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Morphological Evolution of Indian Gondwana Megaspores

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ABSTRACT

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The occurrence of abundant dispersed fossil megaspores in the Indian Gondwana sediments indicates the presence of heterosporous early lycopsid plants which are themselves uncommon. Study of megaspores is, hence, significant since it reflects on the evolution of early land plants. A variety of megaspores are recorded from various Gondwana basins of India. They are categorised on the basis of their shape, presence and absence of tri-radiate ridges and nature of exosporium and mesosporium. On the basis of their structural diversity, Permian megaspores show a distinct evolutionary trend. However, in the Mesozoic, no such trend is observed, probably because of paucity of megaspore records and also lack of complete information on mesosporium characters. A careful, detailed and comprehensive study is, therefore, required for a better understanding of the evolutionary trend of Mesozoic megaspores..

Key-words—Heterospory, Megaspores, Permian, Mesozoic, Evolutionary trend.

भारतीय गोंडवाना स्थूलबीजाणुओं का आकारिकीय विकास

रजनी तिवारी

सारांश

भारतीय गोंडवाना अवसादों में प्रचुर परिक्षिप्त जीवाश्म स्थूलबीजाणुओं की प्राप्ति विषमबीजाणुकी प्रारंभिक लाइकोप्सिड वनस्पतियों की विद्यमानता इंगित करती है जो कि अपने आप में अनूठी हैं। स्थूलबीजाणुओं का अध्ययन, इस प्रकार, उल्लेखनीय है क्यों कि यह प्रारंभिक स्थलीय वनस्पतियों का विकास व्यक्त करता है। भारत की विभिन्न गोंडवाना द्रोणियों से स्थूलबीजाणुओं की विविधताएं अभिलेखित की गईं हैं। उन्हें उनकी आकृति, विद्यमानता तथा त्रि-विकिरण कटक की अनुपस्थिति और बीजाणु बहिःचोल व बीजाणुमध्यचोल की प्रकृति के आधार पर श्रेणीबद्ध किया गया है। उनकी संरचनात्मक विविधता के आधार पर, पर्मियन स्थूलबीजाणु एक विशिष्ट विकासात्मक प्रवृत्ति दर्शाते हैं। फिर भी, मीसोज़ोइक में, संभवतः स्थूलबीजाणु अभिलेखों के अभाव तथा बीजाणुमध्यचोल लक्षणों की पूर्ण जानकारी की भी कमीं के कारण, इस प्रकार की प्रवृत्ति नहीं प्रेक्षित की गई है। मीसोज़ोइक स्थूलबीजाणुओं की विकासात्मक प्रवृत्ति को बेहतर समझने के लिए एक ध्यानयुक्त, विस्तृत एवं बोधगम्य अध्ययन की जरुरत है।

संकेत-शब्द—विषमबीजाणुता, स्थूलबीजाणु, पर्मियन, मीसोज़ोइक, विकासात्मक प्रवृत्ति।

INTRODUCTION

MEGASPORES and microspores or the larger and smaller spores, respectively, are the reproductive units of heterosporous early land plants. Heterospory-the phenomenon of production of two types of spores (micro- and mega-) is an important step in the evolutionary history of early land plants. Microspores are male reproductive units which on germination give rise to male gametophytes; whereas, megaspores are the female reproductive units and give rise to female gametophytes. The presence of megaspores indicates the presence of cryptogams. In fossil conditions, where the nature of the gametophyte produced by spores is not known, micro- and megaspores are differentiated on the basis of their

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respective sizes. Generally, spores larger than 200 microns are considered as megaspores. Study of fossil megaspores is not only significant in deciphering the evolutionary history of land plants but also useful in biostratigraphy and interpretation of source vegetation. The origin of heterospory lies in the late Early Devonian (Scott & Hemsley, 1996).

Permian Gondwana megaspores from India have been reported by many workers (Mehta, 1943; Surange *et al*., 1953; Pant & Srivastava, 1961, 1964; Kar, 1968; Bharadwaj & Tiwari, 1970; Agashe, 1979; Lele & Chandra, 1974; Lele & Srivastava, 1983; Pant & Mishra, 1986; Jha & Srivastava, 1984; Jha & Tewari, 2003, 2006; Jha *et al*., 2006, 2007; Maheshwari & Tewari, 1988, 1989; Tewari, 1991; Tewari & Maheshwari, 1992; Tewari *et al*., 2004, 2007; Tripathi, 1997, 1998a, 1998b, 1999; Tripathi & Mishra, 1997, 2001; Srivastava & Tewari, 2001, 2002, 2004).

Indian Mesozoic Gondwana megaspores are reported by Sukhdev (1961), Singh *et al*., (1964), Maheshwari & Banerji (1975), Banerji *et al*. (1978), Pant & Basu (1979), Banerji *et al*. (1984), Jana & Ghosh (1997), Pal *et al*. (1997), Patil & Premchand (2001) and Jana (2004). Forty five genera are reported from Indian Gondwana of which thirty two genera are reported from Permian and thirteen from Mesozoic. Previously, Lower Gondwana megaspores were recorded from the Damodar and South Rewa basins mainly (Early Permian). However, during the last five years comprehensive work has been done in this area and megaspores have been studied from the Satpura, Wardha (Barakar) and Godavari (Barakar and Raniganj) basins. The megaspores are now known from all the major Gondwana basins of India (Fig. 1) from Early and Late Permian.

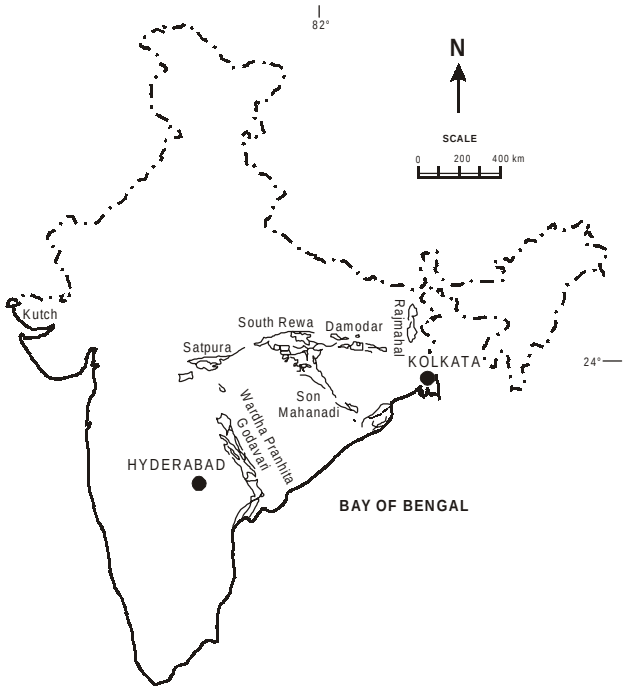


Fig. 1—Map of India showing Indian Gondwana basins.

Other Gondwana countries from where the megaspores are reported include Brazil (Carruthers, 1869; Zeiller, 1895; Lundquist, 1919; Sommer, 1953; Trindade, 1954, 1959a, b,1960, 1961, 1962, 1964, 1966, 1967; Pant & Srivastava, 1962; Dijkstra, 1955, 1957, 1959, 1971, 1972; Piérart & Dijkstra,1961; Trindade & Sommer, 1966; Arai & Rosler, 1980, 1984; Faria *et al.*, 2007), South Africa (Høeg *et al.*,1955; Høeg & Bose, 1960; Pierart, 1959, 1975, 1978a, b; Piérart & Dijkstra,1961; Glasspool, 2003b) and Australia (Dettmann, 1961; Helby, 1967; Helby & Martin, 1965; Scott & Playford, 1985; Wood & Beeston, 1986; Hemsley & Scott, 1989; McLoughlin, 2000; Glasspool, 2000, 2003a, b).

CATEGORISATION OF MEGASPORES

Gondwana megaspores have been classified on the basis of shape, distribution pattern of ornamentation on the exosporium (outer wall layer), type of ornamentation and nature of mesosporium (inner wall layer). Shape of the megaspores in polar view is mainly circular, triangular or, sometimes, oval.

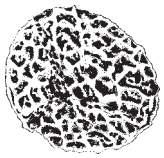
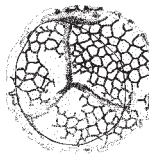
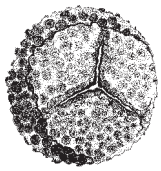
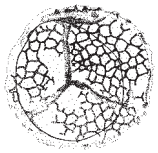
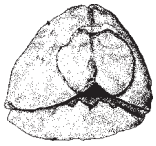
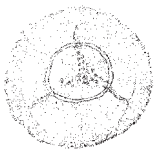
Three kinds of megaspores have been categorised on the basis of distribution pattern of ornamentation, viz. (a) azonate, (b) zonate and (c) gulate. In azonate megaspores the ornamental processes are distributed uniformly on the exosporium. In zonate megaspores the ornamental processes are reduced and rare in the vicinity of contact area and are denser and more pronounced beyond the contact area forming a zone and in gulate megaspores a cone-like structure also known as gula, is formed due to elevation of tri-radiate mark and contact area into a neck like projection (Bharadwaj & Tiwari, 1970). The polar diameter is usually larger than the equatorial diameter in these megaspores. According to Jha and Tewari (2006), gula is not a taxonomic character but a germ tube and gulate megaspores were probably preserved during germination.

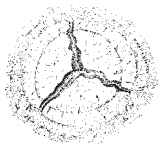
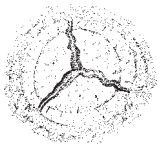
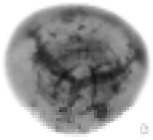
Parameters adopted for circumscription of Indian megaspore taxa include study in both dry and macerated conditions, involving shape, extension of tri-radiate ridges, exosporium and mesosporium characters which appropriately categorise the megapores in an organised way. However, recently, Glasspool (2003b) classified megaspores on exosporium characters only, on the grounds of rapid identification. He ignored the mesosporium characters since its study involves maceration, is time consuming and there is a possibility of loss of exosporium characters during maceration. However, none of the wall characters, i.e. exosporium and mesosporium can be ignored since they constitute an integral part of the megaspore taxonomy. Therefore, work done on Indian megapores is more complete and reliable, whereas, purely exosporium based classification has its own limitations and demerits.

Earlier workers circumscribed megaspores on the basis of nature, viz. unequal, sinuous or straight tri-radiate ridges. Circumscription was also based on width of the ridges.

Taxa	Early Permian			Late Permian		Early Triassic			Late Triassic	Early Cretaceous			
	1	2	3	4	5	6	7	8	9	10	11	12	13
Duosporites Høeg *et al.*, 1955	*	*	*	*									
Talchirella Pant & Srivastava, 1961 emend. Bharadwaj & Tiwari, 1970	*	*	*	*	*	*	*						
Banksisporites Dettmann 1961; Banerji *et al.*, 1978	*	*	*		*	*	*	*	*		*		*
Saccarisporites Sukhdev, 1961		*								*	*		*
Shahdolia Pant & Mishra, 1986		*											
Ancorisporites Pant & Mishra, 1986		*	*										
Barakarella Lele & Srivastava, 1983		*	*										
Jhariatriletes Bharadwaj & Tiwari, 1970		*	*	*	*								
Surangeaesporites Bharadwaj & Tiwari, 1970		*	*	*	*								
Biharisporites Potonié 1956 emend. Bharadwaj & Tiwari, 1970		*	*	*	*	*	*			*			
Bokarosporites Bharadwaj & Tiwari, 1970		*	*		*				*				
Aneuletes Pant & Mishra, 1986			*										
Canaliculites Pant & Mishra, 1986			*						*				
Cystosporites Schopf, 1938			*										
Gundalaspora Jha *et al.*, 2007			*										
Pantiella Maheshwari & Banerji, 1975			*			*	*						
Hughesisporites Potonié, 1956			*						*		*		*
Lagenicula (Bennie & Kidston, 1886) Potonié & Kremp, 1954			*					*					
Lagenoisporites Potonié & Kremp, 1955 emend. Dybova-Jachowicz *et al.*, 1979			*										
Manumisporites Bharadwaj & Tiwari, 1970			*										
Penchiella Srivastava & Tewari, 2001			*		*								
Pilatriletes Pant & Mishra, 1986			*										
Ramispinatispora Pant & Mishra, 1986			*		*								
Saksenasporites Tripathi, 1999			*										
Satpuraspora Srivastava & Tewari, 2002			*										
Sethiaspora Srivastava & Tewari, 2001			*										
Setosisporites Ibrahim, 1933 emend. Potonié & Kremp, 1955			*										
Singhisporites Potonié, 1956 emend. Bharadwaj & Tiwari, 1970			*		*	*		*					
Singraulispora Tripathi & Mishra, 1997			*										
Sporites (Potonié, 1956) Schopf, 1938			*										
Kamthispora Jha & Tewari, 2003					*								
Noniasporites Maheshwari & Bajpai, 1984					*								
Maiturisporites Maheshwari & Banerji, 1975						*	*						
Verrutriletes van der Hammen, 1954 emend. Potonié, 1956						*	*		*		*		
Umiaspora Singh *et al.*, 1964							*				*		
Grambastisporites Pant & Basu, 1979								*					
Trikonia Pant & Basu, 1979								*					
Nathorstisporites Jung, 1958									*				
Erlansonisporites Potonié, 1956									*		*		*
Horstisporites Potonié, 1956									*		*		*
Minerisporites Potonié, 1956										*	*	*	*
Dijkstraisporites Potonié, 1956											*		*
Valvisisporites Ibrahim, 1933 emend. Potonié & Kremp, 1954											*		*
Bacutriletes van der Hammen, 1954 emend. Potonié, 1956											*		*
Paxillitriletes Hall & Nicolson, 1973											*		*

Fig. 2—Distribution of megaspore genera in Indian Gondwana (1-Talchir, 2-Karharbari, 3-Barakar, 4-Barren Measures, 5-Raniganj, 6-Maitur, 7-Panchet, 8-Lower Tiki, 9-Late Triassic, 10-Jabalpur, 11-Bhuj, 12-Umia, 13-Athgarh).

Age	Megaspore taxa	Morphological characteristics
Early Cretaceous	 *Horstisporites biswasii* Banerji *et al.* 1984  *Paxilitriletes battenii* Banerji *et al.* 1984  *Hughesisporites singhii* Banerji *et al.* 1984  *Horstiporites aerolatus* (Harris 1935) Potonie 1956	Tri-radiate ridges indistinct, associated with a number of branched or unbranched appendages which are joined at bases or along whole length; exosporium spinose forming reticulum, mesosporium indistinct or absent
Late Triassic	 *Jhariatriletes obscurus* Banerji *et al.* 1978  *Horstisporites aerolatus* (Harris 1935) Potonie 1956	Shape circular, exosporium verrucate, granulate, tri-radiate and arcuate ridges distinct, mesosporium indistinct, subcircular
Early Triassic	 *Maiturisporites distinctus* Maheshwari & Banerji 1975  *Trikonia emarginata* Pant & Basu 1979  *Pantiella bharadwajii* Maheshwari & Banerji 1975  *Talchirella dubia* Maheshwari & Banerji 1975	Shape subtriangular, tri-radiate ridges and arcuate ridges either indistinct or distinct, in Trikonia tri-radiate ridges notched at angles, exosporium smooth to finely granulate, conate, mammillate cavate, verrucate, spinose, mesosporium usually triangular with cushions either absent or arranged in one row along tri-radiate mark
Late Permian **Raniganj**	 *Surangeaesporites raniganjensis* Bharadwaj & Tiwari 1970  *Noniasporites harrisii* Maheshwari & Bajpai 1984  *Singhisporites radialis* Bharadwaj & Tiwari 1970  *Kamthispora ramanamurtyi* Jha & Tewari 2003  *Singhisporites baculatus* (Kar 1968) Bharadwaj & Tiwari 1970  *Ramispinatispora nautiyalii* Pant & Mishra 1986	Alete, trilete zonate, shape circular, oval, exosporium smooth granulate, verrucate, baculate spinose, spines simple, bifurcate or multifurcate, rarely showing rill like structures, mesosporium with or without cushions, cushions either arranged in one row or in multiple rows along tri-radiate mark

Age	Megaspore taxa			Morphological characteristics
Late Permian **Barren Measures**	 *Singhisporites radialis* Bharadwaj & Tiwari 1970	 *Jhariatriletes baculosus* Bharadwaj & Tiwari 1970		Alete, trilete, zonate, shape circular, subcircular, triangular or subtriangular exosporium verrucate, baculate; bacula massive, sparsely or uniformly distributed; tapering, dome shaped or blunt, sometimes with elongate, ribbose, simple or bifurcate filamentous or fleshy processes, spherical, subspherical, triangular, mesosporium thin or translucent or with dark contents; either without cushions or with one row of cushions arranged biseriately along tri-radiate mark or with few irregularly arranged cushions
Early Permian **Barakar**	 *Manumisporites distinctus* Bharadwaj & Tiwari 1970	 *Ramispinatispora nautiyalii* Pant & Mishra 1986	 *Gundalaspora spinosus* Jha *et al.* 2006	Azonate, alete, trilete, circular, triangular or oval, triradiate and arcuate ridges distinct, former sometimes extending beyond contact area, exosporium psilate, granulate, verrucate, finely verrucate, mixed verrucate, baculate - bacula may be thin, slender, small, massive tapering or flattened at tip or dome shaped; spinose, conate; numerous variations, mesosporium spherical or subspherical, subtriangular, triangular, globular, membraneous, thin, hyaline, translucent or with dark contents, smooth or granulate; (a) either devoid of cushions; (b) with one row of cushions arranged along trilete mark; (c) numerous cushions arranged trigonally along triradiate mark; (d) with irregularly arranged cushions
	 *Bokarosporites rotundus* Bharadwaj & Tiwari 1970	 *Bokarosporites* sp. (in Tewari *et al.* 2007)	 *Talchirella trivedii* Pant & Srivastava 1961, emend. Bharadwaj & Tiwari 1970	

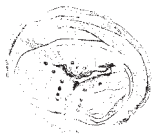
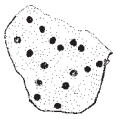
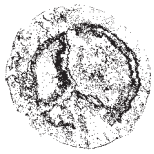
Age	Megaspore taxa			Morphological characteristics
Early Permian **Karharbari**	 *Bokarosporites rotundus* (Singh) Bharadwaj & Tiwari 1970	 *Ancorisporites venkatachalae* Maheshwari & Tewari 1989	 *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari 1992	Azonate, alete, trilete, circular, triangular or oval, tri-radiate and arcuate ridges distinct, former sometimes extending beyond contact area, exosporium smooth, granulate, verrucate, reticulate, baculate, conate, spinose, setate, covered with bifurcate appendages apices of which are either pointed, tapering or recurved hook like; mesosporium spherical, subspherical, subtriangular, triangular; thin or thick walled, devoid or with one row of cushions arranged biseriately along tri-radiate mark or a number of cushions arranged trigonally or irregularly along triradiate mark
	 *Barakarella pantii* Lele & Srivastava 1983	 *Banksisporites utkalensis* (Pant & Srivastava) Tewari & Maheshwari 1992	 *Barakarella prakashii* Tewari & Maheshwari 1992	
Early Permian **Talchir**	 *Duosporits congoensis* Høeg *et al.* 1955	 *Duosporits congoensis* Høeg *et al.* 1955	 *Banksisporites indicus* (Singh 1953) Tewari & Maheshwari 1992	Azonate, trilete, circular or triangular, tri-radiate and arcuate ridges distinct, exosporium granulate-verrucate, mesosporium with numerous cushions arranged trigonally along tri-radiate mark or without cushions

Fig. 3—Diagrammatic representation of megaspores showing evolutionary trends through Indian Gondwana.

Accordingly, taxa were differentiated on the basis of uniformly wide tri-radiate ridges or tri-radiate ridges that were narrow at tri-junction and broad at ends or else, tri-radiate ridges that were broad at trijunction and narrow at ends. However, these features are preservational in nature. The tri-radiate ridges usually end at contact ridges. However, in the genus *Duosporites* Høeg *et al.*, 1955 they reach beyond contact ridges. Except for some seed megaspores or alete megaspores all the heterosporous plants show trilete megaspores, i.e. presence of a tri-radiate mark, through which the megaspores of a tetrahedral tetrad are attached with each other. Seed megaspores are formed due to maturation of only one functional megaspore in a tetrahedral tetrad, while other three disintegrate. These megaspores assume an elongate, oval shape and are without a trilete mark, i.e. they are alete, e.g. *Cystosporites* (Trivedi, 1953), *Saccarisporites* Sukhdev 1961 and *Kamthispora* Jha & Tewari, 2003. Alete megaspores indicate advance stage of heterospory, a step further towards seed habit. Homospory, heterospory and seed habit are successive evolutionary stages (Chaloner & Hemsley, 1991).

The specific circumscription of megaspore taxa was earlier also based on the nature of contact ridges and contact area, e.g. less curved contact ridges with circular contact area as in *Surangeaesporites,* moderately curved contact ridges

with trilobed contact area as in *Talchirella trivedii* and highly curved contact ridges with deeply trilobed contact area as in *Biharisporites spinosus* (Bharadwaj & Tewari, 1970).

The exosporium or the outer wall of megaspores is either (a) smooth, i.e. laevigate or (b) ornamented. Ornamentation ranges from granulate (*Banksisporites*), verrucate (*Talchirella*), baculate (*Barakarella*), conate (*Biharisporites*), spinose (*Kamthispora*), pilate, mammilate (*Mammilaespora*). Sometimes, the ornamentation include ribbon-like, fleshy simple or bifurcate processes (*Singhisporites*), apically lobed mammilate appendages (*Singraulispora*), elongate filamentous simple processes with rounded tips (*Pilatriletes*) and appendages with two to many apical branches with pointed tips (*Ramispinatispora*). Additionally, reticulate exosporium is observed in Mesozoic megaspores (*Horstisporites*, *Maiturisporites*).

The mesosporium or inner wall of megaspores is usually a hyaline, sac-like structure. Its shape in polar view may be circular or triangular. The presence or absence of cushions is an important generic feature. Cushions are knob/pit like structures present along tri-radiate mark and exosporium is attached to the mesosporium through these structures. The arrangement of cushions may vary in different species of a genus, e.g. (a) numerous cushions may be present and arranged in multiseriate rows, trigonally along tri-radiate mark, e.g. *Talchirella trivedii, Barakarella pantii,* (b) few cushions which may either be arranged irregularly, e.g. *Talchirella flavata* or (c) in a single row along tri-radiate mark, e.g. *Duosporites congoensis.*

DISTRIBUTION OF GONDWANA MEGASPORES

A review of the distribution of Gondwana megaspores indicates that there are about 45 megaspore genera (Fig. 2), of which twenty two are distributed exclusively in Permian, thirteen exclusively in Mesozoic and nine megaspore genera are found both in Permian and Mesozoic. Some of them are restricted to a particular horizon while others show a wide vertical distribution.

Megaspore genera showing wide vertical distribution are *Banksisporites, Bokarosporites, Biharisporites, Talchirella, Duosporites, Hughesisporites* and *Jhariatriletes*. The genera *Banksisporites, Biharisporites* and *Hughesisporites* extend from Early Permian to Early Cretaceous but *Banksisporites* is absent in Barren Measures Formation and *Biharisporites* is absent in Late Triassic. *Talchirella* and *Singhisporites* extend from Early Permian to Early Triassic. *Bokarosporites* is found in Early Permian and Late Triassic but is absent in Early Triassic. *Duosporites* and *Jhariatriletes* are found only in Permian and extend from Early to Late Permian.

Megaspore genera with restricted distribution are *Shahdolia* which is restricted to Karharbari Formation; *Cystosporites, Gundalaspora, Manumisporites* and *Pilatriletes* which are restricted to Barakar Formation; *Noniasporites* and *Kamthispora* are restricted to Raniganj Formation; *Grambastisporites* and *Trikonia* are restricted to Lower Tiki (Early Triassic) Formation, and *Nathorstisporites* is restricted to Upper Tiki (Late Triassic) Formation.

AFFINITIES OF DISPERSED FOSSIL MEGASPORES

Heterospory is known in diverse groups of extant vascular plants. In the fossil plant groups megaspores occur in the Lycopsida (Lepidodendrales), Filicopsida (Coenopteridales), Sphenopsida and Noeggerathiopsida. Affinity of dispersed fossil megaspores with lycopsids is now well established on the basis of widespread prevalence of heterospory in the group. Besides, dispersed fossil megaspores are also comparable with *in situ* megaspores of lycopsids in presence of pronounced ornamentation like spines, etc. Megaspores of *Isoetes* are similar to the genus *Duosporites* (Høeg *et al.*,1955). A number of dispersed megaspores from Cretaceous, viz. *Paxillitriletes vittatus* Kovach & Dilcher, *P. dakotaensis* (Hall) Hall & Nicolson, *P. cutchensis* (Singh *et al.*) Banerji *et al.*, *P. battenii* Banerji *et al.*, *Minerisporites susserassuis* Tschudy and *M. mirabilis* (Miner) Potonie, *Maiturisporites rewaensis* Wood & Beeston are apparently closely related to megaspores of *Isoetes* (Srivastava, 2000). Similarly, megaspores of extant genus *Isoetes dixitei*, possessing well developed auriculae resemble megaspores of *Valvisisporites auritus* (Zerndt) Potonié & Kremp and *Valvisisporites appendiculatus* (Kowaleska-Mslankiewicz) Potonié & Kremp, and; megaspores of *Isoetes janaianus* are comparable with *Valvisisporites.*

CONCLUSIONS

An analysis of Fig. 2 suggests that during deposition of the sediments of Talchir Formation (Early Permian), the number and variety of megaspores are few but increase during Karharbari and Barakar time. In the Late Permian (Raniganj Formation) though the number is less, structural diversity is unaffected. Therefore, during Permian, a distinct evolutionary trend is observed (Fig. 3). However, in Mesozoic time, the exosporium is highly diversified but mesosporium characters are not so well known. This may be due to the fact that either they were not preserved because of harsh climatic conditions or else their detailed studies were avoided due to lengthy and time consuming procedure (Glasspool, 2003b). The latter seems to be more relevant because had the climatic conditions been responsible for non-preservation, the exosporium should have been affected more than the mesosporium, which is not the case. An endeavour has to be made in this direction for better comprehension of evolution of the early land plants.

A comparison of lycopsid megafossils and megaspore distribution in India exemplifies discrepancy in their

preservation potential. The quantitative and qualitative superiority of megaspores over megafossils is probably due to their stupendous production and structural adaptability. The diversity in exosporium ornamentation from laevigate to verrucate, baculate to conate/spinose and the nature of spines (viz. simple, bifurcate and multifurcate) indicates structural diversity and complexity thus reflecting on the richness and variety of the megaspore assemblage. The prolific and diversified megaspore assemblage throughout the Permian and Mesozoic indicates that lycopsids persisted throughout Gondwana though their megafossil records are scarce. Probably, the fragility of the plants was the limiting preservational factor.

Future Prospects—Recently, study on megaspores have been extended in most of the Indian Gondwana basins, but there is scope for study, especially of Permian sediments of the Mahanadi Basin. Mesozoic, megaspores are reported primarily from Kutch and South Rewa Gondwana Basin. There is need to study them from other basins as well for a better understanding of evolution of various heterosporous groups of cryptogams. Further, for a complete morphotaxonomic understanding of dispersed fossil megaspores, details of all the morphological characters, viz. shape, nature of exosporium and inner wall layer/mesosporium, should carefully be studied. There is a pressing need to study the details of mesosporium especially in the Mesozoic megaspores, since such information is largely unreported.

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