

A Gramminoid Plant from the Cretaceous of the Middle East

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Abstract—A new genus and species *Geroftia lorchii* gen. et sp. nov. is erected on the basis of a fossil infructescence from the lower Turonian of Israel. This is the earliest macrofossil of graminoid monocotyledons evidencing their early appearance in the evolutionary history of angiosperms. Problems in the homology of spikelets and florets of grasses and sedges are discussed.

INTRODUCTION

The graminoid group of herbaceous monocots include, in addition to grasses, the habitually similar Cyperaceae and Restionaceae, as well as fossil forms of which the taxonomic position within these extant forms is ambiguous. The latter on the other hand might belong to some extinct families. The origin and morphological evolution of glumiflorous monocots, including the largest extant angiosperm families, the Cyperaceae and Poaceae, is as yet poorly documented in the fossil record, while their morphology remains controversial. As a reminder they are assigned to a single order Cyperales by Cronquist (1981) but to different orders and even subclasses by Takhtajan (1966), although in other aspects the macrotaxonomic systems of these authors are quite similar.

Conceivably, in graminoids, many of which are ecologically dominant in herbaceous plant communities, the life form similarities are largely convergent. Their reproductive structures are generally considered as highly advanced. They consist of spicate inflorescences with extremely reduced flowers protected by bracts and scales, the homology of which both within and outside the group is far from clear. Some morphologists consider the floral units of graminoids, or of some of them, as flower-like inflorescences. However all the morphological hypotheses in this field are solely based on extant data. Palaeontological material is too scanty to clarify phylogenetic relationships within graminoid groups and between them and other monocots.

The appearance of graminoids is usually assigned to the Eocene although there are a few earlier records of dispersed achenes, such as *Carex tsagajanica* Krassilov from the Paleocene of the Amur Region (Krassilov, 1976) and the slightly earlier Late Maastrichtian pollen record of Restionaceae (Muller, 1970; Hochuli, 1979; Krassilov, 1989). A still earlier find of *Taldysaja*, a graminoid inflorescence from the Santonian–Campanian of Kazakhstan (Krassilov *et al.*, 1983) may indicate an extinct Late Cretaceous group. The new findings described below push the graminoid record at least

25 million years back in time, placing them among the early, i.e., mid-Cretaceous, angiosperms. The early differentiation of graminoids does not fit the current view of their highly advanced position in angiosperm phylogeny. At the same time our material has some bearing on the problem of floral homologies of grasses and sedges.

MATERIAL

A single rock slab containing an incomplete infructescence and a number of detached glumes and fruits was collected from the Maale Grofit locality situated at Zomet Ketura on the left slope of the Geroft (Grofit) Valley near its confluence with the Arava Valley, about 62 km north of Eilat by the Eliat–Dead Sea highway (local coordinates 1572/9337). The locality was discovered by Lorch (1965, 1967). In his popular account of “Fossil plants in Israel” he reported on the racemes of undetermined plants from Maale Geroft older than 90 My (Turonian, Late Cretaceous). The associated fossil plants are represented by platanoid and dryophylloid leaves, as well as the remains of aquatic dicotyledons. Fossil plants came from the Ora-Shale Formation of thick red and green shales with sandstones, marly shales, dolomites, and fossiliferous limestones widespread in the Arava and Negev areas (Bartov *et al.*, 1972). Plant remains occur in the pale grey marly shales of the uppermost member of the Ora Shale Formation. Their geological age is determined by the early Turonian ammonites in the underlying Ora members and the Late Turonian *Radiolites preasauvagesi* Toucas in the overlying Geroft Formation. These deposits are confined to the slowly subsiding Arabo-Nubian Carbonate Platform. The terrestrial plant material, including fragmented fructifications of marsh herbs, may presumably have been washed in from episodically emerging land.

The infructescence is preserved as a brownish grey impression powdered by a dispersed coaly substance. Its branches and detached achenes were partly imbed-

ded in the rock matrix and were uncovered using fine needles under a stereoscopic microscope that provided a clearer view of the infructescence general structure and its terminal units. Fragments of the latter were mounted for the SEM to study details of venation and relief. The material is deposited in the Institute for Biological Sciences, The Hebrew University, Jerusalem collection "T".

SYSTEMATICS

Genus *Geroftia* Krassilov et Dobruskina, gen. nov.

E t y m o l o g y. From the locality, Maale-Gerofit.

T y p e s p e c i e s. *Geroftia lorchii* sp. nov.

D i a g n o s i s. Infructescence loosely paniculate corymbiform, with two branch nodes, distal branches ascending above apex. Branches (paracodia) racemose, apically fasciculate, with crowded terminal units. Terminal units spicate, bearing five to seven imbricate bracts (glumes) of which the distal axillates form two scales enveloping fruit, and shed with it. Scales of axillar complex awned, longer than glumes, dimorphic, the abaxial thick carinate, adaxial slightly shorter, membranous, with parallel veins connected by cross-veins, their awns converging over fruit forming pincers-shaped beaks.

S p e c i e s c o m p o s i t i o n. Type species alone.

C o m p a r i s o n. In the structure of inflorescence (infructescence) this plant differs from all fossil graminoid, including the Cretaceous genus *Taldysaja* (Krassilov *et al.*, 1983), the latter having a fasciculate radial inflorescence with spinulate glumes. Corymbiform inflorescences are common in the extant Cyperaceae, whereas the morphology of the axillar units is comparable with that of both grasses and sedges, but at the suprageneric level alone (see discussion below).

Geroftia lorchii Krassilov et Dobruskina, sp. nov.

Plate 6, figs. 1–9

E t y m o l o g y. In honor of Professor J. Lorch.

H o l o t y p e. Institute of Biological Science, Hebrew University, Jerusalem, no. T-244, Maale-Gerofit locality, southern Israel, Cretaceous, Early Turoanian, Ora-Shale Formation.

D i a g n o s i s. As for the genus.

D e s c r i p t i o n (Figs. 1 and 2). The fossil plant is an impression of a single compound infructescence with scattered fruit and bracts on the same slab, obviously detached from it in the course of deposition and burial. The infructescence is paniculate, with a short main axis bearing two whorls of lateral branches. The proximal branches are much stronger than the distal ones, the latter ascending above the apex to form a corymbiform structure (following a classification of inflorescence morphotype by Fedorov and Atryushchenko, 1979). The first order branches are compound one-sided racemes bearing spikes that are subtended by short bracts. The axillar complex is formed of two

awned scales of unequal length (the abaxial one longer than the adaxial) enveloping the fruit (some of them might still contain a floret with a distinct floral part, see below).

The main axis is terminated in a mass of spikes that apparently belong to the terminal raceme. The lateral branches arise in two successive nodes 9 mm apart, marked by transverse grooves. The distal branches diverge at an wide angle and are directed forward overhanging the main axis. They are about 20 mm long, proximally terete for about 7 mm, distally repeatedly forking at short intervals of a few mm giving rise to a mass of spikes. Of the proximal whorl, the better preserved left branch is recurved and, although not traceable for its full length, is visibly much longer than the distal branches. It gives off a secondary branch 30 mm long, compressed across the main axis. This second order branch is in turn dichopodially divided giving off the fascicles of five to six densely crowded spikes (Plate 6, fig. 1). The intervals and angles of branching progressively decrease towards the terminal fascicle.

A reflexed subtending bract—or a thick decurrent basal part of a supposedly caudate bract—is discernible at the base of the left distal branch. At other places, slender linear processes occasionally protruding from under the masses of spikelets might suggest awned bracts or prophylls (Pl. 6, fig. 4), but their attachment is impossible to make out.

The spikes are 7–9 mm long, bearing five to seven spirally arranged, imbricate, short triangular bracts (glumes) two or three of which are empty, the rest axillate a pair of larger scales of which the abaxial is the stronger developed. Their awned apices form a pincers-shaped beak, occasionally gaping, with a fruit apex protruding between them (Pl. 6, figs. 2, 3, and 5). Small scaly appendages, presumably of a floret, are seen between the larger scales in occasional longitudinally cut axillar complexes (Pl. 6, fig. 5).

The scale morphology is better discernible in detached axillar complexes. The abaxial scale is lanceolate, about 4 mm long, sessile, one-keeled with an awn 0.5 mm long, concave and finely longitudinally striated in the central part, with flat smooth margins. The adaxial scale is membranous, elongate, about 3.5 mm long, 1.5 mm broad, with a shorter awn, basally constricted to a minute stalk, thickened as a callus at the base. Impressions of the abaxial scale show a distinct venation marked by slightly undulating ribs diverging from the middle of the base and running parallel over most of the blade length. Between them, a scalariform pattern of thin cross-veins is discernible with a SEM (Pl. 6, fig. 8).

The fruit are detached with their enveloping scales forming a loosely adnate utricle with a split beak (Pl. 6, figs. 6 and 7). The impressions convey soft, rather than rigid or brittle, fruit bodies. On the bedding plane, most detached fruit are turned with their convex lower scale



Fig. 1. Inflorescence and detached fruit of *Gerofitia lorchii* Krassilov et Dobruskina, sp. nov., holotype no. T-244, $\times 5$.

to the observer; only a few of them showing a flat ribbed surface of the upper scale (Pl. 6, fig. 9).

DISCUSSION

In our previous paper on Early Cretaceous (Aptian) fruit (Krassilov and Dobruskina, 1995) we suggested a Middle Eastern centre of angiosperm evolution related to the regionally prominent rift zone. The first appearance of graminoid monocots in the same region seems to support its significance in the initial angiosperm diversification. These findings might have some bearing not only on the chronological sequence of the major angiosperm orders, but also on the morphological evolution of compound inflorescences, as well as homology and structural interpretation of their functional units.

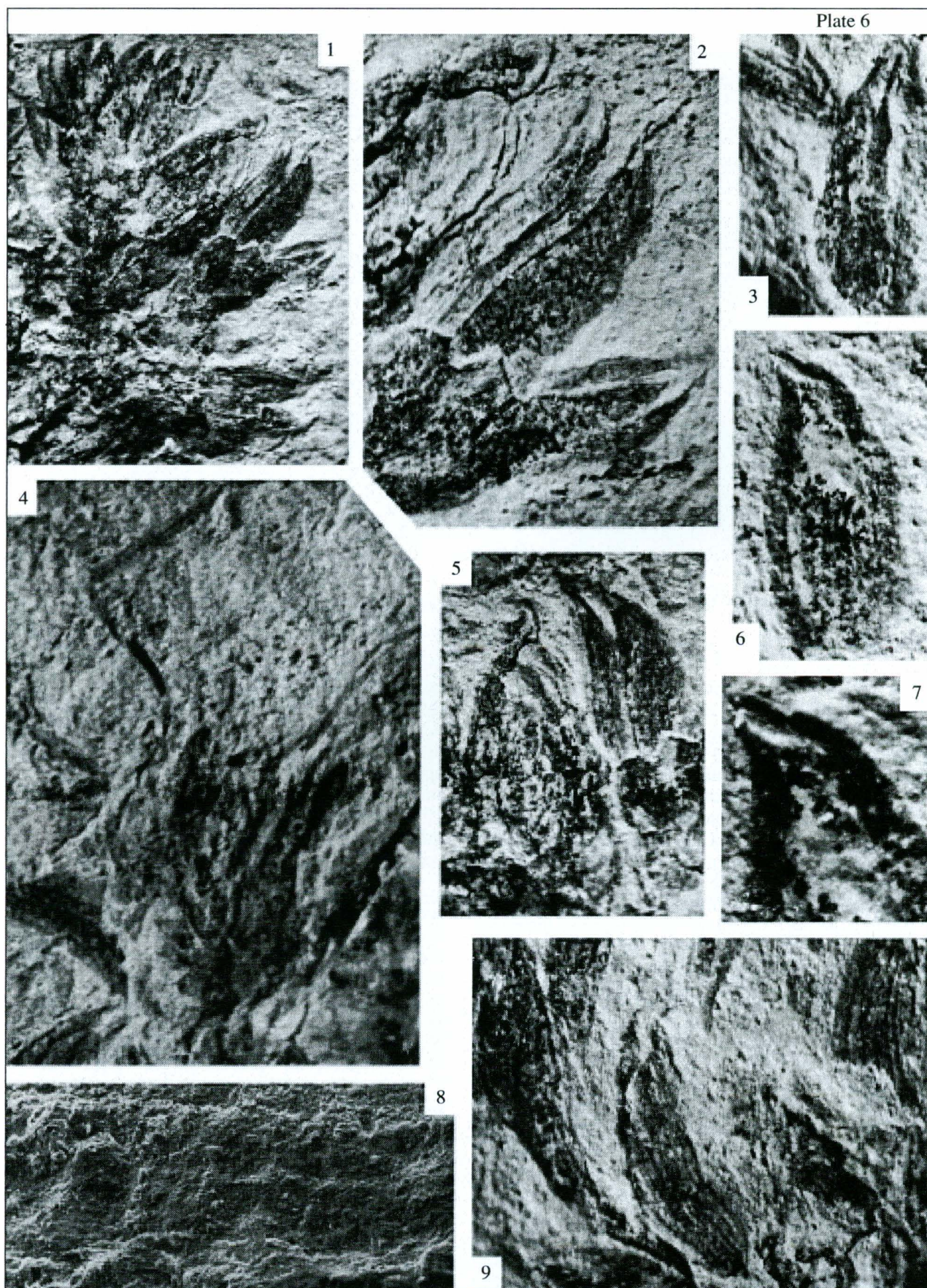
Among the extant angiosperms, the corymbiform inflorescences typically occur in families such as the Cyperaceae that are placed high on phylogenetic trees. Therefore the early appearance of these types of compound inflorescences in the mid-Cretaceous is of interest for the evolutionary morphology of angiosperms.

It has to be mentioned, however, that compound inflorescences had already appeared in the Early Cretaceous gnetophytes in which there was a tendency to diminution and structural reduction that sometimes led to a definitely graminoid habit (Krassilov and Bugdaeva (in press)). On this evidence, the graminoid

inflorescences might have developed on the basis of fairly advanced proangiospermous structures rather than, as the classical theory suggests, from perfect solitary flowers with a complete set of floral organs. Compound inflorescences have also simultaneously appeared in other herbaceous angiosperm lineages, such as *Caspiocarpus* (Vachrameev and Krassilov, 1979). Contrary to some widely held views, compound inflorescences seem more typical for the mid-Cretaceous evolutionary stage than solitary flowers.

Even for morphologists working with extant material, structural interpretation of glumiflorous axillar units in graminoid monocots is met with considerable difficulties. At the graminoid level of morphological transformation, the distinctions between one-flower spikelets and solitary flowers are, for most groups, conventional, depending on traditions and terminological preferences. In particular, the pseudanthial interpretation of the cyperacean "perfect flower" goes back to the 19th century morphologists Goebel and Pax. More recently it has been revived by Schultze-Motel (1959 and elsewhere) for the entire family and by Eiten (1976) for the subfamily Mapanioideae, while rejected with respect to the rhynchosporoid tribes. In graminology, the pseudanthial concept is much less popular than in cyperology, and the inner scales of glumiflorous complexes are traditionally interpreted as members of transformed perianths. However, unambiguous morphological evidence is lacking for either of the groups.

Plate 6



Explanation of Plate 6

Figs. 1–9. *Gerofitia lorchii* Krassilov et Dobruskina, sp. nov., holotype no. T-244: (1) part of basal branch with fascicles of spikes, $\times 6$; (2) short bracts axillating gluniflorous complexes of two dimorphic scales, their own pincers-like converging over the fruit apex, $\times 16$; (3) detached utriculate fruit enveloped in the adaxial (left) and abaxial scales, $\times 16$; (4) fascicle of spikes with protruding linear bracts or prophylls of the first order lateral branch, $\times 16$; (5) longitudinally cut axillar complex (left) with small inner scales discernible, $\times 16$; (6) detached fruit, the upper membranous scale facing the observer, $\times 16$; (7) the same fruit showing a bifid beak, $\times 30$; (8) upper scale, cross-veins between parallel veins, SEM, $\times 140$; (9) detached fruit with a well preserved upper scale (center) showing parallel venation, $\times 16$.

Such terms as “glume” might have a different meaning when applied to grasses and sedges, while their differently interpreted parts of the axillar glumiflorous complexes might have been strictly homologous.

In cyperology, the origin of utricles (perigynia) and their homology is a controversial problem linked with an even more complicated problem of the pseudanthial nature of cyperacean flowers. In the widely held opinion initiated by Kunth in the 1830s, the typical perigynia are derivable from the prophyll of the spikelet axis, an adaxial sheathing scale opposite the subtending glume. The cyperaceous prophylls are highly variable structures with differently developed keels and venation, sometimes interpreted as double leaves (reviewed in Blazer, 1944). However, the utricles might arise in parallel in specialized members of different clades, thus not necessarily homologous within the family. The distally bifid utricles may have been formed from two homomorphous or even dimorphous scales with a possible involvement of the true glumes subtended by glume-like bracts, or pseudoglumes (reviewed in Shah, 1962). In the genera *Lagenocarpus*, *Microdracoides* and *Cephalocarpus*, the intraperigynal spikelets may lose their morphological identity by reduction of the rachilla and the ensuing terminal position of the solitary flower. In such cases, the glumes might appear as

perianth members (a glumaceous perianth) while replaced in their original position by pseudoglumes.

The morphology of axillar glumiflorous units in the mid-Cretaceous *Gerofitia* may suggest a basic structure of two juxtaposed scaly organs of which the stronger developed abaxial scale is both topologically and morphologically homologous to the lemma of grasses and the glume of sedges, whereas the relatively slender adaxial is comparable to the palea although differing from a typical bicarinate awnless form of the latter in the leafy shape and venation. The parallel venation with commissural cross-veins is common in graminoid leaf morphotypes. Therefore it is here considered as evidence of a prophyll origin of the adaxial scale in *Gerofitia*. In this fossil genus the adaxial scale is involved in the utriculate structure thus suggesting homology with cyperaceous prophylls, in turn homologous to the upper floral scale (palea) of grasses. The characters indicative of the double origin of the palea find their analogy in the double prophyll structure in the Cyperaceae. Additional support to these comparisons comes from a morphological variability of the palea including utriculate forms.

It follows from the above discussion that the traditional interpretation of graminoid flowers have to be reconsidered. In particular, the so called floral scales might have been of an extrafloral origin, derivable from glumes and prophylls of the spikelet, as in the flower-like spikelets of lagenocarpoid sedges. The existing fossil data are obviously not enough for settling this controversial problem, although what can be made out of the axillar scale complex in *Gerofitia* seems in favor of a reduced one-flower spikelet.

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Fig. 2. *Gerofitia lorchii* Krassilov et Dobruskina, sp. nov., holotype no. T-244, infructescence structure.

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