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Lower Gondwana seeds

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ABSTRACT

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The seeds of Lower Gondwana are found attached, detached, dispersed and mixed with other organs of being detached from the plants, which produced them. Like other plant fossils, seeds are also preserved in a variety of ways depending upon their structure and the conditions that prevailed during the time of deposition. They may be found as petrifaction or occur as impressions, cast and moulds or as carbonized compressions. Generally seeds are longer than broad but few are broader than long. All these seeds are platyspermic. There are about thirty two compressed seed genera are known from Lower Gondwana out of which twenty are described with complete structural details. The structural details and pollination of these seeds suggest that during the Palaeozoic time, seeds of at least three major groups of gymnosperms existed in Lower Gondwana countries, viz. Glossopteridales and allies, Cordaitales or Ginkgoales and primitive Coniferales.

Key-words—Lower Gondwana, Archegonia, Tent pole, *Glossopteris*, Upper Palaeozoic, Pollination.

निम्न गोंडवाना बीज

एस.पी. तिवारी

सारांश

पादपों से विलग्न होते हुए निम्न गोंडवाना के बीज संलग्न, विलग्न, परिक्षिप्त व अन्य अंग के साथ मिश्रित पाए गए हैं, जिन्होंने उनको उत्पन्न किया। अन्य जीवाश्मों की भाँति, बीज भी परिरक्षण काल की परिस्थितियों एवं बीजों की संरचना के अनुसार विभिन्न प्रकार से परिरक्षित हुए। वे अश्मीभवन के रुप में पाए जाते हैं अथवा छाप, ढाँचा एवं साँचा अथवा कार्बनीकृत छापों के रुप में पाए जाते हैं। सामान्यतः बीज चौड़ाई की अपेक्षा लंबे होते हैं किंतु कुछ लंबे से अधिक चौड़े हैं। ये समस्त बीज चिपिटबीजी हैं। निम्न गोंडवाना से लगभग बत्तीस संपीडित बीज वंश प्रसिद्ध हैं जिनमें से बीस संपूर्ण संरचनात्मक विवरण सहित वर्णित हैं। इन बीजों के संरचनात्मक विवरण एवं परागण संकेत देते हैं कि पुराजीवी काल के दौरान, निम्न गोंडवाना देशों के अस्तित्व में अनावृतबीजी के कम-से-कम तीन प्रधान समूहों के अर्थात ग्लोसोप्टेरीडेल्स एवं संबद्ध, कार्डेटेलीज या गिंकगोएल्स तथा आधारी कोनीफेरेलीज थे।

संकेत-शब्द—निम्न गोंडवाना, स्त्रीधानी, तंबू ध्रुव, *ग्लोसोप्टेरिस,* ऊपरी पुराजीवी, परागण।

INTRODUCTION

THE Southern Land mass was very distinct during Carboniferous-Permian times and was populated by the Lower Gondwana Glossopteris flora. The flora are dominated by Gymnosperms which bear the naked seeds. A large number of seeds are described from Lower Gondwana but mostly remained structurally uninvestigated. Unlike seeds of extant plants, the fossil seeds are usually found dispersed in the sediments and mixed with other organs after being detached from the parent plants that produced them. The seeds were described under *Alatocarpus, Cardiocarpon, Cardiocarpus, Cordaicarpus, Cornuspermum, Cycadospermum, Eucerospermum, Nummulospermum, Indocarpus, Samaropsis, Talchirospermum* and *Karharbariospermum* by different workers (Lele, l969; White, 1908; Zeiller, 1902; Feistmantel, 1879, 1882; Walkom, 1921, 1922, 1928, 1935; Johnston, 1888; Maithy, 1965; Hoeg & Bose, 1960; Feruglio, 1942; Seward & Sahni, 1920; Biswas, 1955; Ganguli, 1959; Lele, 1966; Lele *et al*., 1968; Plumstead, 1962; Millan, 1967a, b, 1977; Saksena, 1955; Rigby, 1972 a, b, 1978; Shirley, 1902; Surange & Chandra, 1975a, b; Seward, 1917; Schopf, 1961; Oliveira, 1980;

Bhattacharya, 1963; Holmes, 1995; Khan, 1969; Srivastava & Chandra, 1982; Maheshwari & Tewari, 1986; Singh *et al*., 2003, 2005; Tewari & Srivastava, 1996, 2000) and are structurally unknown. Pant 1958, described the structural details of the compressed seeds from Mukuru Coalfield, Tanganyika. Afterwards many workers, viz. Pant and Nautiyal 1960, 1963, Pant and Srivastava 1963, Srivastava 1954, Banerjee 1969, Pant *et al.* 1984, 1985, 1999 and Pant *et al*. 1995 reported the structural details of various compressed Lower Gondwana seeds.

Majority of the seeds are impressions which lack structural details. Similarly the seeds preserved as cast and moulds are also un-useful for study of anatomical details, though they may be sight to a third dimension. Petrified seeds are the best material to study the structural details but their occurrence is rare. Gould and Delevoryas (1977) reported petrified seeds found attached to a dorsiventral fructification. Nishida *et al.* (2003, 2004) described anatomically preserved fossil Glossopterid ovules from the Late Permian of Queensland, Australia, that contain several pollen tubes at various stages, releasing flagellated sperms. Each sperm is approximately 12.7 µm long and 13.9 µm wide with a conspicuous spiral structure comprised of a series of dots that resemble the position of basal bodies of flagella, aligned along the multilayered structure. This configuration is similar to the helically arranged flagella in the sperm of Cycads, Ginkgo and many Pteridophytes. Seeds which come next to petrifactions in the preservation of internal structure are compressions where the original substance of the seed is compressed and squashed between the layers of sediments and got compacted with the time.

There are only 20 compressed seed genera described from the Lower Gondwana with complete structural details. These are *Cornuspermum, Maheshwariella, Platycardia, Pterygospermum, Spermatites, Walkomiellospermum, Cerviculospermum (Collospermum), Retortistoma, Palispermum, Bulbospermum, Palaeocarpus, Shivacarpus, Otofeistia, Buriadiospermum, Birsinghpuria, Stephanostoma, Semenites, Talchirospermum, Karharbariospermum* and seeds of *Birsinghia*. All these seeds genera are platyspermic.

In this paper diversity of Lower Gondwana seeds on the basis of morphology and structural details have been reviewed and their mode of pollination and evolutionary trends are also being discussed.

SEEDS AND OVULES

According to Chadefaud (1944) an ovule becomes a seed after fertilization. However, it is quite difficult to decide whether or not a fossil seed-like body is fertilized. Embryos are as a rule absent in Lower Gondwana seed like bodies but it is quite possible that they remained embryo less because they were shed soon after fertilization and got immediately fossilized before the development of embryos. In this connection it is important to recall that the seeds of modern Ginkgo and Cycads also have long resting period after fertilization on the ground. Palaeobotanists have therefore, been calling even embryo less ovule-like or seed-like bodies as seeds (Tiwari, 2004). Earlier workers like Arnold (1948), Florin (1950) and Eames (1955) have advocated the use of term seed for such reproductive bodies. Eames justified the use of term "seed" by saying " the ancient "seed" without embryos are unfertilized ovules or seeds with early stages of embryos and that the absence of embryos suggests a resting period at the time of shedding or soon thereafter". Accordingly, the structures described from Lower Gondwanas are all termed as seeds. Majority of Lower Gondwana seeds are either impressions or compressions which are either found as attached or detached.

Attached seeds

(a) Impressions

Seeds attached to fertilinger *Arberia minasica* (Fig. 1N) were described by White (1908) and Rigby (1972 a). *Dolianitia* (Fig. 1O) was reported from Brazil by Millan (1967a) who thought that it was possibly the seed bearing organ of *Glossopteris* or *Gangamopteris*. Holmes (1974) found *Cordaicarpus* type of seeds attached to fructification *Australoglossa* (Fig. 2B) from New South Wales, Australia. A number of seed bearing reproductive organs have been described under various names viz., *Denkania* Surange and Chandra (1973b) (Fig. 2E), *Partha* Surange and Chandra (1973c), *Plumsteadia* Rigby (1963), *Lidgettonia* Thomas (1958) (Fig. 1P), *Rusangea* Lacey *et al*. (1975). The structure of all the above seeds is unknown.

(b) Compressions

Pant and Nautiyal (1963) described some structurally preserved seeds attached terminally to dichotomizing axes as *Maheshwariella bicornuta* (Fig. 1H, I). They also described some *Ottokaria* like fructification (Fig. 2A), bearing seeds of *Platycardia* and *Pterygospermum* (Pant & Nautiyal, 1965; Pant, 1977). Pant and Nautiyal (1967) again described the structure of attached seeds of *Buriadia heterophylla* (Feisimantel) Seward and Sahni (Fig. 1L). Banerjee (1969) found structurally preserved seeds *Cornuspermum* attached to fructification *Senotheca*. Surange and Chandra (1973a) reported seeds of *Platycardia* and *Pterygospermum* type occurring in close association with *Dictyopteridium*. Srivastava and Chandra (1982) described *Talchirospermum indicum* from Talchir Formation and *Karharbariospermum surangei* from Karharbari Formation of India. Maheshwari and Tewari (1986) reported *Maheshwariella spinicornuta* reported from Karharbari Formation. Pant *et al.* (1995) described the structure of seeds of *Birsinghia* from Karharbari Formation of India (Fig. 1J).

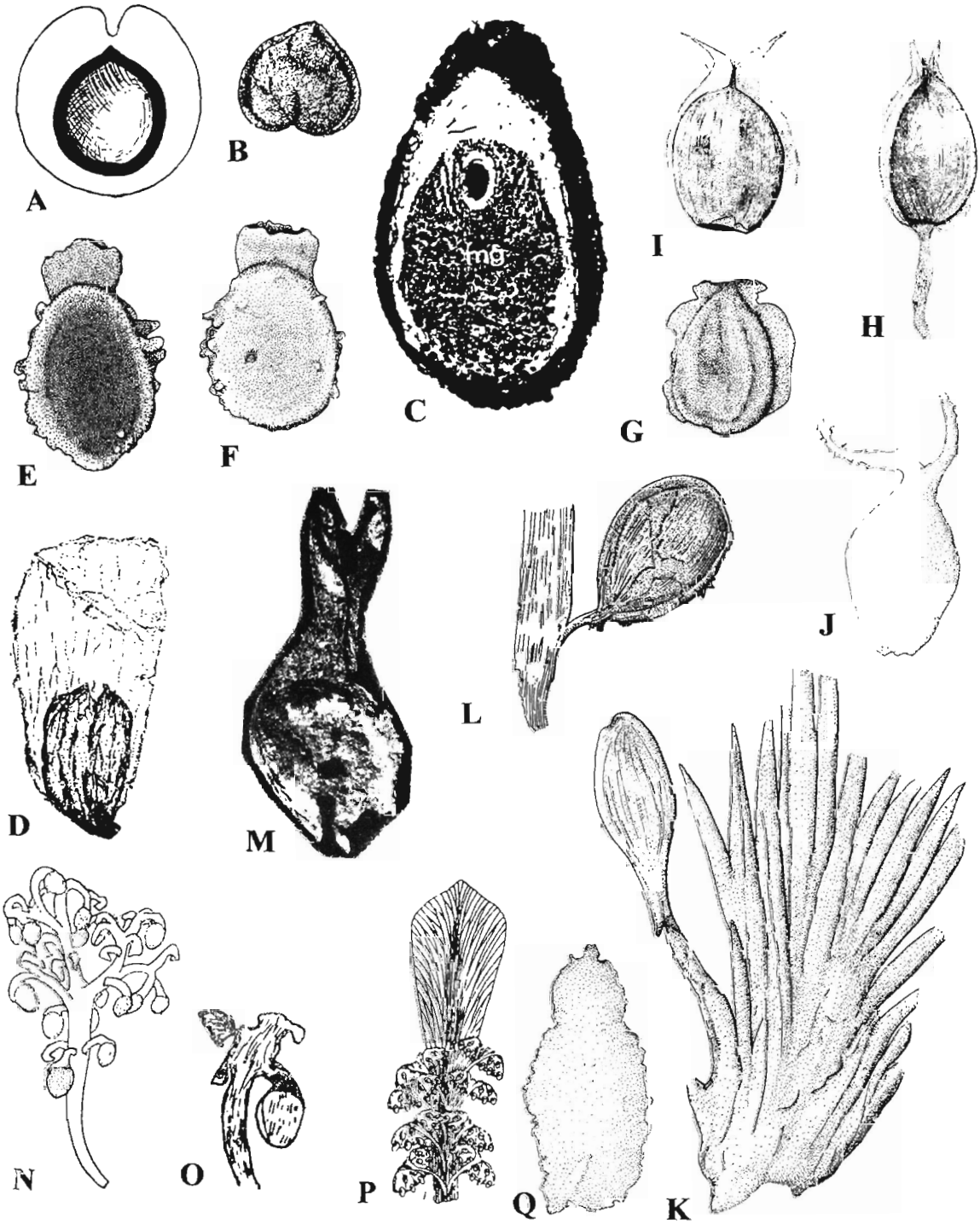

Fig 1—**A.** *Samaropsis emerginata,* with wide wing. x 2. **B.** *Cordaicarpus cordai* with narrow border. x 2. **C.** Longitudinal section of ovule, from *Dictyopteridium* type ovulate organ with a large archegonium in mega gametophyte (mg). x 47. **D.** *Indocarpus.* x 7. **E, F.** *Stephanostoma crystallinum,* compressed seeds showing a funnel like structure at the micropylar end and a number of processes on the sides. **E** x 20, **F** x 20. **G.** *Pterygospermum raniganjense* seed with a narrow wing. x 15. **H, I.** *Maheshwariella bicornuta* compressed seeds. **H** shows almost straight micropylar horns and a long slender stalk at chalazal end. x 6. Seed in **I** shows lateral horns and marginal border. x 14. **J.** Seed of *Birsinghia florinii* with two horns and hairs on the horn. x 7. **K.** Apical portion of the shoot of *Buriadia heterophylla* showing an inverted seed with its a micropylar horn and a slender stalk. x 10. **L.** An axis of *Buriadia heterophylla* bearing a shortly stalked inverted seed. x 14. **M.** A seed *of Buriadiospermum sewardii* showing micropylar horn and a stalk. x 12. **N.** Reconstruction *of Arberia minasica* x 1.25. **O.** *Dolianitia crassa* x 1.25. **P.** *Lidgettonia* cupule. x 0.75. **Q.** *Bulbospermum surangei,* an incarcerated seed showing a bulbous part below micropylar canal. x 20. (**A,** after Goeppert & Berger **B,** after Geinitz. **C,** after Nishida *et al.* 2003. **D,** after Surange & Chandra 1975. **E, F, G,** after Pant & Nautiyal 1960. **H, I,** after Pant & Nautiyal 1963. **J,** after Pant *et al.* 1995. **K, L,** after Pant & Nautiyal 1967 **M,** after Pant *et al.* 1984. **N,** after Rigby 1972. **O,** after Millan 1967 **P,** after Surange & Chandra 1974. **Q.** after Pant *et al.* 1985).

Detached seeds

(a) Impressions

Feistmantel (1879, 1881, 1882, 1886) reported a number of seeds under the name *Carpolithes, Samaropsis* and *Cardiocarpum* (?) from the beds of Talchir, Karharbari and Raniganj formations of India. In subsequent years numerous other seeds were described under the above generic names as well as under *Cardiocarpon, Cardiocarpus, Cordaicarpus, Cycadospermum, Cornucarpus, Indocarpus, Nummulospermum, Trigonocarpus(?)* and *Eucerospermum.* These seeds were reported from India (Zeiller, 1902; Seward & Sahni, 1920; Saksena, 1955; Surange & Lele, 1956; Maithy, 1965; Surange & Chandra, 1975a); South Africa (Seward, 1897, 1917; du-Toit, 1927; Hoeg & Bose, 1960; Walton, 1929); South America (White, 1908; Seward, 1917; Feruglio, 1942; Millan, 1967b, 1969, 1977, 1979; Oliveira, 1980; Rigby, 1972b); Australia (Johnston, 1988; Arber, 1902; Walkom, 1921, 1922, 1928, 1935; Rigby, 1972a, b; Holmes, 1995) and Antarctica (Schopf, 1961; Plumstead, 1962).

Brongniart (1881) and several other workers adopted the name *Cardiocarpus* for *Cardiocarpon, Cardiocarpum* and *Cordaicarpus*. Seward (1917) proposed the name *Cordaicarpus* for all such " Platyspermic seeds, preserved as casts or impressions". At the same time Seward (1917) put *Carpolithes milleri, Cardiocarpus indicus, Cardiocarpus bercellosum* and *Cardiocarpon seixasi* in *Samaropsis.* The genera *Cordaicarpus* and *Samaropsis* (Fig. 1A, B) were the dominant forms of seeds of Lower Gondwana. However, it has to be admitted that the two genera are rather artificial groups, based on morphological differences, like the width of the wing which intergrades from one genus into the other.

Maithy (1965) has mentioned only two Lower Gondwana seeds, viz. *Stereocarpus* (Surange, 1957) from Raniganj Coalfield and *Rotundocarpus* from Karharbari Stage of Giridih in Bihar (India) as radiospermic. However, *Stereocarpus* and *Rotundocarpus* are also platyspermic seeds. So all the seeds reported from Lower Gondwana are platyspermic (Pant *et al*., 1985).

(b) Compressions

Srivastava 1954 for the first time reported maceration resistant cuticles in the Lower Gondwana seed, *Spermatites indicus* but he has not described the details of integument, nucellus, megaspore membrane, etc. Saksena (1947, 1958) failed to recognize his specimen as seed and described it upside down as *Capsulites gondwanensis*, thinking the micropylar canal as the seta of moss capsule and chalazal hole as stomium. According to Cridland (1963) the seed *Stereocarpus emarginatuss* (Surange, 1957) which has only two cuticles and no micropyle or chalaza is certainly a scale leaf. Subsequently Chandra and Surange (1977) designated it as *Eretmonia emarginata.* So it is necessary that the following attributes to be observed in a compressed seed-like body before calling it a seed:

(1). It should yield envelopes, which could be reasonably regarded as outer and inner cuticles of integument, the nucellar membrane and the megaspore membrane.

(2). It should show a chalazal hole and a micropylar canal where pollen grains may be seen inside the canal and or on the nucellar tip.

Pant 1958 was the first person who described the compressed Lower Gondwana seeds according to the above criteria. He included such seeds under two species of *Spermatites.* Later, Pant and Nautiyal (1960) redescribed the above seeds as *Stephanostoma crystallinum* Pant and *Semenites tetrapterus* Pant. If we see the distribution of Lower Gondwana seeds in various parts of Lower Gondwana countries, we find that maximum number of seeds are reported from India (see Figs 3 & 4).

External morphology of Lower Gondwana seeds

Lower Gondwana seeds show a great variation in size. The smallest seeds are less than l mm long and largest are about 5 cm in length. Their width also varies from about half a mm to about three and half a centimeters. All the seeds are platyspermic (Pant *et al*., 1985). They are generally orthotropous but seeds of *Buriadia* (Fig. 1L, K) and *Palaeocarpus* are anatropous. Some seeds are definitely stalked, e.g. *Maheshwariella bicornuta* (Figs 1H, 2D), *Shivacarpus johillensis* (Fig. 2C) and *Otofeistia milleri* (Fig. 2F). Most of the seeds are longer than broad but *Shivacarpus latus* (Fig. 2J), *Alatocarpus indicus* and *Alatocarpus johillensis* are broader than long. *Pterygospermum* (Fig. 1G) shows a wing on its remnants while *Maheshwariella* (Figs 1I, H) and *Cornuspermum* show a narrow border around the seed. *Otofeistia milleri* (Fig. 2K), *Maheshwariella bicornuta* and *Semenites tetrapterus* seem to show a median ridge in the seeds flattened along the principal plane. The apical ends of the seeds of *Cerviculospermum ovalis* (Fig. 5G) are prolonged into a single neck like projection, while in *Retortistoma* (Fig. 5C) it is curved and in *Bulbospermum* (Figs 1Q, 5D) it forms a bulbous structure at the base of micropyle. The micropylar ends *of Maheshwariella bicornuta, Maheshwariella spinicornuta* and *Buriadiospermum* (Fig. 1M) bear micropylar horns. *Stephanostoma* (Figs 1E, F) and *Cornuspermum* are characterized by a funnel like structure at the micropylar end. Seeds of *Palaeocarpus* and *Otofeistia* (Fig. 2K) show centroterminal sinuses. Seeds of *Palaeocarpus, Shivacarpus* and *Otofeistia* (Figs 2C, G, K, L) show a massive integument which is differentiated into an outer fleshy layer (Sarcotesta) and an inner stony layer (Sclerotesta), but others show a rather thin mainly fibrous integument.

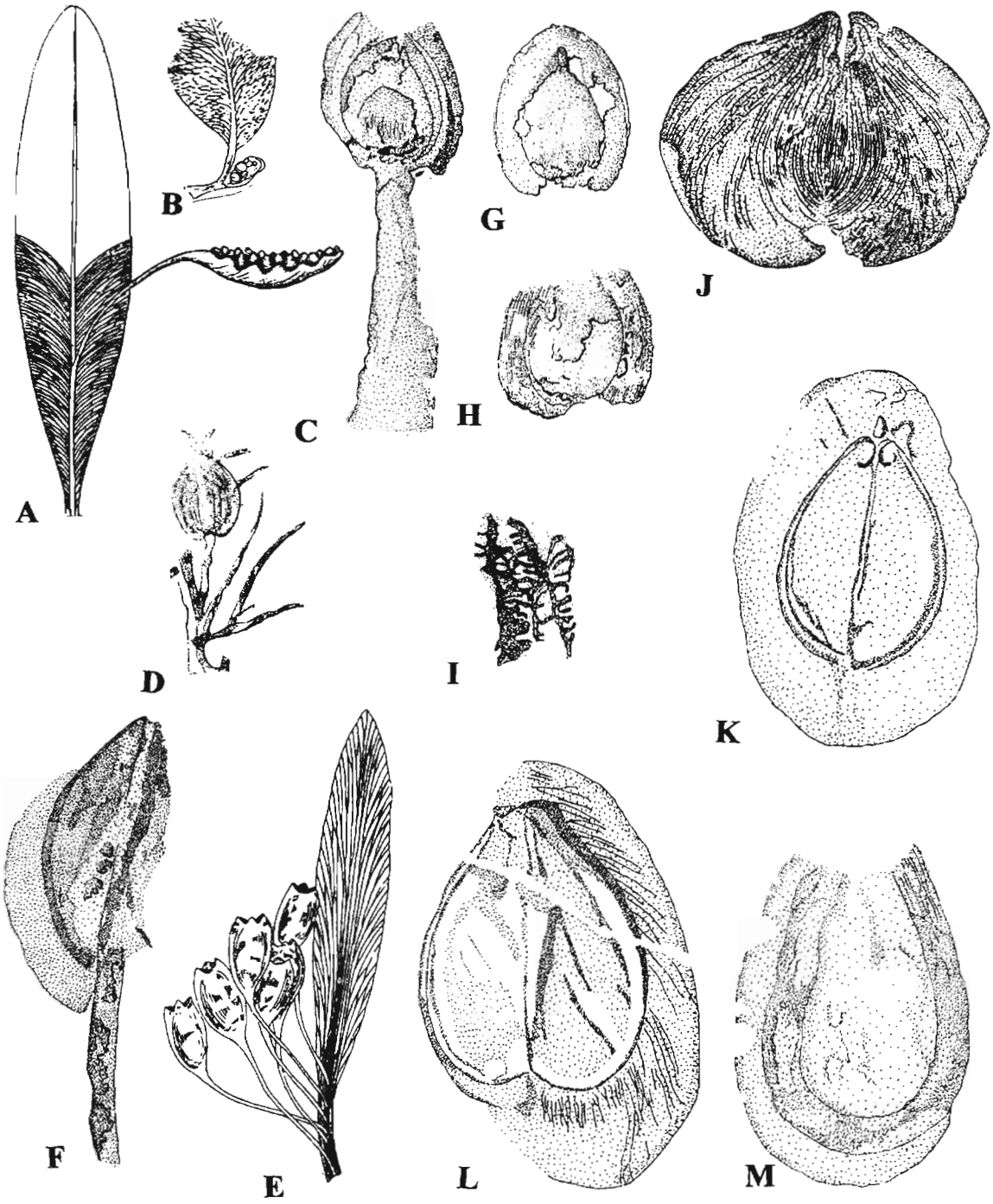

Fig. 2—**A.** a reconstruction of *Glossopteris* leaf bearing an *Ottokaria* (presenting side view). x 2. **B.** *Australoglossa walkomii.* x 2. **C.** *Shivacarpus johillensis,* dry seed with sarcotesta and central nucule, long stout stalk. x 2. **D.** *Maheshwariella bicornuta,* seed is attached terminally to a fork of dichotomizing axis. x 4. **E.** reconstruction of *Denkania.* x 1.4. **F.** *Otofeistia milleri,* stalked seed. x 1.5. **G.** *Shivacarpus johillensis,* dry seed with wide sarcotesta and central nucule. x 2.5. **H.** *Palaeocarpus birsinghpurensis,* seed shows impressions of integumentary fibers. x 2.5. **I.** scalariform tracheids from seed stalk in Fig. **C.** x 300. **J.** *Shivacarpus latus,* a compressed un-macerated seed showing wide sarcotesta and impressions of fibers throughout the surface of sarcotesta and sclerotesta. x 3. **K-M.** *Otofeistia milleri.* **K.** a compressed seed with wide border of sarcotesta and a median ridge, sarcotesta wider at base and micropylar end. x 1.5. **L.** seed with wide sarcotesta and impression of fibres. x 1.5. **M.** laterally compressed seed with wide sclerotesta compressed along secondary plane. x 1.5. (**A,** after Pant & Nautiyal. **B,** after Holmes 1974. **C, F, G, H, I, J, K, L, M,** after Pant *et al.* 1985, **D.** after Pant & Nautiyal 1963. **E,** after Surange & Chandra 1975).

Genera and species	India	Australia	Antarctica	S. Africa	S. America
Alatocarpus indicus Lele, 1969	+				
Alatocarpus pincombei (Walkom) Holmes, 1995		+			
Alatocarpus sp.	+				
Cardiocarpon oliveiranum White, 1908					+
C. moreiranum White, 1908					+
C. barcellosum White, 1908					+
C. seixasi White, 1908					+
Cardiocarpus indicus Zeiller, 1902	+				
Carpolithes milleri Feistmantel, 1879	+			+	+
Carpolithus circularis Walkom, 1935		+			
C. striatus Walkom, 1935		+			
C. tasmanicus Johnston, 1888		+			
Carpolithus sp.	+				
Cordaicarpus barbosanus Millan, 1977					+
Cordaicarpus emerginatus Walkom, 1935		+			
C. furcata Surange & Lele, 1956	+				
C. irapuensis Oliveira, 1980					+
C. *karharbarense* Maithy, 1965	+				
C. *ovatus* Walkom, 1935		+			
C. mucronatus Hoeg & Bose, 1960				+	
C. patagonicus Feruglio, 1951					+
C. prolatus Walkom, 1935		+			
C. rocha-camposii Oliveira, 1980					+
C. zeilleri Maithy, 1965	+				
Cordaicarpus sp. cf. *C. cordai* Seward & Sahni, 1920	+				
Cordaicarpus sp.	+				
Cordaicarpus sp.	+				
Cordaicarpus sp. Plumstead, 1962			+		
Cornucarpus cerquiensis Millan, 1977			+		
Cornucarpus striatus Walkom, 1935		+			
Cornucarpus sp.				+	
Cornuspermum pennatus Banerjee, 1969	+	+			
Cycadospermum dawsoni Shirley, 1902		+			
Eucerospermum opium Feruglio, 1942					+
E. nitens Feruglio, 1946					+
E. patagonicum Feruglio, 1942					+
Nummulospermum bowense Walkom, 1921		+		+	
Nummulospermum cf. *bowense* Maithy, 1965	+				
Maheshwariella bicornuta Pant & Nautiyal, 1963	+				
Platycardia bengalensis Pant & Nautiyal, 1960	+				
Platycardia jugus Maithy, 1969	+				
Pterygospermum raniganjense Pant & Nautiyal, 1960	+				
Rotundocarpus ovatus MaIthy, l965	+				
R. striatus Maithy, 1965	+				
Indocarpus elongates Surange & Chandra, 1975	+				
Semenites tetrapterus (Pant) Pant & Nautiyal, 1960				+	
Spermatites indicus Srivastava, 1954	+				
Stephanostoma crystallinum (Pant) Pant & Nautiyal, 1960				+	
Stephanostoma (cf.) *crystallinum* Plumstead, 1962			+		
Samaropsis argentina Feruglio					+
S. bainhensis Millan, 1967					+
S. bautkofi Hoeg & Bose l960				+	
S. (cf.) *barcellosa* White, 1908					+
S. criciumensis Millan, 1967					+
S. dolianitii Millan, 1977					+
S. etheridgei Walkom, l922		+			
S. feistmantelii Maithy, 1965	+				
S. ganjrensis Saksena, 1955	+				
S. goraiensis Surange & Lele, l956	+				
S. intermedia Hoeg & Bose, l960				+	
S. johillensis Saksena, 1955	+				
S. kurtzii Leguizamon, 1971					+
S. leslii Seward, l917				+	

S. longii Schopf, 1961				+			
S. mendesii Rigby, 1972							+
S. millaniana Oliveira, l980							+
S. moravica Walkom, 1935			+				
S. pincombei Walkom, 1928			+				
S. ovalis Walkom, 1935			+				
S. raniganjensis Seward & Sahni, 1920	+						
S. rigbyi Millan, 1977							+
S. sancti-marci Oliveira, l980							+
S. thomasii Schopf, 1961				+			
S. yoshidae Rigby, 1972							+
S. zambesicus Hoeg & Bose, l960					+		
Samaropsis sp.	+						
Trigonocarpus (?) *ellipticus* Walkom, 1935			+				
T.(?) ovoideus Walkom, 1935			+				
Walkomiellospermum indicum Pant & Srivastava, 1963	+						
Birsinghpuria indica Pant *et al.,* 1985	+						
Bulbospermum surangEi Pant *et al.,* 1985	+						
Buriadiospermum sewardii Pant *et al.,* 1985	+						
Cerviculospermum ovalis Pant *et al.,* 1998	+						
Otofeistia milleri Pant *et al.,* 1985	+						
Palaeocarpus birsinghpurensis Pant *et al.,* 1985	+						
Palispermum ovalis Pant *et al.,* 1985	+						
Platycardia papillata Pant *et al.,* 1984	+						
Retortistoma crystallinum Pant *et al.,* 1985	+						
Shivacarpus johillensis Pant *et al.,* 1985	+						
Shivacarpus latus Pant *et al.,* 1985	+						
Karharbariospermum surangei Srivastava & Chandra, 1982	+						
Talchirospermum indicum Srivastava & Chandra, 1982	+						
Maheshwariella spinicornuta Maheshwari & Tewari, 1986	+						
Seeds of *Birsinghia florinii* Pant *et al.,* 1995	+						

Fig. 3—Distribution of seeds in different Gondwanaland Countries.

Internal structure

The outer cuticle of integument varies in texture, thickness and the size and shape of cells in different types of seeds. Outer cuticle of *Stephanostoma* (Fig. 6C), *Pterygospermum raniganjense*, *Platycardia bengalensis* and *Retortistoma crystallinum* show marks of crystals and *Shivacarpus johillensis* (Fig. 6B), *Buriadiospermum sewardii* and seeds of *Birsinghia* have stomata in their outer cuticle of integument. Likewise, the inner cuticle of integument presents distinctive features like occurrences of papillate cells in *Birsinghpuria indica*, *Maheshwariella bicornuta,* and *Shivacarpus latus* (Fig. 6H) or the occurrence of simple pits in anticlinal walls of *Cerviculospermum ovalis* (Fig. 6D). In most of the seeds this inner cuticle is closely appressed to nucellar cuticle but in *Palispermum ovalis*, it is not easily separable and in *Cerviculospermum ovalis* it is separated from the nucellus by a wide gap (Fig. 6J). Generally, the micropylar tube which is formed by the inner cuticle is straight but in *Retortistoma* it is curved (Fig. 5C). The seeds of *Cerviculospermum* and *Retortistoma* are characterized by long micropylar canal while others have short micropylar canal.

In *Shivacarpus johillensis* and *Platycardia bengalensis* the fibrous layer in between cuticles shows impressions of cells bearing scalariform thickenings like those of tracheids. Others show elongated fibres but *Palaeocarpus birsinghpurensis* shows short sclereids (Fig. 6E).

The nucellar cuticle also shows characteristic features in its cells. *Platycardia bengalensis*, *Stephanostoma crystallinum* , *Cornuspermum pennatus* show sinuous walled cells while in other seeds it shows straight walled cells. The nucellar surface in *Shivacarpus, Palaeocarpus* (Fig. 6G) and *Cornuspermum* shows papillate cells and that of *Shivacarpus latus* shows occasional stomata. The nucellus of *Cerviculospermum* (Fig. 5G) and *Palispermum* is prolonged into nucellar beak above the pollen chamber.

The pollen chamber wall of some seeds presents characters which enable us to distinguish them from others, e.g. the rim of the pollen chamber wall show elongated processes in *Platycardia bengalensis*, *Stephanostoma crystallinum* (Fig. 5B), *Pterygospermum raniganjense* (Fig. 5A) and *Cornuspermum pennatus* while in others it is continuous. In *Bulbospermum* the pollen chamber forms a bulbous dome shaped structure at the base of the micropylar canal (Fig. 5E).

Genera and species	Talchir	Karharbari	Barakar	Barren Measures	Raniganj
Alatocarpus indicus Lele, 1969		+	+		
Alatocarpus sp.			+		
Cardiocarpus indicus Zeiller, 1902		+			
Carpolithes milleri Feistmantel, 1879		+	+		
Carpolithus sp.		+			
Cordaicarpus furcata Surange & Lele, l956	+	+			
C. karharbarense Maithy, 1965		+			
C. zeilleri Maithy, 1965		+	+		
Cordaicarpus sp.	+		+		
Cordaicarpus sp. cf. *C. cordai* Seward & Sahni, l920			+		
Cornuspermum pennatus Banerjee, 1969					+
Indocarpus elongatus Surange & Chandra, 1975					+
Maheshwariella bicornuta Pant & Nautiyal, 1963		+			
Nummulospermum cf. *bowense* Maithy, 1965		+			
Platycardia bengalensis Pant & Nautiyal, 1960					+
P. jugus Maithy, 1969		+			
Pterygospermum raniganjense Pant & Nautiyal, 1960					+
Rotundocarpus ovatus Maithy, 1965		+			
R. striatus Maithy, 1965		+			
Samaropsis feistmantelii Maithy, 1965		+			
S. ganjrensis Saksena, l955		+	+		
S. goraiensis Surange & Lele, l956	+	+			
S. johillensis Saksena, 1955		+	+		
S. raniganjensis Seward & Sahni, 1920					+
Samaropsis sp.	+	+	+		+
Spermatites indicus Srivastava, 1954					+
Samaropsis sp. cf. *goraiensis* Lele, 1966	+				
Stereocarpus emarginatus Surange, 1957					+
Walkomiellospermum indicum Pant & Srivastava, 1963	+				
Birsinghpuria indica Pant *et al.*, 1985		+			
Bulbospermum surangei Pant *et al.*, l985		+			
Buriadiospermum sewardii Pant *et al.*, l984		+			
Cerviculospermum ovalis Pant *et al.*, 1998		+			
Otofeistia milleri Pant *et al.*, 1985		+			
Palaeocarpus birsinghpurensis Pant *et al.*, 1985		+			
Palispermum ovalis Pant *et al.*, 1985		+			
Platycardia papillata Pant *et al.*, 1984		+			
Retortistoma crystallinum Pant *et al.*, 1985		+			
Shivacarpus johillensis Pant *et al.*, 1985		+			
Shivacarpus latus Pant *et al.*, 1985		+			
Karharbariospermum surangei Srivastava & Chandra, 1982		+			
Talchirospermum indicum Srivastava & Chandra, 1982	+				
Maheshwariella spinicornuta Maheshwari & Tewari, 1986		+			
Seeds of *Birsinghia florinii* Pant *et al.*, 1995		+			

Fig. 4—Distribution of seeds in different Lower Gondwana formations of India.

The megaspore membrane of *Cerviculospermum* (Fig. 5G) and *Palaeocarpus* (Fig. 5H) is raised and prolonged into a "tent pole" like structure. Below the surrounding depression 2 or 3 spherical dark bodies (archegonia) are seen.

The pollen grains are present in the micropylar canal or on nucellar tips. The seeds of *Cerviculospermum, Retortistoma, Palispermum, Platycardia, Stephanostoma, Semenites, Pterygospermum, Cornuspermum, Bulbospermum* and *Palaeocarpus* are pollinated by disaccate pollen grains. The body of pollen grains may be striate or non-striate. *Shivacarpus, Birsinghpuria* (Fig. 7A), *Maheshwariella* and seeds of *Birsinghia* show pollination by monosaccate pollen grains. Unwinged, monocolpate pollen grains are present inside the pollen chamber of *Buriadiospermum* (Fig. 5F) and *Walkomiellospermum*. The pollen grains found inside the cuticle of nucellar tip obviously lie inside the pollen chamber wall (see Fig. 8).

A source of disaccate pollen grains could be the sporangia of *Arberiella* (Figs 7C, G) which produce disaccate striate pollen grains (Pant, 1958; Pant & Nautiyal, 1960). Further, similar

sporangia are attached to fructifications of *Eretmonia* (Lacey *et al.,* 1974, 1975; Surange & Maheshwari, 1970; Surange & Chandra, 1975b) (Fig. 7F) and *Nesowalesia* (Pant, 1958, 1977) (Fig. 7H) which are attributed to *Glossopteris* and its allies. The sources of one winged spores of the type found in *Maheshwariella bicornuta, Shivacarpus latus, Shivacarpus johillensis, Birsinghpuria indica* and seeds of *Birsinghia* are presently unknown. However, Pant *et al*. (1995) reported *Paliandrolepis singularis* (Fig. 7J) a detached elongated bisporangiate microsporophyll with a pointed apex and truncated base. Microsporangia are elongated, oval and parallel to each other and contain numerous oval, monosaccate pollen grains. It may be source of monosaccate pollen grains. Surange and Chandra (1975a, b) reported *Kendostrobus* (Fig. 7M) a pollen producing cone that has been suggested as having glossopterid affinities. It consists of a central axis with helically arranged, naked, exannulate sporangia arranged in groups. The surfaces of sporangia are covered with minute pits. Pollen of *Kendostrobus cylindricus* is elliptical-sub circular. Extending over the surface is a series of parallel ridges and on surface there is a suture described as monolete. The source of unwinged monocolpate spores which are found in *Buriadiospermum* and *Walkomiellospermum* are presently unknown and they suggest the affinities of these seeds are more uncertain. This fact further emphasizes the need for work on microsporangia and microsporangiate organs of the Glossopteris flora, so that the sources of the diverse pollen grains found in seeds and in the dispersed condition could be traced.

DISCUSSION AND CONCLUSION

The structural details of compressed Lower Gondwana seeds are very much helpful in tracing the affinities of *Glossopteris* and its allies. Surange and Chandra (1975b) have suggested that leaves of *Glossopteris* may belong to two rather different groups of gymnosperms, viz. Pteridospermales and the Glossopteridales. On the other hand Pant (1977) and Gould and Delevoryas (1977) suggested that *Glossopteris* may be a Pteridosperm. Pant in particular points out that the attachment of the cupule stalk to the midrib of a leaf is a pteridospermous feature even though the attachment of a cupule to a simple leaf was previously unknown in other seed ferns. One could therefore, continue to keep these plants in the pteridosperms in the manner of the Caytoniales, Corrystospermaceae and Peltaspermaceae, the attachment of whose microsporophylls, megasporophylls is unknown. Pant 1977 also points out that if the fructification is axillary as seen in *Glossopteris taenioides* (Pant & Singh, 1974) and as sometimes assumed for *Scutum* also then the Glossopteridales would undoubtedly be very different.

A third view is held by Schopf (1976) and according to him "the glossopterids may be hypothetically derived from ancient cordaiteans if allowance is made for a large gap in the phyletic record occasioned by a long glacial hiatus…… The most distinctive feature of the glossopterids is the ovulate fertiliger with its foliar bracts. The vascular bundles of leaf veins are reasonably comparable to those of cordaitean leaves and it is postulated that the foliar bract is derived from the cordaitean-type leaf and that the fertiliger stalk and capitulum, much condensed and modified, corresponds morphologically to the fertile spike of the cordaiteans. No similar basis for comparison is afforded by the Pteridosperms, which apparently do not bear seeds directly on stem-like structures". The seeds of *Palaeocarpus birsinghpurensis* and *Cerviculospermum ovalis* having circular archegonia, tent-pole and two winged pollen grains inside the pollen chamber may suggest that they belong to plants allied to Cordaitales. However, except for the above mentioned features the seeds are just like other seeds which are suspected to belong to the Glossopteridales and this may indirectly support the view about cordaitean affinities of *Glossopteris* held by Schopf (1976).

There is also a possibility that the seeds which are pollinated by monosaccate pollen grains may belong to Cordaitales or some primitive conifers. However, they could even belong to some hitherto undiscovered plants which had monosaccate pollen grains. In this connection it is important to point out that although *Cordaites* like leaves of *Noeggerathiopsis* have been described from Gondwanaland, but no cordaitean fructifications have so far been found in this region and the attribution of the seeds to Cordaitales must, for the present, remain questionable. Another group which has spherical archegonia is the Ginkgoales but the pollination of the seeds by one winged pollen grains rules out the possibility of the seeds belonging to the Ginkgoales.

The structural details of the dispersed seeds and also the previous studies by Pant 1958, 1966, 1977, 1982, Pant and Nautiyal 1960, 1963, 1967, Pant and Srivastava 1963, Banerjee 1969, Surange and Chandra 1975b, Pant *et al*. 1984, 1985, Tiwari 2004 suggest that during the Palaeozoic times seeds of at least three major groups of Gymnosperms were existing in India and also other parts of Gondwana Land. These are:

1. Seeds of *Glossopteris* and allies, which are pollinated by disaccate pollen grains. Their plants may have been related to the Pteridosperms.

2. Seeds of plants possibly closely or distantly allied to Cordaitales and Ginkgoales. Their leaves may have been of *Noeggerathiopsis* type. Such seeds have spherical archegonia and pollinated by monosaccate pollen grains. Other seeds which have been referred to Cordaitalean genera like *Cordaicarpus* and *Cycadospermum* may also belong to this alliance but since their structural details are unknown, this is even more uncertain. However, as long as no typical fructification and stems referable to Cordaitales have been reported the occurrence of this group in Gondwanaland must be regarded as doubtful.

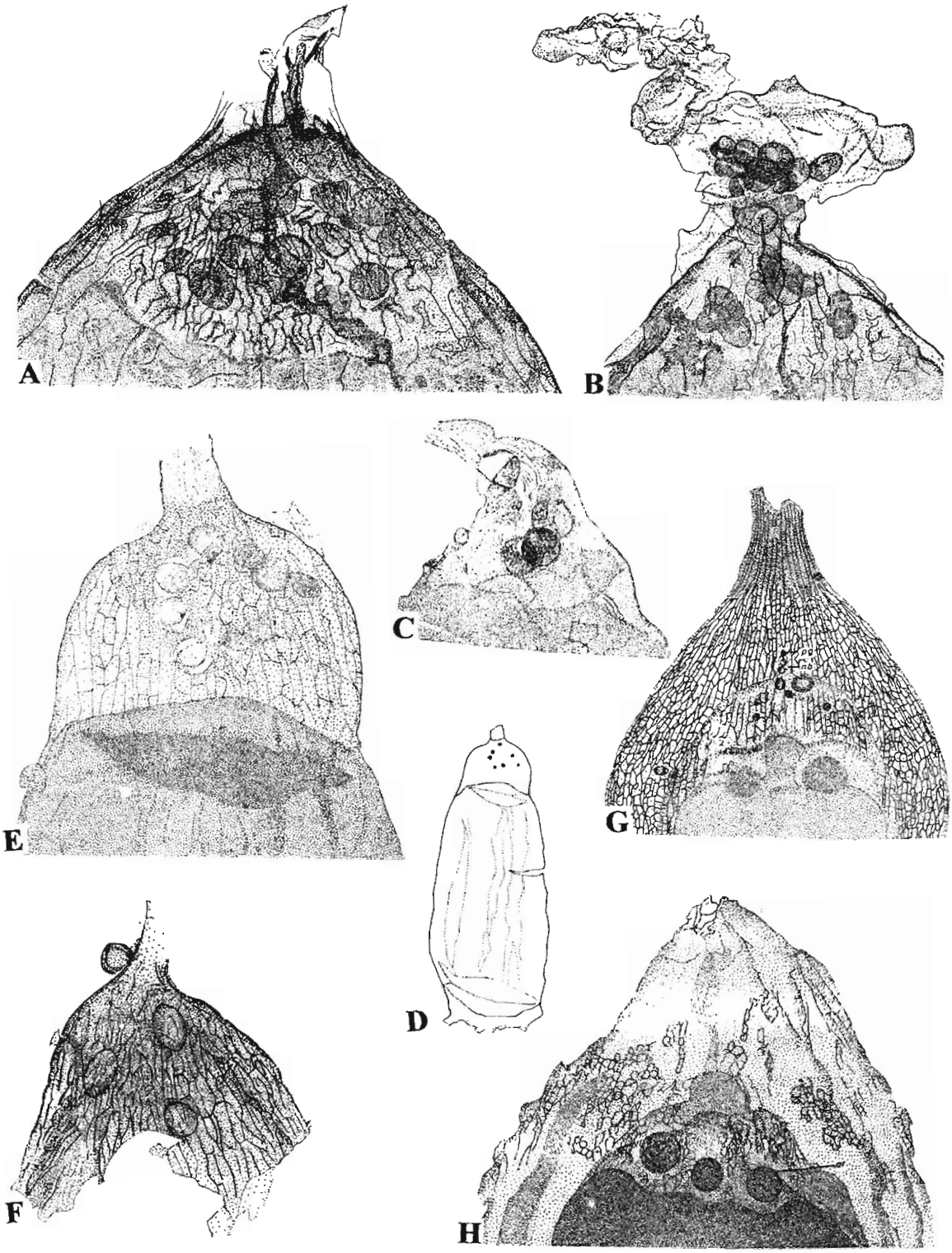

Fig. 5—**A**. *Pterygospermum raniganjense* seed with numerous pollen grains inside the pollen chamber, nucellar processes arising from the rim of pollen chamber wall have entered in the base of the micropylar canal. x 150. **B.** micropylar end of the seeds of *Stephanostoma crystallinum* showing numerous pollen grains inside the funnel like structure and the pollen chamber x 85. **C.** micropylar end of *Retortistoma crystallinum* with curved micropyle and pollen grains inside the pollen chamber. x 50. **D.** outline of the macerated seed of *Bulbospermum surangei* showing micropylar canal, swollen pollen chamber, megaspore membrane and chalazal hole. x 25. **E.** micropylar end of *Bulbospermum surangei* with bulbous pollen chamber with pollen grains and micropylar canal. x 80. **F.** micropylar end of the seed of *Buriadia heterophylla* with pollen grains. x 80. **G.** seed of *Cerviculospermum ovalis* showing tent-pole like structure in megaspore membrane, nucellar beak and pollen grains inside the pollen chamber. x 30. **H.** seed of *Palaeocarpus birsinghpurensis* showing tent-pole, nucellar beak and three dark archegonia. x 30. (**A, B,** after Pant & Nautiyal 1963, **C, D, E, G, H,** after Pant *et al.* 1985. **F,** after Pant & Nautiyal 1967).

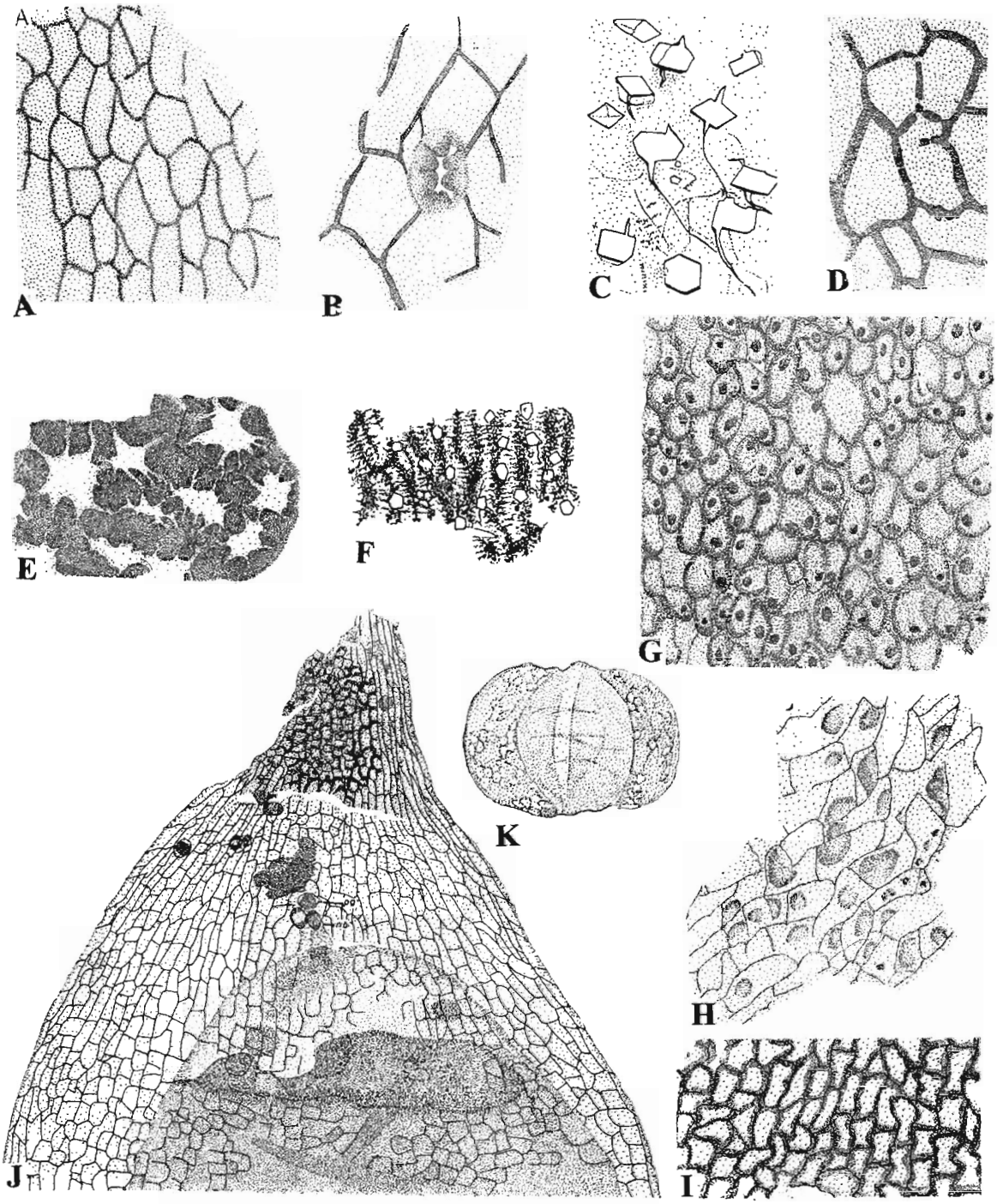

Fig. 6—**A-B.** *Shivacarpus latus.* **A.** outer cuticle of integument showing narrowly elongated rectangular cells. x 90. **B.** a portion of outer cuticle of integument more magnified to show stoma and papillate subsidiary cells. x 250. **C.** crystals with stalk like structure in outer cuticle of integument in seed *of Stephanostoma crystallinum.* x 350. **D.** inner cuticle of integument showing simple pits on anticlinal walls. x 300. **E.** sclerieds with simple pits recovered from stony layer of *Palaeocarpus birsinghpurensis* x 250. **F.** membrane found inside the outer cuticle of integument with imprints of scalariform elongated cells and crystals. x 135. **G.** nucellar cuticle of *Shivacarpus johillensis* showing papillate cells. x 90. **H.** inner cuticle of integument showing papillate cells in *Shivacarpus latus.* x 125. **I.** thick walled nucellar cuticle showing middle lamellae in seed of *Palaeocarpus birsinghpurensis.* x 125. **J.** micropylar end of seed of *Cerviculospermum ovalis* showing megaspore membrane, nucellar beak and disaccate pollen grains. x 35. **K.** a disaccate pollen grain recovered from seed of *Cerviculospermum ovalis.* x 600 (**A, B, D, E, G, H, I, J, K,** after Pant *et al.* 1985, **C, F,** after Pant & Nautiyal 1963).

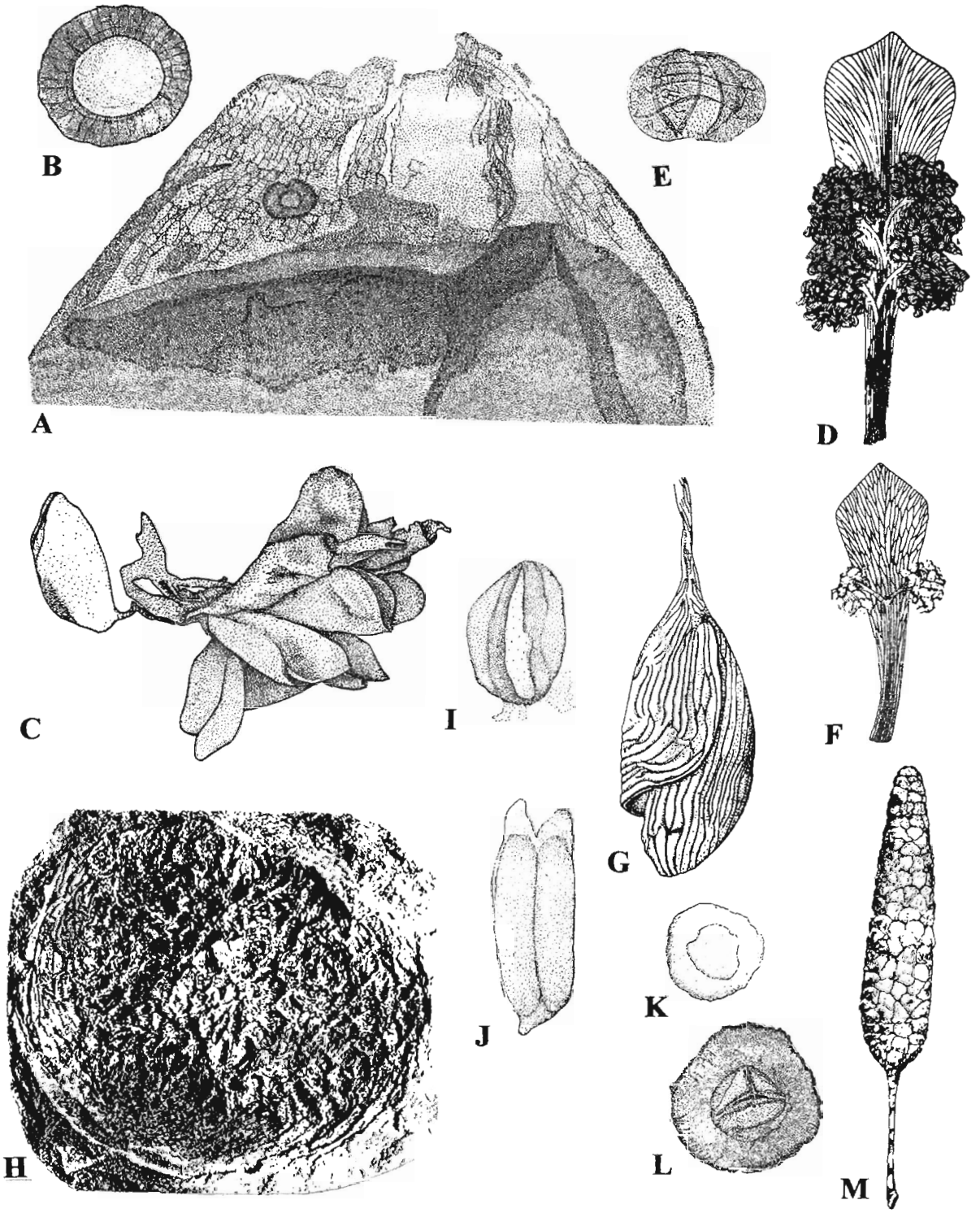

Fig. 7—**A**. *Birsinghpuria indica,* micropylar end of the seed more magnified to show the details of pollen chamber and monosaccate pollen grain inside the pollen chamber. x 170. **B.** monosaccate pollen grain. x 50. **C**. group of sporangia attached to a branching axis. x 15. **D.** *Glossotheca.* x 2. **E.** disaccate pollen grain. x 300. **F.** *Eretmonia* x 1.5. **G.** a single dehisced sporangium of *Arberiella.* x 35. **H**. *Nesowalesia,* a disc showing attached *Arberiella* type sporangia flattened in various planes. x 4. **I.** unwinged monocolpate pollen grain recovered from the nucellar tip of seed of *Buriadia heterophylla.* x 350. **J.** *Paliandrolepis singularis,* microsporangiate organ. x 2. **K., L.** monosaccate pollen grains. K x 100, L x 250. **M.** *Kendostrobus.* x 1.5 (**A, B, E, L,** after Pant *et al.* 1985, **C, G, H**, after Pant 1958, **D, F,** after Surange & Chandra 1975, **I**, after Pant & Nautiyal 1967, **J, K**, after Pant *et al.* 1995).

Name of the seeds	Size in mm.	Exomorphic features and integumentary characters	Integument		Micropylar canal and its length in µm	Commonly pollinating grains size in µm	Nucellar cuticle	Pollen chamber	Megaspore membrane
			Outer cuticle	Inner cuticle					
Platycardia Pant & Nautiyal, 1960 Type species *P. bengalensis* Loc. Raniganj Coalfield	1.9-3.04 x 1.26-2.68	Oval, platyspermic, unwinged with small processes on surface.	Thin, cells straight -walled showing crystals in cells and anticlinal walls.	Thin and delicate, appressed to nucellar cuticle.	Straight, 153	Disaccate, 60 x 45	Tough with sinuous-walled cells.	Excavated, rim of pollen chamber divided into elongated processes.	Present or absent
Stephanostoma (Pant) Pant & Nautiyal, 1960 Type species *S. crystallinum* Loc. Mukuru Coalfield	1-1.5 x 1-1.1	Oval, platyspermic, unwinged but with a prominent micropylar funnel and prominent processes only at margins.	-do-	-do-	Straight, 90	Disaccate, 50 x 30	-do-	-do-	Not seen
Pterygospermum Pant & Nautiyal, 1960 Type species *P. raniganjense* Loc. Raniganj Coalfield	.94-2.5 x .54- 1.8	Oval, platyspermic but with a wing or its remnants in the principal plane.	-do-	-do-	Straight, 147	Disaccate, 44 x 36	-do-	-do-	Present or absent
Maheshwariella Pant & Nautiyal, 1963 Type species *M. bicornuta* Loc. Giridih Coalfield	4-5 x 2-3	Oval, platyspermic with two micropylar horns, a narrow border in principal plane and longitudinal ridge in secondary plane.	Tough up to 5 µm thick, granular in texture, crystals absent.	-do-	-	Monosaccate 130-223 x 90-143 Wing 31.	Tough but cell walls straight.	Excavated pollen chamber with a continuous rim.	Not seen
Walkomiellospermum Pant & Srivastava, 1963 Type species *W. indicum* Loc. Talchir Coalfield	1.7 x 1.5	Oval, platyspermic without surface processes, horns or wing.	Tough, smooth and without crystals.	-do-	Straight, 124	Non saccate, 36 x 25	-do-	-	Present in single seed
Cornuspermum Banerjee, 1969 Type species *C. pennatus* Loc. Jharia Coalfield	3-3.2 x 2-2.2	Oval, platyspermic, with a broad wing and a funnel like structure at micropylar end, surface processes absent.	Thick with slightly wavy cell walls.	"Thin and delicate"	-	Disaccate, 76 x 58	Tough with deeply sinuous cell walls having peg like growths.	As in *Platycardia.*	-
Spermatites Miner *S. indicus* Srivastava, 1954 Loc. Bokaro Coalfield	1105 x 650 µm	"Flat and oval" but details unknown.	"With rectangular cells."	-	-	-	"With wavy cell walls".	-	-

Rotundocarpus Maithy, 1965 Type species *R. striatus* Loc. Giridih Coalfield	6-10 x 3-4	Reportedly radiospermic, unwinged, spindle shaped, surface with vertical striations.	Outer coat thinner.	-	-	-	"Thick with sinuous walled cells, surface of cells with small peg like projection."	-	-
Alatocarpus Lele, 1969 Type species *A. indicus* Loc. Singarauli Coalfield	1.32-2.3 x 2.3- 2.5	Oval, platyspermic but broader than long appearing pear shaped showing micropylar beak and a median ridge of sclerotesta, sarcotesta widest in middle, sinuses present on proximal and distal ends of sclerotesta.	With irregularly arranged polygonal cells.	A sclerotesta showing double layered cuticle, outer layer with polygonal cells and inner layer pulpy but no cells.	-	-	-	-	-
Talchirospermum Srivastava & Chandra, 1982 Type species *T. indicum* Loc. Birsinghpur, Pali, M.P.	2.0-2.5 x 1.2- 1.5	Oval, narrow, platyspermic, without any surface processes or wing.	Integument thin, cells narrow, elongated	-	-	-	Thick, cells linear and narrow.	Quite wide	Present
Karharbariospermum Srivastava & Chandra, 1982 Type species *K. surangei* Loc. Umaria, M.P.	3-5 x 2-4	Oval, flattened, platyspermic, surface smooth without any processes.	Thin with narrow and elongated cells.	Tough, granular and reticulate in appearance with polygonal cells.	Straight, 165	Disaccate, 80 -120 x 40 60 µm	Tough, appressed to inner cuticle	Excavated pollen chamber	Present, circular
Cerviculospermum (Collospermum) Pant *et al.* 1999 Type species *C. ovalis* Loc. Birsinghpur Coalfield	2.5-4 x 1.5-3	Oval, platyspermic without any process, wing, funnel, border or ridges, seeds showing a neck like prolonged straight micropyle.	As in *Platycardia* but without crystals.	Thick with simple pits on anticlinal wall of cells, cuticle showing a wide gap in between inner cuticle of integument and nucellar cuticle.	Straight, 587.	Disaccate, 59 x 49.	Tough, granular with straight-walled cells and a prominent micropylar beak.	As in *Maheshwariella*	Present but showing a tentpole and dark bodies (archegonia) towards micropylar end

Buriadiospermum Pant *et al.* 1984 Type species *B. sewardii* Loc. Giridih Coalfield	3-6 x 2-5	Oval, platyspermic with two micropylar horns, one gradually tapering and the other is bluntly truncated, a narrow marginal border and a shallow median ridge present	Tough, edge of carineae showing hairs and the two surfaces papillate, a few stomata also present.	-do-	Straight, length unknown.	Unwinged, 55-99 x 23-83 µm	-do-	-do-	-
Palispermum Pant *et al.* 1985 Type species *P. ovalis* Loc. Birsinghpur Coalfield	2-3 x 1.5-2	Oval, platyspermic.	As in *Cerviculospermum*	As in *Platycardia* but not easily separable from nucellar membrane.	Straight, 118	Disaccate, 48 x 27	Tough, cells large, straight-walled and polygonal, beak present.	-do-	Present
Bulbospermum Pant *et al.* 1985 Type species *B. surangei* Loc. Birsinghpur Coalfield	2-2.5 x 1-1.75	Oval, platyspermic showing a bulbous swelling towards micropyle.	-	As in *Platycardia.*	Straight, 142	Disaccate, 49 x 31	As in *Retortistoma,*	Prominently bulbous with continuous rim.	Present
Birsinghpuria Pant *et al.* 1985 Type species *B. indica* Loc. Birsinghpur Coalfield	2.2-3.3 x 1.6-2.5	Oval, platyspermic.	Delicate, granular but without crystals.	Tough with smooth large papillate cells. Papillae about 6 µm thick.	Straight, 235	Monosaccate, 130 x 113	-do-	As in *Maheshwariella*	Present
Palaeocarpus Pant *et al.* 1985 Type species *P. birsinghpurensis* Loc. Birsinghpur Coalfield	6-10 x 4-10	Oval to cordate, platyspermic, integument differentiated into sarcotesta and sclerotesta. Sarcotesta wider in middle, integument massive enclosing central cordate nucellar part.	Tough about 2 µm thick without crystalline imprints.	As in *Platycardia.*	-	Disaccate, 55 x 40	Tough, cells papillate and with very thick walls (about 10 µm).	-do-	As in *Cerviculospermum*

Shivacarpus Pant *et al.* 1985 Type species *S. johillensis* Loc. Birsinghpur and Manendragarh coalfields	10-14 x 9-13	Seed oval to cordate, platyspermic, longer than broad, sarcotesta up to 5 mm wide, widest towards micropylar end, narrower at base, central part cordate, seed stalked.	Thin granular and Stomatiferous	As in *Platycardia.*	Straight, 800	Monosaccate, 113 x 89.	Tough, cells papillate and with very thick walls (about 10 µm).	As in *Maheshwariella*	Present
Otofeistia Pant *et al.* 1985 Type species *O. milleri* Loc. Giridih Coalfield	18-48 x 15-35	Oval, platyspermic, stalked, sarcotesta up to 6 mm wide, widest in middle part, up to 12 mm, apical and basal sinuses and a median ridge.	Thin, smooth and non-stomatiferous.	-do-	-	-	Tough with thick-walled non papillate cells.	-do-	Present
Retortistoma Pant *et al.* 1985 Type species *R. crystallina.* Loc. Birsinghpur Coalfield	3-4 x 1.5-3.5	Oval, platyspermic, showing a recurved micropylar beak, surface processes absent.	As in *Platycardia.*	Granular showing hexagonal cells and appressed to nucellar membrane.	Curved, 455	Disaccate, 121 x 92	As above but without a beak.	-do-	Present
Seeds of *Birsinghia florinii* Pant *et al.* 1995 Loc. Birsinghpur Coalfield .	2.5-3.5 x 1.5-2.3	Broadly oval, platyspermic, with two to three backwardly directed gradually tapering micropylar horns. Horns diverging at wide angles, sometimes forked and form two short hairy lobes.	Tough with longitudinally elongated cells, sometimes stomata present.	As in *Platycardia*	Straight, short	Monosaccate, 50-110 µm x 20-140 µm.	Smooth but tough and form prominent nucellar beak.	Excavated pollen chamber with continuous rim.	

Fig. 8—Comparative generic characters of different Lower Gondwana seeds whose structural details are known.

3. Seeds belonging to plants of a possible primitive coniferous stock, e.g. *Buriadia* and *Walkomiella.* Such seeds are pollinated by asaccate, monocolpate pollen grains.

Some seeds may belong to a fourth group. These may be represented by seeds which Walkom (1935) has referred to *Trigonocarpus* (?) although no Medullosan stem and other remains referable to this alliance have been reported from Gondwanaland. Accordingly the existence of the Medullosales is extremely doubtful.

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