

# An argument for the origins of heterospory in aquatic environments

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## ABSTRACT

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The bifid, grapnel-like processes and apical prominence (acrolamella) found in some heterosporous Middle-Late Devonian spores closely resemble to the bifid processes of acritarchs, dinoflagellates, and some Cretaceous - Recent heterosporous aquatic ferns and the lycopsid *Isoetes*. The spongy wall ultrastructure of *Protobarinophyton pennsylvanicum* and *Barinophyton citrulliforme* shows some similarities to the megaspore wall structure of *Azolla*, *Salvinia*, *Isoetes* and *Marsilea*. The difference between the microspore and megaspore wall structure seen in *B. citrulliforme* and *P. pennsylvanicum* is comparable to the difference found in megaspore and microspore wall structure of *Azolla*, *Salvinia* and *Isoetes*. As the spongy wall structure found in heterosporous aquatic ferns provides buoyancy in an aquatic environment, the same may have been true for *Protobarinophyton* and *Barinophyton* and we suggest they probably were aquatic in the dispersal of their spores. These genera are among the oldest heterosporous megaspores known and we suggest that the earliest line of heterospory evolution may be linked to aquatic dispersal of spores and out crossing in their fertilization during the Middle Devonian. This paper is a review of relevant literature and information. We use these data to support our hypothesis that the reproduction of plants by heterospory has its origins in aquatic environments.

**Key-words**—Heterospory, Middle-Late Devonian, Pteridophyta, Aquatic plants, Plant evolution.

## जलीय पर्यावरण में विषमबीजाणुता के उद्गम पर कुछ विमर्श

रंजीत कुमार कर एवं डेविड एल. डिलचर

### सारांश

कुछ विषमबीजाणुविक मध्य-अन्तिम डिवोनियन बीजाणुओं में पाए गए द्विशाखी काँटे की भाँति के प्रवर्ध तथा शिखाग्र उन्नत (एक्रोलैमेल्ला) एक्रोकार्क, घूर्णीकशाओं के द्विशाखी प्रवर्धों तथा कुछ क्रिटेशस-अद्यतन विषमबीजाणुविक जलीय फर्न तथा लाइकोसिड आइसोइटीज़ के समरूप हैं। प्रोटोबैराइनोफाइटॉन पेन्सिलवेनिकम तथा बैराइनोफाइटॉन साइट्रुल्लाइफार्मी की स्पंज की भाँति की भित्ति परासंरचना एज़ोला, साल्वीनिया, आइसोइटीज़ तथा मार्सीलिया की भित्ति संरचना के गुरुबीजाणुओं से कुछ समानता प्रदर्शित करती है। बी. साइट्रुल्लाइफार्मी तथा पी. पेन्सिलवेनिकम में प्रेक्षित सूक्ष्मबीजाणु तथा गुरुबीजाणु भित्ति संरचना में भिन्नता एज़ोला, साल्वीनिया तथा आइसोइटीज़ की गुरुबीजाणु तथा सूक्ष्मबीजाणु में पाई गई भिन्नता से तुलनीय है। चूँकि स्पंज युक्त भित्ति संरचना, जो विषमबीजाणुविक जलीय फर्न में पाई गई है, एक जलीय पर्यावरण में प्लवकता प्रदर्शित करती है। अतः यही तथ्य प्रोटोबैराइनोफाइटॉन तथा बैराइनोफाइटॉन हेतु भी सत्य होना चाहिए। प्रस्तावित किया जाता है कि ये अपने बीजाणुओं के परिक्षेपण में सम्भवतः जलीय थे। ये वंश अभी तक ज्ञात प्राचीनतम विषमबीजाणु गुरुबीजाणुओं में से हैं। अतः यह भी प्रस्तावित किया जाता है कि विषमबीजाणुविक विकास की प्रारंभिकतम

सीमा मध्य डिवोनियन के दौरान बीजाणुओं के जलीय परिक्षेपण तथा उनके निषेचन में बहिःसंकरण से सम्बन्धित है। हमने इन आंकड़ों का उपयोग अपनी इस अवधारणा की पुष्टि करने हेतु किया है कि विषमबीजाणुविकता द्वारा पौधों के प्रजनन का उद्गम स्थल जलीय पर्यावरण है।

संकेत शब्द—विषमबीजाणुविकता, मध्य-अन्तिम डिवोनियन, टेरिडोफाइटा, जलीय पादप, पादप विकास.

## INTRODUCTION

**H**ETEROSPORY is found today in the Lycopsidea in *Selaginella* and *Isoetes*, and the Pteropsida in *Marsilea*,

*Salvinia* and *Azolla*, as an effective means of reproduction. Four of these genera are aquatic while *Selaginella* is widely distributed from moist forest floors to seasonally dry habitats (Bateman & DiMichele, 1994). Dilcher *et al.* (1992) proposed

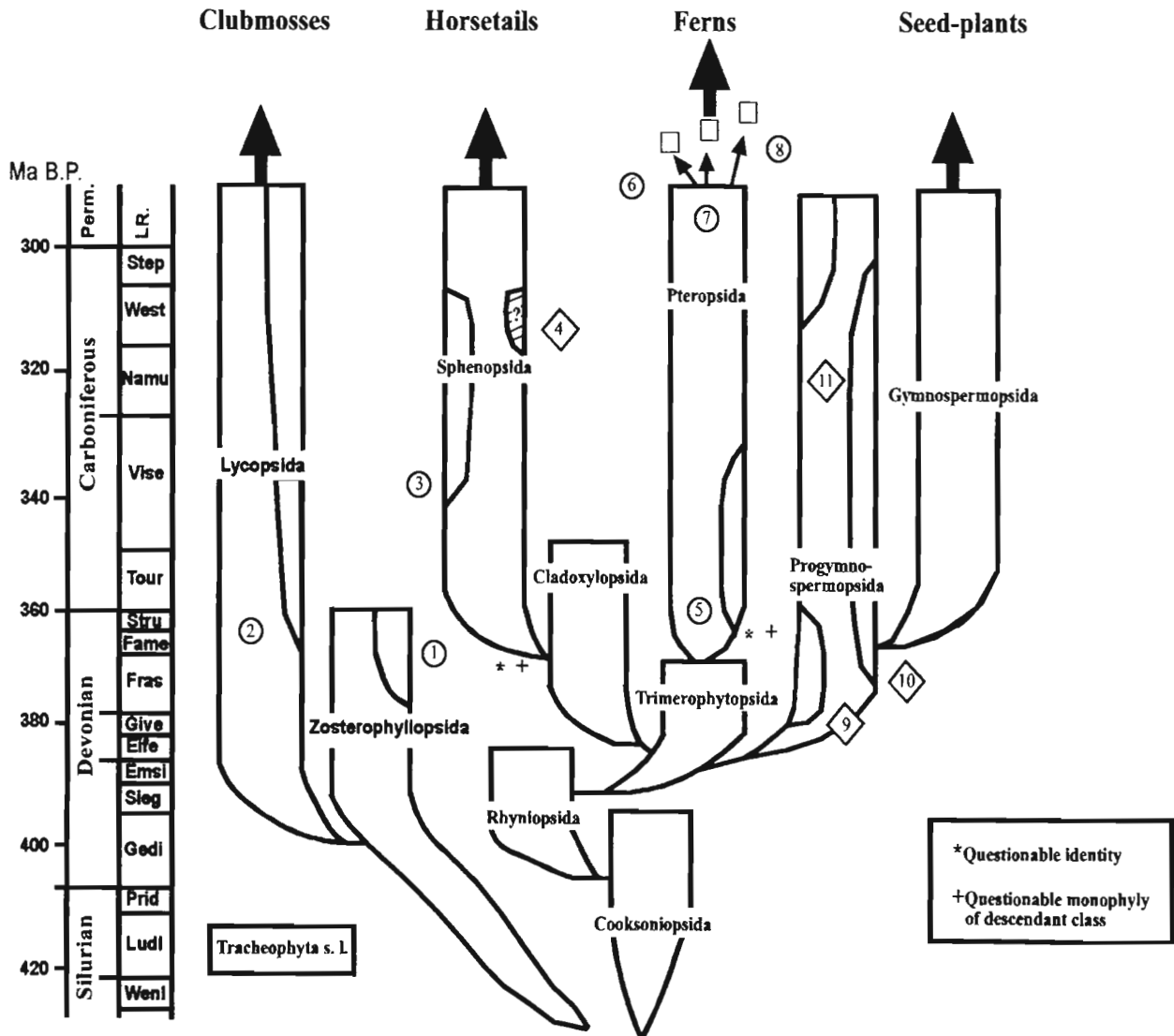


Fig. 1—Tentative non-numerical phylogeny of all tracheophyte classes, showing putative ancestor-descendant relationships and divergence dates: note that the class-level radiation occurred within the Devonian. Stippling indicates the minimum number of potentially independent origins of heterospory: (1) some Barinophytales, (2) all Selaginellales and Rhizomorphales, (3) some Equisetales, (4) some Sphenophyllales (doubtful), (5) some Stauropteridales, (6) all Salviniales, (7) all Marsileales, (8) some Filicales (e.g., *Platyzoma*\*), (9) some Aneurophytales, (10) some Archaeopteridales, ?all Protopotyales, all Cecropsidales, (11) some Noeggerathiales. Note that the Gymnospermopsida inherit heterospory from their putative progymnospermopsid ancestor. Open circles indicate probable aquatic, open squares indicate possible aquatic (modified from Bateman & DiMichele, 1994).

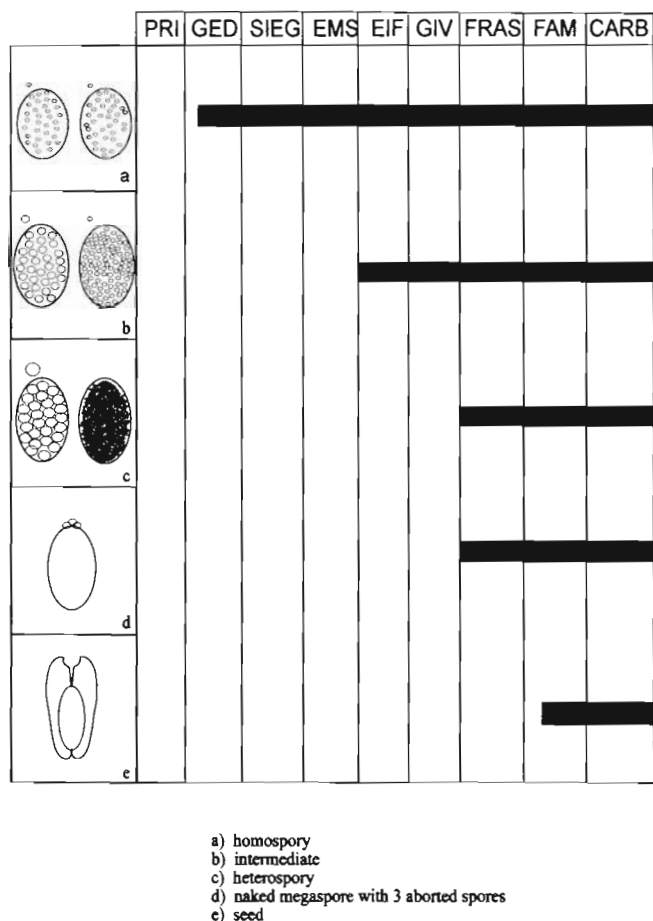


Fig. 2—Diagrammatic record of the time of first appearance of different types of reproductive structures in Devonian fossil plants. a. Sporangia with spores of same size (e.g., in *Cooksonia*). b. Sporangia with spores of two sizes (e.g., in *Chaleuria*). c. Sporangia with mega- and microspores (e.g., in *Archaeopteris*). d. Megaspore tetrad: one large, presumed fertile, three small presumed abortive (e.g., in *Cystosporites*). e. Radiospermic (*Archaeosperma*) and platuspermic (*Spermolithus*) seeds (modified from Chaloner & Sheerin 1979).

that many megaspores and microspores of the Middle Devonian had morphological features that suggested that they were dispersed in fresh water and demonstrated parallel morphological features with those megaspores and microspores of the aquatic ferns that evolved about 240 million years later during the Lower and Upper Cretaceous. It is obvious from the paleobotanical record presented by Bateman & DiMichele (1994) (Fig. 1) that heterospory has evolved repeatedly in various major groups of plants at various times during the history of land plant evolution.

We suggest that the major stimulus for the initial evolution of heterosporous reproductive systems in plants is to accommodate out-crossing in an aquatic environment. In such an aquatic environment, a two dimensional dispersal system is available in which out-crossing is encouraged. Therefore, it

could be considered possible that the potential to capture a new dispersal strategy which increased out-crossing was an important driving force in evolution of heterospory in or near aquatic environments. The megaspores and microspores when released in the water could drift freely mixing microspores and megaspores from diverse populations of the same species and after fertilization further drifting to areas distant from either parent population where the new sporophyte generation would then mature. The data for consideration of such a hypothesis is presented here.

In this paper we are addressing only questions of initial morphological changes that were driven by selection pressures as mentioned by Tiffney (1981). We suggest these selection pressures were directed by the potential for increased out-crossing encouraged by heterospory in aquatic environments. We do not carry this argument further to include modifications of heterospory that might have carried these further to the evolution of the seed habit or seed-like habit (Bateman & DiMichele, 1994) or prepollen so common in the later Paleozoic seed land plants as discussed by Poort *et al.* (1996).

During the Middle Devonian (Givetian), there were many new innovations in land plants (Banks, 1968; Chaloner & Sheerin, 1979; Gensel & Andrews, 1984). By this time, some land plants, such as *Aneurophyton* had attained an arborescent habit that included the production of secondary tissue and major branching systems. Heterosporous taxa were present at this time, some which must have been the precursors of seed plants (Stewart, 1983). The seed habit represented an important innovation in the evolution of plants and became the normal habit of the various groups of vascular plants that were to become the dominant vegetation on the earth (Fig. 2).

Early Devonian spores were simple with a trilete mark, mostly azonate with smooth, apiculate or spinose ornamentation (Traverse, 1988). Early Devonian genera (Figs 3, 4) such as *Retusotriletes*, *Calamospora*, *Lophotriletes*, *Acanthotriletes*, *Punctatisporites*, *Apiculatisporis*, *Leiotriletes* and *Emphanisporites* are examples of these early spores (Banks, 1968). Large spores of 150-200  $\mu\text{m}$ , some pseudosaccate and some zonate, are known from the Middle Devonian Eifelian and Givetian stages (Owens & Richardson, 1972; Richardson, 1974; Turnau, 1986). At that time we also see several spores with bifurcate processes such as *Ancyrospora*, *Hystricosporites*, *Perotriletes*, *Nikitinsporites* and *Dicrospora* while there are some genera that have small bifurcate processes such as *Densosporites devonicus* and *Rhabdosporites langii*. In the Late Devonian (Frasnian) continental and marginal marine facies, there often is dominance of spore genera with grapnel like processes. Pseudosaccate/camerate spores are also found as common elements in these assemblages (Figs 3, 4). Richardson (1969) observed that 50% of the palynological assemblage from the Middle Old Red Sandstone of the Orcadian Basin, Scotland consists of *Ancyrospora* and *Rhabdosporites langii*. Abundance of *Ancyrospora*, *Hystricosporites* and *Rhabdosporites langii*

Series or Stage	Banks, 1980	McGregor, 1977		Richardson, 1974
Post Famennian Tn 1b Tn 1a	?			<i>V. nitidus</i>
FAMENNIAN	<i>Rhacophyton</i> Assemblage - zone VII			<i>V. pusillites</i> <i>S. lepidophytus</i>
FRASNIAN	<i>Archaeopteris</i> Assemblage - zone VI			<i>L. cristifer</i>
GIVETIAN	<i>Svalbardia</i> Assemblage - zone V			<i>optivus - bullatus</i>
EIFELIAN	<i>Hyenia</i> Assemblage - zone IV	<i>devonicus - orcadensis</i>		<i>Triangulatus</i>
		<i>velata - langii</i>		<i>Densosporites devonicus</i>
UPPER EMSIAN	<i>Psilophyton</i> Assemblage - zone III	<i>annulatus - lindlarensis</i>	<i>Grandispora</i>	<i>Rhabdosporites langii</i> <i>Acinosporites acanthomanmillatus</i>
LOWER			<i>sextantii</i>	<i>Calyptosporites biornatus - proteus</i>
SIEGENIAN				<i>Emphanisporites annulatus</i>
		<i>caperatus - emsiensis</i>		<i>Dibolisporites cf. gibberosus</i>
GEDINNIAN	<i>Zosterophyllum</i> Assemblage - zone II			<i>Emphanisporites micornatus</i>
		<i>micornatus - proteus</i>		<i>Streelispora newportensis</i>
PRIDOLIAN	<i>Cooksonia</i> Assemblage - zone I	<i>chulus - ? vermiculata</i>		<i>Synorisporites tripapillatus</i>

was also noticed in the Frasnian freshwater deposits of New York State (Richardson, 1969). In the Famennian Stage of the Late Devonian, a progressive decrease of the spores with bifurcate processes, pseudosaccus and zona is observed (Fig. 4).

Dilcher *et al.* (1992) advocated that the bifid, anchor like processes and the apical prominence (acrolamella) found in these heterosporous Middle-Late Devonian spores were produced in order to increase the potential to entangle and hold megaspores and microspore masses in close proximity while the spermatozoa were released (Fig. 5). Also they mentioned there might be some increase in volume ratio which would provide necessary buoyancy in the water. The presence of bifid processes in the Palaeozoic acritarchs (e.g., *Micrhystridium shinetonensis*, *Polygonium gracilis*), Mesozoic, Tertiary (e.g., *Achomosphaera ramulifera*, *Homotryblium tenuispinosum*) and Recent dinoflagellates, Cretaceous (*Arcellites*) and Tertiary aquatic heterosporous hydropterideae as well as the extant Salviniaceae all demonstrate similar functional morphologies. This is probably related to the fact that many of these microspores and megaspores accomplished their fertilization in water. The observation of Taylor *et al.* (1980) of the presence of smaller microspores between the spines, or in the apical prominence (acrolamella) of the megaspore *Nikitinsporites canadensis*, and of Winslow (1962) on the presence of smaller *Archaeoperisaccus* grains associated with *Nikitinsporites*, as in extant *Azolla*, provides additional support for this contention. *Archaeoperisaccus* and *Nikitinsporites* are mostly confined to Frasnian and according to McGregor (1979) are restricted to north of the palaeoequator (Fig. 6). Marshall & Allen (1982) noted the simultaneous occurrence of four larger and smaller species of *Auroraspora* and two species of a similar nature in *Rhabdosporites* from the Devonian sediments of Shetland. Turnau and Karczewska (1987) also observed that nearly all the large spore species described by Fuglewicz and Prejbisz (1981) from the Middle Devonian of Poland are associated with smaller but otherwise similar spores. These genera are *Apiculiretusispora*, *Biharisporites*, *Coronispora*, and *Grandispora*. The spores of the smaller size class are themselves relatively large and their mean ranges from 90-207  $\mu\text{m}$ . Turnau and Karczewska (1987) suggest the reason for the size increase of the isospores was to enhance the nutritional capability for the developing gametophyte. They also postulated that in the course of development of heterospory, endospory preceded size differentiation and presumably sex differentiation (Fig. 7). Similarly, spores of one sporangium of *Faironella* reported by Gerrienne (1996) from the Early Devonian of Belgium have size ranges from 37-210  $\mu\text{m}$ . This

according to the author may exhibit the beginning of biometric heterospory.

Chaloner (1967) showed, in a series of histograms, a progressive increase in maximum spore size through the Early and Middle Devonian and then a gradual segregation into small spores and large spores and thus the commencement of heterospory (Fig. 7). The overall picture according to Chaloner (1967) seems to be consistent with a progression from a phase beginning early in the Devonian with a low degree of heterospory and continuing later in the Middle and Late Devonian to a much more pronounced size difference between microspores and megaspores. According to Sussex (1966) the fossil record suggests that there was an early and widespread occurrence of heterospory in almost all the major groups of land plants. By the Late Devonian or Early Carboniferous *Lepidostrobis*, *Sigillariostrobus*, *Pleuromeia*, *Lepidocarpon*, *Mazocarpon* and *Miadesmia* of Lycopsidea; *Palaeostachya* and *Calamostachys* of Sphenopsida; *Archaeopteris*, *Lagenostoma* and *Trigonocarpus* of Pteropsida and many other plants as well had attained heterospory.

Cichan *et al.* (1984) considered that the term heterospory has traditionally been used to describe plants that have spores of two different sizes (morphological heterospory). However, because of the consistent correlation in extant plants between a bimodal distribution in spore size and the production of endosporic dioecious gametophytes, this term has also come to denote a particular pattern of reproduction (biological heterospory). To ascertain whether or not a plant is heterosporous (in the biologically heterosporous sense), small and large spores must be germinated and correlations between spore size and archegonial versus antheridial production observed (Cichan *et al.*, 1984; Bateman & DiMichele, 1994). *Platyzoma* (Tryon, 1964) is the first example of a dioecious condition in a heterosporous, terrestrial plant where the spores of two different sizes are found and the small spores bear the antheridia while the larger spores produce archegonia. DiMichele *et al.* (1989), however, think that the gametophytes of *Platyzoma* lack colonizing capabilities and that the life cycle is not comparable to heterosporous species with endosporic gametophytes. The ecological constraints inherent in the life history of *Platyzoma* make it an unlikely candidate for evolutionary intermediate. DiMichele *et al.* (1989) advocated heterochrony to explain the independent evolution of heterospory in most lineages of the lower vascular plants.

Galtier (1964), Brack (1970) and Brack-Hanes (1978) suggest that in fossil plants, where developmental studies are not possible, a biological definition of heterospory can only be applied in cases of morphological heterospory where mature gametophytes bearing either antheridia or archegonia are found preserved within the spore wall. In the cases when micro-



Fig. 3—Showing the comparison of tentative megafossil generic assemblage zones in Devonian with palynological zones suggested by McGregor (1977), Richardson (1974) and Banks (1980) (after Banks, 1980).



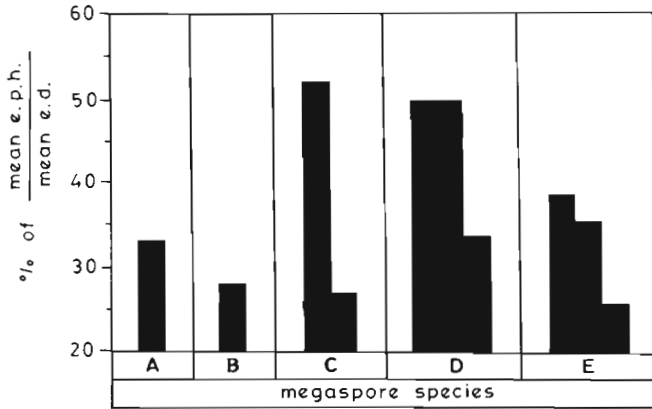


Fig. 5—Givetian and Frasnian megaspore species with apical prominence. a.p.h. = apical prominence height, e.d. = equatorial diameter (modified from Allen, 1972).

and megagametophyte development are imperfectly known, they infer that biological heterospory was probably present based upon a correlation with living plants. In cases where the contents of the spores are not preserved, the precise nature of the large and small spores is uncertain because the difference in spore size may merely have been incidental and not significant in a biological sense (Sussex, 1966). Bateman and

DiMichele (1994) suggest a spore size of 200  $\mu\text{m}$  is sufficient to designate megaspores as probably containing archegoniate-bearing gametophytes.

Unfortunately, the contents of dispersed spores from the Devonian are not preserved and the parent plants of the Devonian spores with bifurcate processes, and most of the other megaspores, are not known. Balme and Hassell (1962), Potonié (1965), Banks (1968) and Gensel (1980) detailed *in situ* spores of Devonian plants. According to Gensel (1980) spores described from the Devonian sporangia consist of 30 genera and 40 species. She concluded that spore morphology seems to be similar between the various species of some genera e.g., *Psilophyton*, *Pertica* and *Archaeopteris*. Sometimes different genera may have the same type of spores e.g., *Tetraxylopteris* and *Rellimia*. Also, plants of quite different affinities have more or less similar types of spores e.g., *Krithodeophyton*, *Cooksonia*, *Crassipariatalis* and *Psilophyton* producing spores assigned to *Apiculiretusispora*.

*Protobarinophyton* and *Barinophyton* are exceptions because the *in situ* spores of these two genera are small and large spores (Cichan *et al.*, 1984). Both these genera exhibit intrasporangial heterospory, i.e., the spores within a single sporangium conforms to a bimodal size. According to Cichan *et al.* (1984) microspores of *Protobarinophyton pennsylvanicum* are 30-42  $\mu\text{m}$  and the megaspores are 410-560

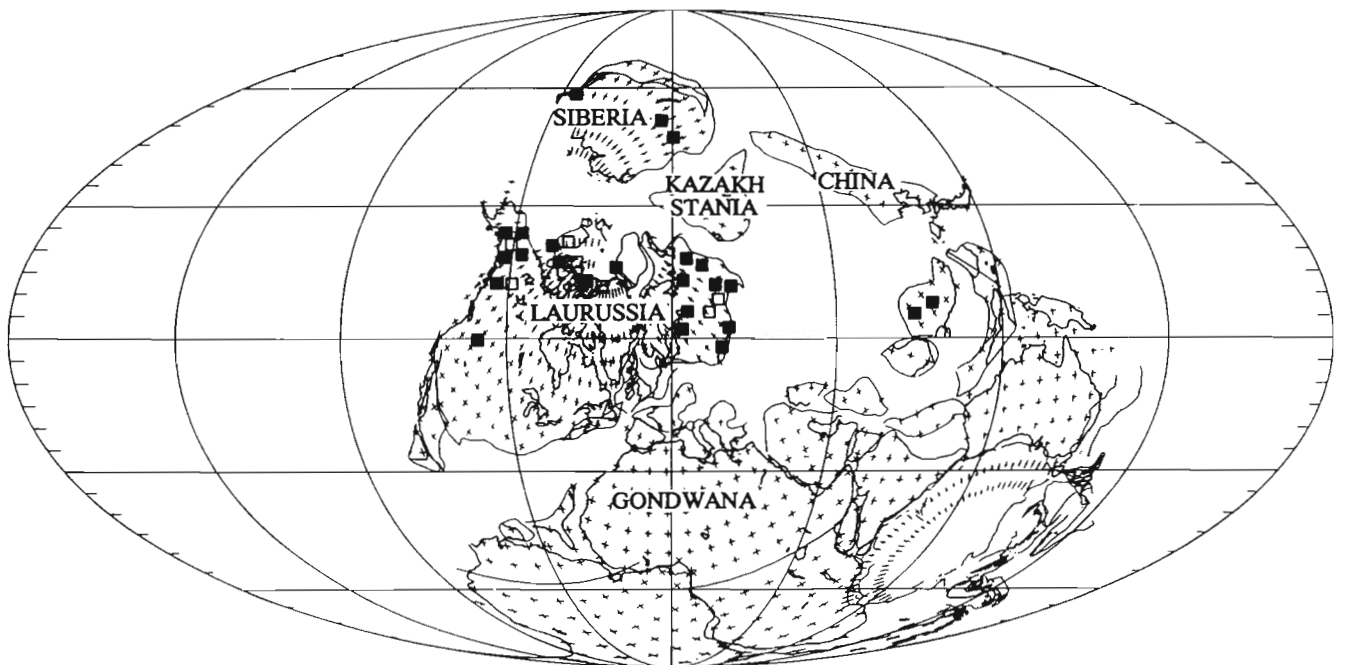


Fig. 6—Geographical distribution of *Archaeoperisaccus* (black squares) and *Nikitinsporites* (white squares) (modified from Streele *et al.*, 1990; map modified from Scotese & McKerrow, 1990).



Fig. 4—A table showing the first and last appearance of Devonian spore genera (modified from Chaloner, 1967).

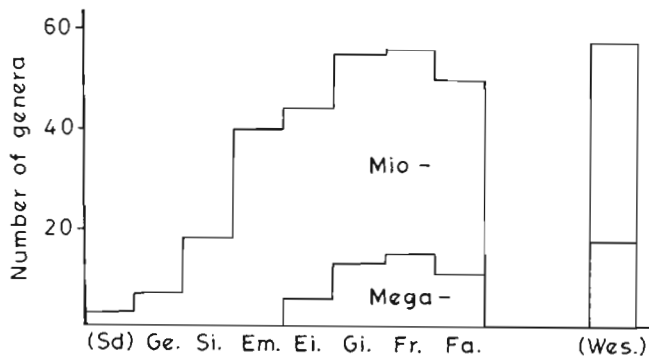


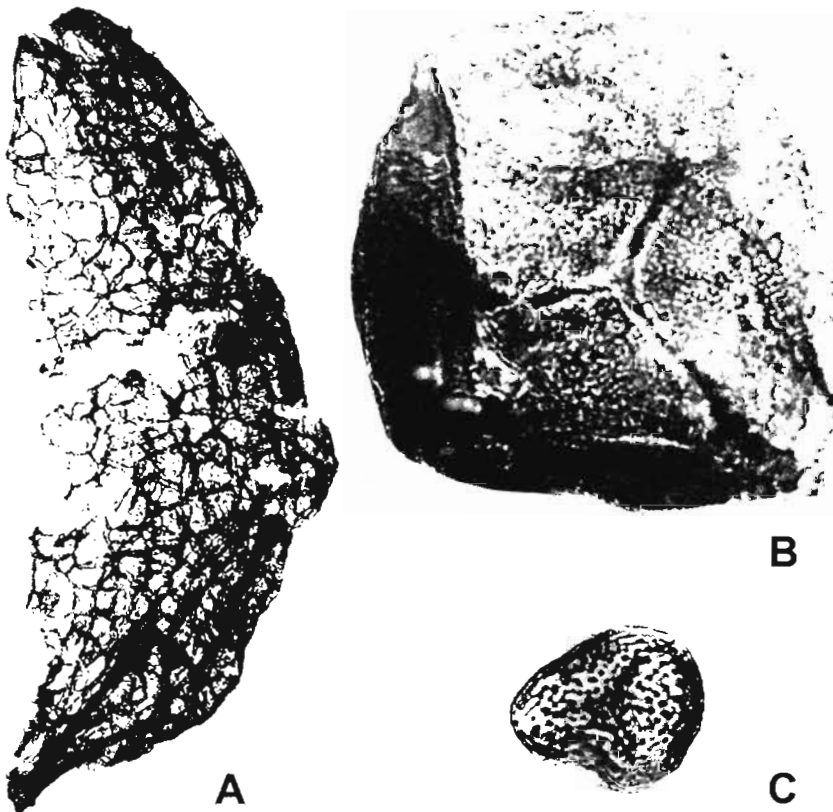
Fig. 7—A histogram showing the numbers of those genera which contain species with a mean size exceeding 200  $\mu\text{m}$  as megaspores (mega) in contradistinction to miospores (mio) (modified from Chaloner, 1967).

$\mu\text{m}$ . The microspores of *Barinophyton citrulliforme* are 30-50  $\mu\text{m}$  and the megaspores are 650-900  $\mu\text{m}$ . The sporangia of *Chaleuria cirrosa* (Andrews *et al.*, 1974) also produce two kinds of spores. The smaller ones are 30-48  $\mu\text{m}$  in size whereas the bigger ones range from 60-156  $\mu\text{m}$  and both types are produced in the different sporangia. The larger spores are subcircular-circular in shape and sculptured with closely

packed minute grana. The smaller spores, on the contrary, are triangular in outline and ornamented with baculi, coni, etc. (Gensel & Andrews, 1984). The size range of the megaspores of *Chaleuria cirrosa* falls far below 200  $\mu\text{m}$ , a conventional size often used to mark heterospory in dispersed spores (Pl. 1).

Taylor and Brauer (1983) considered that *Barinophyton citrulliforme* might be regarded as a transitional stage in the evolution of heterospory because the spores already differ in size, wall structure and most importantly sexual expression but are still found in the same sporangium. Cichan *et al.* (1984) considered that in plants with spores distinct in size as well as structure, there is a strong possibility that biological heterospory was also present. They thought that differential sporoderm ultrastructure in conjunction with dimorphic spore size might potentially be a more viable indicator of heterospory than differences in spore size alone. Using such evidence they suggest that *Protobarinophyton pennsylvanicum* and *B. citrulliforme* were biologically heterosporous. In the extant lycopods some species of *Selaginella* have micro- and megaspores in the same sporangium. The same phenomenon was recorded by Goswami and Arya (1970) in *Isoetes pantii* and by Mondal (1978) in *Isoetes coromandelina*.

The most characteristic feature of the megaspore of *Protobarinophyton pennsylvanicum* and *Barinophyton citrulliforme* is the wall structure. Both of them are spongy



#### PLATE 1

*Chaleuria cirrosa*.

- A. One single sporangium x 45.
- B. A presumed megaspore x 640.
- C. A presumed microspore x 640 (after Andrews *et al.*, 1974).



and in *P. pennsylvanicum* SEM study reveals a porous surface layer while the subsurface layer is alveolate and seems to be composed of superposed sheets of wall material with numerous oval/circular lacunae. In *B. citrulliforme*, the sporoderm layer of the megaspore is loosely arranged giving a spongy appearance. The microspore wall of *B. citrulliforme* has a homogeneous sporoderm and the microspore wall of *P. pennsylvanicum* is also different from that of the megaspore (Taylor & Brauer, 1983; Cichan *et al.*, 1984). The spongy megaspore wall structure of *P. pennsylvanicum* and *B. citrulliforme* shows some similarity to the megaspore wall structure of *Azolla*, *Salvinia*, *Isoetes*, *Marsilea*, as well as *Selaginella*. Fitting (1900), Pettitt (1966), Fowler and Stennett-Wilson (1978), Lugardon and Husson (1982) and Zhiyan (1983) observed several layers of spongy sporoderm in the megaspore wall of *Azolla* where the sporopollenin elements forming the ektexine have ramifying rodlets. Pettitt (1966), Lugardon (1973) and Lugardon and Husson (1982) also recorded fairly comparable sponginess in the megaspore wall of *Isoetes* and *Marsilea*. Similar differences between the microspore and megaspore wall structure found in *P. pennsylvanicum* and *B. citrulliforme* were also observed in the microspore and megaspore walls of *Azolla*, *Salvinia*, *Marsilea*, *Isoetes* and *Selaginella* by Pettitt (1966), Stainer (1967), Lugardon (1972) and Lugardon and Husson (1982). An exception to this observation is found in the wall structure of the microspores and megaspores of *Archaeopteris*. Here the wall structure in both microspores and megaspores found in the microsporangia and megasporangia in organic connection have similar wall features. Pettitt (1966) thinks the spores of *Archaeopteris* cf. *jacksoni* was not far advanced from a homosporous stage and the wall structure of the microspores and megaspores had not differentiated much beyond that of the common ancestral isospore type.

The spongy wall structure of the megaspores found in *Protobarinophyton* and *Barinophyton* of the Devonian and extant *Azolla*, *Salvinia*, *Marsilea*, *Isoetes* and *Selaginella* is indeed very striking. Except for *Selaginella*, all are aquatic heterosporous water plants. Dilcher *et al.* (1992) have postulated that the presence of grapnel like processes in extant aquatic *Azolla*, and in aquatic megaspores *Arcellites* and *Ariadnaesporites* from the Late Cretaceous suggests that the heterosporous genera, *Ancyrospora* and *Hystricosporites* from the Middle and Late Devonian, also had an aquatic habit. While the megaspores of *Protobarinophyton* and *Barinophyton* are devoid of bifid processes, the spongy nature of the megaspore wall, which is comparable to the extant megaspore walls of *Azolla*, *Salvinia*, *Isoetes* and *Marsilea* strongly suggests that they had an aquatic habit also. Differences between the microspore and megaspore wall structure of these plants may also suggest such a habit.

Dodd and Stanton (1990) assumed that palaeoenvironmental reconstruction depend upon a

comprehensive understanding of the ecological significance of each organism. Such ecological context consists of an understanding of the ways in which present day organisms function within their ecosystems, how their external characters and physiology are adapted to their lives and the way in which their morphology fits the environments. The spongy wall structure of the megaspores of *Azolla*, *Salvinia* and *Marsilea* provide buoyancy in aquatic environments. Thus it may also be postulated that the same character found in *Protobarinophyton* and *Barinophyton* megaspore walls were adapted to the same kind of environment. In the opinion of Dodd and Stanton (1990), the analogy of morphological similarities for individual entities or populations can be regarded as a valid argument for environmental interpretations that are time independent. Lorenz (1974) advocated that whenever we find two kinds of life that are unrelated to each other with a similarity in form it is probably caused by parallel adaptations to similar environmental pressures. When we correlate the megaspore wall structure of *Protobarinophyton pennsylvanicum* and *Barinophyton citrulliforme* with the wall structure of megaspores of living heterosporous aquatic ferns and lycopods, we have to assume that these heterosporous Devonian plants also lived in an aquatic environment. This raises the possibility that heterosporous may have originated in aquatic environments. DiMichele *et al.* (1989) reasoned that the heterosporous sexual system is most advantageous in aquatic and semi-aquatic habitats because these exhibit physical conditions more consistently favourable for the release of sperm and eggs. They further suggest that in such environments the heterosporous species may have a distinct advantage over homosporous forms.

Allen and Friend (1968) and Banks (1968, 1975) wrote about the palaeoecology and palaeogeography of the Devonian. According to them, when vascular plants appeared on land all the continents were joined to form a megacontinent and there may have been only about 2% oxygen in the atmosphere. In the uplands there were abundant metamorphic rocks and a predominance of mechanical over chemical weathering. The earliest land plants seem to have occupied chiefly mud flats. However, Banks (1975) assumed that the *Rhynia* chert flora of Emsian age is a good example of an inland intermontane bog (Fig. 6). Dineley (1979) remarked that as much as 85% of the surface of the earth was covered by water during Middle-Late Devonian time in addition to the presence of continental ice in the south polar region. None the less, the volume and the area covered by Devonian sediments are greater than those of other Palaeozoic systems (Raup, 1976). Gregor (1970) calculated that about 1.5 cubic kilometers of sediment accumulated per year during this period, which is more than double that of the Cambrian, Ordovician or Carboniferous periods. According to Dineley (1979) this seems to reflect the vigour of the geological cycle during the Devonian. In North Atlantic, Devonian sedimentation took

place widely and rapidly with thick greywackes and associated clastic rocks, cherts and volcanics. In north-west Europe-Russian platform volcanic activity was in full swing during Early-Middle Devonian. In northern Asia, several cratonic blocks collided and fused and stabilization was in progress during the Devonian (Dineley, 1979). This turmoil in a vast area was perhaps responsible for one of the three great Phanerozoic phases of extinction of marine invertebrate life mostly referred to as Frasnian - Famennian mass extinction (McLaren, 1970; Cooper, 1977). Obviously, such palaeogeographical and palaeoecological conditions were not congenial for the plants to thrive in the terrestrial realm. The marginal lacustrine environment where *Ancyrospora*, *Hystricosporites* and *Rhabdosporites langii* are found in abundance could easily harbour and nourish the megaspores at the cradle of their evolution.

## SUMMARY

The hypothesis is proposed here that aquatic environments have provided plants with the potential to develop a heterosporous mode of reproduction. Heterospory has occurred independently in several groups (clades) of vascular land plants at different times ranging from the Middle Devonian to the Cretaceous. Many of the extant heterosporous plants, that had their origins in these early times, are still living in aquatic environments. An aquatic environment provides increased potential for out-crossing between microspores and megaspores and provides a safe environment in which to disperse microspores and megaspores. The heterosporous plants that gave rise to seed plants and heterosporous land plants owe their origins to aquatic ancestries.

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