Morphological evolution of pteridophytic spores in relation to free floating environment

R. K. Kar

Kar RK 1992. Morphological evolution of pteridophytic spores in relation to free floating environment. *Palaeobotanist* **41** : 128-131.

The free floating ferns are mostly heterosporous with a trilete mark on the spores. They first evolved in the Early Cretaceous, radiated in the Late Cretaceous and except for *Azolla* and *Salvinia*, all of them died out by the Late Maestrichtian. The common genera are: *Arecellites, Molaspora, Balmeisporites, Ariadnaesporites, Glomerisporites, Parazolla, Azollopsis, Azolla* and *Salvinia*. The morphological evolution and adaptation of these genera in relation to the free floating environment is discussed.

Key-words—Morphology, Palynology, Evolution, Adaptation, Free floating ferns.

R. K. Kar, Birbal Sahni Institute of Palaeobotany, 53 University Road, Lucknow 226 007, India.

साराँश

स्वतंत्र आप्लावित वातावरण से सम्बद्ध टेरीडोफ़ाइटी बीजाणुओं का आकारिकीय विकास

रंजीत कुमार कर

स्वतंत्र आप्लावित फ़र्नों के बीजाणु त्रिअरीय चिह्न से युक्त होते हैं तथा विषम प्रकार के बीजाणु उत्पन्न करते हैं। ये फ़र्न सबसे पहले प्रारम्भिक क्रीटेशी कल्प में विकसित हुए, अनंतिम क्रीटेशी में इनका बृहत् विस्तार हुआ तथा **अँज़ोला** और **साल्वीनिआ** को छोड़कर सभी अनंतिम मास्ट्रिक्शियन कल्प में विलुप्त हो गये। **अरेसेल्लाइटिस**, **मोलास्पोरा**, **बाल्मीस्पोराइटिस**, **एरिएडनीस्पोराइटिस**, **ग्लोमेरीस्पोराइटिस**, **पैराज़ोला**, **अँज़ोलॉप्सिस**, **अँज़ोला** एवं **साल्वीनिआ** नामक इनकी सामान्य प्रजाति हैं। इस शोध-पत्र में इन प्रजातियों के आकारिकीय विकास एवं स्वतंत्र आप्लावित वातावरण हेतु इनमें उपयुक्त परिवर्तनों की विवेचना की गई है।

PROFESSOR Birbal Sahni (1925, vide Sahni, 1941) identified fossil *Azolla* from the Deccan Intertrappean beds. He observed several anchor-shaped glochidia entangled in a frothy pseudovacuolate mass (massula) with few microspores. Reid and Chandler (1926) instituted *Azolla prisca*, and Berry (1927) described *Azolla tertiaria* from western Nevada, U.S.A.

Sahni and Rao (1934) instituted the species *Azolla intertrappea* which was later redescribed by Sahni (1938, 1940, 1941). Taking Rao's work (1935) on extant *Azolla pinnata* R. Brown as a clue that massulae become anchored to the megaspore in the month of September, Sahni advocated that the volcanic eruption around Sausar took place in the same month because in *Azolla intertrappea* massulae were observed attached to the megaspore in the same fashion. As heterosporous aquatic fossil and living ferns were one of his favourite subjects it was thought that a befitting tribute to him during the centenary year would be a paper dealing with the free floating ferns.

Ferns and fern-allies need more water than angiosperms yet very few thrive in free floating environments. In fact, they have excelled more in adapting to xeric environments than aquatic environments. Tryon and Tryon (1982) mentioned about 100 species of xeric pteridophytes belonging mostly to the genera *Cheilanthes, Notholaena* and *Pellaea* in Mexico. On the other hand, true aquatic pteridophytes, viz., *Salvinia* and *Azolla* (Salviniaceae) have only 16 species distributed throughout the tropics (Tryon & Tryon, 1982). In addition, there are some pteridophytes like *Marsilea, Regnellidium* and *Pilularia* (Marsileaceae),

Essays in Evolutionary Plant Biology
Editors : B. S. Venkatachala, David L. Dilcher & Hari K. Maheshwari
Publisher : Birbal Sahni Institute of Palaeobotany, Lucknow

Equisetum (Equisetaceae), *Isoetes* (Isoetaceae), *Ceratopteris* (Parkeriaceae), and *Acrostichum* (Polypodiaceae) that live in a watery medium for some parts of their life.

A perusal of the above list would reveal that most of the heterosporous pteridophytes except *Selaginella* are potential hydrophytes and the true aquatic forms belong to this group. Heterospory, in the opinion of Pettitt (1970), originated in the Late Devonian more or less simultaneously in lycopods, progymnosperms and *Barinophyton* (Chaloner, 1976). In the Carboniferous, heterosporus plants were many and both mega- and microspores exhibit much morphological diversity. It is also noteworthy that no pteridophytes producing monolete spores are aquatic though a very large number of ferns produce this type. Kremp (1967) studied spores of 277 genera of ferns and observed that 49 per cent of them produce obligatory monoletes, while 22 per cent show mixed or transitional types having either a monolete or a trilete. Monolete spores first appeared in lycopods in the Late Devonian (McGregor, 1969) and are found in a number of families in the Late Carboniferous. Chaloner (1976) contended none of them was heterosporous. The natural deduction that could be drawn from this observation is that bilaterally symmetrical monolete spores do not show heterospory as well as aquatic habitat. The only exception to this inference is the microspores of some species of *Isoetes* (Berthet & Lecocq, 1977).

It is interesting to note that though heterospory developed in the Late Devonian and was a common phenomenon in the Carboniferous and Permian, there are no preserved megafossil remains known of free-floating aquatic heterosporous plants. The known heterosporous plants then were gigantic trees. None of them was modified for a free floating aquatic environment. Perhaps the evolutionary tendency of the heterosporous plants was towards the development of the seed habit rather than adaptation to water. Pettitt and Beck (1968) and Pettitt (1970) described *Archaeospermia arnoldii*, a cupulate seed from the Late Devonian which may be regarded as a precursor of the seed habit. Here in a small cupulate structure containing integumented sporangia there is a single large elongated megaspore, bearing at its apex the remains of the three aborted megaspores of the same tetrad (Chaloner, 1976).

The highly specialized free floating ferns like *Salvinia* also exhibit more or less the same kind of development. Here the sporocarps from the initial stage bear one kind of sporangia in which only a single megaspore comes to maturity. In *Azolla*, the sporocarps in the beginning contain both megaspores and microspores but in later stages one of them aborts to produce finally either megasporangia or microsporangia (Turrill, 1959). The character which appeared in Palaeozoic roughly 360 Ma ago in some groups of plants reappeared again in this aquatic fern approximately 85 Ma ago in the Late Cretaceous. Hall (1974) listed marsileaceous and salviniaceous heterosporous genera which include *Arcellites, Molaspora, Balmeisporites, Ariadnaesporites, Glomerisporites, Parazolla, Azollopsis, Azolla* and *Salvinia.* Of these, *Arcellites* is recorded from the Neocomian, *Balmeisporites* from the Aptian and *Molaspora* and *Ariadnaesporites* from the Cenomanian. The remaining genera are all recorded from the Campanian. In addition, spores of *Acrostichum* and *Striatriletes* are dispersed spores of *Ceratopteris* known from the Palaeocene and the Middle Eocene, Respectively (Kar, 1984a).

There are many morphological adaptations to aquatic environments. But all these modifications are primarily meant for providing bouyancy to the plants. We would, however, restrict ourselves to the response of spores to meet the challenge.

Acrostichum aureum L. lives in mangrove swamps and is pantropical in distribution. It is an erect and rather a strong pinnate plant attaining a height of 2 m. It has apparently developed no morphological adaptation for aquatic environment; except for the lower part, the whole plant lies above the water level. The microspores for this reason also do not exhibit any morphological variation.

The genus *Ceratopteris*, an aquatic to subaquatic annual, has 4 species (Lloyd, 1972) that grow in quiet water habitats of the tropics. These plants are occasionally found floating on water for months. Kar (1984a) advocated an Indian origin of *Ceratopteris* during Middle Eocene.

The spores of *Ceratopteris* are homosporous and very easily identified in dispersed condition. The exine of the spores is costate. Normally one set of costae appears as bands running more or less parallel to each other in one inter-radial area and its correspondingly distal side. This type of costate ornamentation is not observed in any other group of pteridophytes except for *Anemia* and *Mohria* which have two distinct sets of costae on proximal and distal surfaces. When the spores are shed in water the concentric nature of the costate exine helps it to float by maintaining the subspherical shape and gives additional bouyancy to cover a long distance with grace and perfection. Thus the costate exine of *Ceratopteris* is a development towards efficient water dispersal. Without undergoing any drastic morphological changes to face the free floating environment, *Ceratopteris* spores have developed only the costae and invaded pantropical areas within a span of 50 million years.

Arcellites (= *Pyrobolospora*) is a marsileaceous hydropterid, a Cretaceous marker. It has the oldest record of all Cretaceous heterosporous megaspores and has distinct megaspore and microspore. Megaspores are large (average 259 μm) and they have developed a special device for floating on water. The outer layer of exoexine of the spores has 6 long leaf-like appendages on the proximal side (mean length 357 μm). These leaves are folded lengthwise, margin is crenulate or fimbriate and generally exhibit torsion of about 180°. In some specimens, microspores assignable to *Crybelosporites striatus* are observed on these leaves. The spores of *C. striatus* have morphological similarity to the microspores of different species of *Pilularia* and *Regnellidium*. In addition to the leafy appendages, the exoexine also bears many long tubular appendages uniformly distributed on the body; both provide buoyancy to the megaspores for efficient floating. The thin blade-like shape of the leaves with torsion and fimbriate margin developed to cater the same need. In addition, the leaves also catch the microspores for fertilisation of the megaspore. Frequent presence of *Crybelosporites striatus* on the leaves cannot be ruled out as a mere coincidence but a testimony to this assumption. This microspore has also spongy exoexine by means of which it can float at ease.

Balmeisporites, restricted to Aptian to Cenomanian, possesses a two-layered exoexine. Instead of being pendulous, leaf-like in *Arcellites*, the outer layer of the exoexine in *Balmeisporites* is transformed into three acrolamella around the trilete rays. The exoexine is also modified to form three, drilled, translucent wings to provide additional floating capacity to the megaspores.

Ariadnaesporites is one of the best known genera of heterosporous hydropterideae for its wide geographical but restricted stratigraphic distribution. Little did Miner (1932) realise when he described this type of spore as *Selaginellites ariadnae* from the Late Cretaceous of Greenland that he was opening a new vista into the realm of heterospory.

Ariadnaesporites is also unique in having structurally similar mega- and micro-spores. The difference lies only in the size ranges of the two. Hall and Peak (1968) raised this question and wondered that being amongst typical heterosporous ferns (Hydropterideae) *Ariadnaesporites* should behave in this bewildering fashion. Like *Balmeisporites*, the exoexine is also modified to form 3 acrolamella in association with the trilete rays. A novel adaptation to enhance floating, and effective fertilisation is the presence of hairs on the perispore, predominantly on the distal surface, although Hall (1975) observed them on proximal surface in *Ariadnaesporites varius*. He also observed float-like structures associated with hairs on the proximal surface of this species. The floats though immaturely developed are also two-layered and the outer layer is irregularly foveolate. The hollow bases and long length of the hairs not only help the spore to float but also entangle the microspores together enhancing the chance of fertilisation of megaspore. With this kind of mechanism for floating *Ariadnaesporites* was a very widespread hydrophyte as this genus is found particularly in Campanian and Maastrichtian throughout the world. Perhaps the innovation of the hair did the trick.

Glomerisporites confined to the Campanian. Instead of long hairs as in *Ariadnaesporites*, *Glomerisporites* bears many minute hairs throughout the perispore surface. The acrolamella is also present but not so well developed as in *Ariadnaesporites*. *Glomerisporites* is the first genus to have well-developed floats for floating. These are small, subcircular and only 19-30 μm in diameter. The floats are numerous, distributed all over the body but are generally concentrated on the proximal side. The microspores are borne alone. The hairy perispore is particularly well-developed at the distal end. The pseudoacrolamella is vacuolate and foveolate. The hairs are coiled and may be regarded as rudimentary glochidia.

The floats in *Azollopsis* are also distributed all over the megaspore (Hall, 1968). They are subcircular, pseudovacuolate and are generally enmeshed within the perisporial layer. The microspores bearing massulae are also subcircular, more or less of same size as the floats and are often attached to the megaspore. The massulae are equipped with strong and stout multibarbed glochidia which help in anchoring them to the massulae near the megaspore. *Parazolla* which like *Azollopsis* is restricted to Campanian and Maestrichtian, bears floats only on the proximal side. Columellae are lacking in these genera. These features provide a more or less bilateral symmetry to the megaspore. In addition *Parazolla* microspores did not develop specialized massulae. Instead, they have simple, hair-like glochidia which resemble perisporial hairs of the megaspore.

Azolla and *Salvinia* of the family Salviniaceae are recorded from Campanian to recent sediments world wide. These are the only two genera of the heterosporous hydropterideae which crossed the K-T boundary and thrive in modern times. These two genera have also evolved the highest degree of heterospory as has been mentioned earlier. Adaptation of *Azolla* to aquatic fertilisation has resulted in highly ornate megaspores. However, the microspore remains are very simple. The megaspore of *Azolla* is adorned with floats.

The number and disposition of these swimming structures varies but the prime function is to provide buoyancy to the megaspore when it comes to the surface of the water. The columella which generally holds the float is spongy, pseudovacuolate and provide additional buoyancy. The flappy perispore and hairs along the surface of the megaspore are also meant for negotiating the watery medium. The small, subcircular, psilate microspores are embedded in a spongy, subcircular massulae. The massula is bedecked with hairy outgrowths known as glochidia. These may be either simple, hooked, knobbed or barbed. They not only helped in floating but also anchored the massula firmly on the megaspore so that fertilisation may occur. Within a short span of geological time (Early Cretaceous onwards) the water ferns introduced many innovations which helped them disperse throughout the world. However, inspite of their ingenuinity and adaptability all the genera except *Azolla* and *Salvinia* became extinct at the end of the Maestrichtian. Vagaries of the climate at the K-T boundary acted directly on them. *Azolla* and *Salvinia* survived perhaps due to their capability of long periods of dormancy. It may be recalled that in *Azolla pinnata* as observed by Rao (1935), the megaspores remains for sometime under water before floating on the surface for fertilisation. The phenomenon of 'hibernation' is also known in other species of *Azolla*. If the duration of remaining under water could be prolonged or if some of the megaspores could reactivate after a long period of submersion then *Azolla* could have surmounted the conditions that prevailed during the K-T boundary.

Azolla and *Salvinia* may be thus regarded as 'crisis species' which not only faced the utmost adverse conditions of the K-T boundary but also overcame them and flourished in the later period. Some of the nannoplankton like *Braarudosphaera bigelowii* and calcareous dinoflagellates, viz., *Thoracosphaera operculata* and *Th. saxea* also have similar histories (vide Perch-Nielson, McKenzie & He, 1982).

So it seems that survival of organisms during the critical period does not depend on size and relative strength. *Azolla* and *Braarudosphaera* crossed the K/T boundary whereas the dinosaurs and ammonites perished.

ACKNOWLEDGEMENTS

The author is grateful to Dr B. S. Venkatachala, Director, BSIP, Lucknow and Prof. D. L. Dilcher, University of Florida, U.S.A. for kindly going through the manuscript and providing fruitful suggestions. Thanks are also due to Dr S. A. Jafar for discussion.

REFERENCES

Berry EW 1927. Flora of the Esmeralda Formation in Western Nevada. *Proc. U.S. natn. Mus.* **72** : 1-15.

Berthet R & Lecocq M 1977 Morphologie sporale des especes Francaise due genre *Isoetes* L. *Pollen Spores* **19** : 341-359.

Chaloner WG 1976. The evolution of adaptive features in fossil exine *In* Ferguson IK & Muller G (editors)—*The evolutionary significance of the exine.* 1-14. Academic Press, London.

Hall JW 1968. A new genus of Salviniaceae and a new species of *Azolla* from the Late Cretaceous. *Am. Fern. J.* **58** : 77-78.

Hall JW 1974. Cretaceous Salviniaceae *Annls Mo. bot. Gdn* **61** : 354-367.

Hall JW 1975. *Ariadnaesporites* and *Glomerisporites* in the Late Cretaceous : ancestral Salviniaceae. *Am. J. Bot.* **62** : 359-369.

Hall JW & Peake NM 1968. Megaspore assemblages in the Cretaceous of Minnesota. *Micropalaeontology* **14** : 456-464.

Kar RK 1984a. India : the original homeland of *Ceratopteris* Brongniart (Parkeriaceae). *Palaeobotanist* **31** : 255-262.

Kremp GOW 1967. Tetrad markings of pteridophytic spores and their evolutionary significance. *Rev. Palaeobot. Palynol.* **3** : 311-323.

Lloyd RM 1972. Species delineation in the genus *Ceratopteris* (Parkeriaceae) *Abstract. Am. J. Bot.* **59** : 676.

McGregor DC 1969. Devonian plant fossils of the genera *Kryshtofovichia, Nikitinsporites,* and *Archaeoperisaccus. Bull. geol. Surv. Canada* **182** : 91-106.

Miner EL 1932. Megaspores ascribed to *Selaginellites,* from the Upper Cretaceous coals of western Greenland. *J. Washington Acad. Sci.* **22** : 497-506.

Perch-Nielsen K, McKenzie J & He Q 1982. Biostratigraphy and isotope stratigraphy and the catastropic extinction of calcareous nannoplankton at the Cretaceous/Tertiary boundary. *Geol. Soc. Am. Spec. Pap.* **190** : 353-371.

Pettitt JM 1970. Heterospory and the origin of the seed habit. *Biol. Rev.* **45** : 401-415.

Pettitt JM & Beck CB 1968. *Archaeosperma arnoldii*—a cupulate seed from the Upper Devonian of North America. *Contrib. Mus. Paleont. Univ. Michigan* **10** : 139-154.

Rao HS 1935. The structure and life-history of *Azolla pinnata* R. Brown with remarks on the fossil history of the Hydropterideae. *Proc. Indian Acad. Sci.* **11**(2) : 175-200.

Reid EM & Chandler MEJ 1926. The Bembridge flora, in Catalogue of Cainozoic plants *Br. Mus. nat. Hist.* **1** : 1-206.

Sahni B 1938. Recent advances in Indian palaeobotany. *Proc. 25th Indian Sci. Congr., Calcutta* : 133-176.

Sahni B 1940. The Deccan Traps : an episode of the Tertiary Era. *Proc. 27th Indian Sci. Congr. Madras* : 1-20.

Sahni B 1941. Indian silicified plants 1. *Azolla intertrappea* Sahni & Rao. *Proc. Indian Acad. Sci.* **14** : 489-501.

Sahni B & Rao HS 1934. The silicified flora of Deccan Intertrappean Series. Part IV. *Azolla intertrappea. Proc. 21st Indian Sci. Congr., Bombay* : 26-27.

Tryon RM & Tryon AF 1982. *Ferns and allied plants with special reference to tropical America.* Springer-Verlag, New York.

Turrill WB 1959. *Vistas in botany.* Pergamon Press, London.