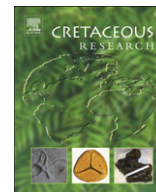




Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

New Albian macro- and palynoflora from the Negev (Israel) with description of a new gymnosperm morphotaxon

Valentin Krassilov^{a,b,*}, Eckart Schrank^c^a Institute of Evolution, University of Haifa, Mount Carmel, Haifa 31905, Israel^b Paleontological institute, Profsoyusnaya 123, Moscow 117647, Russia^c Institut für Angewandte Geowissenschaften, TU Berlin, Sekr. EB 10, Straße des 17. Juni 145, 10623 Berlin, Germany

ARTICLE INFO

Article history:

Received 23 March 2010

Accepted in revised form 1 October 2010

Available online xxx

Keywords:

Paleobotany

Palynology

Cretaceous

Albian

Early angiosperms

Gnetophytes

Negev

Israel

ABSTRACT

New plant macrofossil localities are found in the middle-upper part of the Albian Upper Hatira Formation of Makhtesh Qatan, an erosion crater in the northern Negev. These are so far the only outcrop localities in the Negev containing plant compressions and well-preserved sporomorphs. Their age assignments are controlled by the ammonite *Knemiceras* records below and above the plant-bearing sequence in the adjacent Makhtesh Hatira. The macrofossil assemblages are strikingly different in the sandy fluvial and shaly lacustrine facies, the former being dominated by *Araucaria*, *Athrotaxopsis*, *Brachyphyllum* and pinnatifid *Sapindopsis*, comparable at the plant assemblage and leaf morphological levels to the early to early late Albian assemblage of the North American Potomac flora. The lacustrine shale macrofossil assemblages appear archaic on account of their diverse pteridophyte component and sparse angiosperm remains. A new supposedly gnetophytic genus and species *Qataniaria noae* Krassilov, gen. et sp. nov. is dominant in the shale horizon. The sporomorph assemblages are strongly dominated by psilate trilete spores (87–93%). In the absence of elaterate forms, the angiosperm pollen *Afropollis jadinus*, *Pennipollis*, *Tricolpites* spp. and *Walkeripollis* sp. is consistent with the early Albian age. The abundance and diversity of conifers and the prominence of the fern bog assemblage suggest a relatively humid phase of the regional Albian climates.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Cretaceous deposits are widespread in Israel, being represented by the non-marine or marginal marine clastic lithofacies in the Lower Cretaceous and by the predominantly marine carbonates since the latest Albian. The major Lower Cretaceous plant localities are confined to the Aptian – Albian of erosional depressions (or “craters”, makhteshim in Hebrew), of the northern Negev: Makhtesh Ramon, Makhtesh Hatira and Makhtesh Qatan (Hazera). The Upper Cretaceous localities occur in the Arava Rift Valley, southern Negev (Fig. 1).

The Early Cretaceous plants have been first found in the Makhtesh Ramon, but only a list of provisional taxonomic assignments has been published (Lorch, 1963; Lorch in Nevo, 1968). The Turonian flora of Arava and the arthropod leaf damages are monographically described in Krassilov et al. (2005) and Krassilov and Rasnitsyn (2008). The materials collected by Krassilov and his

former PhD student Natalia Silantieva in the Makhtesh Ramon in 2005–2007 are only partly published (Silantieva and Krassilov, 2006a,b) and are presently under monographic study.

In the Makhtesh Qatan, fossil plants were first found in 2007 by Noa Fruchter, a student of Hebrew University, Jerusalem, in the course of geomorphologic survey of the crater. In 2007–2009 field seasons, two plant-bearing horizons were found and excavated by Krassilov assisted by Sophia Barinova, Natalia Silantieva (University of Haifa) and Dmitry Vassilenko (Paleontological Institute, Moscow). Eckart Schrank discovered the third, uppermost floristic horizon and made palynological sampling. The Makhtesh Qatan localities are the richest and so far the only outcrop localities in the Negev that yielded plant cuticles and well-preserved palynomorphs.

2. Materials and methods

The macrofossil remains are ferruginous impressions lacking organic matter in sandstones (locality IQ2, see below), but with diffused organic matter and fragmented compressions in the shale horizons (locality IQ1). They are partly immersed in the rock matrix and require excavation with thin needles. The compressions are not

* Corresponding author. University of Haifa, Institute of Evolution, Mount Carmel, Haifa 31905, Israel. Tel.: +972 4 8249799; fax: +972 4 824647.

E-mail address: vkrassilov@gmail.com (V. Krassilov).

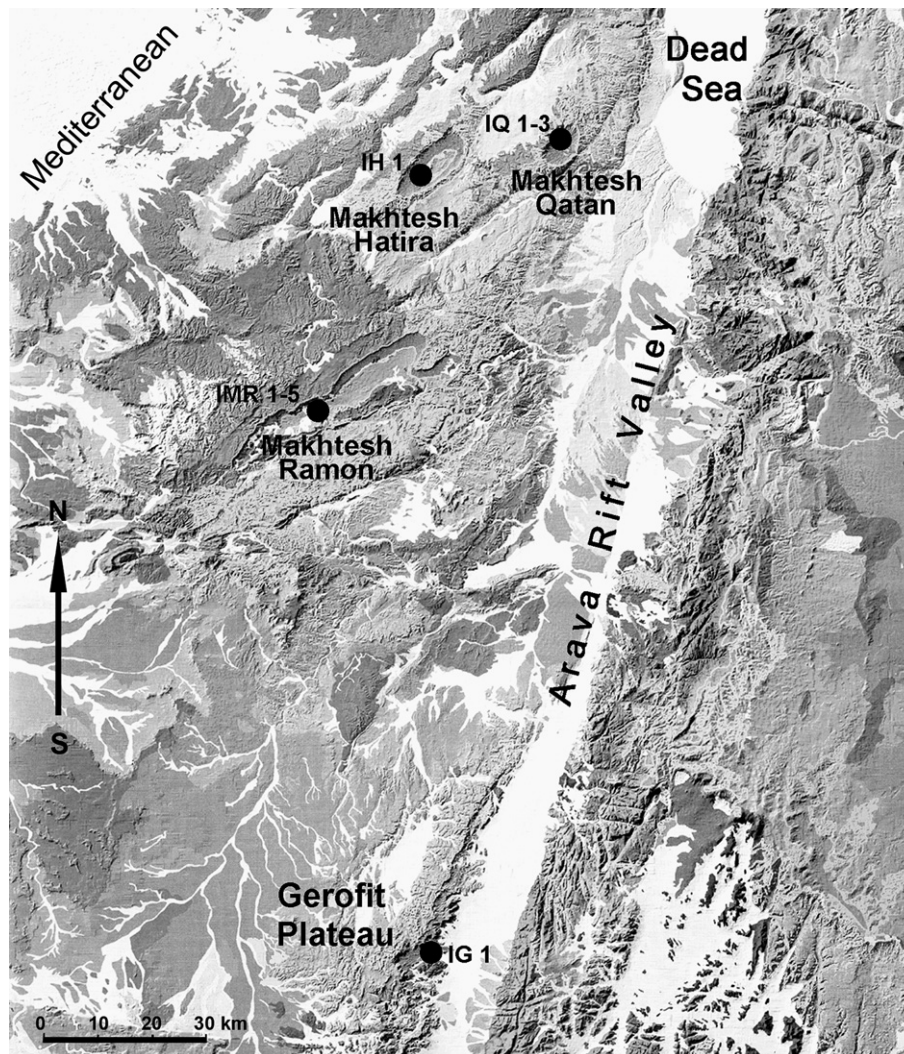


Fig. 1. Map of the study area based on the digitally shaded topographic map of Israel, 1: 5000 000, Geological Survey of Israel, 1997. Plant localities (dots) are designated as in the fossil plant depository of the Institute of Evolution, University of Haifa (IMR for Makhtesh Ramon, IH for Makhtesh Hatira, and IQ for Makhtesh Qatan).

mechanically separable and had to be macerated with small pieces of rock matrix. The cuticles are weathered and extremely fragile, cleared by a brief (about 7 min) exposure to concentrated nitric acid followed by a dilute potassium hydroxide treatment. *In situ* spores were extracted from sporangia by the same treatment. The photographs were obtained under stereomicroscope Leica MZ6 with camera Leica DEC320 and dissection microscope Nikon Eclipse 80i with camera Nikon DS-Fi1.

Plant macrofossil materials are housed at the Institute of Evolution, University of Haifa, the depository collection designations IMR1 – 5 for the Makhtesh Ramon localities, IH1 for the Makhtesh Hatira locality, and IQ1 – 3 for the Makhtesh Qatan locality. The respective symbols in the text and in Figs. 1 and 2 refer to these designations.

The chemical processing, including treatment with hydrochloric and hydrofluoric acids (HCl–HF–HCl) and sieving (mesh width 10–15 µm), and further study of palynological samples was done at the Technical University Berlin. The acid-resistant residues and palynological slides are deposited at the Technical University Berlin.

3. Stratigraphy of the early Cretaceous plant localities

In the northern Negev, the clastic Lower Cretaceous of the erosional craters are assigned to the Lower and Upper Hatira

formations. In the larger craters Makhtesh Ramon and Makhtesh Hatira, the Lower Hatira Formation lies unconformably on the mid-Jurassic Mahmal Formation. The Lower Hatira sequence begins with conglomerates and fluvial sandstones followed by the Zuweira Marine Tongue that comprises an alternation of sandstones, siltstone, and dolomites with bivalves, gastropods, *Lingula*, crustaceans and plant remains (Gvirtzman et al., 1996; Krassilov et al., 2004). This marine horizon is traced in outcrops and boreholes over the southern and central Negev and is correlated with marginal marine deposits of the Abu Ballas Formation of southern Egypt and the gastropod shales (“Couches à Gasteropodes”) of Lebanon (Barthel and Böttcher, 1978; Gvirtzman et al., 1996). The Lower Hatira Formation is topped by basaltic flows, pyroclastics and their covering lateritic redbeds.

On magnetostratigraphic evidence and on isotopic dating of the basalts, the Lower Hatira Formation has been assigned to the Barremian (?) – Early Aptian (Gvirtzman et al., 1996) and more recently to the Aptian – early Albian (Segev et al., 2005). Early angiospermoid pollen appeared at about this level (Schrank, 1992; Brenner, 1996) or even earlier (in the late Valanginian to early Hauterivian: Brenner, 1996), but the plant macrofossils are mostly ferns *Weichselia* in the marginal marine deposits and gymnosperms in the interbasaltic shales. The fruit-like *Afrasita lejalmnicoliae* Krassilov et Lewy, first described from the Abu Ballas Formation of Dakhla Basin, southern

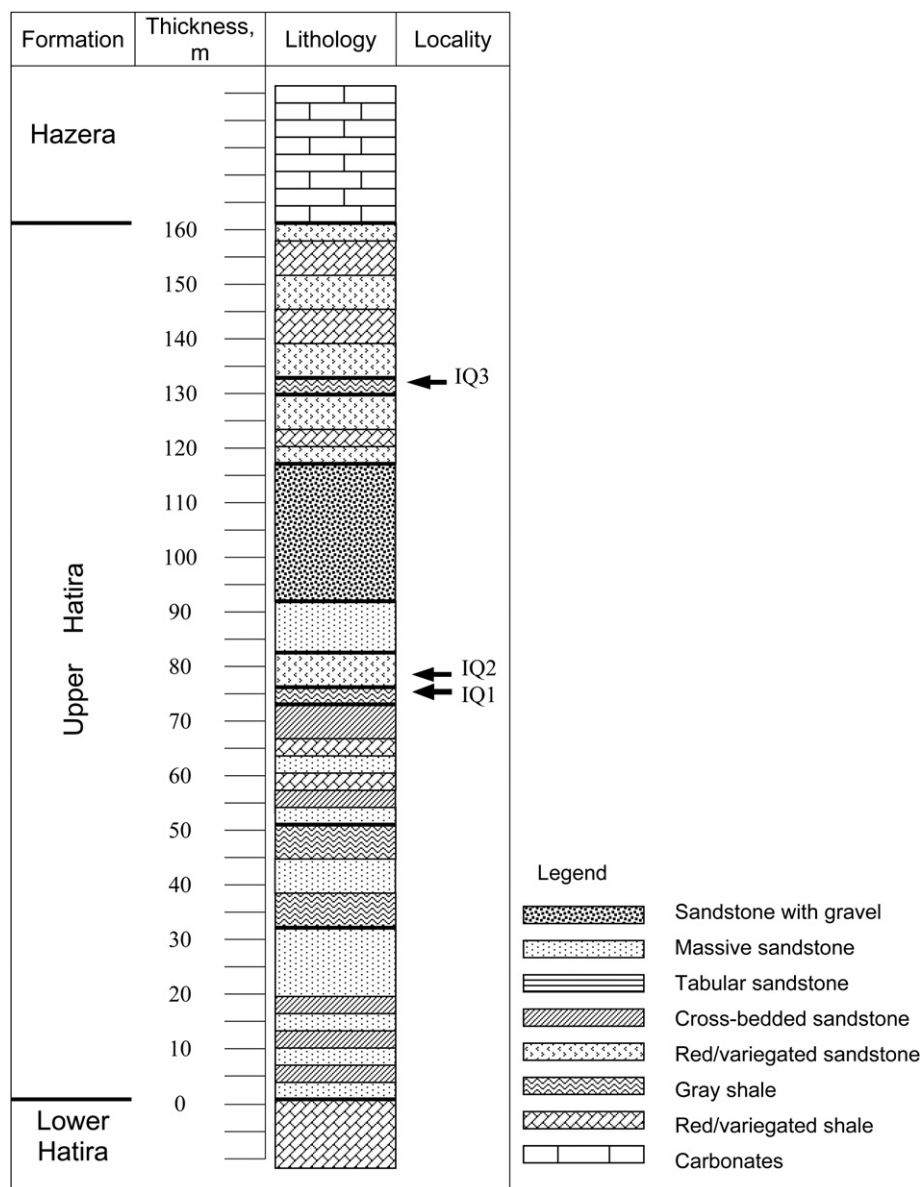


Fig. 2. Generalized stratigraphic section of the Upper Hatira Formation in the Makhtesh Qatan, northern Negev, indicating the fossil plant-bearing beds IQ1 – 3 (designated as in the fossil plant depository of the Institute of Evolution, University of Haifa). Thick horizontal lines are boundaries of lithological units described in the text.

Egypt as an early angiosperm (*Leguminocarpon*: Lejal-Nicol, 1981) has been re-interpreted as proangiospermous of gnetophytic affinities, representing the same evolutionary grade as the gnetophyte records in the Lower Cretaceous of Central Asia (Krassilov et al., 2004).

In the Makhtesh Ramon, *Weichselia* almost disappeared during the Aptian uplift that was accompanied by basaltic extrusions, but recovered in the Albian tidal-flat deposits above. The Upper Hatira sequence, conformable on the Aptian redbeds, consists of two large sedimentary cycles with fossil plant horizons in their shaly members. Platanoid leaves were found in the lower fossil plant horizon, whereas the upper horizon is dominated by *Weichselia*, accompanied by *Araucaria*, *Brachyphyllum*, *Nageiopsis* and the narrow-leaved angiospermoids of *Acaciaephyllum* type, as well as aquatic forms. The broad-leaved *Vitiphyllum* and platanoids are rare members of the younger Upper Hatira assemblage (Silantjeva and Krassilov, 2006a).

In the Makhtesh Hatira, the Barremian – Aptian sequence with marine intercalations is overlain by sandy deposits with terrestrial plant remains in the lower part and with shallow-water marine

mollusks in the upper part. These are followed by an argillaceous marl horizon with oolitic ironstones (the Deragot marine tongue: Segev et al., 2005), with *Knemiceras* sp., a representative of Albian ammonite fauna (Avnimelech et al., 1954). This part of the Upper Hatira Formation probably corresponds to *Knemiceras gracile* Zone (early Albian) of Sinai (Abu-Zied, 2008). The sandstone, siltstone and clay sequence above contains two fossil plant-bearing horizons and grades upward into a carbonate unit (the Uza marine tongue) with *Knemiceras dubertreti* Basse, a member of a late Albian *Knemiceras* group widespread in the Tethys realm (Robaszynski et al., 2008). Variegated sandstones separate this marine intercalation from the limestones and dolomites of the upper Albian – Cenomanian platform carbonates, a readily recognizable stratigraphic marker all over the Negev.

In the Makhtesh Qatan, the Jurassic limestones are exposed in the dry Hazera channel over the deepest part of the crater. They are unconformably overlain by about 200 m thick clastic deposits equivalent to the Barremian – Aptian Lower Hatira Formation of the Makhtesh Hatira and Makhtesh Ramon depressions (above). At

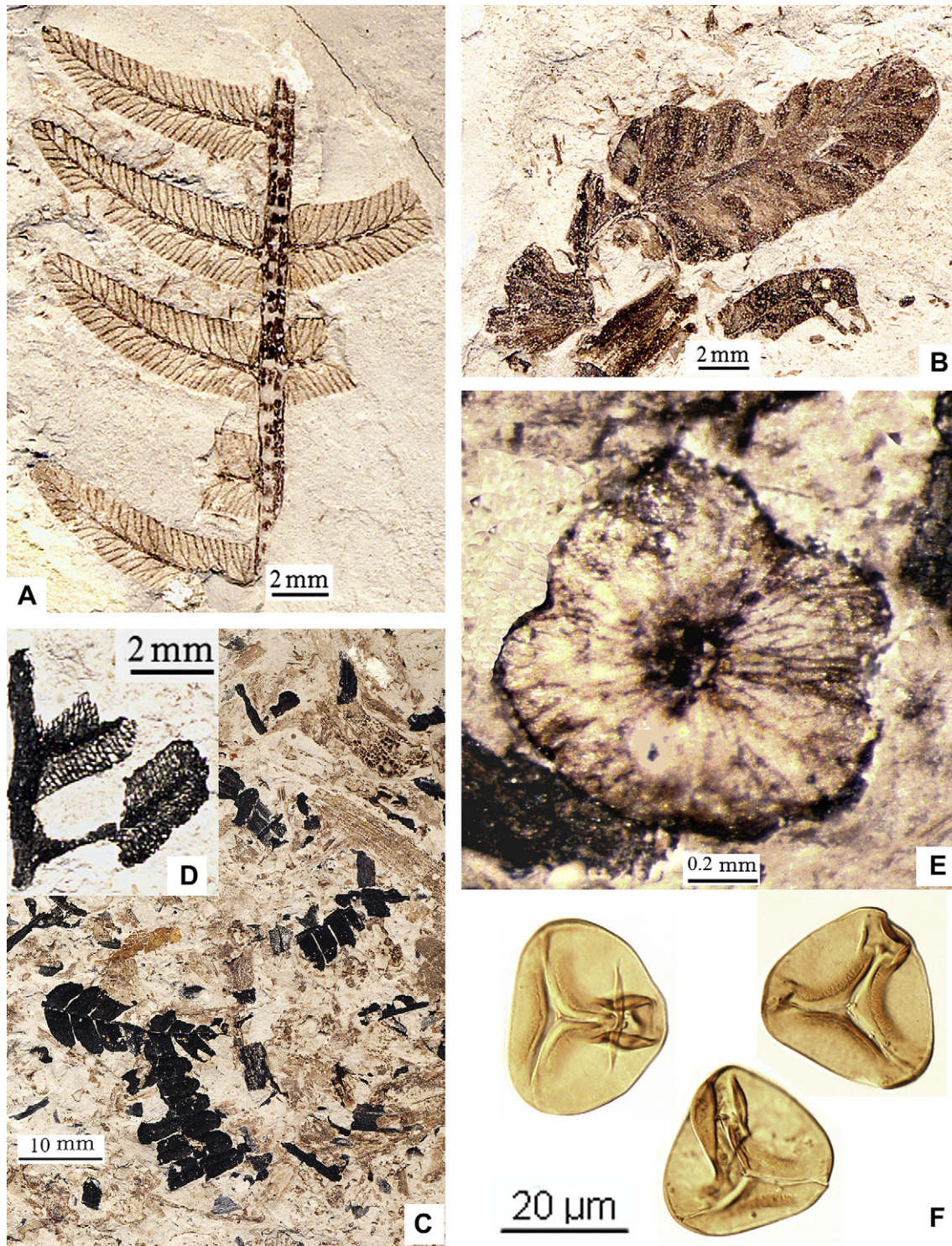


Fig. 3. IQ1 and IQ3 assemblages, Makhtesh Qatan, ferns: A, specimen IQ1-4, *Cladophlebis* cf. *denticulata* (Brongniart) Fontaine; B, specimen IQ1-16, *Asplenium* sp. (sp. nov); C–F, *Weichselia negevensis* Silantjeva et Krassilov (C, D, specimens IQ3-2 and IQ1-191, fusainized pinnules; E, specimen IQ1-104a, shed synangium, F, specimen IQ1-104b, in situ spores).

the top of the sequence, there are redbeds spotted with greenish inclusions of tuffaceous material, about 10 m thick, corresponding to the thick lateritic deposits over the Ramon Basalts. They are conformably overlain by the Upper Hatira sequence, about 160 m thick, striking NW, studied in the nearly continuous outcrops on both sides of the Hazera canyon, traversing the central and western parts of the crater along the strike. The generalized stratigraphic sequence includes from base upward (Fig. 2):

- (1) Tabular cross-bedded grey sandstones with massive pink interbeds, 33 m;
- (2) Grey and greenish-grey calcareous shales with sandy interbeds, 18 m;
- (3) Tabular cross-bedded whitish and yellowish-grey sandstones with reddish-brown shaly interbeds, 25 m;
- (4) Thin-bedded grey shales, 2.5 m, with fossil plant remains in the lower 0.5 m (locality IQ1);

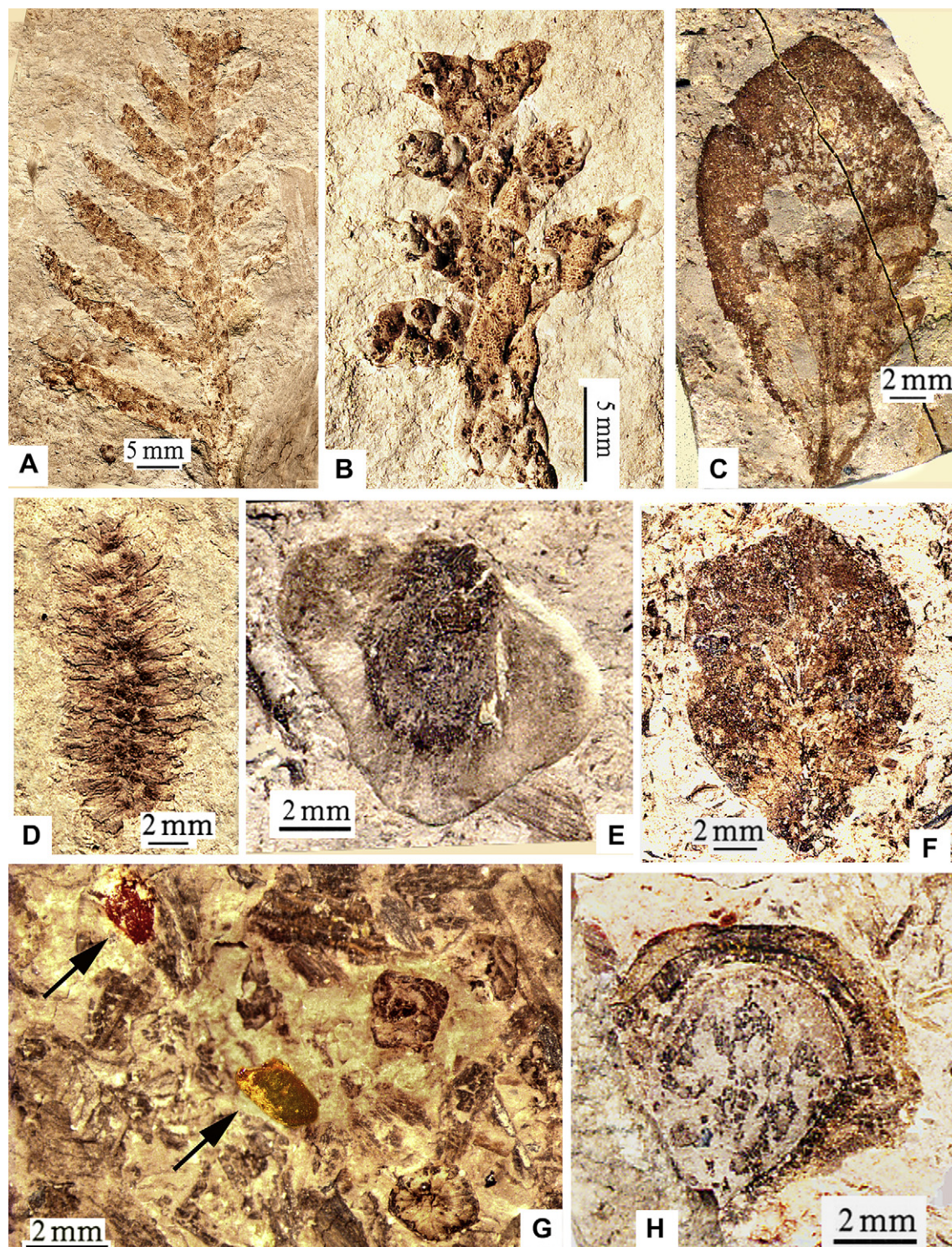


Fig. 4. IQ1 and IQ3 assemblages, Makhtesh Qatan. A, B, specimens IQ3-90 and IQ3-21, conifer *Brachyphyllum* cf. *crassicaule* Fontaine; C, F, specimens IQ1-129 and IQ1-111, angiosperm *Parvileguminophyllum* sp.; D, specimen IQ3-58, male cone, associated with *Qataniaria noae*, gen. et sp. nov.; E, H, specimens IQ1-43 and IQ1-114, samaras, supposedly of a gnetophytic plant; G, specimen IQ1-53, mesofossil assemblage with synangia of a fern *Weichselia negevensis* Silantjeva et Krassilov; arrows on pieces of amber.

- (5) Variegated sandstones of alternating yellowish-grey, reddish-brown and purple ferruginous bands, 6 m, with fossil plant remains (locality IQ2);
- (6) Massive yellowish-grey sandstone, 10 m;
- (7) Cross-bedded whitish-grey sandstone with strings of gravel, 20 m;

- (8) Massive reddish-brown and yellow sandstones with variegated shale packets, 15 m;
- (9) Thin-bedded whitish (yellowish) grey calcareous shales, 2 m, with plant remains (locality IQ3);
- (10) Alternation of light yellowish-grey or pink sandstones and variegated, locally flaser-bedded calcareous shales, about

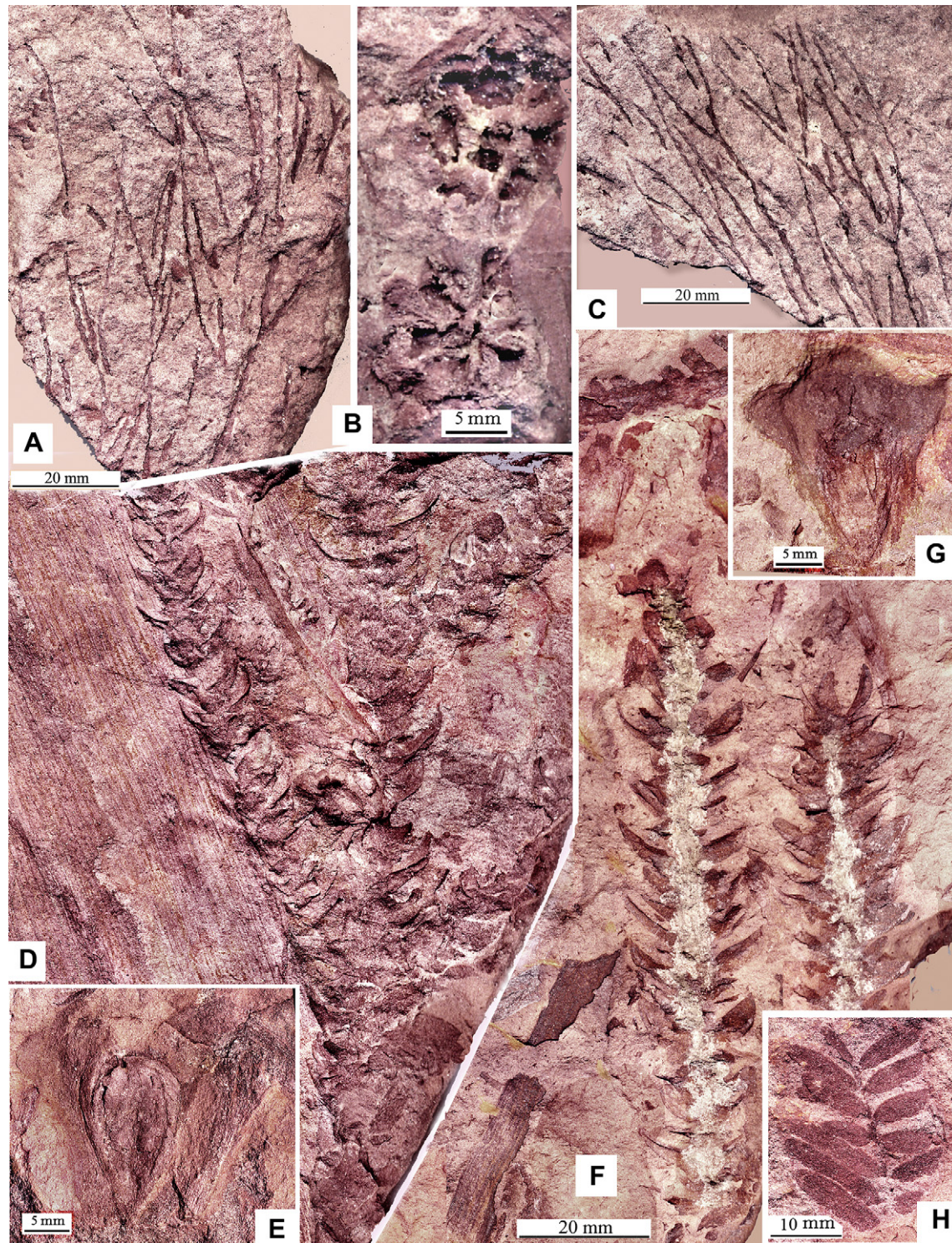


Fig. 5. IQ2 assemblage, Makhtesh Qatan, conifers. A–C, *Athrotaxisopsis cf. expansa* Fontaine (A, C, specimens IQ2-130 and IQ2-131, leafy shoots; B, IQ2-230, cones); D–G, *Araucaria* sp. (specimens IQ2-133 and IQ2-141, shoots; E, G, specimens IQ2-2 and IQ2-145, seed cone scales); H, specimen IQ2-56, *Nageiopsis* sp., leafy shoot.

30 m, overlain by the uppermost Albian – Cenomanian limestones of the regional Hazera Formation (= Hevyan Formation: Segev et al., 2005).

The Albian sequence thus comprises two sedimentary cycles, the lower cycle comprising the beds 1–4 and the upper cycle comprising the beds 5–10, about 78 m and 83 m respectively, both commencing with thick fluvial sandstones and culminating with

lacustrine – lagoonal shales. Bed 2 of the lower cycle sequentially corresponds to the ammonitic *Knemiceras* shales of Makhtesh Hatira, but no marine fossils were found in Makhtesh Qatan. The uppermost variegated shale horizon contains the flaser-bedded tidal-flat facies. Plant remains are found in the shaly upper parts of both cycles and in the basal sandstones of the upper cycle and are correlated, respectively, with the lower and upper fossil plant-bearing horizons of the Upper Hatira sequence of Makhtesh Ramon (above).

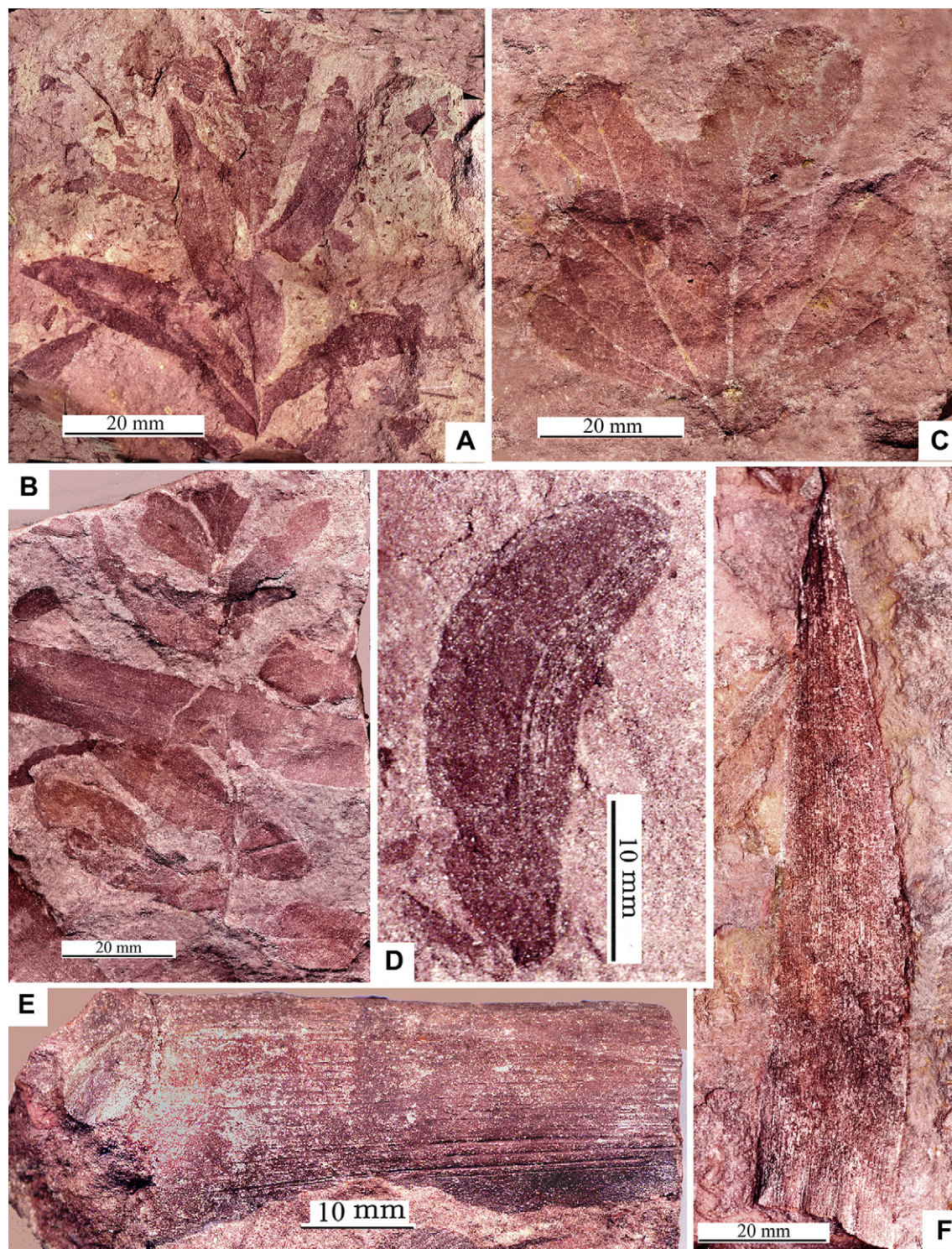


Fig. 6. IQ2 assemblage, Makhtesh Qatan, gymnosperms of gnetophytic alliance and angiosperms. A, B, specimens IQ2-158 and IQ2-44, *Sapindopsis* cf. *heterophylla* Fontaine, compound leaves; C, specimen IQ2-37a, platanoxyllous leaf; D, *Afrasita* cf. *lejalnicoiae* Krassilov et Lewy, seed scale; E, F, specimens IQ2-86 and IQ2-48, supposed stem and leaf of the same plant (also seen in Figs 5D and 6B).

4. Macro- and mesofossil plant assemblages

4.1. Plant-bearing facies and taphonomic associations

The locality IQ1 occurs in a siltstone/claystone alternation (bed 4 of the log, Fig. 2), in which the most remarkable features of sedimentary matrix are pyrite inclusions indicative of a reducing

deposition environment, as well as small pieces of amber, about 5 mm across, scattered over the bedding planes and probably re-deposited from a larger accumulation. Dense debris of fragmentary wood, leaves and reproductive parts covers the siltstone lamellae as a seasonal wash-out. The determinable leaves are rather rare, belonging to ferns, conifers and angiosperms. The predominant preservation form is impression (which is not a mechanical

imprint, as the term implies, but a clayey subcutaneous film, see Krassilov and Makulbekov, 1996), often covered with a crumpled cuticle. Fusainized wood splinters are rather frequent, as well as fusainized *Weichselia* pinnules (Fig. 3C, D). Dispersed synangia of this fern are the most common mesofossils (Figs. 3E and 4G). Tubular cases, supposedly of caddis flies, are built of small debris, including synangia of *Weichselia*.

Dominant in the IQ1 assemblage are the scattered leaves and cataphylls of a new gymnosperm genus *Qataniaria* of a supposed gnetophytic affinity (described in the systematic section below). The leaves are resiniferous, suggesting that *Qataniaria* might have been a source plant for amber. The conifers *Araucaria* and *Brachyphyllum* are infrequent and poorly preserved, coming as allochthonous elements (they are much better represented in the sandstone assemblage IQ2 above). The ferns are common, but *Weichselia* is less abundant than in the Makhtesh Ramon tidal-flat facies (Silantjeva and Krassilov, 2006b) and the whole fronds are rare in comparison with pinnules and dispersed synangia, indicating transportation from a distant source. Also common and more likely autochthonous are the leaf pinnae of *Cladophlebis* (a form-genus for sterile leaves with open dichotomous lateral veins, typical of *Osmunda*, *Todites* and the other osmundaceous natural genera) and fertile *Asplenium* (Aspleniaceae). On account of numerical representation and preservation mode, the source vegetation might have been a *Qataniaria* bog forest or shrubland, as well as an osmundaceous fern bog. Notably, no remains of aquatic macrophytes were found. The only angiosperm that might belong to the bog forest assemblage is *Parvileguminophyllum* represented by a few relatively well-preserved leaflets (Fig. 4C, F).

The locality IQ2 comprises two fossil plant assemblages, the stratigraphically lower of which is confined to the coarsely laminar river-channel sandstones about 0.7 m thick, with abundant shoots and cones of a taxodiaceous conifer *Athrotaxopsis* cf. *expansa* Fontaine (Fig. 5A–C), accompanied by the crumpled leaflets of an angiosperm leaf morphogenus *Sapindopsis*. The plant remains are not accumulated on the bedding planes, but are immersed in the sandy matrix, indicating a rapid deposition from running water. The globose cones of *Athrotaxopsis* might have been rolled over the channel bedrock. This conifer is confined to this depositional environment alone, most likely representing a riparian growth nearest to the channel.

The silty sandstones in the upper part of unit 5 consist of quartz grains coated with iron oxides. The plant remains are coarsely preserved as ferric impressions. Absolutely dominant among them are the large ribbon-shaped leaves forming mat-like accumulations on the bedding planes, with articulate stems occasionally preserved as three-dimensional moulds (Fig. 6E, F). The ribbon-shaped leaves are accompanied by *Afrasita*, a fruit-like fossil of a probable gnetophytic affinity (Krassilov et al., 2004). Likewise abundant in the same plant bed, but obviously representing a different type of vegetation are the branching shoots and cone scales of *Araucaria* (Fig. 5D–G). Its taphonomic associates are the less frequent, but common *Brachyphyllum* and *Nageiopsis*. Angiosperms, next in abundance to conifers, are represented by polymorphic *Sapindopsis* and a few platanophylls (Fig. 6A–C).

A reed-like growth in iron-rich shallow ox-bow water is the most plausible interpretation of the mats of ribbon-shaped leaves. The “reeds” were buried under a sediment flow bringing the diverse plant material from the forested land in the upper reaches of the river basin. *Araucaria* is found in all depositional settings of the IQ2 locality, both as allochthonous components of the ribbon-leaf mats and mixed with the other conifers and with angiosperms in the coarser sedimentary facies, as can be expected of a dominant canopy tree of a coniferous forest with a species-rich understorey, including the broad-leaved angiosperms. Insofar as araucarian

remains are found in the fluvial facies of IQ2, while being extremely rare in IQ1 and lacking in IQ3, may indicate transportation from river benches or lower slopes rather than a flood-plain source.

The locality IQ3 is confined to the indistinctly laminated white and whitish-grey silty claystones, with scattered leaf impressions on bedding planes. The fossil plant assemblages are monodominant, consisting of the detached leaves and occasional leafy shoots of *Qataniaria* admixed with the much rarer shoots of a scale-leaved conifer *Brachyphyllum* (Fig. 4A, B). Aquatic angiosperms (*Nelumbites*) are present, but infrequent. The fusainized fronds of *Weichselia* occur on a single bedding plane at the base, whereas a few angiosperm leaves are found in the uppermost silty bed of the white claystone sequence. Except in the *Weichselia* bed, the mesofossil debris is much less abundant than in the locality IQ1 (above). There is no taphonomic evidence of a fern bog, and the overall input of organic material must have been less voluminous. This is also reflected in the fewer caddis-fly cases built of plant material. This locality represents a low energy depositional environment, suggesting a flat source area, which can also explain the decrease of conifers and disappearance of *Araucaria* from the fossil record.

4.2. Floristic composition

A number of plant macrofossils form the Albian flora of Qatan may represent new species. The others are quite similar to those known from North American and European localities, but their species level identity has to be validated by further studies. Therefore, we are compelled to confine ourselves to the genus level analysis. The flora consists of about 18 genera, including ferns (4), conifers (4), gymnosperms of gnetophytic alliance (4), and angiosperms (6). *Weichselia* of the monotypic family Weichseliaceae is a tree fern having connate sporangia with three cell layer walls, suggesting the affinities with the eusporangiate ferns (Silantjeva and Krassilov, 2006b). It is dominant in the tidal-flat assemblages of Makhtesh Ramon, which implies a coastal wetland habitat. Yet it is far less prominent in Makhtesh Qatan, being mostly represented by allochthonous debris of detached pinnules and dispersed synangia in IQ1 and the somewhat larger, but rare frond fragments in IQ3 upsection. In situ spores are moulds in the Makhtesh Ramon material (Silantjeva and Krassilov, 2006b), but are organically preserved in IQ1, showing details of the margo and ornamentation (Fig. 3F). *Cladophlebis* is a ubiquitous Mesozoic morphotype, mainly including the foliage of extant and extinct osmundaceous genera. A fern with linear sori on anterior branches of arcuate lateral veins (Fig. 3A) represents a relatively recent group, matching the extant *Asplenium* (Aspleniaceae) in the shape and arrangement of sori, the main diagnostic characters of the genus (Kramer and Viane, 1990).

The conifers constitute a numerically dominant group, with the most abundant shoot and cone scale remains from locality IQ2 assignable to a natural genus *Araucaria* on account of both vegetative and reproductive features, such as the fastigiate shoots with radially spreading subulate scale leaves and the bilaterally winged awned cone scales with a solitary embedded seed and transverse subapical ridge, representing the ligule (Fig. 5D–G).

The slender scale-leaved shoots bearing small globose cones (Fig. 5A–C) are practically indistinguishable from *Athrotaxopsis expansa* Fontaine from the roughly contemporaneous Potomac flora of Virginia, U.S.A. (Fontaine, 1889). Its peltate cone scales with minute winged seeds in two tiers suggest an alliance with giant sequoias of the genus *Sequoiadendron* (Sequoiaceae, Taxodiaceae). *Nageiopsis* Fontaine is a morphotaxon for coniferoid shoots and leaves with many parallelodromous veins (Fig. 5H), also prominent in the North American Albian floras, though occasionally recorded from Europe and eastern Asia (Seward, 1895; Kimura et al., 1988; Bartiromo et al., 2009). *Brachyphyllum* and associated cones

represent a widespread Mesozoic family Cheirolepidiaceae, which is traditionally included in the Coniferales, but is separated by Krassilov (2009) into a gnetophytic order Cheirolepidiales.

The gymnosperms of gnetophyte alliance are recently recognized as a major group of Mesozoic plants (reviewed in Krassilov, 2009) distinguishable on the basis of their seed organ morphology. Their leaf morphology is diverse, as in the recent Gnetales. The *Proherbatype* ribbon-shaped parallelodromous leaves are grass-like (Krassilov and Bugdaeva, 1999), which challenges the monocotyledonous affinities of Mesozoic leaves usually described under such names as *Phragmites*, *Typha* or *Pandanites*. In the locality IQ2, large ribbon-shaped leaves with acuminate apices are found in association with *Afrasita*, the fruit-like fossils abundant in the Aptian of Makhtesh Ramon. If actually of the same plant, the leaves were buried not in the season when the fruits were shed. *Afrasita* has been interpreted as a polyspermous gnetophytic cupule (Krassilov et al., 2004). The new find does not add to interpretation, but provides a plausible candidate for the leaves of the *Afrasita* plant.

Another plant of a probable gnetophytic affinity, dominant in both IQ1 and IQ3 localities, is described below as a new leaf genus *Qatanaria*. The associated fruit-like bodies are wrapped in cataphylls similar to the foliage leaves. The 2–3-lobed samaras from IQ1 (Fig. 4E, H) are also considered to be gnetophytic, with the wing lobes probably corresponding to persistent bracteoles as in *Welwitschia*.

Angiosperms are the most diverse, but numerically insignificant group, except *Sapindopsis* that is common in both the *Araucarian* and *Athrotaxopsis* assemblages of IQ2, also occurring as leaf fragments in the other localities. The genus is common in the Potomac flora of Virginia (Fontaine, 1889; Berry, 1911; Hickey and Doyle, 1977) and is also reported from the Cenomanian of Lebanon (Dilcher and Basson, 1990; Krassilov and Bacchia, 2000). The leaves from Qatan are extremely polymorphous, including both compound and pinnatifid morphotypes. In the *Araucaria* bed they are associated with broad-leaved platanophylls that also accompany *Sapindopsis heterophylla* in the Potomac flora (Fontaine, 1889; Berry, 1911). The detached terminal and lateral *Parvileguminophyllum*-type leaflets are infrequent, but conspicuous in IQ1. The other angiosperms, including *Ranunculaecarpus* and *Nelumbites*, are the single-specimen records.

5. Sporomorph assemblages

Three samples were collected in April 2009 from an intercalation of grey shales of the macrofossil plant locality IQ1 (above). Sample WP48/1 (slide number 313-BMJ) represents the exposed base of the shale horizon. WP48/2 (slide number 314-BMK) and WP48/3 (slide number 315-BML) are 20 cm and 48 cm above the base, respectively. All three samples have yielded abundant and well-preserved palynomorph assemblages which are strongly dominated by psilate, trilete spores, most commonly *Dictyophyllidites*, *Deltoidospora* and *Triplanosporites*, less commonly *Cyathidites*, *Concavisporites*, *Cibotiumspora* and *Matonisporites*. The triplan spores represent mainly lateral (equatorial) views of *Dictyophyllidites* and *Deltoidospora*. The estimated percentages of psilate spores range from 87% (WP48/3) to 93% (WP48/1–2) of the total palynoflora. The quantitative estimates are based on a count of at least 200 palynomorphs larger than 15 µm from the acid-resistant residue. A total of several thousand palynomorphs was encountered out of count, so that also rare forms, including the palynostratigraphically significant angiosperm pollen (see below), could be taken into consideration. Selected representatives of the sporomorph assemblage found are illustrated in Fig. 7A–P.

Pteridophytic spores other than psilate triletes include *Concaviisporites*, *Gemmatriletes* (both 0.4% or present out of count),

Cicatricosisporites (out of count, WP48/2), *Verrucosisporites* (out of count, WP48/3), *Sestrosporites* (out of count, WP48/2) and the megaspore *Balmeisporites* (out of count, WP48/1).

Gymnosperm pollen is represented by the *Araucariacites/Inaperturopollenites* group and *Balmeiopsis* (together 2–4%), *Callialasporites* (out of count, WP48/2), cf. *Partitisporites* sp. (out of count, WP48/1–2; 1%, WP48/3), *Classopollis* (out of count, WP48/1–2; 1%, WP48/3), *Eucommiidites* (out of count, WP48/1–2; 0.4%, WP48/3), and *Ephedripites* (out of count, WP48/2–3).

Angiosperm pollen grains occur as a minor element in all three samples studied so far. Notable among them are *Clavatipollenites* (0.5%, WP48/1; out of count, WP48/2–3), *Pennipollis* (out of count, WP48/2–3), *Retimonocolpites* (out of count, WP48/1–2), *Tricolpites* (out of count, WP48/1–2; 0.4%, WP48/3), *Rousea* (out of count, WP48/2) and *Walkeripollis* (out of count, WP48/2–3).

It should be noted that *Clavatipollenites* grains (Fig. 7N), *Eucommiidites* and small *Tricolpites* occasionally form dense pollen masses. These are probably parts of sporangia that have been transported as a unit and are therefore counted as one grain.

Afropollis, a pollen genus present in the Makhtesh Qatan sample WP48/3 (out of count), has been assigned to early angiosperms, but this opinion is sometimes doubted in favour of a gymnospermous affinity (e.g. Doyle, 1999; Heimhofer et al., 2007). *Afropollis* specimens in the studied material probably belong to *Afropollis jardinus*, which is an Albian species according to Doyle (1999).

6. Floristic comparisons and geological age

6.1. Macroflora

In Israel, the Cretaceous paleofloristic succession can be traced from the late Neocomian to Turonian, with the richest fossil plant localities in the Albian of Negev (Silantjeva and Krassilov, 2006a and this paper) and the Turonian of Arava (Krassilov et al., 2005). The Neocomian – Aptian stage is mostly represented by single-species assemblages, such as the *Afrasita* assemblage of Makhtesh Ramon (Krassilov et al., 2004).

In the neighboring countries, the Neocomian locality Quehmeiz/Beskintaa near Beirut contains coniferous wood and leafy shoot remains (Barale et al., 2003). The Late Jurassic – Early Cretaceous flora of Libya (El Chair et al., 1995) is also non-angiospermous, evidencing a gradual transition from the Jurassic to Neocomian floras. The Sabaya Formation of the Dakhla Basin, deposited after retreat of the Aptian sea, contains a diverse assemblage of conifers, *Araucaria* among them (Barthel and Böttcher, 1978; Klitzsch and Lejal-Nicol, 1984) and a few angiosperms, including an *Alalioephyllum* type leaf (Schrank, 1999). The Upper Aptian – Lower Albian flora of South Tunisia is of a “mixed” aspect, including *Weichselia*, *Podozamites* and brachyphyllous conifers that are associated with narrow-leaved angiosperms and aquatic forms (Barale and Ouaja, 2001).

The Albian flora of the Negev shows a great advancement in diversification of all major plant groups relative to the Neocomian – Aptian assemblages. The fossil plant-bearing horizons of Makhtesh Qatan and Makhtesh Ramon are stratigraphically equivalent, being confined to the upper parts of two sandy/shaly sedimentary cycles of the Upper Hatira Formation. In both, the uppermost plant-bearing beds are situated about 30 m downsection from the overlying fossiliferous limestones, a uniform stratigraphic marker of the Negev. However, the composition of plant assemblages is dissimilar owing to differences in the depositional environments. Tidal-flat facies are widespread in Makhtesh Ramon (Silantjeva and Krassilov, 2006a), whereas in Makhtesh Qatan they are recognizable only in the uppermost Upper Hatira, the main part of which is built up of fluvial deposits. The Makhtesh Ramon fossil plant localities

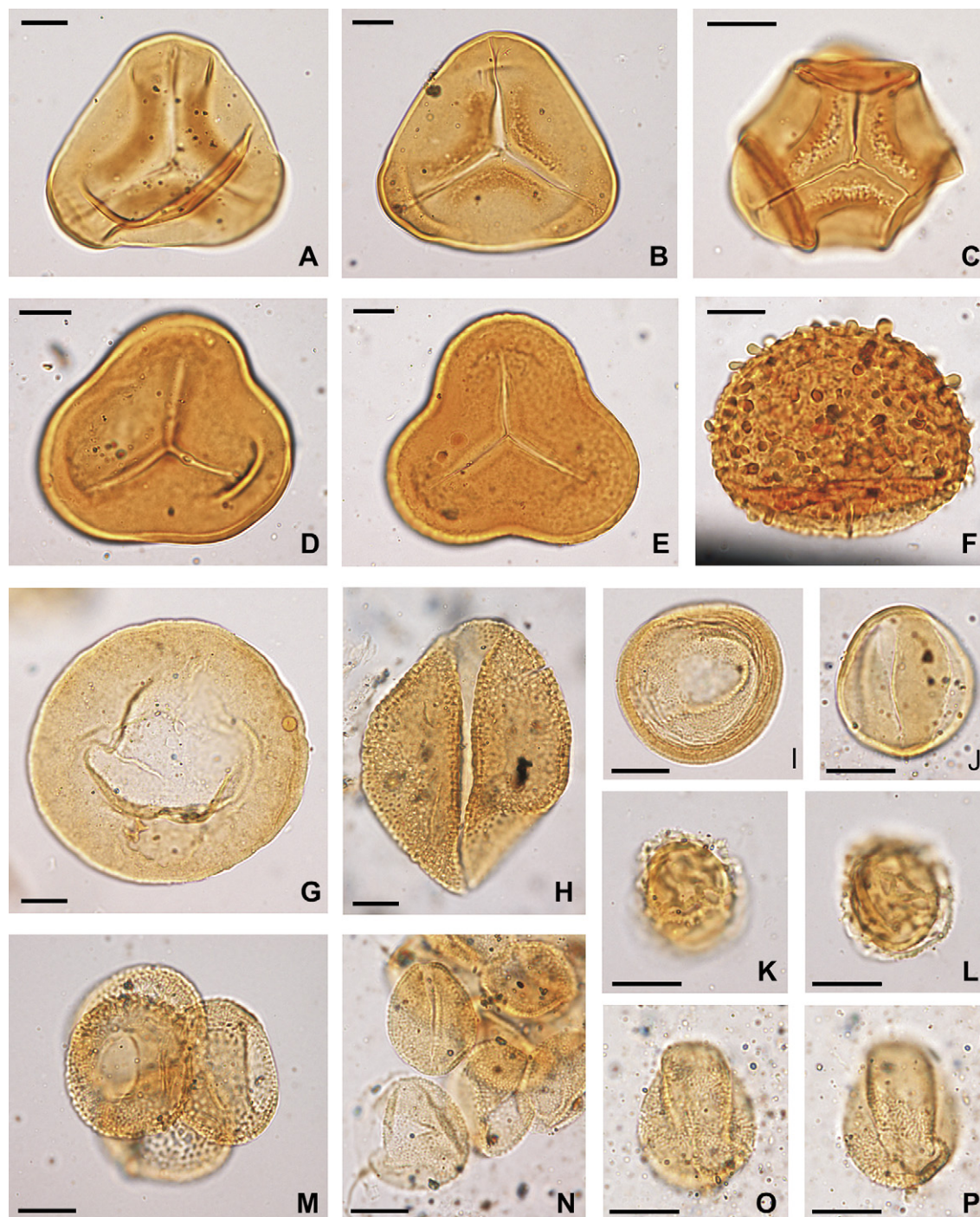


Fig. 7. Selected miospores from the grey shales of the fossil plant locality IQ1, Makhtesh Qatan. The name of the taxon with author citation if applicable is followed by a TU Berlin photo and slide number and England finder coordinates. The scale bar on all figures equals 10 μ m. A, *Dictyophyllidites harrisii* Couper 1958, MH9, 313-BMJ2, V49. B, *Deltoidospora psilostoma* Rouse 1959, MQ1, 314-BMK2, G30/2. C, *Cibotiumspora juriensis* (Balme, 1957) Filatoff 1975, MJ11, 313-BMJ4, F54. D, *Cyathidites australis* Couper 1953, ML5, 314-BMK1, F56/1. E, *Concavissimisporites punctatus* (Delcourt and Sprumont, 1955) Brenner, 1963, MU6, 315-BML1, S28/4. F, *Gemmatriletes clavatus* Brenner, 1968, MU23, 315-BML2, R45. G, *Balmeiopsis limbatus* (Balme, 1957) Archangelsky 1979, MT8, 315-BML1, J47. H, *Retimonocolpites* sp., MJ5, 313-BMJ3, S25/3. I, *Classopollis major* Groot and Groot 1962, MJ14, 313-BMJ4, J52/4. J, *Eucommiidites minor* Groot and Penny 1960, MR16, 314-BMK3, L25/1. K, L, *Pennipollis peroreticulatus* (Brenner, 1963) Friis, Pedersen and Crane 2002, MN16-17, 314-BMK2, K41. M, *Walkeripollis* sp. A in Doyle et al. (1990), MS17, 314-BMK4, H23/1. N, *Clavatipollenites* sp., pollen mass, MG18, 313-BMJ1, T35. O, P, *Tricolpites albiensis* Kemp 1968, s.l., MK12-13, 313-BMJ4, N42/2.

represent coastal wetlands with *Weichselia* and narrow-leaved *Acaciaephyllum*. Conifers are a rare allochthonous component that increases further inland. In Makhtesh Qatan, conifer remains prevail in both the river-bank and slope facies, whereas the role of gnetophytes (*Qataniaria* and the ribbon-shaped leaves) increases in the flood-plain wetlands.

The Early Cretaceous floras of the Negev and the roughly contemporaneous floras of southern and northern Mediterranean (e.g., Barale and Ouaja, 2001; Bartiromo et al., 2009) and Crimea (Krassilov, 1984) share a few cosmopolitan elements. The rich Albian floras of Kazakhstan (Vakhrameev, 1952; Vakhrameev and Krassilov, 1979; Krassilov et al., 1983) and Primorye, Russian Far

East (Krassilov, 1967; Krassilov and Volynets, 2008) have a few conifer elements in common with Qatan, such as *Athrotaxopsis*. However, the role of *Araucariaceae* and *Nageiopsis* is subordinate in the northern Asiatic floras. Platanophylls are prominent in the Upper Albian of Kazakhstan and elsewhere, while the ranunculids *Caspiocarpus*, *Hyrantha*, *Achaenocarpites*, *Ternaricarpites* and the other morphotypes constitute the most diverse angiosperm group (Krassilov and Volynets, 2008) that is not so far recorded from the Negev.

At the same time, the Potomac flora of North America appears fairly close at the plant assemblage level, with abundant *Araucaria* (*Araucarites*), *Athrotaxopsis*, *Nageiopsis* and *Sapindopsis* represented by the same or closely related species, such as *Araucarites aquinensis* Fontaine, *A. expansa* Fontaine, *Brachyphyllum crassicaule* Fontaine, and *Sapindopsis magnifolia/variabilis* Fontaine. The most closely comparable assemblages are assigned to Subzone II-B, early – early Late Albian, of the Potomac Group (reviewed in Upchurch et al., 1994), while the pinnatifid *Sapindopsis* morphotype is confined to the upper, Late Albian part of subzone, where it is associated with broad-leaved platanophylls as in the IQ2 locality of Makhtesh Qatan.

The Cenomanian of Judean Mountains contains a few single-species *Sapindopsis* localities. This genus is also important in the Nammoura locality of Lebanon in association with small-leaved xeromorphic angiosperms (Dilcher and Basson, 1990; Krassilov and Bacchia, 2000; Dalla Vecchia et al., 2002). A well-dated Cenomanian flora from the Bahariya Formation of southwestern Egypt (Lejal-Nicol and Dominik, 1990) comprises *Weichselia* and angiosperms, assigned to the extant families Magnoliaceae, Lauraceae, Cornaceae, Vitaceae, and Proteaceae. An angiospermous Cenomanian flora of Jordan, with a single gymnospermous species *Nilssonophyllum benderi* Mädlar (Bender and Mädlar, 1969), apparently represents the same evolutionary level. The mid-Turonian flora of Arava is fully angiospermous (Krassilov et al., 2005), comparable to the Late Cretaceous flora of Sudan (Schrank and Rüffe, 2003).

6.2. Palynoflora

Among the stratigraphically significant pollen morphotypes of the Makhtesh Qatan assemblage, *Pennipollis*, a non-columellar monosulcate angiosperm pollen (formerly *Brenneripollis*) is indicative of an age not older than Aptian (e.g. Brenner and Bickoff, 1992; Doyle, 1992, 1999; Schrank, 1992). The association of *Pennipollis*, *Tricolpites* and *A. jadinus* is recorded from Egypt and elsewhere in the Albian deposits and probably extended into the early-middle Cenomanian (e.g. Brenner and Bickoff, 1992; Schrank and Ibrahim, 1995; Gvirtzman et al., 1996; Ibrahim, 1996; Mahmoud et al., 2007). The absence of elaterate pollen grains that are typical elements in the late Albian to early Cenomanian of the region (e.g. Schrank and Ibrahim, 1995) probably precludes the Late Albian or younger ages.

The presence of *Walkeripollis* sp. A of Doyle et al. (1990) (see Fig. 7M) in Makhtesh Qatan enables correlation with the Cretaceous sequence of Zohar 1 Well in the northern Negev. This pollen type was originally described as a winteraceous tetrad from core 5 of Zohar 1, and its age was given as late Aptian – early Albian (Walker et al., 1983; Brenner, 1996, p. 107) or (more likely) early Albian (Brenner, 1996, p. 115).

Notably, the macrofossil comparisons are mainly restricted to the sandy facies assemblage IQ2, whereas the shaly facies assemblages IQ1 and IQ3 appear archaic on account of the diverse, essentially Mesophytic, fern elements and poor representation of angiosperms. Since the palynological samples are obtained from the shaly IQ1 alone, the facies differences might have caused a slight discrepancy of age assignments based on the macrofossils and microfossil data.

7. Palaeoenvironmental implications

7.1. Sedimentary environment

In Makhtesh Qatan, the thickness of tabular cross-bedded sandstones is greater than in the erosional windows to the west and the gravel content in the upward-coarsening sequence up to the bed 7 (see description of the log above) is conspicuously higher, indicating a strong river discharge, with gravel progradation from the rising drainage area over the present day Arava – Dead Sea rift valley. The intercalated lacustrine shales with pyrite, amber, plant cuticles and well-preserved palynomorphs are evidence of sediment decomposition in sulfur-rich anoxic bottom layer of a meromictic lake uptaking a considerable input of organic-rich water from surrounding wetlands of a vast flood plain. The lake had no or insignificant floating vegetation, while the presence of freshwater algae (*Ovoidites* and/or *Botryococcus*) in all palynological samples and of dinoflagellate cysts in one sample (WP48/2, out of count) suggest a nutrient-poor surface layer and open water surface as in the present day Lake Kinneret of Galilee, in which dinoflagellates are periodically blooming (Zohary, 2004). Also as in the Kinneret, the reed-like wetlands expanded with progradation of the river deltas.

7.2. Vegetation

The overall abundance of plant material, representing several fairly distinct plant assemblages, indicates a dense vegetation cover of the drainage area and a constant influx of terrestrial organic debris. The diverse fern macrofossils, as well as the overwhelming dominance of fern spores are consistent with an extensive fern bog as a major source of organic input. The relatively rare and often fusainized *Weichselia* might have been transported from a raised and drier bog zone. A different types of flood-plain wetland are represented by the one-species assemblages of *Qatanaria* and the reed-like growths of *Afrasita* or allied plant.

The conifer diversity and abundance are much greater in the Albian of Makhtesh Qatan than in the preceding and succeeding regional Cretaceous assemblages. *Araucaria* is numerically dominant in the fluvial deposits (locality IQ2) and is found as an allochthonous component elsewhere, suggesting a coniferous forest, with *Brachyphyllum* and *Nageiopsis* as co-dominants on slopes of the river valley. Broad-leaved angiosperms are subordinate members of this type conifer-dominated assemblage. On the other hand, *Athrotaxopsis*, a taxodiaceous conifer preserved as a monodominant fossil plant assemblage in the laminated river-channel sandstones may represent a coniferous wetland, perhaps ecologically equivalent to the pure stands of water cypresses over the waterlogged fluviodeltaic planes.

Both sedimentary environments and vegetation thus indicate a relatively humid phase of climate evolution during the mid-Cretaceous. Angiosperms diversified under canopy of conifer forests during the pluvial event and emerged as a dominant plant group after it.

8. Systematics

Genus *Qatanaria* Krassilov, gen. nov.

Derivation of Name. After the type locality.

Type species. *Qatanaria noae* Krassilov, sp. nov.

Diagnosis. The foliar blades are distichous, alternate and sessile on a thin slender axis. The blade shapes are typically elongate or elliptical, about 20–60 mm long, straight or somewhat falcate, their margins are bordered with a thick narrow rim. The apex is mucronate, the base is sheathing, cordate or truncate, with

a thickened (callous) arcuate detachment scar. Occasional small broadly elliptical obtuse leaves are linked with the typical form by intermediate shapes and are interpreted as cataphylls of the same plant. About 7–10 veins enter the leaf base. They are basally forked or unbranched, in the long elongate leaves, nearly parallelodromous, ascending the whole length of the blade and slightly converging towards the apex, a few running into the margin, in the shorter elliptical leaves nearly acrodromous, on flanks running into

the margins, converging to the apex and terminating shortly before the mucro. Veins are more prominent and sparser in the cataphylls and intermediate forms. The leaf compressions are hypostomatic, the upper cuticle showing rows of rectanguloid cells with barbed anticlinal walls, the lower cuticle differentiated into stomatal and stomata-free zones of irregular rectanguloid or elongate cells. The stomata are elongate-elliptical, in 2–4 rows per zone, longitudinal, seldom oblique, amphicyclic, with 5–6 papillate subsidiary cells

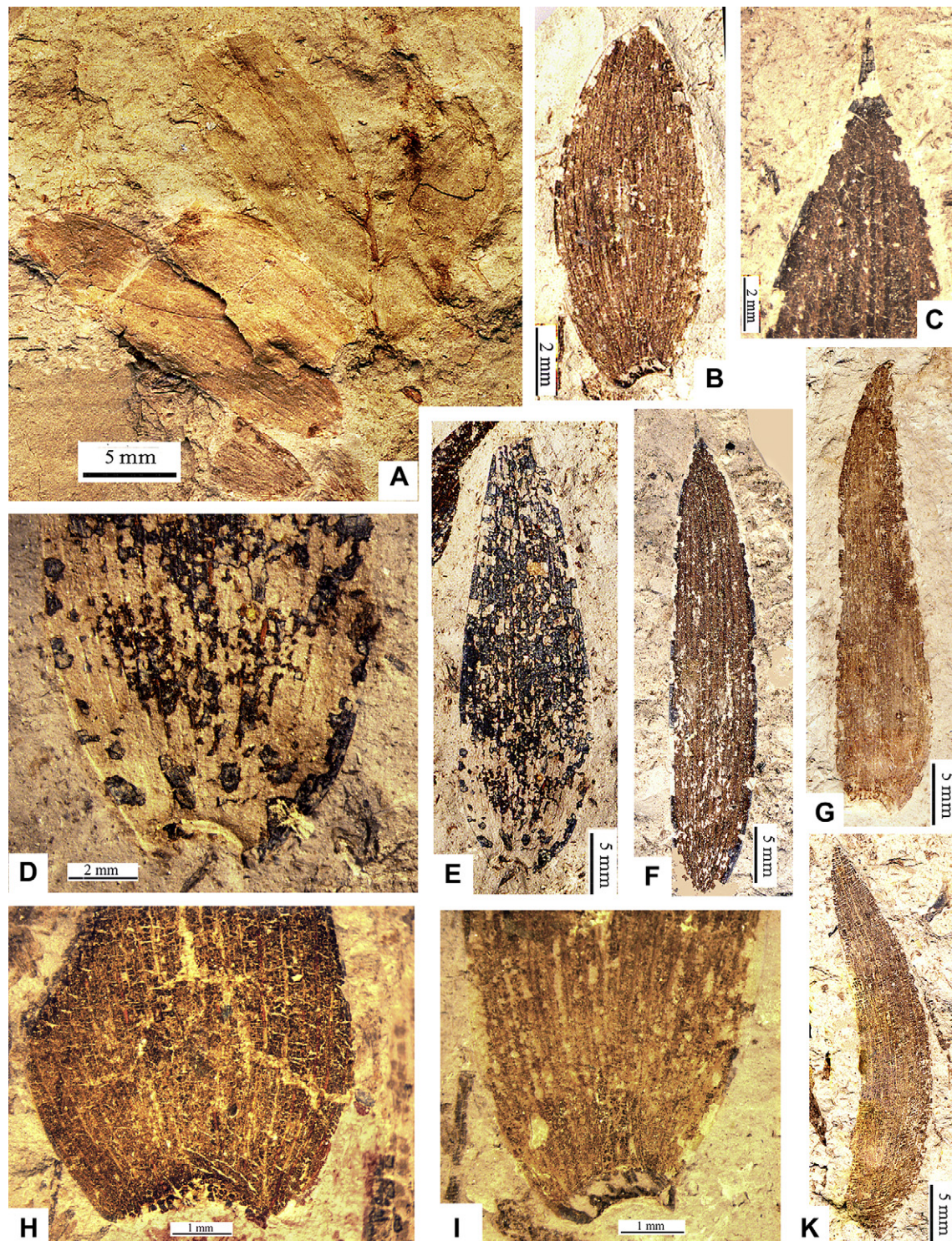


Fig. 8. *Qataniaria noae*, gen. et sp. nov. from localities IQ1 and IQ3, Makhtesh Qatan. A, IQ3-85, leafy shoot, B–K, detached leaf shapes, detachment scars and apical mucro magnified; resin ducts seen as continuous or dashed lines in D and H (B and I, IQ1-54, C and F, IQ1-48, D and E, holotype IQ1-24, G, IQ1-58; H, IQ1-94; K, IQ1-66).

and irregular encircling cells. The resin ducts are continuous or segmented slender tubes under the costal zones.

Discussion of the new genus. The elongate-elliptical foliar blades with open venation of several to many parallelodromous–acrodromous veins occur in the extant Araucariaceae and Podocarpaceae. In the Mesozoic, such leaves are widespread, representing both extant and extinct conifer families, as well as

extinct ginkgophytes and gymnosperms of uncertain taxonomic affinities, such as the “leaf family” Miroviaceae (Bose and Manum, 1990). The comparable leaf morphologies are assigned to the fossil morphogenera *Podozamites* Braun in Münster (1843), *Nageiopsis* Fontaine, 1889, *Pseudotorellia* Florin, 1936, *Araucario-dendron* Krassilov, 1967, and *Mirovia* Reymanówna, 1968. The latter genus has been originally described as ginkgophytic

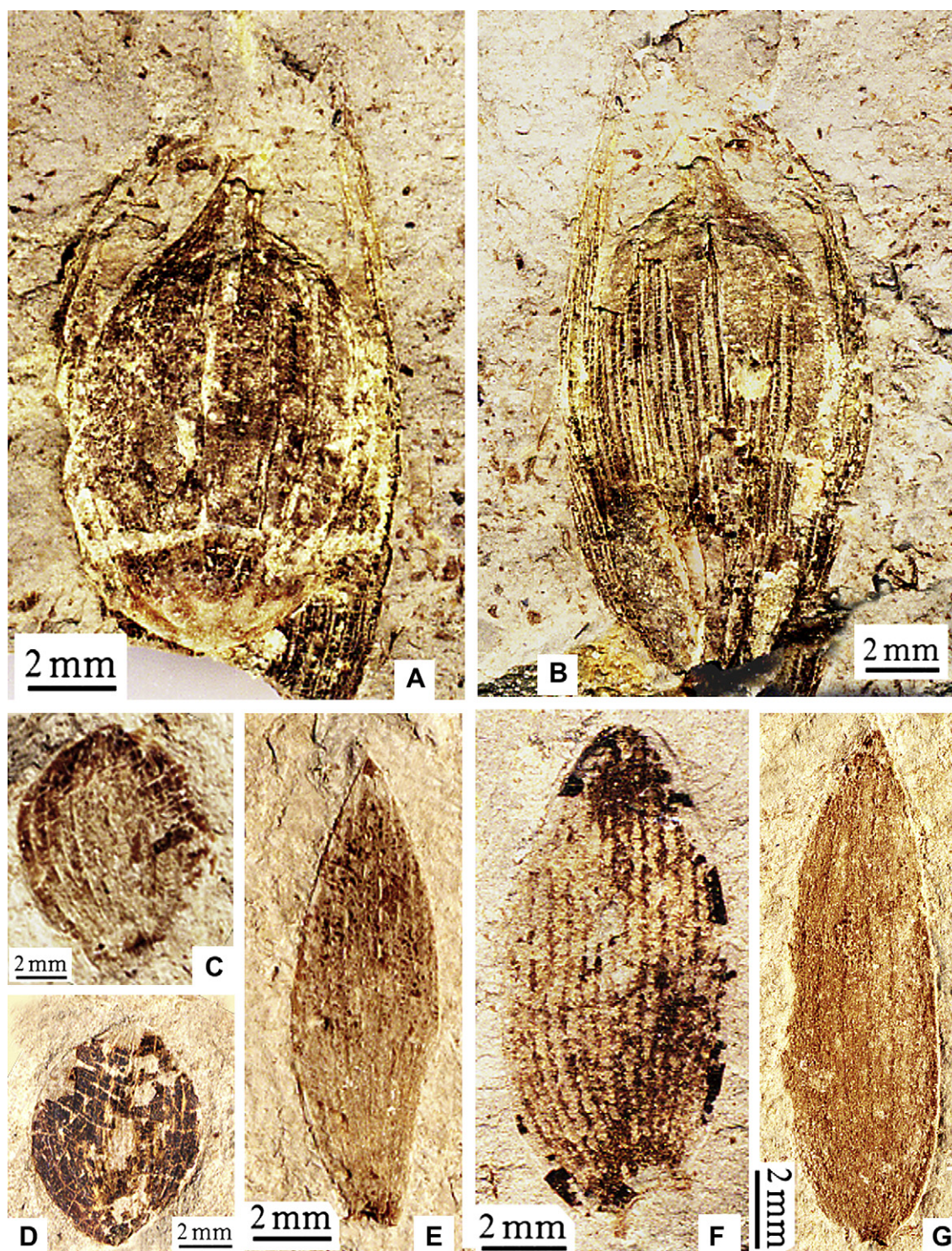


Fig. 9. *Qataniaria noae*, gen. et sp. nov. and associated reproductive structures from localities IQ1 and IQ3, Makhtesh Qatan. A, B, IQ1-40 and IQ1-47, part and counterpart of a fruit-like body wrapped in cataphylls; C–G, cataphylls and transitional form between leaves and cataphylls; resin ducts are seen as dashed lines in D (C, IQ3-34a; D, IQ3-20; E, IQ3-48; F, IQ1-67; G, IQ3-71).

(Reymanówna, 1968), close to *Pseudotorellia* (Krassilov, 1972). Both genera are sometimes assigned to conifers (Watson et al., 2001). *Qataniaria* differs from all these forms in auriculate leaf base with a callous detachment scar, as well as in the spreading veins running into the margins in the proximal part of the blade.

Some cycads, such as extant *Encephalartos*, are similar in the shape and venation of their mucronate pinnae. The pinnae with obliquely sheathing bases also occur in bennettites. In particular,

Otozamites Braun (in Münster, 1843) has auriculate pinnae not unlike *Qataniaria*. Yet, in both cycads and bennettites, the pinnae are regularly distichous, whereas the arrangement of foliar blades in *Qataniaria* suggests spiral phyllotaxis. Leaf shedding is implied by the taphonomy of abundant detached foliar blades, whilst only few leafy axes are preserved, bearing the irregularly overlapping blades.

The leaf base features find their closer analogues among gnetalean plants with sheathing leaves. In *Ephedra*, the leaf blades are

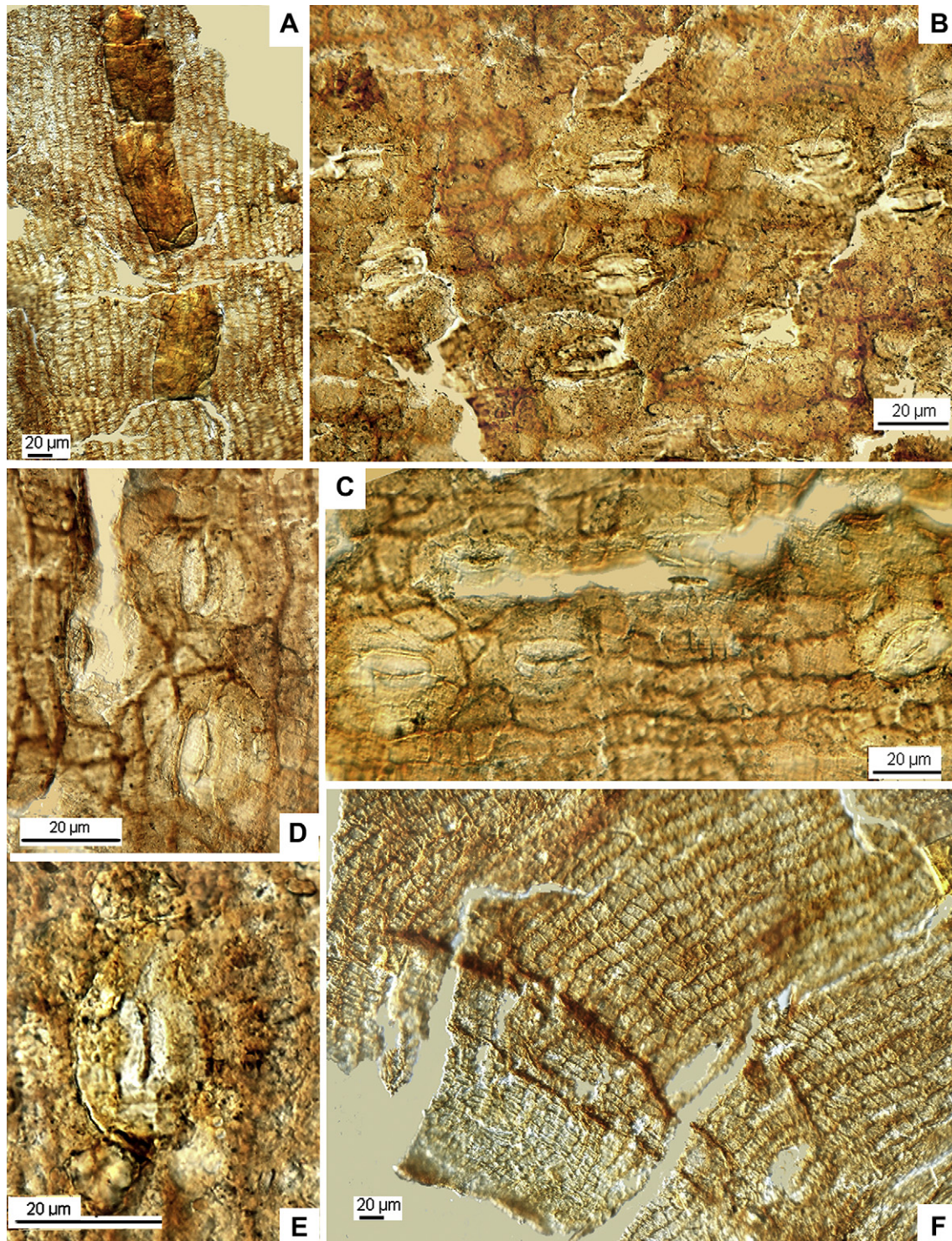


Fig. 10. *Qataniaria noae*, gen. et sp. nov. from localities IQ1 and IQ3, Makhtesh Qatan, cuticles. A, IQ1-50, upper cuticle with a massive median resin duct; B–E, holotype IQ1-24, stomata (B, C, stomatal bands; D, amphicyclic stomata; E, stoma with papillate subsidiary cells); F, IQ1-50, upper cuticle with a detachment scar marked with an arcuate fold.

commonly attached at a prominent arcuate callosity (Fig. 11) and may represent a reduced variant of *Qataniaria* foliage, but differ in decussate leaf whorls.

Among the fossil leaf-genera, *Nageiopsis* (Fontaine, 1889) is an impression genus that was shown by Berry (1911) to be a taxonomically heterogeneous assemblage of leafy shoots, possibly including also compound leaves with elongate or elliptical leaflets. None of these are sheathing or showing arcuate detachment scars. Both *Araucariodendron* and *Podozamites* are fairly distinct in cuticular characters (Krassilov, 1967). *Pseudotorellia* is similar in having continuous leaf-long resin ducts and in disposition of stomata, but differs in the leaf base features. In this genus, the leaves are supplied by two vascular bundles, as is typical of ginkgoalean foliage (Krassilov, 1972). Contrary to the opinion held by Watson et al. (2001), there is no evidence for assigning *Pseudotorellia* to conifers or including it in the so-called “Miroviaceae”. Their associating reproductive structures are of widely disparate taxonomic provenances.

In the Makhtesh Qatan locality IQ1, *Qataniaria* is accompanied by a ribbed fruit-like structure wrapped in cataphylls that are similar in venation to detached cataphylls assigned to this leaf genus (Fig. 9A, B). The reproductive structures are superficially similar to bennettitalean flowers, as well as to *Afrasita* Krassilov and Lewy, a fruit-like many-seeded cupule of a gnetophytic alliance (Krassilov et al., 2004). While bennettites are ruled out by the anomocytic stomatal structures, gnetophytes remain a viable possibility for taxonomic affinities of *Qataniaria*.

Qataniaria noae Krassilov sp. nov.
Figs. 8A–K, 9C–G and 10A–F.

Derivation of name. After Noa Fruchter, Hebrew University, Jerusalem, who first found fossil plants in the Albian of Makhtesh Qatan.

Holotype. Institute of Evolution, University of Haifa, collection IQ1, specimen IQ1-24, leaf impression with compression fragments (Figs. 8D, E and 10B–E); designated here;

Type locality. Makhtesh Qatan (Hazera), the northern Negev Desert, Israel (30° 58' 17" N. 35° 10' 55" E.).

Stratigraphic horizon. The Upper Hatira Formation, the early – early late Albian.

Diagnosis. As for the genus.

Description. This species was collected in two localities, IQ1 and IQ3. In both it is represented by numerous detached leaves. The holotype is a leaf of the most common elongate-lanceolate morphotype with a prominent arcuate detachment scar and the basally spreading veins. It is selected on account of the patchy compression material preserved all over the blade, yielding the relatively well-preserved adaxial and abaxial cuticles, as well as resin ducts (Fig. 10B–E). Despite the considerable leaf polymorphism (described below) the leaves figured as paratypes (Fig. 8A–C, F–K; Fig. 9C–G; Fig. 10A, F) share with the holotype the basal scar and venation features, as well as recognizable cuticular characters.

Only three fragmentary leafy shoots are found in the locality IQ3. These have a slender axis that becomes slightly sinuous distally, offset at the leaf nodes, obliquely clasped by the leaf bases. The detached leaves are polymorphic. Their size range is 20–67 mm long, 3–12 mm wide. The leaf blade shapes show a somewhat discontinuous variation between elongate-lanceolate (Fig. 8E, F), elliptical (Fig. 8B), falcate (Fig. 8G, K), and rounded-elliptical (Fig. 9C, D), the last two shapes being rather rare. The leaf apices seem to have been mucronate in all the blade shapes, but the mucro, spreading at an angle to the blade, is seldom preserved for its full length as in the leaf shown in Fig. 8C. The membranous marginal fringe is a constant, but fragile feature that is only patchily preserved along the leaf length. However, the detachment scar is usually well-preserved as a double arcuate line, forming a major distinguishing feature of the leaves. The basal auricles are asymmetrically developed (e.g., Fig. 8D, H, I), adjusted to oblique clasping of the axis. The scars are thick and apparently callous, well-marked on the leaf cuticle that extends down the leaf sheath (Fig. 9F).

Venation is well-marked on one (supposedly abaxial) side of the leaves, with about 7–8 veins entering the leaf blade at the detachment scar, some forking shortly above the base. In the elongate-lanceolate leaf variety, the veins only slightly diverge at the base, a few running to the leaf margins, whereas in the elliptical



Fig. 11. *Ephedra campylopoda* A.C. Mey, growing wild in suburbs of Haifa, Israel, fruits and leaves of male shoots for comparison with the fruit-like structures (Fig. 9A, B) and cataphylls (Fig. 10, E, F) of *Qataniaria noae* sp. nov.

variety the basal divergence is stronger and more veins on the flanks meet leaf margins below the middle of the blade length. Those running the whole length more conspicuously converge toward the apex, forming an acrodromous pattern. The rounded-elliptical leaves are smaller than the rest and have a more prominently acrodromous venation. They are interpreted as cataphylls, whereas the small elliptical leaves with about twice sparser than normal and relatively prominent veins (Fig. 9 E–G) are morphologically transitional between the cataphylls and regular leaves.

The resin ducts are developed in both foliage leaves and cataphylls, extending along the costal zones and continuous for the most of the leaf or broken into short segments, appearing as a dash line (Fig. 9E). In a few leaves, a thicker resin duct runs along the midline groove (Fig. 10A).

While the upper cuticle is rather frequently, although patchily, preserved, the lower is brittle and difficult to prepare. Fragments removed from the holotype (Fig. 10B–E) show intercostal stomatal bands that are scarcely sunken, comprising irregular files of longitudinal and occasionally oblique stomata (Fig. 10C) that are normally well-spaced, the adjacent apparatuses seldom shearing a lateral or a polar encircling cell. The guard cells are well-exposed, with the aperture extending nearly to the poles, the apertural ledges being feebly if at all developed. The subsidiary cells are not appreciably thickened, showing stumps of large papillae on the borders of stomatal pit. They are radially disposed, forming an irregular ring, with the encircling cells erratically cut off and intruding the ring. Small rounded hair bases are scattered over both the upper and lower cuticles.

9. Conclusion

Early Cretaceous plants were recorded, but never systematically studied in Israel. Our collecting in Makhtesh Ramon and recently in the new localities of Makhtesh Qatan, the northern Negev, has revealed a rich fossil flora of considerable taxonomic, paleoecological and paleogeographic significance. It is so far the only outcrop locality in the Negev yielding plant compressions and well-preserved palynomorphs.

The fossil plants came from three horizons in the upper part of the Upper Hatira Formation, the stratotype of which in the adjacent Makhtesh Hatira depression contains Albian ammonites *Knemiceras* in the lower part. The overlying uppermost Albian – Cenomanian platform carbonates are uniformly spread all over the central and northern Negev. The Upper Hatira sequence comprises two thinning-upward cycles of tabular cross-bedded sandstones and laminated shales. A sandstone locality from the base of the second cycle contains diverse assemblage of conifers and angiosperms, closely comparable to the early – early late Albian Subzone II flora of the Potomac Group, Atlantic coast of North America, in particular on account of pinnatifid *Sapindopsis* typical of the upper part of the unit. The shale assemblages appear less advanced, with diverse ferns and a minor angiosperm component. A palynological assemblage from the lower fossiliferous shale contains such stratigraphically important forms as *Pennipollis* and *Walkeripollis*, jointly indicative, in the absence of elaterate forms, of an early Albian age.

The facial differences strongly affect floristic composition and are even telling on the age inferences. The sandstone assemblages are dominated by *Araucaria* accompanied by *Brachyphyllum*, *Nageiopsis*, *Sapindopsis* and platanophyllous angiosperms, representing a mixed coniferous–broad-leaved forest of drainage area. Occasional plant beds contain monodominant assemblages with a taxodiaceous conifer *Athrotaxopsis* or with a reed-like plant, supposedly gnetophytic. The shale assemblages are dominated by diverse pteridophytes and a new gymnosperm genus/species *Q. noae*, representing

two types of flood-plain vegetation: a fern bog and a gymnosperm bog forest or woodland, respectively. Pyrite, amber, plant cuticles, *Ovoidites*, *Botryococcus* and dinoflagellate cysts in the shales suggest a meromictic meso-oligotrophic lake with open water surface, receiving a massive influx of organic material from surrounding wetlands. Both sedimentary and vegetation evidence imply a humid phase of the regional Albian climates.

Acknowledgements

We acknowledge the assistance in the field work by Noa Fruchter, Zeev Lewy, Sophia Barinova, Natalia Silantjeva, and Dmitry Vassilenko. Professor Wilhelm Dominik (TU Berlin) is thanked for his support of the project. The palynological processing at TU Berlin was done by Alexander Hartwig.

This work is supported by the German–Israeli Foundation of Scientific Research and Development, Grant No. 1-888-159.8/2005.

References

- Abu-Zied, R.H., 2008. Lithostratigraphy and biostratigraphy of some Lower Cretaceous outcrops from Northern Sinai, Egypt. *Cretaceous Research* 29 (4), 603–624.
- Avnimelech, M., Parness, A., Reiss, Z., 1954. Mollusca and foraminifera from the lower Albian of the Negev (Southern Israel). *Journal of Paleontology* 28 (6), 835–839.
- Balme, B.E., 1957. Spores and pollen grains from the Mesozoic of Western Australia. Council of Scientific and Industrial Research Organization of Australia, Coal Research Section T.C. 25, 1–48.
- Barale, G., Ouaja, M., 2001. Découverte de nouvelles flores avec des restes à affinités angiospermiennes dans le Crétacé inférieur du Sud Tunisien. *Cretaceous Research* 22, 131–143.
- Barale, G., Philippe, M., Gèze, R., Saad, D., 2003. Nouvelles flores crétacées au Liban. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 2003 (7), 400–414.
- Barthel, K.W., Böttcher, R., 1978. Abu Ballas formation (Tithonian/Berriasian; southwestern Desert, Egypt) a significant lithostratigraphic unit of the former 'Nubian Series'. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie, historische Geologie* 18, 153–166.
- Bartolomeo, A., Barale, G., Barone Lumaga, M.R., Bravi, S., Barattolo, P., 2009. The early Cretaceous flora from Profeti, Caserta, southern Italy. *Review of Palaeobotany and Palynology* 158 (1–2), 101–116.
- Bender, F., Mädler, K., 1969. Die sandige Schichtenfolge der Kreide mit einer Angiospermen-Flora in SüdJordanien. *Beihefte zum Geologischen Jahrbuch* 81, 35–92.
- Berry, E.W., 1911. Systematic paleontology, lower Cretaceous. In: Clark, W.B. (Ed.), *Lower Cretaceous. Maryland Geological Survey*, Baltimore, pp. 214–508.
- Bose, M.N., Manum, S.B., 1990. Mesozoic conifer leaves with "Sciadopitys-like" stomatal distribution. A re-evaluation based on fossils from Spitsbergen, Greenland and Baffin Island. *Norsk Polarinstitut Skrift* 192, 1–81.
- Brenner, G.J., 1963. The spores and pollen of the Potomac Group of Maryland. *Maryland Department of Geology. Mines and Water Resources Bulletin* 27, 1–215.
- Brenner, G.J., 1968. Middle Cretaceous spores and pollen from northeastern Peru. *Pollen and Spores* 10, 341–383.
- Brenner, G.J., 1996. Evidence for the earliest stage of angiosperm pollen evolution: a paleoequatorial section from Israel. In: Taylor, D.W., Hickey, L.J. (Eds.), *Flowering Plant Origin, Evolution & Phylogeny*. Chapman & Hall, New York, pp. 91–115, etc.
- Brenner, G.J., Bickoff, I.S., 1992. Palynology and age of the Lower Cretaceous basal Kurnub group from the coastal plain to the northern Negev of Israel. *Palynology* 16, 137–185.
- Dalla Vecchia, F., Venturini, S., Tentor, M., 2002. The Cenomanian (Late Cretaceous) Konservat-Lagerstätte of en Nammouira (Kesrouane Province), northern Lebanon. *Bollettino della Società Paleontologica Italiana* 41 (1), 51–68.
- Delcourt, A., Sprumont, G., 1955. Les spores et grains de pollen du Wealdien du Hainaut. *Mémoires de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 5, 1–73.
- Dilcher, D.L., Basson, P.W., 1990. Mid-Cretaceous angiosperm leaves from new fossil locality in Lebanon. *Botanical Gazette* 151, 538–547.
- Doyle, J.A., 1992. Revised palynological correlations of the lower Potomac group (USA) and the cocobeach sequence of Gabon (Barremian–Aptian). *Cretaceous Research* 13, 337–349.
- Doyle, J.A., 1999. The rise of angiosperms as seen in the African Cretaceous pollen record. In: Scott, L., Cadman, A., Verhoeven, R. (Eds.), *Proceedings of the Third Conference on African Palynology*, Johannesburg, 14–19 September 1997. *Palaeoecology of Africa and the Surrounding Islands*, vol. 26. A.A. Balkema, Rotterdam, pp. 3–29.

- Doyle, J.A., Hotton, C.L., Ward, J.V., 1990. Early Cretaceous tetrads, zonosulcate pollen, and Winteraceae. I. Taxonomy, morphology, and ultrastructure. *American Journal of Botany* 77, 1544–1557.
- El Chair, M., Kerp, H., Thiedig, F., 1995. Two florules from the Jarmah member of the Early Cretaceous Mesak formation at Jabal Tandah south of Awbari and northeast of Sabha, Libya. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 11, 659–670. 1995.
- Florin, R., 1936. Die fossilen Ginkgophyten von Franz-Josef-Land, nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters. Allgemeiner Teil. *Palaeontographica* 82B, 1–72.
- Fontaine, W.M., 1889. The Potomac or younger Mesozoic flora. U.S. Geological Survey Monograph 15, 1–377.
- Gvirtzman, G., Weissbrod, T., Baer, G., Brenner, G.J., 1996. The age of the Aptian stage and its magnetic events: new Ar-Ar ages and paleomagnetic data from the Negev, Israel. *Cretaceous Research* 17, 293–310.
- Heimhofer, U., Hochuli, P.A., Burla, S., Weissert, H., 2007. New records of early Cretaceous angiosperm pollen from Portuguese coastal deposits: implications for the timing of the early angiosperm radiation. *Review of Palaeobotany and Palynology* 144, 39–76.
- Hickey, L.J., Doyle, J.A., 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Botanical Review* 43, 3–104.
- Ibrahim, M.I.A., 1996. Aptian-Turonian palynology of the Ghazalat-1 well (GTX-1), Qattara depression, Egypt. *Review of Palaeobotany and Palynology* 94, 137–168.
- Kimura, T., Ohana, T., Mimoto, K., 1988. Discovery of a podocarpaceous plant from the Lower Cretaceous of Kochi Prefecture, in the Outer zone of Southwest Japan. *Proceedings of the Japan Academy B, Physical and Biological Sciences* 64 (8), 213–216.
- Klitzsch, E., Lejal-Nicol, A., 1984. Flora and fauna from strata in southern Egypt and northern Sudan. *Berliner geowissenschaftliche Abhandlungen, Reihe A* 50, 47–79.
- Kramer, K.U., Viane, R., 1990. Aspleniaceae. In: Kubitsky, K. (Ed.), *The Families and Genera of Higher Plants, 1. Pteridophytes and Gymnosperms*. Springer, Berlin, pp. 52–57.
- Krassilov, V.A., 1967. Early Cretaceous Flora of South Primorye and Its Stratigraphic Significance. Nauka, Moscow. 264pp. (in Russian).
- Krassilov, V.A., 1972. Mesozoic Flora of Bureya River. Ginkgoales and Czekanowskiales. Nauka, Moscow, 152 pp. (In Russian).
- Krassilov, V.A., 1984. Albian–Cenomanian flora of Kacha–Bodrak intershed, Crimea. *Bulletin of the Moscow Society of Nature Explorers* 59 (4), 104–112 (in Russian).
- Krassilov, V.A., 2009. Diversity of Mesozoic gnetophytes and the first angiosperms. *Paleontological Journal (Moscow)* 43 (10), 1272–1280.
- Krassilov, V.A., Bacchia, F., 2000. Cenomanian florule of Nammoura, Lebanon. *Cretaceous Research* 21, 785–799.
- Krassilov, V.A., Bugdaeva, E.V., 1999. An angiosperm cradle community and new proangiosperm taxa. *Acta Palaeobotanica (Suppl. 2)*, 111–127.
- Krassilov, V.A., Lewy, Z., Nevo, E., 2004. Controversial fruit-like remains from the Lower Cretaceous of the Middle East. *Cretaceous Research* 25, 697–707.
- Krassilov, V.A., Lewy, Z., Nevo, E., Silantjeva, N., 2005. Late Cretaceous (Turonian) Flora of Southern Negev, Israel. *Pensoft, Sophia*, 352 pp.
- Krassilov, V.A., Makulbekov, N.M., 1996. Plant subcrustations. *Paleontological Journal* 2, 125–128 (in Russian with English summary).
- Krassilov, V.A., Rasnitsyn, A.P., 2008. Plant – Arthropod Interactions in the Early Angiosperm History. *Pensoft, Brill, Sophia, Leiden*, 229 pp.
- Krassilov, V.A., Shilin, P.V., Vakhrameev, V.A., 1983. Cretaceous flowers from Kazakhstan. *Review of Palaeobotany and Palynology* 40, 91–113.
- Krassilov, V.A., Volynets, Y., 2008. Weedy Albian angiosperms. *Acta Palaeobotanica* 48 (2), 101–109.
- Lejal-Nicol, A., 1981. Nouvelles empreintes de la "Lingula Shale Unit" dans la région d'Abu Ballas (Égypte). 106 Congrès national des Sociétés savantes, Perpignan, 1, pp. 15–27.
- Lejal-Nicol, A., Dominik, W., 1990. Paléoflore à Weichseliaceae et à angiospermes du Cénomanien de la région de Bahariya (Égypte du Sud-Ouest). *Berliner geowissenschaftliche Abhandlungen, Reihe A* 120, 957–992.
- Lorch, Y., 1963. The fossil flora of Makhtesh Ramon. *Israel Geological Society, Makhtesh Ramon Symposium*, p. 15.
- Mahmoud, M.S., Soliman, H.A., Deaf, A.S., 2007. Early Cretaceous (Aptian-Albian) palynology of the Kabrit-1 borehole, onshore northern Gulf of Suez, Egypt. *Revista Española de Micropaleontología* 39, 169–187.
- Münster, G.G., 1843. Beiträge zur petrefacten-Kunde pt. 6, pp. 100.
- Nevo, E., 1968. Pipid frogs from the early Cretaceous of Israel and pipid evolution. *Bulletin of the Museum of Comparative Zoology* 13, 255–318.
- Reymanówna, M., 1968. *Mirovia sazaferi* gen. et sp. nov. (Ginkgoales) from the Jurassic of the Kraków region, Poland. *Acta Palaeobotanica* 25, 3–12.
- Robaszynski, F., Amédéo, F., González-Donoso, J.M., Linares, D., 2008. The Albian (Vraconian)–Cenomanian boundary at the western Tethyan margins (Central Tunisia and southeastern France). *Bulletin de la Société Géologique de France* 179, 245–266.
- Schrank, E., 1992. Nonmarine Cretaceous correlations in Egypt and northern Sudan: palynological and palaeobotanical evidence. *Cretaceous Research* 13, 351–368.
- Schrank, E., 1999. Mesozoische Floren aus Nordost-Afrika und ihre Beziehungen zum Klima am Paläoäquator. In: Klitzsch, E., Thorweih, U. (Eds.), *Nordost-Afrika: Strukturen und Ressourcen. Ergebnisse aus dem Sonderforschungsbereich "Geowissenschaftliche Problem in ariden und semiariden Gebieten"*. Wiley-VCH, pp. 137–166. DFG.
- Schrank, E., Ibrahim, M.I.A., 1995. Cretaceous (Aptian–Maastrichtian) palynology of foraminifera-dated wells (KRM-1, AG-18) in northwestern Egypt. *Berliner geowissenschaftliche Abhandlungen, Reihe A* 177, 1–44.
- Schrank, E., Rüffle, L., 2003. The Late Cretaceous leaf flora from Jebel Mudaha, Sudan. *Courier Forschungsinstitut Senckenberg* 241, 119–129.
- Segev, A., Weissbrod, T., Lang, B., 2005. ⁴⁰Ar/³⁹Ar dating of the Aptian–Albian igneous rocks in Makhtesh Ramon (Negev, Israel) and its stratigraphic implications. *Cretaceous Research* 26, 633–635.
- Seward, A.C., 1895. The Wealden Flora. II. Gymnosperms. *Catalogue of the Mesozoic Plants in the Department of Geology. British Museum (Natural History)*, London, 259 pp.
- Silantjeva, N., Krassilov, V.A., 2006a. Evolution of early angiosperm ecosystems: Albian – Turonian of Negev, Israel. In: Barrett, P.M., Evans, S.E. (Eds.), *Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota. Natural History Museum, London*, pp. 118–122.
- Silantjeva, N., Krassilov, V.A., 2006b. *Weichselia* Stiehler from Lower Cretaceous of Makhtesh Ramon, Israel: new morphological interpretation and taxonomical affinities. *Acta Palaeobotanica* 46 (2), 119–136.
- Upchurch Jr., G.R., Crane, P.R., Drinnan, A., 1994. The megaflora from the Quantico locality (Upper Albian), Lower Cretaceous Potomac group of Virginia. *Virginia Museum of Natural History Memoir* 4, 1–57.
- Vakhrameev, V.A., 1952. Stratigraphy and Fossil Flora of Western Kazakhstan. *Academy of Sciences, USSR, Moscow, Leningrad*, 340 pp. (in Russian).
- Vakhrameev, V.A., Krassilov, V.A., 1979. Reproductive organs of angiosperms from the Albian of Kazakhstan. *Paleontological Journal (Moscow)* (1), 121–128 (in Russian).
- Walker, J.W., Brenner, G.J., Walker, A.G., 1983. Winteraceous pollen in the lower Cretaceous of Israel: early evidence of a magnolialean angiosperm family. *Science* 220, 1273–1275.
- Watson, J., Lydon, S.J., Harison, N.A., 2001. A revision of the English Wealden flora, III: Czekanowskiales, Ginkgoales, and allied Coniferales. *Natural history Museum of London Bulletin (Geology)* 57 (10), 29–82.
- Zohary, T., 2004. Changes to the phytoplankton assemblage of Lake Kinneret after decades of a predictable, repetitive pattern. *Freshwater Biology*. 49, 1355–1371.