

Observations on morphology and anatomy of *Equisetum* L.

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ABSTRACT

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Observations on morphology and anatomy of *Equisetum* are presented, including those on fossil specimens of *Equisetites* known since Late Palaeozoic. Stem is jointed, ribbed and green with a horizontal/oblique rhizome. Adventitious roots arise from nodes and may form root tubers. Nodal sheath is circular with reduced teeth like leaves. Stomata are syndetocheilic in one or two rows on sheath and in furrows. Nodal and internodal anatomies are quite distinct. In an internodal bundle, xylem is reduced and differentiated into carinal xylem and lateral xylem with well developed phloem. Nodal bundles are well developed without differentiation of proto- and metaxylems with poorly represented phloem. Formation and functioning of nodal and internodal xylems are described and a modified interpretation is suggested about the path of vasculature in the jointed stem.

Key-words: *Equisetum* L., sphenopsid, scouring rush, morphology, anatomy, vasculature.

INTRODUCTION

Linnaeus (1753) instituted the genus *Equisetum*. Linnaeus (1763) identified six species of this genus, viz. *E. arvense*, *E. hyemale*, *E. palustre*, *E. fluviatile*, *E. sylvaticum* and *E. giganteum*. Schleicht (1797) erected *E. variegatum* var. *variegatum*, whereas Desf (1800) established *E. ramosissimum*. Michx (1803) found a small sized horsetail and named it *E. scripoides*. It has only 3 ribs on stem surface and 3 teeth like leaves on the nodal sheath. Willd (1810) established *E. elongatum*, a large sized plant. Schleicht and Chamber (1830) described one of the tallest horsetail, *E. myriochaetum*, with a height of 8-10 m. Milde (1867) published a monograph on *Equisetum* systematics and morphology. He divided the genus into two subgenera, viz. *Equisetum* and *Hippochaete*. This view was

accepted and followed by Schaffner (1912, 1931), Browne (1912, 1922, 1941), Hauke (1957, 1963, 1977, 1978, 1987), Duckett (1970, 1972, 1973), etc. Goebel (1887) published a book entitled 'Outline of classification and special morphology of plants' which includes a detailed description of *Equisetum*. Du-Buysson (1888) also published an account of morphology and anatomy of *Equisetum*. Systematics, morphology and anatomy of this taxon have also been published by Vaucher (1817, 1821, 1823), Pringsheim (1853), Ramey (1855), Cramer (1855), Hofmeister (1862), Bower (1894, 1908, 1935), Campbell (1895, 1940), Browne (1912, 1922, 1941), Eames (1936), Smith (1955), Foster and Gifford (1959), Bierhorst (1971), Bold et al. (1987), Gifford and Foster (1988), etc.

Browne (1912, 1922, 1941) studied anatomy of vegetative and fertile axes of *Equisetum* and suggested the way of formation of nodal and internodal vasculature. Golub and Wetmore (1948a, b) described in detail the anatomy and development of vegetative shoots of *E. arvense* and regarded nodal vasculature a siphonostele and internodal one an eustele. Bierhorst (1958a, b) studied tracheary elements of *Equisetum* and reported the presence of vessels bearing scalariform and pitted types of thickenings (Bohra et al. 1980). Bierhorst (1971) described the presence of carinal and lateral xylems in the internodal bundles of stem and did not agree with the use of terms protoxylem and metaxylem for them (Eames 1936, Foster & Gifford 1959). Sharma and Bohra (1979) and Sharma et al. (1986, 2001) also agreed with Bierhorst's opinion. Purohit and Rathore (2007) described the apical meristem of *Equisetum* and favoured Golub and Wetmore (1948a) and Sharma et al. (1986). In *E. ramosissimum*, apical dome of young shoots is protected by special scales called ochrole (Hauke 1987, Sharma 1992). Stomata are syndetocheilic and are restricted to stem furrows, nodal sheath and teeth like leaves. In subgenus *Equisetum*, stomata are in a single row whereas in *Hippochaete*, there are two rows of stomata. There are transverse silica bars either on the subsidiary cells or on the guard cells (Hauke 1957, Kedves 1958, Saxena 1976).

In India, study on *Equisetum* was started by Kashyap (1917). Sethi (1928) studied the life history of *E. debile*. Chatterji (1964), Pant and Mehra (1964), Agashe (1968), Pant and Kidwai (1968), Mohan Ram and Chatterji (1970), Sen and Sen (1973), Bir (1978), Saxena (1976, 1978), Sharma (1992), Sharma and Bohra (1979) and Sharma et al. (1986, 2001, 2010) contributed to the morphology, anatomy and experimental studies on Indian species of *Equisetum*. The information provided in the present paper is based on the study of extant and extinct sphenopsid taxon. *Equisetum* is the only extant representative of Arthropsidea.

MATERIAL AND METHOD

Observations presented here are based on published literature on *Equisetum* and *Equisetites*. The

living material was collected from Rajasthan and other parts of the country. Microtome sectioning was done as suggested by Johanson (1940). Sections were stained with the combinations of safranin and haematoxylin, and safranin and fast green. Slides were mounted in dilute canada balsam.

DESCRIPTION

Morphology

Equisetum is a small, green, herbaceous, scouring rush ranging in height from 12-15 cm (*E. scirpoides*) to 8-10 m (*E. myriochaetum*, *E. giganteum*). Plant has a branched/unbranched, jointed, horizontal/oblique brown to black rhizome bearing adventitious roots arising from the nodes (Text-figure 1A). In some species, like *E. diffusum*, root tubers are reported (Bir 1978). Green aerial branches originate from the nodes of rhizome either solitary or in whorls. Aerial branches also have ribs on stem surface and nodal sheath which terminate into small/large teeth like leaves. The ribs are alternate in the adjoining internodes. In *Calamites*, these are in continuation (Andrews 1961). Number of leaves per sheath is variable, e.g. 3 in *E. scirpoides* and 8-24 or more in *E. arvense* and *E. maximum* (Text-figure 1C). The fossil stem *Equisetites arenaceous*, which has a diameter of 20 cm, bears 120 teeth like leaves (Scott 1920). Leaf sheath is generally found preserved on the fossil stems of *Equisetites*, e.g. *E. lyelli* (Text-figure 5C) (Seward 1894), *E. columnare* (Text-figures 5D-F) (Seward 1900) but not always. In a thick stem cast of *E. beani*, ridges and furrows are visible but leaf sheath is not preserved (Text-figure 5B) (Seward 1900). Normally, an embryoid stem comes out vertically upward from the gametophyte (Text-figure 5A) but sometimes, due to formation of a larger leaf in a whorl, the young stem adapts spiral twisting organization as in *Equisetum palustre* and *E. hyemale* (Bierhorst 1971). According to Milde (1867) and Hauke (1963, 1978), there are two basic types of equiseta. In the first type, there is no differentiation of vegetative and fertile branches and all branches bear terminal cones, as found in subgenus *Hippochaete* (e.g. *E. ramosissimum*, *E. debile*). In the second type, vegetative branches are green and originate in whorls while the cone bearing



Text-figure 1. A. *Equisetum arvense*, with distinct vegetative and fertile shoots. B. *E. pratense*, shoot with recurrent whorls of sporangiophores and bracts. C. *E. maximum*, upper portion of fertile axis with loose whorls of sporangiophores. Nodal sheath with long leaves. D. Same, sporangiophores in various orientations. E. *E. sylvaticum*, plant with secondary stalked sterile cones axillary to bracts. F. *E. kansanum*, shoot unbranched, internode long, terminate into a cone. G. *E. ramosissimum*, L.S. of epidermis showing a young stoma with sunken guard cells and covering them the subsidiary cells (A-F: after Bower 1908, G: after Pant & Kidwai 1968).

shoot is unbranched, pale green and terminates into a cone, as found in subgenus *Equisetum* (e.g. *E. arvense*, *E. diffusum*, etc.). There are many more morphological variations in the genus *Equisetum*, e.g. existence of recurrent whorls of sporangiophores and bracts, as found in *E. pratense* (Text-figure 1B) (Bower 1908). In *E. maximum* (Bower 1908), there are many teeth on a long nodal sheath (Text-figure 1C) and the cone has loosely arranged and irregularly placed whorls of sporangiophores (Text-figure 1D). In *E. sylvaticum* (Text-figure 1E), secondarily produced long stalked strobili are present. These are axillary to small young branches at a node of the main axis. However, these strobili are generally sterile. In *E. kansanum*, the plant is normally unbranched and a cone is produced terminally on the stem (Text-figure 1F). Internodes are long but the nodal sheath is short.

Leaf sheath is green and bears rows of stomata which continue up to the leaf tip (Mital 1979). During ontogeny, the stomatal meristemoid is either divided by a periclinal division (Duval-Jouve 1864) or by an anticlinal division (Text-figure 1G) (Johnson 1933, Hauke 1957, Pant & Mehra 1964, Pant & Kidwai 1968).

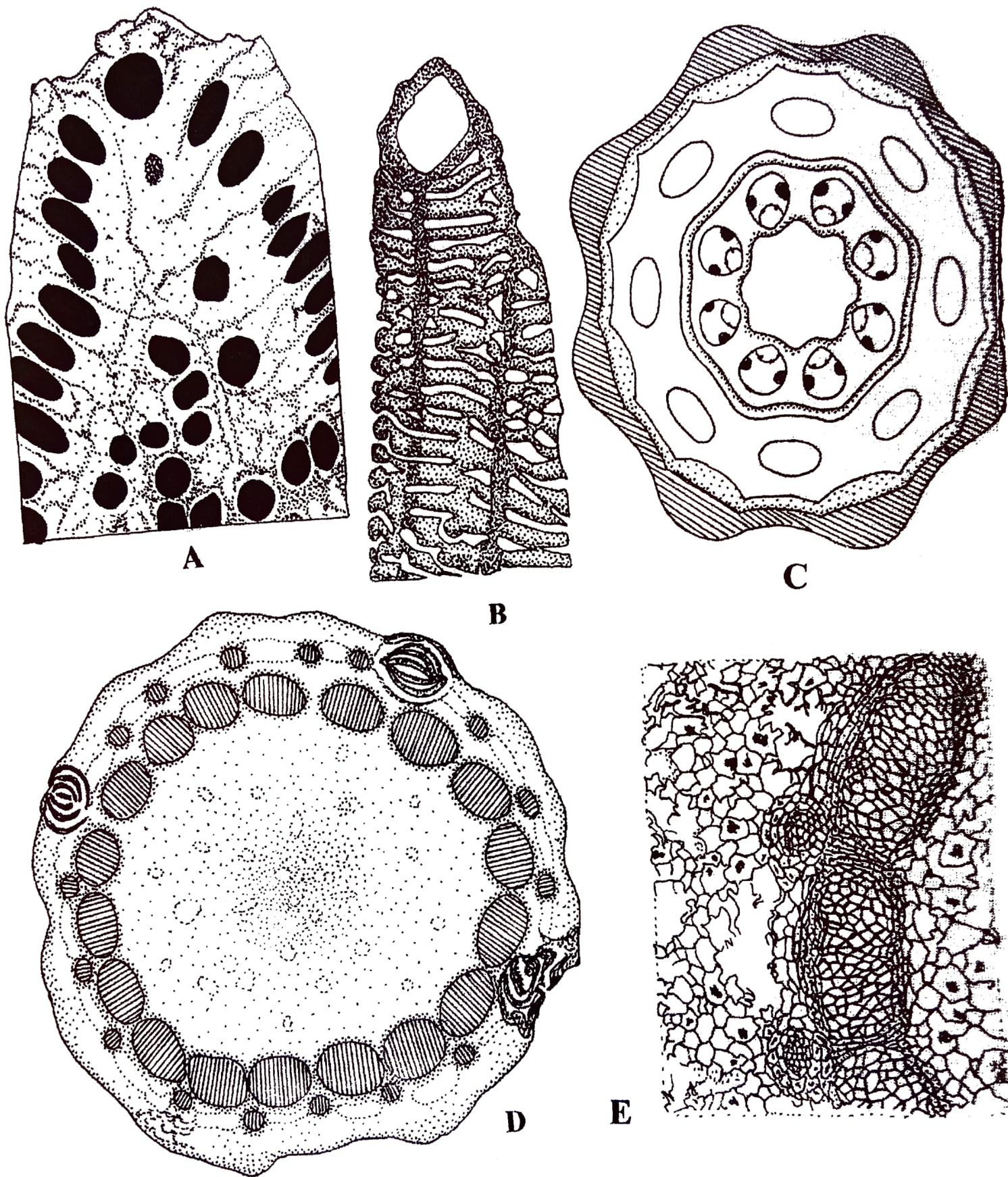
Cone size may be variable in different species of *Equisetum* but in plan of construction all are identical. There is a sterile ring or annulus at the base of the cone with several whorls of sporangiophores above it. Each whorl has 3-8 sporangiophores. On the inner side of peltate head, there are 8-9, closely placed, sessile bag shaped, eusporangiate, homosporous sporangia. Spores are green and each is enveloped by four mucilaginous thread like elaters. Beer (1909) believed that out of four coats of the spore wall the middle and the perispore are utilized in elater formation, whereas others consider their origin from extraneous material (Bierhorst 1971). Despite being homosporous, spore germination and sexuality of gametophytes are variable and depend on physical, chemical and genetic factors, i.e. a spore may form unisexual, bisexual or non-sexual gametophytes (Mohan Ram & Chatterji 1970, Hauke 1977).

Gametophyte is a green, branched multicellular structure with a thick horizontal portion from which rhizoids originate on the lower side and green vertical branches on the upper side (Text-figure 4A). Antheridia are produced terminally or subterminally on vertical branches (Text-figure 4B). The archegonia are axillary to the vertical branches (Text-figure 4C). Antheridium produces multiflagellate spiral antherozoids (Text-figures 4D, E). In an archegonium, the venter is embedded in the gametophyte while a 4 cells thick long neck projects outside the prothallus (Text-figure 4F). Embryo development is exoscopic (Text-figures 4F, 5A).

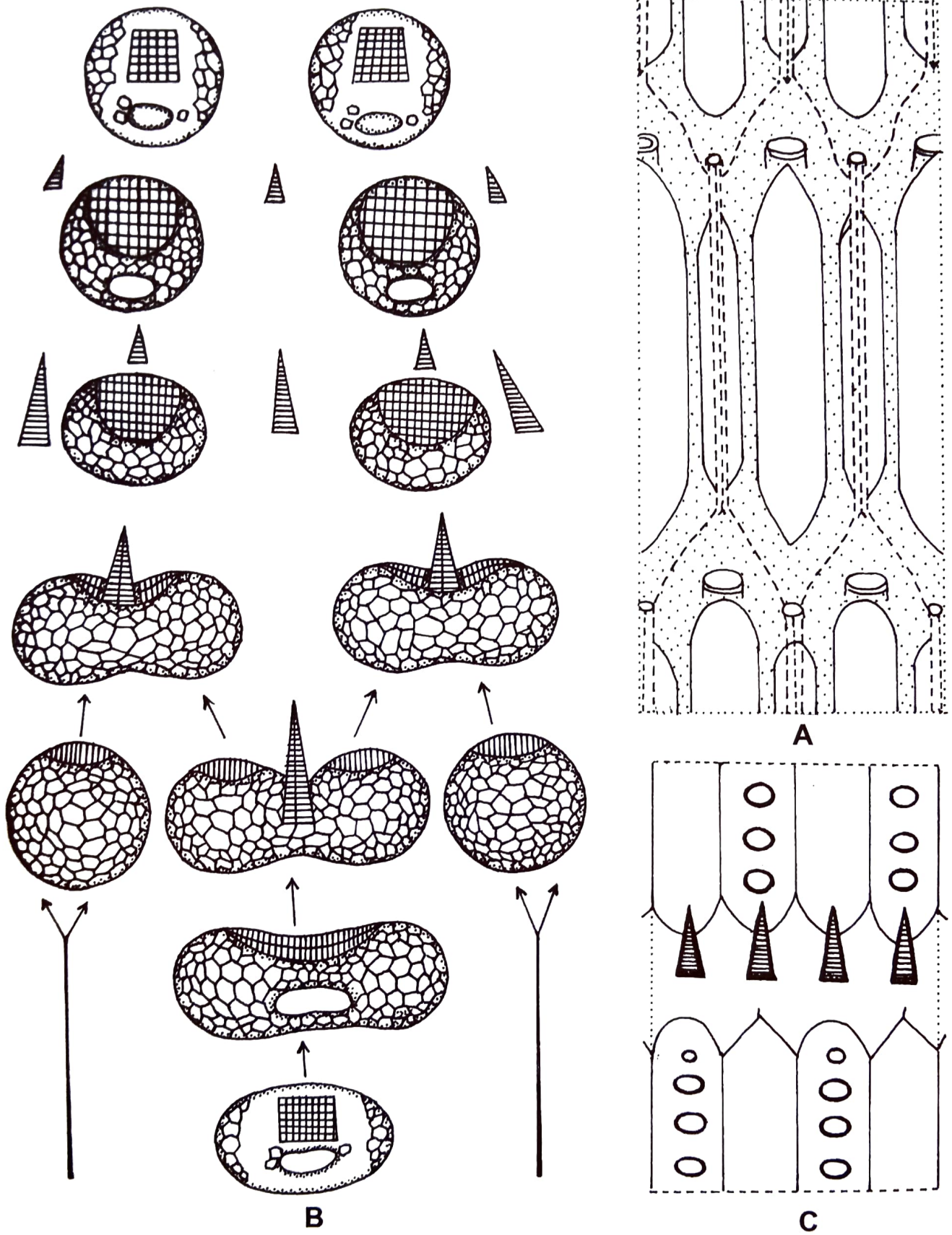
Anatomy

Internodal and nodal anatomies are quite distinct and different from each other (Text-figures 2C, D). A cross section through internode shows presence of vallecular cavities in cortex, a large pith cavity and one carinal canal in each bundle (Text-figure 2C). Position of endodermis is variable, e.g. outer common endodermis, outer and inner common endodermis and outer common endodermis, and each bundle has its own endodermis. Pfiftzer (1867-1868) used endodermis location in the taxonomy of this genus. Each bundle has two lateral rows of xylem one on either side of the phloem and one or two tracheids on either side of the carinal canal. The former is termed as lateral xylem and the latter as carinal xylem (Bierhorst 1971). In majority of books, the lateral xylem has been called as metaxylem while the carinal xylem as protoxylem (Eames 1936, Smith 1955, Foster & Gifford 1959). The tracheary elements of carinal xylem do not have typical annular thickenings of the protoxylem whereas the lateral xylem may have its own protoxylem. Bierhorst (1971) and Sharma et al. (1986, 2001) considered them as two separate xylems. Carinal xylem is the remnant of the nodal xylem left due to fusion and dissolution during formation of the carinal canal (Sharma et al. 2001, Text-figures 12-15). The lateral xylem originates separately and secondarily (Bierhorst 1971).

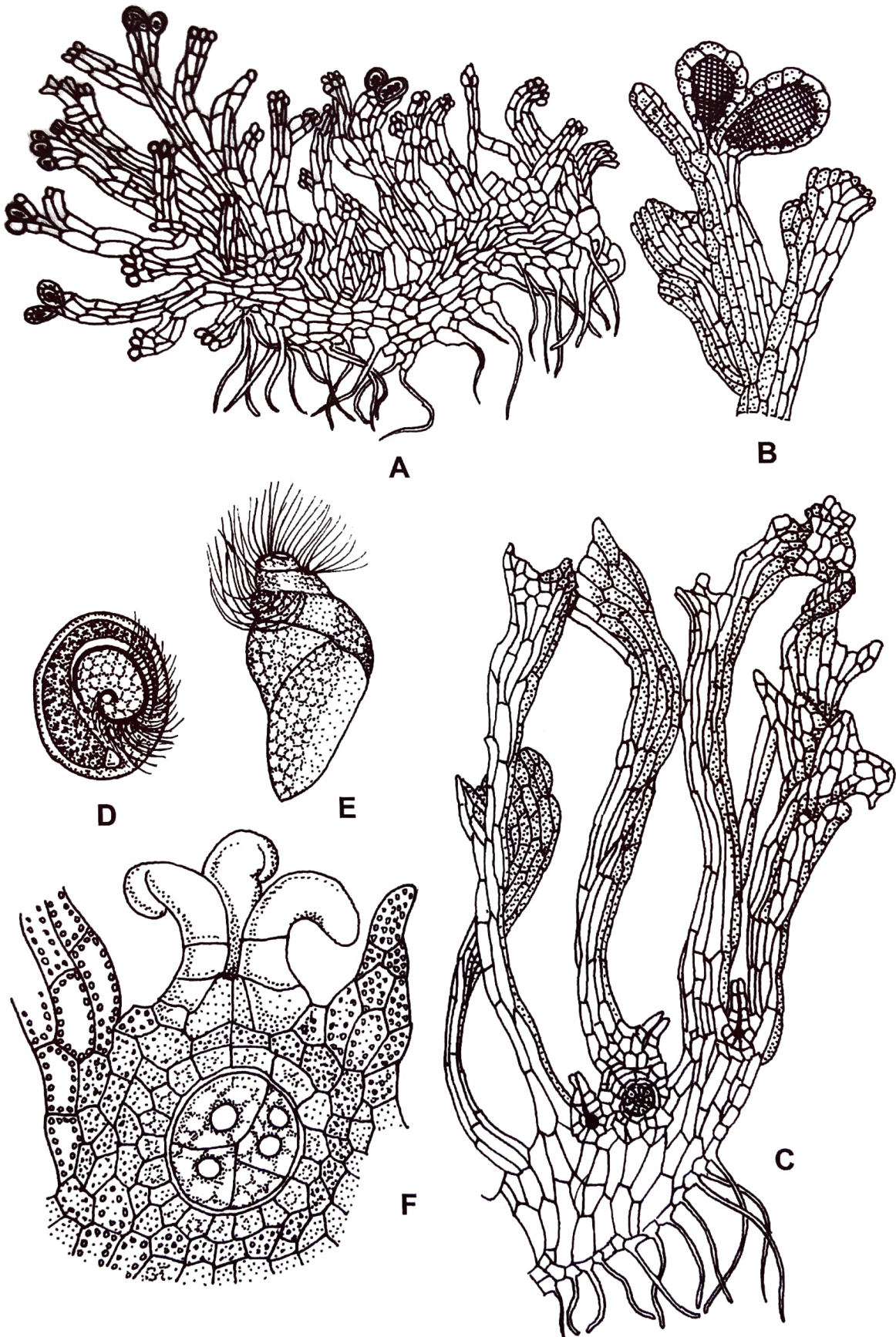
A cross section through the nodal plate shows disappearance of all kinds of cavities, i.e. vallecular, carinal and pith cavities. The bundles are double in number to the internodal bundles (Text-figure 2D).



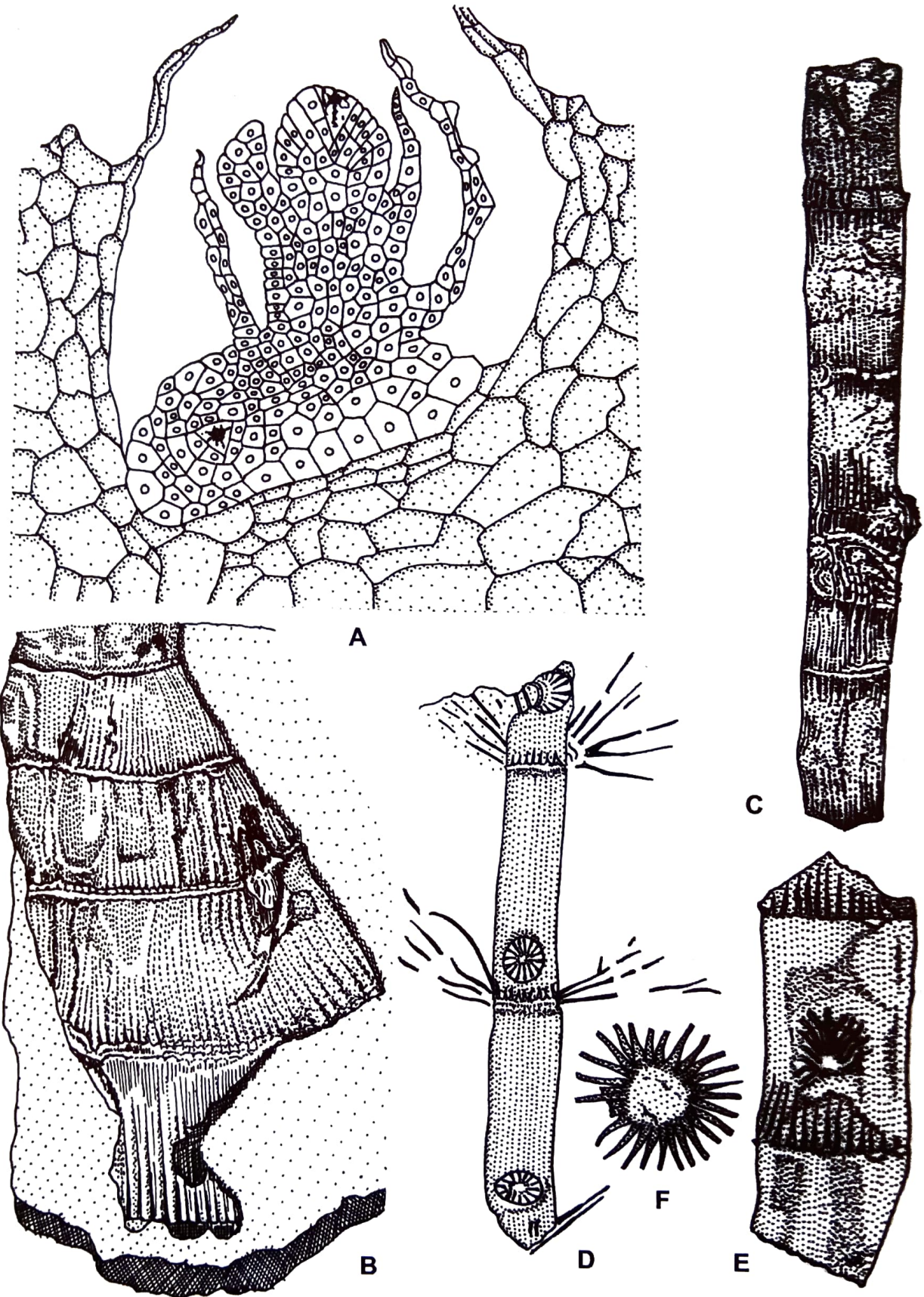
Text-figure 2. A-E. *Equisetum ramosissimum*. A. L.S. of stem apex with a large apical cell and downward sextant cells. B. Vessel element with scalariform and pitted types of thickenings. C. C.S. of stem internodal portion having cavities and poorly developed bundles below the ridges. D. C.S. of nodal portion with double the number of well developed bundle; alternating are small leaf traces. Branch traces visible in cortex. E. A portion of nodal vasculature enlarged. Xylem well developed while phloem poorly represented.



Text-figure 3. A. *Equisetum giganteum*, Browne's (1922) plan of construction of path of vascular bundles through nodal and internodal portions. Origin of branch (larger) and leaf traces (smaller) is also shown. B. *E. ramosissimum*, changes in vasculature internodal to nodal portion and formation of internodal bundles at alternate positions are shown. Leaf traces originate at dichotomy of nodal bundles. C. Same, diagrammatic representation of nodal anatomy and origin of leaf traces. (A: after Browne 1922, B-C: after Sharma et al. 2001).



Text-figure 4. A. *Equisetum maximum*, gametophyte with antheridia at the tips of vertical branches. B. A vertical branch enlarged bearing a pair of antheridia. C. *E. arvense*, gametophyte with archegonia axillary to vertical branches. D, E. An immature and a mature multiflagellate, spiral antherozoid. F. Young embryo in the venter of an archegonium. (A-B, D-E: after Bierhorst 1971, C, F: after Hofmeister 1862).



Text-figure 5. A. *Equisetum arvense*, median section through a mature embryo showing exoscopic development. B. *Equisetum beani*, cast of a thick stem with ridges and furrows. Leaf sheath not visible. C. *E. lyelli*, stem with ribs and bases of branches. D-F. *E. columnare*, D. Stem with whorls of branches arising from nodes. Flattened diaphragm visible on internodal portion. E. Same, enlarged. F. Diaphragm enlarged bearing number of teeth like leaves. (A: after Smith 1955, B, D-F: after Seward 1900, C: after Seward 1894).

Xylem is well developed while phloem is poorly represented. Xylem consists of vessels (Text-figure 2B) and tracheids (Sharma & Bohra 1979, Bohra et al. 1980, Sharma et al. 1986, 2001). Endodermis is also not distinct in the nodal region. Alternating to the cauline bundles, there are small sized leaf traces (Text-figures 2D, E). The cauline bundles may extend laterally and form a siphonostele (Golub & Wetmore 1948a, b).

A longisection through the nodal portion shows an increase in amount of xylem in the upper portion of internode, i.e. below the nodal plate (Sharma et al. 2001, Figure 7). The tissue between the phloem and the carinal canal becomes active and cuts off the tracheary elements. The xyleary cells so formed divide into two. This explains the doubling of cauline bundles at the nodal plate. The branched tissue (bundles) meets with those of the adjoining bundles and reduce in number thus to half and at the alternating position (Text-figures 3A-C) to the bundles of the lower internode. Leaf traces arise from the points of dichotomy of the nodal (cauline) bundles (Text-figures 3A-C). Each leaf trace is concentric and has a distinct bundle sheath (Sharma et al. 2001, Figure 6). Branch traces originate by the meeting of two or more cauline bundles in the nodal region (Sharma & Bohra 1979).

A longisection through the apical portion of stem shows a distinct large apical cell (Text-figure 2A). It divides by 3 cutting faces and forms 3 segment cells. Anticlinal divisions of these cells form six cells per plate called sextant cells. The first primordial leaf sheath is formed of 10-12 cells down the apical cell (Golub & Wetmore 1948a). In some species of *Equisetum*, e.g. *E. arvense* and *E. ramosissimum*, the apical dome of the shoot is protected by a special scale called ochreole or a prophyllar sheath (Hauke 1987, Sharma 1992, Figure 9).

Equisetum root is typically di- to tetrarch with a narrow cortex. Sieberer and Timmers (2009) reported presence of microtubules in root hairs of *E. hyemale* and noted their role in cell polarity and tip growth. Likar et al. (2009) reported diversity and seasonal variations of mycorrhiza and rhizosphere in *E. arvense*. Earlier, there was no record of mycorrhizal association with *Equisetum*.

DISCUSSION

On the basis of morphological study, Milde (1867) and Hauke (1963, 1978) divided the genus *Equisetum* into two subgenera, viz. *Hippochaete* and *Equisetum*. However, these two subgenera are more or less identical in anatomy and basic plan of vasculature. Stomata are syndetocheilic and have transverse silica bars. Vallecular cavities are present below the furrows in internodal portion of stem/rhizome and disappear in the nodal plate. Variations in endodermis position have been observed in both the subgenera (Bierhorst 1971, Gifford & Foster 1988). An internodal bundle has differentiation of carinal and lateral xylems. Phloem is well developed between the two arms of the lateral xylem. Carinal canal is present in all internodal bundles. Vessels are present in xylem. Nodal bundles have well developed xylem and originate in an identical manner in both the subgenera. Leaf traces are concentric and poorly developed. Ochreole has been seen in species of both the subgenera (Hauke 1987, Sharma 1992). Basic chromosome number is: $n=108$ (Love & Love 1961, Abraham et al. 1962). Hybridization work has been done on both the subgenera (Sharma et al. 2010). Both are homosporous, with spores identical in morphology and behaviour. Gametophytes are similar in morphology, structure of sex organs and sexuality (Mohan Ram & Chatterji 1970, Duckett 1970, 1972, 1973, Hauke 1977). All these similarities raise questions on the systematic studies and division of the genus *Equisetum* L. into two subgenera *Hippochaete* and *Equisetum*. Pteridologists have made use of SEM study and silica deposits (Page 1972) in the subgenus *Equisetum* and divided it into 3 sections. Modern tools and techniques are also being used (Zhang 2004, Aguirre et al. 2007) which, in coming days, may help in deciding in favour or disfavour of division of *Equisetum* into two subgenera.

It is generally believed that parenchyma tissue present between phloem and carinal canal of an internodal bundle becomes meristematic and cuts off tracheary cells in the upper portion of an internode, i.e. just below the nodal plate. This increase in tracheary cells in the nodal portion is related with the disappearance of cavities and reduction in phloem

elements. The increase in number of bundles in the nodal plate is due to dichotomy of the secondarily formed xyleary tissue in the upper portion of the internode and formation of cauline bundles. However, these bundles remain active for a short distance and then unite with the adjoining bundles and reduce in number to half in the upper internode and at the alternate position. Browne (1922) explained it with the help of a diagrammatic sketch (Text-figure 3A). Browne considered carinal xylem a protoxylem and suggested its continuation through the nodal plate. On the other hand, Sharma et al. (1986, 2001) do not agree with Browne's view. Leaf traces arise from the point of dichotomy of the nodal bundles (Text-figures 3B, C). Phylogeny of this peculiar type of vasculature in the stem remains unknown till the discovery of petrified specimens of *Equisetites*. Majority of fossil specimens of *Equisetum* or *Equisetites* have been collected either as impressions or casts (Taylor & Taylor 1993, Stewart & Rothwell 1993).

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