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Weichselia Stiehler from Lower Cretaceous of Makhtesh Ramon, Israel: new morphological interpretation and taxonomical affinities

NATALIA SILANTIEVA and VALENTIN KRASSILOV

Institute of Evolution, University of Haifa, Mount Carmel 31905, Haifa, Israel and Palaeontological Institute,
123 Profsoyusnaya, Moscow 117647, Russia; e-mail: krassilo@research.haifa.ac.il

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ABSTRACT. Our material from the Lower Cretaceous of Israel provides new evidence on reproductive morphology and habitats of *Weichselia*, a peculiar Mesozoic fern genus. The material is assigned to a new species, *W. negevensis* sp. nov, differing form the widespread *W. reticulata* in the much less numerous sporangia per cluster and other qualitative characters. In distinction from the commonly hold view of *Weichselia* as a leptosporangiate fern of matoniaceous affinities, we propose a new interpretation of its spore-bearing organs, based on SEM study, as the foliar sporocarps enclosing eusporangiate synangia. The Weichseliaceae is, therefore, compared with the Marsileaceae on account of sporocarps and with the Marattiaceae on account of synangia, but is sufficiently different to be separated in a distinct order. In this coastal, perhaps pre-mangrove, arboreal fern, angiosporangy might have developed as an adaptation to excessive moisture or salinity.

KEY WORDS: fossil pteridophytes, fern systematics, fern morphology, mangroves, palaeoecology, Cretaceous, Israel

INTRODUCTION

Weichselia is assigned to a monotypic family Weichseliaceae, presumably the only fern family that became extinct during the Mesozoic. It is widespread in the Lower Cretaceous of Europe, Northern Africa and the Middle East, extending to India, Far East and western North America, and a subject of numerous palaeobotanical studies (briefly reviewed below).

However, both morphology and palaeoecology of this peculiar fern are matters of lingering controversies. *Weichselia* produced spherical spore-bearing structures for which no close analogues were found either among extant ferns or in the fossil record (Alvin 1968, Sender et al. 2001). The nature of sporangial aggregates within the spheroids is but poorly understood and the comparisons with matoniaceous ferns (Alvin 1968) is based on inadequately studied material. On the basis of stem anatomy *Weichselia* was compared to the Marattiales (Edwards 1933, Koeniguer 1966, 1975).

Xeromorphic (scleromorphic) features of *Weichselia* gave rise to the widely differing reconstructions of its habit and habitat, from a dry land xeromorph (Barale 1979, Watson & Alvin 1996) to a coastal helophyte (Daber 1968, Krassilov 1972, Retallack & Dilcher 1981).

Our material from the Lower Cretaceous of Israel provides new evidence of reproductive morphology and habitats of *Weichselia,* bearing both on taxonomic affinities and palaeoecology of this remarkable Mesozoic fern.

HISTORICAL OVERVIEW

Weichselia is common in the Neocomian to Albian of Europe, northern Africa, Middle East, India, Russian Far East (reviewed in Barale 1979) and Japan (Yabe 1927) locally surviving till the Cenomanian (Stromer 1914, Smith et al. 2001, Schweitzer et al. 2003).

Vegetative material of *Weichselia* is represented by bipinnate fronds occasionally found attached to a massive axis. According to Lipps (1923) and Daber (1968), *Weichselia* had a single whorl of forking fronds up to 1.2 m long that crowned a short stem. These authors described wing-like aphlebia at the base of the fronds. On the other hand, Alvin (1971) followed Bommer (1911) in considering such remains as pedate fronds comparable with *Matonia pectinata* R. Br.

Schuster (1930) has assigned to *Weichselia* a fossil wood genus *Paradoxopteris* Hirmer, first described from the Lower Cretaceous of Egypt (Hirmer 1927). Edwards (1933) suggested its affinities with marattialen ferns on account of its mucilage canals alternating with meristeles, tannin cells, and large sieve-tubes. In the development of sclerenchyma *Paradoxopteris* resembles a Palaeozoic tree fern *Psaronius* Cotta. Koeniguer (1966) came to similar conclusions concerning the relationship of *Paradoxopteris* and the similar, but perhaps taxonomically distinct European *Alstaettia* Remy & Remy with the extant Marattiaceae and *Psaronius*.

Spherical objects found with *Weichselia* fronds were first described as *Conites minuta* Seward (Seward 1900) and interpreted as synangial clusters of this fern by Bommer (1911). Lipps (1932) and Daber (1953) confirmed by their studies of fertile material from Germany that *Weichselia* had spherical “fructifications” 2–4 mm in diameter attached to the ultimate rachises of fertile fronds. Reymanówna (1965) described dispersed peltate disks as parts of disintegrated spheroids. Alvin (1968) studied compressed spherical bodies from Belgium in serial sections and reinterpreted them as aggregates of 12–44 (22) sclerotic peltate indusia, each covering a whorl of about 12 sporangia attached to a central receptacle. The sporangia were described as free, with a vertical annulus, containing trilete spores, comparable on account of these features with the Matoniaceae, although perhaps assignable to an allied extinct family (van Konijnenburg-van Cittert 1993.). However, neither the indusial nature of sclerotic peltae, nor the attachment of sori to a central receptacle were convincingly illustrated. The sporangial wall was not studied in any detail and the so-called annulus might have represented a longitudinal section of exannulate wall with a layer of thickened cells. Despite these uncertainties, Alvin’s interpretation was almost unanimously accepted (Diéguez & Meléndez 2000, Sender et al. 2001, Diez et al. 2005) without any further attempt to clarify the morphology of sporangial structures.

Weichselia (*Paradoxopteris*) is commonly regarded as xerophytic on account of strongly developed sclerotic tissue, large-celled supposedly water-storing pericycle, and the mucilage ducts (Edwards 1933). Thick upfolded pinnules and papillate epidermis agree with such interpretation (Reymanówna 1965, Alvin 1971). It was reconstructed as representing sparse vegetation of an arid landscape (Barale 1979), perhaps a fire climax, and releasing spores when scorched by the fire (Watson & Alvin 1996).

Alternative interpretations were inferred primarily from taphonomic observations. Association of *Weichselia* with strand deposits was repeatedly noted by Gothan (1910), Carpentier (1929), Schuster (1930), Daber (1953, 1968), and (for *Paradoxopteris*) by Koeniguer (1975). Coastal marsh or mangrove habitat was suggested for this fern by Krassilov (1972), Retallack and Dilcher (1981), El-Khayal (1985), Smith et al. (2001), and Schweitzer et al. (2003).

MATERIAL AND METHODS

Weichselia is common in the Lower Cretaceous (Aptian–Albian) of Makhtesh Ramon, the largest eroded anticline (“makhtesh”: cirque in Hebrew) of Central Negev (Fig. 1). Stems and leaf remains of this tree-fern occur in the Hatira Formation unconformable on the non-marine Jurassic deposits and overlain by the upper Albian–Cenomanian limestones. The lower Zuweira member of Hatira Formation represents a shallow marine intercalation with shell beds of gastropods and bivalves, occasionally containing fruit-like seed-bearing structures of gnetophytic *Afrasita* Krassilov & Lewy also known from contemporaneous deposits of Dakhla Basin in southern Egypt (Krassilov et al. 2004). Ferruginous trunks and frond rachises of *Weichselia* (fossil wood genus *Paradoxopteris*) were found in Zuweira Member and the overlying sandstones show borings by marine bivalves (Lewy 2003). On biostratigraphic and magnetostratigraphic evidence as well as isotopic dating of overlying Ramon basalts, the Lower Hatira Formation is assigned to Barremian (?) – Early Aptian (Gvirtzman et al. 1996). *Weichselia* is lacking from the fossil plant assemblages of interbasaltic clayey deposits (Nevo 1968).

The Upper Hatira Formation conformable on the Aptian basalts comprises the cross-bedded sands with lenticular whitish yellow to purple claystone inter-

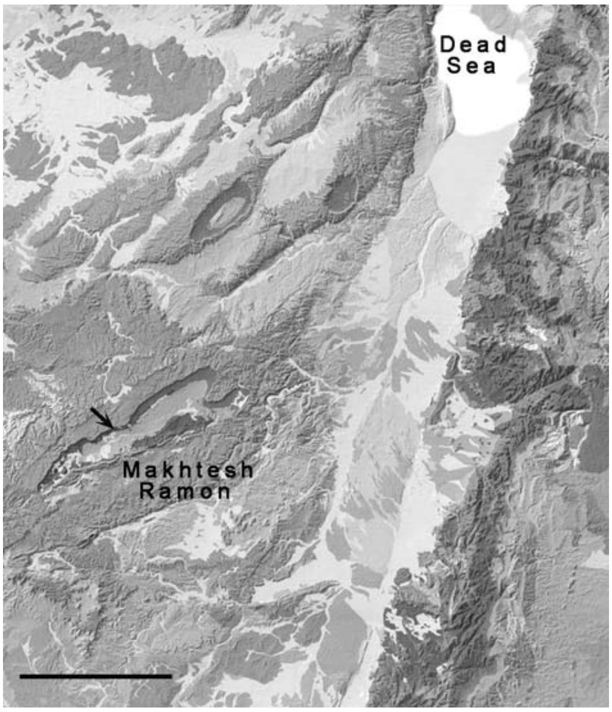

Fig. 1. Map of central – northern Negev: arrow on the area of present study on the northern slope of Makhtesh Ramon cirque. Scale bar = 25 km

beds and a marl horizon containing Albian ammonites (Gvirtzman et al. 1996). We collected macroscopic plant remains from seven outcrops on the northern slope of Makhtesh Ramon. *Weichselia* is abundant in all of them in association with conifers and narrow-leaved angiosperms. It is represented by sterile and fertile leaf impressions and ferruginous moulds of three-dimensional sporangial aggregates. These structures were studied under stereomicroscope Leica MZ6 and photographed with digital camera Leica DFC320. Fragments of three-dimensional moulds were mounted for scanning electron microscopy (CAMSCAN).

MORPHOLOGICAL DESCRIPTION

STERILE LEAVES

Weichselia leaf fragments in our collection are invariably bipinnate, although the rachises vary in thickness from about 3 mm to 20 mm. The pinnae are opposite or subopposite departing from the rachis at angles 75–90°, equidistant at intervals of about 10–12 mm. Although flattened in the bedding plane, they always show evidence of original imbricate arrangement, the rock matrix intervening between the overlapping blades. Most of the pinnae in our material are broken on ends, the preserved fragments being up to 15 cm long. The pinnae rachises are about 1.5 mm thick, expanded at the base, smooth, straight or somewhat arched, apparently flexible.

The pinnules are borne in catadromous series: the basiscopic (lower) pinnule arisng before the opposite acroscopic one. The basal pinnule of acroscopic series is strongly reflexed across the rachis. The distal pinnules are broadly webbed appearing as lobes, decreasing toward an elongate terminal pinnule of imparipinnate arrangement. The pinnule shapes are typically lingulate, in smaller pinnules triangular, sessile, on average 7 mm long, 3 mm wide, attached at open angle, occasionally slightly reflexed. Their apices are bluntly pointed or more typically rounded, the bases are expanded and slightly auriculate, the acroscopic auriculae onlapping the rachis. The pinnules of opposite rows are up-folded as butterfly wings and are raised above the level of the rachis leaving oblique lines of attachment in side view (Pl. 1, fig. 1).

The venation of pinnules is reticulate, with a thick abaxially prominent midrib that is distally upcurved and lost in forking before the apex. Adaxially, the midrib is marked by two series of narrow elongate areoles. Lateral venation appears as oblique series of polygonal, rhombic or rectangular areoles arising at about 75°. Usually the angle of departure is somewhat wider and distally increasing in the acroscopic half-blade, while on the basiscopic side it is distally decreasing (Pl. 1, fig. 3). The areoles are isometric near the midrib, about 0.2–0.3 mm wide, stretched toward the margin to becoming rectangular, about 0.3 mm long, 1.5 mm wide in the intramarginal row.

Stomates, as observed in SEM (Pl. 2, fig. 9) are crowded in the areoles of lateral veins, irregularly oriented. The guard cells are elliptical, about 35 μm long, usually one cell apart, but occasionally showing incomplete ring of subsidiary cells.

FERTILE STRUCTURES

The fertile structures in our material are fragments of lamina-less pinnae bearing reticulate spheroids in two overlapping lateral rows (Pl. 1, figs 4, 5). Occasional fertile pinnae are terminated by a circular pinnule resembling spheroids in outline and dimensions except that it is flat, showing a flabellate pattern of coarse areoles (Pl. 2, fig. 2). Another abnormal pinnule (Pl. 2, fig. 1) is evidently detached from a fertile pinna; there are remains of sporangial aggregates stuck to it. The pinnule is reniform with flabellate venation. Midrib is lacking, but two diverging rows of narrow fusiform areoles, like those marking midribs in ordinary pinnules, may indicate derivation of this abnormal reniform pinnule by marginal fusion of two lingulate pinnules.

Fertile spheroids are sessile on the rachis of fertile pinna and those of the opposite rows overlap. Occasionally spheroids are flattened at the base, appearing as a residual lamina of a fertile pinnule (arrow in Pl. 1, fig. 5). They are preserved as impressions or ferruginous moulds, some of them cut at various angles showing interior structures. There are also dispersed wall fragments and sporangial clusters from disintegrated spheroids (Pl. 2, figs 3–8).

Intact spheroids are about 3 mm in diameter, their reticulate surface structure consisting of polygonal to rhomboid areoles. The enclosed sporangial clusters are impressed upon the reticulate wall, their receptacles appearing as prominent knobs or pits, equidistant all over the surface, with sporangial partitions radiating from them. Our SEM photograph (Pl. 3, fig. 1) shows areoles that are continuous over sporangial clusters, but thickened around the receptacles. Plate 4, figure 2 shows the interior surface of spheroid wall, with sclerenchymos strands radiating from the base of receptacle. At maturity the spheroid wall split at the contacts of areoles into thick peltoid lamellae that are often found dispersed. These lamellae (“peltoids”) are preserved as moulds or impressions with radial striation representing sclerenchymous strands described in Reymanówna (1965). On their concave inner surface, they show a pit of receptacle surrounded by minute scars (Pl. 2, figs 4, 5). Such scars seem authentic rather than preservational for they were observed in a number of peltoids.

Ferruginous moulds of intact spheroids are cut at various angles showing about 8–12 enclosed sporangial clusters pending from the wall (Pl. 3, fig. 2). Each sporangial cluster comprises 5–6 sporangia radial on a thick columnar receptacle. In Plate 4, figure 3 a longitudinally cut sporangial cluster shows the mould of a columnar receptacle and the radial faces of two sporangia. The pattern of sclerenchymous strands is continuous over the receptacle and the thick walls of sporangia that envelop the sporangial cluster as an integral synangial structure. The common outer wall with sclerenchymatous strands is seen also in the tangentially cut sporangial cluster in Plate 4, figure 1.

Frequent preservation of dispersed sporangial clusters implies that they were shed intact from disintegrated spheroids. Dispersed sporangial structures are preserved as impressions or moulds of shallowly lobed ellipsoids with a large central pit (receptacle) and with deep furrows radiating from it (Pl. 2, figs 3, 5). The furrows mark partitions of five or six compartments corresponding to individual sporangia that are fused along their radial contacts. In SEM (Pl. 3, fig. 4), the outer wall is continuous over the slightly depressed contacts of individual sporangia marked by one or two rows of narrow fusiform cells. The central column is surrounded by a ring of radial thick-walled cells uninterrupted at the boundaries of individual sporangia. The thick-walled cells also form a continuous ring around the receptacle obliquely cut by the bedding plane (Pl. 2, fig. 8).

The sporangia are ovate, about 0.7 mm long, 0.6 mm wide, wedging toward the receptacle. In longitudinally cut sporangia (Pl. 3, figs 1, 4), the wall shows three layers: (1) thick outer layer of sclerenchymous cells, enveloping the sporangial cluster, (2) middle level of thick transverse bars, and (3) thin membranous indistinctly granular inner layer surrounding the sporogenous tissue. The bars of the layer (2) are often broken, but when better preserved, extend over the circumference of the exposed sporangial wall (Pl. 3, fig. 3). The bars are rounded or elliptical in transverse section, about 20 µm thick.

Spores, no less than 88 per sporangium, trilete, about 30 µm in diameter, slightly lobed, faintly scabrate, proximally convex with a raised Y-mark of long, somewhat curved, ridged, narrowly bordered rays extending to the equator (Pl. 4, figs 4, 5).

SYSTEMATICS

There is little doubt about generic assignment of our material: the sterile leaves, pinnules, venation, fertile spheroids and their dispersed lamellae are quite similar to the type material from Quedlinburg, Germany (Daber 1968) and conspecific remains from other European localities. The first binominal published under this generic name was *Weichselia ludovicae* Stiehler (1857) from Quedlinburg, generally considered as synonymous to *Pecopteris reticulata* from Sussex (Stokes & Webb 1824). Previous interpretation of fertile structures (Alvin 1968) was based on the Belgian material supposedly conspecific with those from Germany and England. The other species from northern Europe, such as *W. erratica* Nathorst, were synonymised with *W. reticulata* (Edwards 1933).

Stem anatomy suggests splitting of *Weichselia* (*Paradoxopteris – Alstaettia*) into two broad-range species or even genera (Koeniguer 1975), but no clear-cut distinctions were found in the foliar structures of Boreal European and Mediterranean weichselias.

It must be noted, however, that some taxonomically significant features, such as arrangement of pinnules in catadromous versus anadromous series, or differentiation of basal pinnules, are poorly if at all studied in the European material, and the dimensions of pinnules are not systematically measured. In northern European weichselias, mean pinnule lengths, when indicated, are 4.3 mm (Alvin 1971) and 5 mm (Reymanówna 1965). In southern European and African – Middle East material it is about 7–9 mm (Edwards 1933, Lejal-Nicol & Dominique 1990, Diéguez & Meléndez 2000), except the specimens from Saudi Arabia, for which El-Khayl (1985) gives length range 4–13 mm, mean length 4.5 mm.

Well-preserved fertile spheroids are figured form the Lower Cretaceous of Spain (Diéguez & Meléndez 2000), but their interior structure was not studied in detail. The fertile material from Israel (this study) differs from those from European localities in a number of features, most of which can be preservational or interpretational. However, the spheroids are slightly smaller and contain less numerous sporangial clusters than in the European material, but these distinctions may fall in the variation range of a polymorphic species. The spores are smaller, perhaps underdeveloped. Yet there is at least one clear-cut distinction: the number of sporangia per cluster is 5–6 in our material against 12 in the European material (Alvin 1968). This feature is fairly constant – not a single sporangial cluster shows more than six compartments – therefore warranting separation at the species level.

Weichselia negevensis Silantieva & Krassilov, **sp. n.**

Pls 1–4

Holotype. IMR-A5-1, sterile and fertile pinnae (Pl. 1, fig. 4)

Type locality. Northern slope of Makhtesh Ramon, Negev, downslope from Mitzpe Ramon Town, locality IMR-A5.

Type horizon. Upper Hatira Formation, Lower – Middle Albian.

Derivation of the name. From Negev Desert.

Diagnosis. Leaves at least bipinnate, pinnae and pinnules of opposite rows upfolded as butterfly wings. Pinnae imparipinnate. Pinnules in catadromous series, about 7 mm long, slightly auriculate at base, obliquely clasping the rachis. Venation reticulate, of polygonal or rhombic areoles in oblique series, stretched toward the margin. Midrib thick, lost in splitting before the apex. Fertile spherules (sporocarps) borne on pinnae rachises in the position of pinnules, about 3 mm in diameter showing a continuous surface reticulum sclerified at the bases of sporangial clusters and split at maturity into polygonal to irregular lamellae. Sporangial clusters (synangia) 8–12 per spheroid, released intact at maturity, consisting of 5–6 fused sporangia (compartments). Sporangial wall 3-layered, comprising the outer sclerified layer continuous over the cluster, thick parallel bars beneath it and the inner membrane. Spores trilete with a raised Y-mark; laesurae long, ridged, narrowly bordered.

Material. Forty fragments of sterile leaves, nine fragments of fertile pinnae and numerous dispersed synangia from eight localities in the Upper Hatira Formation, Negev Desert, Israel (Aptian – Albian).

INTERPRETATION

Current interpretations of sporangial structures in *Weichselia reticulata* are based on serial sections of compressed spheroids made by Alvin (1968) who reconstructed them as soral clusters of distinct (free) radially arranged sporangia covered with peltate indusia. Each sorus typically consists of 12 sporangia showing incomplete vertical annuli of thickened cells. Reymanówna (1965) described dispersed peltoids ("indusia") attesting to disintegration of ripe spheroids. The other records (Sender et al. 2001, Diez et al. 2005) seem consistent with these interpretations, but in neither of them the sporangial structures were described in sufficient detail. We describe a new species, *Weichselia negevensis* sp.n., which is closely allied, with quantitative distinctions, to *Weichselia reticulata*. However, our three-dimensional material clearly shows several important features that were not seen or were misinterpreted in the compressed material. We, therefore, propose a different interpretation of spore-bearing organs of *Weichselia*.

In the first place, the sporangial wall consists of more than one cell layer, which shows that *Weichselia* was not leptosporangiate, as it was erroneously interpreted on the basis of ill-preserved and inadequately studied sporangial structures, but rather eusporangiate.

Secondly, the outer sclerenchymatous layer is continuous over the sporangia of a radial cluster, thus forming a synangium. When this layer is destroyed or lost in maceration, the sporangia, clad in the inner layer of thick-walled cells alone, may appear as free. The bars of the inner layer of thick cells are often broken and superficially may produce an erroneous impression of an annulus, but actually they embrace the whole circumference of the eusporangia. The synangia were shed from the spheroids as intact structures.

Finally, the fertile spheroids are not the cone-like structure of sporangial clusters with peltate indusia, as they were depicted in (Alvin 1971) and elsewhere. The surface layer of spheroids is a continuous reticulum of rounded-polygonal areoles like in the sterile pinnules, with no evidence of indusia. The receptacles appear as knobs (pits on the impressions) on the wall of spheroids and are equidistant all over their surface. The spheroid wall is patchily sclerified around the bases of columnar receptacles forming polygonal to irregular thickened areas that are separated along their grooved contacts and are shed from disintegrating spheroids.

On account of their analogous disposition on the pinna rachis and their similar venation patterns, the fertile spheroids are here interpreted as involute fertile pinnules enclosing their abaxial synangia. Occasional fertile pinnae contain aberrant circular pinnules (Pl. 2, fig. 2) that appear as incipient spheroids, as do the occasional reniform blades with flabellate venation, evidently formed by fusion of two ordinary pinnules (Pl. 2, fig. 1).

According to this interpretation, spheroids of *Weichselia* correspond to sporocarps of heterosporous aquatic ferns, which are commonly interpreted as modified foliar organs formed of two or more laminate pinnules (Eames 1936, Bierhorst 1971, Kramer 1990). This interpretation does not imply close affinities, because *Weichselia* differs from all heterosporous aquatic ferns in its vegetative morphology, sporangia, and homospory. More plausibly, sporocarps can be seen as parallel developments for protection of developing spores from excessive moistening and/or salinity.

Based on the sporangial structures and certain anatomical features (Edwards 1933, Koeniguer 1966, 1975), the affinities of *Weichselia* must be sought with the Marattiaceae (Marattiales), among which *Christensenia* Maxon is similar to *Weichselia* in reticulate venation and radial synangia. In this and the other Marattiaceae, sporangial walls contain a layer of thick-walled cells that are most conspicuously developed in *Angiopteris* Hoffmann (Camus 1990). On account of minute scales at the base of receptacle, *Weichselia* can be compared to the marattiaceous genera with receptacular hairs or scales, as in *Marattia* and *Angiopteris*. Certain characters of stem anatomy (*Paradoxopteris*) also indicate affinities with *Angiopteris* and the Palaeozoic marattialean fern *Psaronius* (Edwards 1933). At the same time, *Weichselia* is fairly distinct from the marattialean ferns on account of its peculiar sporocarps, deserving separation in a monotypic taxon of ordinal rank.

PALAEOECOLOGY

Our observations are in full agreement with the current views assigning *Weichselia* to the coastal habitats. The Lower Aptian deposits of Makhtesh Ramon (Zuweira Member of the Lower Hatira Formation) represent an alternation of tidal flat and near-shore marine facies reflecting low amplitude fluctuations of subsidence and sedimentation rates. The alkalic basalts on top of the Early Aptian sequence mark an episode of uplift and intracontinental rifting followed by subsidence and paralic deposion in the Albian. The fossil wood and leaf material of *Weichselia* are abundant in the delta plain, tidal flat and near-shore marine facies, but are lacking in the interbasaltic playa lake deposits. Evidently, the weichselian wetlands were reduced by the uplift and volcanism and then recovered with resumed subsidence. The best preserved material came from ferruginous mudstones (bog-iron) of coastal swamps interbedded with variegated sandstones and claystones of the tidal sand flat-mud flat sequences. The earliest angiosperm macrofossils appearing at this stratigraphic level are associated with *Weichselia*.

Yet the taphonomy of *Weichselia* beds does not discriminate between the upper tidal and supratidal environments. Although *Weichselia* seem to produce adventitious roots (Alvin 1971), there is no evidence of special mangrove adaptations, such as the system of anchoring and breathing roots or viviparous propagation. *Weichselia* developed angiosporangy, supposedly for protecting spores from excessive moistening or salinity, but spore germination within the sporocarps was not so far observed.

Weichselia can be compared to the so called mangrove fern *Acrostichum* L. (Pteridaceae), which is abundant and often dominant in the back-mangrove swamps, but also grows beyond the tidal influence and is thereby considered as a mangrove associate rather than a member of mangroves proper (Tomlinson 1994). The Albian assemblages of *Weichselia* and narrow-leaved angiosperms *Sapindopsis* might have been precursory of the later appearing mangroves (Krassilov et al. 2005), but such evolutionary relationships require a better documented palaeoecological sequence.

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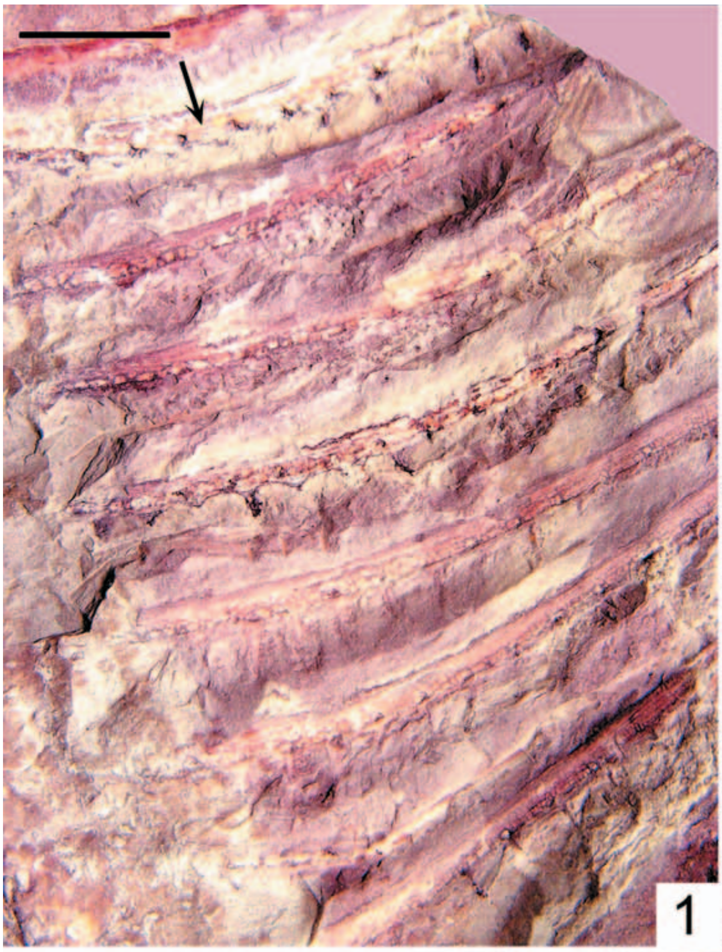
PLATES

Plate 1

Weichselia negevensis sp. n. from the Lower Cretaceous of Makhtesh Ramon, Israel

Scale bar (1) = 1 cm, (2) = 5 mm, (3) = 0.5 mm, (4), (5) = 5 mm

1. Bipinnate leaf fragment, note oblique scars of pinnule attachement on the pinna rachis (arrow), paratype IMR-A2-32
2. Pinnule shape and arrangement, paratype IMR-A2-107
3. Pinnule venation, paratype IMR-A2-108
4. Fertile pinnae with spheroid sporocarps, holotype IMR-A5-1
5. Fragment of fertile pinnae showing reticulate sporocarps, occasionally inflated (arrow), paratype IMR-A5-2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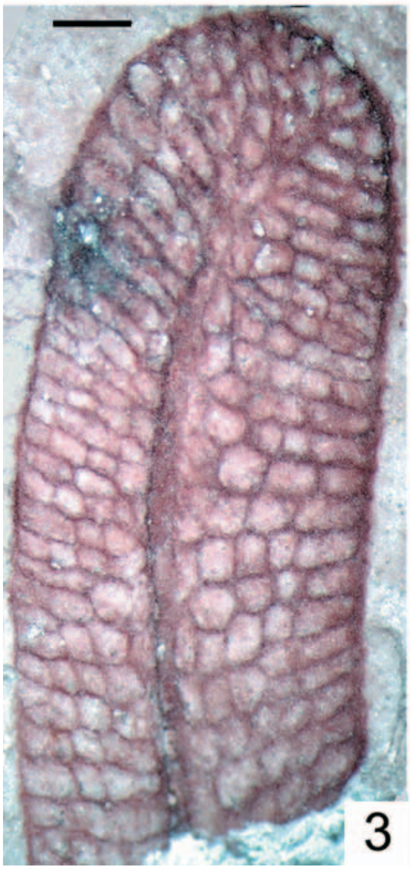
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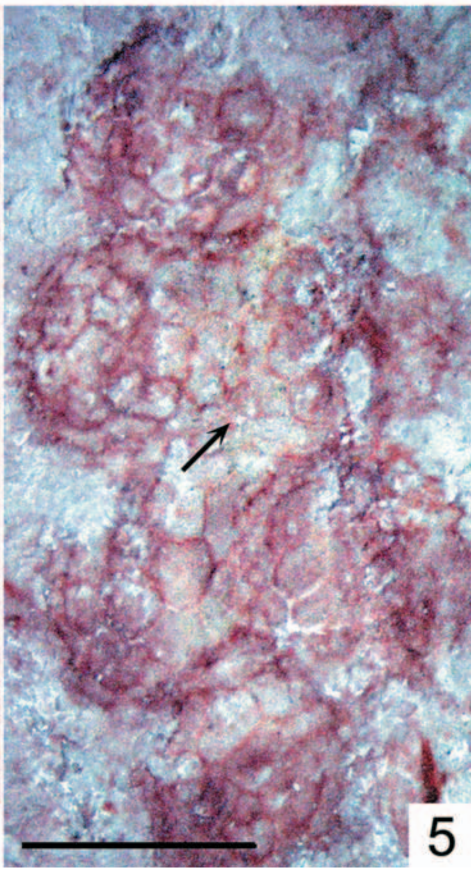
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Plate 2

Weichselia negevensis sp. n. from the Lower Cretaceous of Makhtesh Ramon, Israel

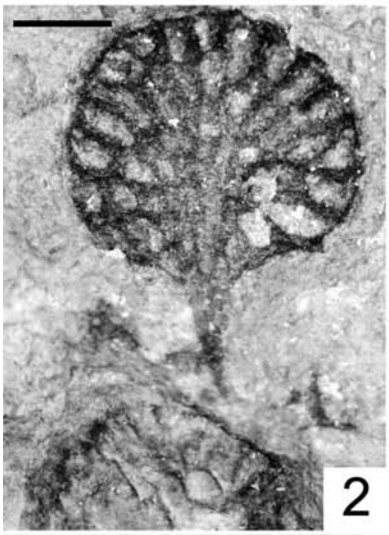
Scale bar (1), (2) = 1 mm, (3)–(5) = 0.5 mm, (6)–(8) = 0.25 mm

1. Abnormal flabellate pinnule with a detached synangium, paratype IMR-A8-1
2. Abnormal rounded pinnule of fertile pinna bearing spheroids (bottom), paratype IMR-A2-106
3. Synangia of disintegrated sporocarp, the bottom one in oblique side view showing 3-dimensional structure, paratype IMR-A8-1

4, 5. Dispersed peltoids (sclerified fragments of sporocarp wall) showing minute scars (trichome bases?) in the middle, paratypes IMR-A3-25 and IMR-A3-25

6. Detached synangium with radial partitions of six compartments, paratype IMR-A8-1
7. Impression of sporangial walls showing transverse bars; arrow on the partition of two compartments, paratype IMR-A8-1
8. Obliquely cut synangium with a complete ring of thick cells around the central receptacle, paratype IMR-A8-1
9. Stomates, SEM


1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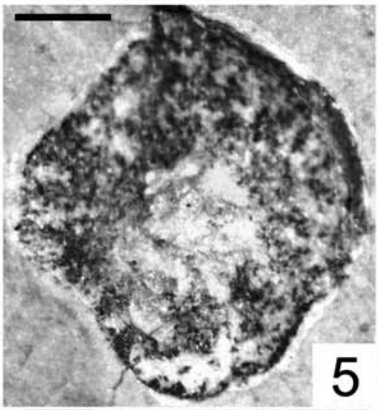
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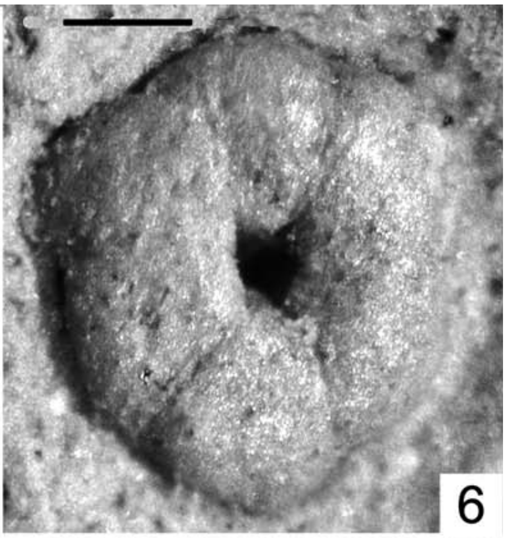
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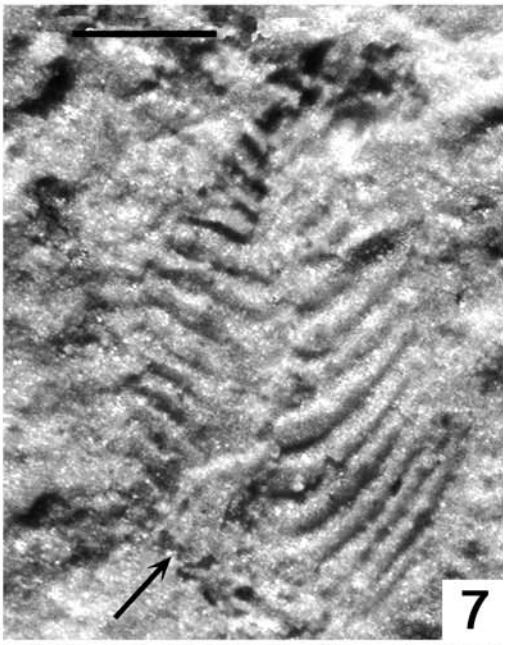
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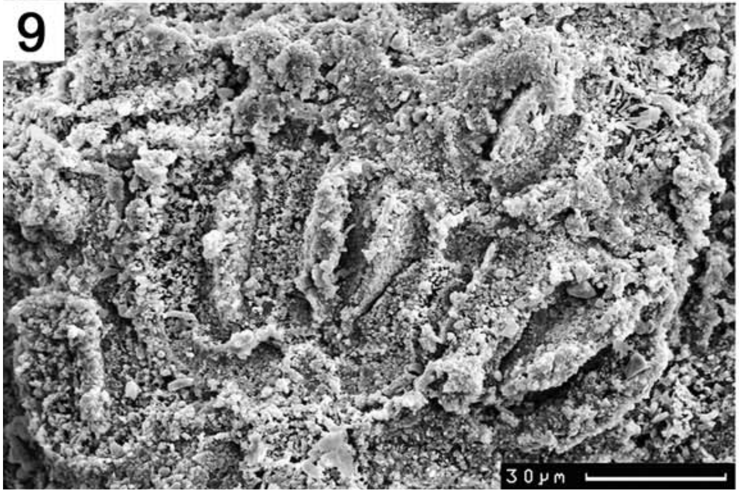
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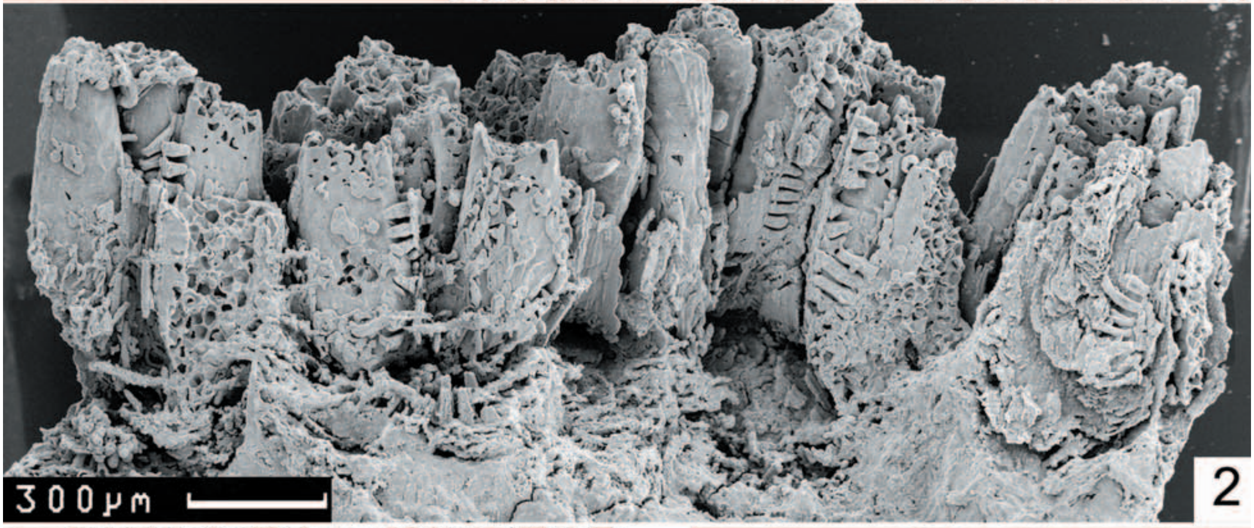
Plate 3

Weichselia negevensis sp.n. from the Lower Cretaceous of Makhtesh Ramon, Israel, SEM

1. Part of sporocarp showing areoles of the continuous surface reticulum (arrow on contacts of areoles) and the enclosed synangia; **R** – a central pit at the base of receptacle, paratype IMR-A6-1
2. Sporocarp wall removed exposing synangia, paratype IMR-A6-1
3. Synangium showing transverse bars across the compartments, paratype IMR-A6-1
4. Synangium of five compartments, paratype IMR-A8-1


1
R
300µm


300µm
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100µm

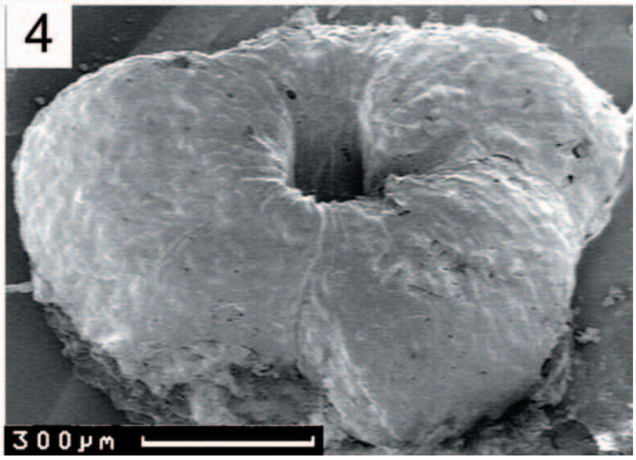
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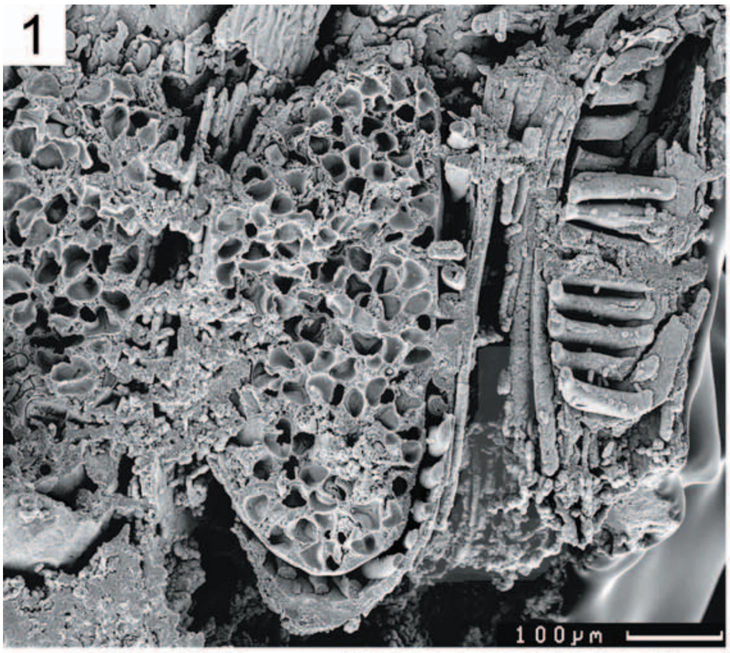
Plate 4

Weichselia negevensis sp.n. from the Lower Cretaceous of Makhtesh Ramon, Israel, SEM

1. Sporangia showing the external layer of sclerotic fibers and transverse bars of the thick-walled cells (marked in fig. 4), paratype IMR-A6-1
2. Sclerotic cells radiating from the base of receptacle, paratype IMR-A6-1
3. Base of synangium showing continuous sclerotic layer around the central column and the compartments; **s** – external sclerotic layer, **b** – middle layer, bars of thick-walled cells, **m** – inner membranous layer; paratype IMR-A6-1
4. Tangentially cut sporangium showing spores and the 3-layered wall with transversely cut bars of the thick-walled layer (symbols as in fig. 3); paratype IMR-A6-1
5. Spores, paratype IMR-A6-1

1



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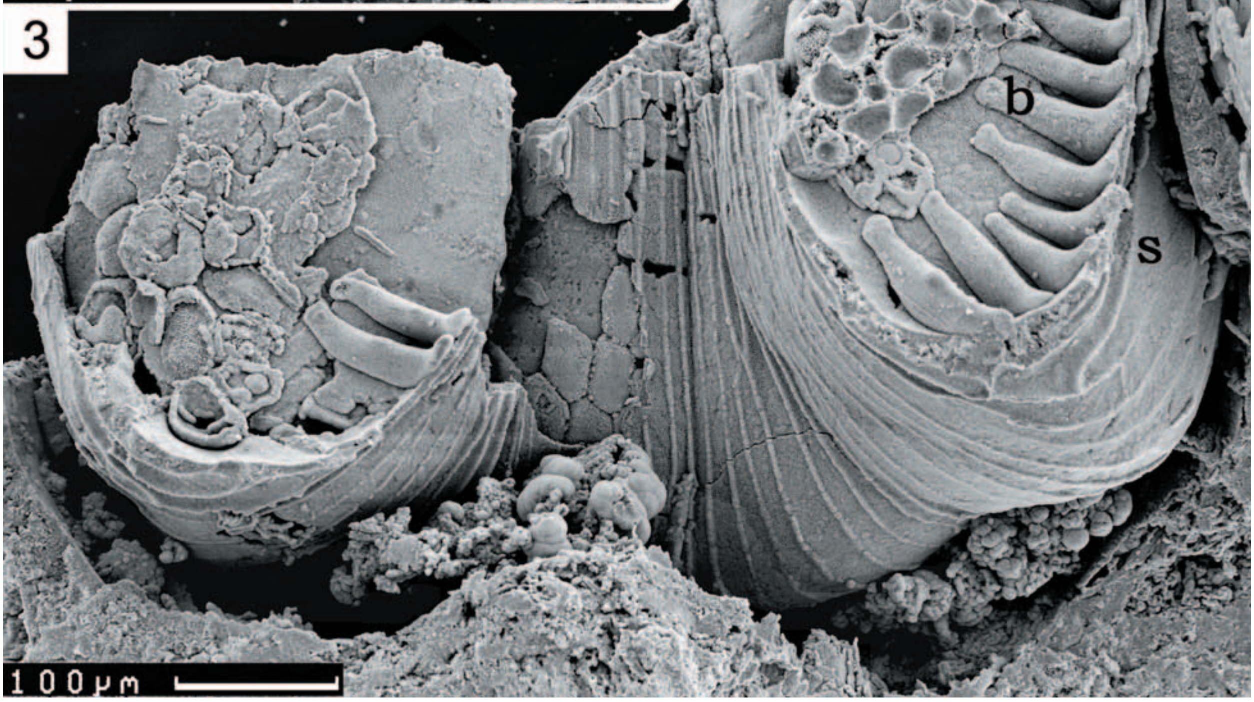

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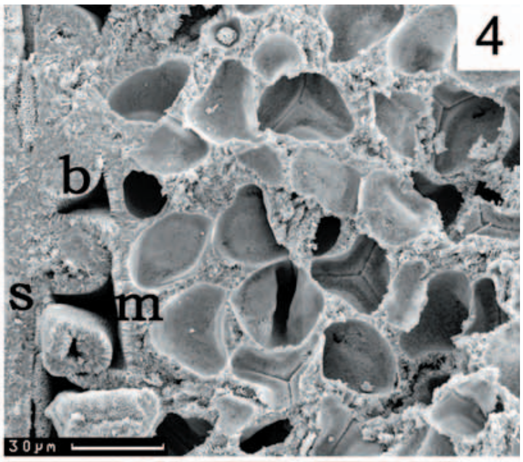

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