which is bi or tri seriate. Inside the capsule wall, the sporogenous tissue is differentiated into spores and elaters. The spores are 18- 30*u* and elaters 6- 10 *u* in diameter. The spore-elater ratio is 3 :1. Elaters are long, very slender, gradually tapered to their tips. They are bispiral. The spore wall has numerous, short blunt papillae.

The mature capsule dehisces by a single, longitudinal slit along one side in ***H. beumii*** or by 4 longitudianal slits along 4 discrets lines of dehiscence.

4B.2-D AFFNITIES OF CALOBRYALES

No near relatives of Calobryales were known before 1958. Discovery of Thakakia by Proskaur (1962) and Schuster (1966- 67) revealed that the two genera Haplomitrium and Takakia share many common significant features between

them such as rhizomatous, gametophyte, erect flesy axes of gametophore radially organized leafy shoot, absence of rhizoids, the possession of mucilage hairs and a massive undoubtedly primitive type of archegonial structure. These common features indicate close relationship between Calobryales & Takakiales.

The Calobryales resemble the fossil bryophyte Naiadita and some acrocarpous mosses and are considered to be the most primitive bryophytes of Hepaticopsida by the proponents of Regressive theory.

The Calobryales show closer relationship to the Metzgeriales in having in (i) Anacrogynous condition of archegonia, (ii) almost no resistance to drought (iii) scattered arrangement of antheridia (iv) lack of Collenchyma (v) Occasional copios secretion of mucilage (vi) elaters are long, narrow, tapering to wards both ends.

The spore in Calobryales is globose and unicellular with poorly ornamented exine. On the basis of spore morphology of a vast number of hepatics, Mehra & Sood (1968) came to the conclusion that the Calobryales and anacrogynous Jungermaniales are the least specialized orders of the Hepaticopsida possessing the most primitive type of spore.

Calobryales show some superficial resemblance to the primitive Jungermanniales (Herbertia and Anthelia) such as erect habit, leafy organization, basically triradiate arrangement and anisophyllous condition.

Recently Duckett *et al*. (1982) who studied spermatozoid morphology found that the spermatozoids of Haplomitrium have features such as accessory band of microtubules in common with homosporous forms. These workers thus sugget that the Calobryales is an extremely divergent group of Bryophytes that represent the closest living organism linking Bryophytes to Tracheophytes.

Smith, a supporter of 'Progressive Theory' is of the view that Calobryales developed in the same line as the Jungermanniales but they departed earlier so that they retain the least specialized type of sex organs among the hepatics and a simple sporophyte coupled with the most elaborate type of gametophyte. Thus they exhibit a strange combination of advanced and primitive characters.-

4B.3 QUESTIONS FOR EXERCISE (Long type Answer)

1. Describe Calobryales in detail and mention its affinities.
2. Explain the structure & reproduction of Takakiales in detail.

Short Type Answer

Write Short notes on ——

1. Affinities of Takakiales
2. Sex organs of Takakiales
3. Salient features of Takakiales
4. Gametophyte of Calobryum
5. Sexualreproduction in Calobryales
6. Capsule of Calobryum

4b.4 SUGGESTED READINGS

1. Bryophyte by B.R. Vashishta, A.K.Sinha, Adarsh Kumar

   (S. Chand & Company Ltd.)

2. Bryophytes: Morphology, Growth and differentiation by Dr. (Mrs.) Prempuri (ATMA RAM & SONS)

3. An Introduction to Embryophyta : Vol.-1, Bryophyta by N.S. Parihar (Central Book Depot).