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Controversial fruit-like remains from the Lower Cretaceous of the Middle East

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Abstract

The marginal marine Lower Aptian deposits of Makhtesh Ramon, Israel contain abundant fruit-like fossils of the type previously described from the Dakhla Basin, southern Egypt as *Leguminocarpon abbubalense* Lejal-Nicol, 1981, which supposedly represent remains of early angiosperms. On the basis of new finds from the gastropod beds of the Hatira Formation, Israel, these fossils are re-interpreted as cones of succulent scales subtending large seeds. The arrangement of cones on rock slabs indicates their clustering at successive nodes of a branching axis. The scales show a coarse reticulate network of sclerotic fibres and a thick, supposedly water-storing, palisade tissue of tracheid-like cells. Large, slightly curved, seeds are exposed in slits between gaping scales. The seed coat consists of an outer spongy layer that is only patchily preserved, a longitudinally ridged middle layer that is truncated below the apex, and an apically protruding inner layer forming a thick bulge at the base of the micropylar tube. Abundant remains of detached scales and seeds suggest disintegration of ripe cones. The fruit-like fossils are described under the new name *Afrasita lejalnicoliae* gen. et sp. nov. and compared to extant gnetophytes and the Mesozoic *Vardekloeftia* Harris, 1932, *Gurvanella* Krassilov, 1982 and *Eoantha* Krassilov, 1986, the latter two being related to gnetophytes. There is evidence of insect fluid feeding on the ovules.

Keywords: Fossil plants; Gnetophytes; Plant morphology; Plant palaeoecology; Cretaceous, Israel

1. Introduction

In their paper on the Abu Ballas Formation (known at the time as the "*Lingula* shales") of the Dakhla Basin, southern Egypt, Barthel and Böttcher (1978) illustrated "numerous fruits of unknown provenance". Their plate 12, fig. 4 shows scattered crescent-shaped, transversely striated objects about 30 mm long. They were found in association with the widespread Mesozoic fern *Weichselia* and a few conifers assigned to *Araucaria* and *Brachyphyllum*. More problematic plants were tentatively described as *Hausmannia*, a dipteridaceous fern with reticulate venation, and the unnamed rhizomes of monocotyledons. Lejal-Nicol (1981) re-assigned "*Hausmannia*" to the new, supposedly angiospermous, genus *Klitzschophyllites*, whereas she assigned the "fruits" to a new species, *Leguminocarpon abuballense*. They were interpreted as pods of a legume containing small seeds. Unfortunately, no holotype was designated, which makes this name invalid according to the International Code of Botanical Nomenclature (2000), Article 37.1.

"*Leguminocarpon abuballense*" has been cited in several papers on the geology of the "Nubian Series".

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In his analysis of sedimentary environments, Böttcher (1982, p. 277) has suggested that this and other plants from Abu Ballas Formation "might have grown near or in the marine water, owing to their good preservation and the fact that they are absent in the floras of the coastal and continental environments". It was assumed that this kind of vegetation was predominantly angiospermous. The plant-bearing beds contained abundant naticid gastropods, together with *Lingula*, *Modiolus* and *Archaeoniscus*. Ahmed et al. (1993) figured "*Leguminocarpon abuballense*" from the south-western Aswan area noting that it is more abundant in the poorly sorted quartz sandstone facies on the southern fringe of Dakhla Basin than in the contemporaneous clayey deposits further north.

In Israel, plant fossils undoubtedly conspecific with "*Leguminocrpon abuballense*" were found by Zeev Lewy in the Hatira Formation of Makhtesh Ramon, the largest erosional cirque of Negev, southern Israel, exposing predominantly non-marine Triassic–Lower Cretaceous deposits (Fig. 1). The cirque is an elongate structure transcurrent to the Arava Rift to the east. A marine intercalation in the lower part of Hatira Formation, known as the Zuweira Tongue, contains a diverse marine fauna as well as plant macrofossils and pollen grains. On biostratigraphic and magnetostratigraphic evidence, the Zuweira Tongue is assigned to the Lower Aptian and is correlated with the Abu Ballas Formation of southern Egypt, and the Lower Cretaceous gastropod shales ("Couches à Gasteropodes") of Lebanon (Gvirtzman et al., 1996). Plant macrofossils, mostly ferns and gymnosperms, were found, together with pipid frogs and salamanders, in lacustrine deposits at about the same stratigraphic level on the south-western rim of Makhtesh Ramon (Nevo, 1963, 1968; Nevo and Estes, 1969). Both the Abu Ballas and Hatira formations contain angiosperm pollen grains (Schrank, 1982, 1983, 1992; Gvirtzman et al., 1996).

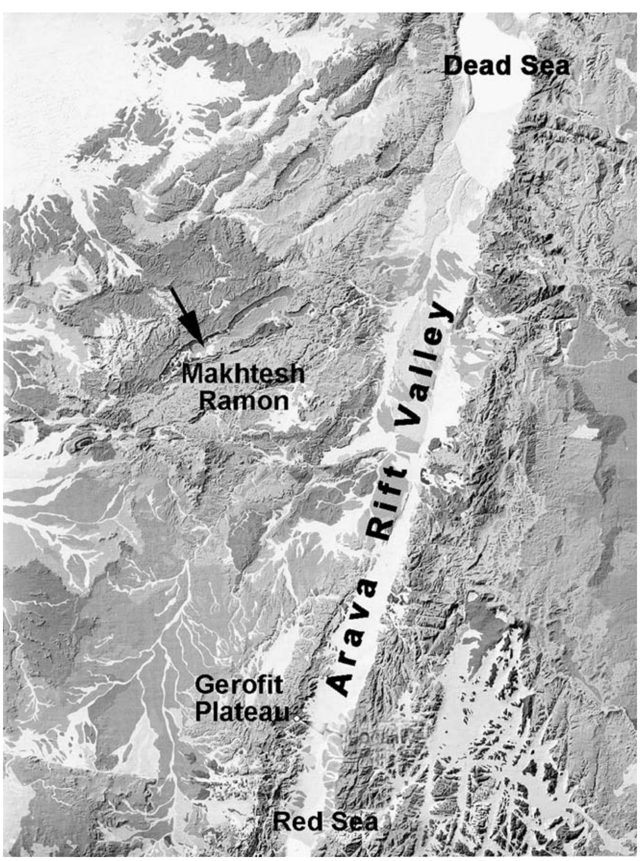


Fig. 1. Satellite photograph indicating the plant locality in the Lower Cretaceous Hatira Formation on the northern border of Makhtesh Ramon Basin (arrow).

The material collected by Lewy incorporates more complete specimens than those figured from contemporaneous Egyptian assemblages, providing material for a revision of the morphology and systematics of this enigmatic fossil.

2. Material and methods

The material consists of about 30 slabs of quartz sandstones containing ferruginous casts and moulds of seeds and seed-bearing structures. Compressed material is only fragmentarily preserved as crumples of coaly substance. The seeds are three-dimensionally preserved and can easily be removed from the rock, whereas the apparently softer seed-bearing structures are strongly compressed. Some are split at various angles showing interior aspects of their structural elements. The casts preserve micromorphological features that were studied under a dissecting light microscope and an SEM (scanning electron microscope). Some small pieces of compressed tissues occasionally showed cellular structures under the SEM.

For several years the fossils were with Professor Andrew Greller of Queens College, City University, New York. Greller and his collaborators sectioned several seed-bearing structures and prepared a few slides that, although differently interpreted, show essentially the same micromorphological features that we observed with the SEM. All the material is now deposited in the Institute of Evolution, University of Haifa, Israel. Morphological interpretation of the fossil plant and feeding traces on it are by Krassilov.

As will be shown in the following sections, the fruit-like fossils from the Dakhla Basin and Makhtesh Ramon are neither pods of a legume nor other angiosperm fructifications. Therefore, the name *Leguminocarpon* Goeppert, which is based on a Miocene fruit (Goeppert, 1855), cannot be applied to them. In fact, these fructifications are unique, only remotely resembling reproductive structures of some fossil gymnosperms.

3. Systematic palaeontology

Genus *Afrasita* Krassilov and Lewy, gen. nov.

Derivation of name. From Africa and Asia, this genus being found in both Egypt and Israel.

Type species. *Afrasita lejalnicoliae* Krassilov and Lewy, sp. nov., Early Cretaceous (Aptian).

Diagnosis. Seed-bearing structures ellipsoid, consisting of radially arranged scales subtending large seeds. Scales laterally sutured for their whole length, gaping at maturity, thick, crescent-shaped in lateral view, with a coarse network of reticulate subepidermal fibres and with abundant palisade tissue of tracheid-like cells. Seed locules impressed on adjacent scales. Seeds axial, nearly as long as the scales, slightly curved, with a fleshy coat consisting of three envelopes. The inner envelope protrudes as a conical bulge over the orifice of the middle envelope.

Afrasita lejalnicoliae Krassilov and Lewy, sp. nov.
Figs. 2–9, 11

Derivation of name. In honour of palaeobotanist Annie Lejal-Nicol who described this species from Egypt (Lejal-Nicol, 1981).

Holotype. IMR1-2 (Figs. 4A, 6A), Institute of Evolution, University of Haifa.

Type locality and stratigraphic horizon. Makhtesh Ramon, southern Israel; Hatira Formation, Lower Cretaceous (Aptian).

Diagnosis. As for the genus.

Description. Most of the specimens are radially symmetrical ellipsoid bodies segmented by longitudinal furrows (Figs. 2A–C, 4A). The segments are dorsiventral, laterally adhering or somewhat gaping, with large seeds protruding between them (Fig. 4C, E). Split or abraded specimens show seeds (Fig. 2B) or empty locules (Figs. 2C, 4A, B) impressed on two adjacent segments. Insofar as the seeds are inserted between the segments, the latter are either bracts or interseminal scales rather than carpels. Therefore, the segmented bodies are here interpreted as cones rather than fruits. Morphological details of the seed-bearing structures and seeds seem consistent with such an interpretation.

The largest specimen, 100×80 mm, shows about ten (perhaps more, but those in the polar view are squashed one upon another) small, probably immature, ellipsoid cones ca. 25–30 mm long and 20–25 mm wide. Their exposed surfaces are traversed by longitudinal furrows cutting segments of a uniform width of ca. 5 mm. No axial structures are preserved, but the cones appear densely clustered or whorled at the closely spaced successive nodes of a branching axis (Fig. 2A; reconstruction in Fig. 3).

Other specimens are clusters of fewer but larger cones, ca. 40–45 mm wide, showing whorls of 6–8 radially spreading scales. The cones are compact with the dorsal faces slightly convex and in contact over their whole length, divided by deep, narrow furrows (Fig. 2C), although in several specimens the scales are gaping, exposing seeds or their empty locules (Fig. 4B, C, E). The variation in the condition of the scales, either in contact or gaping, might have been developmental as well as preservational.

Casts and moulds of intact scales show their outer (dorsal, or abaxial) face or, in split cones, also their ventral face and lateral facets. There are also moulds of detached scales that can be removed from the rock. The scales are thick, crescent-shaped, ca. 30–35 mm long and 7–10 mm wide. The abaxial face shows a coarse polygonal network of subepidermal ridges (Fig. 5A–C). In abraded scales, the ridges appear as interlaced sclerotic fibres. At joints they form prominent bulges of sclerotic tissue (Fig. 6B). The adaxial face is traversed by subparallel ridges.

Under the SEM, fragments of compressed material show a thick palisade tissue of rod-shaped cells arranged in rows along the transverse ridges of the scales (Fig. 7). The palisade cells are adpressed or separated by narrow slits. They are tracheid-like, slightly angular in cross-section, ca. 1–8 μm wide, showing spiral thickenings and a fine striation between the coils. Their lateral walls are minutely pitted.

Adaxially, the scales are flanked by elongate depressions or furrows left by the seeds. The locules are elongate, pointed at both ends, wedged in somewhat obliquely between the lateral facets of adjacent scales, with the slopes slightly asymmetrical relative to the median line (Fig. 4B, D). Since they are reflected in the surface sculpture of the scales, the seed locules are developmental features rather than mechanical impressions. On detached scales, seed locules are marked on both flanks, one of them usually somewhat broader than the other, their asymmetry perhaps reflecting an oblique lateral overlap of the scales. The polygonal pattern of sclerotic ridges is interrupted by the locules that are smooth or feebly longitudinally striated. Two series of minute dots on their flanks are traces of transverse fibres traversing the adjacent scales. In a few cases (Fig. 4B) the flanking scales seem contiguous below the intervening seed cast. Therefore, the scales might have been proximally fused, at least before the ripe stage.

The locules extend almost the whole length of the scales, nearly reaching the poles of the cone. In abraded cones (Fig. 6A), casts of vascular traces entering the

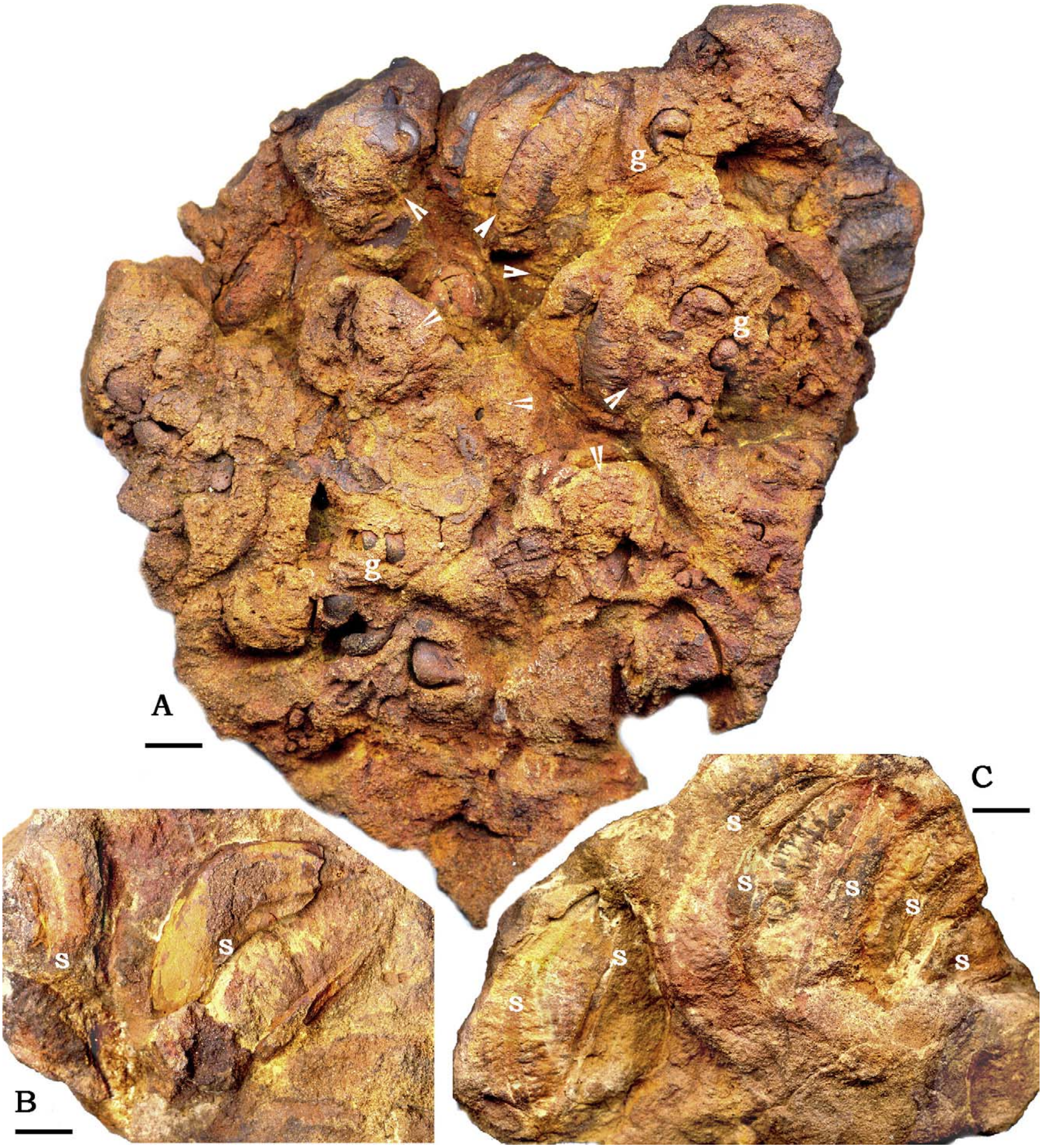


Fig. 2. *Afrasita lejalnicoliae* gen. et sp. nov. from the Lower Cretaceous of Makhtesh Ramon, Israel. A, IMR1-1, ferruginous sandstone with gastropod shells (g) and about ten fruit-like cones apparently borne in a branching system. Arrowheads point to the cones clustered at two successive nodes. B, IMR1-14, split cone showing seeds (s). C, IMR1-13, two cones with seed locules (s) as narrow furrows between the scales. Scale bars represent 7 mm (A, C) and 5 mm (B).

locules diverge close to the base, apparently from the cone axis rather than from scales.

Intact seeds exposed between gaping scales (Figs. 2B, 4C, E) are elongate, 20–25 mm long, 5–6 mm broad, curved conformably with the flanking scales. Their base is stalk-like (Fig. 4E), never preserved to full length, but traced down nearly to the base of the cone in abraded specimens. The apex is beaked, probably extended into a long micropylar tube that is invariably broken at or shortly above the base. The seed coat is smooth or, in some cases, shows low transverse folds (Fig. 4E).

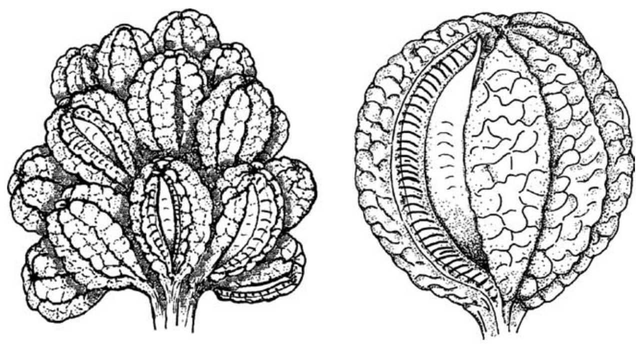


Fig. 3. *Afrasita lejalnicoliae* gen. et sp. nov. from the Lower Cretaceous of Makhtesh Ramon, Israel. Reconstruction of fruiting branch and cone with one of the seeds partly exposed.

The detached (shed) seeds are elongate elliptical to fusiform, ca. 22–30 mm long, 5–8 mm broad, slightly curved, with micropyle and chalaza at opposite ends, but not in line with each other (Fig. 4F, G). They are gradually tapered to the narrow base. The apex is conical, with a rounded scar of the micropylar tube (Fig. 8A, B). Three structural layers are discernible in the seed coat. The outer layer, which is only patchily preserved, is of a loose spongy structure consisting of irregularly interlaced fibres. The middle layer is glabrous, showing uniformly spaced longitudinal ridges and a fine striation between them. This layer is truncated below the apex forming a circular orifice. The inner layer protrudes as a dome-like apical structure bulging over the orifice (Fig. 9A). Punctures in this layer (Fig. 9B) are caused by piercing insects (see below).

Remarks. The morphology of seed-bearing structures does not comply with their previously presumed (Barthel and Böttcher, 1978; Lejal-Nicol, 1981) angiospermous affinities. These structures consisted of whorled scales surrounding large seeds. This arrangement restricts comparison to the bennettites and gnetophytes. In the Bennettitales, stalked seeds were surrounded by interseminal scales. In such derived gynoecial structures as *Vardekloeftia* (Harris, 1932; Pedersen et al., 1989), only a few relatively large orthotropous ovules were produced, their apices protruding between the polygonal heads of interseminal scales. Seeds were shed from these structures, supposedly by pushing through the heads of interseminal scales at maturity (Pedersen et al., 1989). The seeds show a ribbed outer envelope (a cupule) that is truncated below the apex in much the same way as the middle seed coat in *Afrasita*.

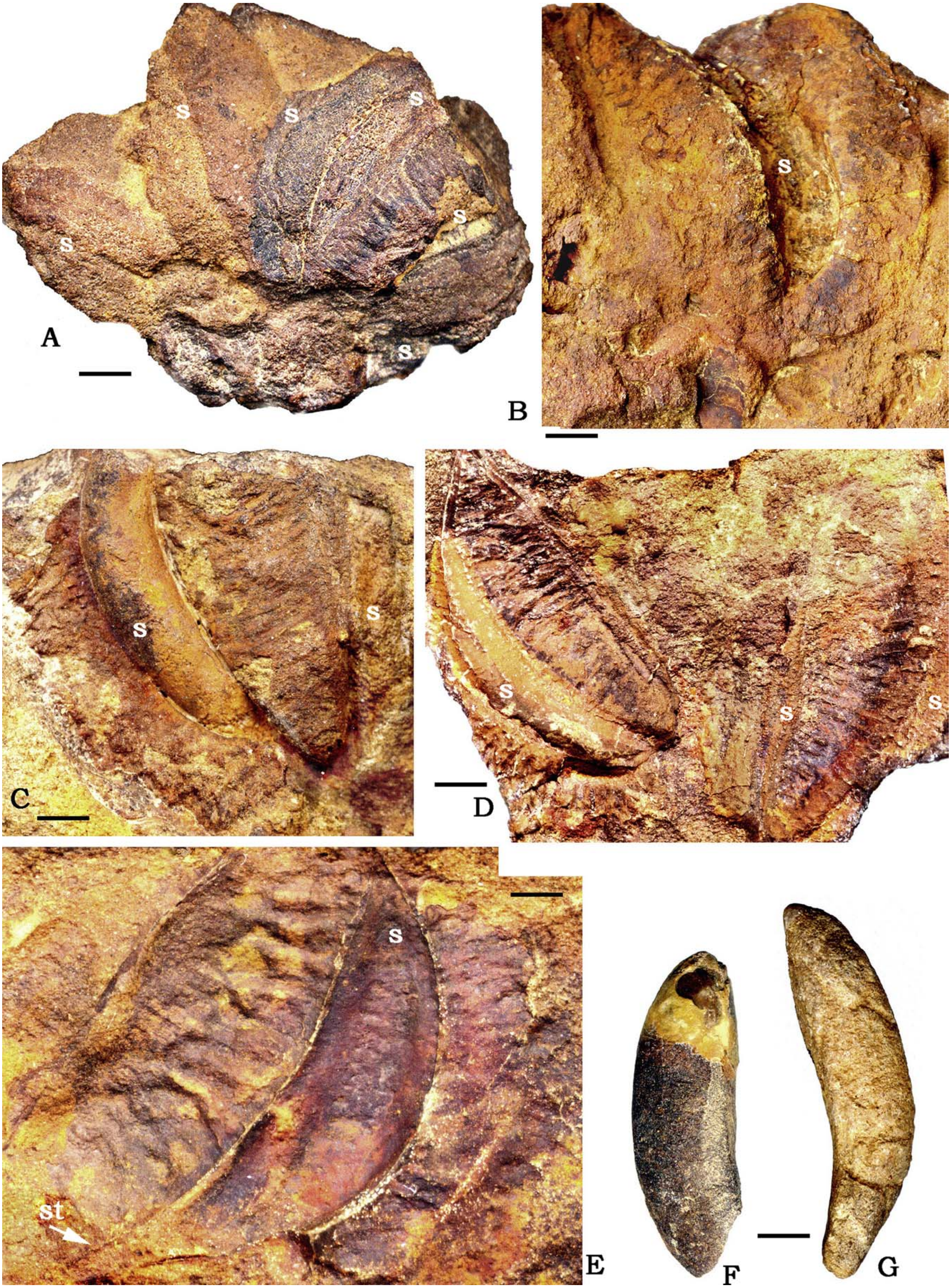
Another point of similarity is the polygonal fibrous network on scales that conceivably might have been derived from coalescent interseminal scales of a bennettitalean gynoecium. Stockey and Rothwell (2003) have found completely fused interseminal scales in the Late Cretaceous bennettite that they assigned to *Williamsonia*. Thus, a tendency to fusion actually manifested itself in the late representatives of the order and at an advanced stage the interseminal scales, as well as the aborted ovules between them, might have lost their morphological identity. However, this possibility remains speculative at the moment. From a morphological point of view, our fossil is readily distinguishable from *Vardekloeftia* in the segmentation of its fruiting bodies, and its large whorled scales and curved seeds.

The gnetophytes are essentially similar in having their ovules surrounded by scales that are described as bracts and bracteoles (Martens, 1971). In *Welwitschia*, the cone bracts subtend a solitary ovule flanked by a median pair of bracteoles that expand as wings at maturity. The bract is thickened over the midline by a network of interlaced fibres. In *Gnetum*, the coalescent bracts form collars beneath the whorls of ovules. In principle, the collars can be derived by a shortening of whorled cone scales of the type met in our Early Cretaceous fossil. There is a striking similarity in the seed structures with three envelopes, of which the innermost protrudes over the truncated middle one, expanding over it as an apical bulge (in our fossil) or a flange (in extant *Gnetum*).

Among fossil plants related to gnetophytes, *Eoantha* from the Lower Cretaceous of Transbaikalia produced pedicellate flower-like, cupular structures of four whorled scales each subtending an orthotropous ovule (Fig. 10A). Costate pollen grains were found in the pollen chambers of the ovules (Krassilov, 1986, 1997; Krassilov and Bugdaeva, 2000). In *Eoantha* the scales are much smaller than in *Afrasita*, but they show a similar pattern of coarse ridges. If related to the roughly contemporaneous plant from Negev, *Eoantha* is much advanced in the miniaturization of its seed-bearing structures and in its flower-like aspect.

Another Asiatic fossil comparable to *Afrasita* is *Gurvanella* from the Lower Cretaceous of Mongolia and China, initially described as an angiospermous fruit (Krassilov, 1982), but later re-interpreted (Akhmetiev and Krassilov, 2002) as a samaroid cupule of four decussate scales each subtending a crescent-shaped seed. The wing was formed of the median pair of scales (Fig. 10B). Although morphologically dissimilar, the cupules of *Eoantha* and *Gurvanella* were built upon the same structural plan (Akhmetiev and Krassilov, 2002). *Gurvanella* resembles the seed-bearing structures from Negev in both the crescent-shaped seeds curved conformably with the scales and the polygonal fibrous network on the latter. Yet the seed cones of *Afrasita* consist of a larger number of radial scales and the seeds were shed from the cones rather than being dispersed with samaroid scales.

Our knowledge of these plants is admittedly incomplete and the interpretations may change with better preserved material. As interpreted here, they were gymnospermous, related to bennettites and gnetophytes,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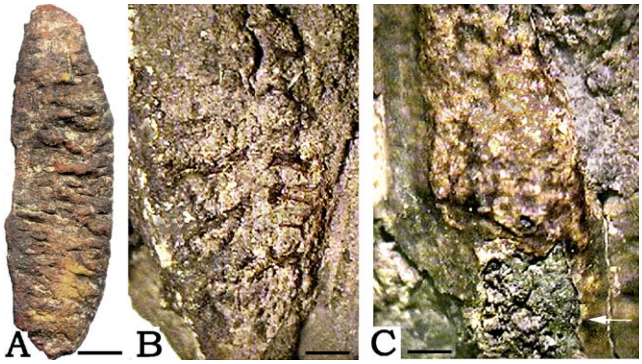

Fig. 5. *Afrasita lejalnicoliae* gen. et sp. nov. from the Lower Cretaceous of Makhtesh Ramon, Israel. A, IMR1-3, detached scale, abaxial view. B, IMR1-15, abraded scale showing interlacing fibrous strands. C, IMR1-16a, scale with a polygonal pattern reflecting subepidermal fibrous network exposed where the epidermal cast is pulled-off (arrow). Scale bars represent 4 mm (A) and 2 mm (B, C).

but closer to the latter on account of seed morphology. Their morphological affinities are with the central Asiatic plants described as proangiosperms of gnetophytic origin (Krassilov, 1986; Krassilov and Bugdaeva, 2000; Akhmetiev and Krassilov, 2002). Their seed bearing structures are variations on the same theme, representing parallel developments in the distant regional settings of Cretaceous rift valleys of Central Asia and the Afro-Arabian landmass.

4. Feeding punctures of sucking insects

Description. A detached seed of *Afrasita abuballensis* under the SEM shows deep punctures on the apical bulge of the inner envelope (Figs. 9B, 11A, B). There are eight punctures irregularly distributed over the apex (three of them seem to be in line with each other, but this may be a serendipitous arrangement) at ca. 100–200 μm from each other. Their external openings are crater-like, ca. 40–50 μm in diameter, with a flange of minutely cracked brittle material (Fig. 11B) surrounding the central duct ca. 12–15 μm wide and extending down the puncture as a sheath of the duct. Occasional punctures are capped by concentric accumulations of an amorphous material that is spread irregularly over the epidermis (Fig. 11E).

Between the deep punctures there are slightly depressed areas of many small punctures separated by short epidermal ridges. These areas vary in outline from elongate or elongate-polygonal to nearly circular, about 80–150 μm across. They are strewn with small droplets of amorphous (resinous?) material (Fig. 11D). The punctures themselves are triangular with concave sides or nearly rhombic in outline. An ill-defined sunken area with a few small punctures shown in Fig. 11A is situated midway between the adjacent deep punctures. Fig. 11C shows rather dense punctures and bulges aligned along the median line of a narrow depression, whereas in Fig. 11F the epidermal ridges spread radially from a small puncture in the center of a shallow sunken area. The puncture is triangular, with sharp, slightly curved points as if made with a barbed tool.

Discussion. Of the diverse plant-sucking insects, those of the order Homoptera leave stylet tracks that are

Fig. 6. *Afrasita lejalnicoliae* gen. et sp. nov. from the Lower Cretaceous of Makhtesh Ramon, Israel. A, holotype IMR1-2, base of an abraded cone showing casts of vascular traces (arrow) entering seed locules. B, IMR1-16b, subepidermal cast of scale showing bulges (arrow) at the joints of the fibrous network. Scale bars represent 3 mm (A) and ca. 1 mm (B).

Fig. 4. *Afrasita lejalnicoliae* gen. et sp. nov. from the Lower Cretaceous of Makhtesh Ramon, Israel. A, holotype IMR1-2, cone with radially spreading scales flanking seed locules (s). B, IMR1-11, two gaping scales exposing a seed locule (s). C, IMR1-8, gaping scales exposing an intact seed and an empty locule to the right (s). D, IMR1-10, adaxial view of two scales flanked by seed locules (s). E, IMR1-9, intact seed with partly preserved stalk (st). F, G, IMR1-5, IMR1-6, detached seeds. Scale bars represent 4 mm (A), 6 mm (B), 3.5 mm (C, D), 2.5 mm (E), and 3.5 mm (F, G).

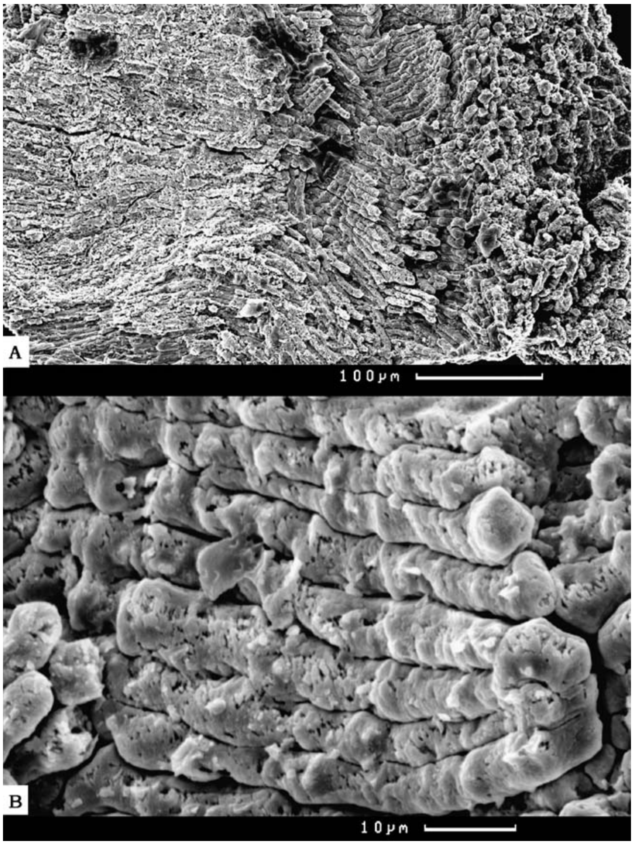

Fig. 7. *Afrasita lejalnicoliae* gen. et sp. nov. from the Lower Cretaceous of Makhtesh Ramon, Israel, scanning electron micrographs. A, IMR1-16b, compression fragment of cone scale showing palisade layer. B, palisade cells enlarged, spiral thickenings are seen as transverse lines.

Fig. 8. *Afrasita lejalnicoliae* gen. et sp. nov. from the Lower Cretaceous of Makhtesh Ramon, Israel. A, IMR1-17, seed cut at the chalazal end (arrow), lateral view. B, another aspect of the same seed showing scar of micropylar tube on the apical cone. Scale bars represent 3.4 mm (A) and 1.1 mm (B).

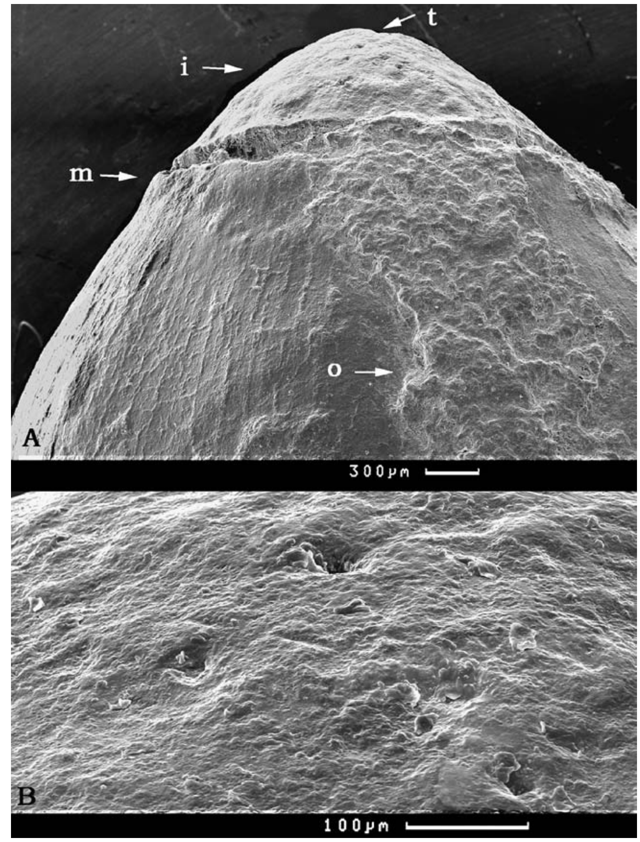

Fig. 9. *Afrasita lejalnicoliae* gen. et sp. nov. form the Lower Cretaceous of Makhtesh Ramon, Israel, scanning electron micrographs. A, IMR1-17, seed (same as in Fig. 8) showing a strip of the outer spongy layer (o) and the ridged middle layer (m) separated by an annular furrow from the inner layer (i), the latter forming the apical cone, with the scar of the micropylar tube (t) on top. B, punctures on the apical cone (see Fig. 11).

readily recognizable owing to their durable sheaths, which remain intact as the stylet bundles are withdrawn from the puncture (Chrystal, 1926; Miles, 1968; Meyer, 1987). Insofar as the sheath is secreted by the insect concomitant with the penetration of stylets, it is often called a ''salivary sheath'', yet in several cases the sheaths are reported to contain callose apparently secreted by the affected plant cells (Chrystal, 1926; Evert et al., 1968, 1973). The external deposits of saliva on the epidermis form a flange or collar around the puncture (Miles, 1968; Evert et al., 1973). Feeding ducts are always filled with saliva mixed with the percolating sap. Both mandibular and maxillary stylets of homopterous insects, in particular the aphids, are sharply pointed and provided with distal barbs. Besides the deep feeding punctures reaching to the main source of sap, aphids (their larvae) make shallow probes by stinging through the epidermis with their barbed stylets (Lewis and Walton, 1958; Meyer, 1987).

Probing activity in aphids was reviewed by Pollard (1973), who noted that the insects sting with their stylets whenever they encounter an obstacle, such as an epidermal ridge. Such punctures are usually clustered. Their frequency varies systematically in different families. As some insects remain in one place for hours or even days they leave behind an extensively punctured area. The

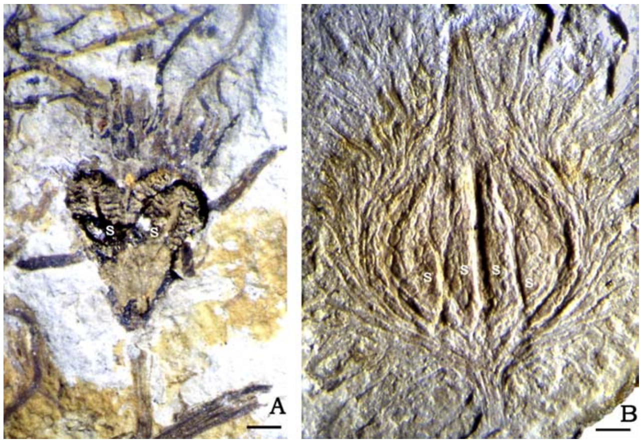

Fig. 10. Seed-bearing structures of gnetophytic plants from Central Asia for comparison with *Afrasita lejalnicoliae* gen. et sp. nov. from the Lower Cretaceous of Makhtesh Ramon, Israel. A, *Eoantha zherikhinii* Krassilov, from the Lower Cretaceous of Transbaikalia (Krassilov, 1986), a cupule of four decussate scales subtending orthotropous ovules (s). B, *Gurvanella dictyoptera* Krassilov, from the Lower Cretaceous Yixian Formation, north-west China (Krassilov, 1982; Akhmetiev and Krassilov, 2002), a cupule of four scales bearing crescent-shaped seeds (s), the median pair of scales forming membranous wing. Scale bars represent ca. 1 mm.

probes may be perfunctory to making a feeding duct, but sometimes a small amount of sap is sucked from epidermal cells or mesophyll. Plant reactions to the penetration of stylets are highly diverse, including plasmolysis of cells adjacent to the sheath and secretion of resinous material (Meyer, 1987; Pollard, 1973).

Several features in common lend support to a hypothesis that punctures on fossil seeds from Makhtesh Ramon were made by sucking insects belonging or related to the hemipteran order Homoptera. The flanges of opaque material around the larger punctures obviously correspond to the external collars of salivary sheaths consolidating the stylet tracks of extant aphids. The concentric surface deposits plugging some punctures might have been formed by sap percolating through the sucking ducts.

Small, shallow punctures are evidence of probing activity. Since the feeding punctures are nearly equidistant, the probing punctures between them might have been inhibited by a defense reaction of plant cells around the adjacent stylet tracks (see discussion of probing inhibition in Walker, 1983). The arrowhead punctures with sharp points (Fig. 11F) might have been left by a laterally barbed stylet, as in extant aphids. The depressed areas of shallow punctures betray a plasmolytic effect of probing on epidermal cells that sank and shrank as minute ridges. Secretion of resinous droplets is another reaction of plant cells to the penetration of stylets.

However, punctures on the fossil seeds are much larger than those made by modern Hemiptera, suggesting relatively robust mouthparts in the Mesozoic sucking insects. For example, in modern aphid nymphs, the stylet bundle rarely exceeds 3.5 µm in diameter, whereas the external collar of the duct is about 4.5 µm wide (Pollard, 1973). On the other hand, the Palaeozoic palaeodictyopteorid insects that were similar in their piercing and sucking habits to the extant Hemiptera had much larger beaks (Labandeira and Phillips, 1996). Their target was primarily the phloem of vascular bundles, yet deep punctures through a seed coat reaching to the nucellus were also recorded in Palaeozoic material (Sharov, 1973).

Punctures described by Labandeira and Phillips (1996) on the Pennsylvanian tree fern *Psaronius* were made with stylets about 0.45 mm wide, which is rather small for Palaeodictioptera, but far too large for Hemiptera. The punctures on the Cretaceous seeds are intermediate between the lowest values for Palaeodictyptera and the highest values for Hemiptera, but closer to the latter. The probing habit is essentially hemipteran, as yet not recorded in the related fossil groups.

Our material is peculiar in that the punctures are confined exclusively to the apical bulge, which indicates a fairly specialized feeding habit. This part of the seed is formed by the inner envelope alone and evidently was the least resistant to penetration. Moreover, the bulge at the base of micropylar tube might have contained a secretory gland for producing a sugary liquid for a pollination drop. This might have been the main target of the sucking insects. If so, then the ovules must have been attacked at about the time of pollination.

5. Other palaeoecological remarks

Found at the same stratigraphic level and in similar settings of coastal deposition in the Dakhla Basin of Egypt and the Makhtesh Ramon Basin of Israel, *Afrasita* attests to a vegetation continuity between these two areas. Seeds and seed-bearing structures of this peculiar plant are the only plant remains found in the coastal sand-flat facies of the Aptian locality in Makhtesh Ramon. It was not found among the diverse plant macrofossils from the contemporaneous lacustrine deposits (Nevo, 1968). This suggests an abundant local source, such as a monodominant stand of coastal vegetation.

Preservation of large fruit clusters suggests insignificant transportation damage, yet many fruiting bodies are abraded as if they had been dragged or rolled by tide currents. Their association with gastropod shells that are often found stuck to the scales also indicates long immersion in sea water before burial. It is not clear whether the seeds were shed in the course of maturation or released by disintegration of the fruiting bodies, but the latter seems more probable because detached scales are nearly as common as the seeds.

The scales are described as succulent on account of the fibrous hypodermal layer and thick palisade

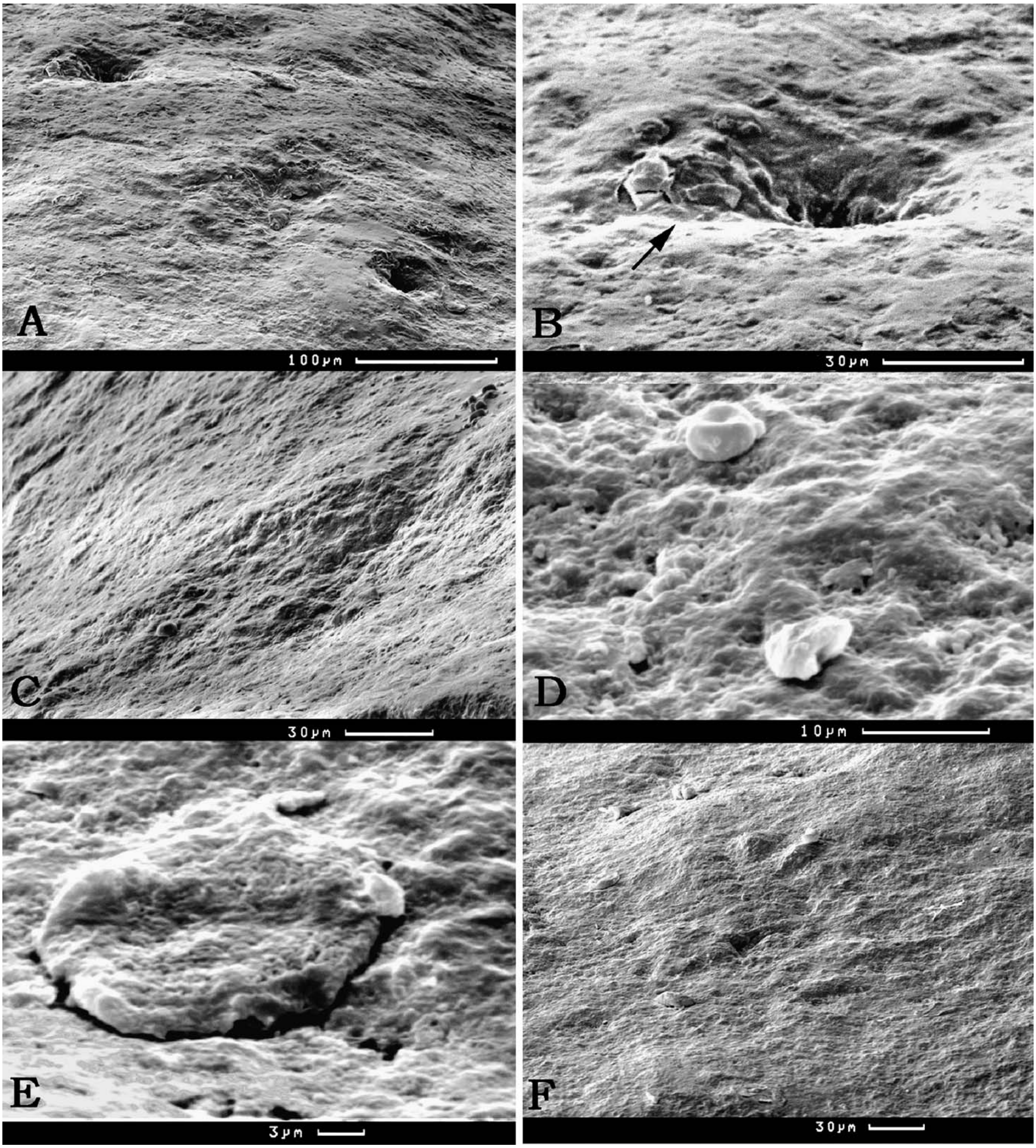

Fig. 11. Feeding punctures on *Afrasita lejalnicoliae* gen. et sp. nov. from the Lower Cretaceous of Makhtesh Ramon, Israel, IMR1-17, scanning electron micrographs. A, two feeding punctures of a sucking insect and a shallowly punctured sunken area between them. B, puncture showing a broad flange (collar) of opaque material (arrow). C, elongate area of dense small punctures (probes). D, droplets on a probed surface. E, flap of concentrically ridged substance (percolate sap) capping a feeding puncture. F, radial epidermal ridges around a shallow triangular puncture with sharp points (a sting with a barbed stylet).

parenchyma (on association of this histological feature with succulent habit see Shields, 1951). Moreover, the palisade cells are mostly in contact with each other leaving only very narrow intercellular spaces, which is also characteristic of xeromorphic plants. Tracheid-like cells occur in the palisade parenchyma of some xeromorphic halophytes, such as *Salicornia*. Their function as water-conducting and/or water-storing cells was discussed by Fahn (1967).

The ovules must have been well exerted at anthesis when they were attacked by the sucking insects. This feeding habit would have promoted insect pollination.

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