

Significance of mesosporium in taxonomic resolution of fossil megaspores

NEERJA JHA AND RAJNI TEWARI

Birbal Sahni Institute of Palaeobotany, 53 University Road, Lucknow 226 007, India.
Email: neerjajha@yahoo.co.uk, rajni.tewari@gmail.com

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Heterosporous-formation of two kinds of spores, viz. mega- and microspores is a significant phenomenon in evolutionary history of early land plants. Fossil microspores and megaspores are differentiated on the basis of their respective sizes. Generally spores more than 200 μm are regarded as megaspores (Zerndt, 1937).

Dispersed megaspores are circumscribed on the basis of type of megaspore, i.e., alete or trilete, shape (triangular, circular, oval), contact area and arcuate ridges, characters of wall layers (Pant & Srivastava, 1961, 1962, 1965; Bharadwaj & Tiwari, 1970; Pant & Mishra, 1986). Outer wall layer, i.e., exosporium is variously sculptured and is characterized by different types of ornamentations, viz. grana, bacula, coni, verrucae, setae and spines. Spines may be simple, bifurcate, multifurcate, straight, curved or hook-like. Inner wall layer is mesosporium. It has also been called as the inner sac, basal lamina, inner body or nexine by different workers (Pant & Mishra, 1986 and references cited therein).

The mesosporium is attached only on the proximal side with the exosporium leaving a cavity or open space all around. Mesosporium (mesospore) was introduced by Fitting (1900) in the megaspores of modern representatives of the genera *Isoetes* and *Selaginella*. It is mostly a hyaline sac-like structure which may be circular, oval or triangular in shape, with or without cushions (Fig.1). Cushions have been variously described as raised circular/knobbed/pit-like structures.

When present, these may be arranged in a single row, trigonally in multiple rows or irregularly along the triradial mark.

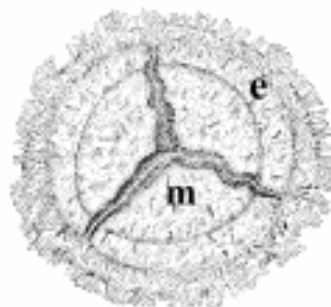
In dispersed fossil megaspores mesosporium was first identified and described in detail by Høeg *et al.* (1955) in the genus *Duosporites congoensis*. This taxon was created on the basis of presence of double wall layers and cushions/pits in a single row along triradial mark on mesosporium. Since the institution of *D. congoensis*, mesosporium has been considered as important taxonomic character for the identification of megaspores and various genera have been proposed by various workers, viz., Kar (1968), Bharadwaj & Tiwari (1970), Lele & Srivastava (1983), Pant & Srivastava (1961, 1962, 1965), Pant & Mishra (1986), Jha & Srivastava (1984), Maheshwari & Tewari (1989), Tewari & Maheshwari (1992), Tripathi (1997, 1998a, b, 1999), Tripathi & Mishra (1997, 2001), Patil & Premchand (2001), Srivastava & Tewari (2002a, b, 2004), Jha & Tewari (2003), Tewari *et al.* (2004), Jha *et al.* (2006), Tewari *et al.* (2007) and Tewari *et al.* (2009). The study of mesosporium is not only of immense significance in determining the range of structural variability in various taxa (Fig. 1) but also provides a basis for determination of evolutionary pattern in megaspore development thereby in understanding the development/evolution of ovule/seed habit. Evolutionary history of land plants suggests that heterosporous land plants gave rise to seed plants (Sprone, 1965). One of the possibilities is that



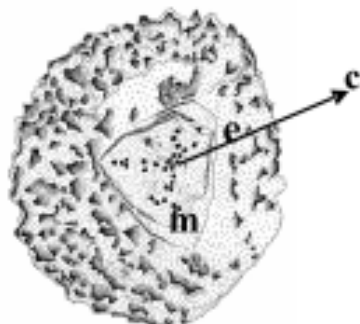
Singhisporites radialis

(after Bharadwaj & Tiwari 1970)

Mesosporium without cushions

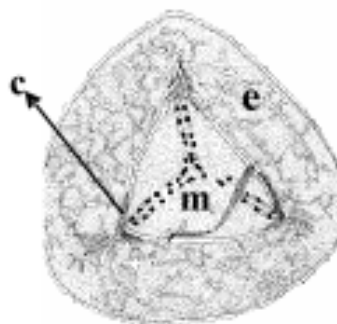


Manumisporites distinctus



Pantiella bharadwajii

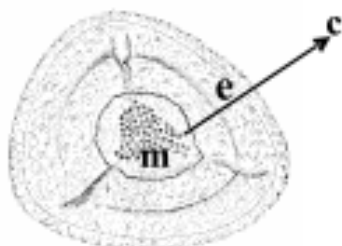
Mesosporium with irregularly distributed cushions



Pantiella bosei

Mesosporium with uniseriate cushions

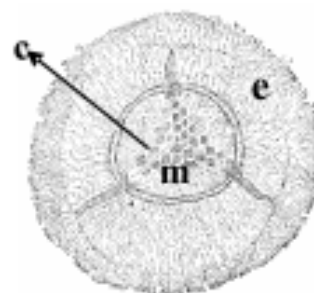
(after Maheshwari & Banerji 1975)



Duosporites multipunctatus

(after Hoeg & Bose 1960)

Mesosporium with multiseriate cushions



Surangaesporites raniganjensis

(after Bharadwaj & Tiwari 1970)

Fig. 1—Megaspore taxa showing different kind of mesosporia. e - exosporium, m - mesosporium, c - cushions

mesosporium in megaspores of these heterosporous plants might have developed as ovule and the attachment point of exosporium with mesosporium by means of cushions was probably a higher stage of evolution which might have evolved as the stalk of ovule in seed plants.

Presence of mesosporium has always been considered as important character for identification of megaspores (Pant & Srivastava, 1962; Stubblefield & Rothwell, 1981; Tryon & Lugardon, 1978; Taylor & Brack Hanes, 1976; Archangelsky & Villar de Seoane, 1990). Occurrence of mesosporium has also been recorded in megaspores found in attachment with *Selaginella harrisiana* from Kungurian (Permian) of Australia (Townrow, 1968).

Recently, the taxonomy proposed by Glasspool (2003) for Permian Gondwana megaspores is based on exosporium characters only. It does not include the features of the inner body or mesosporium. He has omitted the study of mesosporium character on the pretext of rapid identification of Gondwana megaspores and based his identification on SEM studies alone discarding the character examined under light microscopic studies. SEM study has its own limitations as it shows only external characters. According to Glasspool, study of mesosporium is time consuming, is a lengthy process and involves “destructive maceration”. Presence of inner body/mesosporium was accordingly not given any importance for the morphographic grouping or classification, and megaspores with and without a mesosporium have been included within the same genus. However, it is imperative to examine the mesosporium features in order to understand the basic principles of plant evolution (Grauvogel-Stamm & Lugardon, 2001; Srivastava, 2000). SEM studies are applicable only to the surface structures, whereas, studies under transmitted light, though time taking, involve LO analysis and provide detailed, comprehensive, complete and more reliable study of both internal and external characters of fossil megaspores. Internal characters are equally important as the external characters for complete description/understanding of any organism and cannot be ignored on the grounds of time consumption for the study.

Accordingly, the technique used for study of megaspores includes their study in dry condition under incident light for exosporium characters and involves careful, controlled, differential maceration for study of mesosporium in wet condition with care and caution.

Glasspool (2003) has merged Indian megaspores without considering original specimens which are based on external (exosporium) and internal (mesosporium) characters and clearly show distinct mesosporia. The study of a large number of megaspores from different Indian Gondwana basins and type specimens available in the repository of Birbal Sahni Institute of Palaeobotany, Lucknow, indicates that both exosporium and mesosporium are important features and can very well be studied in transmitted light after treating the megaspores with schultz's solution with mild alkali. Almost all the Gondwana megaspores are identified and described on the basis of external morphological features. The importance of mesosporium in megaspore taxonomy cannot be ignored. Moreover, Glasspool has himself cited the importance by showing the mesosporium in his new species *Singhisporites tubbus* (Glasspool, 2000, Pl.3, Fig.7).

SEM studies of torn megaspores and section of megaspores of many extant species, viz. *Isoetes coromandelina* Linnaeus (Bajpai & Maheshwari, 1985) and *Selaginella delicatula* Desv., *S. inequalifolia* Hook. & Grev., *S. monospora*, *S. nummularia* and *S. plumosa* (Bajpai & Maheshwari, 1986) have clearly shown occurrence of two distinct layers, i.e., exosporium and mesosporium. SEM and TEM studies by Archangelsky & Villar de Seoane (1990) have also revealed mesosporium in megaspores of *Verrutritetes*. Additionally, they too have discussed the significance of mesosporium in megaspore taxonomy.

Records of megafossils of heterosporous early land plants are sporadic in Indian Gondwana. Megaspores are the only indicators/representatives of these plants. For a comprehensive study and proper understanding of the diversity of the heterosporous early land plants, it is imperative to use all the taxonomical parameters available in the megaspores. Realising the importance of mesosporium in systematics of megaspores, the study

of mesosporium character in megaspores along with all the other characters is emphasized in the present communication.

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