

Anthoceros:

Systematic Position of Anthoceros:

Division	:	Bryophyta
Class	:	Anthocerotopsida
Order	:	Anthocerotales
Family	:	Anthocerotaceae
Genus	:	<i>Anthoceros</i>

Distribution and Habitat of Anthoceros:

Anthoceros is represented by about 200 species. All species are terrestrial and cosmopolitan in distribution. The species grow in very moist and shady places like slopes, rocks or sides of the ditches. Some species are found growing on decaying wood (Cavers, 1911). Unlike other bryophytes Anthoceros is usually not well adapted to resist dry conditions.

In India Anthoceros is represented by about 25 species. Out of these three species of Anthoceros viz., *A. himalayensis*, *A. erectus* and *A. chambensis* are commonly found growing in the Western Himalayan region at an altitude of 5000-8000 feet (Kashyap, 1915). These species are also found growing in Mussoorie, Kulu, Manali, Kumaon, Chamba valley, Punjab, Madras and in plains of South India.

Mehra and Handoo (1953) reported *A. himalayensis* and *A. erectus* from Simla, Nainital and Dalhousie. Some other species of Anthoceros and their places of occurrence are—*A. dixitii*, *A. sahyadrensis* (Poona and neighbouring hills), *A. crispulus* (Lucknow), *A. assamicus* (Assam), *A. shvianandani* (Kerala) etc. The species of Anthoceros may be perennial (*A. himalayensis*) or annual (*A. erectus*).

Gametophytic Phase of Anthoceros:

External Features:

The gametophytic plant body is thalloid, dorsiventral, prostrate, dark green in colour with a tendency towards dichotomous branching. Such branching results into an orbicular or semi orbicular rosette like appearance of the thallus.

The thallus is bilobed (*A. himalayensis*, Fig. 1 A) or pinnately branched (*A. hallii*) or spongy with large number of sub-spherical spongy bodies like a gemma (*A. gemmulosus* fig. 1 C) or raised on a thick vertical stalk like structure (*A. erectus*, fig 1. B).

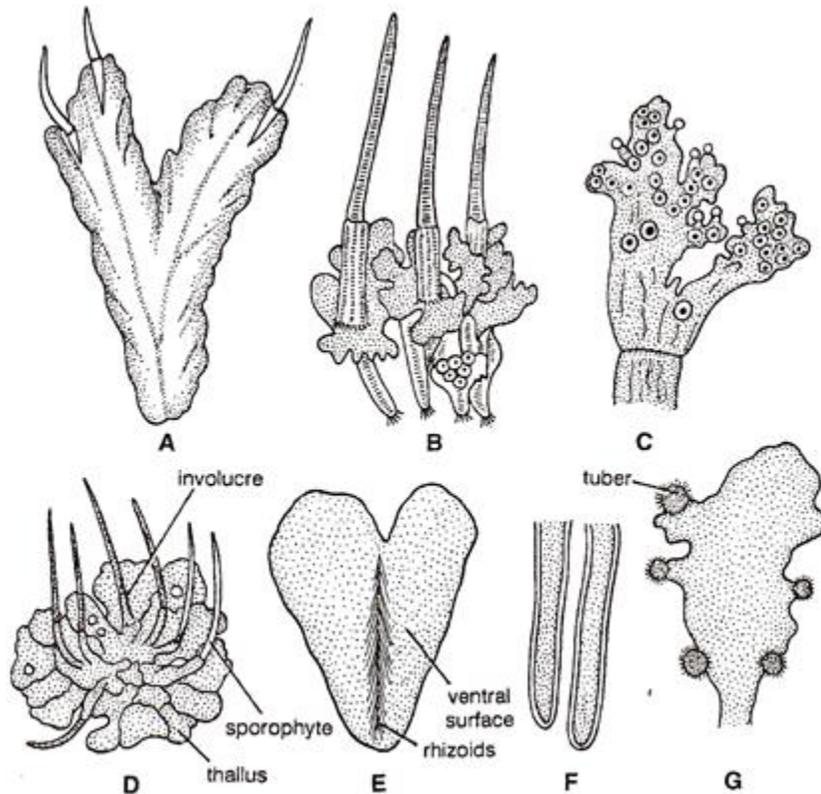


Fig. 1. (A-F). *Anthoceros*. External features (A) *A. himalayensis*, (B) *A. erectus*, (C) *A. gemmulosus*, (D) *A. crispulus* (dorsal surface), (E) Ventral surface, (F) Smooth-walled rhizoids, (G) Thallus with tubers.

Dorsal Surface:

The dorsal surface of the thallus may be smooth (*A. laevis*) or velvety because of the presence of several lobed lamellae (*A. crispulus*) or rough with spines and ridges (*A. fusiformis*). It is shining, thick in the middle and without a distinct mid rib (Fig. 1 D).

Ventral Surface:

The ventral surface bears many unicellular, smooth-walled rhizoids (Fig. 1 E, F). Their main function is to anchor the thallus on the substratum and to absorb water and mineral nutrients from the soil. Tuberculated rhizoids, scales or mucilaginous hairs are absent. Many small, opaque, rounded, thickened dark bluish green spots can be seen on the ventral surface. These are the mucilage cavities filled with *Nostoc* colonies.

In the month of September and October the mature thalli have erect, elongated and cylindrical sporogonia. These are horn like and arise in clusters. Each sporogonium is surrounded by a sheath like structure on its base. It is called involucre (Fig. 1 D).

Internal Structure:

The vertical transverse section (V. T. S.) of the thallus shows a very simple structure. It lacks any zonation (Fig. 2 A, B). It is uniformly composed of thin walled parenchymatous cells. The thickness of the middle region varies in different species.

It is 6-8 cells thick in A. laevis, 8-10 cells thick in A. punctatus and 30-40 cells thick in A. crispulus. The outer most layer is upper epidermis. The epidermal cells are regularly arranged, smaller in size and have large lens shaped chloroplasts. In A. hallii the epidermal layer is not distinguishable.

Each cell of the thallus contains a single large discoid or oval shaped chloroplast. Each chloroplast encloses a single, large, conspicuous body called pyrenoid, a characteristic feature of class Anthocerotopsida (Fig. 2 C, D). 25-300 disc to spindle shaped bodies aggregate to form pyrenoid.

The number of chloroplasts per cell also varies in different species. In A. personi each cell has two chloroplasts and in A. hallii the number may be even four. The nucleus lies in the close vicinity of the chloroplast near the pyrenoid (Fig. 2 D). Sometimes the chloroplast enfolds

The air chambers and air pores are absent in Anthoceros. However, in a few species intercellular cavities are present on the lower surface of the thallus. These cavities are formed due to break down of the cells (schizogenous).

The cavities are filled with mucilage and are called mucilage cavities. These cavities open on the ventral surface through stoma like slits or pores called slime pores (Fig. 2 B). Each slime pore has two guard cells with thin walls (Fig. 2 F). The guard cells are non-functional and do not control the size of the pore.

The pore remains completely open. These pores are formed by the partial separation of two adjacent cells. The slime pores represent the vestigial remnants of a previously existing aerating system. With the maturity of the thallus the mucilage in the cavities dries out.

It results in the formation of air filled cavities. The blue green algae Nostoc invades these air cavities through slime pores and form a colony in these cavities. The

presence of Nostoc colonies in the thallus of Anthoceros is beneficial for the growth of gametophyte is not definitely known.

Pierce (1906) assumed that the thalli without Nostoc grow better than the ones containing the endophytic algae. However, according to Rodgers and Stewart (1977) it is a symbiotic association.

The thallus supplies carbohydrates to the Nostoc and the latter, in turn, adds to nitrate nutrients by fixing atmospheric nitrogen. The lowermost cell layer is lower epidermis. Some cells of the lower epidermis extend to form the smooth-walled rhizoids (Fig. 2 B).

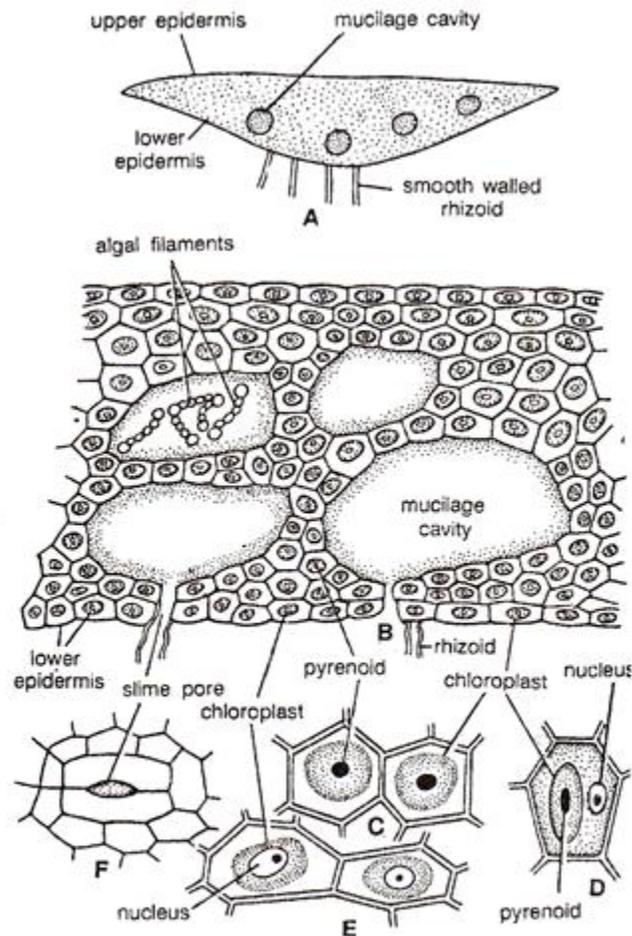


Fig. 2. (A-F). *Anthoceros*. Internal structure of the thallus. (A) Vertical transverse section (V.T.S.) of thallus (diagrammatic), (B) V.T.S. of thallus (a part cellular), (C) Cells showing chloroplast and pyrenoid, (D) cells showing chloroplast, pyrenoid and nucleus, (E) Parenchymatous cells with chloroplast and nucleus, (F) Surface view of slime pore.

Reproduction in Anthoceros:

Anthoceros reproduces by vegetative and sexual methods.

Vegetative Reproduction

It takes place by the following methods:

1. By death and decay of the older portion of the thallus or fragmentation:

The older portion of the thallus starts rotting or disintegrates due to ageing or drought. As it reaches up to the place of dichotomy, the lobes of the thallus get separated. Thus, detached lobes develop into independent plants by apical growth. This method is not so common in Anthoceros as in liverworts.

2. By tubers:

Under unfavorable conditions or prolonged drought, the marginal tissues of the thallus get thickened and form the perennating tubers. (Fig. 1 G). Their position varies in different species. They may develop behind the growing points (*A. laevis*) or along the margins of the thallus (*A. hallii*, *A. pearsoni*). In *A. himalayensis* the tubers are stalked and develop along the margins on the ventral surface of the thallus.

The tubers have outer two to three layers of corky hyaline cells which enclose the tissue containing oil globules, starch grains and aleurone granules. They are capable to pass on the unfavorable conditions. On resumption of favourable conditions tubers produce new thalli.

3. By Gemmae:

In some species of Anthoceros like *A. glandulosus*, *A. propaguliferus*, *A. formosae* many multicellular stalked structures develop along the margins of the dorsal surface of the thallus. These structures are called gemmae. When detached from the parent thallus, each gemma develops into new plant.

4. By persistent growing apices:

Due to prolonged dry summer or towards the end of the growing season, the whole thallus in some species of Anthoceros (*A. pearsoni*, *A. fusiformis*) dries and gets destroyed except the growing point. Later it grows deep into the soil and becomes thick under unfavorable conditions. It develops into new thallus. It is more a method of perennation than multiplication.

5. By apospory:

In Anthoceros, unspecialized cells of the many parts of the sporogonium (for e.g., intercalary meristematic zone, sub epidermal and sporogenous region of the capsule) form the gametophytic thallus. This phenomenon is called apospory (Schwarzenbach, 1926, Lang, 1901). The thalli are diploid but normal in appearance e.g., A. laevis.

Sexual reproduction:

Sexual reproduction is oogamous. Male reproductive bodies are known as antheridia and female as archegonia. Some species of Anthoceros like A. longii, A. gollani, A. fusiformis, A. punctatus, A. crispulus and A. himalayensis are monoecious while some species like A. erectus, A. chambensis, A. hallii, A. pearsoni and A. laevis are dioecious. The monoecious species are protandrous i.e., antheridia mature before archegonia.

Antheridium:

Structure:

A mature antheridium has a stalk and club or pouch like body. The stalk attaches the antheridium to the base of the antheridial chamber. Stalk may be slender and composed of four rows of cells (e.g., A. punctatus, A. erectus, Fig. 3 I) or more massive (e.g., A. laevis Fig. 3 J). A single or a group of two to four or more antheridia are present in the same antheridial chamber (Fig. 3 H). A single layered sterile jacket encloses the mass of androcytes which metamorphosis into antherozoids.

In some species for e.g., A. punctatus and A. erectus jacket layer is formed of four tier of cells. Each tier appears to be composed of elongated rectangular cells (Fig 3 I). In A. laevis and A. himalayensis jacket is composed of many relatively smaller and less regularly arranged cells (Fig. 3 1).

The cells of the upper most tiers are triangular with a narrow end towards the apex (Fig. 3 J). Each cell of the jacket consists plastids. At maturity these plastids change their colour from green to red to bright orange. Young antheridia are, therefore, green and mature one turn bright orange or reddish.

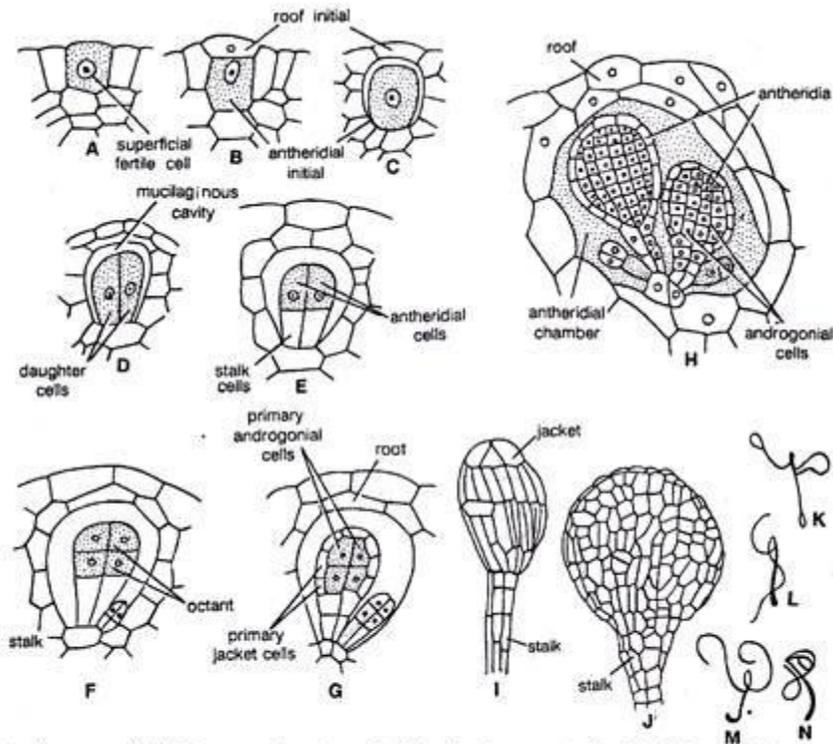


Fig. 3. (A-N) *Anthoceros*. (A-H) Successive stages in the development of antheridium, (I) Mature antheridium of *A. punctatus* (J) Mature antheridium of *A. laevis*, (K, L) Antherozoids of *A. laevis*, (M, N) Antherozoids of *A. punctatus*.

The Antherozoid:

A mature antherozoid is unicellular, uninucleate, bi-flagellated and has a linear body. The flagella are of almost the same length as the body (Fig. 3 K, L). Proskauer (1948) observed that in the body of antherozoids show some degree of residual curvature (Fig. 3 M, N).

Dehiscence of Antheridium:

Water helps in the dehiscence of the antheridium. As the antheridia mature the roof of the antheridial chamber breaks down irregular, exposing the antheridia in a cup like chamber. The antheridia absorb water and the uppermost tier of triangular cells fall apart releasing a mass of antherozoids.

After dehiscence the antheridium loses turgor and collapses. It is followed by another antheridia to converge towards the opening in the roof and in this way a continuous stream of antherozoids is possible. It explains the formation of large number of sporophytes Hornworts. (fig 4).

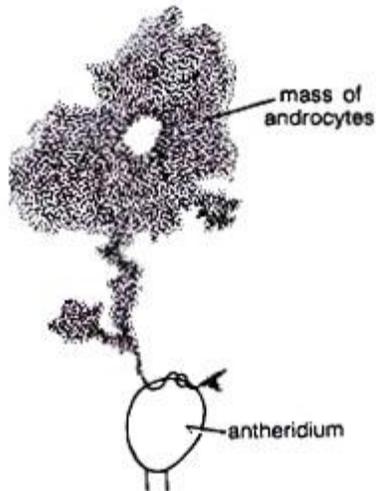


Fig. 4. *Anthoceros*. Dehiscence of antheridium.

Archegonium:

Archegonia develop in the flesh of the thallus on dorsal surface. The place of an archegonium on a thallus can be identified by the presence of a mucilage mound (Fig. 5).

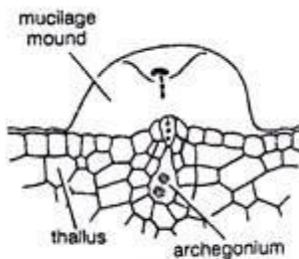


Fig. 5. *Anthoceros*. Mature archegonium with mucilage mound.

Structure:

A mature archegonium consists of two to four cover cells, an axial row of four to six neck canal cells, a venter canal cell and an egg. The jacket layer is not distinct from the other vegetative cells like other Bryophytes (Fig. 6 G, H).

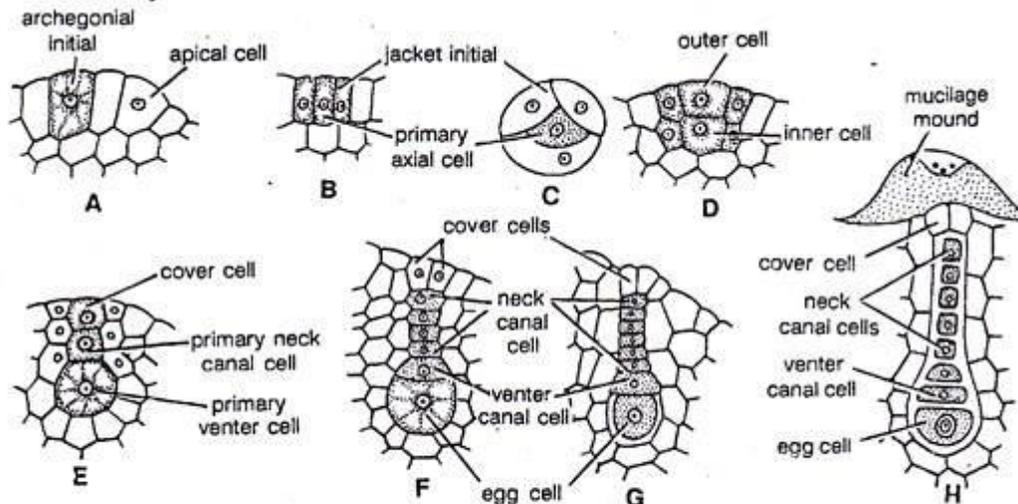


Fig. 6. (A-H). *Anthoceros*. Development of archegonium. (A-H). Successive stages in the development of archegonium.

Fertilization:

Water is essential for fertilization. In the mature archegonium, the venter canal cell, neck canal cells disintegrate and form a mucilaginous mass. It absorbs water, swells up and becomes out of the archegonial neck by pushing the cover cells apart. This mucilaginous mass becomes continuous with the mucilage mound and in this way an open passage down to egg is formed.

The mucilaginous mass consists of chemical substances. Many antherozoids caught in the mucilage enter in the archegonial neck because of the chemotactic response, reach upto the egg, and fertilization is effected. Prior to fertilization, egg enlarges and fills the cavity of the venter. Fusion of both male and female nuclei results in the formation of diploid zygote or oospore. Fertilization ends the gametophytic phase.

Sporophytic Phase:

After fertilization the diploid zygote or oospore still enlarges in size and fills the cavity of the venter of the archegonium. It secretes an outer cellulose wall.

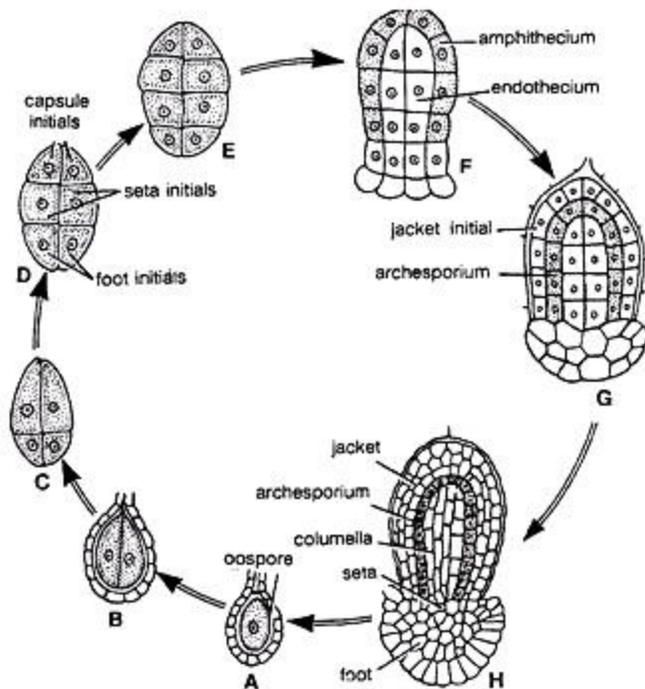


Fig. 7. (A-H). *Anthoceros*. Successive stages in the development of sporophyte.

On maturity the archesporium gives rise to two types of cells: spore mother cells and elater mother cells. These cells are arranged in alternate manner one above the another (Fig. 8 A).

Spore mother cells are spherical or oval with dense cytoplasm and large nuclei. These cells divide by meiotic divisions to form spore tetrads (Fig. 8 A). Elater mother cells are elliptical with small nuclei. These cells divide mitotically to form four celled elaters.

The four cells of the elaters may remain attached to each other or may break into 1-celled, 2-celled or 3-celled units. The broken units are called pseudo elaters. (The elaters are without thickening bands and therefore, called pseudo elaters, Fig. 8 A). By the activity of the meristematic zone various tissues of the capsule are continuously produced so that it becomes elongated.

The young sporophyte of the *Anthoceros* is surrounded by a fleshy covering or sheath. It is called involucre (Fig. 8 A). It is developed partly from the tissue of the archegonium and partly from the tissue of the gametophytic thallus. In young stages the sporophyte is completely surrounded by involucre.

Structure of Mature Sporogonium:

The mature sporophyte consist a bulbous foot and a smooth, slender, erect, cylindrical, structure called capsule. Capsule varies in length from two to fifteen centimeter in different species. The sporogonium appears like a 'bristle' or 'horn', hence, the species are called 'hornwoits' (Fig. 1 A, 8 A).

Internal structure:

A mature sporogonium can be differentiated into three parts viz., the foe: seta and the capsule.

Foot:

It is bulbous, multicellular and made up of a mass of parenchymatous cells. It acts as ac haustorium and absorbs food and water from the adjoining gametophytic cells for the developing sporophyte (Fig. 8 A).

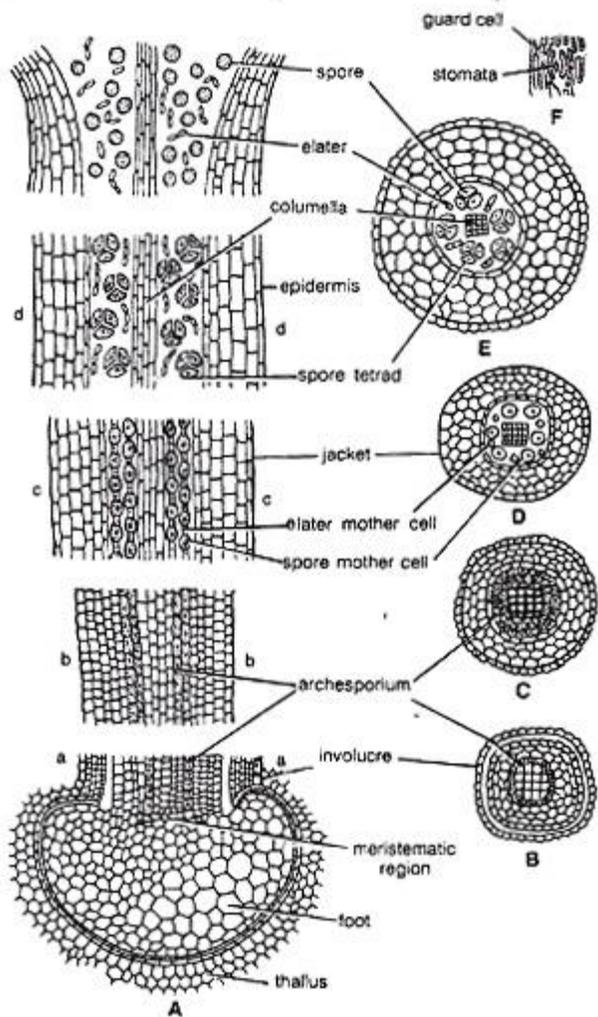


Fig. 8. (A-F). *Anthoceros*. Internal structure of the sporogonium (A) Longitudinal Section (L.S.) through the mature sporogonium. (B) Cross section of the sporogonium at a-a level, (C) cross section of the sporogonium at b-b level, (D) cross section of the sporogonium at c-c level, (E) Cross section of the sporogonium at d-d level, (F) Structure of stomata from the epidermis of sporogonium wall.

Meristematic Zone or Intermediate Zone or Intercalary Zone:

Seta is represented by meristematic zone. This is present at the base of the capsule and consists meristematic cells. These cells constantly add new cells to the capsule at its base.

The presence of meristem at the base enables the capsule to grow for a long period and form spores. It is a unique feature of *Anthoceros* and is not found in any other bryophyte. We are able to see different stages of development from base upwards in the sporogonium of *Anthoceros* (Fig. 8 A).

Capsule:

Its internal structure can be differentiated into following parts:

Columella:

It is central sterile pan, extending nearly to its tip. It is endothecial in origin. In young sporophyte it consists of four vertical rows of cells but in mature sporophyte it is made up of 16 vertical rows of cells (4 x 4). In a transverse section these cells appear as a solid square (Fig. 8 D, E). It provides mechanical support, functions as water conducting tissue and also helps in dispersal of spores.

Archesporium:

It is present between the capsule wall and the columella. It extends from base to the top of the capsule. It originates from the inner layer of amphithecium. In young sporophyte it over arches the columella (a feature in contrast to liverworts).

In a few species of Anthoceros for e.g., *A. crenatifrons*, *A. hawaiiensis* and *A. erectus*, the archesporium may remain one cell in thickness throughout its further development.

However, in *A. pearsoni* and *A. himalayensis* it may become two layered thick a little above the base. In *A. hallii* it may even become two to four cells in thickness (Fig. 8 A, a-a). In upper part of the capsule it is differentiated into sporogenous tissue which produces spores and pseudo elaters.

Pseudo elaters may be unicellular or multicellular, branched or un-branched and may consists more or less elongated cells (Fig. 9 A-D). The spiral thickenings are absent (characteristic of Anthoceros) but in *A. physocladus* the cells have long and thick walls with extremely reduced lumen (Pande, 1960). In some species of Anthoceros their secondary walls possess helical thickenings (Proskauer, 1960).

Capsule wall:

It consists of four to six layers of cells, of which the outermost layer is epidermis (Fig. 8 A, d-d). The cells of the epidermis are vertically elongated and have deposit of cutin on their walls. The continuity of epidermis is broken by the presence of stomata. The stomata are oriented vertically with the axis of the sporogonium and are widely separated from each other.

Each stoma consists a pore surrounded by two guard cells (Fig. 8 F). The cells of the inner layers have intercellular spaces and contain chloroplast. Thus, the sporogonium is partially self-sufficient to synthesize its own organic food but partially it depends on the gametophyte for the supply of water and mineral nutrients.

Dehiscence of the capsule:

Capsule dehisces basipetally i.e., from apex to base. As the capsule matures, its tip becomes brownish or black. Vertical lines of dehiscence appear in the jacket layer (Fig. 9 E). The dehiscence of the capsule is usually by two longitudinal lines, occasionally it is by single line (Fig. 9 F) or rarely by four lines. The capsule wall dries and shrinks at maturity.

Consequently narrow slits appear in the capsule wall all along the shallow grooves (line of dehiscence), which gradually widen and extend, towards the base. (In *A. crispulus* capsule splits first along one line of dehiscence and it is followed by splitting along other line of dehiscence). It results in the formation of two valves of the capsule wall (Fig. 9 G).

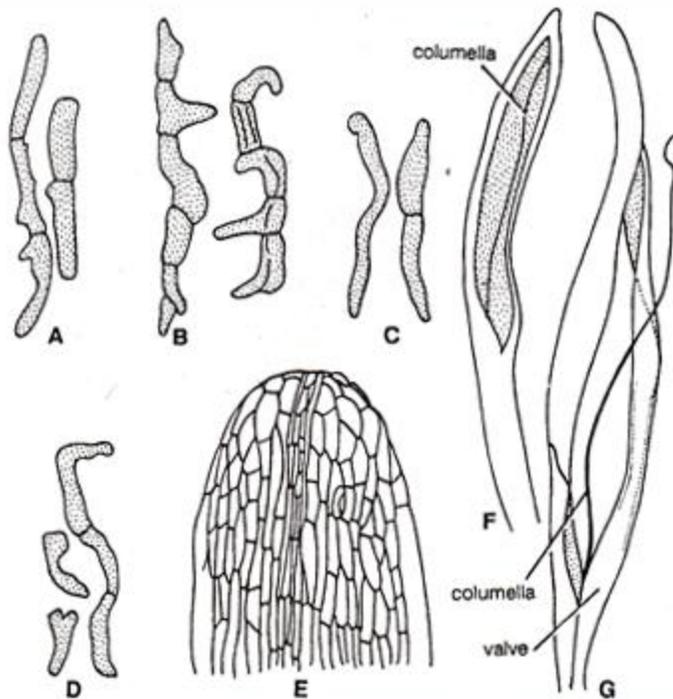


Fig. 9. (A-G). *Anthoceros* (A-D). Pseudoelaters of different species, (E). Apex of the capsule with line of dehiscence, (F) Single line of dehiscence, (G) Bivalved dehiscence.

Still attached at the tip and exposing the columella is the mass of spores and pseudo elaters. The two valves thus separated, diverge and twist hygroscopically. The pseudo elaters also dry out, twist and help to loosen the spores. Thus, the twisting of the valves and the movement of the pseudo elaters in the exposed spore mass helps in the shedding of the spores. Air currents also help in the dispersal of spores.

Structure of Spore:

The spores are haploid, uninucleate, semicircular with a conspicuous triradiate mark (Fig. 10 A).

Each spore remains surrounded by two wall layers. The outermost layer is thick ornamented and is known as exospore. It varies in colour from dark brown to black (e.g., *A. punctatus*) or yellowish (e.g., *A. laevis*). The inner layer is thin and is known as endospore. Wall layers enclose colourless plastids, oil globules and food material.

Germination of spore and formation of young gametophyte:

Under favourable conditions the spores germinate immediately in *A. erectus* and *A. punctatus* (Mehra and Kachroo, 1962).

However, in *A. fusiformis* the spores undergo a resting period of few weeks or months before germination (Campbell, 1928). At the time of germination spore absorbs water and swells up Exospore ruptures at the triradiate mark and endospore comes out in the form of a tube. It is called germ tube (Fig. 10 B).

Contents migrate into the germinal tube where the colourless plastids turn green.

Two successive transverse walls are laid down at the tip of a the germinal tube resulting in the formation of three celled filament (Fig. 10 C, D). The upper cell divides by a vertical division (Fig. 10 E) followed by similar vertical division in the lower cell (quadrant stage Fig. 10 F).

These four cells again divide by a vertical division at right angle to first to form eight cells (octant stage). This octant stage is known as sporeling. The **o.otal** tier of four cells function as apical cells and form the new gametophyte. First rhizoid develops as an elongation of any cell of the young thallus (Fig- 10 G, H). As the growth proceeds, the mucilage slits appear on the lower surface and these slits are infected by *Nostoc*.

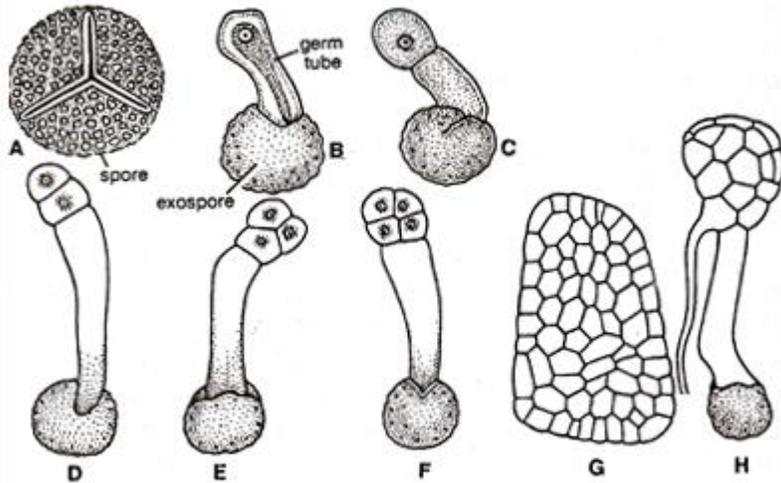


Fig. 10. (A-H). *Anthoceros*. Successive stages in the germination of spore and formation of gametophyte.

Alternation of Generation:

The life cycle of *Anthoceros* show regular alternation of two morphologically distinct phases. One of these generations is haplophase and the other is diplophase.

Haplophase or gametophytic phase:

In *Anthoceros* this phase is dominant and produces the sex organs. Sex organs produce gametes to form a diploid zygote.

Diploid phase of sporophytic phase:

Zygote develops into sporophyte. In *Anthoceros* sporophyte is represented by foot, meristematic zone and capsule. The sporophyte produces the spores in the capsule. The spores on germination produce the gametophyte.

So, in *Anthoceros*, two morphologically distinct phases (haplophase and diplophase) constitute the life cycle. The life cycle of this type which is characterised by alternation of generation and sporogenic meiosis is known as heteromorphic and diplohaplontic. (Fig. 11,12).

Affinities of *Anthoceros* or Primitive and Advanced Characters of

Anthoceros:

The thallus of *Anthoceros* shows both primitive and advanced characters. *Anthoceros* on one hand forms a connecting link with the Chlorophyceae (green algae), liverworts, mosses and on the other hand it is linked with primitive Pteridophytes.

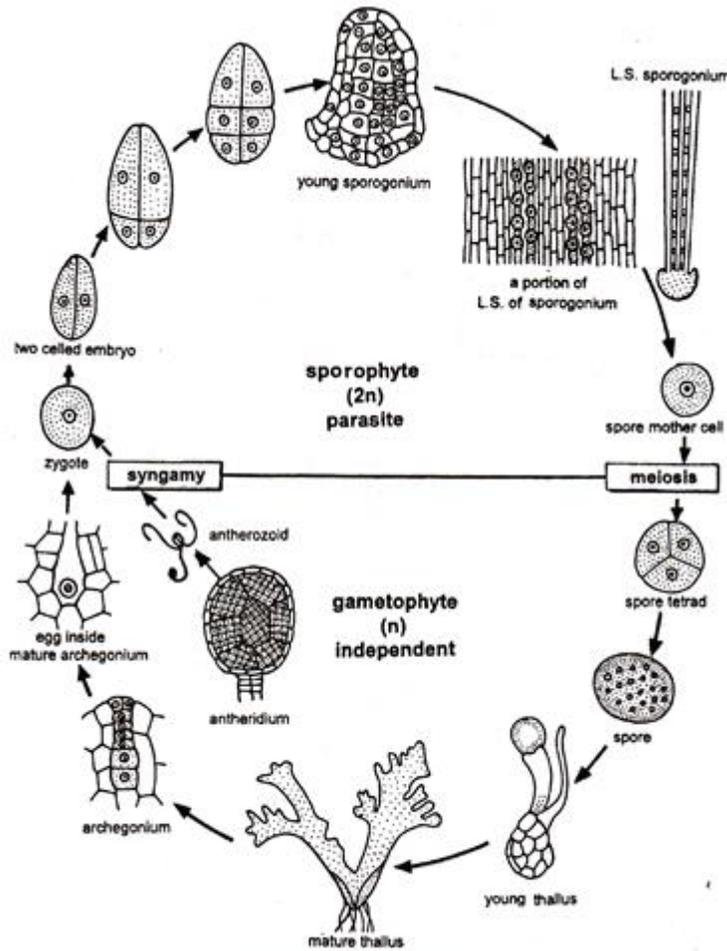


Fig. 11. *Anthoceros*. Diagrammatic life cycle.

Primitive Characters:

1. Resemblances with chlorophyceae (green algae):

(a) Simple, green, gametophytic thalloid plant body.

(b) Presence of less number of chloroplasts per cell.

(c) Definite shape of the chloroplast.

(d) Presence of pyrenoid.

(e) Structure and function of pyrenoid is similar to that of green algae (form starch grains at periphery).

2. Resemblances with liverworts:

(a) Simple, green, gametophytic plant body, without any differentiation of tissues like Pellia.

(b) Similar apical growth.

(c) Biflagellated antherozoids.

(d) Periclinal division separates amphithecium and endothecium.

(e) Archegonium is differentiated into spore mother cells and elater mother cells.

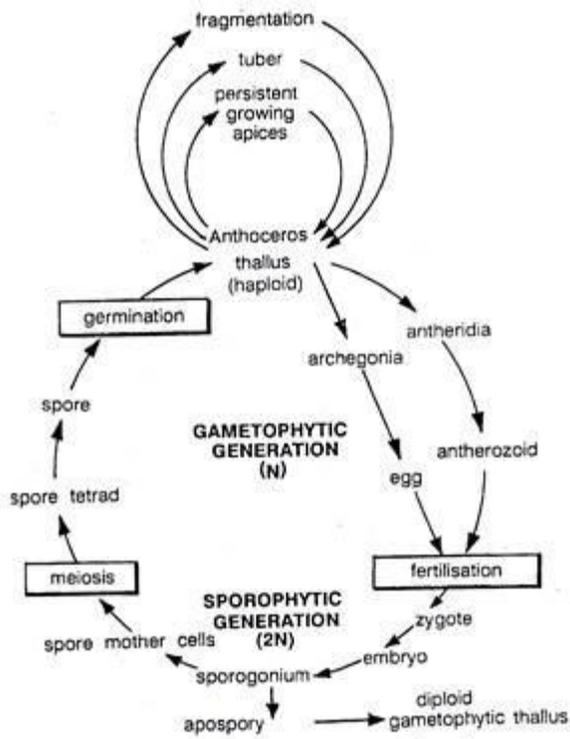


Fig. 12. *Anthoceros*. Schematic life cycle.

Advanced Characters:

1. Resemblances with mosses:

(a) Presence of highly differentiated and ventilated system in the capsule wall.

(b) Presence of columella (endothelial in origin).

(c) Presence of reduced archesporium.

(d) Archegonium arches over the columella like Sphagnum.

2. Resemblance with Pteridophytes:

(a) Gametophytic plant body resembles with fern prothallus.

(b) Sunken sex organs.

(c) Structure of archegonium is similar.

(d) Semi-parasitic sporophyte of Anthoceros resembles with primitive fossil vascular plants of order Psilophytales.