Jurassic flora of the Negev Desert: Plant taphonomy, paleoecology and paleogeographic inference

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ABSTRACT

Jurassic fossil plants of Makhtesh Ramon, the northern Negev, are collected from the Early Bajocian paralic Inmar Formation conformably overlain with the marine Mahmal Formation, which contains ammonite markers of the Middle–Upper Bajocian age. Plant remains occur in the thin ferruginous layers traceable all over the questa exposures, composed of re-deposited sand at the base and the fine-grained ferro-alumosilicate lamella on top. Plants are preserved as ferruginous molds of leafy shoots and reproductive material, buried by turbid run-over sand flows and embedded in the back-wash clayey deposits as calcified plant debris. On account of their peculiar taphonomy and elementary composition, the fossiliferous horizons are interpreted as tsunamites. The coastal plant assemblages are endemic at the syntaxonomic level, with Gondwana affinities extended to insular landmasses north of the Tethys. The abundance of bennettitalean plants and the inferred proximity of *Araucaria*-like brachyphylls give the Bajocian Inmar flora a thermophilic paratropical aspect, while the Bathonian flora of Sinai is of a more temperate aspect, suggesting a major mid-Jurassic climate change.

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1. Introduction

The mid-Jurassic flora of Makhtesh Ramon is one of a few representative fossil plant assemblages of this age in the Northern Africa and Middle East bearing on floristic development, climate change and geological history of the region, the currently controversial geotectonic reconstructions of which are reviewed in (Robertson and Mountrakis, 2006). The fossiliferous rocks and sedimentary environments are peculiar in many aspects, in particular in the plant remains being confined to the lithologically distinct sheet-like layer mantling the vast area of dune sandstones, hypothetically interpreted as a tsunami generated taphonomic environment. Perhaps our analysis would attract more attention to this type of fossil plant taphonomy.

The well-exposed fossil plant localities of Makhtesh Ramon ("Circus Ramon") in the northern Negev Desert have been for many years exposed to unprofessional collecting, the material being kept in private collections or lost. The first taxonomic description was published by Lorch (1967). The taphonomy, paleoecology and paleogeographic significance of the flora remained unexplored.

2. Material and methods

The material was collected during several collecting trips to fossiliferous Inmar Formation of Makhtesh Ramon (Fig. 1). Several hundred slabs

with well preserved plant remains were transported to the Institute of Evolution (IOE), University of Haifa for morphotaxonomic studies and housed in the IOE fossil plant depository, collection MRJ nos. 1–500. Material of lower preservation quality was used for counting numerical representations and left at the localities.

Taphonomic observations reveal a vast area of continuous fossiliferous layers that have a bipartite structure; fossil plants are preserved as ferric impressions in the fine-grained capping lamella and, locally, as ferruginous sandstone molds and casts in the underlying sandy layer. Those exposed by splitting of the ferruginous matrix are covered with a thin and brittle film of calcium sulfate. In the lack of compressed material or cuticles, morphological studies have been conducted under stereomicroscope Leica 300 and scanning electron microscope FE1 Quanta 200. Spectral analysis was performed with the scanning electron spectrometer EDS9 (methodology after Scott et al., 1995).

3. Taxonomic notes

A full-fledged taxonomic discussion would shift the focus of the paper, but a few notes on taxa making the bulk of the fossil assemblage seem pertinent. The fern genus *Piazopteris* Lorch, 1967 is described as having palmate-bipinnate leaves, but all the available specimens are 2–3-pinnate (except a small leaf rosette, perhaps a sporeling). The genus was originally typified by *Phlebopteris branneri* (Whyte) Lorch from Brazil. However, a specimen from Makhtesh Ramon was figured as the holotype (Lorch, 1967, Pl. 6, b). Thus both nomenclature and taxonomic diagnosis are problematic, but we postponed revision for a more comprehensive taxonomic treatment.

Fig. 1. Study area (arrow) on the digitally shaded topographic map of Israel, 1:5000,000, Geological Survey of Israel, 1997.

The bennettitalean flowers have been assigned to *Williamsonia*, a female fructification genus, but at least some specimens (Lorch, 1967, Pl. 12d) show microsporophylls. Our material reveals monoclinous (bisexual) structure, with the androecial whorl detached at maturity, a new feature of bennettitalean floral morphology.

The bennettitalean leaves are likewise a problem, partly because the traditional ill-defined leaf genera are inadequate for representing the immense morphological diversity of the group. We acknowledge the necessity of a more detailed classification, with new generic names, such as *Banatozamites* (Czier, 1996), representing a leaf morphotype of *Zamites*–
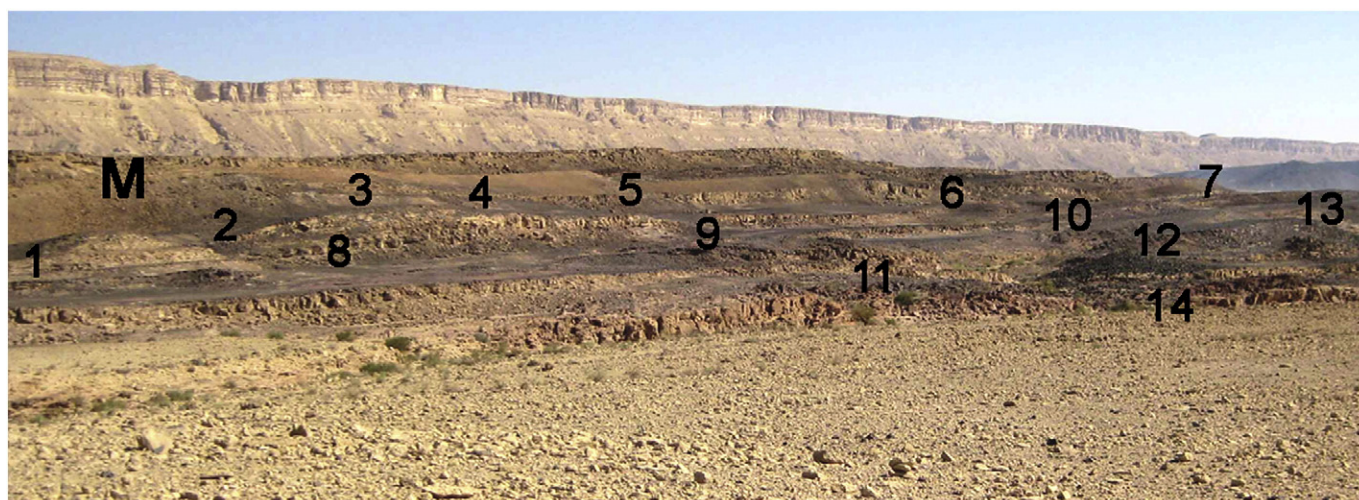

Fig. 2. Brown Questa of Makhtesh Ramon exposing the Middle Jurassic deposits, with numbers of collecting points.
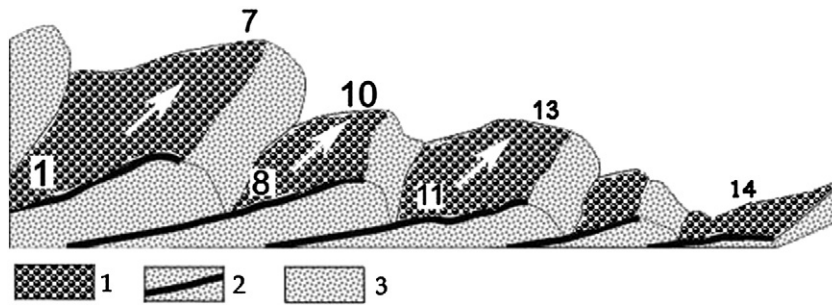
Fig. 3. Scheme of Brown Questa with erosional surfaces tilted as the strata. Numbers of fossil plant localities increasing in the direction of the arrows are indicated for each of the benches. Legend: 1, 2—ferruginous layers with fossil plants; 3—sandstones exposed at scarps.

Otozamites group, but not assignable to any of these genera on account of the pinnule attachment characteristics. Controversial interpretations of such leaves as one- or bipinnate have to be resolved by further morphological study and emendation of taxonomic diagnoses, if necessary.

4. Results of taphonomic and paleoecological studies

4.1. Geomorphology and stratigraphic position of fossiliferous horizons

Makhtesh Ramon and the other "circuses" of the northern Negev are currently interpreted as erosional windows through the thick cover of the Cretaceous shelf carbonates, exposing the predominantly clastic Triassic to Lower Cretaceous deposits in a broken homoclinal sequence. The Middle Jurassic sandy deposits compose a prominent ridge ("Brown Questa"), extending NE for about 6.5 km, with broad benches tilting at about 15° NW conformably with the tilt of the strata, thus forming a typical questa geomorphology (Easterbrook, 1999). This structure is favorable for interpretation of plant taphonomy, because fossiliferous horizons can be continuously traced for several kilometers along strike (Figs. 2, 3).

The Mahmal sandstone/limestone sequence overlies the undulate surface of the Inmar dune sandstones, but there is no evidence of stratigraphic unconformity at the boundary. The Mahmal fauna is assigned to the *Teloceras–Normannnites* ammonite assemblage of the Middle–Late Bajocian age (Parnes, 1982). The Inmar floristic assemblages are of a uniform composition over the fossiliferous interval downsection, thus assignable to Early Bajocian by their stratigraphic position, but with the lower boundary only tentatively dated (Fig. 4).

The Inmar Formation is 35–40 m thick at the questa escarpment, composed of pale yellowish gray to variegated coarse to medium-grained massive, cross-bedded and cross-laminated sandstones. The thickness variation corresponds to the gentle rises and lows of the downgraded dune relief. Massive coarse-grained sandstones prevail in the lower part of the sequence, with the medium-grained cross-laminated series increasing upsection. The sandstones are barren of fossils, except the ramified tracks and burrows of benthic fauna on hardground layers a few centimeters thick near the bottom of the escarpment (Fig. 5). The ichnofossil layers are traced along strike over the whole fossiliferous area. Occasional fragments of hardground lamina are re-deposited and embedded in the fossil plant-bearing horizons upsection (Fig. 6).

4.2. Scanning electron spectrometry of fossiliferous layers (examples in Supplement II)

The fossiliferous beds are purple to (weathered) dark gray layers 1–3 cm thick, locally expanded to 4–6 cm, of a thinning upward sand to silt granulometric composition. At the thicker points, the layer is divided into sandy and clayey lamellas that differ in texture and color, as well as containing different plant fossils. The lower lamella consists of angular quartz grains glued with reddish ferruginous clayey substance. Fresh splits of the upper lamella show scattered or patchily amassed quartz grains in the purplish-brown silty matrix with small plant debris (Fig. 7).

Discernible in the back-scattered electron mode at magnifications 100–10,000 are ferrosilicate and silicate fractions, the former as the major component of the matrix and the latter as angular grains of sand to silt granulometric grades. The matrix contains a subordinate alumosilicate component representing a smectite group clay mineral with occasional inclusions of zirconium sulfate and organic matter. Titanium oxide occurs as a finely dispersed quantitatively variable fraction of the matrix. The structurally preserved plant remains embedded in the ferruginous layer are preserved as a white film of calcium
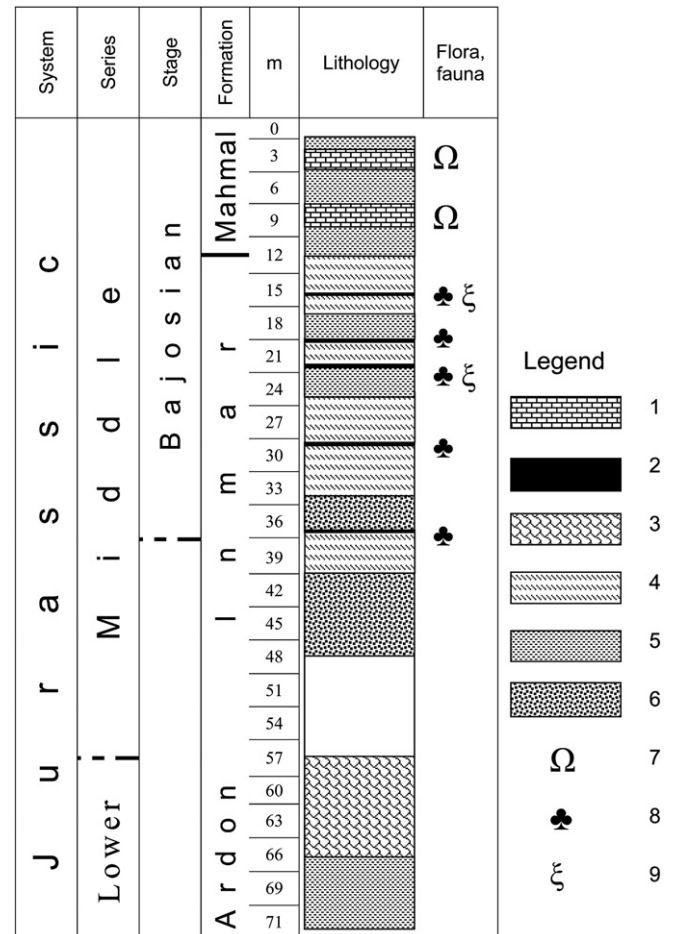

Fig. 4. Stratigraphic column of Jurassic deposits at the Brown Questa and adjacent Ramon channel of Makhtesh Ramon, the northern Negev. Legend: 1—dolomitic limestones; 2—fossil plant beds; 3—variegated shales/red beds/evaporites of the Lower Jurassic Ardon Formation; 4—cross-bedded sandstones; 5—plate sandstones; 6—massive sandstones; 7—ammonites, 8—plant fossils, 9—ichnofossils.

Fig. 5. Bedding plane with multiple trails and burrows in the basal part of fossiliferous sequence (field photograph, coin for scale 23 mm).

sulfate with an iron sulfide residue. The dispersed organic particles reveal high chlorine content.

The fossiliferous layers are of uniform electron spectrometric characteristics over the area of fossiliferous deposits, exhibiting a constant composition of electron distinctive mineral phases and insignificant quantitative variability of elementary constituents, indicating re-deposition and mixing of sand platform material.

4.3. Fossil plant assemblages

Insofar as fossil plant remains are found all over the nearly continuous exposure over the Brown Questa between 30°36′997″N, 34°50′822″E and 30°37′612″N, 34°51′162″E, this area can be considered as a single locality of about 12 km². However, plant fossils are unevenly distributed over this area, being typically represented by leaf fragments scattered over the top lamella, but locally forming matted accumulations in the sandy part of the ferruginous top layer. The numbered localities are points at which fossil plants were excavated and counted. Scattered plant remains between these points are registered out of count.

We identified 14 localities in the main fossiliferous area (Figs. 3, 5) and two supplementary localities nos. 01 and 02 west of the main area where only a few specimens have been found. Among the upper bench localities, no. 1 (30°37′444″N, 34°50′801″E) in the eastern part of the study area is the most representative, with a relatively thick (about 6 cm) sandy layer, containing a single species assemblage of crowded *Nipponoptilophyllum* (cf. *N. bipinnatum* Kimura et Tsujii), a bennettitalean plant with bipinnate foliage with *Ptilophyllum*-type comb-like pinnae (Kimura and Tsujii, 1984), covered with a white film of calcium sulfate. The capping lamella is imprinted with scattered pinnae of *Nipponoptilophyllum* and *Piazopteris*, a tree fern with reticulate venation of alethopteroid pinnules, both preserved as ferruginous relief impressions of a similar general aspect. *Brachyphyllum*-type scale-leaf shoots are occasionally found as a numerically minor component of the cap rock surface assemblage (Fig. 8). Such mixed assemblages repeatedly occur in the upper bench localities nos. 2–7.

At locality no. 9 on the 2nd bench downsection (30°37′544″N, 34°51′040″E), the fossiliferous layer is about 5 cm thick, with a single species accumulation of *Banatozamites* (cf. *B. chlamydostomus* Czier), a large-leafed bennettitalean species with the obliquely clasping "sunblind" pinnule arrangement (Czier, 1996). The relatively thick sandy layer contains stem cortex impressions, floral buds at different developmental stages, sometimes still attached to leafy twigs, and disintegrated flowers. The leaves are irregularly matted or amassed
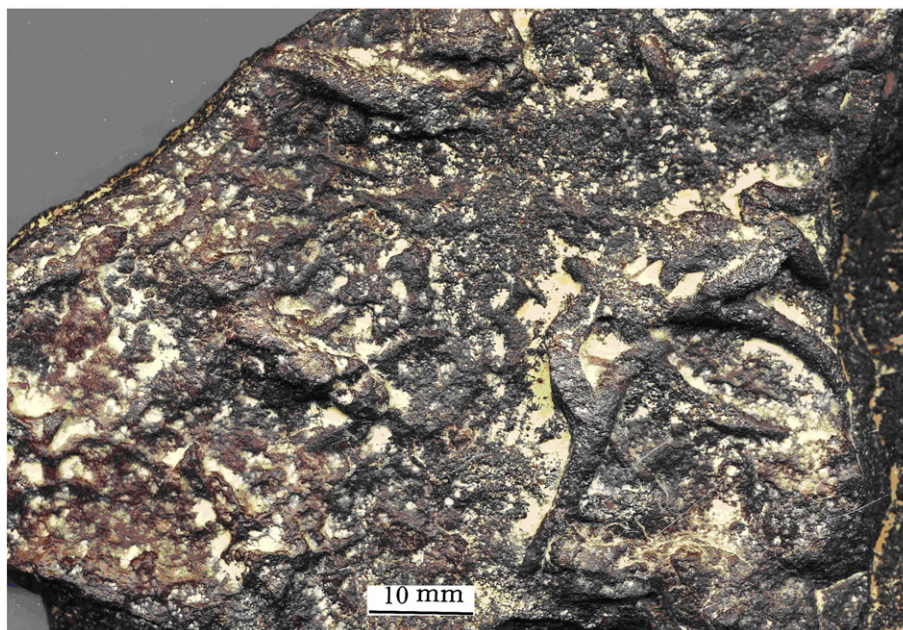
Fig. 6. Ichnofossils on a slab embedded in the fossil plant bearing horizon, locality no. 10, MRJ-61 (field photograph).

obliquely to the bedding plane, the overlapping pinnules separated by 1–2 mm of sandy matrix (Fig. 9). Flowers are preserved as three-dimensional molds. These features indicate instantaneous burial of unsorted plant material by rapid sand deposition. The capping surface association contains sparse pinnae of *Piazopteris*, as well as logs about 25 cm in diameter, disintegrated to heaps of splinters, their piths filled with sandy mold (Fig. 10). The logs are assigned to *Piazopteris* on evidence of occasionally preserved U-shaped leaf traces with circinate arms characteristic of this fern.

The lower bench localities nos. 11–14 (30°37′502″N, 30°51′072E″–30°37′536N, 34°51′216″E) yielded the predominantly fern assemblages, with matted *Piazopteris* leaves amassed in the sandy matrix. The capping surface association consists of crowded and scattered pinnae of the same species, thick defoliate rachises with oblique scars of detached pinnae, and occasional fragments of *Nipponoptilophyllum* and *Brachyphyllum*, the latter somewhat more frequent than in the debris assemblages upsection (Fig. 11). Small debris of fern pinnules and slender cheirolepid shoots incrusted with calcium sulfate are chaotically embedded in the capping lamella (Fig. 7A).

5. Discussion

5.1. Differentiation of plant assemblages

Inferred from above descriptions, the Jurassic fossil plant assemblages of Makhtesh Ramon are of two taphonomic types: (1) overrun and instantaneously buried by sand flows, forming dense accumulations, and (2) transported and scattered in the matrix and on top of the capping layers.

Type (1) includes single-species assemblages (nos. 1 and 2 with small-leafed *Nipponoptilophyllum*, nos. 8 and 9 with large-leafed *Banatozamites*, and nos. 11 and 13 with *Piazopteris*). Type (2) includes mixed assemblages of 4–5 species, numerically dominated by *Piazopteris* (up to 90% of counted specimens) in association with *Nipponoptilophyllum*, up to 50% (locality no. 2), but decreasing to 10% (no. 3) and about 5% (no. 13) further east. The *Araucaria*-like brachyphyllous shoots indiscriminately occur in the *Piazopteris*, *Nipponoptilophyllum*, and *Piazopteris–Nipponoptilophyllum* capping surface assemblages, constituting up to 5% (no. 12), but more often as an occasional out of count component. The ramified cheirolepid shoots of *Watsonicladus* type are rather frequent among small debris embedded in the capping layer (nos. 10–13).

Thus, the bulk of the plant deadmass was produced by only three species, an arboreal fern *Piazopteris* and two bennettitaleans *Nipponoptilophyllum* and *Banatozamites*, forming in situ or both in situ and ex situ accumulations (Figs. 8, 9) and recognized as dominant growth forms of the tidal flat vegetation. *Piazopteris* emerges from this study as a tree fern related to Cretaceous *Weichselia*, a pre-mangrove tree fern according to Silantieva and Krassilov (2006a,b), ecologically comparable with Paleozoic *Psaronius*, as well as the present day "mangrove ferns" more prudently assigned to mangrove associates (Tomlinson, 1994). The Mesozoic bennettites were ecologically diverse, with *Encephalartos* shrublands of South Africa as a modern analog. Yet saline habitats have been inferred for xeromorphic representatives of the group based on their leaf taphonomy (Krassilov, 1975). The co-occurring *Piazopteris* and *Nipponoptilophyllum* are represented by bipinnate or tripinnate leaves of similar general aspect suggesting morphological conversion.

In contrast, the scale-leafed *Brachyphyllum* shoots are a numerically minor, but widespread component of the mixed plant assemblages. Their taphonomy suggests an abundant distant (inland) source. The problem of their taxonomic affinities cannot be solved with only vegetative remains at hand. Yet the morphology of stout cord-like shoots about 10 mm thick with uniform overlapping scaly leaves in distinct parastichi (Fig. 12) is like that of deciduous shoots of *Araucaria columnaris*, shed and accumulated under the trees in dry season. The Inmar *Araucaria*-like *Brachyphyllum* material might have come from a similar source. In contrast, the slender cheirolepid brachyphylls *Watsonicladus* more probably belong to the tidal flat debris.

As usual, the minor components are difficult to assign, but their provenance would not affect our general conclusion: the bulk of the material came from the tidal flat fern–bennettitalean communities, with numerically subordinate, but constant contribution of *Araucaria*-like remains from an inland source.

5.2. Taphonomic interpretation

In sandy coastal deposits, plant macrofossils are usually accumulated in lenticular silty/clayey bodies of highly variable thickness, granulometric structure and mineral composition, representing a diversity of local plant communities. The fossiliferous horizons of Inmar
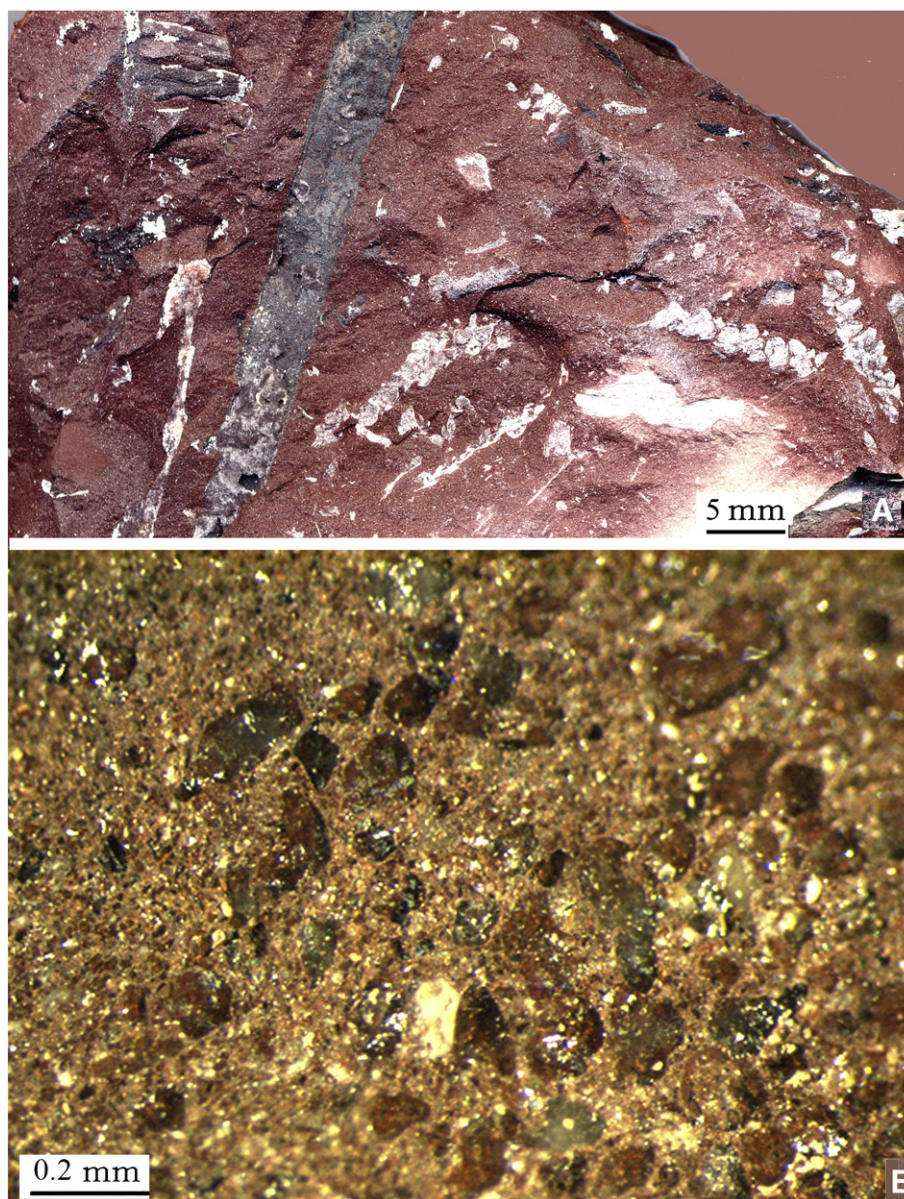
Fig. 7. Split cap rock lamella with white plant debris sampled for EDS (A) and ferrosilicate matrix with embedded quartz grains (B).

Formation are fairly different in being spread over a vast area as continuous ferruginous sheets of uniform composition over thick cross-bedded sandstones that are barren of plant fossils, but contain marine ichnofossils. The ferruginous capping layers contain accumulations of instantaneous buried autochthonous plant material, with scattered plant debris on top. The uniformly mixed plant material came from local as well as distant inland sources. Stem molds of arboreal plants stuck in the silty cap rock among small plant debris are evidence of high energy turbid flow over the sandy tidal flat platform.

Scanning electron spectrometry of fossiliferous capping layers (Section 4.2) testifies to uniform distribution of electron-distinctive mineral phases and insignificant quantitative variability of elementary composition over the study area. These features are incompatible with a massive influx from heterogeneous inland sources, as in deltaic deposition, indicating a tidal flat provenance of the capping layer material, re-deposited and purified by tide action. The influx of soil compounds, organic material and sea water resistant metallic residues (Ti enrichment) from terrestrial sources was evenly distributed all over the deposition area. The pyrite to calcium (strontium) sulfate substitution in the mineral coating of plant remains indicates deposition of plant material in anoxic water-logged, but rapidly exposed and dried up sediment. A relatively high chlorine content of dispersed organic matter can be ascribed to halophytic source plants.

Both sedimentological and plant taphonomic evidence thus comply with episodic large scale re-deposition of sandy tidal flat sediment stirred by high energy turbid flows and covered with backwash with organic remains from inland sources mantling the abraded surface of the coastal land forms. Such deposition events can be inflicted by an exceptionally strong storm surge or tsunami, both depositing widespread layers of distinctive lithologies and fossil content (reviewed in Dawson and Shi, 2000). However, tsunami flows run some distance upslope penetrating deeper inland and depositing continuous sedimentary sheets over wider areas, with inland material in the backwash (Clague and Bobrowsky, 1994).

Tsunami impacts on tidal flat deposition are now studied in many coastal settings. Vertical differentiation of tsunamites into sandy/silty lamellas corresponds to the runover and backwash deposition (Atwater and Yamaguchi, 1991; Atwater and Moore, 1992; Clague et al., 1994; Bondevik et al., 1997; Shanmugam, 2006; Shanmugam et al., 2011). The
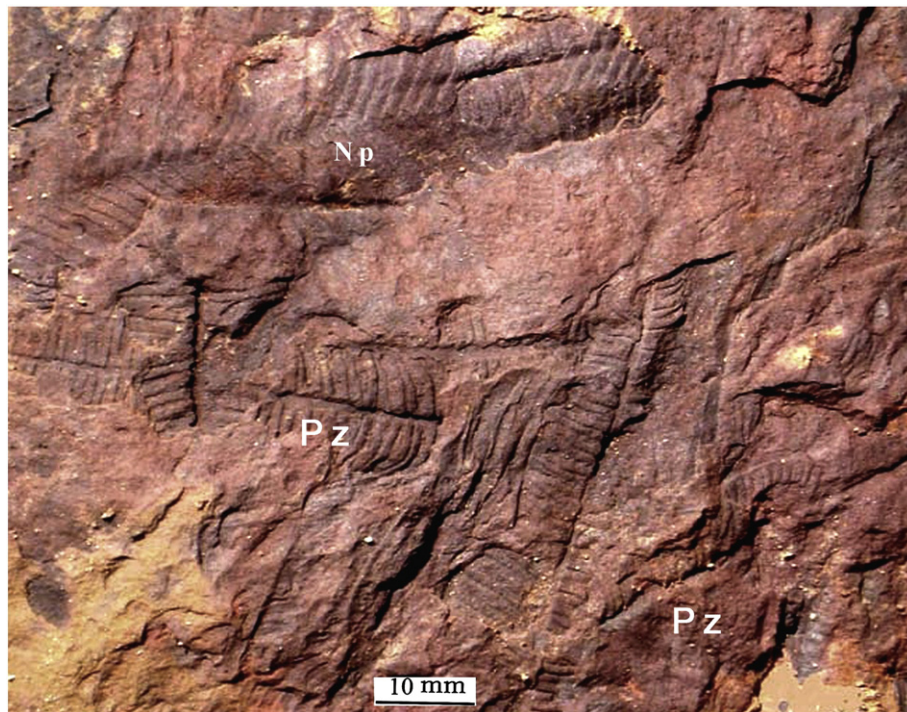
Fig. 8. Fragmentary *Piazopteris* (Pz)–*Nipponoptilophyllum* (Np) association on ferruginous capping lamella, locality no. 1 (field photograph).

advancing tsunami wave is a turbulent mixture of water and sand causing instantaneous burial of tidal flat vegetation (Dawson and Shi, 2000), whereas capping layers deposited after retreat of major wave are covered with drifted plant debris (Clague et al., 1994), which is what the Inmar plant-bearing beds exhibit. Such sedimentological and taphonomic features are also important as evidence of co-depositional seismic activity offshore.

Fig. 9. Locality no. 9, instantaneously buried *Banatozamites* leaves and floral structures (field photograph). On insertions: floral bud attached to a leafy twig (left) and digging at the fossiliferous layer.

Fig. 10. Disintegrated log with splinters scattered over the fossiliferous cap rock. On insertion: wood splinters magnified (field photograph).

5.3. Paleogeographic implications

The Jurassic flora of Makhtesh Ramon represents a low diversity low-land vegetation dominated by a peculiar *Pizopteris–Nipponozamites–Banatozamites* alliance. Its similarities with northern European Jurassic floras have been exaggerated by unreliable taxonomic assignments of fragmented material as "*Onychiopsis*", "*Aspidistes*" and "*Williamsonia*", typically represented in the Jurassic and Early Cretaceous floras of England (Lorch, 1967).

Among the better studied numerically dominant plants, *Piazopteris* was recognized by Lorch (1963, 1967) as a fern genus of Gondwana affinities. It is now reported from the Jurassic and Cretaceous localities of Libya, Tunisia and elsewhere in Northern Africa (El Chair et al., 1995; Barale and Ouaja, 2002). *Piazopteris* was replaced over the Jurassic–Cretaceous transition by *Weichselia* of closely similar stem anatomy and leaf morphology. The cone-like spore-bearing structures of *Weichselia* are derivable from the more conventional lamellar sporophylls of *Piazopteris* (Fig. 13A) by involution of fertile pinnules, probably a case of autochthonous evolution.

The bennettitalean genus *Banatozamites* was erected for bipinnate leaves with zamioid and ptilophylloid pinnules from Jurassic of Banat, Rumania (Czier, 1996, 2008, 2009). Here this generic name is applied

Fig. 11. Surface lamellae assemblage with fragmentary *Nipponoptilophyllum* (Np), *Brachyphyllum* (Br), and *Piazopteris* (Pz), locality no. 12, no. MRj-19.
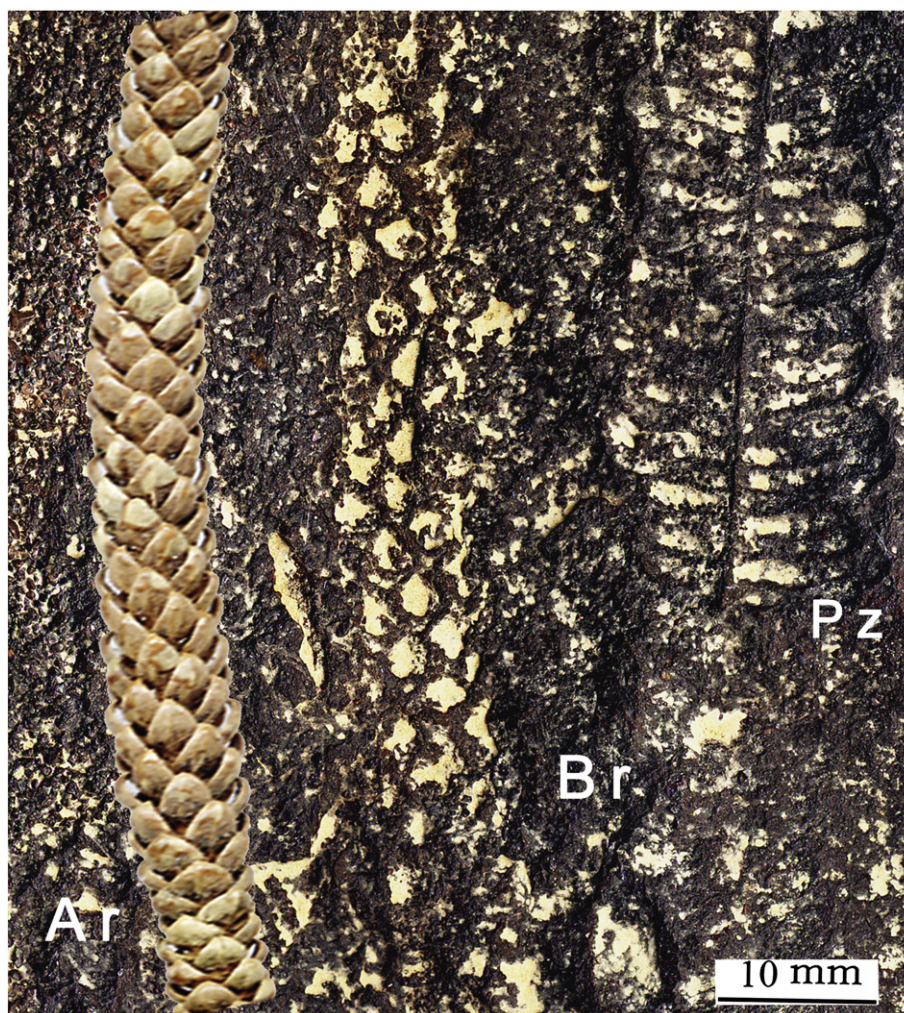
Fig. 12. Deciduous shoot of *Araucaria columnaris* (Ar) placed on fossiliferous layer for comparison with *Brachyphyllum* shoot (Br), no. MRJ-77, also showing a *Piazopteris* pinna (Pz).

to large pinnae with elongate basally decurrent and clasping pinnules like those in the type species (Fig. 13C), whereas the bipinnate leaves with ptilophylloid pinnules are assigned to *Nipponoptilophyllum*, previously known from the mixed Gondwanan/Laurasian Jurassic floras of Japan (Kimura and Tsujii, 1984). The bennettitalean flowers are monoclinous ("bisexual") with involucrate androecial whorl shed at maturity (Fig. 13F, G), comparable with *Amarjolia dactylota* from Rajmahal Hills, India (Bose et al., 1984).

These comparisons suggest floristic connections with the other parts of Gondwana, probably extended through trans-Tethys exchanges to the insular landmasses in the north. Notably, for the Middle Jurassic Inmar flora, the Gondwanaland connections are more evident than for the younger floras of the area (Krassilov et al., 2005).

5.4. Paleoclimate

Paleoclimatological interpretation of fossil floras involves synecological and autecological criteria, both applicable with reservations. Taphonomic analysis (above) suggests a tidal flat provenance of plant material. The present day arboreal tidal flat vegetation is almost exclusively tropical, replaced by marshes up the latitudes. When extended beyond the tropics, the arboreal tidal flat communities are reduced to one- or few species stands like those that the Jurassic *Piazopteris* and *Banatozamites* assemblages represent.

In ferns, reticulate venation as in *Piazopteris* (and *Weichselia*) is usually associated with thermophily. Yet *Piazopteris* has a restricted stratigraphic range being poorly and not quite reliably represented in the younger (Bathonian) flora of Sinai (Van Konijnenburg-van Cittert and Bandel, 2001).

Numerical fluctuations of cycadophyte (cycads plus bennettites) abundances are evidence of climate change through the Mesozoic fossil plant record (Krassilov, 1973). On this criterion, the Jurassic flora of Makhtesh Ramon is fairly thermophilic, with bennettitalean cycadophytes being the most abundant group of gymnosperms preserved as single-species assemblages and amounting to more than 50% in mixed assemblages.

The bennettitalean dominance in the Inmar flora of Makhtesh Ramon is in sharp contrast with their scanty presence in the Bathonian flora of Sinai (Lorch, 1963; Van Konijnenburg-van Cittert and Bandel, 2001), where this group is subordinate to conifers and cheirolepids in both taxonomic diversity and abundance. Zamioid leaf morphotypes are common in the mesozoic tropical–subtropical realm, broadly penetrating the subtropical/warm temperate ecotone over northern Europe and central Asia, but scarcely extending into the temperate Siberian realm north of 50°N (Krassilov, 1972, 2003). Geographic ranges of *Zamites*, *Otozamites* and *Ptilophyllum* broadly overlap, but *Otozamites* alone is found in the temperate/subtropical ecotone localities of central Gobi, Mongolia, being represented there by mass accumulations of shed pinnules, supposedly deciduous (Krassilov, 1982). Notably, it is *Otozamites* alone that represents
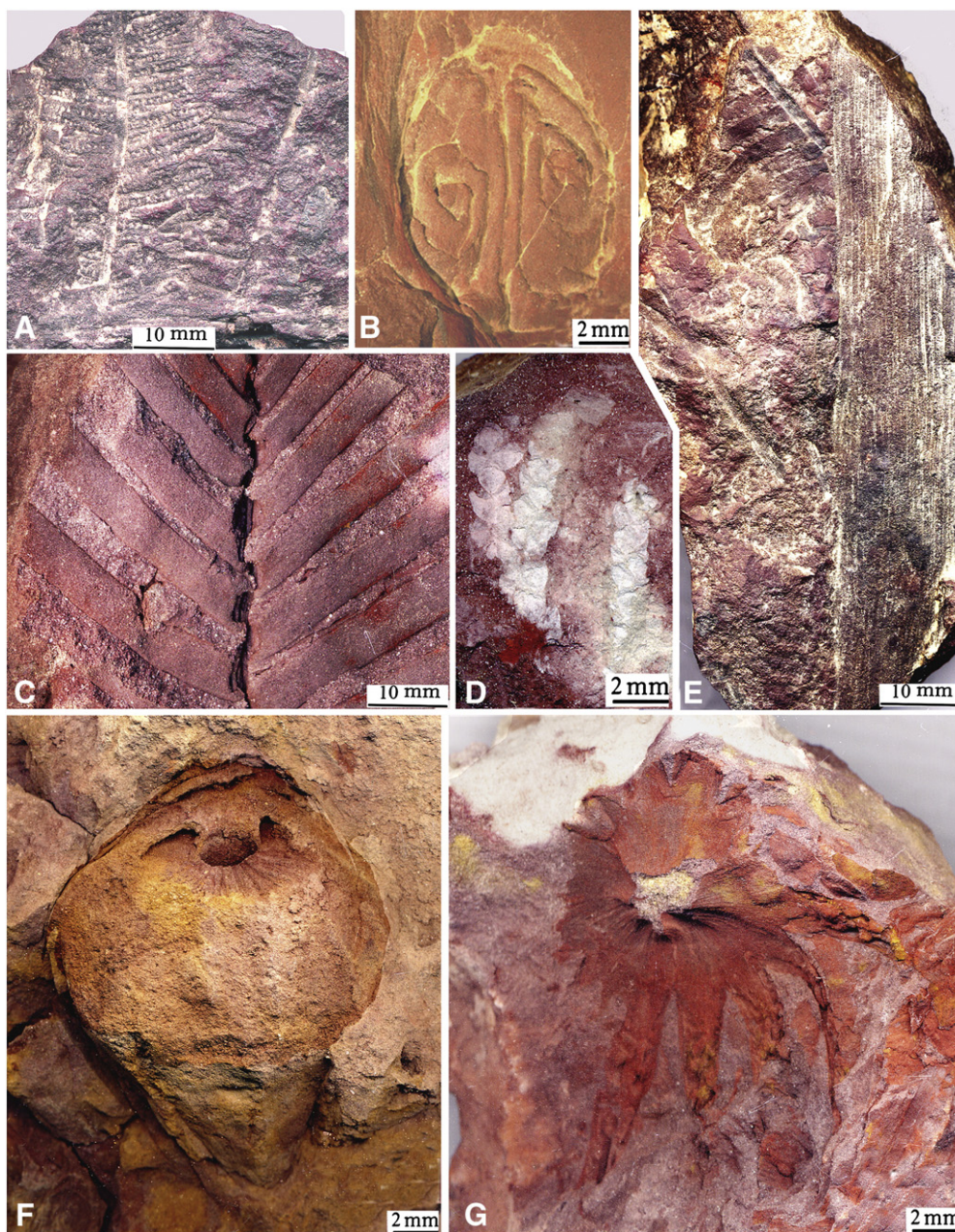
Fig. 13. Dominant plants of the Inmar flora of Makhtesh Ramon: A, *Piazopteris*, fertile leaf, no. MRJ-56; B, *Piazopteris* leaf cushion, MRJ-39; C, *Banatozamites* cf. *chlamydostomus* Czier, bipinnate leaf, no. MRJ-69; D, *Watsonicladus ramonensis* (Chaloner et Lorch) Srinivasan, branching shoot, no. MRJ-14; E, *Nipponoptilophyllum* cf. *bipinnatum*, 2-pinnate bennettitalean leaf, no. MRJ-16; F. Flower bud of *Banatozamites* plant, no. MRJ-47; G, Open flower of *Banatozamites* plant with androecium lobes spread from central hole of shed gynoecium, no. MRJ-40.

zamioid bennettites in the Bathonian flora of Djebel Tih, Sinai (Van Konijnenburg-van Cittert and Bandel, 2001).

The preponderance of *Nipponoptilophyllum* with comb-like pinnae confers a xeromorphic aspect on the Bajocian plant assemblages (paleoecological interpretations of *Ptilophyllum*-type leaves are reviewed in Krassilov, 1975, p. 73–75). Yet it is well known that morphological features converge in climatic xerophytes and edaphic sclerophytes (xero-halophytes). The pronounced xeromorphism of ptilophylloid bennettites from the Inmar localities can be interpreted as a synergistic climatic/edaphic effect of high salinity and pH over the tidal flat habitats.

Additional evidence on seasonality comes from *Banatozamites* plant in flower at locality no. 9, showing full grown leaves at the onset of blooming. Flowers are buried at different developmental

stages, from small buds tightly wrapped in cataphylls to about twice larger fruit-like bodies partly open at corona, and disintegrated into androecial whorl and gynoecial cone. These features indicate asynchronous blooming over a period exceeding flower development and fruit maturation. Unlike simultaneous flowering in sharply seasonal climates, long period of asynchronous blooming suggests rather mild seasonality of the time.

Constantly occurring, but numerically subordinate in the backwash debris are *Araucaria*-like cord-like brachyphyllous shoots, a permanent component of drifted plant assemblages through the Inmar floristic sequence. Their taphonomy indicates a stable inland source within the reach of tsunamis that is about 1 km inland. Presently araucarian forests are widespread over warm temperate to tropical highlands. They descend to sea coast under milder climate like in New Caledonia,

Fig. 14. Scheme of coastal vegetation at the time of Inmar deposition in Makhtesh Ramon. Tree ferns *Piazopteris* (based on reconstruction of *Psaronius* in Morgan, 1959), small-leafed *Nipponoptilophyllum* in front view, large-leafed *Banatozamites* near river mouth (represented by extant *Bowenia* spp.), and *Araucaria*-type brachyphylls at the background (based on *Araucaria columnaris* on New Caledonia: http://www.flickr.com/photos/45295993@N03/4274468822/ NC21, date = 2009-07-02 14:16, author = [http://www.flickr.com/people/45295993@N03 my LifeShow] from Paris, France).

where the coastal "pine forests" are formed of *Araucaria columnaris*, morphologically the closest match to the Inmar *Araucaria*-like brachyphylls (Fig. 12).

The allochthonous part of the Inmar assemblages commonly include small debris of slender cheirolepid shoots *Watsonicladus* (Fig. 7A) that are more common at Djebel Tih, rising to numerical dominance in the Late Jurassic Kidod flora (Raab et al., 1986). Ecology of cheirolepid expansion is insufficiently understood and sometimes attributed to aridization, although their shoots and pollen grains frequently occur in coal-bearing deposits and are locally abundant in off-shore facies. Anyway, different cheirolepid representation in the Bjocian Inmar and Bathian Djebel Tih assemblages signals climate change of a more than regional significance.

6. Conclusion

The Jurassic flora of Makhtesh Ramon is confined to paralic facies truncated by the Middle Bajocian transgression. The taxonomic and syntaxonomic composition is uniform over the succession of fossiliferous horizons indicating high sedimentation rates at the onset of Bajocian deposition. Fossil plants are collected over the continuous exposures of a questa relief that are traced for several kilometers. Plant remains are accumulated in the hard ferruginous layers mantling the cross-bedded tidal flat sandstones.

The fossiliferous layers are sheet-like, a few centimeters thick, with well defined bottom and top planes, sandy with a fine-grained ferro-alumosilicate lamella on top. Scanning electron spectrometry of fossiliferous beds indicates tidal flat provenance of re-deposited sandy matrix with a uniformly distributed backwash material with corrosion resistant metallic residues. The embedded plant remains are coated with iron sulfide–calcium/minor strontium sulfate film. Chlorine in dispersed organic particles suggests saline plant habitats.

Plant remains are instantaneously buried under runover sand flows and scattered as backwash debris on top of ferruginous capping layers. On account of sedimentological and plant taphonomic evidence, the fossiliferous beds are interpreted as tsunami deposits (tsunamites). This type of plant taphonomy, although rarely recognized, is markedly different from the more common plant debris accumulations in lenticular bodies of fine-grained sediment.

The Inmar tidal flat vegetation is reconstructed as single-species stands of arboreal ferns and bennettites, as well as mixed stands with a xeromorphic ptilophylloids amounting to 50% of counted specimens. Inland vegetation is represented by the numerically minor, but widely scattered *Araucaria*-like brachyphylls (Fig. 14). At the syntaxonomic level, the *Piazopteris–Nipponoptilophyllum–Banatozamites* alliance appears endemic, with intermittent floristic exchanges across Gondwanaland and with insular land masses north of the Tethys.

The abundance of bennettitalean plants gives the Inmar assemblages a thermophilic aspect, whereas their xeromorphic features are probably related to xerohaline effect. Yet a relatively low taxonomic diversity of arboreal tidal flat vegetation complies with extratropical rather than tropical provenance. The present day lowland araucarian forests thrive under mildly seasonal climate as in New Caledonia. The bennettitalean floral/fruiting structures instantaneously buried at different developmental stages together with full-grown macrophyllous foliage, testify to asynchronous blossoming, which is typically associated with a mild rather than sharp seasonality. In comparison, the Bathonian flora of Sinai is temperate, suggesting a prominent mid-Jurassic climate change the significance of which for Jurassic paleoclimatology is still to be learned.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2013.03.014.

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