ANGIOSPERM FRUIT FROM THE LOWER CRETACEOUS OF ISRAEL AND ORIGINS IN RIFT VALLEYS

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Abstract: Angiosperms appear in the fossil record as minor elements of the fern-gymnosperm dominated Mesozoic floras. Their pre-Albian macrofossils are very few, and each new find helps to obtain insight into the controversial problem of their origin and early evolution. Our revision of a plant collection from the Aptian intrabasaltic "Amphibian beds" of Makhtesh Ramon, southern Israel, has revealed a samaroid fruit of juglandioid affinities, recording the presence of amentiferous forms among the earliest angiosperms. Insofar as the Negev basalts and their varved lacustrine interbeds resemble the contemporaneous intracontinental rift zone sequences in other parts of the world also containing angiosperm localities, our findings support the idea of early angiosperm evolution in the rift valley environments.

Key words: Earliest angiosperms; samaroid fruits; Makhtesh Ramon; "Amphibian beds"; Lower Cretaceous; Aptian.

Плод покрытосеменных обнаружен в интрабазальтовых амфибиевых слоях Махтеш-Рамона, южный Израиль. Возраст амфибиевых слоев определяется как аптский. Это наиболее ранняя находка сережкоцветных покрытосеменных. Высказывается предложение о том, что рифтовые долины служили центрами развития и расселения новых групп фауны и флоры.

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Angiosperms appear as occasional Neocomian pollen records [1]. They remained a minor component of terrestrial vegetation until the Albian. Stringently dated pre-Albian angiosperm macrofossils are exceedingly rare. Occasional leaves and fruits from the Ptomac Group of eastern North America, the Baquer' Formation of Patagonia, the Zaza Formation of Transbaikalia, the Nikan Series of the Russian Far East, the Gurvan-Eren Formation of western Gobi, and the Koonwarra Formation of southern Australia are considered Aptian though most

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of them lack independent stratigraphic control [2-7]. We report here a rather modern-looking samaroid fruit from the Aptian "Amphibian beds" of Makhtesh Ramon, southern Israel (fig. 1). Makhtesh Ramon is an eroded northern wing of a medially faulted anticline 20 km long, with Triassic and Jurassic deposits in the core zone unconformably overlain by a Lower Cretaceous to Cenomanian sequence on the flanks. The Lower Cretaceous Kurnub Group includes the Arod Formation of basal conglomerates and the Hatira Formation of predominantly freshwater sandstones and shales with marine interbeds and basalt flows. The "Amphibian beds," discovered by E. Nevo during geological exploration of the area in 1954, occur about 50 m below the dolomite marker bed with marine bivalves, between two thick basalts, and consist of tuffaceous fine-grained sandstone and silty clay about 20 m thick, forming varved couples of light and dark lamellae. They outcrop on the northern slope of Amphibian Hill, 30° 32' 20'N, 34° 43'36'E (1236/9945 of the Israeli grid), altitude 720 m. This locality contains numerous remains of pipid frogs and many fewer terrestrial plants. All fossils are preserved as ferruginous impressions with dispersed organic substance.

Nevo has described fossil frogs and discussed the stratigraphy, paleoecology, climatic inferences, and geological age of the locality, which he assigned to the Neocomian [8-10]. However, recent studies of marine intercalations in Makhtesh Ramon, as well as in Makhtesh Gadol and Makhtesh Katan to the north, suggest an Upper Aptian rather than Neocomian age [11, 12].

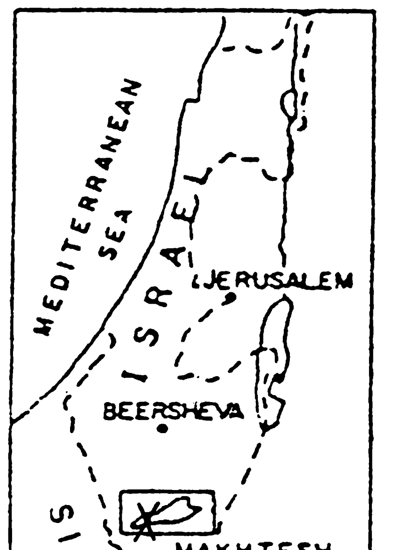


Fig. 1. Location of the Amphibian Hill in Makhtesh Ramon (x), after [10].

Fossil plants from the Amphibian Hill locality have been preliminarily studied by Y. Lorch, who determined several fern and gymnosperm species figured in [8, 10]. Our survey of the collection in the Hebrew University of Jerusalem has revealed a few angiosperm leaf fragments and a single samaroid fruit preserved as a double impression of its abaxial and adaxial faces (fig. 2). The fruit is 25 mm long, 7 mm broad, consisting of a comparatively large bilobed wing, abaxially attached to a nutlet 3 mm long. The wing lobes are lanceolate, acutely pointed, of unequal lengths of 15 and 16 mm. They show an irregular reticulate venation and a fine parallel striation, supposedly reflecting hypodermal fibers. Venation of the wing lobes consists of a midrib and weaker lateral veins diverging to the margins and looping with proximal secondary branches of the midrib in the lower third of the lobe. The secondaries arise at an acute angle and arch to produce a series of strong, distalward diminishing loops bordered by the shorter tertiary loops extending along the margin. Ultimate venation is irregularly areolate with polygonal or rectangular areoles of unequal size. The freely ending veinlets seem absent.

The nutlet is incompletely preserved on both the impressions. The abaxial face shows a medially grooved entire base of the wing and the outline of a broken nutlet with a persistent pedicel 1 mm long. On the adaxial face is a spatulate appendage 4 mm long, onlapping a stylar part of the nutlet with two stigmatic arms spreading in the plane parallel to the wing.

The mode of attachment and venation of the wing suggest a fruit rather than a samaroid seed or seed-scale complex. Moreover, there is a close similarity with samaras of Juglandaceae, although the fossil does not seem to fit any tribe of the family. Superficially, it resembles *Hooleya*, a fossil genus of Platycaryeae, which has two diverging wings with irregular reticulate venation [13, 14]. In Platycaryeae, however, the wings are lateral and their primary veins are flabellate. Engelhardieae is closer in having involucrate fruits, whose involucres consist of a large winglike bract and a much smaller adaxial appendage, or winglet ("prophyll" in [14]) formed of bracteoles and perianth lobes. The nutlet is typically pedicellate, with an extended style bearing biarmed stigma (in *Engelhardia*), and notably, in extant *Oreomunnea* and several fossil species of *Palaeocarya*, is much smaller than the winglet. Lateral veins of the wing lobes in extant *Oreomunnea* and related fossil forms are parallel to the midrib, but in *Alfaropsis* they diverge to the margins, as in the Aptian fruit. *Alfaropsis* is distinct, however, in a much reduced winglet. In addition, all the Engelhardieae have a trilobed, rather than bilobed, bract-wing. The fossil fruit, thus, represents a new taxon.

Ramonicarya Krassilov and Dobruskina, gen. nov.

Name. After locality and genus *Carya*.

Diagnosis. Fruit involucrate with large bilobed abaxial wing and small spatulate adaxial winglet. Wing venation with a midrib and weaker lateral veins, irregularly reticulate. Nutlet pedicellate with biarmed stigma.

Type species. *Ramonicarya nevoi* Krassilov and Dobruskina, sp. nov.

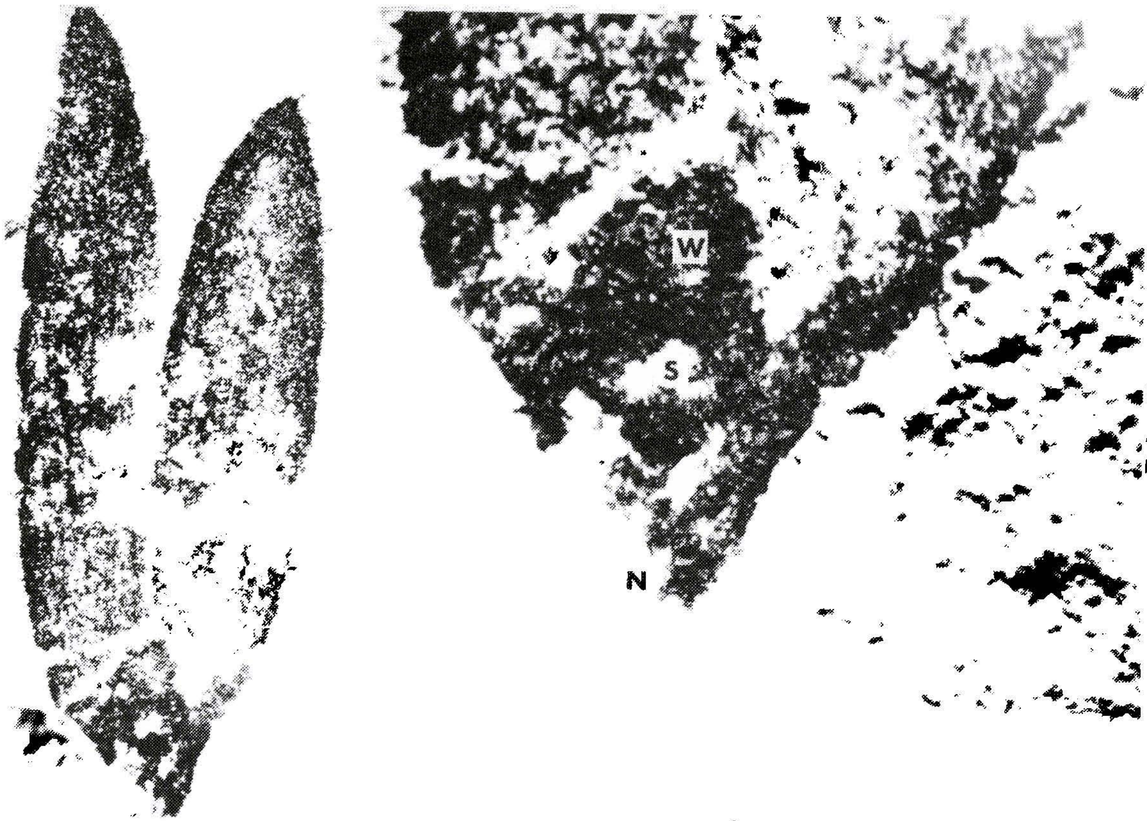
Species name. In honor of Professor Eliatar Nevo.

Holotype. CRE 98, 99, part and counterpart, Depository of the Hebrew University, figs. 2, 3.

Fig. 2. Samaroid fruit *Ramonicarya nevoi* from the Aptian of Makhtesh Ramon, Israel: *a* - adaxial aspect, showing part of nutlet with short pedicel below, (×7); *b* - abaxial aspect, showing bract-wing venation, (×10).

Type locality. Amphibian Hill, Makhtesh Ramon, Negev, Israel; Lower Cretaceous, Aptian.

Juglandaceae, of a modern aspect closely related to extant forms, have appeared in the Paleocene [14] while their *Noempollia*-producing precursors dominated the transatlantic Late Cretaceous floras. Our findings extend the fossil record of juglandioid fruit morphotypes back to the Aptian, thus showing a considerable morphological diversity of the earliest angiosperms



a b

Fig. 3. Samaroid fruit *Ramonicarya nevoi* from Aptian of Makhtesh Ramon, Israel: *a* - abaxial aspect, (×7); *b* - proximal part of (*a*) enlarged to show biarmed stigma, (×15). (N - nutlet, S - stigma, W - singlet).

and the presence among them of supposedly woody amentiferous forms with involucrate, samaroid, wind-dispersed fruits. These fruits might have been transported to the side of deposition from slopes of nearby volcanoes.

The Lower Cretaceous basalts of Makhtesh Ramon evidence an initial rifting phase in the Negev while the intrabasaltic "Amphibian beds" are varved deposits of a stratified lake in which the mass mortality of pipid frogs might have been caused by accidental acidification induced by volcanic activity. Volcanic impact on surrounding vegetation might have disturbed the then-dominant fern-cycadophyte communities, permeating the early angiosperm invasion. The "Amphibian beds" are remarkably similar to the varved deposits of the Aptian rift-valley lakes in other parts of the world, such as the Zaza Formation of the Lake Baikal Rift in Siberia or the Koonwarra Formation of the Strzelecki Rift in Australia. These deposits also contain the earliest angiosperm macrofossil records, thus supporting the idea [15] of rift valleys as the sites of early angiosperm evolution.

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