The functional biology of Devonian spores with bifurcate processes—a hypothesis

D. L. Dilcher, R. K. Kar & M. E. Dettmann

Aquatic heterosporous ferns may have grapnel-like glochidia, e.g., *Azolla*, specialized for anchoring a microspore mass to a megaspore. Thus, in an aquatic system, the free floating microspore mass (glochidia) and megaspores are held in close proximity when the sperm cells are released. Similar structures are known from the Cretaceous and Tertiary megaspores and microspores such as *Azollopsis* and *Ariadnaesporites* and are considered to have functioned in fertilization. This demonstrates that, as part of the evolution of the aquatic heterosporous habit in the ferns during the Cretaceous, functional and structural elements of the megaspores and microspores evolved early. A parallel evolution event can also be observed in the initial radiation of heterosporous plants during the Late Devonian. Megaspores and microspores, with probable lycopod affinities, demonstrate grapnel-like processes which we suggest were similar to the functional/structural elements known from the Cretaceous aquatic ferns. From this we conclude that many of the Middle and Late Devonian heterosporous plants were aquatic and that there were two parallel evolutionary events, one in the evolution of Devonian aquatic lycopods and a second in the evolution of Cretaceous aquatic ferns. Both of these evolutionary events are characterized by similar functional/structural elements in the megaspores and microspores.

Key-words—Parallel evolution, Heterospory, Aquatic plants, Fossil ferns, Fossil Lycopods.

D. L. Dilcher, Palaeobotany Laboratory, Department of Natural Sciences, Florida Museum of Natural History, Gainesville, FL 32611 U.S.A.

R. K. Kar, Birbal Sahni Institute of Palaeobotany, GPO Box 106, Lucknow 226 001, India.

M. E. Dettmann, Department of Botany, The University of Queensland, Brisbane, Queensland 4072, Australia.

सारांश

द्विशाखित प्रवर्धों से युक्त डिवोनी बीजाणुओं का कार्यात्मक अध्ययन : एक परिकल्पना

डेविड एल० दिल्चर, रंजीत कुमार कर एवं मैरी ई० डेटमैन

जलीय विषमीबीजाणु फ़र्नों, उदाहरणतया अज़ोला में ग्रभांकुश-सदृश अंकुशलोम विद्यमान हैं। अतः जलीय प्रणाली में जब पुमणु कोशायें मुक्त होती हैं, स्वतंत्र अंकुशलोम एवं गुरुबीजाणु परस्पर सटे रहते हैं। इसी प्रकार की संरचनायें क्रीटेशी एवं तृतीयक गुरु- एवं सूक्ष्मबीजाणुओं—अज़ोलोप्सिस एवं एरिएडनीस्पोराइटिस से प्राप्त हुई हैं। इससे यह प्रदर्शित होता है कि गुरु- एवं सूक्ष्म-बीजाणुओं में ये कार्यात्मक एवं संरचनात्मक अवयव पहले ही विकसित हो गये थे। इसी प्रकार अन्तिम डिवोनी कल्प में विषमीबीजाणुओं वाले पौधों के आरम्भिक विस्तार के समय इसी प्रकार के समानान्तर विकास की घटना भी प्रेक्षित की जा सकती है। सम्भाव्य लाइकोपोडीय सजातीयताओं से युक्त गुरु- एवं सूक्ष्म-बीजाणु भी ग्रभांकुश-सदृश प्रवर्ध प्रदर्शित करते हैं। जिन्हें क्रीटेशी जलीय फ़र्नों से विदित कार्यात्मक/संरचनात्मक अवयवों के सदृश प्रस्तावित किया गया है। इससे यह निष्कर्ष निकाला गया है कि मध्य एवं अन्तिम डिवोनी विषमीबीजाणविक पौधों में से अधिकतर जलीय थे तथा उस समय दो समानान्तर वैकासिक घटनायें थीं—एक डिवोनी जलीय लाइक्रोपोडों के विकास से सम्बद्ध, तथा दूसरी क्रीटेशी जलीय फ़र्नों के विकास से सम्बन्धित। दोनों ही वैकासिक घटनायें गुरु- एवं सूक्ष्मबीजाणुओं में विद्यमान सदृश अवयवों से लक्षणित हैं।

PARTICULAR characters in organisms evolve to accommodate life in special habitats. More or less the same types of features are repeated again and again in organisms living in similar environments to provide functional adaptations to these environments. Whether this evolution results in homologous or analogous features or is the product of convergent or parallel evolution and is important in establishing the synapomorphies of Hennig (1966) is often debatable (Cain, 1982). However, whatever may be the case, the message remains the

same. Different entities develop more or less similar characters for adaptation to similar environments.

Plants living permanently, temporarily or for a particular phase of their life cycle in water often develop special characters to provide buoyancy and/or attachment. Even the tiny Early Palaeozoic acritarchs such as *Micrhystridium shinetonensis* Downie 1958, *Polygonum gracilis* Vavrdova 1966, *Archaeohystrichosphaeridium zalesskyi* Timofeev 1959, *Vulcanisphaera cirrita* Rasul 1976 are all equipped with long, slender, bifurcate processes important for attachment, movement and floating. This same type of process is maintained throughout the Palaeozoic acritarchs and is repeated in Triassic to Recent aquatic dinoflagellates. *Achomosphaera ramulifera* (Deflandre & Courteville) Davey & Williams 1966, *Homotryblium tenuispinosum* Davey & Williams 1966, *Heterosphaeridium heteracanthum* (Deflandre & Cookson) Eisenack & Kjellström 1970, *Circulodinium distinctum* (Deflandre & Cookson) Jansonius 1986 and *Oligosphaeridium complex* (White) Davey & Williams 1966 are several of the many species that show this adaptation in an aquatic environment. Another example of a common functional morphology of fossil and extant plants are the roots of the Palaeozoic fern, *Psaronius*, that have an arenchymatous cortex similar to the stems of *Cyperis* living today. Such arenchymatous tissue in both is thought to be an adaptation for life in extremely wet or swampy areas in which the roots and stems may be submerged.

It is interesting to note that the spores of some aquatic heterosporous extinct ferns, such as, *Arcellites* Miner emend. Ellis & Tschudy 1964,

Balmeisporites Cookson & Dettmann 1958, *Ariadnaesporites* Potonié emend. Tschudy 1966, *Glomerisporites* Potonié emend. Hall 1975, *Azollopsis* Hall 1968, and *Parazolla* Hall 1969, as well as spores of the extant aquatic heterosporous ferns *Azolla* and *Salvinia*, are covered with delicate tubular grapnel-like processes obviously used for floating and for adherence of the microspores or clusters of microspores to the megaspores to facilitate fertilization. The megaspore floats free on the surface of the water and when it comes in contact with a free-floating microspore or microspore mass, which often are entangled in a mass of thread-like massulae with barbed glochidia, the grapnel-like processes of the megaspores become attached to the glochidia, thus holding the microspore(s) in close proximity to the megaspore when sperms are released.

Arcellites is a Cretaceous marker genus believed to represent megaspores of a heterosporous marsilialean fern (Cookson & Dettmann, 1958). The exospore of the megaspores is modified into long tubular anchor-like appendages uniformly distributed on the spore body. Occasionally, microspores assignable to *Crybelosporites striatus* (Cookson & Dettmann) Dettmann 1963 are seen attached to the leafy-like appendages (acrolamella) of the megaspore which are developed around the haptotypic mark (Pl. 1, figs 1, 2).

In *Ariadnaesporites*, the microspores and megaspore have similar morphological characters and are differentiated only on the basis of size. They have long hair-like exosporal outgrowths for floating and to aid in the clinging of the microspores to the

---

→

PLATE 1

1. *Arcellites reticulatus* (Cookson & Dettmann) Potter 1963. Lateral view showing prominent leaf-like acrolamellae and associated microspores of *Crybelosporites striatus* (Cookson & Dettmann) Dettmann 1963, × 200; Albian, South Australia.
2. *Crybelosporites striatus* (Cookson & Dettmann) Dettmann 1963. Proximal aspect showing trilete aperture, × 500; Albian, South Australia.
3. *Ceratosporites equalis* (Cookson & Dettmann 1958). Polar view showing bacula with capitate distal extremities, × 750; Aptian, Victoria, Australia.
4. *Petrotriletes majus* (Cookson & Dettmann) Evans 1970. Proximal view showing sculpture of bifurcating spinae, × 750; Albian, South Australia.
5. *Grapnelispora evansii* Stover & Partridge 1984. Microsporangium with grapnel-shaped processes, × 375; Maastrichtian, South Australia.
6. *Grapnelispora evansii* Stover & Partridge 1984. Detail of grapnel-shaped process from microsporangium, × 750; Maastrichtian, South Australia.
7. *Nathorstisporites reticulatus* Dettmann 1961. Off-polar view

showing spinae on crests of labra, × 100; Late Triassic, South Australia.
8. *Nathorstisporites reticulatus* Dettmann 1961. Detail of labra on specimen depicted in fig. 7 showing monolete spores enmeshed among spinae.
9. *Nathorstisporites flagellatus* Dettmann 1961. Proximal view showing spinose labra surrounding trilete aperture and sculpture of branched, hook-like spinae, × 100; Late Triassic, Tasmania, Australia.
10. *Heterosphaeridium heteracanthum* (Deflandre & Cookson) Eisenack & Kjellström 1971. Dinocyst with bifurcating processes, × 500; Cenomanian, James Ross Island, Antarctic Peninsula.
11. *Circulodinium distinctum* (Deflandre & Cookson) Jansonius 1986. Dinocyst with slender capitate processes, × 500; Cenomanian, Bathurst Island, Australia.
12. *Oligosphaeridium complex* (White) Davey & Williams 1966. Dinocyst with distally furcate tubular processes, × 400; Cenomanian, Bathurst Island, Australia.
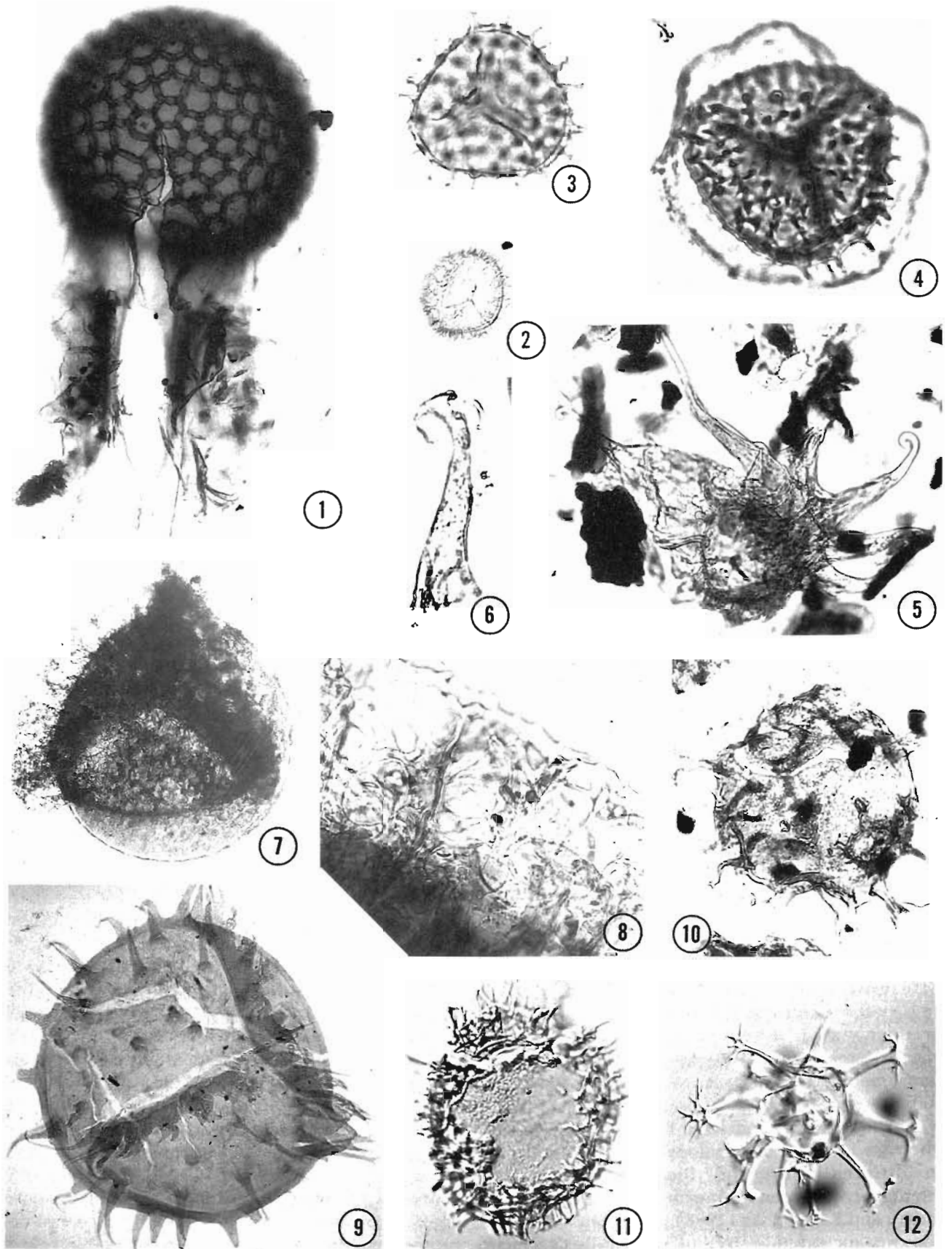
PLATE 1

megaspores for effective fertilization. Like *Arcellites* they also have an apical prominence around the trilete rays made up of exospore that is known as acrolamella. The microspore masses or massulae of *Azollopsis* have strong multi-barbed glochidia to help them anchor on the megaspore (Hall, 1968; Jain & Hall, 1969). The grapnel-like glochidia in *Azolla* may be simple, hooked, knobbed or barbed. With the help of these slender outgrowths, the massula can float easily and anchor firmly on the megaspore to ensure the release of sperm cells in close proximity to the megaspore for effective fertilization. Sahni (1940, 1941) observed that the massulae in fossil *Azolla intertrappea* Sahni are attached to the megaspore by means of glochidia, a feature observed by Rao (1935) and in spores of extant *Azolla pinnata* R. Brown by many in both living and fossil *Azolla*.

In addition to the extant genera *Azolla* and *Salvinia* (Salviniaceae), which are true free-floating aquatic ferns, there are also heterosporous pteridophytes such as *Marsilea, Regnellidium* and *Pilularia* (Marsiliaceae), and *Isoetes* (Isoetaceae) which, during some period of their life cycles, live in an aquatic environment. In addition to these there is also *Selaginella* (Selaginellaceae) which is uniquely drought-adapted or adapted for humid areas in which gravity and wind carry the microspores to the vicinity of the megaspores where some small amount of water must be present for effective transfer of the sperm cells (Bold, Alexopoulos & Delevoryas, 1973).

All the microspores and megaspores of these plants have a trilete mark except for *Isoetes* microspores which are monolete. The microspores are arranged in tetragonal tetrads in contrast to the trilete megaspores which are aligned in tetrahedral tetrads.

Earliest recorded heterospory is from the Middle and Late Devonian (Chaloner, 1967, 1976; Richardson, 1967). According to Turnau and Karczewska (1987), there was no morphological differentiation between microspores and megaspores in earliest heterosporous plants except for their size. The genera *Apiculiretispora* Streel emend. Streel 1967, *Biharisporites* Potonié 1956, *Coronispora* Lu & Ouyang 1978, *Grandispora* Hoffmeister, Staplin & Malloy emend. McGregor 1973 contain small and large forms of spores with otherwise identical morphology. The bearing of size on differentiation and the development of heterospory has been dealt with by Chaloner (1970), Turnau and Karczewska (1987). They concluded that isospores increased in size in Early-Middle Devonian times and heterospory developed during the Upper

Devonian due to different selective pressures.

Moreover, many Middle-Late Devonian genera, e.g., *Hystricosporites* McGregor 1969, *Ancyrospora* Richardson emend. Richardson 1962, contain spores, the size range of which exceeds $200\,\mu m$, and the arbitrary demarcation of microspores and megaspores is difficult to maintain. These genera, as well as other Palaeozoic taxa (e.g., *Nikitinsporites* Chaloner 1959, *Dicrospora* Winslow 1962) and several Mesozoic forms (e.g., *Petrotriletes* Erdtman ex Couper 1953, *Ceratosporites* Cookson & Dettmann 1958) have peculiar slender, cylindrical, sometimes curved, bifid processes (Pl. 1, figs 3, 4). This type of spore is quite common. Brideaux and Radforth (1970) described a Late Devonian miospore assemblage where spores with bifid processes constitute more than half of the total assemblage.

The function of these processes is a matter of conjecture and many hypotheses have been put forward to explain the occurrence of these processes during the dawn of heterospory in the Middle-Late Devonian. According to Taylor, Maihle and Hills (1980), three possible functions that have been advocated for these processes include protection, buoyancy, and a mechanism by which these spores could be attached to other organisms such as arthropods. In addition, the frequent occurrence of the spores with bifurcate processes in the Middle-Late Devonian palynofloras led several authors to postulate that these processes evolved due to some selective pressure (Taylor *et al.*, 1980). The idea that arthropods may have been an important selective pressure on the spores in their evolution of ornate bifid processes was championed first by Taugourdeau-Lantz (1971) and followed by Smart and Hughes (1973) and Kevan, Chaloner and Savile (1975). Tillyard (1928), albeit in a very generalized way, also postulated the same much earlier.

Kevan, Chaloner and Savile (1975), postulated the interrelationship of early terrestrial arthropods and spores with grapnel-like processes. Stressing the simultaneous increase in the complexity of spore exine structure with arthropod diversity, they advocated that some of the arthropods were probably spore-eaters which resulted in the development of an anchor-like process in some spores for dispersal by those arthropod invaders. The processes could have also developed as a means of protection from these organisms. In correlating sculptural attributes with living spore-eating arthropods, they concluded that the elaborate bifid processes in some Middle-Late Devonian spores could be clearly related to arthropod dispersal and protection. They further suggested that the role of arthropods in long distance dispersal of these spores

could have been of great significance in Middle-Late Devonian ecosystems. According to them, ornamented bifid spores would have been attractive and palatable to arthropods, and they dismissed the notion that bifid processes helped to maintain buoyancy.

The theory that spore dispersal was aided by arthropods led to speculations on early plant-animal symbiosis. However, this assumption seems to us to be more speculative than elucidative and more imaginative than conclusive. Kevan, Chaloner and Savile (1975) pointed out that caution is commendable before professing function for a particular structure. The different hypotheses put forward on the probable function of air sacs in some of the conifer pollen is a point to ponder (Doyle, 1945; Wodehouse, 1935; McWilliams, 1958).

Kevan, Chaloner and Savile (1975) also mentioned that one of the probable functions of these processes was protection from animals. If the Middle-Late Devonian arthropods developed a special liking for megaspores then they may have been tempted by less ornate forms such as *Apiculiretusispora, Biharisporites* and *Grandispora* rather than spores with bifid processes like *Hystricosporites* and *Ancyrospora.*

It is also debatable how significant Late Devonian arthropods were in the dispersal of megaspores and microspores as diverse winged arthropods did not evolve until later (Kevan, Chaloner & Savile, 1975). Therefore long distance dispersal by Devonian arthropods seems to be only a remote possibility. The question of desiccation also may have been a factor which might have hindered long dispersal through the air. Middle Devonian-Late Devonian plants mostly grew in swamps or near water, so appropriate dispersal logically could be by means of water rather than land.

The thesis of this paper is not to rule out the possibility that arthropods occasionally fed on megaspores with bifid processes, but to advocate that these processes were functioning for buoyancy, movement, and adherence of microspores to the megaspores in an aquatic environment. Taylor, Maihle and Hills (1980) also postulated that these processes were involved in trapping smaller microspores. During the course of their investigation they observed a large number of small spores between the spines or in the apical prominence of *Nikitinsporites canadensis* Chaloner. Similar apical prominences are found in other Late Devonian megaspores such as *Hystricosporites* and *Lagenicula* Bennie & Kidston ex Zerndt 1934.

Also similar is the acrolamella of the Cretaceous marsilialean megaspores *Arcellites* and *Ariadnaesporites.* In *Arcellites,* the outer layer of the exospore that surrounds the haptotypic mark is modified into six long leaf-like appendages where occasionally microspores assignable to *Crybelosporites striatus* are attached (Cookson & Dettmann, 1958). *Petrotriletes bifurcatus* Richardson 1962 described from the Middle Old Red Sandstone of Scotland may be a microspore (size range 80-130 μm) and its slender bifid processes probably functioned for floatation and adherence to the megaspores. *Grapnelispora* Stover & Partridge 1984, which represents microsporangia, shares a similar functional design (Pl. 1, figs 5, 6). Thus there appear to have been two independent evolutionary events both related to megaspore evolution in aquatic systems. One event is recorded from the Middle and Upper Devonian and involved lycopods and perhaps a few ferns. The second event took place in the Lower and Upper Cretaceous and involved ferns and a lycopod.

The hypothesis that fertilization in some of the Middle-Late Devonian megaspores took place in an aquatic environment is further supported by association of monolete microspores (*Archaeo-perisaccus* Naumova 1937) and the megaspores of *Kryshtofovichia* Nikitin (Nikitin, 1934; Winslow, 1962). Extant *Isoetes* also have monolete microspores that fertilize the trilete megaspores in an aquatic environment. In fact, Nikitin (1934), Chaloner (1959) and McGregor (1969) believed that *Kryshtofovichia* is the possible ancestor to the Triassic-Jurassic strobilus genera *Lycostrobus* and *Cyclostrobus* and possibly to the living genus *Isoetes.* In the opinion of Taylor, Maihle and Hills (1980), the morphological evolution of large trilete megaspores and smaller monolete microspores in heterosporous plants is attained in fossil history only by the lycopsid genera *Cyclostrobus* and *Lycostrobus scottii* Nathorst 1908. *Nathorstisporites,* which accommodates megaspores consistent with those of *Lycostrobus scottii,* is characterized by a trilete aperture surrounded by acrolamellae of bifurcating spinae. Occasionally monolete microspores are found entrapped amongst the spinae. In the present day this phenomenon is observed only in *Isoetes.* Therefore it seems likely that the apical prominence and the bifid prominences of *Nikitinsporites* were adaptations for effective fertilization in an aquatic environment.

GENERAL DISCUSSION

During the Middle to Late Devonian heterospory was in an incipient stage and many genera could be distinguished only by their different ranges in size.

The same condition is also seen in the Cretaceous taxon *Ariadnaesporites*. The Devonian and Cretaceous taxa share similar characters such as apical prominences (acrolamella) and slender hair-like processes. There is no reason why the Late Devonian taxa, depicting more or less similar characters, should not also be considered to represent spores of aquatic plants as is *Ariadnaesporites*, which is thought to represent an aquatic fern.

The diversity of megaspores and microspores are known to represent both aquatic ferns and aquatic lycopods. Most of the diversity is derived from ferns in the Cretaceous while most of the diversity of heterosporous spores in the Upper Devonian are thought to be related to the lycopods.

Azolla and *Salvinia* are extant free-floating heterosporous ferns. There were also a number of related genera living in the Late Cretaceous, but these are the only two fern genera which survived the K-T Boundary and flourished in the Tertiary. The microsporangium in *Azolla* is embedded in a spongy massula which has grapnel-like processes of various kinds. In addition to providing a floating device, the glochidia may anchor the microsporangium on the megaspore. This is important to ensure fertilization when the free-swimming sperm are released.

Needless to say, the glochidia-like processes found in Devonian spores may have also functioned in a similar manner in an aquatic environment. Reports of Devonian microspores attached to megaspores provide additional evidence for this hypothesis.

Most of the Devonian plants preserved in the fossil record lived in or very near to water and some of them probably lived in swampy habitats. Water must have been an important limiting factor in both the vegetative and reproductive stages of the early land plant cycle. Much of the structural evolution of vascular land plants, such as the development of cuticle, epicuticular waxes, stomata and guard cells, and tracheids, relates to the conservation and transportation of water. Because of the probable presence of motile sperm in the gametophyte, water was an essential and a limiting factor for this phase of the land plant life cycle. The homosporous condition of early land plants must have produced homothallic gametophytes, probably bearing both archegonia and antheridia. DiMichele, Davis and Olmstead (1989) address the question of the evolution of heterospory and consider that endosporic development of the gametophytes must be considered as a part of the evolution of heterospory. This is important because the spore dispersal of aquatic heterosporous plants is a means

of increasing outcrossing. Therefore, heterospory provides added advantages over homothalic gametophytes. A sophisticated incompatibility mechanism, such as has been investigated by Haufler and Soltis (1984), may not have evolved yet. Therefore, heterospory was a mechanism to encourage outcrossing (Dilcher, in press). Because the male sperm-bearing cells must be in close proximity to the female gametophyte and because water is necessary for the motile sperm cells, gravity, wind (*Selaginella*), and water (*Azolla* and *Salvinia*) have been effective dispersal mechanisms.

The development of bifid anchor-like processes and the apical prominence (acrolamella) in spores of some heterosporous Middle-Late Devonian plants was perhaps directed towards increasing the surface-to-volume ratio and enhancing buoyancy. The presence of similar characters in Lower Palaeozoic acritarchs, Mesozoic, Tertiary and Recent dinoflagellates, Cretaceous and Tertiary aquatic heterosporous plants and in living Salviniaceae suggests that some heterosporous plants of the Devonian had microspores and megaspores with morphologies especially modified to ensure fertilization. The occasional presence of embedded microspores/massulae on the megaspores of *Nikitinsporites* and *Azolla intertrappea* as well as living *Azolla* further substantiates this assumption. The chances for outcrossing would have been increased in the free-floating dispersal of megaspores and microspores and random contacts from various parent populations.

There is no need to invoke dispersal agents such as arthropods to facilitate fertilization. The hydrophilous Devonian heterosporous plants were capable of doing that themselves by developing spore characters such as those unique to living aquatic heterosporous ferns and fern allies. It is noteworthy that the same reproductive strategy resulting in similar characters are repeated at least twice in geologic history with diverse groups of plants that occupied aquatic habitats.

ACKNOWLEDGEMENTS

REFERENCES

Bold HC. Alexopoulos, CJ & Delevoryas T 1973. *Morphology of*

plants and fungi, 3rd ed. Harper & Row, Publishers, New York.

Brideaux WW & Radforth NW 1970. Upper Devonian miospores from the Escuminac Formation, eastern Quebec, Canada. *Can. J. Earth Sci.* **7** : 29-45.

Cain AJ 1982. On homology and convergence. *In* Joysey, K. A. & Friday, A.E. (editors)—*Problems of phylogenetic reconstruction* : 1-19. Academic Press, London.

Chaloner WG 1959. Devonian megaspores from Arctic Canada. *Palaeontology* **1** : 321-332.

Chaloner WG 1967. Spores and land plant evolution. *Rev. Palaeobot. Palynol.* **1** : 83-93.

Chaloner WG 1970. The evolution of miospore polarity. *Geosci. Man* **1** : 47-56.

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.

Cookson IC & Dettmann ME 1958. Cretaceous "megaspores" and closely associated microspores from the Australian region. *Micropaleontology* **4** : 39-49.

Couper RA 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. *Bull. geol. Surv. N.Z. Palaeont.* **22** : 1-77.

Davey RJ & Williams GL 1966. The genus *Heterosphaeridium* and its allies. *In* Davey RJ, Downie C, Sarjeant WAS & Williams GL (editors)—*Studies on Mesozoic and Cainozoic dinoflagellate cysts. Bull. Br. Mus. nat. Hist. Geol. Suppl.* **3** : 53-106.

Dettmann ME 1961. Lower Mesozoic megaspores from Tasmania and South Australia. *Micropaleontology* **7** : 71-86.

Dettmann ME 1963. Upper Mesozoic microfloras from south-eastern Australia. *Proc. R. Soc. Vict.* **77** : 1-148.

DiMichele WA, Davis JI & Olmstead RG 1989. Origins of heterospory and the seed habit: the role of heterochrony. *Taxon* **38** : 1-11.

Downie C 1958. An assemblage of microplankton from the Shineton shales (Tremadocian). *Proc. Yorkshire geol. Soc.* **31** : 331-350.

Doyle J 1945. Developmental lines in pollination mechanisms in the Coniferales. *Proc. scient. R. Dubl. Soc.* **24** : 43-62.

Eisenack A & Kjellström G 1971. *Katalog der fossilen Dinoflagellaten, Hystrichosphaeren und verwandten Mikrofossilien.* **II.** *Dinoflagellaten.* Schweizerbartsche Verlagsbuchhandlung, Stuttgart.

Ellis, CH & Tschudy RH 1964. The Cretaceous megaspore genus *Arcellites* Miner. *Micropaleontology* **10** : 73-79.

Evans PR 1970. Revision of the miospore genera *Petrotrilites* Erdtman ex Couper 1953 and *Diaphanospora* Balme & Hassel 1962. *Bull. Bur. Min. Resour. Geol. Geophys. Aust.* **116** : 65-81.

Evitt WR 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres and acritarchs. *Proc. natn. Acad. Sci. U.S.A.* **49** : 158-164.

Hall JW 1968. A new genus of Salviniaceae and a new species of *Azolla* from the Late Cretaceous. *Am. Fern J.* **58** : 77-88.

Hall JW 1969. Studies on *Azolla* : primitive types of megaspores and massulae from the Cretaceous. *Am. J. Bot.* **56** : 1173-1180.

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

Haufler CH & Soltis DE 1984. Obligate outcrossing in a homosporus fern : field confirmation of a laboratory prediction. *Am. J. Bot.* **71** : 878-881.

Hennig W 1966. "*Phylogenetic Systematics*" (translated by D. D. Davis & R Zangerl). University Illinois Press, Urbana & London.

Jain RK & Hall JW 1969. A contribution to the Early Tertiary fossil record of the Salviniaceae. *Am. J. Bot.* **56** : 527-539.

Jansonius J 1986. Re-examination of Mesozoic Canadian dino-

flagellate cysts published by S.A.J. Pocock (1962, 1972). *Palynology* **10** : 201-223.

Kevan PG, Chaloner WG & Savile DBO 1975. Inter-relationships of early terrestrial arthropods and plants. *Palaeontology* **18** : 391-417.

Lu L & Quyang S 1978. Devonian megaspores from the Zhanyi District, E. Yunnan. *Acta palaeont. sin.* **17** : 70-80.

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

McGregor DC 1973. Lower and Middle Devonian spores of eastern gaspe, Canada: systematics. *Palaeontographica* **B142** : 1-77.

McWilliam JR 1958. The role of the micropyle in the pollination of *Pinus. Bot. Gaz.* **120** : 109-117

Naumova SN 1937 Spores and pollen of the coals of the U.S.S.R. *Proc. XVII int. geol. Congr.* : 1-17.

Nikitin PA 1934. Fossil plants of the Petino horizon of the Devonian of the Voronezh region-1. *Kryshtofovichia africane* nov. gen. et sp. *Izv. Akad. Nauk SSSR.* **7** : 1079-1092.

Potonié R 1956. Synopsis der Gattungen der *Sporae dispersae* 1. Teil : Sporites. *Beih. geol. Jb.* **23** : 1-103.

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** : 175-200.

Rasul SM 1976. New species of the genus *Vulcanisphaera* (Acritarcha) from the Tremadocian of England. *Micropaleontology* **22** : 479-484.

Richardson JB 1962. Spores with bifurcate processes from the Middle Old Red Sandstone of Scotland. *Palaeontology* **5** : 171-194.

Richardson JB 1967 Some British Lower Devonian spore assemblages and their stratigraphic significance. *Rev. Palaeobot. Palynol.* **1** : 111-129.

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.

Scott AC & Playford G 1985. Early Triassic megaspores from the Rewan Group, Bowen Basin, Queensland. *Alcheringa* **9** : 297-323.

Smart J & Hughes NF 1973. The insect and the plant: progressive palaeoecological integration. *R. ent. Soc. Lond.* **6** : 143-155.

Stover LE & Partridge AD 1984. A new Late Cretaceous megaspore with grapnel-like appendage tips from Australia and New Zealand. *Palynology* **8** : 139-144.

Streel M 1967. Associations de spores du Dévonien inférieur Belgeet leur signification stratigraphique. *An. Soc. Geol. Belg.* **90** : 11-53.

Taugourdeau-Lantz J 1971. Les spores du Frasnien d' une région privilégiée, le Boulonnais. *Mem. Soc. Géol. fr. n. ser.* **50** : 1-88.

Taylor TN, Maihle NJ & Hills LV 1980. Morphological and ultrastructural features of *Nikitinsporites canadensis* Chaloner, a Devonian megaspore from the Frasnian of Canada. *Rev. Palaeobot. Palynol.* **30** : 89-99.

Tillyard RJ 1928. Some remarks on the Devonian fossil insects from the Rhynie Chert beds, Old Red Sandstone. *Trans. R. Soc. Lond.* **76** : 65-71.

Timofeev BV 1959. The oldest flora of the Baltic Province and its stratigraphical significance. *Trudy vses. nauchno-issled. geol.-razv. neft. Inst.* **129**.

Tschudy RH 1966. Associated megaspores and microspores of the Cretaceous genus *Ariadnaesporites* Potonié, 1956 emend. *U.S. geol. Surv. Prof. Pap.* **550-D** : D76-D82.

Turnau E & Karczewska J 1987. Size distribution in some Middle Devonian dispersed spores and its bearing on the problem

of the evolution of heterospory. *Rev. Palaeobot. Palynol.* **52** : 403-416.

Vavrdova M 1966. Paleozoic microplankton from Central Bohemia. *Cas. Miner Geol.* **11** : 409-414.

Winslow MR 1962. Plant spores and other microfossils from Upper Devonian and Lower Mississippian rocks of Ohio. *Prof. Pap.* *U.S. geol. Surv.* **364** : 1-93.

Wodehouse PP 1935. *Pollen grains, their structure, identification and significance in science and medicine.* McGraw-Hill Co., New York & London.

Zerndt J 1934. Les mégaspores du bassin Houiller Polonais. *Acad. Polon. Sci. Let. Trav. géol.* **1** : 1-55.