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Fossilized pollination droplet in a new seed genus from the Middle Triassic of Nidpur, India

NUPUR BHOWMIK and SHABNAM PARVEEN

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The present article reports a fossilized pollination droplet at the micropylar orifice in a compressed seed *Gopadispermum papillatus* gen. et sp. nov. from the Middle Triassic beds of Nidpur, Madhya Pradesh, India. The shapeless droplet forming a convexity above the micropylar orifice is comprised of a resinous crystalline substance. Entrapped within the droplet are a few saccate pollen grains. The seeds are small, oblong to widely elliptical in shape, about 3 mm long and generally 2 mm broad. The micropylar end shows a short straight beak-like micropyle often extended beyond a persistently adhering wrinkled tissue lying outside the seed coat. The seed is composed of four membranes excluding the adherent tissue. They are the outer and inner cuticles of integument, the nucellar cuticle distally modified to form a dark collar-like pollen chamber and the innermost megaspore membrane. Cuticles of the tissue adhering to seed coat are different from seed coat cuticles. The pollen grains inside the pollen chamber are frequently clumped together forming a pollen mass. Individual pollen grains appear spheroidal to ellipsoidal in shape and are saccate. This is the first report of the preservation of a pollination droplet in a compressed seed specimen from the Nidpur Triassic beds. Preservation of the droplet can be attributed to its supposed resinous constitution and the entrapped organic contents (pollen grains). Occurrence of clumped pollen grains inside the pollen chamber also indicated possibility of fluid feeding, pollinivory and insect pollination in the seeds.

Key words: Plantae, Ginkgoopsida, *Rugaspermum*, pollen, seed, pollination, micropyle, compression, Triassic, India.

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Introduction

The Nidpur Triassic beds discovered by Satsangi (1964) have yielded a rich haul of fossiliferous plant material assignable to different groups like algae, bryophytes, pteridophytes and gymnosperms. The dominant vegetation of the region is comprised of gymnosperms assignable to diverse groups of Pteridospermophyta (Srivastava 1969, 1974, 1984; Bose and Srivastava 1970, 1971, 1972, 1973a, b; Pant and Basu 1979; Bhowmik and Parveen 2008, 2012b). Mesofossil remains of diverse reproductive structures like microsporangia, synangia and megaspores have also been described from Nidpur Triassic flora (Pant and Basu 1973, 1977, 1979; Srivastava 1974; Bhowmik and Das 2011, 2012; Bhowmik and Parveen 2012a). The mesofossil assemblage also shows an abundance of dispersed seeds. Quite a number of these seeds have already been described by Pant and Basu (1977), Manik (1987), Srivastava and Manik (1990, 1993, 1996), Bhowmik and Parveen (2012a). The new seed differs from earlier described ones in displaying features indicating possibility of their occurrence inside an envelope or a cupule-like structure at the time of dispersal. Another significant feature is the occurrence of a fossilized pollination droplet above the seed micropyle in a seed specimen of the morphotaxon suggesting possibility of insect-plant interaction. The presence of clumped pollen grains inside the pollen chamber of the seeds is an additional feature supporting insect-plant relationship. Quite contrary to the general belief of wind pollination in Mesozoic pteridosperm, the heavy pollen clumps in *Gopadispermum* also hinted at the pollinating agent being an insect and not wind (Retallack and Dilcher 1988; Anderson and Anderson 2003; Labandeira et al. 2007; Labandeira 2010).

As all these features are hitherto unreported in seeds of the Nidpur beds we decided to undertake a detailed study of *Gopadispermum*.

Institutional abbreviations.—DDPMAU, Divya Darshan Pant Collection Museum, Botany Department, University of Allahabad, Allahabad, India.

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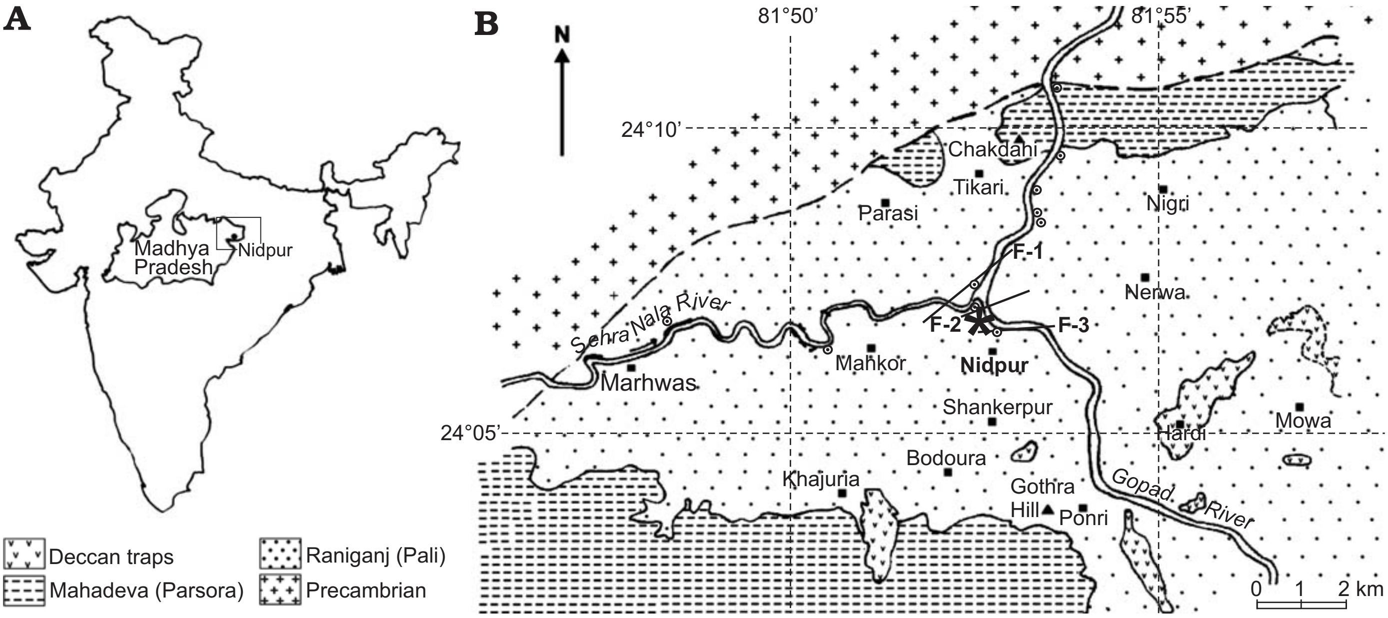


Fig. 1. **A**. Map showing the location of Nidpur locality in Madhya Pradesh, India. **B**. Geological map of north-west Singrauli Coalfield showing Marhwas area, where the Nidpur beds are situated. Circles with dots, yielding samples taken along the traverses; asterisk, position of samples NID-4, 5, 8, 10. F-1–3, faults. Modified after Raja Rao (1983).

Historical background

The evidence of insect-plant inter-relationship in the Early Triassic to Early Jurassic is mostly available from seed plant reproductive structures rather than insect mouthparts. According to Labandeira (2010), several gymnospermous fructifications were probable sources of nutrition for diverse orders of Mesozoic insects feeding on internal and external reproductive tissues. In the case of ovules, fluid food provided was in the form of micropylar secretions of pollen drops, pre pollen, and pollen. Krassilov (1977) has also reported small bees visiting the ovules and producing honey from the drops during the Jurassic. As a consequence of insect feeding, the host plant ovule received the benefit of pollination.

Besides providing nutrition for insects, surface fluids also aided pollinivory as is reported in insects whose lineages extended to the Middle Triassic (Rasnitsyn 1964; Grimaldi and Engel 2005). Apart from the droplet, possibility of strong odors emitted by reproductive structures could have also attracted pollinivorous insects to the ovule. An earlier study by Krassilov et al. (2007), on the pollen load in the gut content of *Ceroxyela dolichocera* Rasnitsyn, 1964, has shown clumps of pollen grains in fore-gut and anus regions, indicating insect dispersal.

Nevertheless, pollination droplet mechanism in ovules do not indicate plant insect relationship always. In the permineralized ovule *Callospermarion pusilla* Eggert and Delevoryas, 1960, from the Middle Pennsylvanian of Illinois, Rothwell (1977) has reported production of a resinous pollination droplet extending from the micropylar orifice probably functioning as an aid in trapping wind dispersed pollen. The numerous pollen grains of *Vesicaspora*-type contained in its pollen chamber are reportedly unclumped.

Out of the several seed genera described so far from the Nidpur Triassic beds, pollen grains within micropylar canals and pollen chambers have been reported only in two seed taxa viz., *Rugaspermum* Pant and Basu, 1977 and *Sahnispermum* Srivastava and Manik, 1993. In both the instances, the pollen grains are non saccate. In the former, they are of *Rugapites*-type (Pant and Basu 1977) while in the latter, they are reportedly of *Weylandites* complex type (Bharadwaj and Srivastava 1969). Interestingly, both the pollen types reportedly exhibited distinctive surface features associated with entomophily (Labandeira 2010; Krassilov et al. 2007) and yet were not reported to occur in clumps. Besides the above, Srivastava and Manik (1996) have reported winged pollen grains occasionally occurring within a species of the seed of *Savitrispermum*, *S. umkomasii*, but the photomicrographs and sketches of *S. umkomasii* are not convincing, as they do not show the winged pollen grains clearly.

The significance of the present article is the report of a fossilized pollination droplet, in a new genus of compressed seeds indicating possibility of plant-insect relationship in the Gondwana Mesozoic.

Material and methods

The compressed seeds of *Gopadispermum* comprise a small fraction of the enormous litter of plant fragments occurring in the Triassic shales of the Nidpur beds located along the bank of the Gopad River near Nidpur village, Marhwas area, Sidhi District, Madhya Pradesh, India. The specimens are well preserved and carbonized with their original three-dimensional form slightly flattened. They were extracted out of the rock matrix after dissolving the shales in 40% hydrofluoric acid. The carbonized plant residue accumulated at the bottom of the container was repeatedly washed in distilled water before being subjected to examination. The seeds were picked up from the deacidified residue under a stereo-binocular (OLYMPUS SZ61). The selected seeds were air dried and mounted on cavity slides. External features of the new seed including surface details were observed under unilateral incident light. Later, some of the extracted seeds were subjected to further maceration in Schulze's fluid, so that their anatomical features could be revealed. Macerated specimens were dissected with a fine needle to tease out the cuticles of the seed coat integument, thereby also revealing the seed micropyle and pollen chamber. The separated integumentary cuticles along with the remaining part of the seed were stained in safranin glycerine jelly and mounted on a glass slide. The mounted slides were examined under a Trinocular microscope (OLYMPUS CH20i). Photographs of the seeds were taken with a Wild Leitz microscope, Leica DM 2500 microscope and SONY DSC-W70 Digital camera.

Geological setting

The seed morphotaxon described in the paper, was extracted from shales of the Middle Triassic (Anisian–Ladinian) Nidpur beds occurring in the Gopad river section in the western part of Singrauli Coalfield, Sidhi District, Madhya Pradesh, India (Ghosh and Banerji 2007; Kovach and Batten 1989). The sediments are exposed downstream, on the bank of the Gopad river about 2 km NE of Nidpur village (E-W 24°7′, N-S 81°53′) and are found between two faults, F-2 and F-3 (Fig. 1). The area south of the confluence of Sehra Nala with Gopad river has been considered to be the "Nidpur beds" and the area as "Marhwas area" (Tiwari and Ram-Awatar 1989). The country around Marhwas and the Nidpur village is flat alluvial plain with exposed Triassic sediments in river cuttings. The Nidpur beds along the Gopad river cuttings contain structurally preserved carbonaceous fossils on grey coloured, medium grained micaceous shale (Majumdar 1981). The sediments above and below the Nidpur beds are unexposed. The plant remains of the bed appear to be allochthonous.

Systematic paleontology

Pinophyta Cronquist, Takhtajan, and Zimmermann, 1966

Ginkgoopsida Meyen, 1984

Genus *Gopadispermum* nov.

Etymology: In reference to the river Gopad in Sidhi District, Madhya Pradesh, India. The Middle Triassic beds of Nidpur are situated along the banks of the river.

Type species: *Gopadispermum papillatus* sp. nov., see below; monotypic.

Diagnosis.—Seeds small, platyspermic, orthotropous, rounded to broadly oblong, micropylar end rounded, with a short straight mucronate micropylar tube. Chalazal end rounded, with a shallowly concave, narrow chalazal hole at centre. Surface of seed generally smooth. Seed outline often irregular due to a persistently attached incompletely preserved carbonaceous layer outside seed coat. Micropylar canal often extended beyond adhering tissue. Outer cuticle of integument thin, delicate, papillate. Inner cuticle of integument thin, delicate, granular, extended apically to form a short micropylar tube. Nucellar cuticle tough, appressed to inner cuticle upto chalazal hole, cell walls conspicuously sinuous. Megaspore membrane large, rounded, tough. Pollen chamber dark, collar-like at base, generally containing clumps of compactly adherent saccate pollen grains. External carbonaceous layer yielding two non-stomatiferous cuticles on maceration. Pollination by droplet mechanism.

Remarks.—The genus *Gopadispermum* is instituted to include small, dispersed seeds exhibiting the following features: pollination by droplet mechanism, droplet substance showing a few entrapped saccate pollen grains, a collar-like pollen chamber below the short micropyle containing saccate pollen grains frequently occurring in clumps. In addition to the above features, seeds of *Gopadispermum* generally lack surface wrinkles and show a delicate outer cuticle of integument, suggesting the possibility of seeds having occurred sheltered inside a cupular or protective structure rather than having been borne exposed. No seed specimen was however, found completely enclosed within a cupulate structure, although several of them exhibited an irregular seed outline, due to the presence of the closely adhering carbonaceous tissue external to the seed coat. The short straight micropyle often extended beyond the margin of the cupule-like tissue as is reported in seeds of Corystosperms (Thomas 1933). The characters of *Gopadispermum* are unique and interesting and to the best of our knowledge, no earlier described seed morphotaxon from the Nidpur Triassic has reportedly exhibited similar features. Therefore, we consider it reasonable to institute a new genus for this fossil seed.

Stratigraphic and geographic range.—Middle Triassic of Nidpur, Madhya Pradesh, India.

Gopadispermum papillatus sp. nov.

Figs. 2B, 3A, 4F.

Etymology: In reference to the papillate feature in outer cuticle of seed integument.

Type material: Holotype: DDPMAU 53,313 has an external coat (Figs. 2, 4) and clumped pollen grains in pollen chamber (Fig. 3).

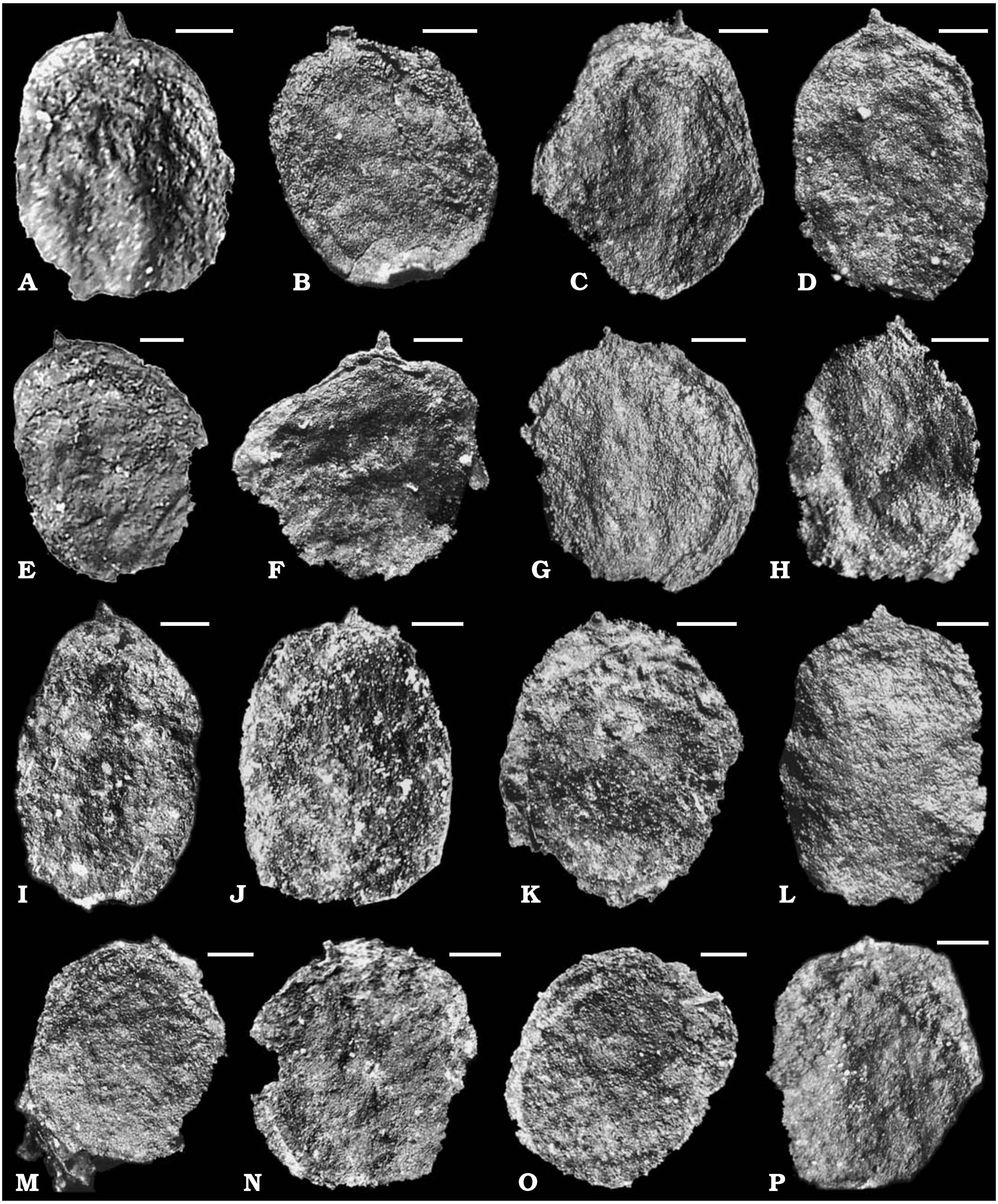
Type locality: Nidpur village, Marhwas area, Sidhi District, Madhya Pradesh, India.

Type horizon: Middle Triassic (Anisian–Ladinian).

Diagnosis.—Seeds platyspermic, rounded to orbicular when compressed along principle plane, averaging 2.5 × 2 mm, broadly oblong in secondary plane, averaging 3 × 2 mm. Both micropylar and chalazal ends broadly rounded. Apex of micropylar end shortly mucronate forming the short, straight micropylar tube. Chalazal end showing a narrow, median, shallowly concave chalazal scar, about 600 μm wide. Surface of seeds generally smooth to finely papillate, sometimes rough, showing irregular folds. Seed margin smooth to finely papillate. Seeds often adhering to an external folded to wrinkled carbonaceous tissue enclosing the seed. Seed micropyle generally extending beyond margin of adhering tissue. Seeds yielding four membranes on maceration. Outer and inner cuticles of integument, nucellar cuticle and megaspore membrane. Outer cuticle of integument delicate, thin, about 2 μm thick, cells polygonal, often medianly papillate. Inner cuticle of integument thinner, about 1 μm thick, granular, extended apically into a short, narrow micropylar tube. Cells narrow rectangularly elongated. Nucellar cuticle thick, tough, about 7 μm thick, cells rectangularly elongated to polygonal, averaging 35 × 15 μm. Cell walls about 5 μm thick, deeply sinuous. Nucellar tissue distally modified into a pollen chamber having a dark coloured collar-like base. Cell walls at distal end of pollen chamber vertically extended, forming acutely pointed processes protruding into cavity of micropylar canal. Micropylar canal and pollen chamber containing saccate pollen grains averaging 55–75 × 25–55 μm, circular, oval or of other shapes, corpus and sacci faintly distinct, corpus circular to subcircular ranging between 25–35 μm in diameter, thick and dark brown coloured, ornamentation indistinct. Saccus generally folded, dark coloured, exine coarsely intrareticulately ornamented. Pollen grains in pollen chamber generally clumped together, rarely occurring isolated. Megaspore membrane large, tough, occupying more than 2/3rd of total seed area, measuring 1.5 × 1.8 mm. Cells large, polygonal. Seeds pollinated by droplet mechanism or its modification. Carbonaceous layer external to seed coat yielding two non-stomatiferous cuticles on maceration.

Description.—The description of *Gopadispermum papillatus* is based on the study of 30 dispersed seed specimens flattened in various planes (Fig. 2A–P). The seeds were isolated after bulk maceration of carbonaceous shales of the Nidpur beds in hydrofluoric acid. The seeds are rounded to oblong, depending on the plane of preservation and broadly flattened. In most specimens, a small beak-like micropyle is seen prominently projecting out of the micropylar end of the seed body (Fig. 2A–N). The surface generally appears smooth to finely papillate, lacking folds or wrinkles but occasionally, irregular folds are visible at the apical end of some (Fig. 2A, D, E, K). The margin in most specimens is smooth but in a few seeds it may appear faintly papillate to dentate (Fig. 2B, H, L, N). The chalazal end is also rounded showing a narrow, transversely elliptical, shallowly concave, chalazal hole at the centre (Fig. 2B–D, I, N). Frequently, the seed outline appears irregular due to the persistence of a closely adherent tissue almost encompassing the seed like a cupule (Fig. 2A–D, F–H, K–P). This external tissue measuring approximately 2.7 × 2.4 mm generally shows folds or feeble wrinkles on the surface suggesting a fleshy nature. Interestingly, most seeds on maceration yielded two additional cuticles besides the cuticles of integument, nucellus and the megaspore membrane. Both the cuticles are structurally distinct from the cuticles of the seed coat. The outer cuticle appeared to be thin and delicate, about 2 μm thick showing faint polygonal cell outlines while the inner cuticle appeared comparatively thick (5 μm), granular and displayed distinct outlines of elongated rectangular cells. Besides carbonized seeds, a number of naturally macerated seeds were also recovered in the macerated residue. In such specimens, cuticles of the adhering tissue and the delicate outer cuticle of seed integument is generally missing while the rest of the seed membranes are found to remain intact. Such naturally macerated seeds were probably dispersed from their cupules long before fossilization and their delicate outer cuticles were not resistant enough to be preserved. Maceration of carbonized seeds in Schulze's fluid yielded four membranes including the integumentary layers, nucellus and megaspore membrane. The outer cuticle of integument is thin and delicate showing vague outlines of papillate to non-papillate polygonal cells arranged in longitudinal rows. The cells averaging 16 × 30 μm have thin, straight to undulated walls (Fig. 3A$_4$). The inner cuticle of integument is also thin and delicate, extending apically to form a short, narrow micropylar canal, about 250 μm long. The cells are narrow and rectangularly elongated, averaging 30 × 5 μm. The cell walls are thin and straight (Figs. 3A$_2$, A$_5$, C$_1$, D, 5A$_2$, B$_2$). The inner integument is free above but fused with the nucellar membrane below (Figs. 4A$_1$, A$_2$, B, 5A$_2$, B, C). The nucellar cuticle is the most resistant and perceptible layer of the seed. All the macerated seeds yielded a very tough and thick nucellar cuticle which is free above but fused to megaspore membrane below (Figs. 3A$_1$, 4A$_1$, B, E$_1$, 5A$_1$, B$_1$). The cells are rectangularly elongated to polygonal with deeply sinuous periclinal walls and vague to obscure anticlinal walls (Figs. 3A$_6$, B, C$_1$, D, 5A$_2$, B$_2$, C). The amplitude of sinuosity ranged between 8 to 15 μm and the wave length varied from 20–38 μm. In many seeds, the periclinal wall of distally situated nucellar cells is extended forward forming pointed processes that seem to protrude into the cavity of the micropyle (Figs. 3B, D, 5B$_2$, C). The nucellus is distally modified forming a pollen chamber having a prominent dark coloured, collar-like base (Figs. 3A$_1$, A$_2$, C$_1$, D, 4A$_1$, A$_2$, D$_1$, E, 5A, B). The cavity of the pollen chamber contains saccate pollen grains clumped together into a dark colored pollen mass of irregular shape, measuring about 400 × 220 μm (Figs. 3A$_1$–A$_3$, B–D, 4A, D$_1$, E; 5). Incidentally, the pollen grains of a pollen clump are so tightly adherent that it is not possible to separate them for examination of morphological features. Besides the clumped pollen grains, a few pollen

Fig. 2. Compressed dry seed specimens of the ginkgoopsid *Gopadispermum papillatus* gen. et sp. nov. from the Triassic of Nidpur, India. **A**. A seed showing a short, micropylar tube. DDPMAU 53,361. **B**. Holotype, showing the externally adherent layer near base of the short micropylar →



tube and a shallow concave chalazal hole at the opposite end. DDPMAU 53,313. **C**, **F**–**H**, **J**–**N.** Specimens showing a short micropylar tube extending beyond the margin of cupule-like externally adherent layer. DDPMAU 53,362; 53,365; 53,366; 53,374; 53,369; 53,372; 53,368; 53,377; 53,380 respectively. **D**, **E**, **I**, **O**, **P**. Specimens compressed in various planes showing feebly wrinkled or folded, faintly papillate surface. DDPMAU 53,363; 53,364; 53,367; 53,381; 53,382 respectively. Scale bars 500 μm.

grains may occasionally also occur isolated (Figs. 3A_2, A_3, B, D, 5B).

In addition to the clumped pollen grains in the pollen chamber, a specimen of the new seed also showed a fossilized pollination droplet extending from its micropylar orifice. Initially, this unmacerated specimen exhibited a small sized carbonized fragment clinging to the micropylar end of the seed. Prior to subjecting the seed to further maceration in Schulze's solution several attempts were made to disengage the foreign fragment from the seed body and when all attempts failed, the seed was macerated together with the attached fragment. Maceration and later mounting of the seed on a slide revealed a convex mass of non-cellular, inorganic, crystalline resinous substance adhering to the tip of the micropyle. Entrapped within the non-cellular residue, could be seen obscure outlines of a few scattered, saccate pollen grains. Surprisingly, the morphological nature of the foreign fragment sticking to the micropylar end of the seed was revealed to be a carbonized fossilized pollination droplet (Figs. 4E, 5A). The pollen grains trapped within the non-cellular mass of the droplet are not clearly evident but appeared to be saccate and quite similar to the pollen grains found clumped as well as isolated inside the pollen chamber and micropyle of the same seed and pollen chambers of other seeds (Figs. 3A_2, A_3, D, 4A_2, 5A, B). They are saccate, appear to be superficially similar to bisaccate grains due to the lateral expansion of saccus. The central body appears circular to subcircular, about 25–35 μm in diameter. The saccus exine is dark coloured, averagely thick and coarsely intrareticulate consisting of moderately broad muri enclosing irregular meshes (Figs. 3A_3, C_2, D, 4E_2, 5).

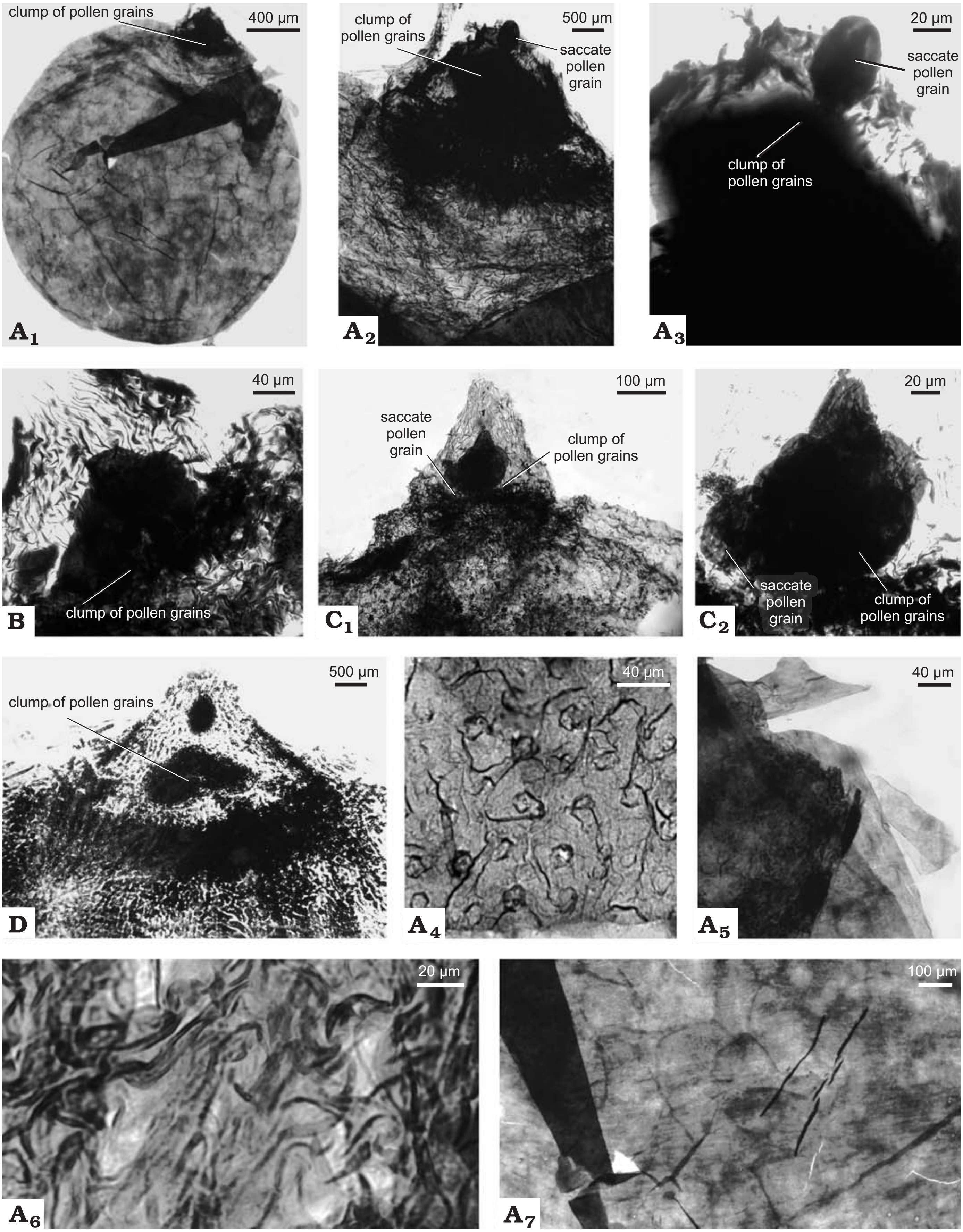
The innermost layer of the seed consists of the megaspore membrane which is dark brown, spherical to oblong in outline occupying a large portion of the seed area (Figs. 3A_1, 4A_1, E_1, 5A_1, B_1). The cells are large, averaging 150 × 100 μm, showing polygonal outlines and are often filled with dark cell contents. The cell walls are uniformly thickened and straight (Fig. 3A_7). In some seeds, one or more rounded dark-coloured spots are visible near the middle region of the megaspore membrane. Such spots presumably represent embedded archegonia (Fig. 4D).

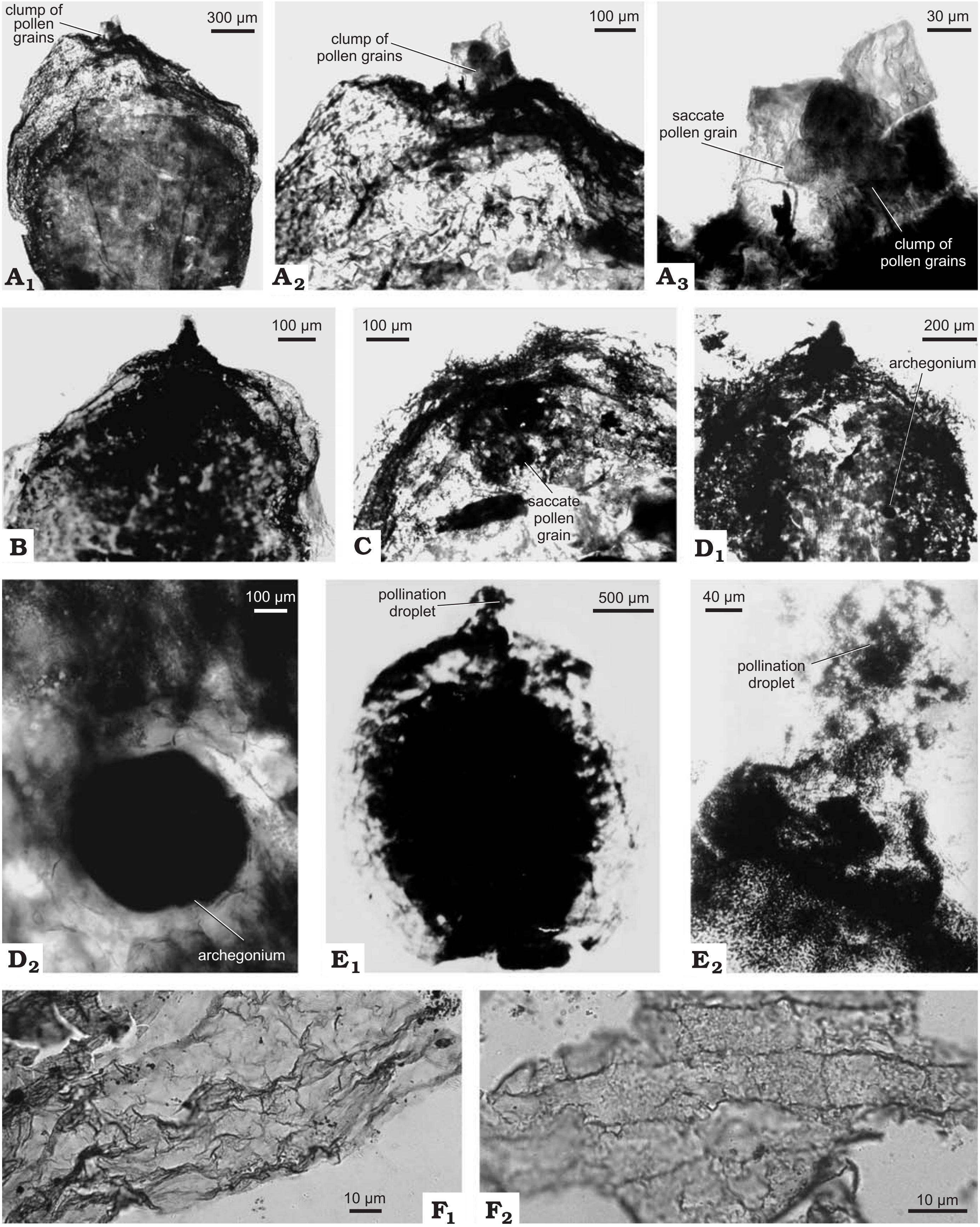
Stratigraphic and geographic range.—Middle Triassic (Anisian–Ladinian) of Nidpur, Madhya Pradesh, India.

Discussion

Dispersed seed genera from the Triassic Nidpur beds have been reported previously by Pant and Basu 1977; Manik 1987; Srivastava and Manik 1990, 1993, 1996; Bhowmik and Parveen 2012a). See Supplementary Online Material at http://app.pan.pl/SOM/app59-Bhowmik_Parveen_SOM.pdf for comparative structural features of all the seeds described so far from the Nidpur beds. The new seed significantly differs from those described earlier in displaying the preservation of a pollination droplet above the micropyle, frequent occurrence of clumped saccate pollen grains inside the pollen chamber and single seeds showing partial to almost complete enclosure inside a cupule-like layer. The first two features are somehow linked to insect fluid feeding, entomophily and palynophagy in the terminology of Labandeira (2010). Evidence of insect fluid feeding and entomophily in the Early Triassic to Early Jurassic comes mostly from seed plant reproductive structures rather than insect mouthparts. But, during the Triassic and into the Jurassic, evidence of palynophagy seemed to come from early mandibulate family of insects that were palynophagus "colonizing" cycadalean, bennettitalean, pentoxylalean and undoubtedly other plant hosts (Labandeira 2010). Fluid food seemed to have been provided in the form of micropylar secretions of pollen drops, pre pollen and pollen in the case of ovules. The outcome of insect feeding often resulted in the host plant ovule receiving the benefit of pollination. In the opinion of Krassilov et al. (2007), characters associated with entomophily seemed to have been consistent for modern as well as fossil pollen and the features of pollen preferred by insects included size and shape of the pollinating grains and surface ornamentation like taeniae or rimulae. Their speculation was based on observations made in the case of some Permian insects where taeniate pollen of gnetophytes was reported in the insect gut. Another possible reason for Palaeozoic and Mesozoic insects preferring pollen with distinctive morphologies and surface ornamentation could be the ability of insects to distinguish only such pollen as edible pollen types (Krassilov et al. 2007). Besides taeniae, rimulae etc. plants foraged by insects are generally believed to have pollen grains that have surface stickiness (Faegri and Van Der Pijl 1966). Moreover, insect dispersed pollen is found in

Fig. 3. Photographs of macerated seed specimens showing internal details and different cuticular membranes in the ginkgoopsid *Gopadispermum papillatus* gen. et sp. nov. from Triassic of Nidpur, India. **A**. DDPMAU 53,313; A_1, holotype showing the pollen chamber with clumped pollen grains at micropylar end and a megaspore membrane below; A_2, the micropylar end magnified to show the dark coloured collar-like base of pollen chamber, clumped pollen grains and an isolated saccate grain at the apex and the micropylar canal above pollen chamber, below the collar of pollen chamber is seen the free nucellar membrane; A_3, a more magnified view of clumped pollen grains and an isolated saccate pollen grain; A_4, a papillate outer cuticle of seed integument; A_5, cuticles of the seed integument, the darkest cuticle is that of the megaspore membrane; outside it, comparatively less dark, the nucellar membrane and external to it are the inner and outer cuticles respectively; A_6, nucellar membrane highly magnified to show the thick sinuous cell walls; A_7, cuticle of megaspore membrane showing large polygonal cell outlines. **B.** DDPMAU 53,362; apical end showing pointed processes of the nucellar membrane at distal end, a clump of pollen grains and the collar-like base of pollen chamber. **C**. DDPMAU 53,361; C_1, micropylar end showing a short micropyle and the pollen chamber containing a clump of pollen grains, cuticles of the seed integument and the sinuous walled nucellar membrane are also visible along the base of pollen chamber; C_2, part of the pollen chamber highly magnified to show the clumped pollen grains, two peripheral grains of the pollen clump show faint details of the monosaccate pollen. **D.** DDPMAU 53,376; apical end showing faint cell outlines of the micropyle outside the pollen chamber containing a clump of grains together with an isolated saccate grain, the collar-like base of pollen chamber and cells of nucellar membrane below are clearly visible. →


clump of pollen grains
400 µm
A1
clump of pollen grains
500 µm
saccate pollen grain
A2
20 µm
saccate pollen grain
clump of pollen grains
A3
40 µm
clump of pollen grains
B
100 µm
saccate pollen grain
clump of pollen grains
C1
20 µm
saccate pollen grain
clump of pollen grains
C2
500 µm
clump of pollen grains
D
40 µm
A4
40 µm
A5
20 µm
A6
100 µm
A7


clump of pollen grains
300 µm
A1
100 µm
clump of pollen grains
A2
30 µm
saccate pollen grain
clump of pollen grains
A3
100 µm
B
100 µm
saccate pollen grain
C
200 µm
archegonium
D1
100 µm
archegonium
D2
pollination droplet
500 µm
E1
40 µm
pollination droplet
E2
10 µm
F1
F2
10 µm

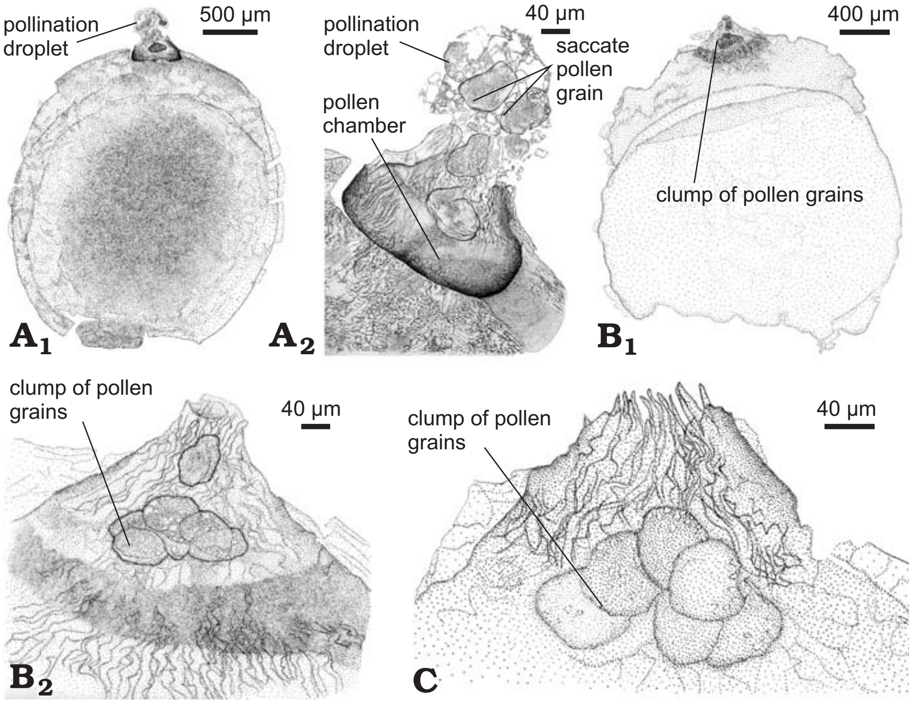


Fig. 5. Photo drawings of macerated seeds of ginkgoopsid *Gopadispermum papillatus* gen. et sp. nov., from Triassic of Nidpur, India. **A**. DDPMAU 53,375; A$_1$, seed showing the fossilized pollination droplet at micropylar orifice, various integumentary membranes and the dark, collar-like pollen chamber containing clumped pollen grains; A$_2$, highly magnified view of micropylar end showing a clump of pollen grains and an isolated one in the dark coloured pollen chamber, a few saccate grains are entrapped in the pollination droplet. **B**. DDPMAU 53,376; B$_1$, seed showing the dark coloured pollen chamber and a cluster of tightly adherent pollen grains below and an isolated grain in the micropylar end, the inner, nucellar and megaspore membranes are also clearly visible; B$_2$, a more magnified view of micropylar end showing a clump of pollen grains below and an isolated grain, the dark, collar-like base of pollen chamber and sinuous walls of the nucellar cells is also clearly visible. **C**. DDPMAU 53,362, a highly magnified view of the micropylar end showing a pollen grain clump and pointed processes of the nucellar cells, cells of inner integument outside the nucellus are also clearly visible.

pollen clumps due to repeated visits of the insect to the forage plant, as shown by an earlier study of the pollen load in the gut compression of a xyelid genus *Ceroxyela dolichocera* (Hymenoptera), where Krassilov et al. (2007) have reported clumps of pollen grains in fore-gut and anus regions. Further, insect vectored pollen is usually large, more the 25 µm in diameter, has a significant shape like spheroidal to ellipsoidal and frequently lacks bladders or sacci (Labandeira 2010).

Coincidentally, characters indicative of insect fluid feeding and entomophily (distinctive surface ornamentation of pollen grains and grains occurring clustered in the pollen chamber of seeds) are also observed in the seed *Rugaspermum* described from the Nidpur beds by Pant and Basu (1977). This taxon is reportedly abundantly represented in the Nidpur beds and has four described species: *R. insigne*, *R. media*, *R. obscura*, and *R. minuta* (see Pant and Basu 1977; Bhowmik and Parveen 2012a). All the species of the genus are easily identifiable on account of their prominent surface wrinkles. The pollinating grains in *Rugaspermum* seeds were assigned to genus *Rugapites* Pant and Basu, 1977 of the sporae dispersae. The grains displayed distinctive surface features like taeniae and rimulae and could have been classed among the "charismatic" pollen grains of Krassilov et al. (2007). The shape of such dispersed, striate, unwinged grains is reportedly spheroidal to ellipsoidal and the ektexine is characteristically ridged. *Rugapites* grains apparently resemble the palynomorphs of *Classopolis* Pflug, 1953, *Vittatina* Luber, 1938, and *Weylandites* Bharadwaj and Srivastava, 1969, occurring in strata ranging in age from Permian to Tertiary (Pant and Basu 1977). The two former genera *Classopolis* and *Vittatina* are considered prominent Mesozoic pollen grains on account of their distinctive surface microstructures and as pollen load of insects also indicated that pollinivorous insects were attracted by pollen grains with ornamental surface patterns (Krassilov et al. 2007). Pollen grains of *Weylandites* type have also been reported in the palynoflora of the Nidpur Triassic beds (Bharadwaj and Srivastava 1969) and in the seed of *Sahnispermum* (Srivastava and Manik 1993).

Besides having a rimulate-type of surface ornamentation, the *Rugapites* grains were also held in loose radial to tangential clusters within the pollen chamber of the *Rugaspermum* seed (see Pant and Basu 1977: text-fig. 1I, 2C, G; pl. 1: 5, 8). On account of these insect dispersal features *Rugapites* grains should also have been considered as "charismatic" pollen grains. Insect dispersed pollination in *Rugaspermum* is also indicated by the structure of the synangiate pollen

← Fig. 4. Photographs of macerated seeds of ginkgoopsid *Gopadispermum papillatus* gen. et sp. nov. from Triassic of Nidpur, India. **A**. DDPMAU 53,383; A$_1$, a macerated seed showing a short micropyle containing loosely clumped pollen grains and cuticles of the seed coat external to the nucellar and megaspore membranes; A$_2$, magnified view of the micropylar end; A$_3$, faint details of clumped pollen grains. **B**. DDPMAU 53,364; specimen showing the short micropyle containing pollen grains, a dark coloured pollen chamber and different membranes of the seed. **C.** DDPMAU 53,377; specimen showing the pollen chamber and various membranes, some saccate grains are found sticking to the membranes. **D.** DDPMAU 53,365; D$_1$, specimen showing a short micropyle containing pollen grains, a dark pollen chamber base and an archegonium at the centre of megaspore membrane; D$_2$, A highly magnified view of the archegonium **E**. DDPMAU 53,375; E$_1$, specimen showing a pollination droplet above the micropyle, it also shows the dark coloured collar-like base of pollen chamber and different membranes of the seed; E$_2$, highly magnified view of the micropylar end, showing the crystallized droplet above micropyle, a pollen chamber containing a pollen grain clump and the characteristic dark, collar-like base of pollen chamber. **F.** DDPMAU 53,313; outer (F$_1$) and inner (F$_2$) non-stomatiferous cuticles of the externally adherent layer of the holotype seed.

organ *Rugatheca* Pant and Basu, 1977 that contained in situ *Rugapites* pollen grains. The reportedly hairy outer cuticle of the synangial wall presumably consisted of glandular hairs that offered nutritional reward for pollinating insects. A similar form of nutritional reward for insects was earlier reported by Retallack and Dilcher (1988) in the microsynangiate structure of the Palaeozoic genus *Pachytesta illinoensis*.

If hairy cuticles of pollen organs are considered to be characters indicative of entomophilous pollination, then, reference can be given of the not too well known male fructification *Nidpuria problematica* reported by Pant and Basu (1979), from the same Nidpur Triassic beds. The fructification reportedly exhibited a profusely hairy axis and pollen sac cuticles, probably attractive to insects. But the pollen grains inside *Nidpuria* pollen sacs are bisaccate and structurally very different from the pollen grains within pollen chamber and in the pollination droplet of the new seed. They are also of two sizes and are associated with tri-and tetra saccate grains. Therefore, it seems unlikely that such grains had pollinated seeds of *Gopadispermum*.

Surprisingly, in comparison to *Rugapites* grains, those pollinating *Gopadispermum* seeds are found to be quite uncharismatic and featureless. They are small, saccate and frequently clumped into a pollen mass. If found dispersed, such grains would presumably be included in the genus *Densipollenites* Bharadwaj, 1962, of the dispersed miospores. Bharadwaj and Srivastava (1969) had described a number of species of *Densipollenites*, from the Triassic beds of Nidpur and the species closest to the clumped pollen grains in *Gopadispermum* is *D. densu*. The pollen grains of *D. densu* are circular, oval or of other shapes because of folds. The central body is circular to sub-circular, thick and dense brown, surrounded by an equatorial saccus ornamented by coarse intra-reticulation. The size of the dispersed grains is however reportedly larger, ranging between 110–137 µm, almost double the size of those found in clumps within the pollen chamber of *Gopadispermum* seeds. It is quite possible that individual pollen grains in a clump might have been of a larger size than given above because extremities of grains appeared almost imperceptible in the dark coloured pollen mass.

Except for *Rugaspermum*, most of the other seeds previously described from Nidpur Triassic are less researched and a detailed comparison of all the seeds with *Gopadispermum* is presently not possible. But out of them three genera viz., *Rotundaspermum* Manik, 1987, *Savitrispermum* Manik, 1987, and *Sahnispermum* Srivastava and Manik, 1993 need special mention as the former two are approximately of similar size and therefore comparable, while the latter, *Sahnispermum*, is larger (about 4 × 3.5 mm) but resembles *Gopadispermum* in having an outer cuticle of integument showing papillate cells. It differs, in having stomata which are absent in the new seed. The two seeds also resemble each other in having a distinct pollen chamber but the pollinating grains inside the pollen chamber of *Sahnispermum* are of the *Weylandites*-complex type and not the *Densipollenites* type, as in *Gopadispermum*.

Of the other two seeds, *Rotundaspermum* Manik, 1987 resembles *Gopadispermum* in having a similar mucronate micropylar end with a short micropyle, a delicate outer cuticle of integument and a cutinized nucellar membrane but differs in lacking a well defined pollen chamber. The description of the pollen grains pollinating such seeds is also not available for comparison.

The seed *Savitrispermum* Manik, 1987 resembles *Gopadispermum* in showing a distinctly delimited pollen chamber but the shape of pollen chamber is reportedly dome shaped, quite unlike that of *Gopadispermum* and pollen grains contained within its pollen chamber are reportedly winged. Further, seeds of *Savitrispermum* differ from *Gopadispermum* in frequently showing a curved micropyle and in having a thick outer cuticle of integument, indicating relationship with non-cupulate seed bearing fructifications. In *Gopadispermum*, the micropyle is short and straight and the outer cuticle is delicate.

Much prior to this report, fossilized pollination droplets have been reported in the petrified Palaeozoic seeds of *Pachytesta* (Stewart 1951) and *Callospermarion* (Rothwell 1977). The earliest reference of the physical presence of a fossilized pollination droplet is found in the Palaeozoic seed fern ovule *Pachytesta illinoensis* (Medullosacceae), of Late Pennsylvanian age, from north-central USA, where a resinous appearing substance was found confined to a small area at the tip of the pollen chamber but not extending from the micropyle. Moreover, the droplet reportedly contained no entrapped pollen and spores. The large ovules were pollinated by *Schopfipollenites* prepollen grains that were unusually large and heavy and most likely dispersed by insects (Taylor 1978).

Another Late Pennsylvanian structurally preserved ovule from Illinois, USA, *Callospermarion pusillum*, also exhibited a non cellular substance extending from the micropyle, into which several palynomorphs were found either embedded or adhering (Eggert and Delevoryas 1960). The ovule was pollinated by *Vesicaspora* pollen (Rothwell 1977). The morphologic nature of *Vesicaspora* was well suited to dispersal by wind, considering the moderate size (37–54 × 30–49 µm; Millay and Taylor 1974) of its pollen and large amount of it produced. The grains were trapped by the resinous pollination droplet extruded from the micropyle of *Callospermarion* ovule. The pollen grains could have floated into the pollen chamber of the ovule or were pulled in by the shrinking droplet (Taylor et al. 2009). Saccae had sometimes been considered the “wing” of wind dispersed pollen, but later they were thought to have served more for orientation and floatation in an inverted pollination drop (Doyle 1945).

Nearly all the specimens of *Gopadispermum* are found to be surrounded entirely or partially by a carbonaceous layer presumably representing remains of a fleshy cupulate structure enclosing individual ovules. Presence of this persistent adherent layer necessitates a comparison of *Gopadispermum* with one of the most common Mesozoic corystospermous seeds *Umkomasia* Thomas, 1933, known widely from Gondwana deposits (Taylor 1996). Compressed cupules of *Umkomasia* are reportedly bilobed showing a wrinkled surface. They contained one or two seeds with a slightly curved bifid micropylar canal which often extended beyond the cupule margin (Thomas 1933; Taylor et al. 2009). Townrow (1962) reported numerous saccate pollen grains embedded in the pollen chambers of several seed specimens similar to those found in the pollen organ *Pteruchus*. Well preserved compressed cupules reportedly also showed stomata on both surfaces of the cupule (Taylor et al. 2009). The new seed taxon *Gopadispermum* resembles the cupulate organ *Umkomasia* in having a wrinkled or folded externally adherent layer but differs in lacking a curved bifid micropylar canal and in containing bisaccate pollen grains similar to those found in the pollen organ *Pteruchus*. It is also dissimilar in lacking stomata on both the surfaces of the adherent cupule-like tissue (Fig. 4F). The micropyle is short, straight and entire in *Gopadispermum* and cuticles of the adherent tissue are non stomatiferous. Moreover, the pollen grains contained in the pollen chamber are saccate (appearing to be bisaccate) and clumped together into a pollen mass. When isolated, they seem to resemble the pollen *Densipollenites* Bharadwaj, 1962, of dispersed spores and not the saccate pollen found in the pollen organ *Pteruchus*. Above all, pollination in the new seed is probably of insect dispersed type, quite unlike that reported for *Umkomasia* (Umkomasiaceae), where pollen in reportedly wind dispersed (Retallack and Dilcher 1988; Labandeira 2010), with the exception of two probable corystosperm seeds of Late Triassic, Molteno Formation, where insect pollination was suggested, based on elongated micropylar extension of the ovules (Labandeira 2010).

Besides the corystosperms, a comparison of *Gopadispermum* with ovules of other Mesozoic seed ferns like *Peltaspermum thomasii* Harris, 1937 (see Anderson and Anderson 2003), of the Peltaspermales also indicated wind pollination. Pollination by means of a pollination drop was unlikely in the majority of Mesozoic Gondwanan peltasperms, since the grains were small (20–40 μm) and oval with a distal sulcus and were produced inside *Antevsia* Townrow, 1960 pollen organs. If dispersed, such grains would be assignable to *Cycadopites* (Retallack and Dilcher 1988; Taylor et al. 2009). Interestingly, there is considerable morphological variety among the pollen organs of the peltasperms. In *Autunia* (Pennsylvanian–Early Permian), bisaccate grains of the *Vesicaspora* type and not *Cycadopites* types are borne inside the pollen sacs (Taylor et al. 2009). Quite strangely, *Vesicaspora* type of pollen grains have also been reported in the pollen chamber of the Pennsylvanian seed *Callospermarion pusillum*. Here too, the morphologic nature of *Vesicaspora* is well suited to dispersal by wind (Taylor et al. 2009) although ovules were apparently aided in trapping pollen by the production of a resinous pollination droplet, that extended from the micropylar orifice (Rothwell 1977). Therefore, entomophily has not been adequately demonstrated for any well known Mesozoic pteridosperm species (Retallack and Dilcher 1988).

Contrary to earlier speculations however, Anderson and Anderson (2003) believed that such taxa as *Peltaspermum thomasii* may have been insect pollinated as the large size of their pollen (up to 40 μm) argued against plants being wind pollinated. Moreover, their pollen sacs reportedly bore glandular swellings on the surface that probably attracted insects (Retallack and Dilcher 1988). Despite much speculation, it is still not clear whether *P. thomasii* had a pollination drop mechanism in it's ovules or not (Labandeira et al. 2007). Thus, other than exhibiting characters of wind pollination, the ovule of *Peltaspermum* further differs from *Gopadispermum* in being tetrahedral (2 × 1 mm) and in having a bifid micropyle.

In comparing *Gopadispermum* with dispersed seed taxa described earlier, from the Nidpur Triassic beds, it was found that the new morphotaxon exhibited a number of unique features hitherto unreported in previously described seeds. Therefore *Gopadispermum* was not assignable to them.

In tracing relationship of dispersed seed genera, the nature of pollen grains (found within the micropyles and pollen chambers) presumed to have pollinated the seeds is regarded as the most reliable character. If such pollen grains are found to resemble pollen contained within pollen organs found associated with the seeds, the dispersed seeds are assigned to the associated pollen organ as in the case of the seed *Rugaspermum* (see Pant and Basu 1977). Contrary to this, tracing affinities is often difficult in instances where the pollinating grains may not have been reported from a pollen organ in situ but belonged to a morphotaxon of the sporae dispersae from the same beds. Unfortunately, the latter incident seems to be true for the pollen grains pollinating seeds of *Gopadispermum* as pollen grains of *Densipollenites* type have not yet been reported contained within any of the several pollen organs described so far from the Nidpur Triassic beds (see Bose and Srivastava 1973a; Pant and Basu 1973, 1977, 1979; Srivastava 1974, 1975, 1984; Bhowmik and Parveen 2008, 2009; Bhowmik and Das 2012).

Discounting the feature of pollinating grains indicating affinity of a dispersed seed genus and considering the cupule-like structure adherent to individual seeds of *Gopadispermum* as helpful, we regret to state that cupulate organs of *Umkomasia* type are so far unreported from the Nidpur beds, even though several species of its pollen organ are reported (Pant and Basu 1973, 1979; Srivastava 1974; Bhowmik and Das 2012). Further, entomophilous features like those reported for *Gopadispermum* have not been described in the ovulate organ *Umkomasia*. Nevertheless, notable understanding may come about when attached specimens are found that combine organs particular to a strata. Till then, *Gopadispermum* may be regarded as one of the unclassifiable, unique Mesozoic pteridosperms which may for the present be included among the genera of ginkgoopsids with uncertain familial position, pending further investigations.

Conclusions

The structurally preserved compressed mesofossil *Gopadispermum* is a seed morphotaxon displaying the following features: (i) the preservation of a fossilized pollination droplet extending from the micropylar orifice in one of its specimens; (ii) the crystallized, resinous substance of the droplet containing organic remains of entrapped saccate pollen grains; (iii) the pollen grains recovered from the micropylar canals and pollen chambers of the seeds being also saccate and presumably assignable to *Densipollenites* Bharadwaj, 1962 of dispersed miospores; (iv) the grains found clumped together in the seed pollen chamber forming a dark coloured pollen mass of variable size. These features are concluded from seed plant reproductive structures rather than from insect mouthparts.

Prior to this report, scanty evidence for insect fluid feeding was available from the Triassic to Early Jurassic of the Mesozoic, as ovulate organs of gymnosperms of this period produced a pollination droplet presumably for trapping wind dispersed pollen. Therefore, the new seed indicates plant-insect inter-relationship in fossils of Nidpur beds. Besides droplet mechanism, the seeds also show exceptional features of the nucellar tissue which is distally modified to form a pollen chamber having a dark collar-like base. The cells of the pollen chamber have thick and characteristically sinuous walls, forming pointed processes at the distal end that appear to project into the micropylar canal. Another significant feature unique to *Gopadispermum* seeds is the exhibition of a cupule-like tissue, externally adherent to the single seeds. The cupule-like structure is comparable to the bilobed cupule of *Umkomasia*, as in both the taxa a short, micropylar tube extended beyond the margin of the cupule.

Apart from these aforementioned features, the orthotropous, unwrinkled seeds show general anatomical features common for all seeds: (i) having a delicate, often papillate outer cuticle of integument; (ii) even more delicate inner cuticle of integument extended above to form a short micropyle; (iii) the nucellus which is fused to the inner cuticle of integument and megaspore membrane below, but free above. Nucellar cells shows distinctive features hitherto unreported for other seeds of Nidpur beds. The characteristic pollen chamber with a dark coloured pollen clump is a diagnostic feature that enables easy identification of the seeds; the innermost layer of seed being the dark coloured megaspore membrane, which occupies a large part of the seed area and sometimes shows one to two embedded archegonia.

Structural details of the new seed have been compared with features of seed morphotaxa described earlier from the region and *Gopadispermum* was found to be quite different. It has also been compared with the Palaeozoic seed taxa *Pachytesta* and *Callospermarion*, on account of the droplet mechanism. Finally, the exclusive and unparalleled characters displayed in *Gopadispermum* do not presently permit it's inclusion under any of the earlier described Triassic seed genera of the Nidpur beds, therefore, a new name is instituted to include all such mesofossil seed taxa that show characters identical to *Gopadispermum*. The new seed has been placed among the ginkgoopsids on account of its cupule-like features.

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References

Anderson, J.M. and Anderson, H.M. 2003. Heyday of the gymnosperms: Systematics and biodiversity of the Late Triassic Molteno fructifications. *Strelitzia* 15: 1–398.

Bharadwaj, D.C. 1962. The miospore genera in the coals of Raniganj Stage (Upper Permian), India. *Palaeobotanist* 9: 68–106.

Bharadwaj, D.C. and Srivastava, S.C. 1969. A Triassic mioflora from India. *Palaeontographica* 125: 119–149.

Bhowmik, N. and Das, N. 2011. Further report on megaspores from the Triassic of Nidpur, M. P., India. *Acta Palaeobotanica* 51: 107–125.

Bhowmik, N. and Das, N. 2012. On three new species of *Pteruchus* Thomas from the Triassic of Nidpur, M.P., India. *Palaeontographica B* 288: 5–39.

Bhowmik, N. and Parveen, S. 2008. *Nidianthus* gen. nov.—a *Caytonanthus*-like Pollen organ from the Triassic of Nidpur, M.P., India. *Palaeobotanist* 57: 389–398.

Bhowmik, N. and Parveen, S. 2009. *Nidistrobus indicus*—a new species of the male cone from Triassic of Nidpur M.P., India. *Proceedings of the National Academy of Scences, India, Sec. B* 79: 289–306.

Bhowmik, N. and Parveen, S. 2012a. *Rugaspermum minuta*—a new species of the seed genus *Rugaspermum* from the Triassic of Nidpur, India. *Turkish Journal of Botany* 36: 141–150.

Bhowmik, N. and Parveen, S. 2012b. On *Vertebraria* Royle from Triassic of Nidpur, Madhya Pradesh. *Journal Geological Society of India* 79: 618–626.

Bose, M.N. and Srivastava, S.C. 1970. *Glottolepis rugosa* gen. et sp. nov. from Triassic beds of Nidpur. *Palaeobotanist* 18: 215–217.

Bose, M.N. and Srivastava, S.C. 1971. The genus *Dicroidium* from the Triassic of Nidpur, Madhya Pradesh, India. *Palaeobotanist* 19: 41–51.

Bose, M.N. and Srivastava, S.C. 1972. *Lepidopteris indica* sp. nov. from the Lower Triassic of Nidpur, M.P., India. *Journal of Palaeontological Society of India* 15: 64–68.

Bose, M.N. and Srivastava, S.C. 1973a. *Nidistrobus* gen. nov. a pollen bearing fructification from the Lower Triassic of Gopad River Valley, Nidpur. *Geophytology* 2: 211–212.

Bose, M.N. and Srivastava, S.C. 1973b. Some micro and megastrobili from the Lower Triassic of Gopad river valley, Nidpur. *Geophytology* 3: 69–80.

Doyle, J.A. 1945. Developmental lines in pollination mechanisms in the Coniferales. *Scientific Proceedings of the Royal Dublin Society* 24: 44–62.

Eggert, D.A. and Delevoryas, T. 1960. *Callospermarion*—a new seed genus from the Upper Pennsylvanian of Illinois. *Phytomorphology* 10: 131–138.

Faegri, K. and Van Der Pijl, L. 1966. *The Principles of Pollination Ecology*. 248 pp. Pergamon Press, Oxford.

Ghosh, A.K. and Banerji, J. 2007. Biostratigraphic significance of megaspores from the Triassic sequence of Peninsular India. *In*: D.K. Sinha (ed.), *Application in Stratigraphy and Paleoceanography*, 81–89. Narosa Publication House Pvt. Ltd., New Delhi.

Grimaldi, D.A. and Engel, M.S. 2005. *Evolution of the Insects*. 755 pp. Cambridge University Press, New York.

Harris, T.M. 1937. The fossil flora of Scoresby Sound East Greenland. Part 5: Stratigraphic relations of the plant beds. *Meddelelser om Grønland* 112 (2): 1–114.

Kovach, W.L. and Batten, D.J. 1989. Worldwide stratigraphic occurrences of Mesozoic and Tertiary megaspores. *Palynology* 13: 247–277.

Krassilov, V.A. 1977. Contributions to the knowledge of the Caytoniales. *Review of Palaeobotany and Palynology* 24: 155–178.

Krassilov, V.A., Rasnitsyn, A.P., and Afonin, S.A. 2007. Pollen eaters and pollen morphology: co-evolution through the Permian and Mesozoic. *African Invertebrates* 48: 3–11.

Labandeira, C.C. 2010. The pollination of mid Mesozoic seed plants and the early history of long proboscid insects. *Annals of the Missouri Botanical Garden* 97: 469–513.

Labandeira, C.C., Kvaček, J., and Mostovski, M. B. 2007. Pollination drops, pollen and insect pollination of Mesozoic gymnosperms. *Taxon* 56: 663–695.

Luber, E.L. 1938. Spores and pollen from coals of the Permian of U.S.S.R. [in Russian]. *Problemy Sovetskoj Geologii* 8: 152–160.

Majumdar, M. 1981. Geology of Bhadoura-Tansar area; north-western part of Singrauli Coalfield, Sidhi District, Madhya Pradesh. *Geological Survey of India Progress Report* 1: 1–15.

Manik, S.R. 1987. Some new genera of Triassic seeds. *Palaeobotanist* 36: 197–200.

Millay, M.A. and Taylor, T.N. 1974. Morphological studies of Paleozoic saccate pollen. *Palaeontographica B* 147: 75–99.

Pant, D.D. and Basu, N. 1973. *Pteruchus indicus* sp. nov. from the Triassic of Nidpur, India. *Palaeontographica B* 144: 11–24.

Pant, D.D. and Basu, N. 1977. On some seeds, synangia and scales from the Triassic of Nidpur, India. *Palaeontographica B* 163: 162–178.

Pant, D.D. and Basu, N. 1979. Some further remains of fructifications from the Triassic of Nidpur, India. *Palaeontographica B* 168: 129–146.

Pflug, H.P. 1953. Zur Entstchung and Entwicklung des angiospermiden pollens in der Erdgeschichte. *Palaeontographica B* 95: 60–171.

Raja Rao, C.S. 1983. Coalfields of India, III. Coal resources of Madhya Pradesh, Jammu & Kashmir. *Geological Survey of India Bulletin A* 45: 119–129.

Rasnitsyn, A.P. 1964. New Triassic Hymenoptera from Central Asia [in Russian]. *Paleontologičeskij žurnal* 1: 88–96.

Retallack, G.J. and Dilcher, D.L. 1988. Reconstructions of selected seed Ferns. *Annals of the Missouri Botanical Garden* 75: 1010–1057.

Rothwell, G.W. 1977. Evidence for a pollination drop mechanism in Palaeozoic Pteridosperms. *Science* 198: 1251–1252.

Satsangi, P.P. 1964. On the occurrence of *Dicroidium* flora in Sidhi District, Madhya Pradesh. *Current Sci*ence 33: 556.

Srivastava, S.C. 1969. Two new species of *Glossopteris* from the Triassic of Nidpur, Madhya Pradesh, India. *In*: H. Santapau and J. Sen (eds.), *J. Sen Memorial Volume*, *Botanical Society of Bengal*, 229–303. J. Sen Memorial Committee and Botanical Society of Bengal, Calcutta.

Srivastava, S.C. 1974. Pteridospermic remains from the Triassic of Nidhpur, Madhya Pradesh. *Geophytology* 4: 54–59.

Srivastava, S.C. 1975. A new microsporangiate fructification from the Triassic of Nidhpur, India, *Palaeobotanist* 22: 19–22.

Srivastava, S.C. 1984. *Lelestrobus*: A new microsporangiate organ from the Triassic of Nidpur, India. *Palaeobotanist* 32: 86–90.

Srivastava, S.C. and Manik, S.R. 1990. *Rostrumaspermum venkatachali* gen. et sp. nov., an archegoniate seed from Triassic of Nidpur, India. *Palaeobotanist* 38: 98–104.

Srivastava, S.C. and Manik, S.R. 1993. Taxonomic diversity of Triassic seeds from India. *In*: R.H. Findlay, R. Unrag, M.R. Banks, J.J. Veevers (eds.), *Proceedings of the Eight Gondwana Symposium, Hobart, Australia, Evolution & Dispersal*, 265–275. Taylor and Francis, Hobart.

Srivastava, S.C. and Manik, S.R. 1996. Reconsideration of *Savitrispermum* from Triassic of Gondwanas. *Geophytology* 26: 1–11.

Stewart, W.N. 1951. A new *Pachytesta* from the Berryville locality of Southeastern Illinois. *American Midland Naturalist* 46: 717–742.

Taylor, T.N. 1978. The ultrastructure and reproductive significance of *Monoletes* (Pteridospermales) pollen. *Canadian Journal of Botany* 56: 3105–3118.

Taylor, T.N. Taylor, E.L., and Krings, M. 2009. *Palaeobotany*: *The Biology and Evolution of Fossil Plants.* 1230 pp. Elsevier Academic Press, Burlington.

Thomas, H.H. 1933. On some pteridospermous plants from the Mesozoic rocks of South Africa. *Philosophical Transactions of the Royal Society of London B* 22: 193–265.

Tiwari, R.S. and Ram-Awatar 1989. Palynodating of Nidpur beds, Son Graben, Madhya Pradesh. *Palaeobotanist* 38: 105–120.

Townrow, J.A. 1960. The Peltaspermaceae, a pteridosperm family of Permian and Triassic age. *Palaeontology* 3: 333–361.

Townrow, J.A. 1962. On some disaccate pollen grains of Permian to Middle Jurassic age. *Grana* 3: 13–46.