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WATER FERNS: THEIR ORIGIN AND SPREAD

BY

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Poona (India).



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T. S. MAHABALÉ

MR. CHAIRMAN, COLLEAGUES, LADIES AND GENTLEMEN

I FEEL honoured by the invitation, authorities of this Institute have extended to me, to deliver the 20th Memorial Lecture in the name of late Sir Albert Charles Seward, my Professor's Professor. I feel it all the more, because it is here that I had my early lessons in Palaeobotany at the hands of Professor Birbah Sahni, F.R.S. after whom this Institute has been named. Work of it has now increased many-fold under the leadership of its present Chairman and active cooperation of highly trained workers, who have made a mark in the world of Palaeobotany by their devotion and distinctive contributions. To Indian Palaeobotanists it is an academic home, a real *Acad.* There is no doubt that the Institute will henceforth progress more and more. Let all assembled here today wish it greater glory, and work in future.

The subject I have chosen for my lecture is of special interest, namely "Water Ferns", as it touches both living and fossil forms, and has provoked a number of problems yet to be solved. Water has been the perpetual source for the origin, organization, and continuation of plant life since the ages. It has also been a storehouse of many groups of plants. The seas, lakes, rivers, their banks, estuaries, mountain tarns, rapidly flowing cascades and glaciers, each encourages unique assemblage of plants today. So they did in the past. Therefore, it has been rightly said

that water is the very life itself, 'Jeevan' as it is called in Sanskrit. No plant life as far as our present knowledge of Exobiology goes, exists without water. The search is on, and one would know in future, whether there is anything similar to it on other planets now, or had it in the distant past. Various plant communities have arisen in water, prospered and have even become extinct since ages. Some others have migrated to land taking temporary shelter on the littoral zone, or on the banks of rivers and margins of lakes. Others have not changed their aquatic habit and habitat, as they found it more congenial to live in water. Still others migrated land-wards. The conquest of land began this way and terrestrial plant life came into existence after a fairly long time when a large proportion of oxygen released by plants accumulated in the air. The early reducing atmosphere of the Earth made way for the oxidizing atmosphere of it as now, and tolerance to it has been a great step forward for the plant life. Here on land they rapidly prospered, and we have a continuous history of them for about 300 to 400 millions of years. But the span of time preceding it is much longer, 1000 to 1200 millions of years. However, not all plants were successful on land and many of them reverted to aquatic life, marine or fresh water. Various taxa and plant communities adapted themselves to conditions of watery environment with

varying degrees of tolerance, and they got spread from highly luxuriant tropical forests to desiccated deserts.

The aquatic plants on land naturally do not have continuous distribution but are segregated into communities at various places in lakes, on river banks, estuaries, mountain lakes covered with snow etc. The limiting factor for their spread naturally is water. Should such isolated plant communities be cut off from each other or be dried up for any reasons, they become progressively less and less in number and their population decreases, and they become sparse. Some become rare and have to face intensive competition from other aquatic biotic groups of plants and animals. Ultimately they become rare and eventually disappear on land. After all rariety is undoubtedly the fore-runner of extinction. This in short is the general story of biology of water plants. As a rule they are wonderfully well adapted to their environment, e.g. mangroves, *cacti* and other plants growing in the deserts of Arizona, Kizil-Kum and Rajasthan, or the Alpine plants. The water ferns are in no way different than others and have to face the same fate in course of their wanderings on different continents in different eras.

They are a small group of Filicales and are supposed to have come into existence during the last part of the Cretaceous period. They have no direct relations earlier. They are supposed to be a highly evolved group amongst ferns. They comprise two small families, the Salviniaceae and Marsileaceae. Of these the Salviniaceae appears to be earlier as it occurs in the Uppermost Cretaceous period. A few fossil spores such as *Arcellites* (*Pyrobolospora*) are claimed to be belonging to the Marsileaceae. They occur in still earlier strata of Holland, Belgium, U.S.A. etc. But the members positively belonging to the Marsileaceae are known only from the Tertiary strata of India in the Deccan

Intertrappean Series. They have been named as *Rodeites* by Professor Sahni (1943) after the distinguished Indian geologist, Professor K. P. Rode of Udaipur University. Members of the other family Salviniaceae, *Azolla* and *Salvinia*, occur, on the other hand, much more widely in U.S.A., U.S.S.R., in Great Britain on the Island of Wight, in Holland, Australia, mostly from post-Cretaceous period till now. Naturally such a distinct group continuing till today is expected to have a continuous history; but alas! such an expectation is far from being realized.

The distinctive characters of the group Hydropteridiniaceae, are heterospory, sporocarps and aquatic habit. It is a highly artificial unit, as quite unrelated groups of plants grow together as an aquatic community in the same place. This has tickled many botanists, and made difficult to trace their origin and relationships. In the earlier works on Ferns it was customary to recognize them as a single group on par with the Eusporangiateae—another very problematic and heterogenous group, and the Leptosporangiateae forming the majority of present day ferns. The Rhizocarpi or Hydropteridiniaceae as they were called, are not related to each other among themselves, although they have two common characters, heterospory and sporocarps. Both families have leaf characters and anatomy modified to suit the life in water and for dispersal. Their original characters are masked by the reduced characters due to aquatic habit and it is difficult to decide what characters are really conservative. They comprise only a few genera. The Salviniaceae has two genera: *Salvinia* with about 10 species and *Azolla* with about 6 well recognized species. The Marsileaceae has three genera: *Marsilea* with about 70 species spread all over the world, many of which are found in Australia, *Pilularia* having six species found in Europe and America, and *Regnellidium* having one species endemic to Southern Brazil. We

have only small material for comparison, and, therefore, analogies drawn mainly on the basis of a common structure such as sporocarp would be erroneous. At the same time suggested relationship of the Salviniaceae with Hymenophyllaceae, and of Marsileaceae with the Cyatheaceae or Schizaeaceae often becomes a scholastic effort. *Hymenophyllum* has 13 as the basic number of chromosomes, whereas *Azolla* has 11 and *Salvinia* has 9. In the majority of species of *Marsilea* this number is 20. In *Regnellidium* it is 19. In Schizaeaceae basic number is 10, and the other numbers known are 10, 77 and 38. In Cyatheaceae, which are tree ferns, $n = 35$. To these three genera of the Marsileaceae one has to add an extinct form genus, *Rodeites*, irrespective of its taxonomic status whether as an independent genus or as a species of *Regnellidium*. This point will be discussed later.

Ferns as a group are essentially shade and water loving plants. Their real home is tropics where there is maximum concentration of genera and species as Manton and Sledge (1954) found. In Temperate regions the density of population of a particular species in an area of comparable size is more, but not many genera and species occur there. Among water ferns *Azolla* and *Salvinia* grow floating as segregates in isolated ponds. *Marsilea* and *Pilularia* form continuous stretches on edges of lakes, rivers and Nallahs, rooted in wet mud. *Regnellidium* and *Pilularia* grow similarly but do not stand competition from others, and very often die due to attacks by aquatic fungi.

Besides these well known five genera of water ferns, there are a few other ferns which grow as hydrophytes or hygrophytes thriving partly or fully in water. Growth in water is a necessary condition for the completion of some stage in their life cycle. Two such important ferns are *Acrostichum* and *Ceratopteris*. *Acrostichum aureum* grows

in salt marshes in the tropical seas. It produces golden coloured sporophylls and has striking spores. Its sori are distributed all over the back side of leaf in a characteristic manner and its spores are typically trilete. They are known to be present in the Lower Miocene pollen flora of the Klodnica Valley of Upper Silesia. Two fossil species of spores are recognized. One is identical with the spores of *Acrostichum aureum* and the other with those of *A. axillare* occurring at present in Java, Sumatra, Borneo, India and Ceylon. The latter species, like its counterpart, is not a mangrove but an epiphyte growing on the branches of trees in deep tropical and sub-tropical forests. In the Indian Tertiaries these spores have not yet been recognized, as very little is known about the tolerance of these species to the degrees of salinity. Consequently the limits of their zonation along sea coast and estuaries are not known. If cultivated *A. aureum* also grows as a fresh water fern.

The other water fern *Ceratopteris* prefers fresh water marshes and lakes. It is a small genus with about four species spread all over the world in tropical and sub-tropical waters in the Old and New World, and also in a few temperate lakes. Its spores occur in various Tertiary and Quaternary formations and have been reported from the Oligocene rocks of Barails of Nahorkatiya region of Assam by Ghosh (1941), Baksi (1962), Biswas (1965) and others under the name *Cicatricosisporites*. Sah and his associates Dutta, Kar and Singh (1966, 1968, 1971, 1972) have shown that they are the same as of *Ceratopteris* and named them *C. macrocostata*. Baksi (1962) found that these spores range from middle Oligocene to Miocene. They occur in the Miocene of Gujarat also and in Makum-Namdang area in East Garo hills. The first definite record of it is from the Lower Eocene of Tura Formation of Garo Hills. Dr. Sah's work suggests that the different spore forms

of this genus serve as good markers for the different formations in that area. It has helped in stratigraphic correlation of Tertiary sedimentary sequence of Assam. Some fossil spores related to *Ceratopteris* have also been described under the new genus *Magnastriatites*, *M. howardi* by Germeraad *et al.* (1968). This spore marks the Oligocene-Miocene horizons of tropical South America, Africa, and South-East Asia. It is interesting to note in this connection that this fern spore is a marker of sedimentary sequence in Oligocene-Miocene horizons in India also. Being a water fern it cannot migrate like other terrestrial ferns and as such it produces several bioforms. As it is very variable, the affinities of *Ceratopteris* as Holtum (1954) points out are not clear.

Besides these two ferns some other ferns grow on river banks and estuaries and in areas periodically flooded with water, such as banks of rivers and Nallahs, in deep tropical jungles. Here these ferns live as hydrophytes in inundated condition for some months. As the water recedes, they produce sporophylls and complete their life cycle. They are: *Humata*, of which one species occurs in Nilgiris, Khasi Hills and Bhutan. *Dipteris lobbiana* is deeply rooted in crevices of rocks in Malayan jungles and for a period it gets inundated on flooded rocks. *Osmunda regalis* and *Thelypteris ciliata* grow under similar situation. *Macrothelypteris ornata* and *M. terresiana* grow close to streams in marshy areas, usually isolated in Khasi and Jaintea Hills in Assam. Many rivers of Deccan arise at high altitudes in Western ghats. There are three or four ferns here which grow in a similar way. They are *Ampelopteris prolifera*, *Egenolfia asplenifolia*, *E. appendiculata*, *Gymnopteris contaminans*, *Schizoloma ensifolia* and *S. heterophyllum*.

It is quite possible that their spores may be found in fresh water sediments of Assam and Nilgiris, as these are the genera that still occur in those areas. It will be clear

from the above that all these Leptosporangiate ferns growing in steady or rapidly flowing waters, partially or fully, are for some part of their life aquatic or semi-aquatic. They share watery habitat as a common feature with the Hydropteridinae; but that need not suggest affinities *inter se*, as they are homosporous. We have, therefore, to treat the members of Hydropteridinae each separately.

Pteridophytic spores are known to occur in various strata of the Earth, and have vertical as well as horizontal distribution. They are good markers of time and strata. From this point of view, the families Parkeriaceae and Schizaeaceae seem to be of special interest as they occur in the possible oil-bearing strata of Miocene and Pliocene strata. The work of Dr. Ghosh, Dr. Bakshi (1962) and Drs. Sah and Kar (1971) of this Institute on the spore forms of *Ceratopteris* is important in co-relating the horizons in different areas, particularly when megafossils or impressions are not available. As a matter of fact this is the special advantage of paleopalynology over other disciplines, as even a small sample of a few milligrams helps to unearth vast information about the sediments and conditions under which they were laid. Hence they are likely to prove of considerable help in oil and coal exploration.

A spore is an extra-ordinary organic unit of life, being an haploid cell. Botanists working on living plants consider it as a definite entity having a definite function in the life cycle of a plant. Some think it to be the first cell of the gametophyte itself; whereas others think it to be a propagule which on its germination gives rise to gametophyte. From the view point of a living plant, its function is two-fold: to disperse plant in new localities and to produce gametes. The small ones ranging from 10 to 30 μ are considered as microspores, meaning thereby that they are not only small-sized spores or miospores, but

also ones which give rise to male gametophyte and male gametes. On the other hand, megaspores are large and range from 50 to 150 μ or more, and give rise to female gametophyte. In Algae and Fungi there are many other kinds of spores besides these, which have a specific function e.g. zoospores, uredospores, teleutospores, etc. During sporogenesis spores assume their definite shape after the polarity is established. Their polarity according to me is fixed at the time of tetrad division. The pointed end where four spores meet in a tetrahedron is proximal, and the other rounded end is distal. First division in germination and the way in which the first cell emerges out of spore is indicative of their polarity. Sporoderm gets differentiated after the polarity is fixed. The palynologists make most of sporoderm characters overlooking the functional aspect of spores and base their conclusions regarding the identity or relationship of spores very often out of proportion. This should serve as a caution to those who deal with "*Sporae dispersae*", and who out of necessity talk of isospores, miospores and macrospores in a different sense. To them the spore is merely a kind of rock-content like a mineral having a particular size and which indicates its composition, age and mode of sedimentation. In doing so they forget that the spore they are dealing with had a function in the life cycle of the plant to which it belonged, and, therefore, it has to be treated differently than minerals, as a live entity of the past. It is not merely a haploid cell of cytogenetists or a propagule of ecologists or a marker of stratigraphists, but an entity having many functions of its own. And therefore, while dealing with them, their full significance must be understood. The spores of *Ceratopteris* are highly significant in this context. Their size, markings on sporoderm differ in different living species, so they did in the past in different Tertiary strata. This is not surprising,

as *Ceratopteris* is known to have two chromosomal complexes $n=40$ and 77. It also shows physiological heterospory, and produces a variety of prothalli. Some of them have midrib with reproductive organs and wings with stomata (Mahabalé, 1948a). Its leaves are dimorphic and venation complex—reticulate. It grows rooted in aquatic mud and even floats on the surface of water in some Assam lakes. When water begins to recede it migrates to rice fields and produces sporophylls and prothalli. Thus its shape and size, chromosomes, nature of annulus and sori, size of spores, prothalli greatly vary. It is no wonder therefore, Miocene strata of Barails, Tipam and other places in Nahorkatiya basin have yielded differently marked spores of different sizes in vertical and horizontal distribution. Only a few spores of pteridophytes have played such an important role in stratigraphic and biological considerations as that of *Ceratopteris*. Leaving these aquatic and semi-aquatic ferns we may turn our attention now to the two members of the Salviniaceae.

The genus *Salvinia* has ten species spread mostly in tropical waters. Only *S. natans* has far wider geographical distribution in Temperate regions in Europe and Australia. It occurs in fossils and about 20 species have been recognized. They fall in three categories: those with oblong leaves, those with upturned leaves, and those with cuculate leaves. They produce distinct bioforms which are not stable. The hairs on the leaves in different species form a distinguishing character. However, many of the species and plants in different areas are sterile, as the meiosis in them is irregular (Mahabale and D'Mello, 1952; Loyal and R. Kaur 1964). Their megasporocarp contains a single megasporangium with one megaspore fully ripened. Megaspore in all species has three-layered wall. The outermost is perisporium which is spongy and facilitates their floating on the surface of

water and helps in dispersal. Many oil globules are present in the distal part which are consumed by the developing sporophyte formed after fertilization at the apical end of the megaspore. The microsporocarps are many in a chain and each sporocarp contains massulae in which the microspores are embedded. They are of two types in the genus. In a species like *Salvinia natans* a massula occupies the entire cavity of the sporocarp after germination and forms a solid frothy mass. This generally happens in fertile species. On the other hand, in sterile species like *S. cuculata* or in many plants of *S. auriculata* the megaspores are infertile due to meiotic irregularities. The microsporocarps produce massulae which are hollow and they float on the surface of water. In 1935, Professor Sahni observed some small seedlike bodies in some cherts collected at Sansar (M.P.). The shape of sporoderm of the megaspore in them was peculiar, and it looked as if they were integuments of a small seed. These bodies, therefore, were named as *Sausarospermum*.

He (Sahni, 1943) also instituted genus *Massulites* for the hollow massula of some water fern, then not known in the living. Later on, however, when I investigated three species of *Salvinia*, *S. natans* a fertile species, *S. cuculata* of Sunderbans which is sterile, and *S. auriculata* from Brazil which is also mostly sterile. I found that the megaspore of the introduced Brazilian species *S. auriculata* is identical with *Sausarospermum* in all details and that the massulae in that species are not solid as in the fertile *S. natans*, but are hollow as in *Massulites coelatus* of Sahni (Mahabale, 1954b). *S. auriculata* is believed to be a tetraploid species, but probably produces some fertile and some infertile races. The interesting fact is, the Paleocene species of India, *S. intertrappea*, found in the Deccan Intertrappeans, shows strong resemblance with the present day South Brazilian species. Further investigation of other fertile species

like *Salvinia oblongifolia* and comparison of it with the known fossil species will throw some more light on the problem which is too well-known to the students of palaeobotany in India viz. presence of South American element in the Tertiary flora of India.

Other floating genus of the Salviniaceae is *Azolla*. About six species of it are found in the warmer parts of the Old World and in the Temperate region of Europe, America and Australia. The genus is very susceptible to cold, and quickly dies without producing fertile plants in different populations. It grows best in tropical waters. Africa is supposed to be its original home. The genus is divided into two sections: *Eu-Azolla* which has glochidia in massulae anchor-shaped, and 3 or 4 float corpuscles. *Azolla filiculoides*, *A. caroliniana*, *A. rubra*, *A. Mexicana* belong to this Section. In the second category of species massulae have curved hair-like glochidia and 6-9 or less float corpuscles as in *A. pinnata*. *Azolla filiculoides* complex is of world-wide occurrence being present in Australia also. The *A. pinnata* is mostly in Volga basin, Australia, India and Japan. The third complex is formed by *A. nilotica* which is a South African species from Rhodesia described by Demalsay (1953). It also produces different clones and varieties. The glochidia are absent in it and float corpuscles are 8 or less. In *Eu-Azolla* generally there are four float corpuscles and in the other Section *Rhizosperma* there could be more, as many as nine. The float corpuscles serve as a pedestal to the megaspore and upraise the growing sporophyte. Glochidia of microspores attach themselves to the glochidia found on the basal part of the megaspore, fixed in the midst of float corpuscles. It opens at the top exposing small gametophyte. The microspores come out of microsporangium and their contents break into small segments forming massulae with glochidia. Glochidia with microspores

get attached to them and germinate in the vicinity of megaspores to which they are attracted presumably by some sort of chemical stimulus. Float-carpuscles merely help the megaspores to float. Microspores germinating in the vicinity of megaspores release sperms near female gametophyte which peep out of the megaspore with one or two archegonia. After fertilization megaspore sinks below the level of water, quite often reaching the bottom or edge of the shallow pond in which the plants grow. Segmentation of the fertilized egg does not begin immediately. For some time oil globules in megaspore are utilized by the fertilized egg. The megaspore becomes light and comes to surface undergoing rapid cell divisions. Thus both in *Azolla* and *Marsilea* the fertilization and developmental mechanism of sporophyte is the same, highly adapted to floating at the surface of water. Reduced stelar system, floating leaves, aerenchyma in stem and other parts, profusely branched roots as well as light sporocarps are similar adaptations in both to resist water. Their vegetative parts are highly adapted to living in water, but the reproductive mechanism is very conservative. It has no parallel in ferns. On the basis of anatomy, simplicity of vegetative parts, fluffy wall of sporocarps, position of sori at the tips of veins have suggested affinity of the Salviniaceae with Hymenophyllaceae. But it seems to me that their simplicity has been achieved mainly through reduction. The chromosome numbers found in the Hymenophyllaceae are $n=13, 18, 21, 34$ whereas *Azolla* has $n=12$ and 22 , *Salvinia* has $n=9$ or 18 . The venation of the leaf in Hymenophyllaceae is open, while that in *Salvinia* and *Azolla* is closed. They, therefore, do not seem to be related, at any rate closely to the Hymenophyllaceae.

Azolla is essentially a Tertiary genus and 10-15 variable species are known from the horizons ranging from Cretaceous to Pleistocene (Sahni, 1941; H. S. Rao, 1935, Hall,

1969). There are three broad complexes. Pre-Tertiary *Azollas* have float corpuscles, generally 3 or 4 or sometimes less and glochidia once or more septate, and the tips anchor-shaped. Upper Cretaceous *Azolopsis* has multibarbed anchor-shaped glochidia and many floats. They broadly can be said to belong to the present day *A. filiculoides* complex. In the second, *A. pinnata* complex, the glochidia are without anchor tips and have 8 or 9 float corpuscles in megaspores: The third complex is formed by *Azolla nilotica* of Africa. There are no glochidia in it and the number of float corpuscles is more than 4, 8 or 9. All the known fossil *Azollas* belong to either "*Filiculoides*" group or *Azolla pinnata* group. The Pre-Cretaceous *Azollas* had more than four float corpuscles. But all the Tertiary *Azolla* species concentrated in the Miocene or post-Miocene period and have anchor-shaped glochidia e.g. *Azolla prisca* of Island of Wight, London Clays, *A. primaeva*, *A. caroliniana* of U.S.A., *A. rubra* of Australia and *A. intertrappea* of India all belong to "*Filiculoides*" complex, but they had variable number of floats. *A. prisca* had 9, *A. teschiana* 2-4-9, *A. primaeva* 3, *A. antiqua* 9. *Azolla pinnata* is found in post-Miocene period. Both the *Azollas*, *A. pinnata* and *A. filiculoides*, are found in Holland, Germany, Volga basin of U.S.S.R. and Japan (see Dorofeev, 1959; Hall, 1969; Hills & Gopal, 1967). Some are intermediate in characters e.g. *A. montana*, *A. primaeva*, *A. prisca*. The genus is thus very variable as regards glochidia and floats and is also far flung in distribution and is supposed to have migrated from Africa. It is difficult to imagine that *Azolla nilotica* endemic to South Africa could be the ancestral form, and could have given rise to present day *Azollas* as well as the past ones belonging to two complexes '*Filiculoides*' and '*Pinnata*', and the intermediate ones also. More evidence would be necessary for accepting such an idea,

as no fossil *Azolla* is known from Africa. None of the fossil species whose reproductive organs are known show similarity with the massulae of *Azolla nilotica* (Mahabale, 1954a and 1954b).

Second family of the Hydropteridinae, Marsileaceae has three members: *Marsilea* with about 70 species of which 57 are well recognized and spread all over the world in the Tropical as well as Temperate waters. The majority of species however, occur in Australia. *Pilularia* with acicular leaves has six species mostly in Temperate waters, and *Regnellidium* from Brazil is monotypic having only one living species, *A. diphylum*. To these Dr. Mrs. Chitaley has added Sahni's form genus *Rodeites* as a distinct genus of the Marsileaceae on par with the three other genera. According to her it combines the characters of *Marsilea* and *Regnellidium*. Sahni thought it to be a distinct fossil species allied to *Regnellidium diphylum*. Chitaley and Paradkar (1971), however, feel that it is a different genus of the Marsileaceae. This is no doubt due to confused and imperfect understanding of the characters of the two genera. Many botanists would rather agree with the original view of it of Professor Sahni for very strong reasons. *Pilularia* with its leaf morphology, radial symmetry of sporocarp — its burrowing habit, imperfect mechanism of dehiscence of the sporocarp, and dispersal of spores by developing cracks into it on decay, undoubtedly suggest that it is a primitive member in the family. It has three doubtful fossil species (Mahabale, 1958).

The genus *Marsilea* has ten doubtful fossil species; but it is necessary to remember that many of the earlier fossil records are in the form of leaves previously described as *Sagenopteris*, which is no longer considered to be a fern. Some megaspores named as *Arcellites* (*Pyrobolospora*) have been reported from Lower Cretaceous and other horizons, and they are similar to the spores of Marsileaceae.

Despite this, one gets no conviction that they really are the members of the Marsileaceae. According to Dr. Mrs. Chitaley spores *Pyrobolospora lobata* described by Dijkstra (1959) seems to agree well with the spores of *Rodeites*, but nothing could be said definitely about them. The third genus *Regnellidium* has unique spores and sporocarps. Like the sporocarp of *Marsilea*, its sporocarp is bivalved but round; the raphe is small and without teeth. Its symmetry is bilateral. The mechanism of dehiscence of the sporocarps in *Regnellidium* and *Marsilea* is alike by the outthrow of a mucilagenous cord having two rows of sori. The sporocarps in *Marsilea* and *Regnellidium* produce a variable number of sori in a sporocarp and each sorus contains a variable number of megaspores total per sporocarp, ranging 2 to 10 in *Marsilea* and upto 90 in *Regnellidium*, all studded in the midst of numerous microspores. The number of sporocarps and megaspores in a sporocarp in some species of *Marsilea*, *M. minuta*, *M. quadrifolia*, *M. erosa* is variable. The number of sporocarps borne at the base of the petiole is also different in different species; in some only one, in some two, and in some many on the petiole of each leaf. In *Regnellidium diphylum* there is only one sporocarp at the base of each leaf, but in the fossil form genus *Rodeites* the number seems to be more as in *Marsilea polycarpa*. The megaspores in a sporocarp are also variable about 90 and they have peculiar appendages at the apical end. In the Tertiary form genus, *Rodeites*, the number of megaspores in a sporocarp, is very large. But no complete reconstruction of this water fern has been made. Till then perhaps it would be better not to create a new synthetic genus for it, because, on the whole, in Evolution divergence of characters is more common than their synthesis. And, therefore, to consider *Rodeites* as a new synthetic genus merely on the similarity of characters between

Rodeites, *Marsilea* and *Regnellidium* is a matter of opinion.

It may be pointed out here that a vast amount of work on the morphology and cytology of *Marsilea* has been done, as also on the morphogenesis and biotypes. The chromosomes recorded in it vary—generally $n=20$, sometimes 36, 40, 105. In *Regnellidium* they are 19. In *Marsilea* there is both irregular meiosis, polyploidy, aneuploidy and parthenogenesis which was first observed by Strasburger (1907). Morphogenetic studies on it show that the genus is highly susceptible to external factors and produces *in vitro*, and in nature, various biotypes and unstable forms. *Regnellidium diphyllum* also yields to morphogenetic treatment producing variable structures. Recently Dr. Loyal of the Punjab University was able to obtain in culture a haploid plant of it. All this ought to suggest that convergence of characters rather than synthesis of divergent characters has resulted in the production of a form genus like *Rodeites*. Obviously there is need for further studies on *Rodeites* in a non-committal way, and also on *Regnellidium diphyllum*.

As early as 1948, I (Mahabale, 1948b) had pointed out that the genus *Regnellidium* is quite unique in many respects among ferns. It is the only genus of ferns which has latex and laticiferous tissue system. It poses many other problems too. One of them is: how a Tertiary fern in the Deccan Intertrappeans of India and living *Regnellidium* of South Brazil could show great similarity, despite their occurrence in two different countries of Southern hemisphere, separated by two oceans and a continent in between. Could they have migrated from some common source in the mid-oceanic islands, now no more, in two directions westward to south America, and Eastwards to India? It is difficult to imagine that this Tertiary species of India *Rodeites dakshini* could have migrated

from India to America. To my mind, this has something to do with the foundering of the Gondwana continent where it must have been in existence before and subsequently wandered. The African continent is supposed to be the home of *Azolla* which has also migrated Eastwards, Westwards and Northwards; but since no fossils of *Azolla*, *Marsilea* or *Regnellidium* have been found in that continent, this will merely amount to guesswork. The mechanism of spore dispersal in *Regnellidium* and *Marsilea* is also quite unique in ferns (Mahabale, 1968). Their sporocarps have the capacity to remain dormant for years. The spores grow even from sporocarps obtained from some old herbarium sheets. This is probably due to their compaction in mucilaginous mass protected by thick wall of the sporocarp. Under conditions of desiccation in Rajasthan desert *Marsilea aegyptica* preserves contents for years, and on return of favourable conditions germinates quickly by imbibing water by the mucilaginous cells and hairs on the sporocarp wall. The morphology of this organ is highly controversial and attempts made to homologize it with the sori—bearing organs of the Cyatheaceae or Schizaeaceae is not without lacunae. I would rather prefer to consider it as an organ *sui generis*, remnant of some ancient fern fructification, rather than attempt to homologize it with that of some highly differentiated modern ferns. Some have compared it even with the seed capsule of angiosperms, but this seems to be a far fetched comparison, just as it would be to consider *Azolla* and *Marsilea* related to each other, simply because both possess heterospory and sporocarps. The morphology of sporocarp suggests that in Salviniaceae it represents a soral envelope enclosing sorus, whereas in Marsileaceae it represents the whole of sporophyll, bearing several sori in positions not yet satisfactorily explained. As a matter of fact these two different ways of

bearing sori is an age-long practice. Some sporangiferous organs of the Devonian genera bore them on organs of intermediate nature which cannot be categorized as stem or leaf. The fact is, various taxa of ferns evolved broadly on these two lines, but similarity as well as deviation from them are not without significance. They indicate parallel tendencies in evolution. Therefore, too much of phylogeny should not be seen in them in order to fit them into our phylogenetic systems with perfect harmony.

The major problem, however, they both provoke is that of heterospory — apart from the nature of sporocarps, extraordinary mechanism for fertilization and spore dispersal by a mucilage cord. Heterospory has been in vogue since long time from Devonian. It has been present on a large scale in Green, Red and Brown Algae. One visualizes a floating mass in sea in which many plants had heterospory both in the physiological and morphological sense. Also there were zoospores, isospores propagating the plants vegetatively. These differences got accentuated with the advance of plants towards land. Green and Brown algae supposed to be precursors of land plants have it in abundant measure. They were followed by Bryophytes, though strangely one finds that they have no heterospory. It would be an extraordinary find of great theoretical significance, should some botanist get a heterosporous member either in Hepaticae or in Musci. So far we know none.

For quite a long time, heterospory was not known in ferns; only peculiar sporangiferous organs, found in the Carboniferous calcareous shales, called *Bensonites* were known to have large spores. The ancient *Lycopods*; *Calamites*, *Progymnosperms* like *Archeopteris* had it. But it was not known in ferns. By a very fruitful chance and critical work, Dr. Surange (1952) was able to show that the ultimate branchlets of

two species of fern *Stauropteris*, *S. oldhamia* and *S. burntislandica* differed to some extent from each other. The microsporangial wall in *S. oldhamia* was multiseriate, but in *S. burntislandica* it was one-celled. Another main difference between the two lay in their megasporangia. *Bensonites* is considered to be a megasporangium of *S. burntislandica*. It had two megaspores well developed within a megasporangium, lodged over a loose epithem-like tissue. Some times there were in addition one or two small possibly abortive spores. Chaloner (1958) confirmed this and further found that there could be two large megaspores and two minute presumably abortive spores. The sporangial wall though cutinized had no definite mode of dehiscence. Sporangium was shed intact in soil and megaspores were released by decay and disintegration of the sporangium wall like the sporocarp wall of *Pilularia*. A large number of such megasporangia, *Bensonites*, are some times obtained in the same matrix. Some of these megasporangia had even more megaspores in a sporangium. This species of Coenopterid had a wide range of distribution in space and time, though originally it was reported from the lime-stones of Pettycur. This is highly significant because it shows that the ferns were in no way lagging behind the contemporary Pteropsids in heterospory.

The strange fact is, when we try to search the origin of heterospory in living ferns we are puzzled, as we do not get any clues to it. The most primitive living ferns — the Eusporangiatae or the advanced Leptosporangiatae are all homosporous. On the other hand Hydropteridiniaceae with their highly modified, or reduced vegetative parts due to watery habitat, and complex reproductive organs, strange mechanism of fertilization and dispersal, are heterosporous. It is generally believed that all modern fern taxa are derived from four major groups: the Coenopteridaceae, Osmundaceae,

Gleicheniaceae, Schizaeaceae. Many things are common between the Coenopteridaceae and Eusporangiatae, and between Coenopteridaceae and Salviniaceae. Similarly there is a good deal of similarity between the Marsiliaceae and Schizaeaceae. But how the Coenopteridaceae, which is earlier than the other three major fern taxa Osmundaceae, Gleicheniaceae and Schizaeaceae, is related to Hydropteridineae is not very clear. Possibly we have to derive Salviniaceae from heterosporous Coenopterid like *S. burntislandica*, though not directly from it. Both have extremely simple tripartite leaves, dichotomy or trichotomy of stem modified heterosporous sporangia, which are extremely simple in *S. burntislandica*.

The sporangial wall in *Salvinia* likewise is simple and profusely hairy and even possesses stomata. It would be worthwhile searching them in *Bensonites* also. Sporocarps in Marsileaceae on the other hand, its general organization of leaf, stem, anatomy are similar to those in Schizaeoid ferns like *Lygodium*, *Aneimia* and *Schizaea* and even *Ceratopteris*. The probability, therefore, is that for the origin of heterospory, at least in the family Salviniaceae, we have to look to heterosporous Stauropteridineae. For that in the other family, Marsileaceae, we have yet no clues. Herein lies a great opportunity for work to pteridologists, palaeobotanists and physiologists.

Literature Cited

- BAKSI, S. K. (1962). Palynological investigation of Sumrang river Tertiaries, South Shillong Front, Assam. *Bull. geol. Min. metall. Soc. India*. **26** 1-21.
- BISWAS, S. K. (1965). A new classification of Tertiary rocks of Kutch, Western India. *Bull. geol. Min. metall. Soc. India*. **35** 1-6.
- CHALONER, W. G. (1958). Isolated megashore tetrads of *Staropteris burntislandica*. *Ann. Bot. N.S.* **22** 197-204.
- CHITALEY, SHYAMALA & PARADKAR, S. A. (1971). *Rodeites* Sahnii reinvestigated. *J. Linn. Soc.* **64**: 109-116.
- DEMALSAY, PAUL (1953). Le sporophyte d'*Azolla nitotica*. *La Cellule* **56** (1): 1-60.
- DIJKSTRA, S. J. (1959). On the megaspores, Charophyte fruits and some other small fossils from the Cretaceous. *Palaeobotanist*. **8**: 8-18.
- DOROFEEV, P. I. (1959). New species of *Azolla* Lam. in Tertiary flora of U.S.S.R. *Bot. Zh. SSSR*, **V**, **44**: 1753-1763.
- GERMERAAD, J. H., HOPPING, C. A. & MULLER, J. (1968). Palynology of Tertiary sediments from Tropical areas. *Rev. Paleobotan. Palynol.* **6** (3): 189-348.
- GHOSH, A. K. (1941). Fossil Pollen in the Tertiary rocks of Assam. *Sci. Cult.* **6** (2) 674.
- HALL, J. W. (1969). Studies on fossil *Azolla*. Primitive types of megaspores and marsulae from the Cretaceous. *Am. J. Bot.* **56** (10): 1173-1180.
- HILLS, L. V. & GOPAL, B. (1967). *Azolla primaeva* and its phylogenetic significance. *Canad. J. Bot.* **45**: 1179-1191.
- HOLTUM, R. E. (1954). The Flora of Malaya. **2**. The Ferns., (Singapore.)
- LOYAL, D. S. & RAJINDER KAUR (1960). Cytological approach to the life history of *Salvinia auriculata* Aublet. *Curr. Sci.* **33**: 344-346.
- MAHABALE, T. S. (1948a). Prothallus of *Ceratopteris thalictroides* Brong. *Bot. Gaz.* **109** 349-354.
- Idem (1948b). The laticiferous system of *Regnellidium*. *Curr. Sci.* **18** 460.
- Idem (1954a). Evolutionary tendencies in the genus *Azolla*. *Mem. Indian bot. Soc.* **4**: 51-54.
- Idem (1954b). The genus *Salvinia* and evolutionary problems related to it. *Proc. VIII int. bot. Congr., Paris*. **I**. 304.
- Idem (1958). Trends of specialization in living and fossil Marsileaceae. *Palaeobotanist*. **5** (2): 66-72.
- Idem (1968). Spores and pollen grains of water plants and their dispersal. *Rev. Palaeobotan. Palynol.* **7**: 285-296.
- MAHABALE, T. S. & d'MELLO (1952). Apogamy in *Salvinia*. *Curr. Sci.* **21**: 227-228.
- MANTON, IRENE & SLEDGE, W. A. (1954). Observations on the Cytology and taxonomy of pteridophytic flora of Ceylon. *Phil. Trans. R. Soc. London*, **238 B**. 127-185.
- RAO, H. S. (1935). The structure and life history of *Azolla pinnata* R. Br. with remarks on the fossil history of Hydropterideae. *Proc. Indian Acad. Sci.* **2** 175-200.
- SAH, S. C. D. & DUTTA, S. K. (1966). Palynostratigraphy of the sedimentary formations of Assam. 1. Stratigraphical position of the Cherra formation. *Palaeobotanist*. **15** (1-2): 72-86.
- Idem (1968). Palynostratigraphy of the Tertiary formations of Assam: 2. Stratigraphic significance of spores and pollen in the Tertiary succession of Assam. *Paleobotanist*. **16** (2): 177-195.

- SAH, S. C. D., DUTTA, S. K., KAR, R. K. & SINGH, R. Y. (1971). Stratigraphic range of *Dandotiaspora* gen. nov. in the lower Eocene sediments of India. *Geophytology*. **1** 54-63.
- SAH, S. C. D. & KAR, R. K. (1972). Palynostratigraphic evolution of the Lower Eocene sediments of India. *Proc. Sem. Paleopalynol. Indian Stratigr., Calcutta*: 235-265.
- SAHNI, B. (1941). Indian silicified plants. I. *Azolla intertrappea* SAHNI & H. S. RAO. *Proc. Indian Acad. Sci.* **14**. 489-501.
- Idem (1943). Palaeobotany in India. IV. Progress Report for 1942. *J. Ind. bot. Soc.* **22**. 171-183.
- SURANGE, K. R. (1952). The morphology of *Stauropteris burntislandica* P. Bertrand and its megasporangium *Bensonites fusiformis* R. Scott. *Phil. Trans. R. Soc. Lond.* **237 B**. 73-91.
- STRASBURGER, E. (1907). Apogamie bei *Marsilea*. *Flora* **97** 123.