Anthoceros

PHYLLUM. ANTHOCEROTOPHYTA

(HORNWORTS)

Characteristic features

1. Gametophytes are simple, flat, lobed and **unspecialised thalloid.**
2. The thallus shows a **uniform internal tissue organisation.**
3. Colonies of **symbiotic cyanobacterium,** *Nostoc* fill small cavities that are scattered throughout the ventral part of the thallus. These colonies appear as scattered blue-green dots when the thallus is viewed from the top.
4. Hornworts differ from all other land plants in having only one large algae-like chloroplast (**chloroplasts with pyrenoids**) on each thallus cell.
5. Like liverworts, the rhizoids are hyaline unicellular, and unbranched.
6. Sporophytes are very strong and lasting for several weeks. Hornworts get their name from their long, **horn-shaped sporophytes.**
7. The sporophyte is differentiated into a long cylindrical capsule and a bulbous foot.
8. At the base of the sporangium, just above the foot, is a mitotically active meristem, which adds new cells to the spore-producing zone throughout the lifespan of the sporophyte.
9. The sporangium releases spores at its apex, at the same time the new spores are being produced by meiosis at its base.
10. With drying, the **capsule opens by splitting into two segments** or **valves.**
11. Release of spore takes place gradually over a long period of time, and the spores are mostly dispersed by water movement rather than by wind. **Pseudoelaters** perhaps take place in spore dispersal.
12. Like liverworts, the protonema of hornworts is globose and forms a single bud (shoot).

ANTHOCEROS

Systematic position

Phyllum.	Anthocerotophyta
Class.	Anthocerotopsida
Order.	Anthocerotales
Family.	Anthocerotaceae

Total number of species : About 200

Number of species found in India : 25

Common Indian species : *Anthoceros erectus, A. himalayansis, A. longii, A. dixitii, A. crispulus.*

Distribution and Habitat – The genus *Anthoceros* is cosmopolitan in distribution and occurs both in the tropical and temperate regions of the world. The plants grow mostly on moist clayey soil and ditches or on the wet rock crevices in very moist shady places, usually in dense patches. Some species grow on the decaying woods that found in moist shady places. In India, it is found all over the Himalayas, in south India and even in the Gangetic plains.

The plant body (The adult gametophyte)

External morphology

The gametophytic plant body is a small greasy dark-brown prostrate, dorsiventral thallus. The thallus is usually dichotomously lobed (e.g. *A. fusiformis*, Fig.6.29B) or sub-orbicular (e.g. *A. crispulus*, Fig. 6.29 A). The thallus is often raised on a thick ascending stalk-like structure (*A. erectus*, Fig. 6.29C & D). Sometimes the thallus is long and pinnately divided (*A. hallii*) or bilobed (*A. himalayensis*) (Fig. 6.29E & F).

The middle part of the thallus is always without a definite midrib, although the thallus is thick. The upper dorsal surface of the thallus may be smooth (*A. laevis*), velvety (*A. crispulus*) or rough (*A. fusiformis*) with ridges. The lower ventral surface bears numerous unicellular, smooth walled **rhizoids** along the median line. **Tuberculate rhizoids, scales** or **mucilage hairs** are absent in *Anthoceros.*

Internal features

The internal structure of the thallus tissue (Fig. 6.30A) shows a very simple organisation without any cellular differentiation. The thallus is comprised of uniform, thin-walled, parenchymatous cells except the epidermis which is made up of comparatively smaller cells. The thallus is several layers thick in the middle and the thick-

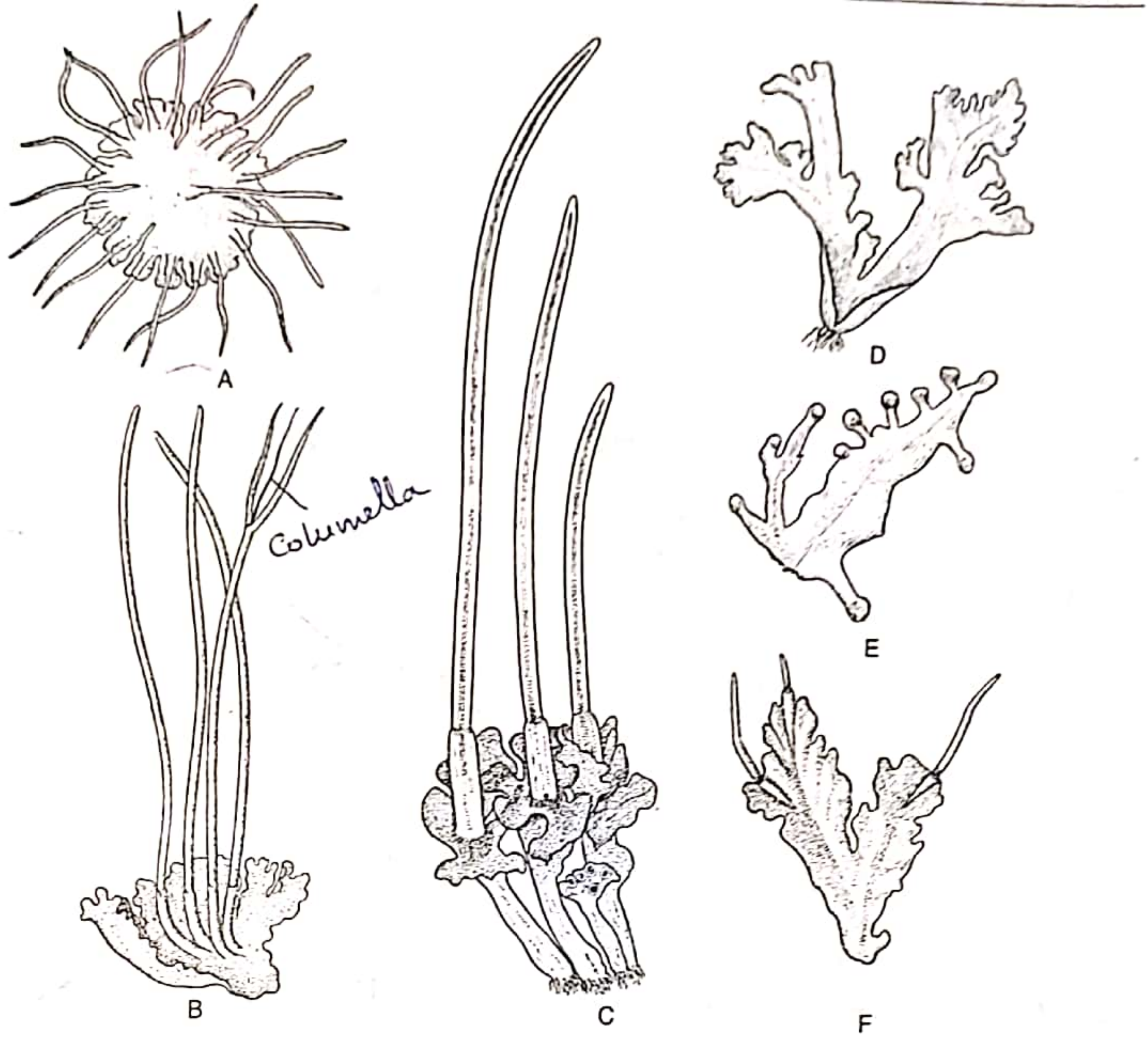

Fig. 6.29 : A. *Anthoceros crispulus* (after Bharadwaj), B. *Anthoceros fusiformis* (after Smith), *A. erectus* : C. (after Bharadwaj) and D. (after Kashyap), *A. himalayensis* : E. (Sterile, bearing tubers) and F. (Fertile) (after Kashyap)

ness of the thallus may vary from 6 to 8 cells in *A. laevis* to 30-40 cells in *A. crispulus*. The thallus, which is thickest in the middle, tapers towards the margins.

The surface cells contain a comparatively large chloroplast and are not cuticularised. Each cell of the thallus (Fig. 6.30B) shows one or more discoid or oval chloroplasts containing many **pyrenoids**. This is the characteristic feature of the class Anthocerotopsida. There are no air chambers or pores in the tissue of the thallus. Instead, intercellular mucilage cavities are present which open on the ventral surface by means of narrow slit called **slime pore** (Fig. 6.30A & C). These mucilage cavities are always invaded by the colonies of endophytic blue green alga, *Nostoc* which enters the thallus through slime pores. (endosymbiotic)

In addition to these mucilage ducts, some schizogenous tubular cavities are present behind the growing point. They are also filled with mucilage and run longitudinally (e.g., *A. crispulus*) or obliquely (e.g., *A. gemmulosus*) through the thallus. This mucilage may be replaced by gaseous contents in other parts of the thallus. The mucilage cavities/ducts are absent in *A. laevis* and *A. himalayensis*.

Apical growth

The thallus usually grows by a single **apical cell** (*A. fusiformis*) or by a group of apical cells (*A. erectus, A. himalayensis*). These cells are located distally in a shallow depression and remain covered externally with mucilaginous substances. Each apical cell has four cutting faces, one each on the dorsal and ventral side and two on the lateral side. The tissue derived from the dorsal and ventral faces contribute to the thickness of the thallus, while derivatives of the lateral faces are responsible for its lateral

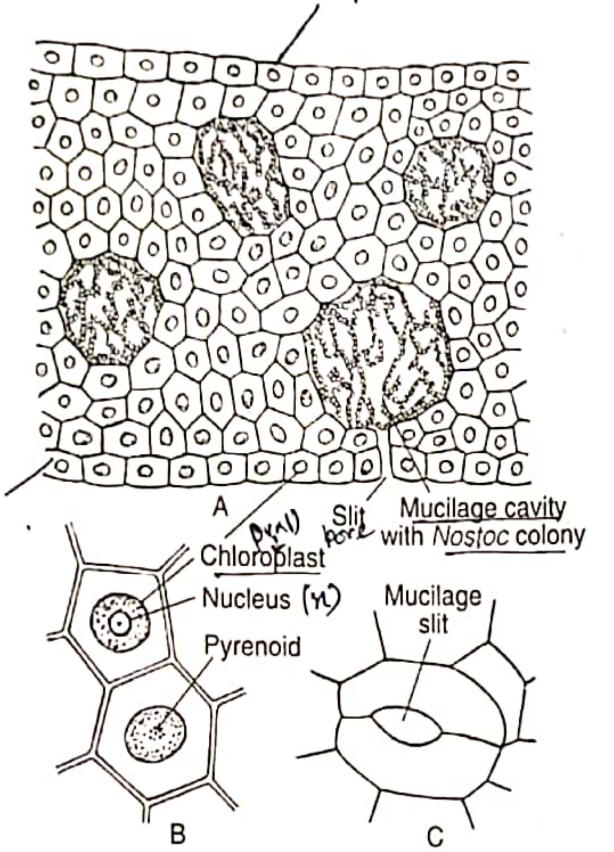

Fig. 6.30 : *Anthoceros* : A. Vertical section through gametophyte thallus showing mucilage cavities with *Nostoc* colonies and opening slit in ventral surface. B. Gametophyte thallus cell showing single chloroplastid, pyrenoid and nucleus. C. Mucilage slit or cleft opening to mucilage cavity from ventral side

expansion. Sex organs and rhizoids develop from the segments of the dorsal and ventral faces, respectively.

Reproduction

The genus *Anthoceros* reproduces both by vegetative and sexual methods :

Vegetative reproduction

Vegetative propagation takes place by the following four methods :

(a) **By progressive death and decay of the older parts of the thallus (fragmentation)**

Vegetative reproduction often takes place by the decay of the older basal parts of the thallus and by continuous growth from the growing point. The tip grows continuously giving rise to separate plants. This method is less common in *Anthoceros* than in other Hepatics.

(b) **By Tubers**

Under unfavourable environmental conditions like prolonged drought, many species of *Anthoceros* (e.g. *A. laevis, A. tuberosus, A. pearsoni, A. hallii*) produce tubers on the marginal patches of the thallus tissue (Fig. 6.29 E). Tubers escape from desiccation with the formation of a resistant layer of cork cells. Tubers store food and function as perennating organ that germinate into new gametophytes on the return of favourable environmental conditions.

(c) **By Gemmae**

Gemmae are known to develop on the dorsal surface of the thallus in some species of *Anthoceros* (*A. gladulosus, A. formosii, A. propaguliferous*). They are stalked and often develop mucilage pores. On separation from the parent plant, the detached gemmae grow into a new gametophyte.

(d) **By persistent growing apices**

During dry summer, the thalli of some species of *Anthoceros* (e.g., *A. pearsoni* and *A. fusiformis*) become completely dry except the apical region with a little of adjacent tissue. These apical parts remain dormant during the dry season and form new thalli on the return of favourable conditions.

Sexual reproduction

Anthoceros is either **dioecious** i.e., **heterothallic** (e.g., *A. himalayensis, A. hallii, A. erectus, A. pearsoni*) or **monoecious** i.e., **homothallic** (e.g., *A. fusiformis, A. gollani, A. punctatus*). Monoecious species are usually protandrous i.e., antheridia mature before archegonia. Antheridia and archegonia are embedded in the dorsal surface of the thallus. They develop in continuous rows just behind the apical growing point.

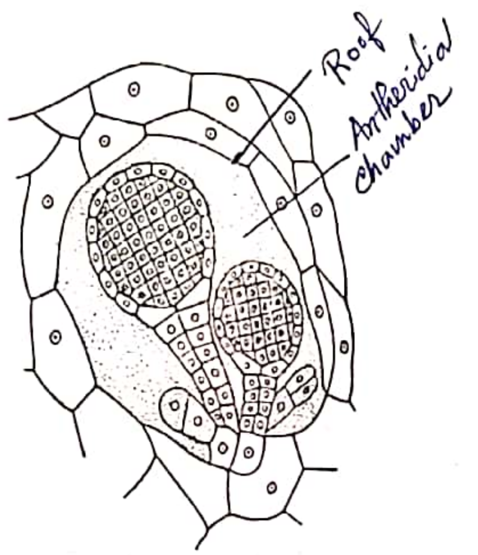

Fig. 6.31 : *Anthoceros* : An antheridial chamber showing a cluster of antheridia

Antheridium

Development and structure

In the species of *Anthoceros*, the antheridium develops from a hypodermal cell as opposed to liverworts. A superficial dorsal cell, lying close to the growing apex, usually divides by a periclinal wall into an upper **roof initial** and a lower **antheridial initial** (Fig. 6.32A-B). The upper roof initial first divides periclinally, followed by many anticlinal divisions to form a multi-celled roof over the antheridium. The antheridial initial is, therefore, hypodermal rather than superficial (Fig. 6.32B). The cavity between the roof initial and the antheridial initial accumulates mucilage. Subsequently, this cavity enlarges to form a antheridial chamber (Fig. 6.31). The antheridial initial may develop a single antheridium (e.g., *A. pearsoni*) or may divide to form several antheridia. (e.g., 7 in *A. crispulus*, 22 in *A. erectus*, 30 in *A. gemmulosus*). Sometimes, younger antheridia also develop from the base of the older antheridium resulting into the development of a cluster of antheridia of different ages in a single antheridial cavity (Fig. 6.31). Just prior to the division, the antheridial initial becomes almost superficial. The antheridial initial undergoes two vertical divisions at right angle to each other forming four cells. This is followed by a transverse division resulting in eight cells, arranged in two tiers of four cell each (Fig. 6.32C-F). The cells of the lower tier are known as **stalk cells**, while the cells of the upper tier are called **antheridial cells**. The basal stalk cells by transverse divisions form the stalk of the antheridium (Fig. 6.32G). The upper antheridial cells divide transversely to form a 8-celled **octant**. Each cell of the octant by periclinal division form eight outer **primary jacket cells** and eight inner **primary androgonial cells** (Fig. 6.32F-G). The primary jacket cells divide anticlinally to form a single layer **jacket** of antheridium. The primary androgonial cells undergo many regular divisions resulting into the development of a mass of **androcyte mother cells**. Subsequently, each androcyte mother cell divides to form two **androcytes**. The androcytes get metamorphosed into biflagellate **antherozoids** very soon (Fig. 6.32H). A mature antheridium now consists of a slender stalk and a club-shaped or pouch-like body (Fig. 6.31). The club-shaped body has a single-layered jacket which encloses a number of biflagellate antherozoids (Fig. 6.32H).

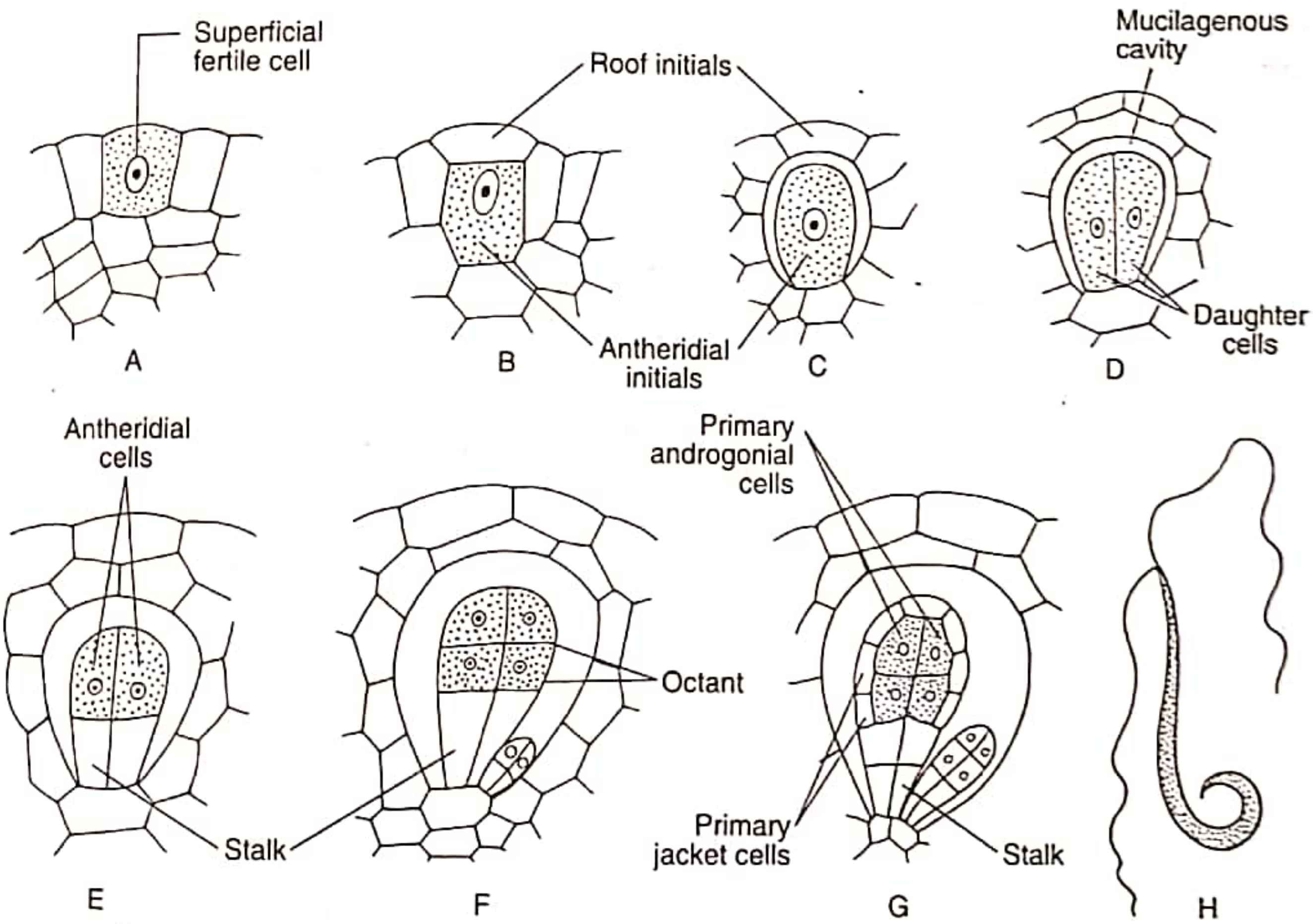

Fig. 6.32 : *Anthoceros* : A-G. Stages of development of antheridium; H. A sperm

Dehiscence

At maturity, the roof of the antheridial chamber ruptures, exposing the antheridia. The apical cell of the antheridial wall, on absorbing water, ruptures by apical aperture. The antherozoids are now liberated to the covering film of water.

Archegonium

Development and Structure

The archegonia produce in acropetal sequence on dorsal surface of the thallus. The archegonia develop from a single superficial dorsal cell close to the apical growing point. In monoecious species, the archegonia are formed later in the same thallus which had borne the antheridia (*A. fusiformis, A. gollani, A. punctatus*).

The archegonial initial (Fig. 6.33 A), by transverse division, gives rise to an outer **primary archegonial cell** and an inner **primary stalk cell.** But according to Mehra and Handoo (1953) the archegonial initial functions directly as the primary archegonial cell. There is no stalk cell. The primary archegonial cell by three transecting periclinal divisions forms three outer **jacket initial cells** and an inner **primary axial cell** (Fig. 6.33B & C).

The primary axial cell, by transverse division, (Fig. 6.33D) forms two cells, the lower **primary ventral cell** and the upper cell which further divides transversely to form a top **cover initial** and a lower **primary neck canal cell** (Fig. 6.33E). The cover initial divides by two vertical walls at right angle to each other forming a rosette of four **cover cells**. The primary neck canal cell by repeated transverse divisions forms a vertical row of 4 to 6 or more **neck canal cells**. The primary ventral cell, by transverse division, forms the **ventral canal cell** and a large **egg** (Fig. 6.33F).

The mature archegonium

The mature archegonia remain completely embedded in the dorsal surface of the gametophyte except the cover cells that protrude slightly above the surface of the thallus. In the growing archegonium, the cover cells are usually associated with a mucilage mound (Fig. 6.33G).

Fertilisation

At the time of fertilisation, the cover cells are thrown off, followed by the disintegration of the neck canal cell and the ventral cell. The egg now becomes directly exposed resulting into the formation of mucilaginous mass. Among the many antherozoids entering the neck, only one fuses with the egg and forms the **zygote** or **oospore.**

THE SPOROPHYTE

Development of the sporophyte

The diploid **zygote** (fertilised egg) is the mother cell of the sporophytic generation. It increases in size and secretes a wall of cellulose around itself and eventually becomes 4-celled by two successive divisions at right angles to each other (Fig. 6.34A). A second vertical division, at

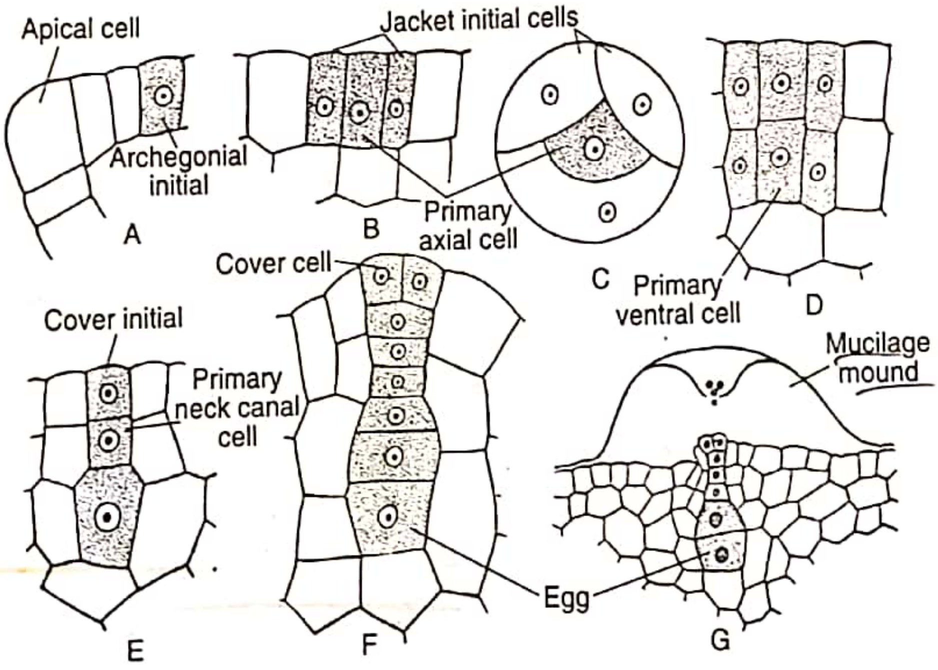

Fig. 6.33 : *Anthoceros* : A-F. Stages of development of archegonium, G. A mucilage mound covering a fully mature archegonium

differentiated into three regions — (a) the lower bulbous **foot**, (ii) the intermediate **meristematic zone**, and (iii) the upper erect, cylindrical **capsule** (Fig. 6.35A) The seta is absent.

The foot

It is the basal part of the sporophyte which is a rounded bulbous structure deeply embedded in the tissue of the thallus (Fig. 6.35A). The lowermost cells of the foot are haustorial which absorb water and mineral nutrients from the gametophyte for the developing sporophyte.

The intermediate meristematic zone

This is a narrow zone of meristematic cells located in-between the foot and the capsule (Fig. 6.35A). It regenerates the capsule from the base, thus the capsules are always in different stages of growth.

The capsule

The capsule forms the major and conspicuous part of the sporophyte. It is a slender smooth upright cylindrical structure that slightly tapers at the apex. It consists of capsule wall, sporogenous tissue and collumela (Fig. 6.35A).

Capsule wall : The capsule wall is made up of 4-6 layers of parenchymatous cells. The cells of the outermost layer, which form the epidermis, are heavily cutinised, vertically elongated and interrupted by the stomata (Fig. 6.35C). Below the epidermal layer is the green parenchymatous, photosynthetic tissue containing chloroplasts. Thus, the sporophyte is capable of manu-

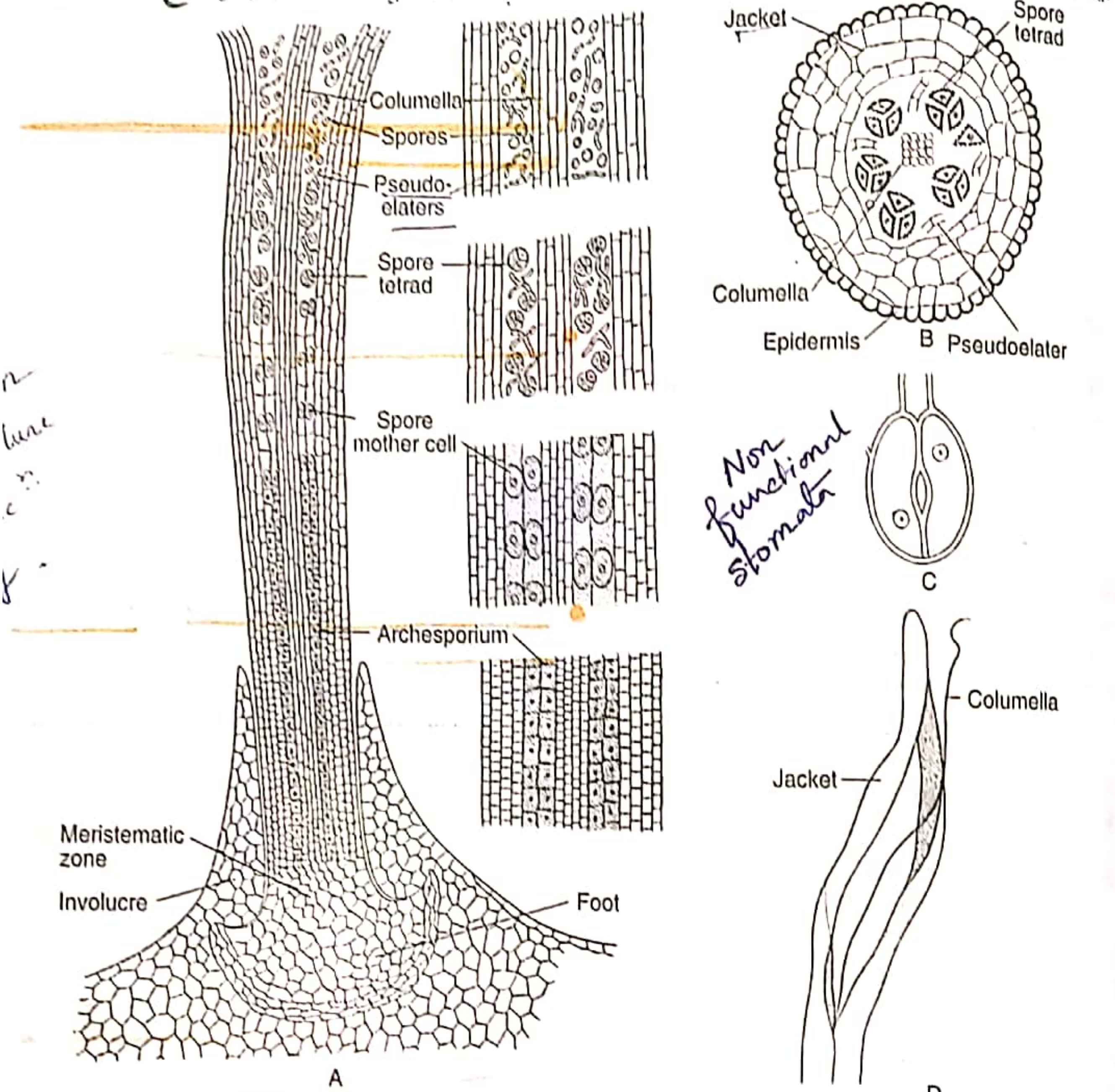

Fig. 6.35 : Mature sporophyte of *Anthoceros* : A. L.S. (semidiagrammatic). Different portions are shown magnified on the right-hand side. B. T.S. at the middle of the sporophyte. C. A stomata in the jacket epidermis. D. Ruptured tip of a mature sporophyte capsule

facturing their own food by photosynthesis, except for the water and minerals for which it depends upon the gametophyte.

Sporogenous tissue : The sporogenous tissue (archesporium) of *Anthoceros* is situated in between the jacket and the collumela. At maturity it differentiates into spore mother cells and pseudoelaters.

Columella : The columella is a solid column of sterile tissue situated at the central part of the capsule. It extends nearly to the entire length. The cells are narrow and elongated and are arranged in 16 vertical rows. In transverse section, the columella appears to be a solid square (Fig. 6.35B). The columella provides mechanical support to the capsule. It also helps the spores to disperse and is associated with the conduction of water and minerals.

Dehiscence of the Capsule

At maturity, the tip of the capsule loses water. In fact, the loss of water from the capsule walls greatly favours the dehiscence. After drying of the capsule, a split appears just below the tip which gradually widens downwards and eventually the capsule wall splits into two to four valves. The hygroscopic movement of the pseudoelaters releases the spores to a distance by air current and at this stage the apical portion of the capsule looks twisted. The tip of the collumela projects out like a flagellum. (Fig. 6.35D).

THE NEW GAMETOPHYTE

The haploid **spore** is the first cell of the gametophytic generation. The wall of the spore is differentiated into an outer thick sculptured **exine** (**exospore**) and an inner thin and smooth **intine** (**endospore**) (Fig. 6.36A). The spore germinates on a suitable substratum either immediately or after a resting period of a few weeks to a few months. The exine rupture through the triradiate ridge and the intine comes out as a long germ tube (Fig. 6.36B). All contents of the spore passes to the germ tube. Here two cells are produced at the tip of the germ tube through two successive transverse divisions. This is followed by two vertical divisions at right angle to each other resulting into the formation of 8-celled **octant** or **sporeling**. The four distal cells of the octant become meristematic and differentiate into a new gametophytic thallus.

Fig. 6.37 shows the diagrammatic life cycle pattern of *Anthoceros*.

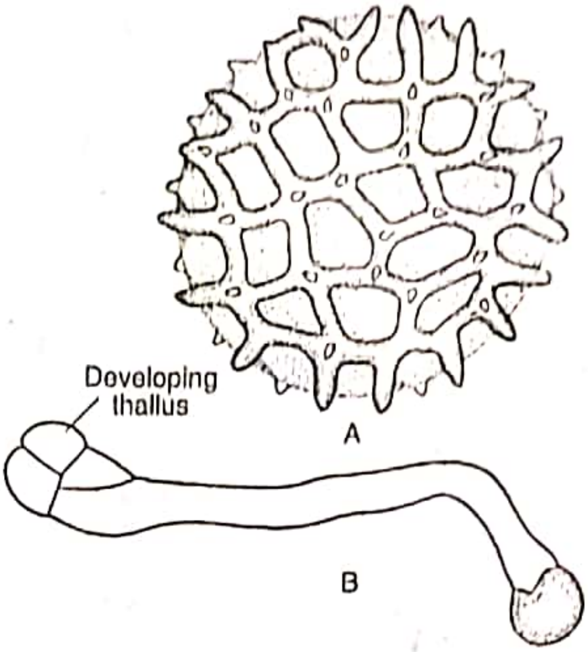

Fig. 6.36 : *Anthoceros* : A. A spore (after Bharadwaj), B. Germination of the spore (after Campbell)

Anthocerotophytes are a distinct but synthetic group of plants :

The phyllum Anthocerotophyta has been called a *synthetic group* as, apparently, it shows characteristics linking it to the algae on one hand and to other groups of embryophyta.

- *Characteristics common with algae :*

1. Simple, green thallus-like plant body and its branching.
2. Presence of a single chloroplast with pyronoids in each cell of the thallus.
3. Biflagellate antherozoids with whiplash flagella.

- *Characteristics common with liverworts (Marchantiophyta)*

1. Apical growth of the thallus taking place by a single pyramidal apical cell with four cutting faces.
2. Gametophytic structure (thallus) resembles *Pellia* (liverwort). In both the members, scales and tuberculate rhizoids are absent.
3. Similarity in the construction of mature sex organs.
4. Separation of amphithecium and endothecium by periclinal divisions.
5. Archesporium gives rise to spores and sterile cells (pseudoelaters). In *Dendroceros* and *Megaceros*, elaters possess spiral bands as in liverworts.

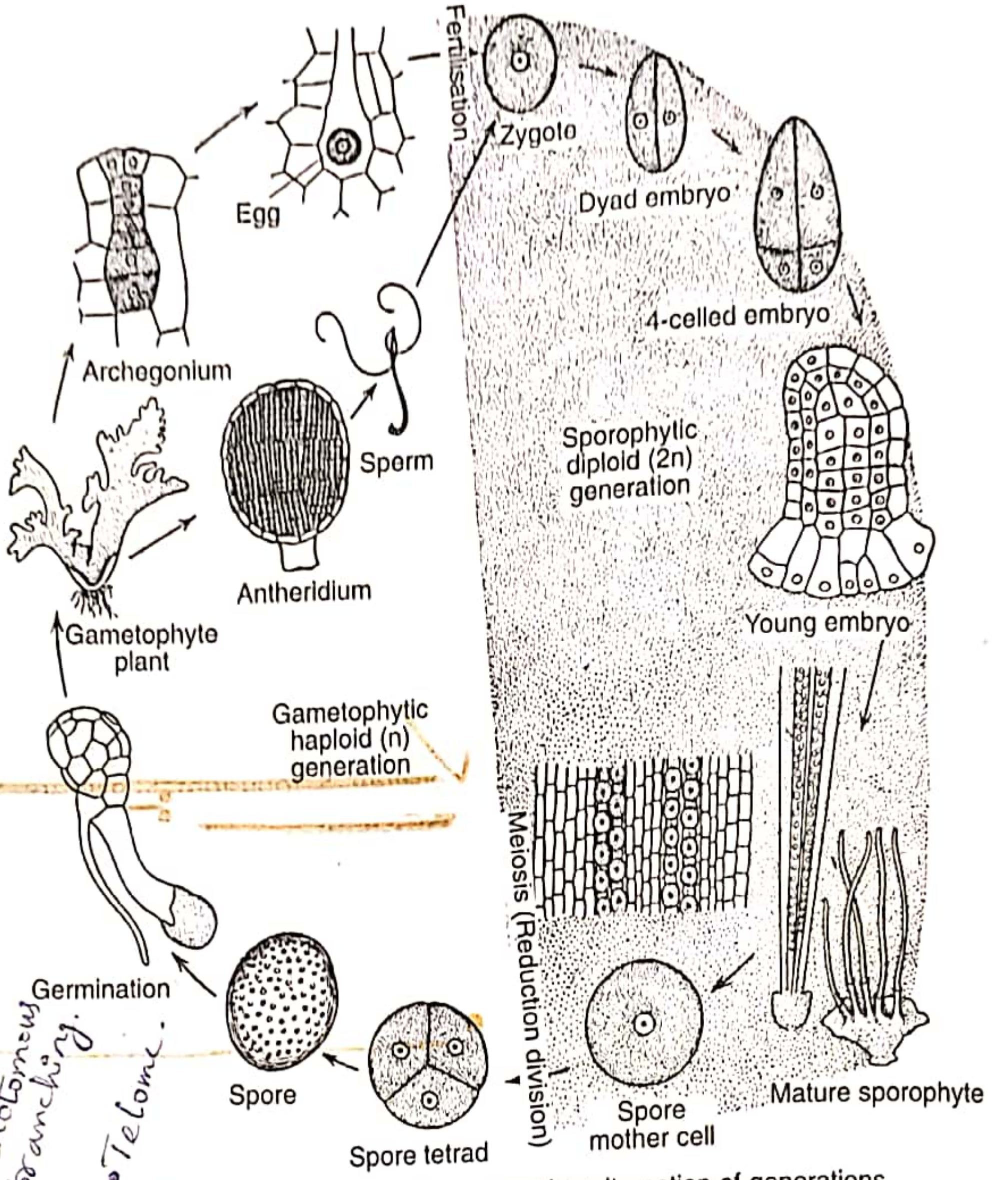

Fig. 6.37 : Life cycle of *Anthoceros* showing alternation of generations

6. In some species of Notothylus (N. levieri) whole endothecium giving rise to archesporium and the amphithecium forming the jacket of capsule. This suggests a connecting link between hornworts and liverworts.

Characteristics common with mosses (Bryophyta)

1. Presence of central columella in the capsule which develops from the endothecium.
2. The sporogenous tissue is greatly reduced.
3. Presence of functional stomata in the capsule wall as in *Funaria* which provides a ventilated photosynthetic system.
4. Archesporium differentiates from the inner layer of amphithecium as in Sphagnales.

Characteristics common with Pteridophytes

1. General similarity in the thallus structure of *Anthoceros* and the fern gametophyte (prothallus).
2. The sex organs are embedded (sunken) in the thallus.
3. Similarity in the structure of mature archegonium.
4. Highly developed semi-parasitic sporophyte of indeterminate growth showing photosynthetic capsule wall with functional stomata.

The elaborate, semi-parasitic sporophyte of *Anthoceros* with its typically ventilated assimilatory system and indeterminate growth denotes the nearest alliance to the independent rootless, leafless, dichotomously branched sporophyte of the primitive vascular plants — the Rhyniopsida.

The features of Anthocerotophytes that are common with lower group of plants, i.e., algae, and the higher groups of plants, like liverworts, mosses and pteridophytes, suggest that the Anthocerotophytes are a distinct but synthetic group of plants.