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ELEVENTH BIRBAL SAHNI MEMORIAL LECTURE

STATUS AND POSITION OF HORNWORTS

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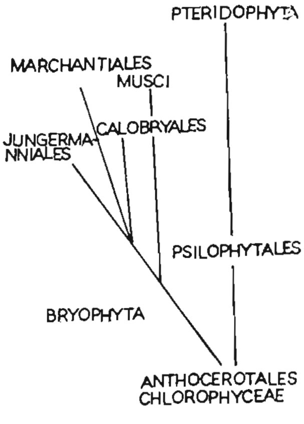
SINCE 1879, when Leitgeb pointed out some anomalies in hornworts (or anthocerotes), a small natural group of bryophytes, their status and position have been a subject of lively discussion.

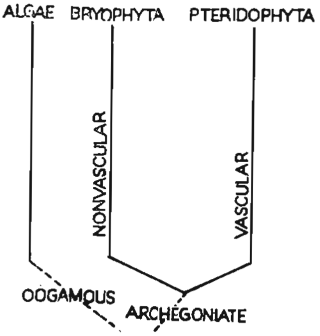
Fulford (1965, p. 3) wrote, " The Anthocerotales or Anthocerotae if you will, is a taxon with very many gametophyte and sporophyte characters unique to itself. Whether it is very closely or more distantly related to other Hepaticae remains to be proved".

Campbell (1895) derived pteridophytes from anthocerotes. Later (1925, 1940) he derived the Psilophytales from the Anthocerotales (Text-fig. 1) which in turn were derived from the Chlorophyceae.

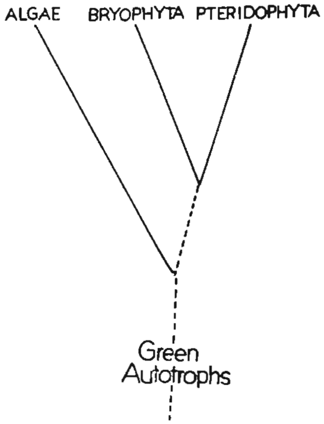


TEXT-FIG. 1 — Phylogeny (after Campbell, 1940).

Goebel (1898, 1905) refuted Campbell and considered the Bryophyta and the Pteridochyta as two independent lines. Later (1930) he concluded that the Bryophyta are not connected with any taxon either upwards or downwards. Bower (1935) supported Goebel (Text-fig. 2). Steere (1969) rejected a direct algal origin of bryophytes, or that they present an evolutionary way station between algae and higher plants, and concluded that they are an offshoot of the Archegoniatae, a " dead end ". An adaptation of the phylogenetic scheme by Zimmermann (1932) expresses these relationships better (Text-fig. 3).



TEXT-FIG. 2 — Relationships (ideas of Bower, Goebel & Steere).



TEXT-FIG. 3 — Phylogeny (adapted from Zimmermann, 1932).

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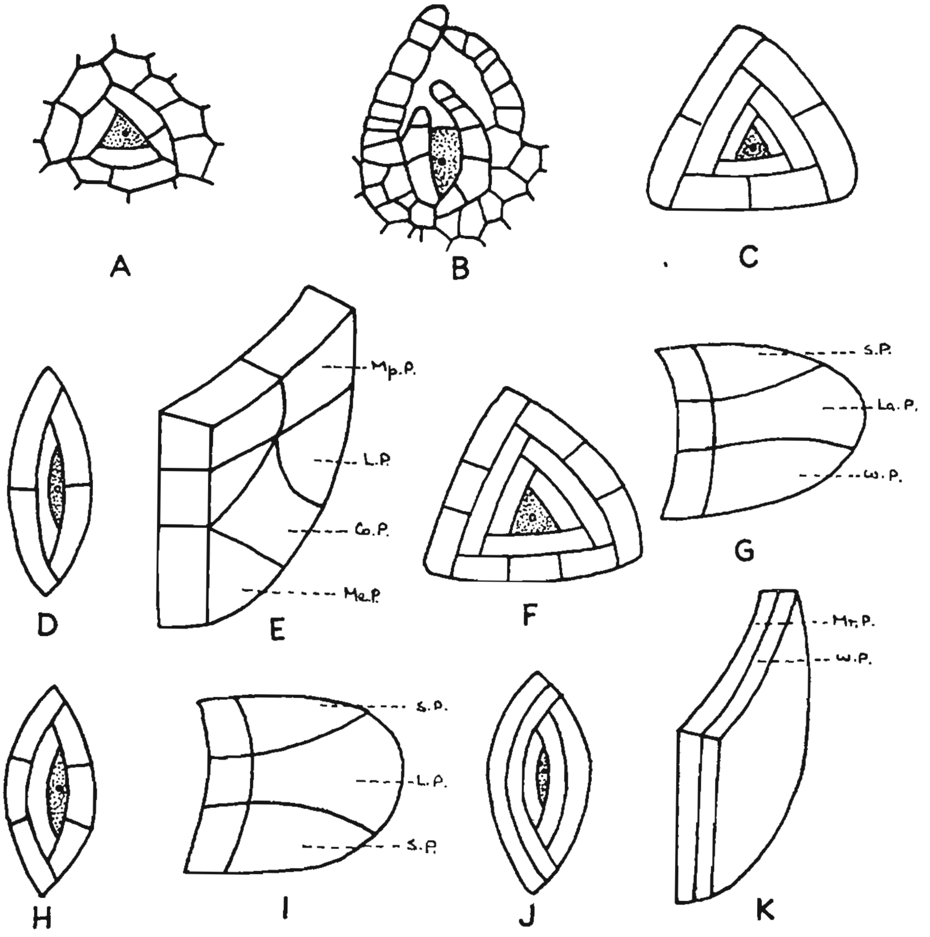
To decide as to the ideas of which school of thought are more tenable than those of the other and to incorporate the comments of various authors, where necessary, it is desirable to cover the entire gamut, considering and evaluating all features, rather than dwell upon a limited number of features (*cf.* Howe, 1898: peculiar chloroplasts, sunken sexual organs, meristematic seta, sterile columella and stomata on the capsule wall).

DATA AND DISCUSSION

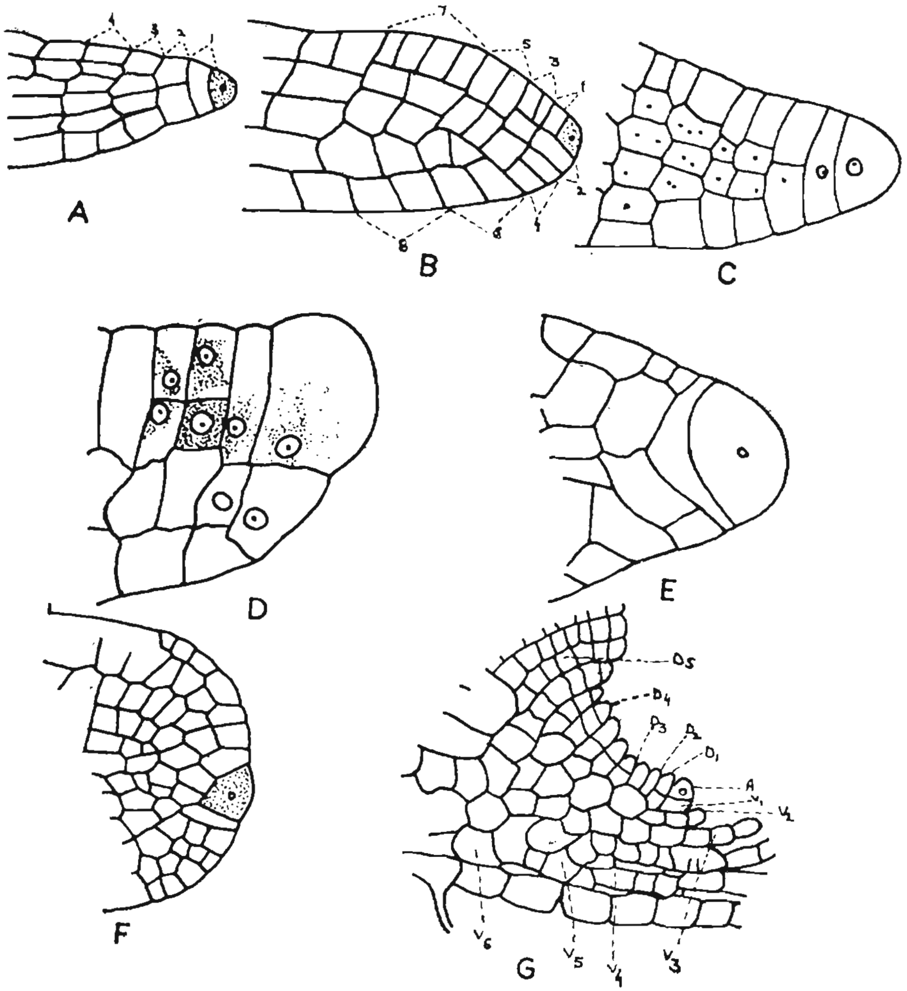
HAPLOPHASE

The habit of growth, but for the presence of colonies of *Nostoc* in the thallus, resembles that of the thalloid Metzgeriales.

Cavers (1911, pp. 90, 91) wrote, " The mode of apical growth is of interest and even of value in helping to understand the morphology of the plant body with special



TEXT-FIG. 4 — Showing sections of apical cell and divisions in segments. **A**, **B**, diagramatic transverse and longitudinal sections respectively. *Haplomitrium gibbsiae* (after Campbell)— **C**, **D**, transverse sections of *Porella* and *Plagiochila* respectively; **E**, a segment of either C or D; **F**, transverse section; **G**, a segment. *Petalophyllum* — **H**, transverse section; **I**, a segment. *Fossombronia* — **K**, a segment. *Metzgeria*. Abbreviations — CoP, cortex stem primordial; LP, leaf primordial; McP, mucilage primordium; SP, stem primordium; LaP, lamella primordium; MrP, midrib primordium.

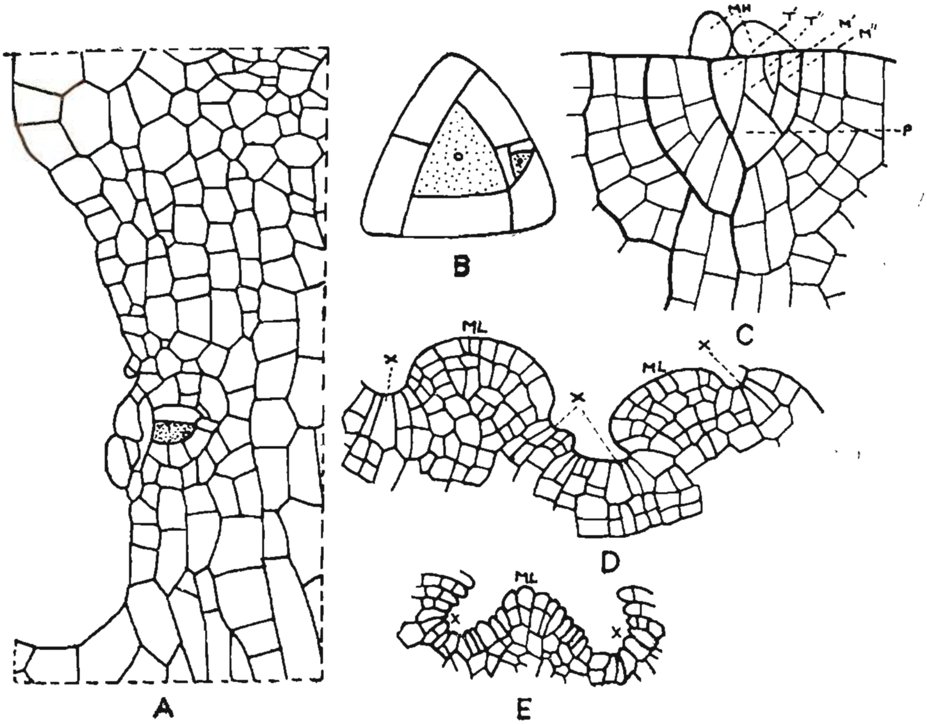


TEXT-FIG. 5 — Vertical longitudinal sections — A, *Dendroceros*; B, *Anthoceros* (schematic after Leitgeb); C, *Notothylas breuteii*, × 600 (after Campbell); D, *Anthoceros* (*Phaeoceros*), × 390 (after Bharadwaj); E, *Pellia epiphylla*, × 450; F, *Pallavicinius cylindricus*, × 225 (both after Campbell); G, *Riccia glauca*, × 325 (after Smith). The numerals indicate the position of apical cell, while D and V stand for dorsal segments. The cells between two epidermis in fig. C are dotted.

reference to the origin of the differentiation into stem and leaves ". This is an apt description with regard to the Calobryales, Jungermanniales and such Metzgeriales as they have two- or three-sided apical cells. Different types (Text-fig. 4) are: Calobryales, Jungermanniales, *Petalophyllum* - *Fossombronia* and *Metzgeria*.

In taxa where the apical cell, as a rule, cuts off four sets of segments (Text-fig. 5) development of the plant body, subject to the interpolation of air-chambers in the Marchantiales, follows more or less the same pattern.

In Calobryales (Text-fig. 6) a cortical cell is transformed into an apical cell of a branch. Several types of branching have been recognized in the Jungermanniales. However, for our limited comparison (Text-fig. 6) we may note intercalary and apical branching. In the former case a branch arises endogenously on the lower side of the stem and in the latter case a branch primordium is developed in one cell either



TEXT-FIG. 6 — Branching. A, vertical section of part of a stem of *Haplomitrium*, × 175 (after Campbell); B, origin (diagrammatic) of a branch primordium in a member of the Jungermanniales; C, horizontal longitudinal section of *Metzgeria furcata*, × 540 (after Strassburger through Goebel); D, horizontal longitudinal sections of *Anthoceros* (after Goebel); E, horizontal longitudinal section of *Riccia glauca* (after Campbell). Abbreviations — mh, mucilage hairs; m' m', first and second grade marginal cells; ML, middle lobe; p, surface cell of the first grade; t' t', old and new apical cells.

of a leaf or an amphigastrium primordium. In the Metzgeriales, where there is always a single apical cell, ventral branching is exogenous and branching in the horizontal plane of the thallus is pseudodichotomous and similar branching in *Sphaerocarpus*, *Monoclea*; in Marchantiales and the Anthocerotales where there is a single apical cell or a group of such cells, is truely dichotomous and is accompanied by the development of ' middle lobe '.

If diverse types like the Calobryales, Jungermanniales, Metzgeriales with three- or two-sided apical cells, and those with four-sided apical cells, *Sphaerocarpus*, *Monoclea* and the Marchantiales (subject to interpolation of air-chambers) can be retained in one taxon by those who segregate the Anthocerotales from the Hepaticae, why should the anthocerotes alone be segregated?

Bower (1935, p. 10) wrote, " A peculiar structural feature, of occasional but not constant occurrence, is the presence of stomata-like clefts on the lower side of the thallus " (Text-fig. 7). Leitgeb (1879) gave the same name to both these structures (Spaltöffung). Goebel (1930) considered these clefts to be homologous with the stomata (Text-fig. 8). Mucilage slits (Text-fig. 7E) have been recorded on the upper surface of the thallus. Bower (1935, p. 23) after due consideration concluded, " A picture would thus be suggested of the original haplophase of the Anthocerotales as a fully equipped photosynthetic structure, probably terete like the present diplophase ". It is of interest to note the presence of stomata on the gametophyte of *Rhynia gwynne-vaughani* (*cf.* Pant, 1962).

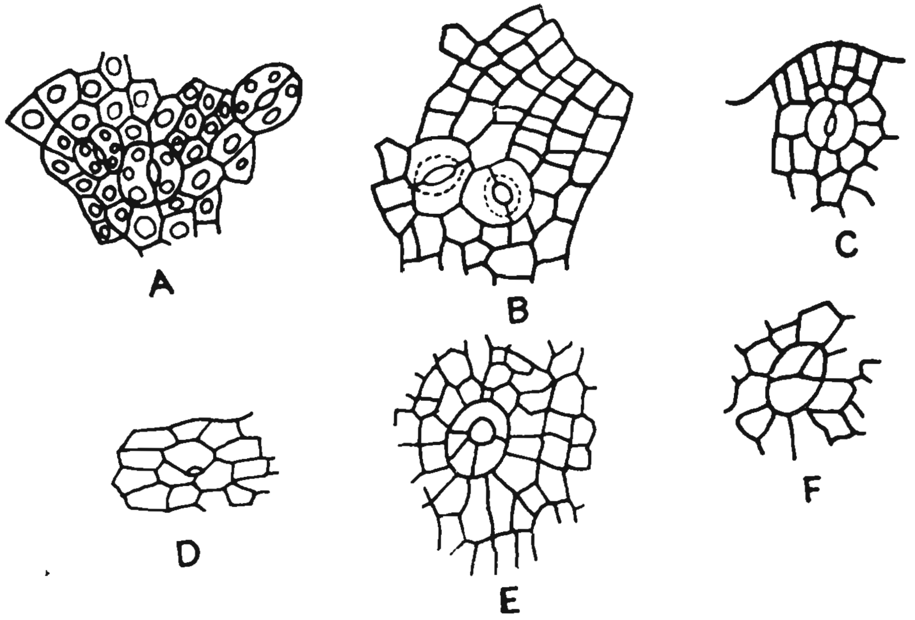
Proskauer (1960) writing on his " common ancestral denominator " speculated the presence of stomata in this hypothetical taxon. It is conceivable that the early archegoniates had stomata on both phases. In the later taxa, this expression was governed by ecological or habit of growth considerations.

In *Cythodium* (Lang, 1905; Kashyap, 1929) pores are present on the lower side of the thallus in small plants (those on the upper side are seen only in large plants) as an adaptation — not to reduce photosynthetic surface in small plants, growing in reduced light.

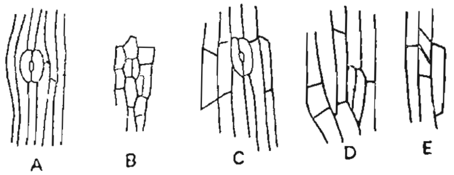
Regression of the mucilage clefts and stomata (to be taken up later) has made a beginning in this taxon, i.e. a trend towards their total elimination, a feature characteristic of other liverworts, has set in.

Combination of this primitive feature with the advanced features of the Marchantiales (shape of the apical cell, development of the thallus and branching in the horizontal plane of the thallus) suggests that the anthocerotes, in their evolutionary march, have travelled longer than any other corresponding group of liverworts. Kashyap (1929), Goebel (1930), Bower (1935) and Campbell (1940) have rightly placed the anthocerotes in a position preceding other taxa.

Cavers (1911, p. 141) wrote, " In every cell there is, in most species of *Anthoceros* a single large chloroplast, with a conspicuous pyrenoid" and on p. 143 he wrote on the chloroplasts in the capsule wall, " each cell contains two chloroplasts ". A part of this concept is considered here and part will be taken up with the sporogonium. Campbell (1905) had expressed the same view in respect of the haplophase chloroplasts and noted the presence of two chloroplasts in a species of *Anthoceros*. Again (1925, 1940) he compared the Anthocerotales with the Ulotrichales. In the later year he noted that: *A. pearsoni* has two chloroplasts, *A. howelli* has four and *Megaceros* as many as twelve in the inner cells of the thallus. A species of *Dendroceros* (Text-fig. 7) has on the lower side of the thallus a single large chloroplast in each cell of the epidermis; but two or three chloroplasts in each guard cell. *A. husnotii*, *A. punctatus* and *Megaceros* have no pyrenoids. Further



TEXT-FIG. 7 — Mucilage clefts on the thallus (all after Goebel). A, *Dendroceros* sp. (epidermal cells have one chloroplast, guard cells have two or three chloroplasts each); B, *Anthoceros* sp.; C, *Anthoceros*; D, *Anthoceros* sp.,— a stoma with a divided guard cell; E, *Megaceros* wih a cleft (from the upper surface); F, *Anthoceros*, a cleft without opening.



TEXT-FIG. 8 — Stomata on the capsule wall. **A**, *Anthoceros*; **B**, *Dendroceros crispulus* (rudimentary); **C**, *Megaceros* (functional); **D**, *Megaceros* (rudimentary); **E**, *Megaceros* stoma-mother cell with oblique division.

studies are likely to add to these examples of more than one chloroplast per cell of the haplophase. This feature is not universal either in the anthocerotes or in the green algae.

Bower (1935, p. 23) wrote, " The Anthocerotales show in this detail of chloroplast-number a scale of variation towards the state habitual in the higher plants, viz., that with numerous small chloroplasts ". This feature does not warrant the segregation of the Anthocerotales, nor their derivation from the green algae, because this resemblance cannot overrule the limitations imposed by oogamous reproduction.

5. Oil-bodies have so far not been recorded in this taxon.

6. Initials of the sexual organ in bryophytes other than the Anthocerotales become papillate and project above the general surface of the haplophase (Text-figs 9, 10). Similar is the case in the antheridium initials in Leptosporangiate ferns. Sometimes (*cf.* Bower, 1935, p. 510, fig. 397) the archegonia too are not sunken in this taxon. In the Anthocerotales, Psilotales, Lycopodiales and Eusporangiate ferns the initials are flush with the general surface of the haplophase. According to Bower (1935, p. 516) this is the simplest method of protection of the archegonium and the young sporogonium. In mosses, except the secondary archegonia of *Sphagnum*, these initials develop apical cells. Howe (1898), Campbell (1905, 1925, 1940) and Mehra (1967, 1968) have over emphasized this feature to segregate the anthocerotes from the Hepaticae.

The antheridium initial (Text-fig. 9) by transverse divisions produces some discs, each of which undergoes two vertical intersecting divisions in the Sphaerocarpales and the Marchantiales. This is followed by periclinal walls in each of the four cells to produce primary wall and primary androgonial cells.

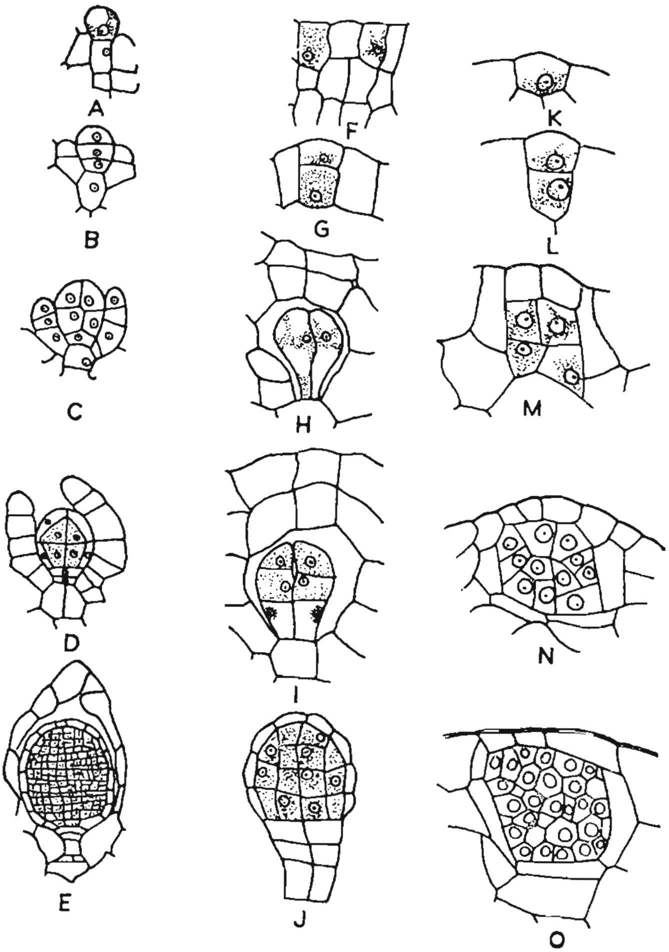
In the Anthocerotales the initial divides transversely into an outer and an inner cell. The outer produces two-cell thick roof of the antheridial chamber. The inner cell produces either one or more antheridia in each chamber. In either case the body of the antheridium develops as in Sphaerocarpales and the Marchantiales.

In *Marattia* the flush initial, as in *Anthoceros*, divides in the same manner. The outer cell produces the roof of the antheridial chamber. Here ends the resemblance with *Anthoceros*. The inner cell develops into spermatogenous tissue, without a stalk and antheridial wall, in the antheridial chamber.

Campbell (1925) noted a developmental similarity between the antheridium of *Notothylas* and *Marattia*. He had done so in 1895 (see Goebel, 1905, pp. 185, 186). Goebel (1905) wrote, " The mature antheridia are constructed like those of other Hepaticae with a wall-layer, stalk, and other parts, and its cellular construction is like what occurs elsewhere amongst Hepaticae, *but is known in none of the Pteridophyta* .... The endogenetic origin is evidently a secondary phenomenon... .... When Campbell endeavours to find an analogy between the antheridium of *Marattia* and an embedded antheridium of *Anthoceros*, which is covered on the outside by a double cell-layer, and to do so has to imagine the wall-layer and the stalk to be absent, the comparison seems to me to be bred of the wish to discover points of relationship between the Bryophyta and Pteridophyta, and not to be founded on facts ".

The spermatozoids in anthocerotes are bicilliate and according to Bower (1953, p. 11) they resemble those of other Hepaticae. In the Marattiaceae the spermatozoids are multicilliate.

Subject to minor details in the sequence of walls and sunken nature in anthocerotes, the development of the archegonium (except the Calobryales, see Campbell, 1920, Campbell, 1959) follows the pattern of *Riccia*, i.e. an axial row of cells is cut off by three peripheral or jacket cells, transverse walls make the archegonium double



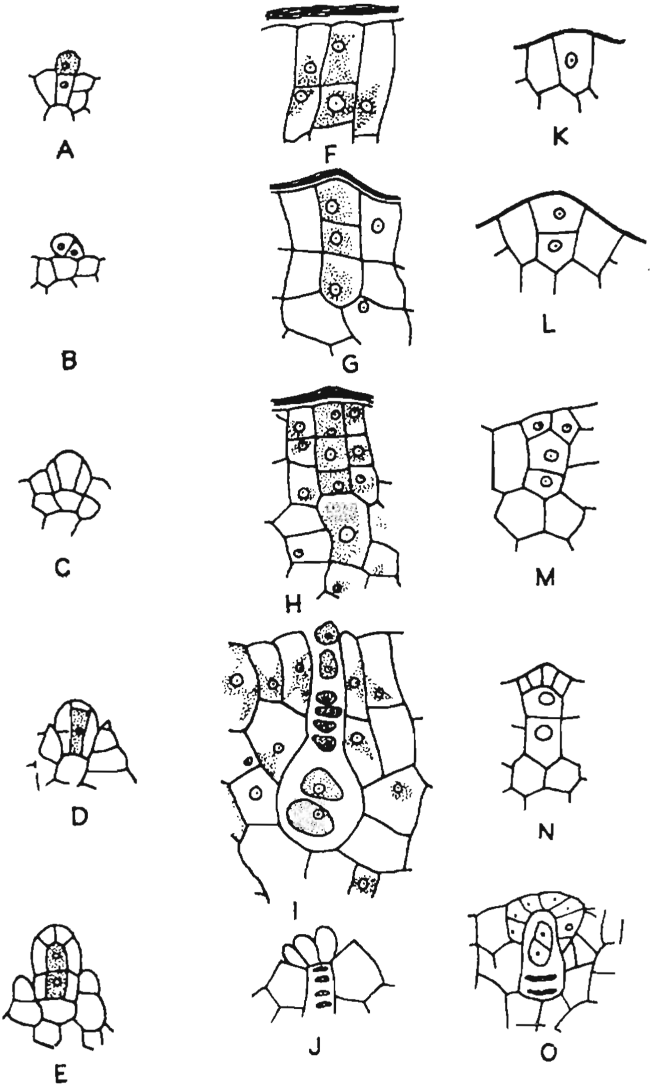
TEXT-FIG. 9 — Vertical sections showing antheridium development (diagrammatic). **A-E**, Sphaerocarpales (after Campbell); **F-J**, Anthocerotales (after Bharadwaj); **K-O**, Marattiaceae (after Campbell).

storied, another transverse wall cuts off the cover cell and this cell takes no part in the development of the neck (Text-fig. 10). Campbell (1940, p. 60) wrote, "The axial cells is next divided by a transverse wall into an outer and an inner cell. From the first by a similar division a terminal, or cap cell, is separated from the primary neck canal cell. The inner cell is later divided into two nearly equal cells — egg cell and venter canal cell. The primary neck canal cell divides into four or five neck canal cells". In spite of this difference the development remains hepatic.

In *Marattia* the initial divides into two or three cells (the lowermost when three take no further part). The top cell undergoes two intersecting vertical divisions. The four cells thus produced divide transversely to produce four rows of neck cells (four rows of neck cells in *Haplomitrium* are due to vertical division in one of the jacket cells instead of being laid in two or three jacket cells). The middle cell divides to produce the axial row of cells.

Campbell (1925) compared the archegonium of *Notothylas* with that of *Marattia* to indicate a close similarity, ignoring the differences in the development of the neck and neck canal cells in the two genera.

Bower (1935, p. 12) rightly remarked, "The sexual organs of the Anthocerotales,



TEXT-FIG. 10 — Vertical sections showing archegonium development (diagrammatic). **A-E**, *Riccia glauca* (after Campbell); **F-I**, *Anthoceros* (after Bharadwaj); **J**, showing cap cells (after Campbell); **K-O**, Marattiaceae (after Campbell).

though differing in certain details from other Hepaticae, are clearly of the Hepatic-type and this is so notwithstanding that they alone are deeply sunk in the fleshy thallus and that the antheridia are even endogenous in origin". (Leitgeb, 1879; Lampa, 1903 noted exogenous antheridia).

Goebel (1905, p. 186) on this topic wrote, "in Anthoceros we have to deal with a derived type which at any rate shows no near relationship to the Pteridophyta. The kinship of Anthoceros to the Pteridophyta is then, so far as the sexual organs are concerned, a mistaken one".

Foregoing comparison and opinions expressed do not warrant:

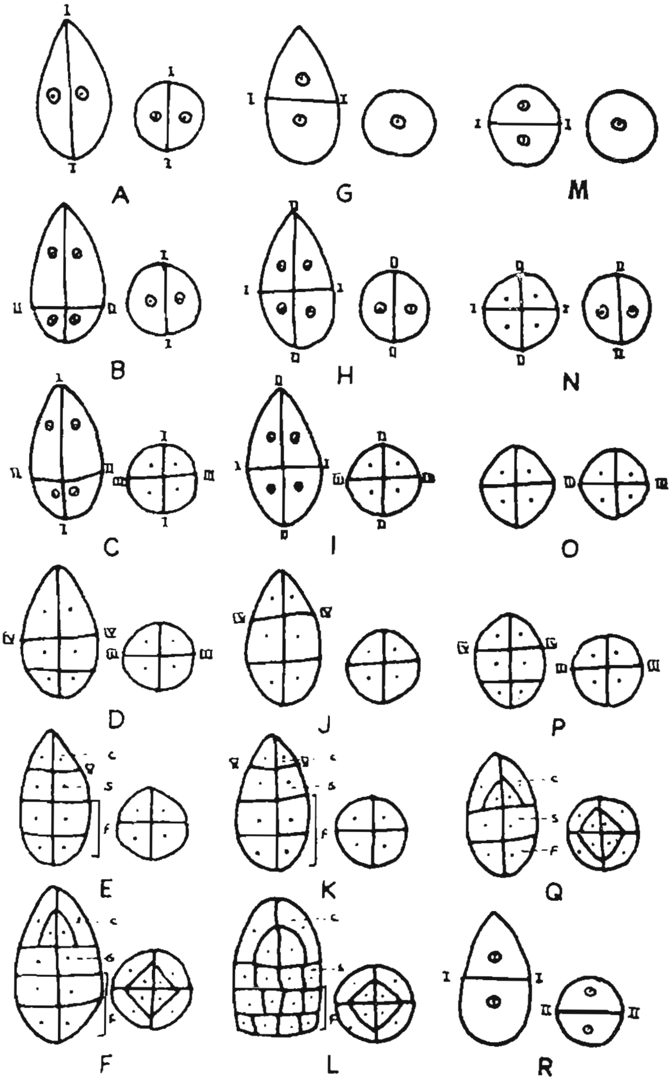
1. Derivation of the Archegoniatae from ancestors like the modern green algae with unicellular gametangia (Bold & Wyne,

1977), not even from *Chara* where growth of pericentral cells encloses the oogonium.

2. Derivation of psilophytes with pteridophytic archegonium (see Pant, 1962) from anthocerotes with hepatic archegonium and *vice versa*.

DIPLOPHASE

The zygote in the Archegoniatae, except most species of the Anthocerotales is more or less spherical and the first wall, except the Anthocerotales and pteridophytes with quadripolar embryo where it is vertical, is transverse. In most of the Anthocerotales (Text-fig. 11) the embryo is spindle-shaped and the first wall is vertical. In mosses and pteridophytes with bipolar, exoscopic embryo the hypobasal half forms the foot and the epibasal half develops an apical cell. In no liverwort does an embryo develop an apical cell and apical growth.



TEXT-FIG. 11 — Embryology of some anthocerotes (diagramatic) in longitudinal and transverse sections. **A-F**, *Anthoceros fusciformis* (after Campbell); **G-L**, *A. crispulus* (after Bharadwaj); **H-Q**; *A. erectus* (after Mehra & Handoo); **R**, *Notothylas orbicularis* four-celled embryo (after Campbell). Roman figures indicate the sequence of walls.

Mehra and Handoo (1953) noted a spherical zygote in *Anthoceros erectus* (Text-fig. 11M-O). Transverse first wall has been recorded by Campbell (1905) in *Notothylas orbicularis* (Text-fig. 11R), Pande in *N. indica*, Bhardwaj (1950) in *A. crispulus* and Mehra and Handoo (1953) in *A. erectus*. According to Bhardwaj (1958) Hofmeister found an oblique septum in *A. laevis*. Leitgeb (1875) mentioned first division in the hypobasal half to be vertical in *Frullania dilatata*.

Campbell (1940, p. 267) wrote, " There is a good deal of variation in the early development of the embryo in *Equisetum arvense* and *E. maximum* the basal wall is transverse and this may be the case in *E. debile*; but in the latter case there is a good deal of variation and the basal wall may be vertical". The spindle-shaped zygote, and the first wall being vertical are derived conditions.

The embryology of the Calobryales is not sufficiently known. According to Campbell (1959) the first transverse wall is not equatorial, the epibasal cell is larger of the two cells. The second wall in each cell is vertical. According to Campbell (1940) the embryo comes to be of four tiers. In most of the Jungermanniales and the Metzgeriales, the hypobasal half produces a haustorium and a filamentous embryo is developed from the epibasal half. However, in *Frullania dilatata* (Leitgeb, 1875; Cavers, 1911) and *Fossombronia* (Campbell, 1940) the hypobasal half produces the foot. In these two taxa the embryo consists of three tiers of four cells each, i.e. foot, seta and capsule tiers. Campbell (1940, p. 136) noted similarity with the embryo of *Anthoceros* in this respect.

According to Campbell (1940, p. 39), " In *Anthoceros*, following the octant division, a second transverse division occurs and the embryo consists of three tiers, each consisting of four equal cells (compare *Frullania* and *Fossombronia*). The two lower tiers develop into the large foot. The upper tier by further transverse divisions, is separated into a terminal segment in which the archesporium arises, and an intermediate zone between this and the foot ". Thus at this stage the embryo is a filament of four tiers of four cells each. *Anthoceros fusciformis* (Campbell, 1905, fig. 69) (Text-fig. 11A-E) shows this type of development.

Bhardwaj (1950, pp. 152-155, figs 19-23) (Text-fig. 11F-L) described the embryology of *Anthoceros crispulus*. In this species the first wall in the zygote is transverse and not vertical. Octant development follows the same pattern as in the Marchantiales and *Anthoceros erectus* (Mehra & Handoo, 1953). Transverse walls are laid both in the hypobasal and epibasal halves to produce a filament of four tiers of four cells each. The lowermost two tiers, as in *A. fusciformis*, develop into the foot, and the upper two tiers give rise to the seta and the capsule as in *A. erectus* and other species where the embryo consists of only three tiers of cells. Elimination of transverse walls in the epibasal half too can result in an octant only. The embryo of *A. crispulus* in having, before periclinal walls are laid, four tiers of four cells each, resembles the filamentous embryo of the Calobryales, Jungermanniales, etc. Growth, following the laying down of periclinal walls, makes it anthocerotalean embryo. This embryology suggests how the octant embryo of the Marchantiales may have arisen. In mosses and pteridophytes the embryo has apical growth at least in the epibasal half; while the Anthocerotaceae like other liverworts lack in apical growth. The embryo is nearest to that of the Hepaticae.

Foot tier is the first to become active and grow into a foot to establish a close contact with the thallus to draw nutrients from the latter. The top tier of four cells, cut off by the first transverse divisions in the epibasal half, differentiates into the ' primary capsule ' (where the seta adds to it from below) or the capsule (where the seta does not add to it). Former is the method of Anthocerotales and a few of the Jungermanniales and latter is the method of rest of the Jungermanniales and the Metzgeriales, etc.

In anthocerotes periclinal walls are laid in the top or terminal four cells. This is followed by differentiation into: columella, archesporium and the capsule wall. The seta tier becomes active and begins to add to the tissues of the primary capsule from below.

Cavers (1911, p. 119, fig. 82G, H, p. 120) enlarged the observations by Leitgeb (1875) on *Frullania dilatata*. Campbell (1940, pp. 136-138) described this and some more cases where the seta does contribute to the basal part of the capsule. He (p. 136) found resemblance among *F. dilatata*, *Fossombronia* and *Sphaerocarpus* on one hand and with *Anthoceros* on the other (i.e. in all these cases the embryo consists of three tiers of four cells each). In these cases the foot develops from the hypobasal half for close contact with the thallus. Other cases described by him are: *Lejeunea serpifolia*, *Radula* and *Cephalozia bidentata*. In these cases the hypobasal half develops into a haustorium and the whole sporogonium is developed from the epibasal half and the seta does add to the basal part of the capsule. In *Radula* (p. 137), " In the terminal segment the first periclinals define the primary archesporial cells, but similar divisions in the segments below the apex also contribute to the archesporium, which is much more extensive than in *Frullania* ".

Meristematic activity of the seta in the Anthocerotales as compared with the Jungermanniales and Metzgeriales is a question of degree and not of kind. Cavers (1911, p. 149) rightly wrote, " meristematic tissue above the haustorium of the sporogonium of the Anthocerotales evidently results from the persistence of a stage which is quickly passed through in the development of the sporogonium in other Hepaticae ".

Campbell (1925, p. 68) correctly expressed the fate of a normal sporogonium of the Anthocerotales. However, as a result of his observations on *Anthoceros fusciformis*, growing under exceptionally favourable circumstances, he (p. 74) concluded that a close resemblance between this sporogonium and the Devonian Rhyniaceae warrants the assumption of a real relationship between the latter and the Anthocerotaceae. He overlooked the fact that this is the only archegoniate taxon with a basal meristem in the sporogonium and the Rhyniaceae had apical growth.

Bower (1935, p. 109) rightly indicated that, " before basal intercalary growth alone no morphological future seems to be open ". Yet Campbell (1940) derived the psilophytes or the Rhyniaceae from the Anthocerotaceae (Text-fig. 1). This had the effect of catapulating this taxon to an unwarranted position. Many authors continue to follow him.

Anthocerotes and sphagna are the only bryophytes where the entire endothecium produces a sterile columella and the archesporium arising from the inner layer of the amphithecium is inverted over it. The condition in *Horneophyton* (see Bower, 1935, p. 120) is similar, though the columella is phloem part of the central stele. In all the three cases the archesporium is essentially axial in contrast with that of living pteridophytes, where it is hypodermal, or superficial in origin. In *Sphagnum* the archesporium is enclosed in a spore-sac and a tapetum surrounds the sporogenous tissue in *Horneophyton*.

On the basis of a survey of the relative extent of the columella and the archesporium, various genera of anthocerotes can be arranged in a series. At one end of this series are types with a well developed columella and a thin archesporium. The latter progressively becomes more massive and the former regresses. At the other end are non-columellate species of *Notothylas*. This genus is reduced and is no closer to other hepatics than is *Anthoceros*. In spite of the difference in the origin of the archesporium, it is nearer to that of other hepactics than any other taxon because of the absence of a spore-sac and a tapetum.

In the primitive taxa of hepatics other than anthocerotes, spore-mother cells and elater-mother cells belong to the same generation. As a result of sporogenesis there come to be four spores for each elater. In the higher taxa divisions are interpolated between the original spore-mother cell and the one that produces four spores. The result is presence of several spores to each elater.

In the anthocerotes converse is the case. In *Dendroceros*, the most primitive genus, the elater mother cells do not divide (see Schuster, 1966), and the ratio remains: four spores to one elater. In other genera the elater-mother cells divide mitotically; the cells generally remain united and the result is: four spores to one compound elater or pseudo-elater. Often the pseudo-elaters break, or undergo extra divisions, or some cells branch.

In *Dendroceros* and *Megaceros* (where the cells remain placed end to end) the elaters/

pseudo-elaters develop spiral thickenings, as in other hepatics. Hepaticae is the only taxon, where elaters/pseudo-elaters are present, no other archegoniate has these. This feature indicates that in spite of a difference in the origin of the archesporium, the anthocerotes are nearer to Hepaticae than to any other taxon.

Cavers (1911, p. 143) and Bower (1935, p. 15) indicated that each cell of the capsule wall contains two large chloroplasts. Campbell (1905, 1940) showed that each guard cell of stomata on the capsule wall of *Anthoceros pearsonii* has a single chloroplast. Bharadwaj (1965) noted that each cell in either phase of *A. communis* contains a single chloroplast. Bower (1935, p. 16), on the authority of Schimper, noted that most of the cells of the sporogonium contain two chloroplasts, but those of the epidermis contain several chloroplasts. A male gamete has no chloroplast, so doubling or increase in the number of chloroplasts in cells of the sporogonium is not due to syngamy but due to fission — a condition that is normal in the Archegoniatae. It was the absence of this clear understanding that lead some early authors to over emphasize a partial truth and suggest a derivation of this taxon from green algae.

Most species of *Anthoceros* and *Phaeoceros* (Text-fig. 8) are stomatose (*A. halli* has a few large stomata on the upper part of the capsule); some species of *Folioceros* are stomatose; while others (*F. fusciformis* and *F. incurvans*) are non-stomatose (see Bharadwaj, 1972); some species of *Megaceros* have poorly developed or no stomata; species of *Dendroceros* either have regressed stomata or none and *Notothylas* in non-stomatose.

Proskauer (1948) indicated that a cross section of *Anthoceros* capsule shcws four lines of dehiscence of which only two are functional. This resembles the Calobryales and Monocleales (with one of the lines being functional), the Jungermanniales and the Metzgeriales. However, according to Proskauer (1948) the capsule does not open by two valves in the beginning (*cf.* the Blyttiaceae). Openings appear along two lines and they coalesce. External agencies cause the opening by two valves.

CYTOLOGY

Mehra and Handoo (1953) on the basis of persistent occurrence of *m*-chromosome in Anthocerotales, Jungermanniales, Sphaerocarpales and Marchantiales suggested a monophyletic origin of these taxa. In no pteridophyte do we find the presence of *m*-chromosome.

Proskauer (1960, p. 17) wrote, " I do not wish at this stage, to go beyond my recent presentation (Proskauer, 1958a) of the cytological evidence suggesting the derivation of the typical karyotype of liverworts from a kayrotype similar to that of typical hornworts. I do not concur with Tautno's (1959) opinion on this point". Do these features not conflict with the " Anthorhyniaceae " concept ?

RELATIONS HIPS

The Anthocerotaceae are considered to be a synthetic taxon and conclusions that are not warranted have been drawn on the basis of these resemblances. It seems desirable to discuss some of these relationships before arriving at a conclusion. Those to be evaluated are: (i) between anthocerotes and other Hepaticae,(ii) between the Anthocerotaceae and mosses through *Sphagnum*, (iii) between anthocerotes and the Rhyniaceae, and (iv) between the last taxon and mosses.

To determine the relationship of the hornworts with rest of the Hepaticeae, matter under data and discussion can be considered under three heads: (i) features that are hepatic, (ii) those that appear to be different, but show a trend towards what is normal in other liverworts, and (iii) those that are anthocerotalean, or nearly so.

Habit of growth, shape and segmentation of the apical cell, further divisions in the segments or merophytes and development of the plant body resemble those of the Metzgeriales, *Monoclea*, *Sphaerocarpus* and the Marchantiales; branching in the horizontal plane of the thallus agrees with the last three taxa. Development and structure of the sexual organs are hepatic and not pteridophytic. It is not fair to ignore these features and over emphasize their sunken nature — the simplest protective device. But for the absence of oil bodies, the haplophase is hepatic. Absence of apical growth recalls hepatic and *Sphagnum* sporogonia. Presence of a *m*-chromosome suggests lack of relationship with pteridophytes and the karyotype is hepatic.

That the meristematic seta is the retention of a stage which is quickly passed through in the Calobryales, Jungermanniales and the Metzgeriales is proved by the embryology of *Frullania dilatata*, *Cephalozia bidentata* and *Rudula*. A single large chloroplast per cell of the thallus and two such chloroplasts per cell of the sporogonium concept is at best a partial statement and a single large chloroplast per cell is not universal in green algae. Increase in number of chloroplasts in the cells of sporogonium is not due to syngammy but due to fission — a condition normal in the Archegoniatae. Elimination of mucilage clefts and stomata is a trend towards what is normal in other liverworts.

Absence of oil bodies and presence of a tierd embryo (though longitudinal cleavage disguise the underlying filamentous nature) and by comparison with mosses and pteridophytes it is nearest to the filamentous type and is actually filamentous in *Anthoceros crispulus*). Entire endothecium producing a columella; the archesporium of amphithecial origin inverted over the columella (remaining essentially axial in contrast to the peripheral or superficial archesporium of pteridophytes); compound elaters in five out of six genera (although the presence of elaters, and those of *Dendroceros* and *Megaceros* with spiral thickenings are features of hepatics); and fully photosynthetic sporogonia, in combination, are features that are not shared with any other group of liverworts in combination.

Bower (1935, p. 19) wrote, " The conclusion from such considerations would be that the place of Anthocerotales is with the liverworts, but not closely with any section of them ". The question does not remain, whether the Anthocerotales are closely or more distantly related to other Hepaticae ? It becomes, what are the status and position of the Anthocerotales in the Hepaticophytina ?

Cavers (1911, p. 196) on the relationship between Sphagnales and the Anthocerotales wrote, " These two aberrant groups show a striking resemblance to each other. If Anthocerotales are to be made a separate class from the Hepaticae, either Sphagnales should be considered a separate class apart from the Musci, thus making four primary divisions of Bryophyta or the Anthocerotales and Sphagnales might be united to form a class ". However, he retained the customary two-fold division of the Bryophyta.

Bower (1935, p. 65) wrote, " *Sphagnum* has always been ranked as a Moss on general grounds of habit. But now not only does the evidence from the sexual organs point to an intermediate position between the mosses and liverworts, but also the primary segmentation and absence of apical growth in the sporogonium and the amphithecial origin and complete dome-shaped archesporium, are all features which point rather to the Anthocerotales than to the true Mosses ". Campbell (1940, p. 185) wrote, " There are some significant points of structure between *Sphagnum* and *Anthoceros*, indicating a possible remote relationship".

Leaving aside ecological adaptations, vegetative development and structure of the haplophase of *Sphagnum* resemble those of other mosses*. *Sphagnum* has no elaters or pseudo-elaters, spores are enclosed in a spore-sac, multistratose capsule wall lacks in intercellular spaces, the capsule has an operculum and opens by an annulus.

Resemblances with mosses outweigh the differences between them, so the sphagna cannot be separated from true mosses. Besides the differences between the sporogonia of *Anthoceros* and *Sphagnum*, the gametophytes are so different that a close relationship between the two taxa is not warranted. Campbell (1940, p. 69) wrote, " It is possible, however, that the highly specialized sporophytes of the higher mosse is a case of parallel development rather than an indication of any close relationships with *Anthoceros*." Bower (1908) and Chopra (1967) considered the Hepaticae and Musci to be diphyletic. Steere (1969) suggested that the bryophytes are polyphyletic. Presumably the Bryophyta are triphyletic, Takakiophytina constituting the third line.

It may be of interest to note that all stages through which the extant fauna and

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**Andreaea* is unique in that the apical cell of the leaf does not cut off two sets of segments. A single segment is cut off by a wall parallel to the posterior face of the apical cell.

flora have passed are not lost. Some of them are retained either as fossils or in some living taxa. A few examples of the latter are: *Takakia*, in having parenchymatous apices of the subterranean axes, and genetically unfixed apical cells in aerial axes, represents a stage between the ancestors without apical cells (green autotrophs) and those with them (Archegoniatae). Liverworts, which have apical cells in the haplophase but lack in them in the diplophase, show an early stage in the evolution of the archegoniate diplophase. Anthocerotes, with peculiar chloroplasts, enable some authors to connect this taxon with green algae. Basal meristem of Anthocerotales, which has no morphological future open to it, is retention of a stage, which is quickly passed through in other orders of the Hepaticae. Presence of mucilage clefts on the thallus and stomata on the capsule wall are retention of a feature of early archegoniates. Sphagna, in retaining hepatic features and the psilophytes, in lacking lignin, are other examples. Cytological and physiological resemblances between the green algae and Embryobionta are the best examples of the retention of features from the pre-archegoniate green ancestors with the same cytological and physiological features. I (1981) named these early ancestors as " green autotrophs ".

Diametrically opposite views have been expressed on the relationship between the Anthocerotales and the Psilophytales. Various authors have suggested the derivation of bryophytes or anthocerotes from pteridophytes or the Rhyniaceae through regressive evolution (for references see Takhtajan, 1953). Miller (1974, p. 166) wrote " Bryophytes in the broadest sense are vascular plants from stocks which arose in the early to middle Devonian from Rhyniophytina and Zosterophyllophytina". I do not propose to add to what I have already written (1981) on this topic.

Campbell (1895), on the basis of what he considered to be similarities between the sexual organs of the two taxa found kinship between *Anthoceros* and pteridophytes. Goebel (1898, 1905, p. 186) wrote, " The kinship of Anthoceros to the pteridophytes is then, so far as the sexual organs are concerned, a mistaken one ". Bower (1935, p. 109) wrote, " Before basal intercalary growth alone no morphological future seems to be open ". According to Proskauer (1960) Kidston and Lang (1920) astutely forebore to consider the point of view that the psilophytes had an origin from Anthocerotes.

Campbell (1925) ignored others' point of view, made a comparison between the sexual organs of *Notothylas* and *Marattia*, noted a close similarity (though wrongly) between the sporogonium of *Anthoceros* and the sporangium of the Rhyniaceae and concluded that a real relationship between the two taxa is warranted. Goebel (1930), Bower (1935) and Zimmermann (1952) did not accept this point of view.

Campbell (1940, p. 72) wrote, " The ancestors of vascular plants, if not actually anthocerotes at any rate closely resembled them ". He (p. 190, fig. 1) did not remove the Anthocerotaceae from its position with the Bryophyta and lump it with vascular plants, as was done by Mehra (1968, p. 24, fig. 9). Zimmermann (1952, p. 464) wrote, " Parallel to the Rhyniaceae the Bryophytes developed from thalassiophytic forms by relative dominance of the gametophyte".

Mehra and Handoo (1953) developed the 'Antho-rhyniaceae' concept. Howe (1898, vide Cavers, 1911, p. 148) enumerated five peculiarities to distinguish anthocerotes from rest of the Hepaticae. Of the features enumerated by Mehra and Handoo four are more or less the same as those of Howe. Instead of the stomata on the capsule wall they added the low number of chromosomes in Anthocerotes. Goebel (1905, p. 185) noted the deviations from the Hepaticae shown by *Anthoceros* and wrote, " But a careful examination does not show a resemblance with peculiarities found in the Pteridophyta".

Mehra and Handoo compared the sporangium of *Horneophyton* with sporogonium of *Anthoceros* and did not derive the latter from the former taxon and rightly so. They derived this stock from the Chlorophyceae.

Proskauer (1960, pp. 15, 16) wrote, " I suspect that the anthocerotalean sporophyte is derived by reduction and specialization from a sporophyte such as that of *Horneophyton*...... In the case of *Horneophyton* itself the occurrence of forked sporangia represents indirect counter evidence...... I do not wish to expostulate at length on the Psilophytic ancestory of Anthocerotales. At present no firm proof can be brought...... I have no quarrel with the postulated "Anthorhyniaceae" of Mehra and Handoo (1953)". He also presented a pen picture of "common ancestral denominator" for these groups.

Mehra (1967, p. 50), on "common ancestral denominator", quoted Proskauer as: "A green parenchymatous land plant; with stomata, single laminate plastids with 'pyrenoid', presumably archegoniate, and with alternation of generations".

According to Zimmermann (1952) origin of an apical cell capable of continuously cutting off segments in a spiral manner, was followed by internal differentiation into a central or medullary and a peripheral or cortical regions. This was an important step in the evolution of the Embryobionta. It made possible the divergence between oogamous and archegoniate plants as well as the internal differentiation of the stem, its branches and the sexual organs of the Archegoniatae.

In the passage quoted above by Mehra no mention is made of an apical cell. It is assumed that Proskauer's "common ancestral denomator", in the absence of an apical cell, was not archegoniate.

Proskauer, continuing (pp. 15, 16) wrote, "It is quite possible that the archegoniate plants arose from a member of the Ulotrichales which not only possessed isomorphic alternation of generations but was itself subaerial and parenchymatous..... Adding stomata, sex organs with sterile outer tissue, etc. we arrive at the "Anthorhyniaceae, but as a group with at maturity free alternating phases, and thus by minimum definition a pteridophytic group". Again no mention is made of an apical cell.

Mehra (1968, p. 23) on Anthorhyniaceae concept wrote, "...... the haploid and diploid phases were morphologically, more or less similar, independent and photosynthetic. Both of them had apical cell segmentation and were radial in organization...... The haploid phase possessed antheridia and archegonia......" The Antho-rhyniaceae of Mehra and Handoo were archegoniate. It is difficult to accept that the diploid phase in all the early archegoniates had apical growth. If so, why such an important feature was lost in the Hepaticae and was replaced by basal growth in the Anthocerotaceae ?

Steere (1969, pp. 137, 138) wrote, "It has been proposed by Zimmermann (1932) and others who promulgate the analogy between isomorphic algae and bryophytes or protobryophytes were identical but separate, and that the present-day epiphytic habit of the sporophyte is derived or secondary, and relatively recent. Although space does not permit a full discussion of the merits of the case, in my opinion the idea is fallacious and should be discarded".

Recently, I have re-confirmed that bryophytes are collaterals of green algae and pteridophytes, offered an explanation of the origin of archegonium and concluded that the advent of archegonium brought about changes, which were not possible in the oogamous green algae. Meiosis was deferred and the zygote continued to develop into a new, hitherto unknown, entity — the embryo. Origin and evolution of an interphase became possible, the function of nourishing the developing sporophyte, was passed on, mainly to the gametophyte.

Bower (1935, pp. 142, 143) after discussing the embryos of *Tmesipteris* and *Anthoceros* (a consideration which can include the embryos of *Sphagnum* and *Rhynia* (cf. Pant, 1962) wrote, "It will be more instructive to enquire what follows in each, as it passes to the adult state...... The alternatives open to the epibasal half are either (i) direct spore-formation without branching or other marked morphological features than intercalary growth, or apical growth soon arrested; or (ii) morphological elaboration with continued apical growth and branching, while spore-formation is deferred. The former is the method of the Bryophyta, with their capsules dependent on the gametophyte; the latter is the method of vascular plants with their independent* sporophyte".

In the light of these remarks is it fair to remove the Anthocerotales from the Bryophyta and lump them with the Pteridophyta ? The place of the Anthocerotales,

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*It should not imply that Bower considered that two phases in the Pteridophyta were free from the very beginning (see Bower, 1935, p. 139, fig. 103A), with hepatic sexual organs, and the sporogonium lacking in branching and apical growth, is with the Hepaticae. The place of Rhyniaceae, with branched axes bearing terminal sporangia and the archesporium with a tapetum, as well as, the pteridophytic archegonium of *Rhynia* is with the Pteridophyta.

Takhtajan (1953) compared the branching axes of *Horneophyton* with branched sporogonia (teratologies) of mosses. According to Mehra (1968, p. 9), " Merker (1959) interprets the creeping part in *Rhynia* and *Horneophyton* is the gametophyte and not the rhizome.... He considers that a circumvellation is present at the region of the junction of the aerial part with the prostrate one which is not the case in a dichotomously branched stem ". Miller (1974, p. 162) credited to Lemoigne (of course with a note that his interpretations are not fully accepted by palaeobotanists) on *Rhynia* as: " He has unquestionably discovered both archegonium-like and antheridium-like structures, which are consistent generally with Merker's observations ". This confirms the discovery of archegonia in *Rhynia gwynne-vaughani* (Pant, 1962).

Hebant (1977, pp. 108, 109, pl. 80) wrote, " It may be noted that the earliest known tracheophytes were more similar in general appearance to certain present day bryophytes than to most contemporary vascular plants. This concerns more particularly certain Rhynophytina such as *Steganotheca* or *Cooksonia*. Their tiny dichotomously branched axes with terminal sporangia are somewhat reminiscent of moss sporogonia. (The latter are unbranched, but some examples of teratological branching are known; in these cases, they are frequently dichotomous)...... As pointed out earlier, the internal organization of these early tracheophytes, with a ring of outer supportive cells and a ' simple ' central strand, is also more or less comparable to that of moss stems".

" With particular reference to *Rhynia*, it must be noted that Kidston and Lang (1920) failed to identify lignified secondary thickenings in the tracheids of *R. major*. Similar observations were made on *Nothia aphylla* by A. G. Lyons...... Similarly, Proskauer (1960) suggested that the water-conducting cells of *R. major* may have been unlignified. These elements in *R. major* and *Nothia* would then be very similar to the hydroids of mosses. Indeed the stele of *Rhynia* as a whole may show an extraordinary resemblance to certain moss steles (figs 339-341). "

It is clear that Rhyniaceae resemble the mosses more than they do with the Anthocerotes and that a moss type sporogonium is not handicaped by a basal meristem as apical growth of the sporophyte is the rule in mosses. I am not tempted to suggest a " Musco-rhyniaceous " stock, nor I suggest an " Antho-sphagno-rhyniaceous " stock because I am fully aware of the limitations inherent in the diplophase of bryophytes. The position of the anthocerotes vis-a-vis other hepatics is the same as that of *Sphagnum* vis-a-vis other mosses and the Rhyneophytina vis-a-vis other sub-divisions of pteridophytes. The resemblances between the Anthocerotales, Sphagnales and the Psilophytales do not warrant any phyletic affinity between these three taxa closer than what exists between the Hepaticae, Musci and the Pteridophyta. Each one of the first three taxa is an early blind offshoot from its respective stock.

CONCLUSION

Bold (1956-57) modified the classical concept of the Bryophyta by raising the rank of anthocerotes, other hepatics and mosses to that of three divisions. Steere (1958) did not concur with him and remarked, " As a professional bryologist, on the other hand, I can go much further than Bold has and with equal justice raise other highly distinctive groups of Bryophytes to divisional rank ". I fully agree with him. I (1975) treated mosses as subdivision Muscophytina, and I still maintain the rank of a division for the Bryophyta. A lot of information is needed to do justice to splitting up of Bryophyta. In my opinion a start should be made by defining the subdivisions and classes before the creation of more divisions.

In 1967, I considered the Bryophyta to be diphyletic and Steere (1969) considered them to be polyphyletic. I (1975) treated Musci as a subdivision. They are at least triphyletic, Takakiophytina being the third suborder.

*Subdivision Takakiophytina** — Prostrate or subterranean axes, lacking in leaves and rhizoids, with parenchymatous apices, bear erect leafy shoots with pyramidal or tetrahedral apical cells; mucilage pads on the lower portions of shoots are composed of crowded, numerous, multicellular and branched hairs, which may possibly be homologous to moss rhizoids (though the functions of the two are different); leaf development from a segment, besides unparalleled form, is unique; oil-bodies are present; antheridia are unknown; pedastaled and spirally twisted archegonium recalls moss archegonium and sporogonium is unknown. Under humid cultural conditions apices of erect shoots become parenchymatous and often the oil-bodies are lost. The chromosomal compliment, as a rule, is $K(n) = 4 = V(H) + V + J + J(h)$, or $K(n) = 5 = V(H) + J + V_1 + V_2 + J(h)$, though sometimes in *T. lepidozoides* an additional " F-derivate " is present.

Subdivision Hepaticophytina — The shoots whether erect or prostrate are with flat leaves, with genetically fixed apical cells in both cases and so are the oil-bodies (except the Anthocerotales); all growth other than that of the plant body is intercalary; elaters or pseudoelaters are almost invariably present.

Subdivision Muscophytina — Leaves are flat, apical cells and oil-bodies are genetically fixed; and growth (except some organs in *Sphagnum*) is apical; and elaters or pseudoelaters are always absent.

Diagnostic features of the three subdivisions of the Bryophyta indicate that the Anthocerotales belong to the Hepaticophytina. This is in conformity with the conclusion arrived at while discussing the relationship of the Anthocerotales with rest of the Hepaticae on the basis of data and discussion (*cf.* Bower, 1935, p. 19: " the place of the Anthocerotales is with the liverworts ").

A combination of features seen in the Anthocerotales is not shared by it with any other section of liverworts. This warrants the status of a class coordinate with other classes into which the Hepaticophytina is to be split up sooner or later.

Resemblances between the two phases coupled with 5 or 6 chromosomes against 8-9-10 chromosome in other hepatics indicate for this class a position at the very bottom of the heirarchy of the Hepaticophytina.

It seems reasonable to presume that the ancestors of modern Anthocerotae or Anthoceropsida parted company from the stock/stocks that gave rise to other modern orders of the Hepaticophytina earlier than did the latter stock/stocks diverge to be the ancestors of modern orders other than the Anthocerotales or classes other than the Anthocerotae or Anthoceropsida.

To sum up, Anthoceropsida or the Anthocerotae, a class of Hepaticophytina, have been considered a synthetic taxon and much, that is unwarranted, has been read in the resemblances between this and other taxa. This class like the other Bryophyta is a collateral of green algae and the Pteridophyta. Ancestors of Anthoceropsida, presumably, were the first to part company or diverge from the stock/stocks that later diverged into other sections of the Hepaticophytina. Modern hornworts, at the very bottom of the heirarchy of the Hepatophytina, are a blind evolutionary line.

I thank all authors whose contributions have provided material for this lecture, particularly Prof. Kashyap, a pioneer botanist and father of bryology in India; Professors Goebel, Bower, Campbell, Zimmermann and Dr Cavers. I am indebted to the Chairman and members of the Governing Body of Birbal Sahni Institute of Palaeobotany for the honour they have conferred on me by inviting me to deliver this lecture on the birthday of the late Professor Birbal Sahni.

Scion of a family of intellectuals, by his qualities of head and heart, care for the progress of juniors, and courage to fight for upholding the right causes, he inspired many persons and endeared himself in their hearts. I consider him a model to be emulated.

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*This diagnosis is based upon the contributions of Hattari *et al.* (1968, 1974) and Schuster (1966a).

REFERENCES

Bhardwaj, D. C. (1950). Studies in Indian Anthocerotaceae. I. The morphology of *Anthoceros crispulus. J. Indian bot. Soc.*, **29** (3): 145-163.

Bhardwaj, D. C. (1958). Studies in Indian Anthocerotaceae. II. The morphology of *Anthoceros cf. gemoulosus. J. Indian bot. Soc.*, 37 (1): 75-92.

Bhardwaj, D. C. (1965b). Studies in the Indian Anthocerotaceae. VI. Some aspects of morphology of *Phaeoceros*. *Phytomorphology*, **15** (2): 140-150.

Bharadwaj, D. C. (1972). On some Asian and African species of *Folioceros*. *Geophytology*, **2** (1): 74-87.

Bold, H. C. (1957). *Morphology of Plant*. New York.

Bold, H. C. & Wyne, W. I. (1978). *Introduction to Algae*. Prentice Hall Inc. Englewood Cliff, New Jersey.

Bower, F. O. (1908). *The Origin of a Land Flora*. Macmillan and Co., London.

Bower, F. O. (1935). *Primitive Land Plants*. Macmillan and Co., London.

*Campbell, D. H. (1895). *Structure and Development of Mosses and Ferns*. Macmillan & Co., London.

Campbell, D. H. (1905). *Structure and Development of Mosses and Ferns*. Macmillan & Co., London.

Campbell, D. H. (1920). Studies on some East Indian Hepaticae, *Calobrium blumei*. *Ann. Bot.*, **34**: 1-12, pl. 1.

Campbell, D. H. (1925). Relationships of the Anthocerotaceae. *Flora. Neve Folge*, **18-19**: 62-74.

Campbell, D. H. (1940). *The Evolution of Land Plants* (*Embryophyta*). pp. 1-731.

Campbell, E. O. (1959). The structure and development of *Calobrium gibbsiae*. *Trans. R. Soc. New Zealand*, **87** (3, 4): 243-254.

Cavers, F. (1911). Interrelationships of the Bryophyta. *New Phytologist*, Reprint no. 4, Oxford.

Chopra, R. S. (1967). Relationship between liverworts and mosses. *Phytomorphology*, **17** (1-4): 70-78.

Chopra, R. S. (1975). *Taxonomy of Indian Mosses* (*An Introduction*). Publications and information Directorate, C.S.I.R., New Delhi. pp. 1-631.

Chopra, R. S. (1981). Origin of Bryophyta. *Misc. Bryol. Lich.*, 9 (1): 1-7.

Fulford, M. (1965). Evolutionary trends and convergence in the Hepaticae. *Bryologist*, **68** (1): 1-31.

*Goebel, K. (1898). *Organographie der Pflanzen*.

Goebel, K. (1898). *Organography of Plants*, translated by Balfour, I. B. Reprint 1969. Hafner Publishing Company, New York and London. pp. 1-707.

Goebel, K. (1930). *Organographie der Pflanzen*. Zweiter Teil. Bryophyten-Pteridophyten. Verlag Von Gustav. Fisher. Jenna.

Hattari, S., Sharp, A. J., Mizutani, M. & Iwatsuki Z. (1968). *Takakia ceratophylla* and *T. lepidozoides* of Pacific North America and a short history of the genus. *Misc. Bryol. Lichen.*, **4** (9): 137-149.

Hattari, S., Iwatsuki, Z., Mizutani, M. & Inoue, S. (1974). Speciation in *Takakia*. *J. Hattari bot. Lab.*, **38**: 115-121.

Hebant, C. (1977). *Conducting Tissues of Bryophyta*. J. Cramer. Fl. 9490 Vaduz, i-xi, and: 1-157, pl. 1-180.

*Howe, M. A. (1898). The Anthoceroteae of North America. *Bull. Torrey bot. Club*, **25**.

Kashyap, S. R. (1929). *Liverworts of the Western Himalayas and the Punjab Plain*, Part I. Panjab Univ., Lahore, reprint by The Chronica Botanica, New Delhi, 1-121, pls. 25.

*Kidston, R. & Lang, W. H. (1920). On old red sandstone plants showing structure from the Rhynie Chert Bed, Aberdeenshire II. *Trans. R. Soc. Edinb.*, **52**: 603-627, pls. 1-10.

*Lampa, Emma (1903). Sex organs of *Anthoceros*. *Oester. bot. Zeitschr.*, **1903**: 436-438, 5 figs.

Lang, W. (1905). On the morphology of *Cyathodium*. *Ann. Bot.*, **19**: 411-426.

Leitgeb, H. (1875). *Untersuchungen uber die Lebermoose*. Heft. II. die Foliosen Jungermannieen. Jena. Reprint J. Cramer, 3301 Lehre.

Leitgeb, H. (1879). *Untersuchungen uber die Lebermoore*. Heft V. die Anthoceroteen Craz. Reprint J. Cramer, 3301, Lehre.

Mehra, P. N. (1967). Phyletic evolution in the Hepaticae. *Phytomorphology*, **17** (1-4): 47-58.

Mehra, P. N. (1968). Conquest of land and evolutionary patterns in early land plants. *15th Sir Albert Charles Seward Memorial Lecture*. Birbal Sahni Institute of Palaeobotany, Lucknow.

Mehra, P. N. & Handoo, O. N. (1953). Morphology of *Anthoceros erectus* and *A. himalayensis* and the phylogeny of the Anthocerotales. *Bot. Gaz.*, **114**: 371-382.

*Merker, H. (1959). Analyse der Rhynien-Bases Und Nachweis des Gametophyten. *Bot. Notiser*, **112** (4): 441-452.

Miller, H. A. (1974). Rhyniophytina, alternation of generations and evolution of bryophytes. *J. Hattari bot. Lab.*, **38**: 161-168.

Pande, S. K. (1932). On the morphology of *Notothylas indica*. *J. Indian bot. Soc.*, **11** (2): 160.

Pant, D. D. (1962). The gametophyte of the Psilophytales, pp. 276-301 in P. Maheshwari, B. M. Johri & I. K. Vasil (eds)— *Proc. Summer School Bot. Darjeeling*. Min. Sci. Cult. Affairs, New Delhi.

Proskauer, J. (1948). Studies on the morphology of *Anthoceros*. II. *Ann. Bot.* (*Lond.*), **12**: 427-439.

*Proskauer, J. (1958a). Studies on Anthocerotales. *Phytomorphology*, **7**: 113-135.

Proskauer, J. (1960). Studies on Anthocerotales. On spiral thickenings in the columella and its bearing on phylogeny. *Phytomorphology*, **10**: 1-19.

Schuster, R. M. (1966). *The Hipaticae and Anthocerotae of North America*. Vol. I. Columbia Univ. Press, New York and London.

Smith, G. M. (1955). *Cryptogamic Botany*, Vol. **2**. *Bryophytes* and *Pteridophytes*. 2nd ed. McGraw-Hill, New York and London, 1-399 pp.

Steere, W. C. (1958). Evolution and speciation in mosses. *Amer. Nat.*, **42**: 5-20.

Steere, W. C. (1969). A new look at evolution and phylogeny in bryophytes, pp. 134-143 in J. E. Gunkel (ed)— *Current Topics in Plant Sciences*. Academic Press, New York & London.

*Tatuno, S. (1959). Chromosomen von *Takakia lepidozoides* und eine studie Zur Evolution der Bryophyten. *Cytologia*, **24**: 138-147.

Zimmermann, W. (1932). Phylogenie in E. Verdoorn (Ed.)— *Manual of Bryology*. Reprint by A. Asher & Co., Amsterdam, 1967.

Zimmermann, W. (1952). Main results of the "Telome Theory". *Palaeobotanist*, **1**: 456-470.

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*Not seen in original.