**Anthoceros L.**

**Habitat and distribution**

The name ‘anthoceros’ means ‘flower horn’, and refers to the characteristic horn-shaped sporophytes that all hornworts produce. The genus *Anthoceros* was first established by Micheli as early as 1729 and later was adopted by Linnaeus (1753).

**Systematic position**

- **Division**: Bryophyta
- **Class**: Anthocerotopsida
- **Order**: Anthocerotales
- **Family**: Anthocerotaceae
- **Genus**: *Anthoceros*

**Habitat and distribution**

*Anthoceros* is a genus of hornworts in the family Anthocerotaceae. With about 250 species, it is widely distributed in the tropical and temperate regions of the world; over 25 species having been recorded from India (Rashid, 2000). Among Indian species, *A. crispulus*, *A. erectus* and *A. bharadwajii* are commonly found in all the major bryogeographical regions of the country, viz. Eastern Himalaya, Western Himalaya and South India. *A. angustus* and *A. punctatus* are distributed in Eastern and Western Himalaya. *A. alpinus*
is confined to Western Himalaya, *A. pandei* to Eastern Himalaya, while *A. subtilis* and *A. macrosorus* are confined to South India. *A. mangalorreus* is extensively distributed in hills of South India and extends up to Western Ghats. *A. khandalensis* abounds Khandala region of Deccan plateau. *A. himalayensis*, *A. erectus* and *A. chambensis* usually occur at an altitude ranging from 5,000 to 8,000 ft. They have been reported by Kashyap (1915, 1916) from Mussoorie, Kulu Manali, outer Himalaya and Kumaon, Chamba Valley, Punjab, Madras and Travancore. *A. erectus* is also found growing in plains of Bihar, U.P. and M.P. Mehra and Handoo (1953) collected *A. himalayensis* and *A. erectus* from Shimla, Nainital and Dalhousie also. *A. westii* has been reported from Rangoon, *A. parkinsonii* from Burma and *A. koshii* from Travancore. Sane (1942) reported *A. dexitti* and *A. sahyadresis* in Pune and the neighbouring hills. Pande and Bhardwaj (1952) described *A. crispulus* from Lucknow. *A. assamicus* has been described from Assam and *A. shivanandani* from Kerela (Kachroo, 1954).

All the species of *Anthoceros* grow on moist clayey soil and on wet rocks in very moist, shady places, usually in dense patches. Sides of moist slopes along
the hill side roads, ditches, along claybanks of streams and moist hollows among rocks are the usual habitats where they are commonly found. A few species of *Anthoceros* occur on decaying wood (Cavers, 1911).

**Thallus morphology**

The plant, as in other bryophytes, is the gametophyte. It is a small, yellowish green or dark-green, dorsiventrally-flattened and variously lobbed thallus, which is spongy in texture, and lacks a definite midrib (Fig. 1). Sometimes the plants form distinct rosettes (usually less than 2cm in diameter) as in *Anthoceros crispulus* (Fig. 2).

In *A. erectus*, the plants are erect, cylindrical in basal portion which become broad (fan out) in apical portion (Fig. 3); while in some other species they form a large patch of overlapping thalli, which are long and...
pinnately branched. The thallus in some species of *Anthoceros* is semi-orbicular in outline and variously lobed. The lobes are thick and fleshy, generally more or less divided to form irregularly-lobed and folded margins, with divided margins overlapping (Fig. 4).

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*), with one-cell thick and several-cells wide leaf like lamellae (Bhardwaj, 1950). The margins of the thallus are generally incised or lobed (Fig. 5).

![Fig. 5. *Anthoceros* thallus with incised lobes](image1)
![Fig. 6. *Anthoceros* thallus bearing gemma](image2)
Thallus is thick in the center and gradually becomes thin towards the margin. Midrib is totally lacking. The upper surface of the thallus is smooth in some species (*A. laevis*), but rough in others (*A. fusiformis*). In *A. angustus* (*A. gemmulosus*), the thallus has number of marginal sub-sessile, sub-spherical spongy bodies called as gemmae (Fig. 6), which help in vegetative reproduction. The ventral surface lacks scales, tuberculate rhizoids and mucilage hairs. However, it bears numerous, unicellular, smooth-walled rhizoids. These anchor the prostrate thallus to the substratum. On the under surface of thallus are seen small dark bluish green spots; which are colonies of cyanobacterium *Nostoc*.

During autumn, the *Anthoceros* thallus bears long, cylindrical, delicate structures. These are sporangia, which arise from the dorsal surface of the thallus. Each sporangium has a tubular sheath around its base called involucre. Some species of *Anthoceros* (as *A. erectus* and *A. punctatus* var. *cavernosus*) are annuals while others (*A. fusiformis*, *A. himalayensis* and *A. laevis*) are perennial.
Thallus anatomy

The thallus of *Anthoceros* is several layers thick, without tissue differentiation. The dorsal surface of the thallus is composed of uniform, thin-walled parenchymatous cells, which are many cells deep in the middle (from 6-8 cells in *A. laevis*, 8-10 cells in *A. punctatus*, 30-40 cells deep in *A. crispulus*). The ventral portion of the thallus has intercellular cavities which remain filled with mucilage (Fig. 7). In addition to the mucilage cavities, some species, such as *A. punctatus* develop schizogenous mucilage-filled tubular cavities behind the growing point which run longitudinally through the gametophyte. Occasionally these cavities may contain gaseous contents, especially in older parts of the thallus.

![Fig. 7. T.S. of *Anthoceros* thallus containing mucilage cavities and chloroplasts with a pyrenoid located in the centre.](image)
Unlike other land plants, some species of *Anthoceros* have variable number of chloroplasts with central minute, distinct pyrenoid bodies (Fig. 8), especially in the deeper cells of the thallus (Proskauer, 1951). The presence of chloroplasts containing pyrenoids is characteristic feature of algae, but is unknown in Archegoniatae; the only exception being *Anthoceros, Isoetes* and *Selaginella*. The pyrenoids of *Anthoceros* are not homologous with those of green algae, as they consist of an aggregated mass of 25 to 300-disc to spindle-shaped bodies, each of which may be converted into rudimentary starch grain without altering its shape or position. 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.

**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), it is somewhat difficult to determine positively whether there is a single cell or a group of apical initials. Leitgeb (1879) reported that the apical growth takes place by a group of marginal apical cells which are meristematic. Mehra and Handoo (1953) observed that growth is initiated by a group of apical cells which occupy a shallow depression at the anterior end of the thallus in *A. erectus* and *A. himalayensis*. 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 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.

**Branching of the Thallus**: The apical cell(s) undergoes repeated vertical divisions to form a transverse row of cells, and a cell near each end of the row starts functioning as an apical cell. With continued growth, the two growing points separate farther and farther from each other. Successive dichotomous
branching result in a compact rosette like thallus. In *A. hallii*, one arm of dichotomy divides more actively than the other, resulting in a long narrow, pinnately branched thallus.

**Mucilage chambers:** The mucilage chambers (Fig. 7) present in the thallus are mainly schizogenous cavities, which appear first as 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.

**Reproduction**

*Anthoceros* reproduces by vegetative and sexual means.

1. **Vegetative reproduction:** Vegetatively the thallus of *Anthoceros* propagates by following methods:
   a) **Fragmentation:** Progressive death and decay of the older parts, and growth of the apical region of a thallus into new plants, is a common method of reproduction in *Anthoceros*, though to a less extent, than that of liverworts.
b) Gemmae: Some authors have reported the formation of gemmae on short stalks on the upper surface and along the margin of the thallus in *A. glandulosus*, *A. formosae* and *A. propaguliferus*. The detached gemma grows into a new thallus. In some other species like *A. angustus* (*A. gemmulosus*) definite spongy bodies develop on the thallus margins, which help in vegetative reproduction.

c) Tubers: In some species, during unfavourable conditions as prolonged drought, tubers are produced which have outer few corky layers to protect the inner tissue with reserve food. The sterile thalli of *A. himalayensis* usually bear stalked tubers (Fig. 9a); they are developed at the apex, along the margin and on the ventral surface of the thallus. The stalks may be long and cylindrical (Fig. 9b). Occasionally the fertile parts of this species also bear sessile and borne ventrally or margin of the thallus (Fig. 9c). Tuber formation has also been reported in other species such as *A. tuberosus*, *A. pearsosi* and *A. hallii* (Fig. 9c). They are developed on the margin of the thallus.
d) **Persistent Growing Apices:** Campbell (1918) reported that the two perennial Californian species, *A. pearsoni* and *A. fusiformis* grow in regions with dry summer. With the approach of summer, these plants dry up except the growing point along with adjacent tissue. The apices persist through the long summer drought and resume growth with the return of conditions favourable for growth.

e) **Apospory:** Lang (1901) reported that *Anthoceros* thallus may arise from the unspecialised cells of the various parts of the sporogonium, particularly the intercalary meristematic zone, sub-epidermal and sporogenous regions of the capsule. In this way, the life cycle is shortened by cutting the spore stage. The thallus (gametophyte) is produced directly from the vegetative cells of the sporogonium. This phenomenon is called apospory.

2. **Sexual reproduction:**
*Anthoceros* shows both the monoecious as well as dioecious sexuality. The former are usually protandrous. Examples of monoecious species are *A. fusiformis*, *A. crispulus*, *A. gollani*, *A. longii*, and *A. punctatus*; while those of dioecious species are *A. angustus*, *A. chambensis*, *A. pearsoni*, *A. halii*, *A. laevis*, *A. dixitianus*, *A. khandalensis* and *A. erectus*. *A. himalayensis* was described as dioecious by Kashyap (1915, 1916), but Mehra and Handoo (1953) reported it as monoecious. In dioecious species, slight sexual dimorphism has been observed in mature gametophytes, the female plants having broader fertile lobes than the male ones. The development of sex organs in *Anthoceros* depends upon photoperiod.

**a) Antheridia:**

(i) **Position:** The antheridia of *Anthoceros* are unique in being normally endogenous. They occur singly or in groups on the upper surface of the thallus within closed cavities called the antheridial chambers. Each antheridial cavity is roofed over by thallus (gametophyte) tissue two cell layers in thickness. The ripe antheridia are bright orange.

(ii) **Structure:** A mature antheridium has multicellular stalk with four rows of Fig. 10. A mature antheridium of *Anthoceros*
cells and a club shaped, clavate or cylindrical, orange coloured antheridial body (Fig. 10). It is raised on a multicellular, short or long, slender stalk. The latter usually consists of four vertical rows of cells. In A. laevis it is thicker. The body of the antheridium, as in the liverworts, consists of a jacket layer or an antheridial wall enclosing a mass of androcytes. Each androcyte forms a single sperm. The jacket is usually unistratose and the cells are arranged in four tiers.

Antheridia are generally present in groups enclosed in a chamber, which forms discrete dorsal areas on the thallus (Fig. 11). These are androecia, which

![Diagram](image-url)

Fig. 11. L.S through the antheridial chamber of Anthoceros
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 appear as scooped areas as in case of *A. erectus*. Inside the androecial chamber antheridia are present in variable numbers at different stages of development. The number may vary upto 30 in *A. angustus*, 22 in *A. erectus* and 7 in *A. crispulus*.

(iii) **Dehiscence**: At the time of maturity, the roof of the antheridial chamber bursts open irregularly. The antheridia now lie in cup-shaped depressions or antheridial ‘craters’ with their orange-coloured contents obvious. The antheridia thus exposed dehisce following absorption of water. This leads to rupture at the distal end of the swollen antheridium. An aperture is thus formed at the distal end of the antheridium. Through it oozes out the matrix containing the sperm vesicles. Finally the sperm vesicles are discharged in the water that caused the rupture by dissolution of the walls of the sperm vesicles.
Proskauer (1948) and Duckett (1973) found that in *A. laevis* following distal rupture, the jacket cells hardly separate and the sperms are thus simply squeezed out.

(iv) **The antherozoid:** The liberated antherozoid is a tiny, biflagellate structure (Fig. 12). The two flagella are equal and almost of the same length as the body (Bagchee, 1924). They are inserted at the slightly broader, anterior end of the slender body which is slightly curved. The unused portion of the cytoplasm of the androcyte remains attached for some time to the swollen posterior portion (Proskauer, 1948). Just behind the front end and beneath the two flagella is an elongated swelling probably a blepharoplast.

**Development of Antheridium**
The antheridia develop endogenously (Fig. 13). They lie in roofed chambers, sometimes singly and sometimes in groups. They are traceable to a single surface cell, which lies close to the growing apex on the upper
surface of the thallus. It has denser cytoplasm and a conspicuous nucleus. It divides periclinal into an inner segment and an outer segment. The former functions as an antheridial initial and develops into an antheridium or an antheridial cluster. The outer segment is the roof initial, which forms the two-layered roof of the antheridial chamber. The antheridial initial before segmentation nearly rounds off. It then either directly develops into a single antheridium (A. pearsoni) or it may divide vertically into two, four or sometimes into more daughter cells (A. erectus). Each of the latter functions as an antheridial initial, so that there is a group of two, four, or more antheridia in the chamber.

**b) Archegonia**
(i) **Position:** Archegonia are present completely embedded in the thallus tissue in acropetal manner. They lie close to the growing point in regular rows and are sunk deep in the fleshy thallus on its upper surface. In the monoecious species the archegonia appear later, on the same thallus which produced antheridia.

(ii) **Structure:** A mature archegonium has 2-4 cover cells, 4-6 neck canal cells, a ventral canal cell and an egg. There is no sterile jacket layer except the distal rosette of cover cells forming its tip. Generally, it is difficult to locate the archegonium in the thallus from external surface, but the presence of distinct broad mucilage mound clearly indicates the presence of archegonium at the site.

**Development of Archegonium**

The archegonia develop from dorsal segment of the apical cell (Fig. 14). The archegonial initial cell becomes evident due to its dense cytoplasmic contents as compared to the adjacent cells.
According to Mehra and Handoo, the archegonium initial directly functions as the primary archegonial cell. It does not project above the general surface of the thallus, nor does it undergo the usual horizontal division. The absence of this division accounts for the sunken nature of the archegonium and its histological continuation with the adjacent cells of the thallus tissue.

The primary archegonial cell divides by three vertical walls, which intersect each other forming outer three peripheral cells enclosing inner axial cell. The axial cell divides transversely into (i) outer and (ii) inner cells. The outer cell further divides transversely forming primary cover cell towards outer side and primary neck canal cell towards inner side. The primary cover cell divides once or twice forming 2-4 cover cells,
while the primary neck canal cell divides transversely to produce 4-6 neck canal cells. The inner cell is the primary ventral cell, which also divides transversely forming ventral canal cell and egg.

**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. This mucilagenous mass remains in continuation with the mucilage mound present on the thallus surface at the apex of archegonium. The biflagellate spermatozoids released from mature antheridium get trapped in this mucilage mound and reach to the egg through neck where the syngamy takes place. The zygote formed as a result of syngamy swells to fill the venter cavity completely. Thereafter the zygote secretes a wall around it. A number of zygotes are formed on a single thallus.

**Sporophyte**

The zygote rapidly grows by cell division and differentiation into an elongated, spindle-shaped structure with a bulbous base called sporogonium or the sporophyte (Fig. 15). The sporophytes usually,
grow in clusters from the upper surface of the thallus, each surrounded at its base by tubular involucres. The mature sporophyte consists of foot and cylindrical capsule (Fig. 16). Seta is totally lacking. In its place, in between the foot and capsule, meristematic zone is present which continuously adds to the capsule tissue.

(i) **Foot**: 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, which often grow out into short, tubular, rhizoid like outgrowths. The latter serve to increase the absorptive surface of the foot and penetrate the tissue of the thallus. The

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Fig. 15. *Anthoceros* sporophytes

Fig. 16. *Anthoceros* sporophytes
foot of *Anthoceros* sporogonium is thus specialised to function as a haustorium. It absorbs food and water from the parent thallus for the sporophyte. The region of contact between the foot and the thallus tissue is well marked in many species. It is called the placenta. The cells on the gametophytic side of the placenta are “transfer cells”. These cells develop long thread-like ingrowths which branch and the branches anastomose to form wall labyrinths. The plasma membrane in these cells follows the contours of the wall and the cell cytoplasm penetrates between the individual ingrowths or into the interstices of the labyrinth. The plasma membrane in the transfer cells is thus greatly increased. The inner cells of foot are parenchymatous, vacuolated and are not regularly arranged.

(ii) **Capsule**: The capsule is elongated, cylindrical, smooth, slender and erect. It is nearly of uniform thickness throughout its length except towards the apex where it slightly tapers. Usually it is 2 to 3cm or in some species up to 15cm long. It is light green at first but turns brown towards maturity. Potentially the sporogonium (capsule) of *Anthoceros* is capable of unlimited growth in length because of the
presence of meristematic zone at the junction of the foot and the capsule. The apex of capsule represents its oldest part. The maturation of spores in the capsule is from the apex downwards.

Internally the capsule shows great elaboration and complexity of structure (Fig. 17a,b). In the centre of the capsule is a slender solid core of sterile tissue called columella. The cells constituting it are narrow, elongated with somewhat uniformly thickened walls. They are arranged in sixteen vertical rows. Often the rows may increase up to 36 or 49 as observed in A. angustus. In the young capsule, however, the columella consists of four vertical rows of cells only. It is endothelial in origin. The columella extends from the base right through the capsule and ends a little behind its distal end. The chief function of columella is to give support to the long, delicate capsule. To some extent it helps in the dispersal of
spore. Some writers look upon it as a primitive type of vascular cylinder.

Around the columella is a double layer of elongate but domed sporogenous tissue. It is in the form of a cylinder between the columella and the capsule wall. Sometimes it is one cell layer thick throughout. It is differentiated from the inner layer of the amphithecium. It extends over the top of the columella like a dome - a feature in sharp contrast to the liverworts. In this respect Anthoceros sporophyte resembles Sphagnum moss. The sporogenous tissue originates in the meristematic zone where it is single layered and is called the archesporium. Higher up it becomes a two-layered sporogenous tissue (A. himalayensis), rarely, 3 or 4 cells in thickness. In A. erectus the archesporiurn remains single-layered throughout. The archesporial cells have denser cytoplasm. In contrast to the liverworts, all parts of the Anthoceros capsule do not mature simultaneously. Thus at successive higher levels spore mother cells, spore tetrads and meiospores are formed. 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. Among the spore tetrads and mature spores are found the pseudoelaters. They form chains of one to four elongated thin or thick walled sterile cells of irregular shape. The pseudoelaters are smooth-walled and are nutritive in function. They lack spiral thickenings and are pluricellular, sometimes unicellular.

External to the fertile zone is the capsule wall. It is several layers (usually 4 to 6) of cells in thickness. The outermost layer of wall is the epidermis. It consists of narrow, vertically elongated cells with their outer walls cutinized. Here and there the epidermal layer is punctured by stomata similar to those of the higher plants. Each stoma consists of a pore surrounded by two guard cells. The cells of the capsule wall within the epidermis are chlorenchymatous. They have intercellular spaces between them. Each cell contains double the number of chloroplasts characteristic of the gametophytic tissue. As a rule there are usually two large chloroplasts per cell. They are similar to those of the thallus. The capsule wall is thus actively photosynthetic in function.
(iii) **Intermediate or intercalary zone**: Due to its position in between the foot and seta, this meristematic zone is often regarded as reduced seta. However, it is entirely different from seta. The meristem constantly adds new cells to the capsule at its base. They become progressively differentiated into columella, archesporium and capsule wall. The presence of a basal intercalary meristem enables the capsule to grow for a long period and form spores.

**Distinctive features of Anthoceros sporophyte**: (i) continued growth from the basal intercalary meristem located between the foot and the capsule; (ii) elaboration of internal tissue into a central columella; (iii) great reduction of fertile (sporogenous) tissue; (iv) archesporium amphithecial in origin and extending like a dome over the top of the columella; (v) green capsule wall several cell layers thick with cutinized epidermis containing stomata; (vi) presence of simple or branched pseudo-elaters intermixed with spores.

**Development of sporophyte**

After syngamy, the archegonial venter. Usually, fertilized egg increases in size filling the entire case of Anthoceros.
**crispulus** the first division is form capsule. In case of *A. transverse* (Fig. 18). *The crispulus*, second division takes place at right angle to the first division forming 4-celled embryo, in which the cells are arranged in 2-tiers. Then it divides vertically forming 8-celled-octant embryo. 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 both the tiers divide transversely forming 4-tiered and 16-celled embryo in which lower two tiers form the foot and the upper two tiers develop into the capsule. The four cells of the uppermost tier which are destined to form the capsule, divide by periclinal walls. This separates a central group of four cells from the surrounding peripheral ones. The former constitute the endothecium and the latter amphithecium. From the

Fig. 18. Development of *Anthoceros* sporophyte: A-F: early stages in the development of embryo; G-I: stages in differentiation; J: Young sporophyte.
entire endothecium originates the sterile columella. The corresponding tissue in the liverworts forms the archesporium. The archesporium in *Anthoceros* is formed from the inner cells resulting from periclinal division of the amphithecium cells. The outer cells of the-series function as jacket or wall initials. The jacket or wall initials undergo repeated divisions to form the capsule wall. The outermost layer of the capsule wall is epidermis. They, as a rule, have two large chloroplasts per cell, sometimes one, rarely as many as four. This photosynthetic tissue communicates with the exterior through the stomata.

The single-layered archesporium is parallel to the elongated axis of the capsule and ‘is dome-shaped. It over-arches the rounded apex of the columella, and extends nearly to its base. In some species the archesporium remains single layered throughout (*A. erectus*) and functions as the primary sporogenous layer. In other species it becomes two-layered above the base of the capsule (*A. himalayensis*). In still others it becomes 2-4 cell layers thick by periclinal divisions and forms the sporogenous tissue. The sporogenous tissue differentiates into two kinds of sister cells namely, fertile cells and sterile cells. The
former give rise to spore mother cells and the latter to pseudoelater mother cells. These two kinds of cells may arise in regularly alternating layers or bands.

(i) **Spore mother cells**: These are large cells oval to spherical in form. Each cell contains granular, denser cytoplasm, a distinct nucleus and a chloroplast. The young spore mother cells increase in size, separate from each other and become spherical in form. Finally each of these undergoes meiosis to form the haploid spores or meiospores. This process is called sporogenesis.

*Sporogenesis*: Prior to meiosis, the single chloroplast in each spore mother cell divides into four chloroplasts. They separate and move to the periphery of the spore mother cell and become spaced equidistantly from each other. The final position of 4 daughter chloroplasts in the spore mother cell indicates the location of the poles of the meiotic spindles in it. The diploid nucleus at this stage undergoes meiosis. The resultant 4 haploid nuclei move to points already occupied by the four chloroplasts. At this stage cell walls are laid simultaneously between the four haploid nuclei dividing the spore mother cell into four cells arranged
tetrahedrally. These are the young spores. As the spores in the young spore tetrad ripen, their walls thicken. The spore coat in the mature spores is irregularly thickened. It is yellow in colour in some species and black with small tubercles in others.

(ii) **Pseudoelater mother cells:** The pseudoelater mother cells are slender, sterile cells with smaller nuclei. These increase in length but do not divide. Finally they become united to form a sort of a network. In their interstices lie the spore mother cells. Towards maturity the network breaks into simple or branched chains of 3 or 4 cells. These are the pseudoelaters. The latter usually lack the spiral thickenings characteristic of elaters but are hygroscopic.

The apical growth of the capsule ceases with the establishment of the archesporium, columella and the wall regions. Further growth is by the activity of the basal intercalary meristem in the median zone. It continually adds cells at the base of the capsule. They become progressively differentiated into the columella, the archesporium and the capsule wall. Consequently the growth and the dehiscence of the capsule extends over long periods. The sporophyte of *Antheceros*
continues to live as long as the thallus lives. It is a feature in sharp contrast to the short-lived sporophytes of the liverworts.

Early growth of the sporophyte is accompanied by an upward growth of the archegonium and adjoining involucre forms a tubular gametophytic tissue. The sheath at the surrounding sheath is base of the mature sometimes called calyptra, sporogonium but involucre is a more appropriate designation for it. The calyptra is carried as a small cap at the top of the sporogonium and the

Dehiscence of the capsule: The spores ripen basipetally from the top downwards. As they ripen the mature portion of the capsule turns grey, brown or black depending upon the species. It loses water, shrinks and consequently ruptures longitudinally along the preformed lines of dehiscence. The ripe Anthoceros capsule usually dehisces basipetally along two longitudinal slits. The portions of the capsule wall between the slits are commonly called the valves. With further drying the valves become spirally twisted owing
to reversible hygroscopic reaction. This results in spore discharge by allowing the wind to blow away the exposed spores. The spore dispersal is further assisted by drying of the columella and the intermixed pseudoelaters which in spite of the absence of spiral thickenings on their walls execute some hygroscopic movements.

**Spores:** The mature spores are usually tetrahedral in shape and thick-walled. The thick spore wall is differentiated into two coats. The outer exospore is thick, opaque and beset with small spines or tubercles. It varies in colour from dark, brown, black or yellow according to the species. It is black and warted in *A. erectus*. In *A. himalayensis* it is yellow and beset with numerous, blunt papillae. The inner endospore is thin. Within the spore wall is the tiny protoplast. It contains a single nucleus, a colourless plastid, oil and other reserve food materials.

**Spore germination:** According to Campbell (1918) the liberated spores in *A. fusiformis* usually enter upon resting period. Mehra and Kachroo (1962) who studied germination in *A. erectus* and *A. punctatus* reported that obligatory resting period is not necessary before
germination. At the time of germination the spores absorb water and swell up. The exospore separate two cells at its ruptures along the triradite apex. The terminal cell ridge. The endospore divides by a vertical wall. protrudes through the cleft in the form of a tube of varying lengths called germinal tube (Fig. 20). The contents of the endospore migrate into the tube where the single plastid present turns green. Two successive transverse walls are laid at the distal end of the germinal tube. These A similar division takes place in the lower cell. A group of four cells is formed. Vertical walls at right angles to the first divide the four-celled structure into an octant. The four apical octants constitute the growing region of the sporeling. No apical cell with two cutting faces is established. Instead it is carried out by a group of 4 or 5 cells lying in front and constituting the apical meristem. First rhizoid appears as an elongation of any cell of the young thallus. On its ventral surface appears Fig. 20. A. Spore of Anthoceros laevis; B-G, Stages in the germination of spore of A.erectus; H-I, Later stage in the formation of
the first mucilage slit close to the growing point. Development of rhizoids and more mucilage slits then follows. *Nostoc* infection takes place as the growth proceeds.

**Life cycle:**

The life cycle of *Anthoceros* consists of two regularly alternating generations viz., gametophyte generation and sporophyte generation, with meiosis and fertilization as its two critical points.

(i) Gametophyte generation: The organs, which include the antheridia, archegonia, a new stage, bear the sex organs. The spores of spore mother cells are differentiated from the spore mother cells. The spores are spore mother cells and archegonia with 4–6 different mating systems. The spore mother cells, with a haplophase starting with the spore mother cells, form a new thallus, which is connected with the gametophyte thallus. The gametophyte is green and independent throughout its life. The generation, with 1n chromosome number.
(ii) Sporophyte generation: The sporophyte generation starts with the fertilized egg or the zygote (G). It has a diploid number of chromosomes (2n). By active segmentation, the zygote forms an embryo (J). The latter by differentiation of cells and continued growth develop into the alternate vegetative individual called sporogonium or sporophyte (K). It produces meiospores and aids in their efficient dispersal. The free spores are scattered by the air currents, which then develop into new gametophytes.
The two phases or generations constituting the life cycle of *Anthoceros* regularly occur one after the other. The life cycle of this type which is characterised by alternation of generations and sporogenic meiosis is termed diplohaplontic.