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EVOLUTION OF FOLIAR VENATION IN EMBRYOBIONTA

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ABSTRACT

A survey has been carried out of the foliar venation in the various 'type' taxa of the Embryobionta as suggested in the classification proposed by Cronquist, Takhtajan and Zimmermann (1966). The study includes not only the true leaves of higher cryptogams but also the scaly leaves of *Psilotum*, *Rhynia*, *Equisetum*, and *Ephedra* have been taken into account. It is seen that usually there is a gradation of complexity in this feature as we go higher up in the ladder of evolution. In several representatives, however, the veins have become less numerous and rarified.

INTRODUCTION

PHYLOGENY is generally regarded as the evolutionary history of a taxon or a group of organisms and attempts to account for its origin and development. As such one of the prerequisite of the phylogenetic studies in Botany is the determination of the origin and relationships of all taxa of both extinct and present-day plants and the classification or 'grouping' of them according to a system that will indicate their genetic or 'blood' relationships. Sufficient work is available on this aspect now taking into account various features or attributes, both of the vegetative and reproductive parts, like archegonium (or the female gametophyte as a whole), pollen (or the male gametophyte as a whole), etc. Similarly, floral characters, nodal anatomy, foliar anatomy, cytology, biometrical genetics, chemotaxonomy, and numerical taxonomy are regarded important parameters, worthy of consideration, from this point of view.

The term 'embryobionta' has been coined by three of the leading present-day taxonomists—Arthur Cronquist (New York), Armen Takhtajan (Leningrad), and Walter Zimmermann (Tübingen) in the year 1966. They also propounded a new system of classification for the embryo-bearing plants. Accordingly, they placed them under the sub-kingdom 'Embryobionta' which includes plants ranging from Bryophyta to Phanerogams of the older systems of classification. They also advanced concrete arguments in support of this new approach.

Necessity was felt by us to provide an understanding of the various stages and aspects of evolution of the foliar features into different groups of the embryobionta based on this arrangement. The present communication is restricted to a consideration of the foliar vascularization alone whereas the epidermal characters form the subject-matter of another article to be published shortly.

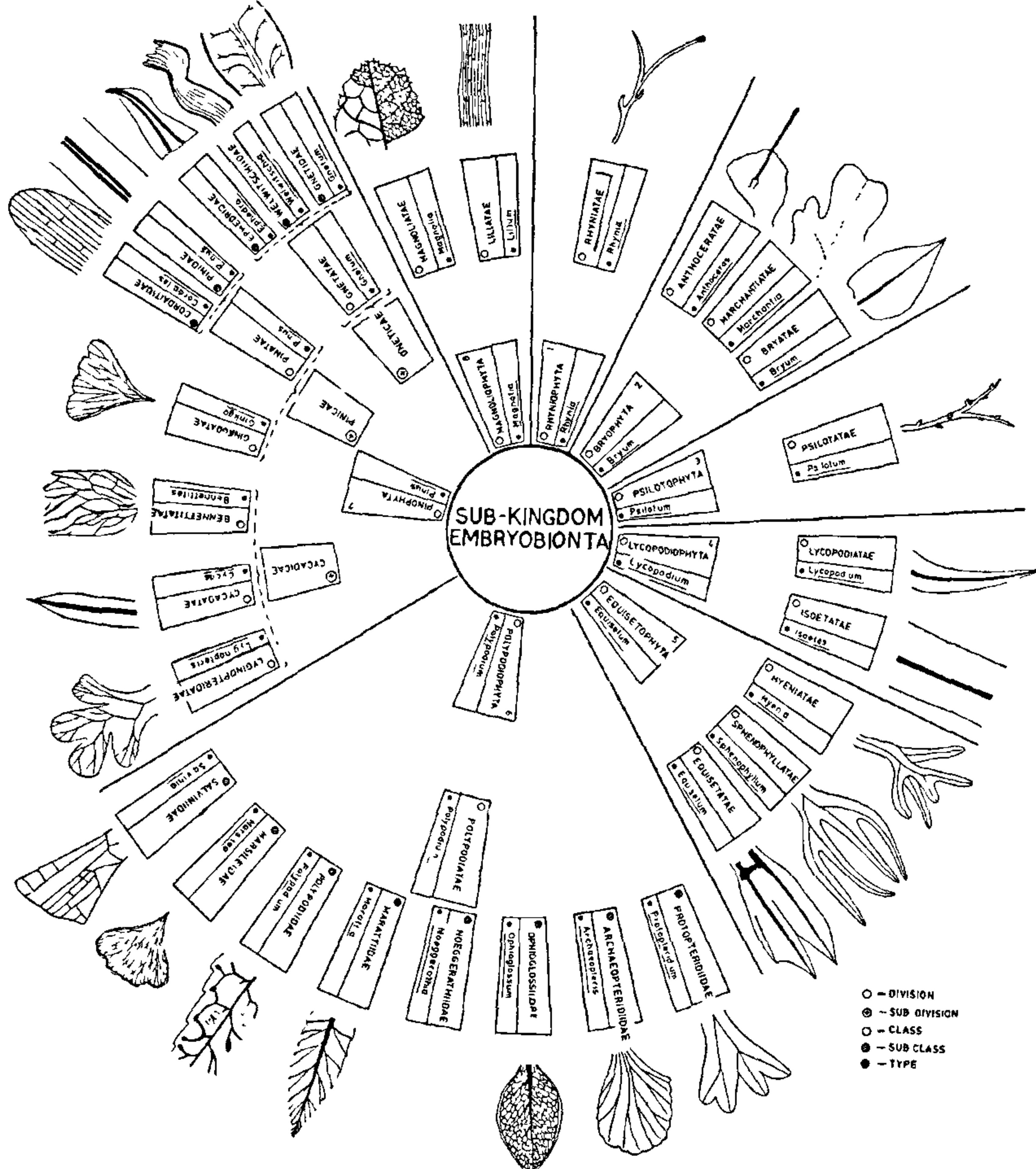
EXPERIMENTAL

Sources of information.—It must be admitted at the outset that in carrying out this survey, we encountered difficulties in procuring both the fossil as well as living materials. Howsoever we wished to study the fossils in detail, we could not do so because of the insufficient information and preparations at our disposal. Specimens of the living materials were collected locally or from the hill stations. Specimens from the herbarium sheets of the Delhi University Botany Department and those from the museum also served us very well. We also attempted to procure data about the fossils from leading palaeobotanists in India and abroad by correspondence but got limited success.

Preparation of the material for microscopic study.—Following the methodology proposed by Paliwal and Kakkar (1969), dried leaves were at first kept in hot water for half an hour, transferred to 3% NaOH for overnight, washed thoroughly with water the next day and placed in the chloral hydrate (100%) + hydrogen peroxide mixture for three hours to overnight. This

was later passed through a chloral hydrate series (75%, 50%, 25%) keeping in each grade for 10 minutes and washed thoroughly with distilled water. It was dehydrated through an ascending series of alcoholic grades and stained with safranin dissolved in a mixture of absolute alcohol and xylol (1:1) for 10 minutes. Mounting was done in piccolyte.

not present but only scaly leaves occur without any vasculature. In *Marchantia polymorpha* the 'midrib' is quite prominent which dichotomizes along with the thallus. However, no such inner tissue differentiation is noticeable as to warrant its description as a vein. In *Anthoceros himalayensis*, the midrib is totally absent. The leaves are leptophyll* in *Bryum* sp., *Psilotum nudum*,



gnemon, and *Magnolia stellata* they are of the mesophyll type.

Origin of Variability.—Primitive vascular plants like *Lycopodium* and *Equisetum* have a primary or 1° vein while those like *Rhynia* and *Psilotum* which are at the bottom of this category lack it completely. Nodal anatomy in all these representatives such as the species of *Lycopodium*, *Psilotum* and *Selaginella*, etc., is alacunar meaning thereby that the vascular system of the leaf does not arise from the main stele (or the stem stele). This may form a part of such a discussion where it is opined that the leaf traces form the stem stele and the stem does not have any vasculature of its own. In *Marchantia polymorpha* the 'midrib' appears distinct externally but it is devoid of any vasculature altogether whereas in *Bryum* sp. and *Cycas circinalis* also a single or 1° vein alone is present. An identical or univeined condition is seen in the young leaves of *Santalum album* (Aggarwal *et al.*, unpublished information) and *Cercis siliquastrum* (Slade, 1957) at the ontogenetic stages of the leaves. This indicates that ontogeny repeats phylogeny.

Primary or secondary vein systems are present in *Marattia* sp., *Polypodium* sp., *Marsilea minuta*, *Salvinia natans* and *Ginkgo biloba*; a little more advanced or 1°, 2° and 3° vein system is present in *Ophioglossum reticulatum*, *Gnetum gnemon*, *Magnolia stellata*, and *Lilium giganteum*. This may be due to increased independence of these taxa from the hydrophytic habitat.

Steps of Evolution.—In taxa like *Bryum* sp., *Lycopodium selago*, *Equisetum ramosissimum*, *Cycas circinalis*, *Pinus roxburghii*, and *Ephedra foliata* only primary or 1° veins are present. However, 1° and 2° vein system is present in *Marattia* sp., *Polypodium spinidosum*, *Marsilea minuta*, *Salvinia natans*, and *Ginkgo biloba* whereas *Ophioglossum reticulatum*, *Gnetum gnemon* and *Magnolia stellata* leaves possess 1°, 2° and 3° vein systems. The most complex vasculature among the taxa studied is of course seen in *Magnolia stellata* wherein the leaves exhibit a further differentiation of the venation system (beyond 3°). Taking stock of the branching of the lateral veins, we find that the primary or 1° vein system has a single midvein which remains unbranched in *Bryum* sp., *Lycopodium selago*, *Isoetes coromandelina*, *Equisetum ramosissimum*, *Cycas circinalis*, *Pinus roxburghii* (where two primary or 1° veins are present) and *Ephedra foliata*. Secondary or 2° vein system has been recorded in *Ophioglossum reticulatum* and *Marsilea minuta* (which also possesses an intramarginal vein). Dichotomously branched situation is seen in *Marattia* sp., *Ginkgo biloba* and *Magnolia stellata* forming compartments or areoles. Distinct areole formation also occurs in *Ophioglossum reticulatum*, *Polypodium spinidosum*, *Marsilea minuta*, *Salvinia natans*, *Gnetum gnemon*, *Magnolia stellata*, and *Lilium* sp.

The Fossil Forms.—*Rhynia* lacks 1° or primary vein system in the fossils. In taxa like *Hyenia* sp., *Sphenophyllum* sp., *Protopteridium* sp., *Archaeopteris* sp., *Bennettites* sp. only primary or 1° veins are present. Primary or 1° single and dichotomously branched veins are seen in *Hyenia* sp., *Sphenophyllum* sp., and *Protopteridium* sp. The primary or 1° veins are several and branched in *Archaeopteris* sp., *Bennettites* sp., and *Cordaites* sp. Arcole formation also seems to occur in the leaves of *Bennettites* sp.

GENERAL COMMENTS AND CONCLUSIONS

Taxonomic evidence (or characters) can be drawn from any part and phase of development of a plant. In practice, however, overwhelming reliance is placed on morphological features, at least for grouping of the various representatives and thereupon erecting classifications. It is also a truthful realization that the primitive morphology of a given part is usually accompanied by specialization of other structures which Bower (1923) called as 'phyletic inertia'. In this connection it is interesting to note that Bailey (1957) has commented on the futile time and effort put in by many workers to show or even 'prove' that certain organs or features of the plant are inherently more conservative than others and, therefore, should have a more dominant role in the analysis of classification and phylogeny. As such the utility of as many characters as can be studied becomes apparent. Taking clue from this fact the argument put forth by some anatomists that endomorphic features are more important than exomorphic structures becomes completely ill founded. Analysis of the angiosperms as a whole shows that such an assumption cannot be fully justified and that each morphological or histological attribute is fundamentally similar and potential of being reckoned for analysis in systematics. It remains, however, true that when looked at under the microscope or with the naked eye, some features are found to be relatively stable in certain groups of plants and show considerable variations in others. It is therefore evident that endomorphic characters such as anatomy are neither more nor less reliable than exomorphic features; perhaps they are of equal valid use. They give us, as Bailey says, more string to our bow.

During more recent years, leaf anatomical features such as stomata, trichomes, venation, etc., have been recognized to play an increasingly important role in the formulation of natural groups. They are also widely used in other aspects of taxonomy and have been largely applied to the elucidation of 'phylogenetic' relationships.

The present observations reveal that there is no linear evolution even among the taxa grouped together indicating that these must have originated from different

and perhaps also 'distant' ancestors. Variable opinions have been expressed in the literature from time to time with regard to the probable lineage of the vascular plants *vis-à-vis* the foliar venation. For instance, Zimmermann (1959) thinks that in gymnosperms the dichotomous foliar venation is the retention of a truly primitive type of vasculature. Hammen (1948) and Lam (1959) consider that instances of primitive dichotomy are still present in the forked pattern of branching of the major leaf veins. Hammen also adds that the accompanying network of veinlets tends to darken the picture.

Looking at the information available for Magnoliophyta we find that Foster (1959 a) recorded for *Kingdonia uniflora* leaf an open type of dichotomous venation pattern which he described to be strikingly like the venation of the leaves of *Ginkgo biloba* and certain fern genera. Other authentic examples of open dichotomous venation in the angiosperms are known in *Circaeter* (Foster, 1961 b; 1963) and *Utricularia* (Subramanyam, 1969; see also Subramanyam and Banerjee, 1967). Foster (1959 b) has discussed the question whether the reticulate type of venation so characteristic of living angiosperms, may not have evolved from open dichotomous vasculature. According to Hutchinson (1959), Foster (1959 a), and Foster and Arnott (1960), this possibility is clearly indicated by the venation pattern in *Kingdonia uniflora*. In this genus the vascular supply at the nodal level consists of four collateral traces which diverge from a single gap into a sheathing leaf base. According to Foster and Arnott (1960) this type of nodal anatomy is comparable to the unilacunar, 2- and 4-traced system found in the cotyledonary nodes of some of the woody Ranales. The vascular system of the tepals is also 2-traced and of the unilacunar type (Foster, 1961 a). Foster and Arnott (1960) consider that from a morpho-

logical point of view *Kingdonia* type of venation is comparable to *Sphenophyllum*, some ferns and *Ginkgo*. This is perhaps an indication of the polyphyletic origin of the different groups of plants included in the subkingdom Embryobionta, although at places we find that some idea becomes available of the 'slide' of venation of representatives of one type becoming like that of the other.

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THE NATIONAL SYMPOSIUM ON RADIATION PHYSICS

The National Symposium on Radiation Physics sponsored by the Department of Physics, University of Mysore, Mysore, will be held during June 10-12, 1976 at the University Physics Department. The last date for receiving abstracts—April 15, 1976, papers—May 30, 1976.

Details can be had from Prof. B. Sanjeevaiah, Convener, National Symposium on Radiation Physics (1976), Department of Physics, University of Mysore, Manasagangotri, Mysore 570 006.

SEMINAR ON ENVIRONMENTAL GEOSCIENCE (JUNE 26-28, 1976)

The Indian Institute of Geological Education has proposed to conduct, in collaboration with other scientific societies, a Seminar on the subject mentioned above along with a workshop on the same

theme in June 1976. Further details can be had from the Secretary, Prof. S. Sambegowda, Central College, Bangalore 560 001.