A NEW PLATYSPERMIC PERMINERALISED SEED
FROM THE MIDDLE JURASSIC OF
QUEEN CHARLOTTE ISLANDS,
BRITISH COLUMBIA, CANADA.

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ABSTRACT.

A description is given of the morphology, anatomy and affinities of a new permineralised seed from South Balch Island in the Queen Charlotte Islands, British Columbia, Canada. The seed is named *Dawsonocarpus haidorum* gen. et sp. nov. This platyspermic seed has features which show relationships with extant members of the Cycadales, coniferopsids and Gnetales together with Palaeozoic seeds e.g. platyspermic cordaites. These seeds are found in association with *Cycadeocarpus columbianus* Dawson in the Yakoun Formation, Vancouver Group, dated as Middle Jurassic (Bajocian), from associated ammonites. The seeds, in common with *Cycadeocarpus columbianus*, are calcified in a pyroclastic matrix and may be readily examined by conventional peel techniques and SEM.

Key Words: *Dawsonocarpus haidorum* gen. et sp. nov., Mid-Jurassic, permineralised platyspermic seed, mesotesta.
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1. INTRODUCTION

1.1 Aims and Objectives.

The main thrust of this research project was directed towards the examination of the platspermic permineralised seeds from the Bajocian of Western Canada. Objectives included the elucidation of the seed anatomy of Dawsonocarpus haidorum gen. et sp. nov. from the examination of several specimens, systematic treatment and naming of the seed, comparison with the structure of Cycadeocarpus columbianus Dawson and other suitable seeds, fossil and extant.

1.2 Geology of the region in which the fossil seeds were found.

Sutherland Brown (1968) and Scudder and Gessler (1989), provide excellent sources for a detailed account of the geology of the Queen Charlotte Islands. Briefly, the islands are at the western edge of the continental shelf seaward of British Columbia. They have a land area of about 9850 square kilometres which is divided into three physiographic units:

1) the Queen Charlotte Ranges on the S.W.

2) Skidegate Plateau in the centre

and 3) the Queen Charlotte Lowlands to the N.E.

The islands were intensively glaciated in the Pleistocene.

The architecture of the Queen Charlotte Islands evolved over the past 230 million years (late Triassic - mid-Jurassic periods), as a result of the accumulation of successive layers of lava intercalated with deposition of sediments of largely marine origin. This accumulation is of the order of some 5000 metres in thickness.

Two Cretaceous sedimentary units, the first flysch-like (syn-tectonic graded interbedded marine shales and sandstones), and the second molasse-like (an association of conglomerates and sandstones of post-tectonic origin), were deposited, and are successively less involved in deformation.

A final early Tertiary episode, largely of sub-aerial volcanism, deposited some 6000 metres of intercalated columnar alkali basalt flows and sodic rhyolite ash flows. These are gently warped, eroded and
overlain by up to 2,000 metres of Mio-Pliocene sands and shales.

Crustal fracturing has been the dominant mechanism of deformation controlling volcanism, sedimentation, intrusion and secondary folding. Major north-westerly lineal faults form a pattern related to the Queen Charlotte fault. The trace of the Queen Charlotte fault runs along the continental slope.

The Queen Charlotte islands form the northern part of the Insular Tectonic Belt of the Canadian Cordillera. Souther (1977). As such they have a stratigraphic and tectonic history very similar to that of Vancouver Island, but with differences of timing and facies which become progressively more important from the beginning of the mid-Jurassic.

In the Queen Charlottes, the rocks ranging in age from late Jurassic to Recent are exposed. Volcanic rocks dominate the stratigraphic column, but they are widely intercalated with fossiliferous marine sedimentary rocks so that a fairly complete stratigraphic record exists. There were three major periods of volcanism separating four main periods of sedimentation. The Yakoun Formation is primarily a volcanic unit dominated by pyroclastic rocks. In addition, the formation includes much volcanic sandstone, some conglomerate, shale, siltstone and minor coal-beds. Many, but not all, of the sedimentary rocks are marine. The Yakoun Formation, the youngest section of the Vancouver Group, spans Middle Jurassic (Bajocian and Bathonian) and earliest Upper Jurassic (Callovian). Bajocian includes lower B member and upper A member [Fig. 1.]

In addition to the occurrence of the ammonites Stephanoceras sp. and Chondroceras sp., South Balch Island is given as a locality for “pelecypods, Cycadeocarpus columbianus Dawson, ‘Cycadeocarpus new sp.’, Nautilus sp. and Trigonia sp.”, by Sutherland Brown (1968).

Sutherland Brown and Yorath (1989) consider that “the rocks seen in the Islands did not all originate at their present sites. On the contrary, only the youngest did and the successively older ones were laid down at progressively greater distances from their present locations. The pattern by which the geology of the Islands formed is complicated and not fully known, but is thought to have begun by a slow northward drift from the site of origin at the latitude of Peru. Two separate crustal fragments (Alexander and Wrangellia terranes), collided somewhere in the Pacific before being welded to North America. More recently, the area
### 1. INTRODUCTION

#### Middle Calovian

<table>
<thead>
<tr>
<th>Age</th>
<th>Stratigraphic Units (Thickness in metres)</th>
<th>Lithology</th>
<th>Fossils</th>
<th>Intrusive Rocks</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>D member (270)</td>
<td>Tuff, lapilli tuff, crystal tuff, cross-bedded tuffaceous sandstone, pebbly sandstone</td>
<td></td>
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<tr>
<td></td>
<td>C member (320)</td>
<td>Porphyritic andesite agglomerate crystal tuff</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>B member (30+)</td>
<td>Shale, tuffaceous shale sandstone</td>
<td>Stephanoceras Chondroceras</td>
<td>Related dykes and sills</td>
</tr>
<tr>
<td></td>
<td>A member (200)</td>
<td>Calcite cemented scoriaceous lapilli tuff</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Highly variable type section used

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Fig. 1. Part of Table of Formations - Queen Charlotte Islands [after Sutherland Brown, (1968)].
of the Islands was disrupted by passage beneath the crust of the Amchin hotspot with consequent rifting and rotation."

A more detailed account of these displaced terranes such as Wrangellia, is given by Jones, Silbering and Hillhouse (1977). The coherent terrane, named Wrangellia, is juxtaposed against unlike sequences of Triassic and older rocks throughout its extent and is interpreted to be allochthonous i.e. having been displaced some considerable distance by tectonic forces. Palaeomagnetic data, obtained from the Nikolai Greenstone, indicate that Middle and/or Upper Triassic rocks in southern Alaska formed in low palaeolatitudes, probably within fifteen degrees of the equator.

1.3 Palaeobotany of the Yakoun Formation.

On a global scale, the Jurassic was characterized by uniform mild climates with highly similar plant communities composed of ferns, pteridosperms, cycads, cycadeoids, ginkgos, and conifers. Mathewes (1989) considers that broadly speaking this general picture is consistent with what is known of the Jurassic flora in the Chariottes. He mentions that the earliest fossil plants known from the Queen Charlotte Islands, which were listed by Dawson (1873), come from the Middle Jurassic, Yakoun Formation. Fossil cycad remains (Cycadeocarpus), from Skidegate Inlet together with wood and pollen spores of Mesozoic plants from coal seams suggest the presence of well developed forests in the Jurassic period.

Of special phytogeographic interest are fossil occurrences of plants not now found on the islands. The fossil bearing sedimentary rocks of the Yakoun Formation encompass the Middle Jurassic Period, about 160-170 million years ago, and Dawson (1873), referred much of the fossil wood samples sent to him to the form genera Cupressoxylon and Taxoxylon suggesting affinities with trees in the cypress and yew families.

Large calcified seeds, are a striking component of the fossil flora, and Dawson described a new genus and species from the Skidegate Inlet collections. Large rounded seeds were named Cycadeocarpus (Dioonites) columbianus, suggesting affinities with living cycads.

A second flattened type of seed was thought to represent a different species and might well have been the type of seed which is the subject of this thesis i.e. a platyspermic seed (bilaterally rather than radially
specymmetrical. Specimens studied here were brought back from South Balch Island by Callomon in 1984, and by Chaloner and Crane in 1991; they mentioned that groups of both types of permineralized seeds were exhibited in the local museum of Queen Charlotte city. The dnospermic seed (radially symmetrical in section), Cycadeocarpus columbianus Dawson, is well documented by Dawson (1873) and by Chaloner & Hemsley (1992).

Both seed types are locally common in exposures along Skidegate Inlet; these exposures also contain ammonites and other marine animal fossils. Along with the cycad remains occur leaf fossils such as those of the pteridosperm Sagenopteris, a genus widely distributed in Mesozoic rocks of the Northern Hemisphere.

Rouse (in Sutherland Brown's Bulletin No. 54), has identified a variety of gymnospermous pollen, including that of conifers and cycad-Ginkgo types from Yakoun coal, for example Classopolis classoides, Cycadopites and Tsugapollenites spp. Thus the presence of coal, wood, leaves, seeds and carbonized twigs together with pollen and spores suggests the existence of vegetation growing near sea level during deposition of the sedimentary sequences of the Yakoun formation.

1.4. Location of the seeds.

The Queen Charlotte Islands are at the western edge of the continental shelf seaward of central British Columbia and lie between 52 degrees and 54 degrees north latitude and 131 degrees and 133 degrees west longitude.

Although remote, these islands received a considerable amount of geological study prior to World War I (1914-18). In the main, this interest was largely concerned with exploration for coal and other mineral deposits.

On South Balch Island, Skidegate Inlet [Fig. 2 and 3], the seeds occur permineralized in calcium carbonate (occasionally with inclusions of iron pyrites), in a marine volcanoclastic sequence, Scudder and Gessler (1989). The matrix is softer than the seeds and, as a consequence, the seeds are found weathered out, protruding from the matrix or loose on the wave-cut platform on the south side of the island.
Fig. 2. Arrow indicates location of Queen Charlotte Islands [after Scudder and Gessler, (1968)].

Fig. 3. Arrow indicates location of South Balch Island [after Scudder and Gessler, (1968)].
This matrix, described by Callomon (1984) as being “coarse volcanoclastics, typical island arc sediments, with ammonites and scattered bivalves”, is from the Yakoun Formation, Vancouver Group, dated as of the Humphriesianum Zone, Bajocian, Middle Jurassic.

South Balch Island (also called locally Logan’s Island), is located in Bearskin Bay, an embayment off Skidegate Inlet at 53 degrees, 13 minutes, 1 second N.lat., 132 degrees, 4 minutes, 44 seconds W.long. It is approximately 400m across, and lies about 3.5 km south of the town of Queen Charlotte. The beach platform on which the seeds were collected is on the south side of the island, and its surface more or less corresponds to the bedding surface of the shaly volcanoclastic unit.

A full account of the geology of the Yakoun formation and of the section at S. Balch Island is given in Sutherland Brown’s bulletin and includes a table of fossils. The fossil seeds are exposed as protrusions on the wave-cut beach platform, and are easily extracted being harder than the matrix. Some were picked up lying loose among the shingle on the platform. A few of the seeds described were collected by Callomon in 1985, with the majority being collected by Chaloner and Crane in August 1991. A total of 28 seeds were examined in the course of this investigation.

In 1985, shortly after returning to UCL from his field excursion to South Balch Island, Callomon passed nine seeds on to Chaloner. These included four radiospermic seeds which Chaloner & Hemsley (1992), deduced as being conspecific with *C. columbianus* Dawson. Of the remaining five seeds, two seemed to be platyspermic, and in their paper the authors mentioned that these “appeared to be platyspermic in character, although it is not at present clear whether this is a preservational effect (flattening of originally radiospermic seeds), or whether they in fact represent entirely different plants.”

The research embodied in this thesis endeavours to investigate fully the anatomy of the principal platyspermic seed in the enlarged collection, referring, where appropriate, to the work carried out by Chaloner & Hemsley on *C. columbianus*. Comparison with suitable extant and fossil gymnosperms has been included.
1.5 Materials and Methods.

The calcified seeds from South Balch Island cut readily and cleanly using standard rock saws. After polishing the sections, cellulose acetate peels were made [Joy, Wills & Lacey (1956)], the etching agent employed was 10% v/v hydrochloric acid solution containing a little household detergent. The detergent, it was found, reduced bubble size during effervescence and seemed to reduce any destructive tendency of the etching process. Etching time was 20 seconds. Following a distilled water wash and drying, propanone (acetone), and cellulose acetate film were applied to the dry etched surface.

Suitable peels were mounted in Canada Balsam and dried in an oven at 80° C.

Sections chosen for SEM, were etched with acid of the strength indicated above, but the time interval was extended to 60 seconds.

1.6. The Geometry of Seed Cutting.

In order to be able to cross refer with reasonable accuracy from peels taken from different seeds or even from various levels within one seed, a labelling technique was adopted which is illustrated in the accompanying sketch [Fig. 4].

Good specimens were easily orientated during cutting, and the micropyle and base of each seed was established without difficulty. All were flattened dorso-ventrally and furrowed longitudinally. Some bore a depressed area at the base which resembled a scar such as might be left after becoming detached from a stalk or ovuliferous scale. Arbitrarily, the face of a seed bearing a basal indentation or ‘scar’ was treated as the ‘lower’ or ventral half of a possibly bivalvate seed. Because it was not possible to ascertain the spatial attitude of the seed in life the terms ‘dorsal’ and ‘ventral’ were used with caution. Again, where features were unclear, coding was delayed until clarification was obtained from internal anatomical detail.

The convention used by Rothwell (1986) was adopted with regard to the designation of longitudinal planes. The wider of the two planes was designated the major or primary plane hence LS1 was used for this, and LS2 for the minor plane. The identity of each seed, or section of a seed, was given by a letter (Callomon collection) or a number (Chaloer/Crane collection).
Diagram of *D. haidorum* showing principal cutting planes TS, RLS1 AND RLS2 yielding 4 or 8 sections, and the terminology used to enable cross-reference to be made of anatomical detail from seed to seed.

\( m \) = micropyle, \( bs \) = base. Scale bar = 1 cm.
The upper or dorsal half section was termed 'A' and the lower or ventral half section 'B'. Using the micropyle as the anterior end '1' and the basal end '2', then when the seed was cut into quarters, the seed viewed from dorsal surface became 'a' and 'alpha' sections left and right respectively.

Immediately below 'a' was 'b' and below 'alpha' was 'beta'. Further cutting to yield eight sections could be accomplished and peels compared with confidence one with another or with sections from other seeds.

A section coded 045: 1a would be a quarter from the Chaloner/Crane seed 045 which would be micropylar and left dorsal relative to appropriate planes. Peels from it could be compared with those from for example B: 1a (Callomon) and 036: 1a (Chaloner/Crane).

In this way peels from several seeds were used to build up a general appreciation of the internal anatomy of the seed with due compensation for loss of tissue in any individual seed through degradation prior to fossilisation.
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2.1 The seed habit.

Steeves (1983) states unequivocally that it is the generally accepted view today that the seed habit is a derivative of free-sporing heterospory, i.e. a condition such as is found in modern Selaginella in which the spores which produce male and female gametophytes are freely shed but differ markedly in size. This concept has been challenged from time to time (Thomson 1934; Doyle 1953), on the grounds that in some modern seed plants there is often little or no difference in size between microspores and megaspores. However, a view stated by Chaloner and Hemsley (1991), thus: “over the intervening years, much evidence has accrued from fossil plant studies which seems to reinforce the suggestion that seeds evolved from heterosporous ancestors, and that this happened not once, but probably several times i.e. that the seed is indeed polyphyletic”, is now widely accepted.

Devonian palaeobotanical studies by Chaloner et al. clearly support Steeves and others that heterospory preceded the seed habit in the fossil record and moreover that the oldest known seeds show an unmistakable structural relationship to typical extant megaspores and megasporangia. Also from the fossil record there is supporting evidence of the reduction in megaspore number from four to one, (Chaloner and Pettitt 1964; Mortimer and Chaloner 1967; Pettitt and Beck 1968). Seed bearing plants appear right at the end of the Devonian (around 360 Ma BP), and gymnosperms were an abundant feature of the land flora from then onwards.

In their paper, Chaloner and Pettitt (1964) clearly show that an evolutionary sequence (although not a simple linear series), exists in the status of megaspore tetrads across the Palaeozoic culminating in a single functional megaspore [Fig. 5]. The authors also give a range of structures dating from the late Devonian to Tertiary times illustrating ovule/seed evolution from a single functional megaspore [Fig. 6].

2.2 The gymnospermous seed.

Gymnosperm literally means “naked seed”. The ovule or seed is not enclosed within a carpel as in angiosperms (although it may be embedded in specialised coverings), but is borne exposed on a sporophyll, scale or some comparable structure. Foster and Gifford (1974), stated that “there is an increasing body of
The changing status of megaspore tetrads in Paleozoic plants. These represent a morphological series and not a time sequence; Archaeopteris and Archaosperma are Devonian, Cycas is Recent and the remainder, Carboniferous. Archaeopteris had a varied number of megaspore tetrads, typically 3-5; (see also Fig. 5). A number of Paleozoic lycopods (e.g. Bothrodendrostrobus) have a single tetrad of megaspores, all of equal status. Bensonites has a unique 2-plus-2 configuration. All up to and including Cardiocarpus have a tetrahedral configuration of the tetrad; Cycas alone of those illustrated has a linear megaspore tetrad, but we have no firm knowledge of when this type of tetrad first appeared in the fossil record.

5.

Fig. 5. The changing status of megaspore tetrads in Paleozoic plants. [Chaloner and Pettitt, (1987)].

6.

Fig. 6. "What is a seed?" [Chaloner and Pettitt, (1987)].
2. THE GYMNOSPERMUS SEED

Palaeobotanical evidence to support the idea that naked seeds probably evolved independently in several Palaeozoic lines of plants." This concept has led to the widespread rejection of the Gymnospermae as a natural taxon, for example, by Arnold (1948), and the recognition, in its place, of several parallel groups of naked seeded plants. Bell and Woodcock (1983), state that "...the affinities of the cycads appear to be pteridospermous, those of Ginkgo cordaitalean. Here then are two groups of plants whose evolution has probably been independent for many millions of years, but which are at the same level of advancement in their reproductive processes. In both, despite their arborescent form, fertilization is still brought about by flagellate spermatozoa, liberated from very similar male gametophytes."

By contrast, siphonogamy is the rule in conifers and in Ephedra, despite the latter having a recognisable archegonium in the female gametophyte. However, Beck (1976), and others consider that the progymnosperms (plants with gymnospermous secondary wood and pteridophytic reproduction), represent a plexus of Devonian age from which cycadophytes and coniferophytes evolved. Hence it is widely believed that Gymnospermopsida arose from Progymnospermopsida.

The progymnosperms produced ovules, which after fertilization, developed into seeds. Palaeobotanically, the distinction between ovule and seed is often uncertain, unless for example, the structure contains an embryo which confirms it as a seed. Hence, the terms ovule and seed are often used interchangeably in discussing fossil gymnosperms.

Meyen (1987), concluded that from successive comparisons of all the best studied gymnosperm genera and by tracing the characters in the history of the taxa, it became apparent that the major phylogenetic lineages of gymnosperms are best reflected in the evolution of seeds and cupules. He divided the oldest seeds into two types: platyspermic e.g. Spermolithus devonicus Johns [Fig. 7, a]), and radiospermic e.g. Hydrasperma sp., a seed with a cupule. He described platyspermic seeds (bilaterally symmetrical), as being longitudinally flattened with two vascular bundles passing along the main plane in the wings produced by an integument. More rarely the bundles divide in the same main plane. Platyspermic seeds lack a cupule. The radiospermic (radially symmetrical) seeds are unflattened, and several bundles arranged in a circular pattern pass through the integument. A cupule may or may not be present. The early appearance of both platyspermic and radiospermic seeds more or less synchronously at the end of the Devonian is a strong argument for a polyphyletic seed origin, (Chaloner et al. 1977; Beck 1981), as referred to earlier in section 2.1 above.
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Fig. 7. 

a) = Spermolithus devonicus [Redrawn from Chaloner, Hill and Lacey (1977)].


Fig. 8. 

Origin and transformation of seed envelopes:

a) megasporangium and surrounding sterile axes in hypothetical ancestor of gymnosperms;

b) oldest seed megasporangial apex is transformed into salpinx, whereas integumental and cupular lobes are modified;

c) formation of integumental micropyle, base of salpinx is transformed into lagenostome with central column;

d) nucellus fused with integument, formation of cupular micropyle.

Key: 1 = integument; 2 = nucellus; cupule lobes and their derivatives in a) - d) stippled, [after Meyen, (1987)].
Meyen further suggested that the cupule, in the course of evolution, became the outer integument whilst coalescence of the inner integument with the nucellus, preserved the vascularisation of the former and resulted in the formation of a “vascularised nucellus” or inner integument. (Fig. 8, a) - d)]. He also postulated that the megasporangial apex underwent a series of transformations over the evolutionary timescale producing structures such as the salpinx and lagenostome (Fig. 7, a) and b), to aid pollen, or prepollen gathering. Later developments, in conjunction with integumentary changes, gave rise to pollen chambers (with or without a nucellar beak), and to the micropyle.

In Palaeozoic seeds there is ample evidence of elaboration at the nucellar apex associated with pollen reception. The salpinx and the lagenostome are examples of devices which enable pollen to be guided downwards towards archegonia. Pettitt (1970), in addition to defining an ovule as an integumented sporangium where the integument forms a micropyle at the distal end, further suggested that a relationship existed between the degree of development of the salpinx and that of the micropyle. The weaker the micropyle, the stronger functionally was the salpinx; this is illustrated in Meyen’s sequence, (Fig. 8, a) - d)].

Long (1961) suggested that a well developed salpinx may have been amongst the first structural refinements of the apex of the megasporangium in the evolution of heterosporous. Moreover, Long (1959, 60 a & b), Andrews (1963) and Stewart (1983) utilised the telome theory of Zimmerman (1952) to account for this progression in megasporangial development which culminates ultimately in a process akin to the complete lateral fusion of telomes. Andrews (1963) also, in a reference to the uniqueness of the salpinx, supports Long thus, “the evolution of a well developed salpinx may have been one of the earliest structural refinements of the megasporangial apex or nucellar beak”.

The “tent-pole” (a central apical prolongation of the megagametophyte), was thought by Long (1944) to rupture the floor of the pollen chamber above exposing the archegonia to microgametophytes and their flagellated sperms. In addition, Stewart considered that the tent-pole may have acted as a plug in the distal end of the micropyle after pollination. Examples of the tent-pole may be seen in the ovules of genera as diverse as Nucellangium (fossil) and Ginkgo (extant).

Foster and Gifford (1974) suggested that the integument is an accessory structure if it is assumed that the nucellus of the ovule is the functional equivalent of a megasporangium. The integument is absent from the megasporangia of lower heterosporous vascular plants and could be regarded as an evolutionary
advance in terms of ovular protection. All extant gymnosperms, with the exception of the Gnetopsida, have a single integument; this is firmly joined to the nucellus at the base of the ovule and is termed the chalaza.

The anatomy of the integument of those gymnosperms most comparable to my seeds, is found in cycads, Ginkgo, Juniperus, taxads and podocarps. The integument is differentiated into three tissue zones; an outer fleshy layer, a middle sclerenchymatous layer and an inner fleshy layer. The degree of development of each of these layers, (where present), varies amongst different groups of gymnosperms. In cycads and Ginkgo the sarcotesta (outer fleshy layer) is relatively thick; this tissue is firm in cycads, but mucilaginous in Ginkgo. The possession of a sclerotesta is much more widespread in gymnosperms, but the development of an endotesta (inner fleshy tissue), may be much reduced, particularly on maturation of the ovule. Vascularisation follows a similar trend: in cycads both fleshy zones are vascularised, but in Ginkgo, Torreya and fleshy podocarps vascularisation is only found in the endotesta. In Dawsonocarpus only the mesotesta was vascularised.

The rate of evolution of each of these principal elements may well have varied depending upon its intrinsic success or lack of it and thus a particular pattern of one group of tissues, for example, the integumentary structure, may be retained over several millions of years whilst profound changes in the anatomy of the reproductive apparatus may have ensued over the same period. By the Lower Mississippian the seed habit was well established as numerous fossil ovules from the Tournaisian of Scotland show, (Long 1966). A sequence of micropylar development, involving progressive fusion of integumentary lobes, may be seen in the structures of Genomosperma kidstoni (incomplete fusion), Genomosperma latens (a rudimentary form), Euryostoma angularare (a more advanced form) and finally Stamnostoma huttonense, (a recognizably complete structure), Fig. [9 a) - d]).

However, all these fossils are of closely similar age and this blurs their evolutionary status.

Paradoxically, it could also be argued that the the integument of Archaeosperma from the Devonian has a more developed micropylar structure than that of Genomosperma from the Mississippian.

Descriptions of fossil seeds of gymnospermous plants (or of their close relatives), are abundant in the palaeobotanical literature. Few however are based upon the examination of permineralised fossils such as those found in the Queen Charlotte’s, but more commonly upon data obtained from impressions, casts, and
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(where possible), cuticular material from them.

From the palaeobotanical standpoint, information is required on the principal structural elements within the seed or ovule for example, integumentary tissues, reproductive apparatus and vascularization, before an opinion may be offered as to its evolutionary status.

In extant gymnosperms, the pre-fertilized ovule normally possesses:

i) an ovular envelope or integument, usually with a vascular system,

ii) a micropyle of the integument,

and

iii) a megasporangium (nucellus) containing a megagametophyte with one or more archegonia,

Of interest diagnostically are:

1. The degree to which the inner surface of integument and outer surface of the nucellus are fused to form the micropylar chamber. In general, early gymnospermous seeds have less fusion between nucellus and integument than later ones. In many Palaeozoic seeds, the lack of fusion is greater than 20% i.e. the micropylar chamber is large.

2. Absence/presence of a 'pollen trapping and guiding' mechanism and its degree of elaboration. Palaeozoic seeds had very elaborate structures.

A further problem with fossil ovules or seeds is to decide the probable state of maturation achieved prior to fossilization. Evidence from extant seeds e.g. cycads & Ginkgo show that the changes in tissue structure as the ripening processes occur are quite considerable as demonstrated by Read and Solt (1986), [Fig. 10. a) and b)].

In addition, and of diagnostic importance comparatively, is the structure of the vascular system and the nature of the tracheidal pitting.
2. THE GYMNOSPERMOUS SEED

Fig. 9. Stages in the evolution of the integument:

a) = *Genomosperma kidstoni*, unfused telomes, b) = *G. latens*, partial fusion of telomes,
c) = *Euryostoma angulare*, fusion of telomes except the upper third of the preovule,
d) = *Stannostoma huttonense*, complete fusion of telomes to form integument and micropyle.

Lower Carboniferous. [Redrawn from Long, (1959, 60a and 60b)], [after Stewart, (1983)].

Fig. 10. Diagrammatic schemes illustrating tissue changes in a *Cycas* seed on maturation. [after Read and Solt, (1986)].

a) = Generalized diagrammatic scheme of *Cycas* seed (slightly enlarged) based on information from Chamberlain, Pant, Swamy and personal observation.

b) = Diagrammatic scheme of mature *Cycas* ovule (slightly enlarged) based on schemes by Chamberlain, Pant, Swamy etc.
2. THE GYMNOSPERMOUS SEED

2.3. Other seeds from the Mid - Jurassic and the Upper Triassic.

To find, in the available literature, gymnospermous seeds of this age in a state of preservation enabling meaningful comparison with Dawsonocarpus haidorum has not been easy. As stated earlier, too many are casts or impression fossils allowing only superficial treatment to be made often limited to the tissues which are visible on the fossil under the microscope, or from a mounted peel or an electron - micrograph.

Thomas and Harris (1960) enlarged upon the structure and affinities of Beania gracilis Carruthers, from the Yorkshire Jurassic, a bilaterally symmetrical seed with a flattened base which was shed from an organ resembling a very lax cone quite unlike any living cycad. Furthermore the slender axis of this cone suggested a pendulous habit. The seed itself was similar in some respects to extant species of Zamia. Mature seeds of B. gracilis, [Fig.11], were up to 16mm x 13mm and, from macerations, Harris (1961) showed that the integument was fused to the nucellus throughout the lower two-thirds of the seed, but free from it at its apex. There was an outer fleshy layer, a middle stony layer and an inner fleshy layer. In the latter was evidence of longitudinally running vascular bundles up to the level at which the integument became free from the nucellus. From all the evidence available, Harris regarded Beania gracilis as a cycad.

Stockey (1980), described the anatomy and morphology of Araucaria sphaerocarpa Carruthers, an ovulate seed cone resembling Araucaria bidwillii Hooker from the Jurassic Inferior Oolite of Somerset. The latter are noted for the ease with which the seeds become detached from the the cone scales on maturation, the cones retaining their empty scales, unlike other araucarians.

Reymanowna (1986), is of the opinion that the podocarps, far from being regarded as a Southern Hemisphere family, occurred widely in the Northern Hemisphere in the Mesozoic. The plant remains (from the Middle Jurassic of the Krakow region, Poland), examined by Reymanowna, were carbonaceous compressions in grey mudstone requiring prolonged bulk maceration. A small seed and integral cone-scale (c. 4mm in length) Harrisiocarpus gucikii gen.et sp.nov. associated with podocarpaceous leafy shoots is described; the structure of the seed shows a closely fitting scale in which distinction between scale and epimatium is rather ill-defined. The scar of attachment of seed to axis was near the base of the adaxial surface rather than exactly opposite the micropyle. Reymanowna assigned H. gucikii to the Podocarpaceae on the combined evidence from the examination of fossil material of shoot, cone, seed and bisaccate pollen. She said "it does not agree with anything living or fossil outside that family."
Fig. 11. *Beania gracilis* diagram of ovule in LS. Ovule is about 1.5 cm in length with internal structure similar to extant cycads. [Redrawn from Harris, (1941,1964), after Stewart, (1983)].

Fig. 12. *Carpolithes rhabdotus* after Barker et al., (1975).

A lateral view has hilum downwards, Type Specimen 44921. Nos. 2), 3) and 4) are unspecified views of Type Specimen V44920, but presumably 2) is seed from above or below, and 3) and 4) represent views of the micropylar end and the base.

Magnification x 6.
The partly exposed ovules found in *Harrisio carpus* are also a feature of genera such as *Dacrydium* Spolander ex Forster, *Saxeogothea* Lindley and *Microcachrys* Hooker. Amongst Mesozoic podocarps Reymanowna mentions *Scarburgia* Harris as the most similar fossil genus to *H. gucikii*, with the cone scale components of ovule, epimatium and bract scale well shown in *S. hildii* Harris. Reymanowna makes the point that *Stalagma samara* Zhou, with its conspicuously winged seeds, is very different from *Harrisio carpus* (she actually cites *H. cracoviensis* comb.nov.), although Zhou also assigns *S. samara* to the Podocarpaceae. The seed of *H. gucikii* is a cordate structure of thickness 0.2mm with length 2.0 - 3.0mm and width of 2.0 - 2.5mm; these dimensions give a winged appearance, but this could be a preservational effect. Comparison of this seed with *Dawsonocarpus haidorum*, is not easy because of the lack of anatomical detail in *H. gucikii*. Both seeds have a perinucellar micropyle and Reymanowna identified a “micropylar canal” which might be an anatomical equivalent structure to the nucellar beak in *D. haidorum*. The apparently intimate association of the bract scale (which may not be separate from the epimatium), with the lowersurface of the seed is different from *D. haidorum*.

Barker et al (1975), whilst investigating a thin cherty layer near the base of the Purbeck Beds in Dorset, gathered a variety of specimens which, in addition to freshwater ostracods, included the remains of some land plants. Amongst this flora were several seeds referred to *Carpolithec* Schlotheim; the seeds were partially petrified, but unfortunately yielded very little information. Of passing interest with regard to *Dawsonocarpus* is a description (with accompanying plates), of a small seed *Carpolithec rhabdotus* sp. nov. The seed is flattened with a ridged and furrowed surface running longitudinally from base to apex. These ridges and furrows (rhabdotus Gk = fluted) commence 2mm from the base and end 1 mm from the micropyle. [Fig 12.]. The authors mentioned the close resemblance of *C. rhabdotus* to *Cycadeospermum schlumbergeri* Saporta (1895), a very similar seed morphologically, found in the Jurassic of France.

Zhou (1983) describes a podocarpaceous conifer *Stalagma samara* gen. et sp. nov. from the Upper Triassic of Hunan, China. Amongst the material are large female cones with platyspermic seeds. The specimens are preserved on small pieces of black shaly mudstone and silt. Although older than the Bajocian seed *Dawsonocarpus, Stalagma samara* is interesting in that the seed is from a Triassic podocarp and is platyspermic. Moreover Zhou shows diagrammatically the structure of this seed and how it was borne on the cone scale (sporophyll). Vascularisation is not shown, so one may conclude that perhaps the manner of fossilisation associated with the mudstone and silt precluded the preservation of this feature, if present in life, in either the seed or cone scale.
2. The Gymnospermous Seed

The seed is small, thin, broadly round or ovate roughly 7.0mm x 7.0mm with thickness varying from 1.9mm at the base to 0.5mm at the obtuse apex. The margin of this winged seed is 1.0mm - 2.5mm at the widest part, narrowing toward both ends; the seed is ridged longitudinally and is attached on an elliptical placenta 1.5mm x 3mm to the cone scale, [Fig 13. i) & j)].
Fig. 13. *Stalagmam samara* Zhou Zhiyan. i). Diagrammatic restoration of seed in median longitudinal section parallel to cone scale. Magnification x 10.

Key: i = inner cuticle of integument, n = nucellus, m = megaspore membrane, s = stony layer, o = outer cuticle of integument.


Both i) and j) after Zhou Zhiyan [Chow], (1983).
3. THE NEW SEED

3) THE NEW SEED -
DAWSONOCARPUS HAIDORUM GEN. ET SP. NOV.

3.1. Systematic Treatment.

Class: Coniferopsida s.l. incertae sedis.

Genus: Dawsonocarpus gen. nov.

Species: Dawsonocarpus haidorum gen. et sp. nov.

Combined generic and specific diagnosis:

Seed cordate to more or less ovate in plan view, 3cm - 6 cm long x 4cm - 7 cm broad and symmetrical (minor longitudinal plane), 2.5cm - 4 cm in thickness, dorso-ventrally flattened, asymmetrical (major longitudinal plane), bivalvate with a prominent equatorial rib and suture in the major radial longitudinal plane running from each side of the micropyle towards the base where it becomes less distinct or is absent.

Longitudinal furrows in the seed surface run from micropyle to within a few millimetres of the base. Apex of seed may be apiculate. A lateral indentation at the base may be present. Epidermis (where preserved), composed of cells 88μm - 163μm wide x 40μm broad, with cuticle 13μm - 40μm thick. Broad outer zone of integument (sarcotesta), consists of large thin-walled cells, typically 175μm x 130μm immediately below the epidermis grading inwards to 67μm x 37μm. A narrow layer of thick-walled cells (mesotesta) typically 82 μm x 27μm (somewhat radially compressed), lies in the major longitudinal plane of the seed forming a boundary between the two presumed valves. Sclerotesta thin, composed of thick-walled cells radially compressed and typically 125 μm wide x 15 μm broad. Central zone - (nucellus), not cellularly preserved, usually occupied by calcite.

Vascular system, forming a plate in the median major longitudinal plane, largely composed of tracheids with uniseriate bordered pits; a vascular plate, bifurcating from the base becomes juxtaposed to the inner face of nucellus. Tracheids diverge laterally from the plate, to form a network. Dis tally, vascular tissue grades from tracheids to transfusion tracheids. Nucellar beak prominent. Nucellus free from integument only at the apex.
The specific epithet is derived from the Haida tribe, in whose territory the seed occurs.

The generic name is in recognition of the work of J. W. Dawson, who first described fossil seeds from the Queen Charlotte Islands. The type specimen is seed SBALCH 036 GSC Type No. 109783b.

Type material is to be deposited with the Type Invertebrate and Plant Collection, Geological Survey of Canada, 601 Booth St., Ottawa, Ontario, Canada K1A 0B8, once research has been completed. The allocated GSC Type Collection numbers are given, where appropriate.

### 3.2. Description of Morphology and Anatomy

The 28 platyspermic seeds which were investigated in the combined collections of 1985 and 1991 varied in size from 3.1 cm x 4.0 cm to 6.0 cm x 7.0 cm. Thickness varied between 2.5 cm and 3.8 cm. Allowing for loss of eroded material in the fossils, the shape of the seed in life was roughly cordate. The seed was evidently dorso-ventrally flattened and had a prominent sutured rib which gave it a bivalvate appearance. This rib, though absent to some extent from the basal area, is well marked from near the base up to the micropyle.

Surface features, common on several seeds, include poorly defined grooves or furrows which run from base to micropyle. The apex was apiculate in one or two examples. Basal features which might indicate the point of attachment of the seed to an axis or sporophyll were lacking in most examples, although some specimens showed an indentation which is interpreted as an abscission scar. [Figs. 14, 15 and 16].

Transverse sections through the base and sub-basal regions indicate that a vascular plate extends to the base of the seed. As mentioned above, seeds examined so far either showed a scar or were extensively damaged, probably as a result of tissue degradation prior to fossilisation. Thus the way in which the vascular tissue passed into the seed base remains unknown.

Without doubt the structure of this mid-Jurassic seed is unusual if not unique. The aspect presented is that of a seed with a pronounced suture in the median equatorial and major plane; this suture is however abscet at the base. It is symmetrical about its minor longitudinal axis, but is asymmetrical in the major longitudinal plane because a) the two parts of an apparently bivalvate structure may vary in size and b) there is a lack of symmetry basally.
3. THE NEW SEED

Fig. 14. *Dawsonocarpus haidorum*, anterior view of a seed showing suture s (arrowed), and micropyle m (arrowed).

Scale bar = 1.1 cm. GSC Type Collection 109783a.

Fig. 15. *D. haidorum*, view of proximal end of a different seed in which the basal indentation, sc (arrowed), which might be a scar left after abscission from the sporophyll, is well shown.

Scale bar = 0.9 cm. GSC Type Collection 109783b.
Fig. 16. *D. haidorum*, a seed having near cordate outline. The eroded micropyle is at the top, and a scar sc (arrowed), [less prominent than in Fig. 2], is at the base.

Scale bar = 1.1 cm. GSC Type Collection 109783a.
A description of the anatomy as seen in longitudinal section involves consideration of the asymmetrical nature of this platyspermic seed. The flattened symmetry gives rise to major and minor radial longitudinal planes passing through the centre of the seed. The seed is bifacial, possessing only one plane of symmetry (Meyen 1984), (Rothwell 1986). Only in the minor longitudinal plane is one half of the seed a mirror image of the other.

Median transverse sections [Figs. 17, 18, 19, 20, 21 and 23] show a marked zonation of tissue types. A typical seed 4.0 cm in width x 3.5 cm in thickness showed seven zones:

a) an epidermal layer (eroded) of cells one cell in thickness and typically 80 - 163 µm x 45 µm, with a cuticle 2.5 µm - 4 µm thick. [Fig. 18],

b) the sarcotesta, a comparatively wide zone 7 mm - 8 mm of large thin-walled cells grading from 67 µm x 37 µm (innermost) to 175 µm x 130 µm sub-epidermally. [Fig. 18],

c) the mesotesta, a narrow zone (1 mm - 2 mm) of thick walled cells somewhat radially compressed and typically 82 µm x 27 µm. [Fig. 17],

d) the sclerotesta, a narrow zone (1 mm - 2 mm) of thick walled cells, more radially compressed than those in c), on average 125 µm x 15 µm. [Fig. 18],

e) vascular tissue, (apparently originating within in the sclerotesta), which is seen in TS as two roughly wedge shaped areas with the base of each wedge abutting against the nucellus and tapering outwards towards the epidermis; the vascular tissue progressively narrows to a sheet a few cells in thickness which persists through most of the mesotesta. [Figs. 26 and 27].

f) innermost zone, a calcified region assumed to have been formerly occupied by the female gametophyte (primary endosperm), typically 23 x 18 mm; traces of megaspore membrane are evident in some examples. [Fig. 19].

and g) an external suture [Figs. 14, 15, 19 and 20].
Fig. 17. *D. haidorum*, a composite section passing through the suture (in TS) showing calcified split, with adjoining mesotesta, and also remnants of vascular tissue at the proximal (left-hand) end of the split.

Scale bar = 1 mm. GSC Type Collection 109784a.

Fig. 18. *D. haidorum*, a composite section of anatomical structure showing progression of tissues from epidermis (left) to calcitised region formerly occupied by female gametophyte (at right).

Scale bar = 1 mm. GSC Type Collection 109784b.
Fig. 19. *D. haidorum* in TS (median). Scale bar = 3.5 mm. GSC Type Collection 109784c.
Fig. 20. *D. hasodorum*, half seed in TS taken 5 - 7.5 mm below the micropyle. Remnants of lower region of nucellar beak and laterally extended vascular plate are visible. 

Scale bar = 3.5 mm. GSC Type Collection 109784d.
South Balch Island Platyspermic Seed
*Dawsonocarpus haidorum*

Segment of seed in median TS passing through the equatorial sutured rib:

- **a. 0.5 - 1 mm** epidermal cells (eroded) 80 x 45
- **b. 8 mm** large thin walled cells gradually diminishing in size towards zone c sarcotesta 175 x 130
- **c. 1 - 2 mm** cells thick walled and in slightly compressed in sutured rib mesotesta 82 x 27
- **d. 1 - 2 mm** cells thick walled and highly compressed radially sclerotesta 125 x 15
- **e. N/A** trachidal mass outer 42 x 32 inner 14 x 14
- **f. female gametophyte - occupied by calcite**

Typical cell dimensions in micrometres

*Cycadeocarpus columbianus Dawson*
(after Chaloner and Hemsley)

Segment of seed in median TS

- **a. 0.5 - 1 mm** epidermal cells (eroded) 150 x 110
- **b. 8 mm** large thin walled cells gradually diminishing in size towards zone c sarcotesta 220 x 220
- **c. 2 mm** cells thick walled, irregular and compressed radially sclerotesta 100 x 30
- **d. 1 - 2 mm** gap filled with calcite
- **e. 2 mm** cells small roughly circular and variable in size - spongy? 40 - 100 diameter
- **f. female gametophyte - occupied by calcite**

Typical cell dimensions in micrometres

Figs. 21. and 22. Comparison of the platyspermic seed *D. haidorum* with the radiospermic seed *Cycadeocarpus columbianus* Dawson. Anatomical structure in TS.

A. Scale bar = 3.5 mm. B. Scale bar = 5 mm.
Fig. 23. *D. haidorum*, in TS (median) showing its platyspermy and its winged appearance. 

- a = epidermis (eroded), b = sarcotesta, c = mesotesta, d = sclerotesta, e = vascular tissue,
- f = female gametophyte (calcite) and g = suture. Scale bar = 5 mm.

Fig. 24. A diagram of *D. haidorum* in RLS1 (major longitudinal axis). Note that in median RLS1, sclerotesta (d elsewhere), is replaced by tracheids or tracheids plus transfusion tissue.

- a = epidermis (eroded), b = sarcotesta, c = areas of mesotesta, d = areas of tracheids or of tracheids + transfusion tissue, f = site of female gametophyte (calcite), i = isodiametric cells,
- m = micropyle and n = nucellar beak. Scale bar = 5 mm.

Fig. 25. Diagram of *D. haidorum* in RLS2 (minor longitudinal axis).

- a = epidermis (eroded), b = sarcotesta, c = mesotesta, d = sclerotesta, e = vascular tissue,
- f = female gametophyte (calcite), i = isodiametric cells, m = micropyle and n = nucellar beak. Scale bar = 5 mm.
The median vascular plate of *D. haidorum* appears wedge shaped in this TS; base of wedge is at the top of the figure tapering below. A mass of possible protoxylem elements has broken away at the base of the wedge (top of figure).

Scale bar = 200 µm. GSC Type Collection 109786a. Composite photograph.

*D. haidorum*, central region of Fig. 26, at a higher magnification. Scale bar = 100 µm.

GSC Type Collection 109786a.

Note that tracheids towards the base of the wedge are seen in TS, but that distally, as wedge narrows, these gradually orientate to LS as the vascular tissue fans outwards to the suture. Also, transfusion tissue becomes interspersed with tracheids distally.
Zones b) and d) clearly conform to tissues generally referred to as sarcotesta and sclerotesta respectively in descriptions of seed anatomy e.g. Pant (1973), Schapiro (1951) and Dehgan & Yuen (1980). In seeds of cycads, Ginkgo and some conifers, the term sclerotesta is synonymous with a hard stony layer, whilst the sarcotesta is a parenchymatous region typically soft or firm within a bounding epidermis.

However, the terminology of zone c) presents a problem, in that if zone d) (sclerotesta) is compared to the stony layer in extant seeds, the former might function, in general, as a transition zone between sarcotesta and sclerotesta with a specialist protective function for the vascular tissue and is referred to here as 'mesotesta'. Corner (1976) uses the term “mesotesta” in a reference to dicotyledonous seeds, but his tissue is entirely sclerotic and therefore different from the vascular elements of Dawsonocarpus.

No fleshy layer inside the sclerotesta (or any remains of it), has been detected in any of the seeds examined so far. However, reference to Read & Solt (1986), commenting on the work of Chamberlain et al, shows how the endotesta can be crushed to a “membrane” and hence become difficult to characterise with certainty when the ovule has developed into a mature seed, as mentioned earlier in section 2.2.

A median longitudinal section through the minor longitudinal plane shows, [Figs. 25 and 28], the relatively thick outer zone or sarcotesta and an inner mesotesta and sclerotesta, the latter predominantly (though not exclusively), enclosing the female gametophyte. The sarcotesta shows groups of cells containing fossil resin, seen as a black reticulate mass [Figs. 30 and 33]. In the basal region, the sclerotesta is continued downwards, but is gradually replaced by a wedge-shaped pad of parenchymatous cells [Figs 25, and 28], seen more clearly in the major longitudinal plane [Figs. 24 and 29].

Distally, the sclerotesta encloses the pollen chamber [Figs. 24, 25, 31 and 32]. About three-quarters of the length from the base to the micropyle of the seed, the sclerotesta splits unequally into two layers. The inner, thinner part, ensheaths the upper nucellus which finally becomes a nucellar beak with a swollen base; there is a cavity within the beak [Fig. 32] for at least part of its length. The outer and thicker layer becomes the lining of the micropylar chamber [Fig. 20].
3. THE NEW SEED

Fig. 28. *D. haidorum* in TLS2. Calcite has penetrated the micropyle and part of the base of the nucellar beak is just visible distally; isodiametric cells below the calcified supposed female gametophyte are well shown; these taper off and in this tangential LS, vascular tissue is evident below them. Note the basal indentation at lower right just above the scale bar.

Scale bar = 3.3 mm. GSC Type Collection 109785a. Tissue details are given in Fig. 25.
Fig. 29.  *D. haidorum*, a seed in RLS1 (the micropylar pole uppermost), note the cordate appearance. Tissue details are outlined in Fig. 24. Some indication of the median planar nature of the vascular system, and of the mesotesta above and below this (making allowance for some buckling in this plane), may be gained from this figure examined in conjunction with Fig. 25. Scale Bar = 1.75 mm. GSC Collection 109785b.

Fig. 30.  *D. haidorum*, one of many resin bodies found in the sarcotesta of the seeds.

Scale bar = 65 µm. See also Fig. 33.
3. THE NEW SEED

Fig. 31. *D. haidorum* in RLS2, nucellar beak which has a (?preservation) cavity within it near the apex. Scale bar = 500 µm. GSC Type Collection 109787b.

Fig. 32. *D. haidorum*, apex of beak and part of micropylar chamber. Scale bar = 500 µm. GSC Type Collection 109787b.

Fig. 33. *D. haidorum*, SEM of resin body from cells of the sarcotesta in TLS1. Structure resembles a solid foam probably resulting from diagenetic effects. Scale bar = 12 µm.
One seed showed what appears to be a stoma on the nucellar surface. In fractures of this specimen the integument came away cleanly from the calcitic mass which was a representation of the female gametophyte. Peels taken from the exposed nucellar region of the cast showed what appear to be haplocheilic stomata. The best of them, with apparently 6 or 7 subsidiary cells, is shown [Fig. 35].

Tracheidal tissue is only seen in tangential longitudinal sections (TLS2 in figures) lending support to the view that the vascularisation of this seed is predominantly in the major radial longitudinal plane (RLS1) and is in the form of a plate roughly wedge-shaped in TS. The base of this wedge of vascular tissue is embedded in sclerotesta and extends laterally, gradually thinning, until the plate is only one or two cells in thickness. This lateral extension from the sclerotesta is sandwiched within mesotesta (see above).

In median longitudinal section through the major longitudinal plane, or in tangential longitudinal section close to the radial longitudinal plane, good specimens are cordate in outline [Figs. 24, 29 and 34]. Vascular tissue appears to originate at the base of the seed at indentations to right and left of a central parenchymatous wedge (sarcotesta) which is surmounted by a roughly conical mass of isodiametric cells. Vascular strands then pass distally, fanning laterally towards the outer edges of the seed and inwards towards the presumed site of the female gametophyte (now calcite). There they appear to merge with the vascular strand adnate to the gametophyte from which they may be separated, at closest contact, by tissue as little as one cell in thickness or indeed may abut directly onto the megaspore membrane. Lateral branches of vascular tissue are subtended from the right and left strands and become adnate to the gametophyte in this major plane.

In the micropylar area, the anatomy is much the same as in the minor radial longitudinal plane (RLS2) except that the female gametophyte is wider, as is the width of the nucellar beak, repeating the dorso-ventral flattening of this platyspermic seed.

Owing to apparent distortion, the sandwich-like structure of the vascular plate, enclosed by layers of mesotesta above and below it, is buckled here and there. It is therefore difficult to obtain a complete view of the vascularisation in RLS1. The buckling gives rise to a patchy effect of vascular tissue and mesotesta [Fig 24].

The tracheids that comprise the vascular plate show uniseriate bordered pits; these are circular or slightly elliptical with the longer axis of the ellipse running in the same direction as the long axis of the
3. THE NEW SEED

Fig. 34. *D. haidorum*, a seed which had split along the major longitudinal plane showing a near cordate outline and the site of the supposed female gametophyte (calcite) with prominent nucellar beak just visible.

Scale bar = 1.1cm. GSC Type Collection 109783c.

Fig. 35. *D. haidorum*, peel of upper nucellar surface showing haplocheilic stoma with 6 or 7 subsidiary cells.

Scale bar = 60μm. GSC type Collection 109787a.
tracheid. Each pit has a wide border; typical dimensions are 8.5 µm x 7.5 µm with a border about 2 µm. The pits [Figs. 36, 37, 38 and 39] most closely resemble those generally described as "podocarpoid" in conifer secondary xylem (Greggus 1955).

Although traces of tracheids with scalariform thickening have been noted, these are rare. Accompanying the tracheids are some shorter cells which may be transfusion tissue (Lederer 1955), or of the "accessory transfusion type" (Pant 1973). Their dimensions are somewhat variable ranging in length from 40 µm - 70 µm, and width from 10 µm - 15 µm. In general the long axis of these elements is greater than the short axis by a factor of four to five times. There are also traces of reticulate thickening on some of these cells.

The innermost tracheids of the vascular plate (a narrow zone some few cells across transversely), seen at the top of Figure 26, are interpreted as protoxylem of an endarch structure. No phloem has been identified.

Where the plate of vascular tissue is closest to the tissues at the base of the female gametophyte and adnate to the latter, the tracheids are the major element in the tissue, but toward the margin of the seed the number of 'transfusion tracheids' increases until they become predominant in the peripheral winged areas of the seed. The vascular plate of conducting elements, enclosed by mesotesta, forms a median layer surrounding the site of the gametophyte for the whole of its length, except for a region below the base of the gametophyte. It is also less evident in its upward extension in the region adnate to the pollen chamber and nucellar beak.
Fig. 36. *D. haidorum*, a section exhibiting vascular detail from Fig. 27., at higher magnification. Tracheids with uniseriate bordered pits are interspersed with transfusion cells. Mesotesta is shown flanking the calcified fissure.

Scale bar = 40 μm. GSC Type Collection 109786a.

Fig. 37. *D. haidorum*, tissue from the central region of Fig. 36, mid-way between innermost and outermost vascular elements showing tracheids with uniseriate pits, and others which have a reticulate or annular thickening.

Scale bar = 10 μm. GSC Type Collection 109786a.
Fig. 38. *D. haidorum*, SEM of part of the vascular wedge showing tracheids with bordered pitting.
Scale bar = 20 µm.

Fig. 39. *D. haidorum*, SEM showing two bordered pits, from Fig. 38., in detail.
Scale bar = 2.2µm.  GSC Type Collection 109786b.
4. COMPARISON OF D. HAIDORUM WITH OTHER SEEDS.

Harris (1947) sounded a warning note to haunt all those attempting to draw comparisons between the Jurassic flora and extant exemplars thus: "The Jurassic flora is too different from the flora of today for us to get much from direct comparison with modern plants." However, an attempt is made in this section to make a comparison of the Dawsonocarpus seed with both fossil and extant exemplars.

Extant plants that produce seeds comparable to Dawsonocarpus with a firm textured, rather broad sarcotesta and a narrow, hard or stony sclerotesta are found among cycads, Ginkgo and some conifers e.g. taxads and podocarps.

The effects of permineralisation and fossilization make it unlikely that in life the sarcotesta of Dawsonocarpus could have been soft and fleshy like the mature seeds of Ginkgo biloba or indeed the aril of Taxus baccata. However, a sarcotesta approximating to the firmer outer tissue of seeds of extant Cycas circinalis might have been more probable in seeds of Dawsonocarpus, or indeed in the seeds of Cycadeocarpus columbianus Dawson, Chaloner and Hemsley (1992), with which they occur in the rock exposures on South Balch Island.

Cycas and the cycads in general [Fig. 40.] contain species which produce seeds of comparable texture to that postulated for this platyspermic seed and some, notably those of C. circinalis, are very large. Platyspermy is known in seeds of the genus Cycas and although Crane (1988), states that the ovules of cycads are generally interpreted as radiospermic, he cites evidence for platyspermy among cycads in that their vasculature is arranged bilaterally. The seed in cycads may be supplied by a single bundle which bifurcates at the base or by two separate bundles which diverge within the megasporophyll. Seward (1917) also notes that bilateral symmetry is most marked in the genus Cycas, and there is evidence of platyspermy in earlier cycads in the fossil genus Primocycas of Zhu and Du (1981). Seeds of extant cycads have a fully double vascular system (Stopes 1905), that is, there is a separate vascular supply to the integument and the nucellus. Tracheids for the most part show spiral or annular thickening. Only Zamia skinneri possesses tracheids with 1-seriate bordered pits.
4. COMPARISON WITH OTHER SEEDS

Fig. 40. A generalised cycadean seed in RLS [after Chamberlain, (1935) and Kershaw, (1912)].

\begin{itemize}
  \item \textit{b} = sarcotesta,
  \item \textit{d} = sclerotesta,
  \item \textit{c} = vascular system,
  \item \textit{m} = micropyle,
  \item \textit{n} = nucellar beak,
  \item \textit{et} = endotesta,
  \item \textit{mc} = micropylar chamber,
  \item \textit{pc} = pollen chamber.
\end{itemize}

Scale bar = 5 mm.

Fig. 41. Ovule of \textit{Ginkgo biloba}, in RLS [after Favre-Ducharte, (1956), and Sporne (1965)].

\begin{itemize}
  \item \textit{b} = sarcotesta,
  \item \textit{d} = sclerotesta,
  \item \textit{e} = vascular system,
  \item \textit{m} = micropyle,
  \item \textit{et} = endotesta,
  \item \textit{mc} = micropylar chamber,
  \item \textit{tp} = tent-pole.
\end{itemize}

Scale bar = 5 mm.

Fig. 42. \textit{Torreya taxifolia}, in RLS, but with the vascular loop as seen in TLS, [after Oliver, (1903)].

\begin{itemize}
  \item \textit{b} = sarcotesta,
  \item \textit{d} = sclerotesta,
  \item \textit{e} = vascular system,
  \item \textit{m} = micropyle,
  \item \textit{fn} = foramen,
  \item \textit{nu} = nucellus and \textit{vl} = vascular loop.
\end{itemize}

Scale bar = 5 mm.

Fig. 43. \textit{Stephanospermum akenoides}, in RLS [after Oliver, (1904)].

\begin{itemize}
  \item \textit{b} = sarcotesta,
  \item \textit{d} = sclerotesta,
  \item \textit{e} = vascular system,
  \item \textit{f} = female gametophyte,
  \item \textit{n} = nucellar beak (micropylar beak),
  \item \textit{et} = endotesta,
  \item \textit{nu} = nucellus,
  \item \textit{pc} = pollen chamber,
  \item \textit{tm} = tracheal mantle.
\end{itemize}

Scale bar = 1.3 mm.
4. COMPARISON WITH OTHER SEEDS

In *Ginkgo* two vascular strands enter the seed at the base and, compared with cycads, there is a reduction in the extent of tissue vascularisation. Only the endotestal region of the seed is vascularised and tracheids, though prominent at the base, begin to become fugitive thereafter distally. Tracheids are reticulate and have bordered pits in a single row on their radial walls. Stripped of its mucilaginous sarcotesta, the seed has a prominent equatorial rib in the major longitudinal plane; this runs from micropyle to base on either side. The symmetry of the *Ginkgo* seed is bilateral and, taken with its slightly flattened dorso-ventral aspect, would indicate platyspermy and possible platyspermic ancestry. Bell & Woodcock (1983), state that these features rule out *Ginkgo* showing affinities with cycads and pteridosperms [Fig. 41.].

Further comparison can usefully be made with some earlier seeds. The apex of the *Dawsonocarpus* seed, when apiculate, resembles *Rhynchospora quinni* gen. nov. (Upper Mississippian), of Taylor and Eggert (1967). The large nucellar beak recalls the structure of some Palaeozoic seeds, and the persistence of nucellar stomata with subsidiary cells could indicate relationships with seeds much earlier than the mid-Jurassic. Schapiro (1949 & 1951) found stomata still persisting on the nucellus and integument of extant *Zamia floridana*, an expression of genes of very great age.

Other large seeds of extant plants with a firm exterior are *Torreya californica*, *T. taxifolia* and *Araucaria bidwillii*. However, the seed of the araucarian has ovuliferous and bract scales adnate to it, and its anatomy lacks some definitive features, including mesotesta and median laminar vascularisation, shown by *Dawsonocarpus*. The seed in *Torreya* is very different from that of a cycad. Although radiospermic it has however only two vascular strands entering from the base and passing up through the sarcotesta, hence the seed is bilaterally symmetrical. The vascular loop, found in this genus, is the only vascularisation associated with the nucellus passing around its outer surface sub-apically.

Pitting of the tracheids in *Torreya* is similar to the podocarpoid type with pits having a large border described and figured by Greggus (1955). The limited amount of vascular tissue and lack of a definitive pollen chamber may be correlated with its siphonogamous mode of reproduction, Oliver (1903), [Fig. 42.].

The Permo-Carboniferous seed *Stephanospermum* although radiospermic, has a prominent nucellar beak (tubular), a vascularised tracheal mantle around the nucellus and an integumentary structure approaching that of a cycad seed. However, the nucellus is free from the outer integumentary tissues except at the base which is a decidedly primitive character, as stated by Oliver (1904), [Fig. 43.].
4. COMPARISON WITH OTHER SEEDS

Fig. 44. *Cardiocarpus* sp., in RLS (major plane) [after Rothwell, (1986)].

- b = sarcotesta,
- d = sclerotesta,
- e = vascular system,
- m = micropyle,
- fn = foramen,
- nu = nucellus,
- pc = pollen chamber and
- vp = vascular plate.  
Scale bar = 1.4 mm.

Fig. 45. *Cardiocarpus* sp., sketched in TS [after Rothwell, (1986)]. Key as for 9 E.
Scale bar = 1.4 mm.

Fig. 46. *Mitrospermum compressum* Arber, [after Taylor & Stewart, (1964)].

Reconstruction of seed:
- a = TS through seed at A-A in b.
- b = Median LS (primary plane).
- c = Median LS (secondary plane).
- m = micropyle,
- nb = nucellar beak,
- nu = nucellus,
- pc = pollen chamber,
- sa = sarcotesta,
- sc = sclerotesta,
- vb = vascular bundle and
- w = wing.  
Scale Bar = 5 mm.
Cardiocarpus, a Permo-Carboniferous seed of cordaitalean stock is platyspermic and although apparently lacking a nucellar beak, has a structure which resembles the swollen base of one. Its vascularisation approaches the double pattern, but is more extensive in the sarcotesta than around the female gametophyte [Figs. 44 and 45].

In *Mitrospermum* seeds, Taylor and Stewart (1964), which are found as calcified petrifications in the Mid-Upper Carboniferous, [Fig. 46], and are also placed in the Cordaitales, the vascularisation of the sarcotesta is more extensive (a massive tracheal plate), differing from that of Cardiocarpus and resembling the vascular pattern found in *Dawsonocarpus*. Where reported, tracheids in the above Palaeozoic seeds tend to have spiral, annular or scalariform thickening. Some tendency for the nucellus to be fused to the outer integumentary tissues at the base and also distally from it has been noted. In *Mitrospermum* particularly, there is evidence of the seed having a valvular platyspermic structure; this was mentioned by Arber (1910), and by Taylor & Stewart (1964). Hence cordaitalean and early coniferalean affinities become more likely for *Dawsonocarpus* with perhaps some particular reference to *Mitrospermum* as a possible ancestor.

In Figure 47, comparable features of four seeds, including the fossil *Dawsonocarpus haidorum*, are set out as an aid to establishing its relationship to other seeds earlier and later than the Bajocian of the mid-Jurassic. Particular references associated with this table are given.
TABLE OF COMPARISON

<table>
<thead>
<tr>
<th>Species</th>
<th>Mitrospermum compressum</th>
<th>Dawsonocarpus haidorum</th>
<th>Ginkgo biloba</th>
<th>Torreya taxifolia</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Seed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>6.5mm - 7.5mm</td>
<td>3.0cm - 6.0cm</td>
<td>Mature “fruit” globe 2.5cm</td>
<td>Mature seed drupe-like and obovate</td>
</tr>
<tr>
<td>Breadth</td>
<td>7.0mm - 8.0mm</td>
<td>4.0cm - 7.0cm</td>
<td>Seed length: 2.0cm</td>
<td>Length: 2.5cm - 3.5cm</td>
</tr>
<tr>
<td>Thickness</td>
<td>1.8mm - 2.2mm</td>
<td>2.5cm - 4.0cm</td>
<td>Breadth: 1.5cm</td>
<td>Steadth: 1.7 cm - 2.3cm</td>
</tr>
<tr>
<td>In major longitudinal plane:</td>
<td>platyspermic, cordate, winged and bivalvate.</td>
<td>Asymmetrical in major longitudinal plane, but symmetrical in minor plane - bifacial.</td>
<td>Symmetry of seed bilateral.</td>
<td>Symmetry of seed bilateral.</td>
</tr>
<tr>
<td>Symmetrical about major and minor longitudinal axes.</td>
<td>Surface furrowed from near base to apex.</td>
<td>Surface furrowed from near base to apex.</td>
<td>Prominent equatorial rib in major radial longitudinal plane running each side of seed.</td>
<td></td>
</tr>
<tr>
<td><strong>Integumentary data</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Three distinct regions distally below thin epidermis:</td>
<td>Three distinct regions distally below thin epidermis:</td>
<td>Three distinct regions distally below thin epidermis:</td>
<td>Three distinct regions distally below thin epidermis:</td>
<td></td>
</tr>
<tr>
<td>Outer - sarcotesta</td>
<td></td>
<td>Outer - sarcotesta</td>
<td>Outer - sarcotesta (arillus) flesh</td>
<td>Outer - sarcotesta (arillus) flesh</td>
</tr>
<tr>
<td>Inner - sclerotesta</td>
<td></td>
<td>Median - mesotesta</td>
<td>Inner - sclerotesta (stony)</td>
<td>Inner - sclerotesta (stony)</td>
</tr>
<tr>
<td>Innermost - endotesta</td>
<td></td>
<td>Inner - endotesta</td>
<td>Innermost - endotesta (fleshy)</td>
<td>Innermost - endotesta (very thin parenchymatous)</td>
</tr>
<tr>
<td><strong>Reproductive structures</strong></td>
<td></td>
<td>Pollen chamber large with small nucellar beak.</td>
<td>Pollen chamber with small nucellar beak.</td>
<td>Lacks definite pollen chamber.</td>
</tr>
<tr>
<td>Nucellus free from integument only near the apex.</td>
<td>Nucellus free from integument except in chalazal region.</td>
<td>Nucellus free from integument near the apex.</td>
<td>Tent-pole absent.</td>
<td>Tent-pole absent.</td>
</tr>
<tr>
<td><strong>Vascular system</strong></td>
<td>Single terete bundle enters base of seed, extends through integument and forms an expanded nucellar platform.</td>
<td>Entry mode of tracheids at base of seed unclear.</td>
<td>Two vascular strands enter seed and vascularise the endosperm region only, becoming progressively fugitive distally.</td>
<td>Vascularisation - limited.</td>
</tr>
<tr>
<td>Tracheids - scalariform.</td>
<td>Vascular plate basal in origin, tracheids bifurcating and becoming juxtaposed to inner face of nucelus then diverging laterally from base forming network.</td>
<td>Tracheids reticulate with bordered pits in a single row on radial walls.</td>
<td>Two vascular strands enter seed and vascularise the endosperm region only, becoming progressively fugitive distally.</td>
<td>Two vascular strands enter seed and vascularise the nucellar dome at about 65% of its length. At some point in its length, a vascular loop passes distally from a foramen on one side of the seed to the other; this loop penetrates the sarcotesta via another foramen on the opposite side of the seed. The loop encircles the nucellus. Tracheids reticulate grading into transfusion tracheids distally from the point of transition.</td>
</tr>
<tr>
<td><strong>Fossil</strong></td>
<td>Fossil - Carboniferous (Pennsylvanian)</td>
<td>Fossil - Mid-Jurassic (Bajocian).</td>
<td>Extant - native of China (Chekiang Province).</td>
<td>Extant - native of NW Florida.</td>
</tr>
</tbody>
</table>
Fig. 47. Table of comparison of *Mitrosporum compressum*, *Dawsonocarpus haidorum*, *Ginkgo biloba* and *Torreya taxifolia*.

*M. compressum* Arber (1910), Taylor and Stewart (1964) and Stewart (1983). Cordaitales, Coniferopsida.


*Torreya taxifolia* Amott (1838), Oliver (1903), Esau (1965), and Dallimore & Jackson (1966). Taxales, Coniferopsida.
The mode of action of the bivalvate structure (if any) in this platyspermic seed is intriguing. It is tempting to speculate on its possible association with the pollination mechanism of the seed and/or perhaps as an aid to the release of the young sporophyte. Other bivalved seeds occur in the fossil record. Harris (1951) cited *Lepidostrobus* (*Czekanowskia*), an ovulate structure bearing capsules, each capsule being composed of two valves like mussel shells with each lobed valve containing a row of small ovules; a protective arrangement resembling the bicarpellary ovary of an angiosperm. Meyen (1988) described the bivalvate *Salpingocarpus bicornutus* from the Angaran flora, and also mentions seeds of similar architecture which he associated with *Glossophyllum-Stiphorus*, *Sporophyllites*, Mesozoic *Ginkgoales*, younger seeds of *Callospermarion* and young *Ginkgo* ovules. He correlated bivalved structure with the possession of a "perinucellar slit dividing the integument into two halves along the major plane of the seed." Arnold (1947), pointed out that fossils of the Angaran Flora "are not limited to the Permian, but include beds as late as the Jurassic." The micropylar entrance of *Dawsonocarpus* is slit-like and, combined with the extensive equatorial suturing, gives a bivalved structure and is firmly placed in the Mid-Jurassic.

There is a possibility that this platyspermic seed, might have relied upon water dispersal in its life-cycle, and indeed it occurs in precisely the same setting as *Cycadeocarpus columbianus* for which Chaloner and Hemsley suggested a possible flotation mechanism when comparing this radiospermic seed with extant species of *Cycas* such as *C. circinalis*. However, although *Dawsonocarpus* lacks the "spongy layer" indicated in the Chaloner and Hemsley paper, it possesses an anatomically distinct tissue (termed 'mesotesta' in this thesis), which may possibly have had a similar function. More probably however, since it surrounds the vascular plate and extends laterally through the winged section of the seed up to the suturing, the mesotesta, (in conjunction with having a bivalved structure), may have had a protective function rather like that suggested in the *Leptostrobus* capsule by Harris. A median TS of *Cycadeocarpus columbianus* (after Chaloner and Hemsley 1992), is shown for purposes of comparison [Fig. 48]; see also [Figs. 21 and 22].

Whether the haplocheilic stomata noted on the seed nucellus had any function in life is doubtful, but their nucellar rather than integumentary location considered along with the possible mode of action mentioned in the above paragraph, might mean that their presence was not entirely vestigial in the Jurassic. Harris (1941) demonstrated that stomata were present on the integument of the *Beania* ovule, and Schapiro (1949 & 1951),
Fig. 48. *C. columbianus* in TS [median], [after Chaloner and Hemsley], (1992).

Scale bar = 5mm.
has shown stomata to be present on the nucellus and on the integument of *Zamia floridana*. Moreover, Schapiro noted that those of the nucellus lacked subsidiary cells and those of the integument were similar to those of foliar origin. Smith (1910) found that in its ontogeny, the ovule of *Zamia* develops its nucellus first. Hence his inference that though the stomata of both nucellus and integument may be vestigial, those of the nucellus must have pre-dated those of the integument.

It is of interest that the haplocheilic stoma on the underside of a leaf of *Sagenopteris phillipsi* (Stewart 1983), resembles that found on the upper nucellar surface of *Dawsonocarpus haidorum* seed. [Fig.35].

In conclusion therefore, it would seem that this platspermic seed *Dawsonocarpus haidorum*, has features which show relationships with extant members of the Cycadales since it possesses some similarity with regard to integumentary structure and also that there is a tendency for platspermmy to be shown by seeds in some species of the genus *Cycas*. However, coniferopsid s.l., affinities seem more likely, particularly when due regard is paid to the morphology of *Ginkgo*, the podocarps and the genus *Torreyia*. Here platspermmy is rare, although seeds are often bilaterally symmetrical, but vascularisation is less extensive than in the ovules and seeds of cycads and, in contrast with cycads, siphonogamy is the rule. However, relationships with seeds from the Palaeozoic may be seen and, in particular, with platspermic cordaites such as *Mitrospermum*.

*Dawsonocarpus*, whilst possessing some affinities with extant genera, has peculiar features of its own for example, the highly stratified median vascular system sandwiched between a mesotesta, and lateral branching in which ‘transfusion tracheids’ gradually replace tracheids distally from the principal strand which is adnate to the female gametophyte. In addition, the nucellar beak is larger than any to be found in extant cycads or conifers. Only in species of *Gnetum* or *Ephedra* are there structures of comparable size, [Figs. 49 and 50], and Thomas and Spicer (1987), in common with others, interpret this as the innermost integument. In archegoniate *Ephedra* this tube is surrounded by a further integument and in *Gnetum* by two integuments. These seeds are radially symmetrical in contrast to *D. haidorum* which is bifacial and platspermic. Thomas and Spicer also suggest that “the widespread distribution of *Ephedra* and *Gnetum* are indicative of probable highly specialised ancestors from different gymnosperm groups; *Ephedra* from Euramerian ancestors and Gnetum from Gondwanan ones”. In addition, they refer to the proposal by Eames (1952), that “the cordaites were probable ancestors of *Ephedra*”. His ideas were based upon what he perceived to be comparable ovuliferous organisations.
Fig. 49. A diagram of *Ephedra* sp. mature ovule sketched in RLS [after Thomas and Spicer, (1987) ex Bierhorst].

a = archegonia, c = pollen chamber, g = gametophyte tissue, i = integument, n = nucellus.

Fig. 50. *Gnetum* sp. ovule prior to fertilisation sketched in RLS [after Thomas and Spicer, (1987) ex Bierhorst].

i = integument, g = gametophyte tissue, n = nucellus, p = pollen tube.
Anatomically though in *Dawsonocarpus*, the tubular nucellar beak might be interpreted as an early trend toward the formation of an inner integumentary structure (this being rudimentary in *Dawsonocarpus*), although the outermost tissues would conform to the criteria stated by Foster and Gifford (1974) thus: “Except for the Gnetopsida, which are frequently said to develop ovules with two integuments, all other living gymnosperms consistently form a single integument which is free from the nucellus only near the upper micropylar end of the ovule.” This would give weight to the notion that this bifacial platyspermic seed *Dawsonocarpus haidorum* has, from the anatomical standpoint, strong affinity with gymnosperms, and possibly even with ancestors of gnetophytes. However, in addition, it possesses features which are unique to this seed and which are unlike seeds of cycadophytes. Also, in common with many gymnospermous seeds from the Mesozoic and extant exemplars, characteristics from seeds of the Palaeozoic persist in this seed.

Perhaps Tom Harris’s warning, mentioned in the opening paragraph of Section 4, requires extension to include fossil exemplars as well as those which are extant. The seed *Dawsonocarpus haidorum*, has features which are hard to find not only in other Jurassic fossils, but also in fossils generally e.g. a vascularised mesotesta associated with a possible bivalved structure.

Relationships with the seeds of older groups point to perhaps cordaitalean ancestry with evolution along stachyospermid lines as cited by Meyen (1987), that is plants with fructifications on modified shoots, referring to cordaites, conifers and ginkgos, and with pycnoxylic wood and platyspermic seeds, rather than on phylloxypermid lines, that is plants with seeds on leaf-like organs, such as pteridosperms, cycads and bennettites, with manoxylic wood and fern-like leaves. From Section 5 and in earlier sections, it would seem that in *Dawsonocarpus*, certain anatomical characters (particularly those of diagnostic importance - see Section 2.2), are but variations on a gymnosperm theme which, from an evolutionary standpoint, might be thought to be vestigial or alternatively advanced. As Meyen said “perhaps palaeobotanists continue believing in (1) the habitual correlation of characters, and (2) the persistence of certain characters within the limits of large taxa, though often there are no rationales for either.”
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