

PTERIDOPHYTES : AN ENIGMATIC GROUP OF PLANTS*

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Pteridophyte (in Greek means 'fern plant') members had a very flourishing past in dominating the vegetation of the earth during the Carboniferous period (280-345 x10⁶ years)** but afterwards the further geological evolution resulted in the dominance of flowering plants in the present day vegetation. Now in comparison to about 2,50,000 species of spermatophytes, the pteridophytes number only 10,000 - 11,000 species. The members of the group have often been called seedless vascular plants or conventionally and more (appropriately 'fern and fern allies' (cf. Wagner 1993) but more recently named as 'ferns and allied plants' or even 'fern worts'. Strictly speaking the members of the group share only few characters as the well developed tracheary system (without vessels), absence of seeds, mostly independent sporophytic and gametophytic generations and swimming spermatozooids. The main link of pteridophytic members is not that much in the similarities of structure but these are linked by the likeness in the life cycle stages.

A perusal of any account on the living or fossil pteridophytes will leave one with the impression that morphologically, structurally and genetically a highly diversified type of plants are grouped together under 'Pteridophytes' and quite often one starts thinking on the lines as whether all these plants do really belong to the same category of plants. The whole difficulty has been because of the nearly total dependence on the characteristics of vegetative organs in classifying the fern allies and on the characteristics of reproductive organs - the sori and sporangia for delimiting the ferns. The results so far achieved make the pteridophytes an enigmatic group of plants - conglomeration of highly diversified plants wherein there has been no evolution of any organ of the order of 'the flower' in angiosperms

which shows the unity of characters of all components.

Having spent more than half the period of my life in the in-depth study of ferns and fern allies I wish to dwell upon as to how much diversified groups of plants do the pteridophytes represent and what are the problems that remain unsolved in the classification of the ferns which constitute more than one-ninth of the total pteridophytic members as they live today on the surface of the earth.

There is absolutely no doubt that the pteridophytes were the first vascular plants on the land but how and when did the simplest of pteridophytic members originate in the fossil history of vegetation is a big question mark even today. A glance over the evolutionary history of world's vegetation as represented by the fossil records confronts us with plant forms that blur the clear-cut picture evolved over the last one and a half centuries through the marvellous studies of palaeobotanists of the stature of H.N. Andrews, T. Delevoryas, T.M. Harris, R. Kidston, W.H. Lang, B. Sahni, A.C. Seward, D.H. Scott and a galaxy of many more. The result is controversial interpretations of interrelationships and phylogeny of major groups. It will be befitting to quote below the remarks of Kramer & Green (1990) :

"As to the classes of Pteridophytes as defined by neobotanists, various intermediate forms are known from the Devonian and Lower Carboniferous. Thus the characters of Lycopods and horse tails are shared by such forms as *Eleutherophyllum*, those of horse-tails and ferns by *Ibyka* and of ferns and lycopods by *Enigmophyton* although the evaluation of these and similar fossils is a matter of continuing palaeobotanical enquiry".

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** For the age of various geological periods highly variable figures are given by different writers (see Smith 1955, Delevoryas 1966, Sporne 1968, Bierhorst 1971)

Even on the basis of study of the extant vegetation, the results are not different in any way. Highly conflicting phylogenetic relationships have been proposed where ever a new evolutionary sequence of pteridophytes or a fern classification has been given. (cf. Bir 1982).

Antiquity and Evolution of Early Pteridophytic Members :

Information about the common fossil genera of fern allies and early ferns as have been described from time to time is provided in Table 1 (as based on Bierhorst 1971). It clearly shows that:

- (1) The fern allies dominated the earth's surface during 600-280 x 10⁶ years period i.e. from Cambrian to Permian.
- (2) The giant sized Calamitean and Lepidopodiaceous, members (*Calmites*, *Lepidendron*, *Sigillaria*, *Bothrodendron*, etc.) constituted the major elements of the forests of the Carboniferous period.
- (3) The generally held view that the pteridophytes first appeared in the Upper Silurian and Lower Devonian over 400 million years ago (cf. Wagner 1993) with *Cooksonia* (Psilophytopsida : Rhyniales) being the earliest vascular plant (cf. Raven 1977), had been put in doubt with the discovery of *Aldanophyton antiquissimum* from the Mid-Cambrian of eastern Siberian Adansk mountains by Kryshstofovich (1953) thus representing the oldest record of the vascular plant. Leclercq (1956) regarded it of Lycopsid affinity representing *Aldanophyton - Baragwanathia - Drapanophycus* line of evolution. With this, it seemed established that prior to the existence of the simplest vascular land plants (*Cooksonia-Rhynia-Horneophyton*), there existed on the surface of the earth, a complex vegetational system comprised of more complex plant body organization. But Stewart (1960) completely discounted the vascular nature of *Aladanophyton* and no sporangia were also found for this ancient plant. This how-ever created a suspicion in the minds of palaeobotanists, phylogeneticists and evolutionists that prior to the known primitive vascular land plants of Silurian-Devonian periods, perhaps there existed more complexity of vegetation that had not been preserved during the early evolutionary history of the earth.

Mehra (1968) while dealing with the evolutionary patterns in the early land plants, stipulated that in the 5 billion years old evolutionary history of the earth, the life originated about 1.7-2.1 billion years ago and the origin of the vascular plants is still shrouded in mystery. He visualized the evolution of Pteridophytes along two main lines: first being represented by *Aldanophylon-Baragwanathia - Drapanophycus* series (lateral sporangiate plexus) evolving into Lycopodiales, Selaginellales, Lepidodendrales, Isoetales, etc. and the second one is the Rhyniaceae stock (terminal sporangiate plexus) evolving into Psilophytales (*Rhynia-Horneophyton* line), living Psilotales, Sphenophyllales, fossil and living Equisetales, etc. with the largest number of genera from the Devonian 300-400 x 10⁶ years old period representing the richest vegetation of fossil fern allies while the Pro-Pteropsida and Pro-Gymnospsida have given rise respectively to Filicales and living (Cycadales Ginkgoales, Coniferales, Gnetales) and fossil (Pteridosperms, Bennettitales, Cordaitales) Gymnosperms (cf. Mehra 1968).

- (4) Several of earlier described Coenopterid genera of early fossil ferns as *Rhacophyton*, *Protopteridium* and *Archeopteris* from the Devonian do not really belong to Pteridophytes but represent a class Aneurophytopsida well established as Progynospermous group.
- (5) *Pseudosporochnus* often regarded as part of Psilophytotales is really a fern genus belonging to Cladoxylales.
- (6) *Baragwanathia* from Lower Devonian still continues to be the oldest record of Lycopodiosida and from Upper Silurian *Cooksonia-Taenioerada* represent the oldest well established and undisputed record of vascular plants of Psilophytalean affinity.

The morphology and structure of early Pteridophytes i.e. fern-allies fossil members from Upper Silurian, Lower and Middle Devonian (*Cooksonia*, *Rhynia*, *Horneophyton*, *Taenioerada*, *Zosterophyllum*, *Psilophyton*, etc.) represented early stage in the development of earth's vegetation and these having less organizational complexities are more conservative in diversification than the later vegetations. As Wagner (1993) has appropriately put it that in the early Devonian the Pteridophytes were all much more closely

Table 1: Distribution of early fossil Pteridophytic Genera in the Palaeozoic Era

Period	Time Period in yrs (x 10 ⁶)*	PLANT GROUPS					
		Rhyniales	Zosterophyllales	Lycopodiopsida	Equisetopsida (Sphenopsida)	Cladoxylales	Coenopteridales
PERMIAN	280						
CARBONIFEROUS							
Pennsylvanian (Upper Carboni.)	310				Equisetales		
Mississippian (Lower Carboni.)	345			Selaginellites Miedesmia	Calamites Sphenophyllum		Botryopteris Stauropteris
DEVONIAN							
Upper	365			Stigmara Lycopodites Bothrodendron Lepidodendron Lepidosigillaria Sigillaria Lepidocarpon	Asterocalamites Pseudobornia Eviostachya		
Middle	390	Rhynia Homeophyton				Cladoxylon Calamophyton	Astropteris Arachnoxylon Indopteris
Lower	395	Trimerophyton Psilophyton Dawsonites	Zosterophyllum Gosslingia		Hyenia	Pseudosporochnus Protohyenia	
SILURIAN							
Upper	?	Taeniochrada Cooksonia		Asteroxylon Drepanophycus Protolpidodendron Baragwanathia			
Middle	415						
CAMBRIAN	600			Aldanophyton			

Aneurophytopsida (*Rhacophyton**, *Protopteridum**, *Aneurophyton-Eospermatopteris*, *Tetraxylopteris-Sphenoxylon*, *Archeopteris**, *Callixylon*, *Protopytis*, etc* Until recently considered as Coenopterid ferns) primarily from Devonian possibly contains ancestral forms of Pteridosperm-Cycadeoid-Cycad line, the Coniferophyte line and the Ophioglossales (cf. Bierhort 1971). Early Seed Plants originated in the Carboniferous-Pteridospermales in the Mississippian and Coniferales-Cordaitales in the Pennsylvanian. + Highly variable figures are given by different writers (see Smith 1955, Delevoryas 1966, Sporene 1968 Bierhort 1971).

related.

Fossil History of Ferns :

As early as 3910 Seward remarked that: "From Jurassic rocks in various parts of the world numerous fossils of ferns have been described under generic names, *Asplenium*, *Aspidium* *Davallia*, *Polypodium* and *Pteris*. In great majority of cases such records leave much to be desired from the point of view of students who appreciate dangers of replying on exter-

nal similarity between vegetative organs and on resemblance found on obscure impression of sori". A few years later he (Seward 1933: 434) stated that very little is known of the early history of Polypodiaceae* since the number of well preserved examples in Mesozoic floras is insignificant. Also the early Cretaceous genera *Onychiopsis* and *Adiantites* implying relationship with Polypodiaceae are for the most part imperfectly known to be of much trustworthy record (Seward 1933 : 393). Not long ago Lovis (1977) has given a fine review of

* Ferns with leptosporangiate sporangium containing 64 spores.

fossil Polypodiaceae while discussing the evolutionary processes and patterns in ferns. He regards the ferns to be "Prominent in the Mesozoic until Lower Cretaceous where after they diminish in importance in direct consequence of vegetation diversification and increasing abundance of angiosperms in the latter half of Cretaceous".

The significant fern elements of the Mesozoic are:

I. Yorkshire Jurassic Flora : This is perhaps the best known so far.

(a) Osmundaceae (*Todites* and *Osmundopsis*) and Dicksoniaceae (*Coniopteris*, *Dicksonia*, *Kylikopteris*, *Eboracia*, etc.) are prominent in number of species and individuals.

(b) Marattiaceae (*Marattia anglica*) and *Angiopteris neglecta* and Schizaceae (*Klukia*, *Stachypteris*). Gleicheniaceae is absent from Jurassic.

(c) Dipteridaceae (*Dictyophyllum*, *Clathropteris*, *Haussmannia*) and Matoniaceae (*Phlebopteris*, *Matonidium*).

(d) *Aspidistes thomsonii* (looks like an early *Thelypteris*).

II. *Aspidistes sewardii* (from Jurassic of Israel) and *A. beckerii* (from lower Cretaceous in England) have also been described but surely they do not belong to Thelypteridaceae and may be Matoniaceae (cf. Lovis 1973).

III. Other Mesozoic Fossils :

(a) *Coniopteris* members resembling *Davallia*, *Lindsaea*, *Schizoloma* and *Odontosoria*.

(b) *Adiantites*, *Australopteris* (comparable to living *Drynaria*)

(c) *Ondontosorites*. A number of sterile and fertile fern fronds are described from Jurassic rocks of Rajmahal Hills, India. Filicinean fronds belong to *Cladophlebis indica*, *C. srivastavii*, *C. sahnii*, *C. kathiawarensis*, *C. denticulata*, *Cladophlebis species*, *Dicksonia rajmahalensis*, *Dryopteris indica*, *Klukia species A & B*, *Marattiopsis reversa*, *Todites indica*, *Sphenopteris* cf. *S. lobifolia*, *Gleichenites species*, etc. (cf. Sharma 1971).

IV. According to Harris (1973) *Gleicheniopsis* and *Aspidistes* are the only Polypodiaceae from the Mesozoic. *Gleicheniopsis* is also recorded from Middle and Upper Cretaceous of Greenland whereas *Gleichenites* is the most abundant in the Greenland Cretaceous vegetation as well *Onychiopsis* is known from Lower Cretaceous.

V. Lovis (1977) mentions that Cyatheoideae were more numerous and diverse in the Later Mesozoic. In the Tertiary period from Palaeocene we have reports of existence of *Allantodiopsis* (*Allantodia* like), *Dennstaedtia* (*Dennstaedtiopsis*), members of Tectarioideae, *Onoclea*, *Salpichlaena*, *Woodwardia*, *Saccoloma*, *Acrostichum*, *Asplenium*, (*Athyrium*, *Diplazium*), etc. *Pteridium* is recorded from Miocene. Surange (1966) in his monograph on the Indian fossil pteridophytes described 85 species under 46 genera and thereafter a number of contributions appeared on the subject which have been reviewed by Sharma (1986). Fossil Pteridophytes are found through out the Gondwana system but more frequently in the Mesozoic era with ferns making the major part of the assemblage while lycopods and sphenopsids are represented by few genera.

Thus we see that the ferns which constituted the common element in the Jurassic and Lower Cretaceous flora became scarce afterwards, their place being gradually taken over by the increasing elements of flowering plants. With this change in situation the ferns and fern allies after the Mesozoic became of lesser numerical importance. According to Chesters *et al.* (1967) and Takhtajan (1969) there was a remarkable transformation in the fossil floras of the world about the Middle Cretaceous; in the Lower Cretaceous angiosperms were still numerically a minor element in fossil record but in the Mid-Cretaceous the angiosperms came rushing on to the stage with many living families including some supposedly primitive and others regarded as advanced already recognizable. By Upper Cretaceous the flowering plants had become the dominant element in the floras of the world (cf. Lovis 1977). In fact the Polypodiaceae came into force rather later than angiosperms (Harris 1973).

Lovis (1977) very rightly asserts that few confi-

dent "Polypodiaceae" fossils are known from any part of Mesozoic period and the situation radically changed early in the Tertiary period and in Palaeocene and Eocene we have records of *Onoclea*, Adiantaceae, Blechnaceae, Denstaedtiaceae and Dryopteridaceae. According to him the main radiation of "polypodiaceous" ferns occurred between Cretaceous and Palaeocene period and the Dennstaedoid radiation was well before Palaeocene, although not yet been certainly detected in the fossil record at an early date. He concluded that: The appearance of the main Polypodiaceous radiation does seem to constitute the most recent major innovation in the evolution of the world flora (Lovis 1977 : 255)".

The whole scrutiny of literature on fossil ferns does reveal one point that there has been lot of misconceptions and confusions about the generic identification and delimitations of fossil ferns and superficial resemblance to the living genera has quite often been instrumental in identification and naming. One example is of *Adiantites* a form genus to which are attributed Carboniferous and Permian fossils which are not even ferns at all, but Pteridosperms (cf. Lovis 1977).

Copeland (1947) thinks the Gleicheniaceae are known by fossils of northern lands perhaps 40 million year old (Miocene-Oligocene epochs) and Antarctica-like Greenland was at sometimes habitable. According to him the whole of the fern world of the tropics is descended from the ferns of old Antarctica and more than half of the living fern species are descendents of migrants from Antarctica since Antarctica has been fit for vegetation at various times in the past and the last such era ended during Miocene. He remarks:

"Free migration in the circumarctic zone ended one billion years ago; in the antarctic region, twenty million years ago. Free migration in the North has had apparently little effect on tropical fern flora and was so recent that almost every Northern fern genus is common to Eastern and Western Hemispheres. In the South the hemispheres have been isolated 20 times as long and many genera are peculiar to one or the other".

Origin of Spermatophytes: Since a reference has

earlier been made that "Polypodiaceae" came into being later than angiosperms it is but obvious that we make a note of as to when did the spermatophytes originate?

Wagner (1993) postulates that the spermatophytes first appeared in the Upper Devonian and they evolved radically to a new highly divergent life cycle involving fundamental changes. Progymnospermosida represented by Aneurophytopsidian genera (*Rhacophyton*, *Archaeopteris-Callixylon*, *Tetraxylopteris-Sphenoxylon*, *Protopteridium*, *Aneurophyton Eospermatopteris* and *Protopytis*) from Middle-Upper Devonian and Lower Carboniferous, is very significant since within it are possibly the ancestral forms of the Pteridosperm-Cycadeoid-Cycad line, the Coniferophyte line and the Ophioglossales (cf. Bierhorst 1971). Quite a many of the members have a dendroid habit. Early seed plants originated in the Carboniferous period (310-345x10⁶ years) but the pre-Cretaceous angiosperms are very few in number. It seems possible that the angiosperms arose and differentiated into several lines long before the Cretaceous from early gymnospermous members which co-existed with the pteridosperms in the upper Carboniferous. From early Cretaceous rocks nearly 30 or more families of angiosperms (mainly from leaf impressions and petrified woods) have been identified. These existed in the floras in which ferns and gymnosperms were dominant (Bierhorst 1971).

How did the spermatophytes evolve the seed bearing character ?

The origin of seed-habit* has been a subject of much speculation. There has been no doubt that the heterosporous condition, a pre-requisite for seed habit, not only had its origin amongst fossil pteridophytes but also got well established in the living ones (Selaginellales, Isoetales, Marsileales, Salviniiales). First clear cut case of heterosporous condition is seen in *Calamostachys casheana* and *C. americana* both members of Sphenopsida from Lower Carboniferous. Heterospory also became well established in members of Lycopsida (Lepidodendrales) also from Lower Carboniferous. In *Lepidocarpon*, three megaspores of the tetrad aborted and only one was functional and retained

* Mehra (1974) gives a complete sequence of events in the evolution of the seed.

in the megasporangium which was protected by an outgrowth of the bract with a radially elongated slit at the top serving as micropyle where microspores have actually been found. In another herbaceous lycopsid of Lower Carboniferous, *Miadesmia membranacea* a single megaspore was retained in the megasporangium and the out-growth of the bract protecting it but with an opening at the distal end where the margin of the out-growth had ciliate or teeth-like processes.

Almost similar situation could be seen in pteropsida. In *Stauropteris burtislandica* again from Lower Carboniferous, there were two abortive mega spores and two functional mega spores retained within the sporangium. Thus we see that the situation regarding retention of enlarged mega spore within the sporangium arose independently in the members of three major groups of Pteridophytes growing almost contemporaneously. This is a seed-like habit though there was nothing like-true integument, a 'pseudo-spermatophyte' situation indeed. Since there was no development of integument so we can not take it as true-seed but the fact remains that the primary stage in the evolution of seed regarding retention of megasporous within sporangium had been achieved in the fossil pteridophytes and this character some how or the other lingered on in some of the living species of *Selaginella* (*S. rupestris*) where the megaspores are retained for some time within megasporangium and germinate right there showing a short of viviparous condition of seed plants. Much accepted line of evolution has been dendroid Aneurophytopsida-Protoseminales-Pteridosperms- Bennettiales-woody Gymnosperms-woody Angiosperms but how this could have happened? There are several wide gaps and it seems highly probable that not only the pteridophytes but also the spermatophytes (gymnosperms and angiosperms) have had polyphyletic origin and various groups can not directly be linked together.

Rhynian Plant Body :

Rhynia and *Horneophyton* the main Psilophytalean genera with the simplest vascular plant body organization so far known (roots absent) were certainly not the most primitive of the pteridophytes. Most widely illustrated plant body of *Rhynia* depicting horizontal, branched rhizome and upright dichotomously divided

stem with terminal sporangia has been questioned morphologically. It was Merker (1959, 1961) who first interpreted the subterranean portions of *Rhynia* and *Horneophyton* plants as gametophytes and not the rhizome because of the presence of sex organ cavities (flask-shaped depressions) and similarity with and occurrence of tracheids as in gametophytes of Psilotales. Pant (1962) considered the small sized axes of *Rhynia gwynne-vaughani* as the gametophyte of possibly *Rhynia major*. This interpretation for Rhynian plant body is now acceptable by and large except that Mehra (1968) expressed an element of skepticism about this. Later on Lemoigne (1968) stated that the gametophyte of *Rhynia* is vascularized and archeqonia anal antheridia are present on that. According to him (Lemoigne 1968, 1973): (i) in case of *R. major* and *R. gwynne-vaughanii*, hitherto considered as two distinct kinds of sporophytes, *R. gwynne-vaughanii* is actually a gametophyte, probably of *R. major*. The gametophyte also shows the stomata, (ii) the correct name for *Rhynia* representative should be *R. gwynne-vaughanii* in accordance with Rules of nomenclature both for the sporophyte (previously called *R. major*) and a vascularized gametophyte (previously called *R. gwynne-vaughanii*) and (iii) the *Rhynia* of Devonian is closely related to *Psilotum* of the present day and these two genera should be classified in the same order Psilotales as family Rhyniaceae: *Rhynia* and family Psilotaceae : *Psilotum* and *Tmesipteris*.

The Rhyniales probably with terminal sporangia in reality gave rise to all groups of vascular plants except the Zosterophyllaceae and lycopsida and that too in the Silurian.

Phylogenetic Position of Psilotales:

The sole family Psilotaceae with no fossil records and two living genera *Psilotum* and *Tmesipteris*, has long been considered to belong to primitive class of fern allies, but more recently suggested as being closer to true ferns, even included in Filicales and grouped together with Stromatopteridaceae to which it is related morphologically and both have affinities with Schizaeaceae and Gleicheniaceae (Bierhorst 1968, 1971, 1973). Later on, Psilotales were treated as ferns by Lovis (1971)*. Majority of the pteridologists how-

* Psilotales placed as first order of 'ancient ferns' followed by Ophioglossales, Marattiales, Osmundales, etc.

ever do not agree with this treatment and retain Psilotaceae amongst fern-allies (Sporne 1968, Pichi Sermolli 1973, Foster & Gifford 1974, Crabe *et al.*, 1975, Love *et al.*, 1977, Ching 1978). While discussing the systematic implications of Psilotaceae Wagner (1977) observed that *Psilotum* and *Tmesipteris* show a number of profound differences from Filicales in respect of structure of aerial organs, vascular patterns, fertile appendages and sporangia and thus Psilotaceae do not belong to Filicales (Polypodiopsida). The idea of closeness of Psilotaceae to Stromatopteridaceae (Filicales) was much opposed by Copper-Driver (1977) and Wallace *et al.* (1983) on phytochemical grounds also.

On the other hand the idea of certain degree of affinity between Psilotales and Filicales got further strength because of similarity in spore structure (Lugardon 1973, 1979). However, the general consensus is that the Psilotales diverge, too far from ferns to be included in that class and merit recognition as a class in its own right (Kramer 1990). According to Bierhorst (1968, 1971) whose knowledge of the group is unparalleled, as a matter of fact, the psilotaceous sporophyte plant body exhibits a conspicuously poor degree of differentiation amongst its parts, the term "stem" and "leaf" are dubiously applied. Therefore, the uniqueness of the sporophytic and gametophytic characters of Psilotopsida makes these plants a category of their own representing a complete mix up of fern and fern allies characters.

Phylogeny as related to Chemical analysis:

It will be appropriate to make a mention of the analysis of distribution of chemical characters as arrived at by Gottlieb *et al.* (1990). They affirmed that :

(a) There is remarkable agreement between primitive pteridophytes and gymnosperms. Since (i) there is wide spread occurrence of biflavanoids in the Psilotaceae and Selaginellaceae on one hand and in the Cycadales and conifers on the other. In all these groups the biflavanoids are based on apigenin and show identical coupling patterns, and (ii) remarkably there is rareness of flavanoids, flavanones and flavanonols in the primi-

tive families of Pteridophytes and these are at least partially absent from gymnosperms. Bot gymnosperms and pteridophytes have been envisaged as sharing the same (Psilophytalean?) ancestor characterised by the presence of fatty @ hydroxyacids and biflavones as well as by the relative scarcity of flavanols and triterpenoids. The similarities acquired during further evolution appear to be due to the action of similar selective pressure extracted upon them.

(b) Strong chemical affinities also exist between advanced pteridophytes and angiosperms.

These workers opined that since no relationship between ferns and angiosperms is acceptable, the appearance of similar chemical substances in both plant groups is another example of *parallelism*. This wide spread occurrence of parallelism was explained by postulating the action of common selective pressures which are related to the plants defence system.

Classification:

The living pteridophytes are subdivided into Psilotatae, Lycopodiatae, Equisetatae and Filicatae (Psilotales, Lycopodiales, Equisetales and Filicales of others) and this classification is largely a compromise between convenience and the present knowledge (Kramer & Green 1990) or we may call them the true ferns and the fern allies (Lycopods, horsetails and Psilotales). The morphological evidence, however casts doubt on the status of Ophioglossaceae as true ferns since there is no circinate vernation in this group and Copeland as early as 1947 was right in considering the family separately from Filicales under Ophioglossales. Kramer (1990) has rightly stressed that the relationships between the classes of traditional pteridophytes are still very difficult to assess, if indeed they are all treated in the sense of being derived from a common source of cormophytes. About the classification of ferns less said the better. In spite the fact that no less than a dozen systems have been proposed in the present century, there are more points of disagreement rather than agreement and the fern classification continues to be in a state of flux* although for herbarium arrangement one could conveniently follow Crab *et al.*

* For details see Bir (1982). Also compare the contents of orders, families and genera as adopted by Lovis (1977), Pichi Sermolli (1977) and Kramer & Green (1990). There are a large number of phylogenetic issues that remain to be settled.

(1975) or Pichi Sermolli (1977) depending on personal choice. Both of these systems are convenient to adopt but at points highly arbitrary or unnatural.

So far so good to recapitulate about the pteridophyte enigmas. Now hence forth I will deal with few of the significant morphological, anatomical, cytological and reproductive biology features of this group of interesting but baffling plants.

(1) *Morphology*: Amongst the fossil members of fern allies there is the greatest amount of diversity of both vegetative and reproductive organs in plant body organization as noticed in Psilophytates, Calamitales, Sphenophyllales, Lepidodendrales, etc. but the fossil members of Equisetales (*Equisetites*), Selaginellales-Lycopodiales exhibit far less complexities and have close similarities with extant members. Isoetales with no fossil record, have plant body very much unlike other pteridophytes. Fossil primitive ferns have organizational complexities which makes their mix up with Pteridospermales particularly when in sterile state. Overall view of the living and fossil pteridophytes reflects *unity in diversity*.

(2) *Anatomy*: The diversity of anatomical features as seen in ferns and fern allies whether living or fossils, is a unique feature of these groups of plants. The simplest of treachery system, the protostele is seen in the Rhyniales, Psilotales, Lycopodiales (modified) of fern allies and the ferns Hymenophyllaceae and Vittariaceae to take one example. How could the same types evolve independently? There is no other explanation than to correlate the structure with plant body organization. The Sphenophyllales, Calamitales and Lepidodendrales together with certain Cladoxylales, Coenopteridales and fossil Osmundaceae, all share the character of secondary growth which is absent in the living members except the small sized *Isoetes* in which cambium forms the primatic tissue i.e. both secondary xylem and phloem on the inner side and secondary cortex on the outside. Such a feature is unique to this group and is not seen any where amongst plants. Lycopodiales, Equisetales, Cladoxylales and Coenopteridales have their own characteristic anatomical features uncorelated with other groups. Whereas in the living true ferns a panorama of structural features characterise each group of families with the total absence of secondary growth

but highly complicated anatomical features in tree ferns, *Dicksoniaceae*, climbing *Stenochlaena*, *Pteridium*, *Matonia*, etc. to cite few but all showing the absence of vessels and 'ontogeny repeat phylogeny' concept of F.O. Bower in the fact that what ever is the adult structure the young sporophyte begins with protostelic condition. Then there is size-structure correlation and megaphyllous condition in ferns governing the presence of leaf gaps i.e. if in higher ferns leaf primordia are removed the rhizome structure is simple and solenostelic but if allowed to grow then dictyostelic and other structural adaptations. The stelar cylinder of rhizome/stem of ferns consists of secondarily interconnected basal regions of leaf vasculatures and some times also vasculatures of leaf associated roots (cf. Nayar 1992). According Loyal & Bir (1991) a peculiar situation exists in the presence of 'vessel members' in the rhizome or root of a dozen species of varied genera of ferns and fern allies from India. They think that in the extant ferns, the vessels might have evolved during a short span of few thousand years when primitive man embarked upon agriculture practice and these vessels developed in fern populations/species which colonized disturbed and newly created habitats as in *Marsilea*. Highly peculiar anatomical features of different taxa lead one to the same inference as to whether Pteridophytes represent a coherent or incoherent groups of members.

Longest tracheids so far known in the vascular plants are present in stem of *Stenochlaena palustris*, a climbing fern of the tropical forests (cf. Mehra & Soni 1971) while Bir *et al.* (1984) showed that depending upon the organ size the tracheidal length is the largest in the petiole or rachis and smallest in the rhizome of the ferns as analysed belonging to *Nephrolepis*, *Pteris*, *Ampelopteris* and *Christella*. On the basis of detailed study of tracheary elements in 110 species of Himalayan ferns of 53 different genera Mehra & Soni (1984) observed that except in Ophioglossaceae and possibly Marattiaceae no where in the Filicales typical round bordered pits are noticeable and this justifies that Ophioglossales and Marattiales should be considered coordinate in rank with the Filicales. This indicates that perhaps the line of descent of all the ferns is not the same.

Stomatal pattern as a feature of considerable importance in deducing phylogeny was found by Mehra & Soni (1983) when these authors noted that members of Psilotales, Lycopodiales, Selaginellales, Isoetales, Ophioglossales and Osmundales have invariably Psilotaceous type (showing absence of subsidiary cells) of stomata, the original or basic type which characterised the early migrants to subaerial conditions of life and during further course of evolution of these early plants, other types of stomata found in Pteridophytes seem to have evolved along several lines. Equisetales and Marattiales have stomata of their own types but in case of leptosporangiate ferns quite often two or even more types of stomata occur together even adjacent to each other on the same frond. This confuses their phylogenetic affinities.

(3) *Fructifications*: Pteridophytes are known to show the widest range of the fructification or the spore bearing organs. From the simplest types in Psilophytales, the fructification gradually grade into complex structures from Psilotales onwards in Equisetales, Sphenophyllales, Lepidodendrales, Isoetales (*Isoetes* having the largest sized sporangium in the plant kingdom), Lycopodiales, etc. but the most complex structures are seen in ArthropHYTA. The organization of sporangia bearing organs in fern-allies has been on plurality of lines. It is with Filicopsida (living or fossil) that some simplification has been noticed beginning with Ophioglossales and two lines of evolution being eusporangiate and leptosporangiate, the later showing the fixity in the number of spores produced per sporangium. But examples are not lacking where sorol similarities have been attained through evolution along different lines of descent i.e. acrostichoid nature being reflected in pteridoid, aspidioid, blechnoid, polypodioid groups. Even then, sorol characters from time to time provided strong basis of fern classification either singly or in conjunction with other characters.

Spore number is infinite in eusporangiate sporangia and fixed in leptosporangiate sporangia and spore structure provides stable characters for comparison but again similarities in palynological features have evolved through plurality of lines.

(4) *Gametophytes*: Except for *Equisetum*, all the homosporous eusporangiate members whether of fern

allies or ferns, have subterranean, partially or fully heterotrophic, long living, cylindrical, tuberous, usually branched gametophytes as seen in *Rhynia* (new plant body interpretation), Psilotales, Lycopodiales and Ophioglossales while heterosporous members as Selaginellales, Isoetales, Marsileales and Salviniales exhibit two types of gametophytes which develop partially or fully within the sporangia. Stromatopteridaceae with 3-layered sporangial wall and 256 spores per sporangium also have subterranean, dichotomously branched gametophytes of a true axial type. Also some Schizaeaceae (*Actinostachys*), another primitive fern family with atypical leptosporangiate condition, show subterranean, tuberous gametophytes of a true axial type. It is the higher leptosporangiate homosporous ferns outnumbering the primitive ferns, which reflect the great diversity in the features of gametophytes which are thalloid, short living but of independent existence. Filamentous gametophytes characterise *Schizaea* and trichomanoid are present in the Hymenophyllaceae. Nothing can explain as to why *Equisetum* has short-living, terrestrial, fully autotrophic gametophytes which are closest to the ancestral types as thought by Nayar (1981), even though the spores producing these are the product of eusporangiate sporangia like other taxa showing subterranean gametophytes ?

Nayar (1981) regards the ribbon-like gametophytes of Hymenophyllaceae representing the derived condition while the cordate form amongst thalloid types is most primitive. Further, the tuberous type gametophyte represents a derived state from the surface growing autotrophic, as a special adaptation. Thus the cylindrical gametophytes of supposedly primitive pteridophytes i.e. certain fern allies and ferns show a derived condition. Really, an anomalous situation, contrary to the accepted evolutionary sequence.

Pteridophytes with distinctive independent gametophytic structures have invariably interpolation of sporophytic and gametophytic generations though the former has far longer life span than the latter but the recent morphogenetic studies for induction of apospory and apogamy, have led to different interpretation of 'alternation of generations' concept. According to Mehra (1972) the mechanism of alternation of generations which occurs with precise regularity in the life

history of land plants seems to owe its explanation neither to 'Antithetic Theory' nor to 'Homologous Theory' but it is to be considered as a part of normal morphogenetic processes of growth and development.

(5) *Cytology* : Beginning with the publication of Irene Manton's book "*Problems of Cytology and Evolution in the Pteridophyta*" in 1950, the pteridophytes today claim to be the best analysed group amongst vascular plants in spite of the fact that only about 25% of the members have been chromosomally analysed. Majority of the homosporous genera have high basic numbers, Psilotales $x = 52$, Lycopodiales $x = 34$ (in 1992 Florence S. Wagner records 23 pairs in *Diaphasiastrum sabinifolium*), Equisetales $x = 108$ (all species of *Equisetum* showing $n = 108$, a high polyploid number), Ophioglossales $x = 45$, Marattiales $x = 39, 40$ and majority of fern genera between 27-42 but tree ferns (*Alsophila*, *Cyathea* and *Hemitelia*) $x = 69$, and *Osmunda* $x = 22$, *Lepisorus* (some taxa) $x = 22$ or 23 or 26? However heterosporous Selaginellales $x = 8, 9, 10, 12$, Isoetales $x = 11$, Marsileales $x = 19, 20$ and Salviniiales $x = 9, 11$ show primarily low numbers. This shows high degree of chromosomal disparities. Does this mean that the evolution of low or high basic chromosome numbers has anything to do with nature of spores or is it a mere coincidence? Polyploidy occurs in the heterosporous and homosporous pteridophytes but with higher frequency in the latter (cf. Klekowski & Baker 1966). By and large, pteridophytes have high chromosome numbers*. According to Klekowski & Baker (1966) the mean gametic number of heterosporous and homosporous members being 13.62 and 57.05. In comparison, the flowering plants usually have $x = 5-15$ and usually low chromosome numbers. High numbers in pteridophytes show their great ancient nature and antiquity of the group. The homosporous pteridophytes have ultra frequent establishment of polyploidy (cf. Klekowski & Baker 1966) which appears to be necessary to create and maintain genetic variation in the face of the homozygotizing effects of habitual self fertilization in the monoecious gametophytes of these groups.

Wagner & Wagner (1980) had put an hypothesis that the ancestral homosporous pteridophytes as well as contemporary species have had high chromosome num-

bers from the beginning but recent evidence suggests that the homosporous pteridophytes had a history of repeated allopolyploidization and in fact all vascular plants probably have original basic numbers of 7-13. The high basic numbers of generic levels of Pteridophytes are the consequence of palaeopolyploidy. In the extant members of Pteridophytes the incidence and grade of polyploidy is also very high to the extent of over 50% in tropical floras whereas some individual genera have even a far higher incidence of polyploidy (e.g. *Asplenium* c. 75%). Recent work (e.g. Haufler 1987), however, suggests that pteridophytes in spite of high numbers, are genetically diploid having essentially the same number of alleles as diploid ancestors (cf. S. Wagner 1992). Cumulative evidence of cytology of pteridophytes does suggest that chromosomal diversity may coincide with morphological diversity of its members which have been involved in the evolution of new taxa throughout the evolutionary history of our flora on earth (homosporous versus heterosporous condition-the former category members having very high chromosome numbers in contrast to the low numbers in the later category).

Concluding Remarks :

Board survey of some aspects of Pteridophytes presented so far leaves one with a major impression that this is really an enigmatic group of plants about the origin, morphology, structure-development, phylogeny and classification of which numerous issues still remain un-resolved. As a matter of fact, pteridophytes show 'unity in diversity' in form, structure and development.

The fore-most question that comes to one's mind is as to why the giant horsetails and lycopods together with others once dominating the earth vegetation during Carboniferous period could not survive the geological upheavals in the evolutionary history of the earth? To my mind the reason could be that possibly the desiccation of the conditions of growth due to global climatic changes in the post-Carboniferous periods made the survival of independent delicate gametophytes (though no fossil evidence has been found, yet presumed to have been like that) and young sporophytes difficult and the regeneration of the then

* Highest chromosome number amongst the plants is shown by *Ophioglossum reticulatum*, $n = 720$.

pteridophytic vegetations became difficult and rather impossible. These gradually declined and were replaced in major part by spermatophytes with simplified gametophytes and fertilization mechanism. The main bottle-neck came in the wake of availability of water film required for fertilization through free swimming spermatozoids. That is why the archegoniatae do not dominate to-day? I do not think high chromosome numbers of homosporous pteridophytes became obstacle in their survival as we very well know that polyploids have better adaptive values in the present day flora. The major replacements of at one time dominating pteridophytic vegetations with gymnospermous and angiospermous vegetations from Cretaceous onwards leading to the present dominating position of flowering plants in the modern floras, has been a boon to mankind because the innovation of 'seed' has been the greatest gift of nature in connection with food supply. Also the gymnospermous and angiospermous forests supply the timbers (though exhaustible). All this would not have been possible had the pteridophytic vegetation continued to dominate the earth's surface till today. The present day descendant pteridophyte members do not have secondary growth and lack the gigantism of plant body organization but the majority of gymnospermous genera and quite a many of woody angiosperms have giant plant body, although to a greater extent the fossilized-Carboniferous floras dominated by pteridophytes, contributed to some of the present day coal reserves.

Today the pteridophytes rank third, next to angiosperms and gymnosperms, amongst vascular plants in constituting the various global vegetations comprised of gigantic trees though they number in terms of genera and species far more than gymnosperms. Their present day survival in the floras provide us with insight into the evolutionary history of the earth and the plants as well as different vegetations. Because of several enigmas connected with ferns and fern allies, these constitute very good subjects for inquisitive botanist's mind who would like to probe the 'whys' about the nature and evolution of these plants. Although of no major economic value except helping in colonization of new

ecological niches* and in soil conservation, the pteridophytic vegetations should be of as much a concern for conservation as the spermatophytic vegetations are today. It will be appropriate to recall the following observations of Jermy (1990) on the subject:

"Pteridophytes have evolved to fill almost every ecological niche but the greatest species diversity is clearly found in the tropical rain forests. The rapid disappearance of this biome throughout the world with many pteridophyte species yet undiscovered let alone described, is of great concern. It is fortunate that the richer mountane forests are the last to disappear. Sustainable logging unfortunately takes mature trees with large canopies frequently covered with rich epiphytic pteridophytes".

Before ending the address I shall wish to express grateful thanks to the Executive Council and the total membership of Indian Botanical Society for unanimously electing me as the President for the year 1993 and giving me whole-hearted co-operation in running the affairs of society. Further, I thank the C.S.I.R., New Delhi for providing me financial assistance under Emeritus Scientist Scheme.

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* Ferns also grow well on lava beds. In Trans Mexican Volcanic Beltg, according to Mickel (1993) there are many flows of various ages and one flow of about 1913 has pockets of vegetation and about a dozen fern species. But on one of these lava fern species are limited to the larva. Certain of the species of surrounding habitats are able to colonize and survive the sig aure of lava living.

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