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TAXONOMIC IMPLICATION OF CONDUCTING ELEMENTS IN THE ACROCARPOUS MOSSES

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ABSTRACT

Present study deals with the structure and development of conducting elements in the nine orders of acrocarpous mosses. The significance of conducting tissues in mosses in relation to their habitat conditions, growth forms and leaf cell patterns has been discussed. Features of cells in different portions of the stem and the laminal cell patterns and costa are taken into consideration. Although water-conducting cells are unspecialized in mosses, yet the study shows that they seem to play a vital role in the conduction and provide additional criteria for the distinction of taxa. Four categories have been determined as (i) Acrocarpous mosses with a distinct thick-walled conducting strand (6-7 layered) as hydrome which is surrounded by patches of leptoids. Cortex consists of thick walled cells (6-10 layered). Costa has stereidal cells and well developed conducting elements in leaf, example *Polytrichum* (ii) Acrocarps with thick-walled, narrow, elongated conducting strand (4-5 layered), cells angular in the cortex (6-8 layered). Leaf cells are rectangular, irregular and porous with incrassate walls, example *Dicranum* (iii) Acrocarps with conducting tissue (2-5 layered) stereidal, thick walled or thin walled varying in the course of development. Leaf cells are mutipapillate, rounded-quadrate, costa is present, examples *Hyophila, Philonotis* and (iv) Epiphytic pleurocarps with conducting cells rudimentary, thickened, scattered (2-4 layers) and parenchymatous, cortical cells (2-3 layered) thick walled. Leaf cells are small, rounded or linear and papillate, costa may be present or absent, example *Leucodon.* The study would constitute a formidable task, especially if intraspecific structural variability is considered. It serves a model system in the eco-physiological aspects.

Keywords : Ectohydric, Endohydric, External Conduction, Leaf cell pattern, Stereidal cells.

INTRODUCTION

Majority of plants on the land are adapted to absorb and conduct water from the soil. Bryophytes adopted the alternative strategy of evolving desiccation tolerance, growing during moist period and suspending metabolism during drought. Bryophytes show remarkable challenges to the water relations. Mosses developed several strategies to absorb water and solutes including external transport, cell-to-cell transport and ability to survive desiccation which make them to occupy diverse habitats. Most bryophytes take up water and nutrients over the whole surface of shoots and leaves through external conduction (ectohydrism), though in some taxa conduction occurs through specialized internal conducting cells. This strategy of bryophytes makes up them a prominent part of vegetation. The growth forms of mosses also make them to hold water in larger quantities. The water retention capacity directly influences the productivity. Most vascular plants are Homoiohydric, i.e. transpiratory water loss is greatly restricted when the potential for evaporative water loss exceeds the rate at which water can be supplied through the xylem from the soil. Bryophytes are Poikilohydric, i.e. the rapid equilibration of the plant's water content to that of the surrounding environment and desiccation tolerant, i.e. to recover after being air-dry at the cellular level. External conduction of water by capillary action has a great significance and considered as an effective path of water supply in numerous mosses. The exact role played by external conduction depends on the morphology and anatomy of the gametophore and also on the environmental factors, mainly the relative humidity. The families Polytrichaceae and Mniaceae represent the well-developed endohydric groups (Proctor, 2000) which has stereome, leptome and a central strand. Leptome is composed of phloem like sieve cells. Hydroids and stereids make up the central strand (Zamski & Trachtenberg, 1976) and collectively called Hydrome**.** Endohydric taxa have well developed rhizoids or more root-like structures, able to abstract water from moist porous substrate, and have relatively water-repellent surface. Hydroids are water conducting cells that lack any horizontal connections. Stereids are elongate, thick-walled,

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and slender and fiber like cells occurring in leaf costa and cortex of the stem. Pleurocarpous forms led to the movement of substances mainly in a horizontal pattern.

The present study is made on the internal structure of the leafy axis of the taxa of various taxonomic groups and the anatomical features are elucidated in relation to the adaptive strategy for water conduction, growth patterns and habitat conditions. The mosses with erect shoot axis absorb the water from the continuous capillary stream of water present along the shoots and also through the conducting cells and developed stereidal cells for mechanical support. The development of the conducting strand varies among different taxa indicating their distribution and habitat type. The present work aims at the survey of conducting elements in some of the mosses to describe organization and distribution of tissue components in the leafy axes in relation to their habitat, laminal cells and costa. As no comprehensive survey of conducting tissues in Indian mosses has yet been completed, this would constitute a formidable task, especially if intraspecific structural variability is considered. It serves a model system in the eco-physiological aspects.

MATERIALS AND METHODS

Mosses from different habitats in the Western Himalaya were collected in polythene bags. They were air dried, and stored in labeled standard-sized (10×15 cm) paper packets. Moss samples were revived in water and regenerated in petridishes and immersed in 0.1% of Safranine solution. Transverse and longitudinal sections were cut down serially by sharp razor. Whole mount of leaves were made in Gum Chloral Mounting Medium.

RESULTS

Significant variations are found in the distribution and the type of the conducting cells in different groups of taxa. In *Sphagnum*, no specialized conducting cells are observed **(Fig. 1A)**.In *Pogonatum,* the conducting strand consists of 5-6 layers of thick walled cells and the cortex of moderately thickened cells **(Figs. 1B,C)**. Members of the orders Pottiales and Bryales show a wide range of differentiation in conducting cells. In *Dicranum lorifolium* (Dicranales), outer portion of cortex has extremely thick stereidal cells (4-5 layered) followed by moderately thick walled parenchymatous cells (8-9 layers) and the central portion has thick-walled, narrow- elongated conducting cells with oblique end walls **(Fig. 1D)**. *Leucobryum humillimum* shows less developed conducting strand **(Fig. 1E)** in comparison to that of *Dicranum lorifolium*. *Dicranum* grows on rocks and hard substrata that need efficient conducting system. *Leucobryum* generally grows on the tree barks or on porous substrata and gets enough moisture from the bark. A well developed conducting strand was observed in *Bryum coronatum.* It consists of a central core of small thick-walled cells in 2-3 layers surrounded by a distinct layer of elongated and pigmented endodermal cells. The cortex is made of 6-7 layers of pentagonal cells **(Figs. C, D)**. In *Bryum plumosum* the central strand was observed to be less developed probably as these plants were found growing on permanently moist and wet substratum and do not require specialized conduction cells. A central core of 3-4 layers of pigmented cells is observed in *Hyophila involuta* **(Fig. 1F)**. In *Plagiomnium* and *Meteorium* conducting cells are poorly developed and conduction is performed by thick walled parenchyma cells **(Figs. 2E, 3A, B)**. *Brachythecium* lacks the specialized conducting cells **(Figs. 3 C,D)**.

Highly developed conducting tissue is observed in those plants which were occurring on impermeable substrata or dry soil as well as on exposed sites. During dry period the available moisture in porous soil particles is absorbed by the conducting cells through rhizoids. The taxa with plagiotrophic shoots form large surface area and are able to absorb water from the air. These plants showed poorly differentiated central core of cells at different stem portions. The conducting cells in the shoots were found to be well developed in those taxa where the laminal cells were small and rounded-quadrate. The conducting cells are poorly differentiated in the taxa where the laminal cells are wide and thin walled. The taxa with narrow laminal cells lack the differentiated conducting cells in the stem.

DISCUSSION

Bryophytes are distinguished from tracheophytes by two important characters – (i) Bryophytes are ecologically persistent. (ii) Absence of lignin containing water-conducting xylem tissue. Despite the typical relegation of Non-Vascular category, conduction has played a major role in the phylogenetic history of mosses. In pleurocarpous mosses internal substances move horizontally (Kawai,1991). Among acrocarpous mosses the axis may have a leptome, a surrounding sheath, a stereome and a central hydrome which constitute a well-developed endohydric pathway. The elongated hydroids typically occur in bryophyte stems (Hébant, 1970), but lack lignin and secondary wall thickenings (Taylor, 1988). Some acrocarpous mosses also show ectohydric pathway, as they absorb water rapidly into the cells by capillary systems (Buch, 1947). Water is being held in the larger capillary spaces between the moss shoots within the moss carpet and the porous cells of the leaf base (Proctor, 1979).

Hébant (1974) described the conducting system in Polytrichales and the development of hydroids. The extent of this development is influenced by various parameters such as moisture substrata, climatic conditions etc. The conducting strands in mosses may be well developed, reduced or absent. The evolutionary significance of distribution patterns of water conducting tissues in mosses has been interpreted in a variety of ways. Hébant (1979) opined that characteristics of conducting tissues can provide additional support to bryophyte systematics and gave three possible views regarding their evolution:

(1) No conducting strand ⟶ reduced strand ⟶ well developed strand

(2) Well developed strand ⟶ reduced strand ⟶ no strand

(3) Well developed strand ⟵ reduced strand ⟶ no strand

On the basis of the present observations, the evolution of conducting cells seems to be related to a number of factors as discussed below:

(A) *Conducting tissue in relation to the distribution* : The taxa, which have a wide distribution scenario, possess a large variation in the presence of conducting tissues. The populations, which are found on higher altitudes and arid areas show well developed conducting strand, whereas the population of the same species growing in moist, temperate or tropical conditions shows poorly developed strand. *Dicranum* growing mainly on barren rocks at higher altitudes shows well developed conducting tissue **(Fig. 1 D)**. *Leucobryum* found in moist areas on tree bark shows less developed conducting strand **(Fig. 1E)**. *Bryum* species show a wide array of conducting elements from well developed to poorly developed strands, depending upon the distribution. Taxa of dry habitats show well developed strand.

(B) *Conducting tissue in relation to the habitat* : The taxa which are found on hard substrates such as rocks (*Pogonatum*, *Bryum*) have a well-developed conducting system **(Figs. 1B, 2C, D)**, whereas those on permeable substrata, have poorly differentiated conducting strand. *Sphagnum* species which occurs in aquatic habit lacks conducting strand at all. Epiphytic Isobryales possess a rudimentary system of central conducting tissues with thick-walled cortical cells **(Fig. 3 B)**. Thick walled cells maintain the turgidity and prevent rapid collapse in dry conditions. *Bryum plumosum* found near damp areas, possessed less developed conducting tissue, whereas *Bryum argentums* var. *lanatum* and *Bryum coronatum*, which were collected from arid habitat showed well developed conducting tissue. Families Polytrichaceae and Mniaceae represent the well developed. endohydric group (Proctor, 2000), but the presently studied population of *Plagiomnium integrum* shows poorly developed conducting strand **(Fig. 3A)**. The taxa of arid areas follow both endohydric as well as ectohydric conduction.

(C) *Conducting tissue in relation to the growth forms* : Mosses show the predominating influence of ground water supply in determining the growth forms. Turf, cushion, weft and dendroid forms are related to dry conditions, so they acquired a differentiated internal conducting tissue as well as take the water through ectohydric system. The mosses with mat and the pendant (*Meteorium* spp.) have rudimentary or undifferentiated conducting cells **(Fig. 3B)** as their plant parts remain in contact with moist substrata or can directly absorb water from the air. The pendant forms require more mechanical strength so they develop more thick walled cells in the cortex. The prostrate forms such as *Brachythecium* spp. totally lack specialized conducting cells **(Figs. 3C, D)**

(D) *Conducting tissue in relation to the leaf cell patterns* : The mosses with the leaves showing plication, linear cell pattern, absence of costa or rudimentary costa represent the poor conducting system (*e.g. Leucodon sciuroides*). The mosses with papillate leaf cells and defined costa, show a well defined tissue for water conduction (*e.g. Bryum* and *Hyophila*). In *Bryoerythrophyllum*, the costa and the leaf cells both show papillae, which indicate water retaining system. *Splachnobryum* spp. have broad leaf cells and ephemeral habit in suitable habitat such that the water economy is compensated and the plant does not need much water but is efficient in assimilation by large leaf cells. In some cases, the leaves possess well developed stereidal cells in the costa region indicating that the plants can survive in prolonged dry conditions and maintain water continuity through leaves and stem. In *Sphagnum*, the hyalocysts can retain enough water for longer duration and the internal specialized conducting cells are not required. There is a trend that the plants with narrow laminal cells possess poorly developed internal conducting system but well developed external conducting system. The plants with large laminal cells have moderate conducting tissue. The conducting tissue is well developed in leaves and stem of the plants that have small, rounded and papillate laminal cells.

Table 1 : Conducting elements in respect to the growth forms, habitat and leaf cell pattern (laminal cells small, rounded or quadrate) :

Taxon	Habitat	Growth form	Leaf cell pattern	Conducting cells
Sphagnum junghuhnianum	Aquatic	Tall turfs	Large hyalocysts and small chlorocyst	Absent **(Fig. 1A)**
Atrichum longifolium	Mineral soil	Turf	Costate, cells small rounded	Distinct thin walled 4-5 layered.
Pogonatum fastigiatum	Rocks	Dendroid	Costate, cells rounded-quadrate	Well defined strand, 5-6 layered, thick walled cells **(Figs. 1B, C)**
Pogonatum proliferum	Porous soil	Dendroid	Costate, cells irregular, thick-walled	Well-developed strand. Cells thick walled and 6-7 layered, surrouned by patches of leptoids
Pogonatum urnigerum	Soil gathered on rocks	Dendroid	Lamina cells are small, thick-walled and quadrate costa present with stereidal cells	Well developed thick walled tissue, 6-7 layered, surrounded by patches of food conducting cells
Dicranella pseudosubulata	Rocks	Cushion	Cells small rectangular. Rectangular cells at the base of lamina.	Well-developed strand of 4-5 layers
Dicranum lorifolium	Exposed rocks	Turf	Costate, cells small and incrassate	Well differentiated central tissue, 4-5 layered **(Fig. 1D)**.
Leucobryum humillimum	Tree barks	Cushion	Broad costa, scabrous pattern of cell type and elevated cells.	Defined zone of central tissue 4-5 layers and have thin walled cells **(Fig. 1E)**
Fissidens zollingeri	Wet rocks	Turf	Costate, cells lax, quadrate-hexagonal, small	Central strand of moderately thickened cells of 4-5 layers
Hyophila involuta	Rocks	Turf	Cells small, mamilose, rounded-quadrate	Conducting cells are 3-4 layered, pigmented **(Fig. 1F)**
Semibarbula orientalis	Old walls and cement floors.	Turf	Costate, small cells multipapillose, rounded quadrate-hexagonal	Thin walled conducting cells-2-3-layered surrounded by stereidal cells.
Bryorythrophyllm recurvirsotrum	Wet soils	Turf	Costate, cells rounded-quadrate, multipapillose	Thin walled cells in centre 3-4 layered surrounded by 2 layers of moderately thickened cells

Table 2 : Conducting elements in respect to the growth forms, habitat and leaf cell pattern (laminal cells wide and large) :

Taxon	Habitat	Growth form	Leaf cell pattern	Conducting cells
Physcomitrium cyathicarpum	Damp soil	Turf	Costate, cells are rectangular, broad and thick walled.	Conducting tissue 4-5 layered
Funaria hygrometrica	Soil	Turf	Costate, cells thick-walled and rectangular	Thick walled conducting tissue of 6-7 layered **(Figs. 2A, B)**
Splachnobryum synoicum	Bricks	Turf	Cells small and hexagonal to rhomboidal	Extremely thin walled conducting tissue of 1-2 layers
Bryum plumosum	Wet soils	Turf	Cells are rhombic and broad	Conducting strand of thin walled cells 2-3 layered
Bryum argenteum var. *lanatum*	Dry soil, rocks	Turf	Wide rhombic, thin-walled cells, costa percurrent	Thin walled cells of 2-3 layered form the conducting strand.
Bryum coronatum	Cemented walls	Turf	Cells are broad and rhomboidal	Well developed and consist of three zones of tissues **(Figs. 2C, D)**
Plagiomnium integrum	Wet soil	Turf	Costa percurrent. Leaf cells lax, thin walled, quadrate-hexagonal	Poorly developed **(Figs. 2E, 3A)**
Philonotis leptocarpa	Calcareous rocks and marshy soils	Turf	Costa percurrent. Leaf cells thick-walled, rectangular, papillose	Thin walled and poorly differentiated, 2-3 layered
Erpodium mangiferae	Bark	Mat	Cells oval-hexagonal and large	Not differentiated
Leucodon sciuroides	Bark	Turf	Cells linear and thick walled, nerve absent	Not differentiated, some thick walled cells are scattered in the cortex.
Meteorium buchananii	Tree branches	Pendant	Costa present, cells narrow and linear	Not differentiated, thick walled cells are scattered in the cortex **(Fig. 3B)**

(E) *Conducting tissue in relation to the systematic placement* : There is some correlation between the development of conducting tissues with regard to their systematic placement (*Tables1* & *2*). The conducting strand is very much prominent in erect, acrocarpous orders such as Polytrichales, Dicranales, Funariales and Eubryales.The members of Pottiales which occur in dry habitats, also show a wide range of conducting tissues in respect to their habitat conditions. Isobryales show poorly developed conducting cells and the conducting cells are absent in the highly specialized group Hypnales. From the evolutionary point of view, the primitive types such as Polytrichales evolved well developed conducting system to compensate the erratic supply of water. However, in advanced groups like Hypnales the plant adjusts the water availability by following the ectohydric strategy.

Inspite of the great efforts made on the study of Indian mosses many areas still remain unexplored. Besides the floristic work on mosses, no attempt has so far been made to study the anatomical details of the mosses of India. The comprehensive survey of conducting tissues in mosses in relation to habitat and environmental conditions is completely lacking. Present study gives an insight to the development of conducting cells in relation to their distribution , habitat , growth forms and leaf cell patterns.

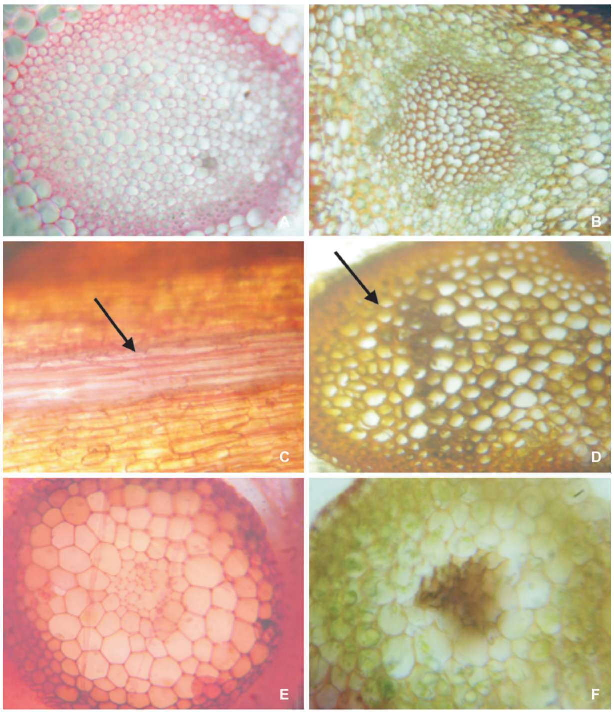

Fig. 1: A-T.S. stem of *Sphagnum* (× 200), B - T.S. stem of *Pogonatum fastigiatum* (× 200) showing, central core of conducting cells, C - L.S. stem of *P. fastigatum* showing prominent conducting cells (arros) (× 300) D - T.S. stem of *Dicranum lorifolium* (× 400) showing stereids in the outer corted (arrow) E - T.S. stem of *Leucobryum humillimum* (× 400), F - T.S. stem of *Hypohila involuta* (× 400).

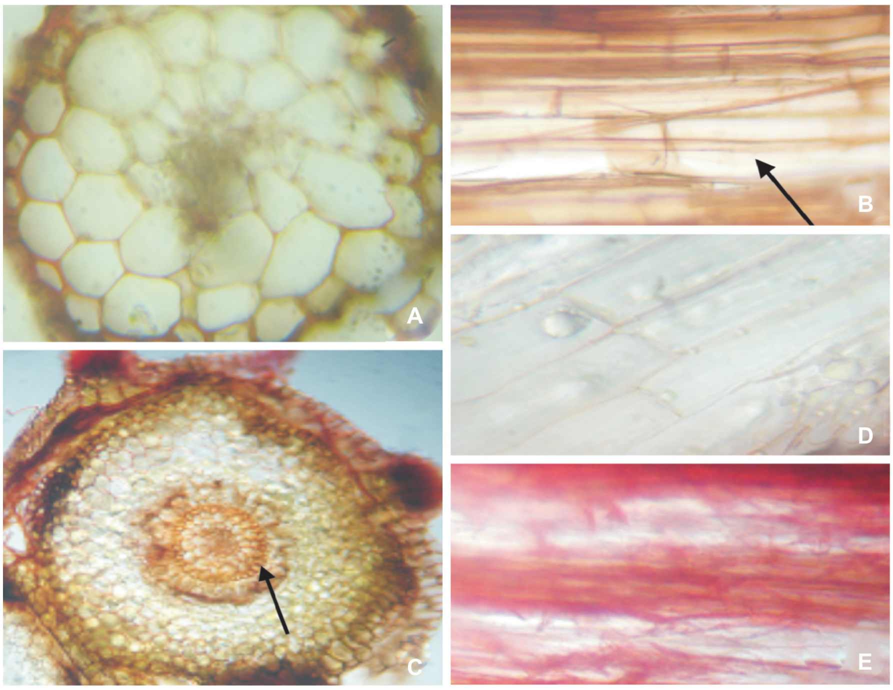

Fig. 2: A-T.S. stem of *Funaria hygrometrica* (× 400) showing poorly developed conducting cells, B - L.S. stem of *F. hygrometrica* showing conducting cells (arrow) (400 ×), C - T.S. stem of *Bryum coronatum* (200 ×) showing central thick walled cells and pigented cells (arrow) surrounding them, D - L.S. stem of *Bryum coronatum*, E - L.S. stem of *Plagiomnium integrum* (× 300).

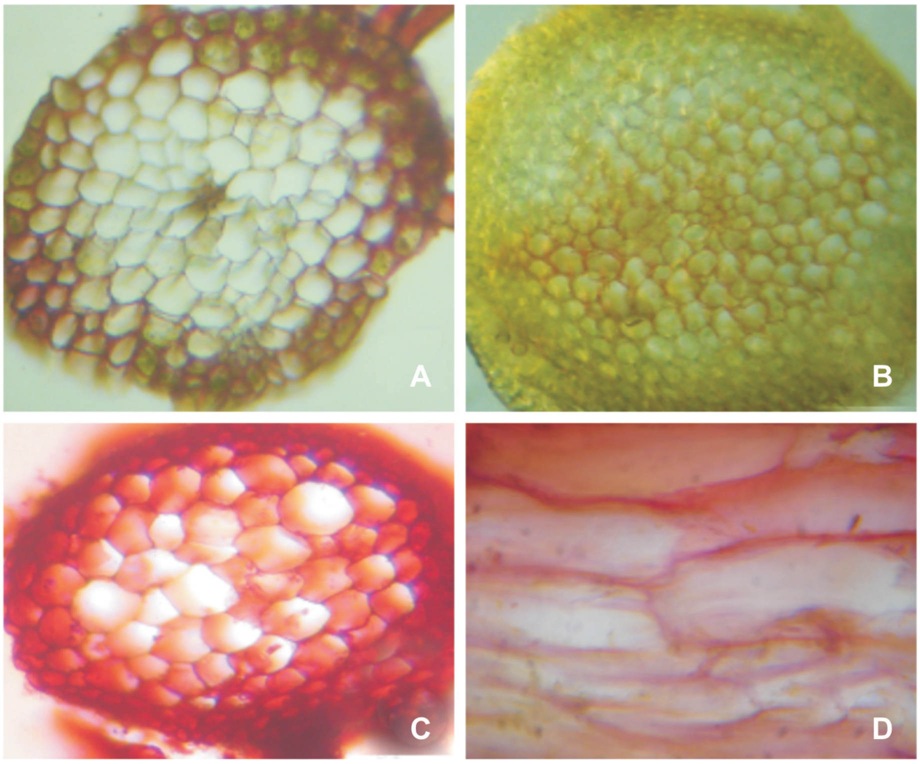

Fig. 3: A-T.S. stem of *Plagiomnium integrum* (× 400), B - T.S. stem of *Meteorium buchananii* showing thick walled cells in the groudn tissue (× 400), C - T.S. stem of *Brachythecium plumosum* (× 400) D - L.S. stem of *B. plumosum* (× 500).

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एक्रोकार्पस मॉस में संचालन तत्त्व का टैक्सोनामिक आशय

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सार संक्षेप

प्रस्तुत शोध में एक्रोकार्पस मॉस के नौ वर्गों में संचालन तत्त्वों की संरचना एवं विकास का वर्णन है। मॉस के आवास स्थिति, बढने का स्वरूप एवं पत्र कोशिका प्रणाली से संबंधित संचालन ऊतकों के महत्त्व की चर्चा है। तना के विभिन्न भागों में कोशिका के लक्षण, पटलीय कोशिका प्रणाली एवं शिरा पर विचार किया गया है। यद्यपिक जल-संचालक कोशिकाएं काई में अविशेषीकृत हैं परन्तु अध्ययन में देखा गया कि संचालन में उनकी जीवंत भूमिका है और टैक्सा के अंतर दिखाने में एक अतिरिक्त मापदंड है।

इनकी चार श्रेणी है (1) लेपट्वाइड की पट्टियों से घिरे हुए हाइड्रोम के रूप में स्प्ष्टत: सघन दीवार वाली संचालन लड़ी (6-7 परत) वाले एक्रोकार्पस मॉस। छाल में सघन दीवार वाली कोशिकाएं (6-10 परत)। शिश में स्टेरिडल कोशिकाएं, पत्तों में सुविकसित संचालनक तत्त्व उदाहरण पोलिट्रिकम (2) सघन दीवार वाले, संकीर्ण, लम्बी संचालक लड़ी (4-5 स्तर) छाल में कोणीय कोशिकाएं (6-8 परत। सूजे हुए दीवार वाले अनियमित व छिद्रयुक्त, अनियमित, चतुज़्कोणीय पत्र कोशिकाएं, उदाहरण डिक्रेनाम (3) विकास क्रम में विविधतापूर्ण मोटे या पतले दीवारयुक्त संचालक।