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Indian Seed - Compressions from Triassic of Nidpur in evolutionary perspective

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RESUMEN

En el Triásico de Nidpur (India) aparecen, junto con restos de aparatos vegetativos, un elevado número de órganos reproductores, excepcionalmente conservados, que han permitido hacer un estudio cuticular detallado.

Los principales aspectos en que se ha basado el estudio han sido la disposición de los tegumentos seminales respecto de la nucela y la paleohistología de sus membranas.

Como resultado de los estudios cuticulares se infieren algunos aspectos paleoambientales y estratigráficos e interesantes conclusiones taxonómicas y evolutivas.

INTRODUCCION

Advent of *Dicroidium* bearing bed at Nidpur in the Triassic of India has brought forth the richest haul of compressed fertile organs co-fossilized with the vegetative remains. Of these fertile structures, occurrence of detached seeds is a matter of ultimate fortuitous discovery of sufficient number of complete and finely preserved specimens permitting detailed observations in all the three dimensions. Practically, this implies more in the study of fossil seeds because of their small size and variable symmetry.

Based upon divergent characters of cutinized membranes, extensive study of these seeds depict variety of morphological forms that have played a vital role in plant-group differentiation. The different morphological entities of seeds are represented by cuticular membranes which are well differentiated and that point towards the fully developed nature of seed. Presence of well developed

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membrane is the result of tissue maturation and therefore, represents the advanced stages in ovule ontogeny.

Besides, it is of further interest to note that the present investigations of carbonized seeds have provided considerable knowledge about the variety of structural modifications met in many of these forms, both at the generic and specific level. The generic delimitation, primarily, has been maintained upon sufficiently distintive seed cuticles and as such there is no overlap of gross morphological plan centred upon epidermal structure of integument. In this way, seed cuticles display adequate differences to require a separate specific name.

Moreover, all the seeds studied over here are platyspermic and had split along a principle plane and specimens depict very little variation in size. But MEYEN (1984) showed two different types of platyspermic seed: primary intrinsically flat and secondarily flattened, however there is no structural differences between these seeds in more advanced taxa that allow recognition of whether their platyspermy is primary or secondary.

Additionally, after examining the seed membranes of Nidpur specimens, the categories of seed cuticle recognized have been noted here under:

I. Where integument is intimately adherent to nucellus,
II. Where outer investment is easily detachable like a sac,
III. Where integument is free only towards the apical portion of nucellus,
IV. Where nucellus is completely free from outer integument except for at the base,
V. Where inner integument is confluent to nucellus,
VI. Where nucellus membrane is closely adnate to megaspore membrane.

Other than these aforesaid notable seed characters, taxa represented in Nidpur assemblage have been identified on the basis of cell shape and size, thickness of cuticle, nature of surface wall whether papillate or nonpapillate, striated, wrinkled or creased, occurrence of folds, ridges or trichomes, thickness of anticlinal walls and the outer integument stomatiferous or non-stomatiferous. These are some of the features which have been used for the taxonomic framework. Also the presence of pollen chamber wheter in reduced stage or altogether absent, has played a significant role in plant group differentiation. Along with these, the micropylar orientation whether sunken or protruding, nature of summit flat or lobed, and the length of micropylar canal are some of the distinguishing characters which offer evidence more especially of probable pollination and seed dispersal adaptations. Further, these micropylar features are also suggestive of pollen drop mechanism and for pollen reception.

Generally, seeds from Nidpur yield three to four membranes which exhibit cellular structure of complex tissues of seed. Based upon the cellular organisation, seed cuticles have been correlated with their vegetative organs already known from Nidpur deposits.

Further, thickness of the cutinized or non-cutinized integumet, the extent of cutinization of nucellus, the presence or absence of megaspore membrane associated with their varied shape, and length of the micropylar canal, are some of the used distinctive and definitive characters for Nidpur seeds being of gymnospermous origin. However, according to SCHNARF (1937 in FOSTER and GIFFORD, 1974) presence of conspicuous megaspore wall is one of the most significant and definitive character of gymnospermous seeds. But this view may not hold true in the study of fossil seeds because the presence or absence of megaspore membrane depends upon preservation whether in compressed or petrified state.

Seeds described in the present investigation have also shown wide variation in the form and upto certain extent in size too. Due to smaller size in the current study, the elaborate observations could be possible in all the three dimensions and moreover, structural complexities and seed morphology could be elucidated more precisely.

As regards the form of seeds, particularly, the genera like *Sahnispermum, Savitrispermum, Delevoryaspermum, Nidispermum* and *Pantiaspermum* are oval but *Pyriformispermum* is typically pear-shaped. The other forms, viz., *Tayloriaspermum* is an oval or almond-shaped seed whereas the seed *Urceolaspermun* is a pitcher or jug-shaped. Seeds like *Cupolaspermum* and *Konaspermum* have got ovale shape while *Rotumdaspermum* is spherical with a mucronate micropylar tip. With these variations marked in shape, it has been visualized that most of the seeds having pteridospermous affinity are oval barring a few which attained dome or pear like form. The shape variation is not of much significance but the robust outer membrane of the seed has revealed that these seeds were not sheltered inside the cupule. Thus these non-cupulate seeds of pteridospermous affinity reflect towards an advancement over the other know seeds of Triassic. Among the seeds of pteridospermic alliance, *Savitrispermum* closely agrees with the Umkomasia seeds, but the detached seed Savitrispermum lacks cupule and appears to have been borne directly over the axis. The outer integument of *Savitrispermum* is also quite tough and indicative of its relationship with non-cupulate-seed-bearing fructifications. The only exception among these seeds in *Cupolaspermum* which has not yielded much robust outer cuticle as has been found in pteridospermous genera of Nidpur, rather is has been isolated into pieces. This shows that the differentiations of outer integument might have not occurred either at the time of fossilization or the seed would have been immatured. However, the occurrence of distinct pollen chamber rules out for the seed *Cupolaspermum* being of immature stage. In this reference, it would be worth to maintain over here, that there has been evidence to indicate that in some of the seeds which were immature, totally lacked pollen chamber while the mature seeds of the same type showed a well differenciated pollen chamber.

Besides, the spherical shape of *Rotundaspermum* affords a fleeting glimpse of an early stage because platyspermy shows an advancement over radiospermy. As the other known seeds from Nidpur are platyspermic, evidently, the genus *Rotundaspermum* must have belonged to some primitive conifers. The occurrence of *Lelestrobus* and *Nidpuria* are the valid examples where structural organization appears to be of lycopsid-type but their pollen constents have distinct relationships with the conifers.

Apart from the general shape of the seed, orientation of cellular pattern has usually been used in delimiting the taxon at the specific level. For instance, in *Sahnispermum* cells are polygonal which is generally met in cellular structure of the plant organs but in *Savitrispermum* cells of outer integument are squarish and quite distinctive. Further, the cellular arrangement is quite symmetrical while in *Sahnispermum*, no set pattern of cells has been marked; however, towards the margin, cells are arranged in a sequence. Likewise, in *Delevoryaspermum* cells appear to be rectangular or polygonal, and in *Nidispermum* too the cellular pattern is more or less the same except for their anticlinal walls which are thinner and at places quite faintly visible. Among the other genera, cells in *Cupolaspermum* become exceptionally shorter and rectangular somewhat compactly arranged but in *Pyriformispermum*, cells are totally different because of being elongated polygonal in several order. Besides, in *Urceolaspermum* cells are polygonal having more or less the same size but varies differently in micropylar and marginal region. In *Tayloriaspermum*, cells are sinuous and in *Konaspermum*, typically cells have attained angular shape. Other tan these, *Rotundaspermum* exhibits polygonal-rectangular cells whereas in *Pantiaspermum* cell outlines are mostly obscured due to heavily infested papillae.

Now it is quite apparent that cellular orientation of seed cuticles accompanied with perceptible differences, provide valuable supplementary evidence in generic delimitation as well as for especific assignation to different seed genera.

In the light of studies made upon homogeneity and heterogeneity of integument, it has been marked that the texture and thickness of integument shows a good deal of variations and the zonation of integument too depicts broad range of morphological variability which appears to be of value in demonstrating the phylogenetic position occupied by the seed.

In Nidpur seeds, integument thickness is highly variable, and therefore, in genera *Delevoryaspermum, Pyriformispermum, Konaspermum* and *Pantiaspermum,* the character has been considered quite useful in delimiting these seed genera. All these genera possess easily separable integument and that shows that the integument is not adherent to nucellus. Genus *Pantiaspermum* since bears strongly develop irregular papillae which is so much in profusion that the cell outlines of outer integument are hardly discernible. Thus the thick outer seed coat in these genera and the presence of intensively cutinized crowded papillae in *Pantiaspermum,* suggest that adaptation to the fluctuating conditions of enviroment. Moreover, thick cuticles also indicate that the species were growing under high light intensity and with reduced moisture contents.

Besides, outer integument of *Sahnispermum* is also tough, and bears well cutinized median papillae throughout the cell surface associated with sunken stomata having papillae overarching the pit. The presence of such protected stomata reflected towards xeromorphic conditions. Any way, since the seed genera bearing thick outer membrane along with variability in papillae development is less in frecuency, it can be more safely regarded as local variation in climate. This has got the supportive evidence by the presence of a few papillate leaf genera occurring in Nidpur beds.

In addition, stomatal frequency bears ecological significance as it may be taken as an environmental humidity. In this reference *Delevoryaspermum* can be cited because it possesses a good number of stomata together with *Dicroidium* leaves in Nidpur shale, and thus could serve as an indicator for environmental conditions.

However, it would be worth to point out over here that in Nidpur, generally the seeds possess delicate and thin outer membrane which can be evidently observed in the taxa: *Savitrispermum, Nidispermum, Cupolaspermum, Urceolaspermum, Tayloriaspermum* and *Rotundaspermum.* Usually these seeds reveal smooth surfaced integument, commonly having straight walled cells but in *Tayloriaspermum,* cells are typically sinuous. Additionally, in *Savitrispermum umkomasii,* lateral and endwalls too, exhibit microsinuosity. Normally, features like delicate cuticle, thinner outer membrane composed of undulated or sinuous cell walls having non-cutinized cell surface, are considered to be indicative of mesomorphic evidence (STACE, 1965) and overall, are suggestive of a favourable growing season with prevailing luxuriant conditions for growth of plants. In addition, it could also be speculated that there must have been plentiful water supply which eventually aided to deduce the climate to be tropical rather than temperate. This is at once supplemented by the evidence of richest haul of cryptogams (bryophytes) which strongly favoures the occurrence of protected shady and marshy spots in the forest of Nidpur during Triassic period (PANT and BASU, 1981).

The inner integument also presents distinctive characters as has been marked in the genus *Pantiaspermum* where cells are broadly polygonal intimately appressed to the nucellus. The delicate and thin inner integument remains completely free upto chalazal end which is quite clear in the genus *Sahnispermum*. Inner cuticle where inseparable remains superimposed, could be marked by cell markings over the nucellus. In such cases, two sets of cell outlines can be clearly demarcated.

As Nidpur, where inner cuticle is preserved, normally surrounds nucellus and continues upto micropylar end. The space between inner and outer cuticles of integument provides the measurement of thickness of integument. Further in totality of structural features of a seed, the inner integument characters has been used mostly for specific identification.

As regards the nucellar membrane, in the present study of seed fossils, a lot of variations have been noticed in the structural features of nucellus. In some of the taxa the preservation of cellular outlines are quite explicit while in others either the cellular structure is ill-defined or intensively cutinized. At times, the structural organisation of some forms have appeared to be contorted. However, the presence of a distinctly differentiated nucellar membrane is the result of tissue maturation.

Nucellar membrane in taxa *Sahnispermum*, *Savitrispermum* are intimately invested by inner integument but outer membrane is typical detached from remainder membranes. Outer integument is not at all adherent to nucellus and the two layers are sharply separable, despite they remain attached at the base. This particular character in conjunction with other features bring these seed genera close to Pteridospermales. Similar is the case with the genus *Delevoryaspermum* and *Nidispermum*, where outer integument remains free upto base. But in *Cupolaspermum* the outer integument es closely adnate to nucellus and the inner integument has been inseparably appressed to outer membrane. However, its distinct pollen chamber shows its alignement with the pteridosperms. In *Pyriformispermum* once again the outer integument is like a sac which can be taken out due to its loose covering and this easily detachable feature predominated consistently in pteridosperms. Moreover, the pteridospermous seeds, namely: *Sahnispermum*, *Savitrispermum*, *Delevoryaspermum*, *Cupolaspermum* and *Pyriformispermum* reveal their integuments laterally free from nucellus but remain connected at the chalazal end. Whereas in genera like *Tayloriaspermum* and *Urceolaspermum*, integument remains adherent to the nucellus but diverge near the mid level of seed with the free portion of nucellus forming an apically differentiated dome-shaped pollen receiving structure. Having nucellar apex free from outer integument is a feature, generally met in cycadean seeds. Additionally, the cutinized nucellar membrane and tenuous outer integument associated with reduced pollen chamber are the other characters which favour the genera *Tayloriaspermum* and *Urceolaspermum to have relationship with Cycadales.*

Thus among Nidpur seeds, the fusion of integument and its adnation to nucellus is quite definitive and depicts obviously that the seeds must have been more advanced.

Other than these taxa, Konaspermum, Rotundaspermum, and *Pantiaspermum* have invariably shown their nucellus free from outer integument over most of the seed and this feature occurs sporadically among living conifers. Therefore, this structural agreement alongwith other supplementary characters such as, degree of cutinization of nucellar membrane and absence of pollen chamber, logically demonstrate the placement of these genera with Coniferales.

Rotundaspermum bears a short micropylar canal, a significant feature indicative of its affinity with conifers. The genus because of its characteristic micropyle offers evidence more especially of probable pollination and seed dispersal adaptations. According to RENAULT (1885), such apical extensions were a dispersal mechanism for seeds, since no ontogenetic sequence is yet known for these extensions, they may be interpreted to have aided in both pollination and dispersal. The subconical micropyle in the present genus could have functioned as efficient pollen traps because narrow surface is more suitable in trapping pollen from moving air than a broad surface (PROCTOR and YEO, 1972). The other genera, namely *Konaspermum* and *Pantiaspermum* also have revealed narrow surface at the micropylar end. The micropylar hole in these genera are narrowly sunken or depressed but with heavy cutinization, and the opening is not that expensive as have been marked in pteridospermous seeds of Nidpur. This decrease in the area of micropyle is suggestive of these genera being quite efficient for pollen reception. Further, the occurrence of microspores inside the micropyle of *Konaspermum* is itself a valid indicator for the taxon to be fully capable for pollen traps.

Besides, the other seeds, viz., *Tayloriaspermum* and *Urceolaspermum* which are allied to Cycadales bearing micropylar opening unevenly cutinized more or less like a bulge or subspherical in appearance with jagged edge. Such micropyles are quite suitable for pollen reception because they are directly exposed to the air and reflects towards pollen drop mechanism The pteridospermous genera *Sahnispermum* depicts usually protruding micropylar end; identical is the case with *Savitrispermum* which bears curved micropylar hole somewhat like a crater-mouth associated with zig-zag cutinization over the opening. The presence of protuberances and constrictions at the apex of seed suggest a potential pollen chamber and pollen drop mechamism. Occasionally, in some forms like *Nidispermum* the micropylar end exhibits cutinized lobes at the summit, this too, appears to have been for pollen reception. In *Delevoryaspermun*, the micropylar end is more or less bowlshaped with intensive cutinization and similar flattening is marked with flaps in *Cupolaspermum;* this kind of structural features are generally marked in pteridospermous seeds where pollen are deposited at the time of fertilization. Apart from these genera, *Pyriformispermum* is a quite peculiar seed where micropylar hole is deeply sunken or depressed having its inner lining sculpted with highly cutinized apparently finger-like appendages and that projects into the pollen-chamber. This sort of unusual structure can be interpreted as a device for concealing the entry of pollen grains after fertilization.

In addition, as opined by LONG (1960), the striking similarities between the apices of seeds suggest a relationship with their parent plant; however, this particular character is well documented among the Nidpur seeds belonging to pteridospermales.

The occurrence of well developed pollen chamber in Nidpur seeds, namely: *Sahnispermum, Savitrispermum, Delevoryaspermum Nidispermum, Cupolaspermum* and *Pyriformispermum* is a usual feature but «salpinx» like structure frequent in Palaeozoic pteridospermous seed is totally missing in present forms. Apart from this, Nidpur seeds bear well developed micropyle while the genera having strongly developed «salpinx» is always accompanied with rudimentary micropyle.

The other outstanding feature is the occurrence of pollen chamber with simple excavation at nucellar tip which is mainly seen in two genera *Savitrispermum* and *Pyriformispermum*. Generally, the rim of the pollen chamber wall has characteristic tapering process which has been marked mostly in the mature seeds but in younger seeds the differentiation of pollen chamber could not be easily detected. Such seeds are however, of arrested development and these specimens throw light on the growth development of a seed.

Pollen chambers in *Tayloriaspermum* and *Urceolaspermum* have depicted considerable reduction and have been distinguished like a crescent-shaped structure in the later form while in the former it has been represented like a flattened apical bulge. Even in the present day cycads, the pollen chambers are usually found extremely reduced.

In the rest seed genera, *Konaspermum, Rotundaspermum* and *Pantiaspermum*, no delimitation of pollen chamber has been marked. In extant conifers too, no such structures have been described.

Additional evidence of pollen grains in pollen chamber, besides other characters, attest that seed has matured at least as far as the pollen receptive stage and thereafter the fossilization occurred.

Of all the structural features of seed, presence of distinct megaspore is considered to be characteristic features of gymnospermous seed. This protected membrane is always thickly cutinized and occupies in the centre of a seed. The megaspore cuticle is highly resistant to maceration. This cutinized membrane is quite varied and exhibits no indication of cell. Mostly it is dark-brown in colour, but at times due to over maceration, the membrane is traversed by cracks which shows indistinct cellular outlines.

In Nidpur seeds it is distinctly recognizable in the genera: *Sahnispermum, Savitrispermum, Delevoryaspermum* and *Pyriformispermum*. In *Nidispermum* it is faintly marked whereas in *Cupolaspermum* the megaspore membrane is not identifiable. In taxa having cycadean affinity i.e. *Tayloriaspermum* and *Urceolaspermum*, the membrane is represented by polygonal markings bearing intensive cutinization whereas in the later form, the membrane is heavily cutinized, and this high grade of cutinization of seeds, is indicative of its affinity with cycads. This particular feature is also implied in Ginkgoalean seed but together with other features, aforesaid seed genera have been assigned to Cycadales.

Further, the occurrence of megapore membrane as one of the layers of seed membrane is amply significant in confirming the fossil structures being dealt as to be a seed definitively, and not a bulb or any other structure (HARRIS, 1954). In addition, megaspore membrane also plays its role in the recognition of a species.

Consequently, the study of compressed and isolated seed fossils based upon the quality and quantity of evidence confirms that all the plant groups were floursing in the vicinity of Nidpur during the Triassic period.

The study has also facilitated to find out the linkage of these seed fossils based upon their epidermal features, between the vegetative and fertile organs described from *Dicroidium* beds of Nidpur. The notable alliances which have been established are: the leaf *Lepidopteris indica*, the pollen organ *Bosea indica* containing *Weylandites*- type of pollen grains and *Sahnispermum indicum* the seed, all attributed to the pteridospermous plant *Lepidopteris indica;* the leaf *Dicroidium nidpurensis* - pollen organ *Pteruchus nidpurensis* and the seed *Delevoryaspermum nidpurensis* all ascribed to the plant *Dicroidium nidpurensis* belonging to Pteridospermales. Besides upon the structural correlation of the epidermal characters of seed cuticle, *Savitrispermum crateriformis* type of seed has been considered to have been borne upon seed organ *Umkomasia*. The seed genus *Savitrispermum* is quite profilic throughout Gondwanaland in midpart of Triassic ashas been represented by *Savitrispermum crateriformis* in

India; *S. douglasii* in Australia; *S. umkomasii* and *S. andersonii* in South Africa. This seed genus occurs in abundance in relatively narrow stratigraphic range and therefore, it has its stratigraphical implication and may be documented as an indicator for Middle Triassic.

Futhermore, other than the pteridospermous alliance, occurrence of putatively derivative cycadean genera *Tayloriaspermum* and *Urceolaspermum* in association of *Taeniopteris glandulata* strengthen the hypothesis that *Taeniopteris* was the leaf of primitive cycads (MAMAY, 1973). Moreover, *Tayloriaspermum sinuosum* the seed and *Taeniopteris glandulata* leaf, both are homologous in their epidermal characters and with this it could be inferred that both belonged to the same parent plant.

As such the botanical affinities of these seed-taxa have been based upon their adnation of integument with nucellus, extent of cutinization, presence or absence of distinct pollen chamber and occurrence of megaspore. The other morphological factors like thickness of cuticle, superficial features like papillae, trichomes, cutinization of anticlinal walls, cell shape, frequency of stomata, intensive or feeble cutinization of nucellar membrane, varied micropylar holes, whether pressed or sunken or lobed or flat, long or short, have been taken into consideration.

Further the study of gymnospermous seed cuticle and the other known plant associates, it could be conceived that Nidpur area must have been a sheltered fresh water lake or estuary bordered by marshy area in which grew besides gymnosperms, bryophytes and pteridophytes. Features like papillae, trichomes, cutinized cell-wall, sinuous cellular outlines must have developed in response to fluctuating climatic conditions prevalent during that period. Thus the investigation of seeds from Nidpur has made revelation of a reasonable reconstruction of palaeoenvironment and also reflects towards in situ burials of vegetation.

In brief, seed a complex, multicellular entity shows much variations in structure. Its cuticles act as an important indicator of taxonomy, evolution, habitat and possibly climate.

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