Journal of Palaeosciences 70(2021): 135–158
0031–0174/2021

The fossil flora of the Dead Sea region, Jordan– A late Permian Garden of Delights

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ABSTRACT

Kerp H, Blomenkemper P, Abu Hamad A & Bomfleur B 2021. The fossil flora of the Dead Sea region, Jordan–A late Permian Garden of Delights. Journal of Palaeosciences 70(2021): 135–158.

The Umm Irna Formation, Jordan, holds one of the most peculiar late Permian plant–fossil assemblages worldwide. Over the last decades of field work, several localities close to the eastern shore of the Dead Sea have yielded a highly diverse ‘mixed flora’ of mesic to xeric environments encompassing elements that are typical either for different floral realms or for different time periods of Earth History. Taxa typical for particular floral realms include, e.g. Cathaysian gigantopterids and *Lobatannularia*, Euramerican conifers such as *Otovicia hypnoides*, or the characteristic Gondwanan seed ferns *Glossopteris* and *Dicroidium*. Moreover, most taxa are typical for the Permian, some assemblages have also yielded precocious occurrences of taxa that have so far been considered typical for the Mesozoic, such as Umkomasiaceae, Bennettitales, and podocarp conifers. In most cases, fossils from the Umm Irna Formation show well–preserved cuticles that allow sound systematic placement and contribute to the reconstruction of dispersed plant parts into whole–plant–taxa. Altogether, the Umm Irna Formation provides an exceptional window into depositional environments and vegetation types that are rarely preserved in the fossil record but that are crucial for our understanding of plant evolution.

Key–words—Late Permian, Mixed Flora, Dead Sea Region, Jordan, Methuselah Taxa, Lazarus Taxa.

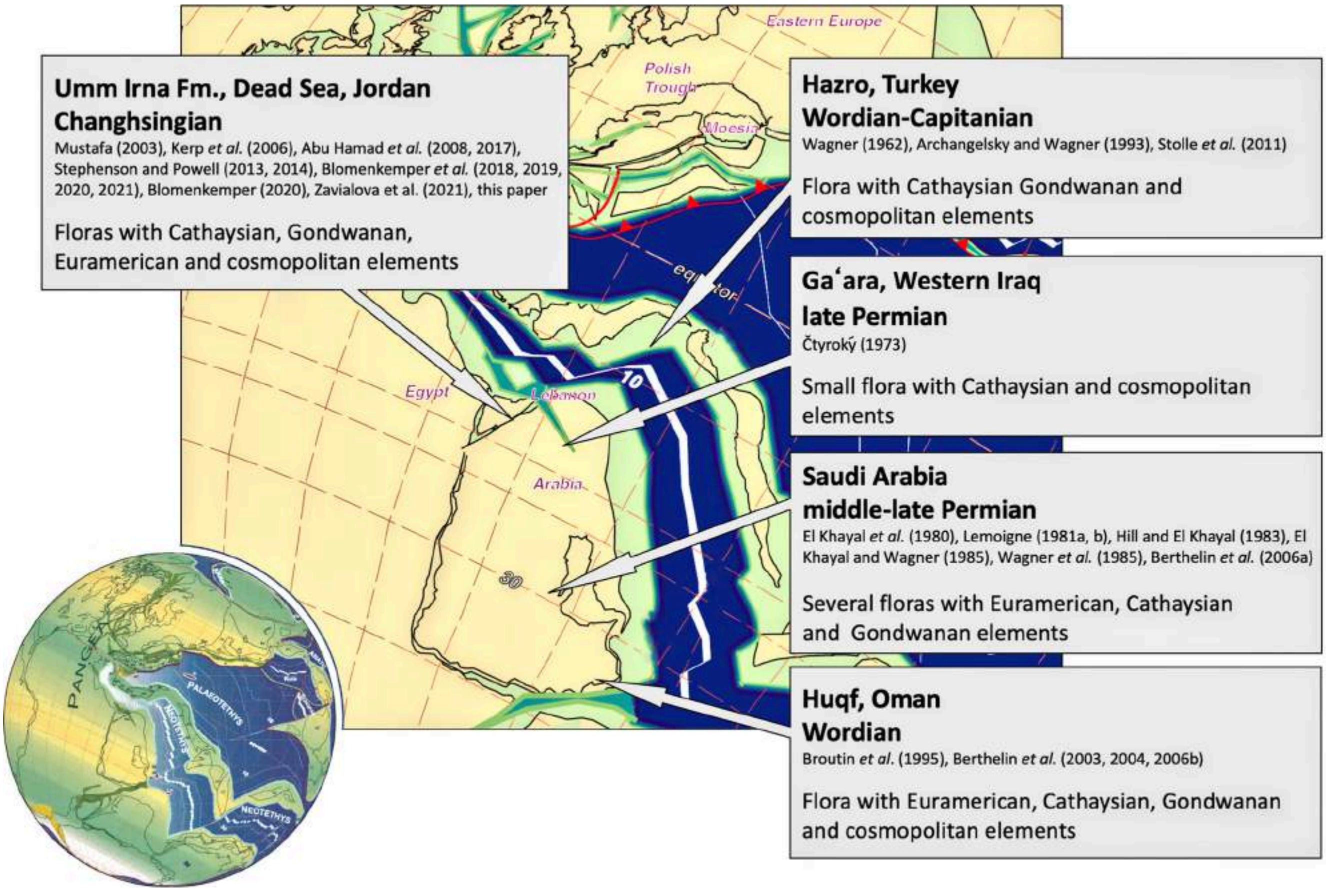
INTRODUCTION

THE Permian–Triassic mass extinction is the most pronounced biotic crisis of the Phanerozoic (Erwin, 1993, 1999; Stanley, 2016) and is most distinct in the marine realm. Unfortunately, the terrestrial record is less clear, and recent debates focus on the question to which extent land plants suffered from the extinction at the P–T boundary at all. Whereas most authors agree that there was a major floral turnover at the P–T boundary (e.g. Bercovici *et al.*, 2015; Cascales–Miñana *et al.*, 2016; Fielding *et al.*, 2019; Vajda *et al.*, 2020), some argue that the fossil record across this interval is too biased and to incomplete to provide robust evidence for any major extinction among land plants (Nowak *et al.*, 2019).

The late Palaeozoic is marked by the transition from an icehouse to a greenhouse climate, which eventually culminated in a hothouse world in the Early Triassic (e.g. Montañez *et al.*, 2007; Roscher *et al.*, 2011; Isbell *et al.*, 2012). Geographic isolation and climatic differentiation resulted in the development of different floral and faunal provinces. Climate change not only had a strong impact on the composition and ecological characteristics of the terrestrial vegetation as a whole, but also resulted in floral migrations and in an extension of the geographical distribution of specific plant groups. Palaeophytogeographically and from an evolutionary perspective, the middle to late Permian floras from the Middle East are of great interest. Most of these are so–called “mixed” floras comprising Cathaysian elements and taxa typical for other floral provinces (e.g. Wagner, 1962; Archangelsky & Wagner, 1983; Berthelin *et al.*, 2003, 2006a, b; Mustafa, 2003). Notably, the first *bona fide* occurrences of three gymnosperm lineages that became highly successful in the Mesozoic were reported from the Umm Irna Formation of the Dead Sea region, Jordan (Abu Hamad *et al.*, 2008; Blomenkemper *et al.*, 2018). Most papers on Permian floras from the Middle East focussed on systematics, the mixed nature and age of these floras, and on the precocious occurrence of typical Mesozoic taxa in the upper Permian. So far, little attention has been given to the composition of the vegetation. This contribution deals with floral associations from the Umm Irna Formation (Changhsingian). The floodplain sediments of the late Permian Umm Irna Formation show rapid lateral and vertical facies changes. Over the last 20 years a large collection has been built up from several localities representing different sedimentary settings, each yielding typical plant–fossil assemblages. The floral associations from the Umm Irna Formation provide new insights in the appearance of new clades and show which vegetation types were most severely affected by the end–Permian biotic crisis.

MIXED FLORAS FROM THE MIDDLE EAST

All Permian floras from the Middle East contain typical Cathaysian elements (Fig. 1). A small flora from the middle to late Permian Ga'ara Sandstone Formation in the Ga'ara Depression in western Iraq seems to comprise only Cathaysian taxa (Čtyroký, 1973). *Lobatannularia heianensis* (Kodaira 1924) Kawasaki 1927 and *Plagiozamites oblongifolius* Halle 1927 are abundant; the other taxa listed, *Pecopteris* sp., *Taeniopteris* sp. and *Protoblechnum* sp., are rare and also known from Cathaysia. It should be noted the most common species of *Protoblechnum–P. wongii* Halle 1927, originally described from central Shanxi, China–was recently transferred to *Compsopteris* Zalessky 1934 (Backer *et al.*, 2019), a genus first described from Angaraland (Zalessky, 1934; Naugolnykh, 1999). Other floras clearly show a mixed composition. The oldest flora is from the Gharif Formation of the Huqf area, central Oman (Berthelin *et al.*, 2003). The terrestrial, plant–bearing Gharif Formation is under–and overlain by the well–dated marine Saiwan and Khuff formations. The Gharif Formation yielded a fairly well–preserved palynoflora (Broutin *et al.*, 1995) and has been dated as early Wordian (Guadalupian) (Berthelin *et al.*, 2003). This flora is a mixture of Cathaysian, Gondwanan and Euramerican elements. Typical Cathaysian taxa are *Sphenophyllum sinocoreanum* Yabe 1920, *Lepidodendron acutangulatum* (Halle 1927) Stockmans & Mathieu 1957, *Gigantopteris* sp., *Gigantonoclea lagrelli*



Umm Irna Fm., Dead Sea, Jordan
Changhsingian
Mustafa (2003), Kerp *et al.* (2006), Abu Hamad *et al.* (2008, 2017), Stephenson and Powell (2013, 2014), Blomenkemper *et al.* (2018, 2019, 2020, 2021), Blomenkemper (2020), Zavialova et al. (2021), this paper

Floras with Cathaysian, Gondwanan, Euramerican and cosmopolitan elements

Hazro, Turkey
Wordian-Capitanian
Wagner (1962), Archangelsky and Wagner (1993), Stolle *et al.* (2011)

Flora with Cathaysian Gondwanan and cosmopolitan elements

Ga'ara, Western Iraq
late Permian
Čtyroký (1973)

Small flora with Cathaysian and cosmopolitan elements

Saudi Arabia
middle-late Permian
El Khayal *et al.* (1980), Lemoigne (1981a, b), Hill and El Khayal (1983), El Khayal and Wagner (1985), Wagner *et al.* (1985), Berthelin *et al.* (2006a)

Several floras with Euramerican, Cathaysian and Gondwanan elements

Huqf, Oman
Wordian
Broutin *et al.* (1995), Berthelin *et al.* (2003, 2004, 2006b)

Flora with Euramerican, Cathaysian, Gondwanan and cosmopolitan elements

Fig. 1—Palaeogeographic map of the Arabian Peninsula and surrounding area during the late Permian showing the occurrences of so–called mixed floras. Map modified after Stampfli and Borel (2001).

PLATE 1

Sphenopsids from the late Permian Umm Irna Formation, Jordan.

1. *Calamites* sp., pith cast.
2. *Calamites* sp., impression of the outer surface, same specimen as 1.
3. *Calamites* sp., pith cast, detail of 1.
4. *Lobatannularia heianensis*.
5. *Lobatannularia spatulata*.

(Halle 1927) Koidzumi 1936, *Cathaysiopteris whitei* (Halle 1927) Koidzumi 1936 and *Tingia* cf. *hamaguchii* Kon'no 1929 and *Tingiostachys* sp. Euramerican elements are the sphenophytes *Calamites gigas* Brongniart 1828 and the conifer *Otovicia hypnoides* (Brongniart 1828) Kerp *et al.* 1990, the latter found in a slightly higher level. Gondwanan taxa include six species of *Glossopteris* as well the associated reproductive organs *Plumsteadia* Rigby 1963, *Lanceolatus* Plumstead 1952, *Arberia* White 1908 and *Lidgettonia* Thomas 1958. A form identified as *Comia* sp. in Berthelin *et al.* (2003) is remarkably similar to *Auritifolia* Chaney *et al.* 2009 from the Leonardian (Cisuralian) of north–central Texas (Chaney *et al.*, 2009). Also, five taxa of silicified wood show a mixture of taxa from three floral provinces (Berthelin *et al.*, 2004). The Hazro flora of eastern Anatolia (Turkey) primarily consists of a mixture of Cathaysian, i.e. *Gigantopteris* Yabe 1904 and *Lobatannularia* Kawasaki 1927, and Gondwanan elements, e.g. *Glossopteris* (Wagner, 1959, 1962). Furthermore, a possible Angaran taxon [?*Angaropteridium cardiopteroides* (Schmalhausen 1877) Zalessky 1932] and a Euramerican pecopterid, *Pecopteris jongmansii* Wagner 1962 occur in this flora. However, the initial identification of *Glossopteris stricta* Bunbury 1861 from Hazro in Wagner (1962) was disputed by Plumstead and Lacey (in: Wagner, 1962), although the presence of *Glossopteris* Brongniart 1828 was not questioned; Archangelsky and Wagner (1983) described another species of *Glossopteris* from Hazro that was later also found in Oman (Berthelin *et al.*, 2006b). The specimen illustrated in Wagner (1962) as *Dicroidium?* vel *Thinnfeldia?* sp. is too fragmentary for a genus assignment. The Hazro flora was originally dated as middle or late Permian (Wagner, 1962) and later as latest Permian (Archangelsky & Wagner, 1983). However, Stolle *et al.* (2011) dated the plant–bearing beds of the Kaş Formation palynologically as late Wordian to early Capitanian (Guadalupian). Two Permian floral associations have been described from central Saudi Arabia. El Khayal *et al.* (1980) published a first brief report on the so–called Unayzah flora from the upper part of the Unayzah Formation (Roadian–Wordian). Later papers on this flora are by Lemoigne (1981a, b), El–Khayal and Wagner (1985), Wagner *et al.* (1985) and Berthelin *et al.* (2006a). The Unayzah flora comprises Cathaysian, Gondwanan and Euramerican taxa. Cathaysian elements include such as *Lobatannularia lingulata* Halle 1928, *Lobatannularia* sp. cf. *heianensis*, *Fascipteris hallei* (Kawasaki, 1931) Lee *et al.* 1974 and *Gigantonoclea* sp. Gondwanan elements are *Pecopteris phegopteroides* (Feistmantel, 1878) Arber 1905 and *Cladophlebis* cf. *roylei* Arber 1901. *Qasimia schyfsmae* (Lemoigne 1981) Hill *et al.* 1983 is a marattialean fern so far only known from the Arabian Peninsula that was originally identified as *Marattiopsis* sp. (El Khayal *et al.*, 1980) and then in part assigned to *Neuropteridium schyfsmae* (Lemoigne, 1981b). According to Berthelin *et al.* (2006) the specimen illustrated in Lemoigne (1981a, b) as *Dadoxylon* belongs to the Euramerican genus *Araucarioxylon*. Palynological studies date this flora as Roadian and/or Wordian (Berthelin *et al.*, 2006a). The second floral association from central Saudi Arabia, the Midhnab flora, is known from several localities, i.e. Jal Khartam, Wadi al Batin and Jal al Watah. The Midhnab flora occurs in the upper part of the Midhnab Member, Khuff Formation, and is dated as Changhsingian (Vaslet *et al.*, 2005; Berthelin *et al.*, 2006b). The Midhnab Member consists of lacustrine limestones, sandstone channels and claystones deposited in meandering river systems and swamps. Plants are found in two different lithologies: in a siltstone channel with drifted trunks, interpreted as a crevasse–splay deposit, and in claystones representing a quieter environment. In the Jal Khartam locality fragments of typical Euramerican conifers are dominant, particularly *Ullmannia frumentaria* Göppert 1850, *U. bronnii* Göppert 1850 and *Culmitzschia* sp., associated with the Gondwanan sphenophyte *Phyllotheca australis* Brongniart 1828 and the Cathaysian fern *Pecopteris chihliensis* Stockmans & Mathieu 1957. At Wadi al Batin the association is dominated by the Cathaysian sphenophytes *Lobatannularia heianensis* and *L. multifolia* Kon'no & Asama 1950, associated with a few *Voltzia*–like shoots. The Jal al Watah association comprises the Euramerican conifers *Pseudovoltzia liebeana* Florin 1927, *U. bronnii* and *Culmitzschia* sp., the Cathaysian noeggerathialean *Discinites* sp. cf. *D. orientalis* Gu & Zhi 1974, the putative ginkgophyte *Pelourdea* sp. cf. *P. hallei* Gu & Zhi 1974, and glossopterids typical for Gondwana, *Glossopteris formosa* Feistmantel 1881, *G. decipiens* Feistmantel 1879 and *Arberia* sp. Except for the conifers that grew in drier environments and are usually preserved as fragments, all forms are typical for humid habitats.

The palynoflora is dominated by a variety of mono– and bisaccate pollen, e.g. *Protohaploxypinus microcorpus* (Schaarschmidt, 1963) Clarke, 1965, *P. amplus* (Balme & Hennelly 1955) Hart 1964, *P. hartii* Foster 1979, *P. bharadwajii* Foster 1979, *P. diagonalis* Balme 1970, *Lueckisporites virkkiae* Potonié et Klaus 1954, *Klausipollenites schaubergeri* (Potonié & Klaus 1954) Jansonius 1962, *Lunatisporites noviaulensis* (Leschik 1956) de Jersey 1979 and *Nuskoisporites* sp. Several of these are typical elements in late Permian floras of Euramerica. Spores include *Calamospora breviradiata* Kosanke 1950, *Laevigatosporites vulgaris* Ibrahim 1933 and *Punctatisporites fungosus* Balme 1963.

THE UMM IRNA FORMATION, JORDAN

The Umm Irna Formation is exposed in a narrow strip along the eastern side of the Dead Sea (Fig. 2). The formation unconformably overlies the Cambrian Umm Ishrin Sandstone Formation and is overlain with an erosional contact by the Lower Triassic Ma'in Formation. In its type section in Wadi Himara, the Umm Irna Formation reaches a thickness of up to 85 m (Bandel & Khoury, 1981; see Fig. 2). Elsewhere,

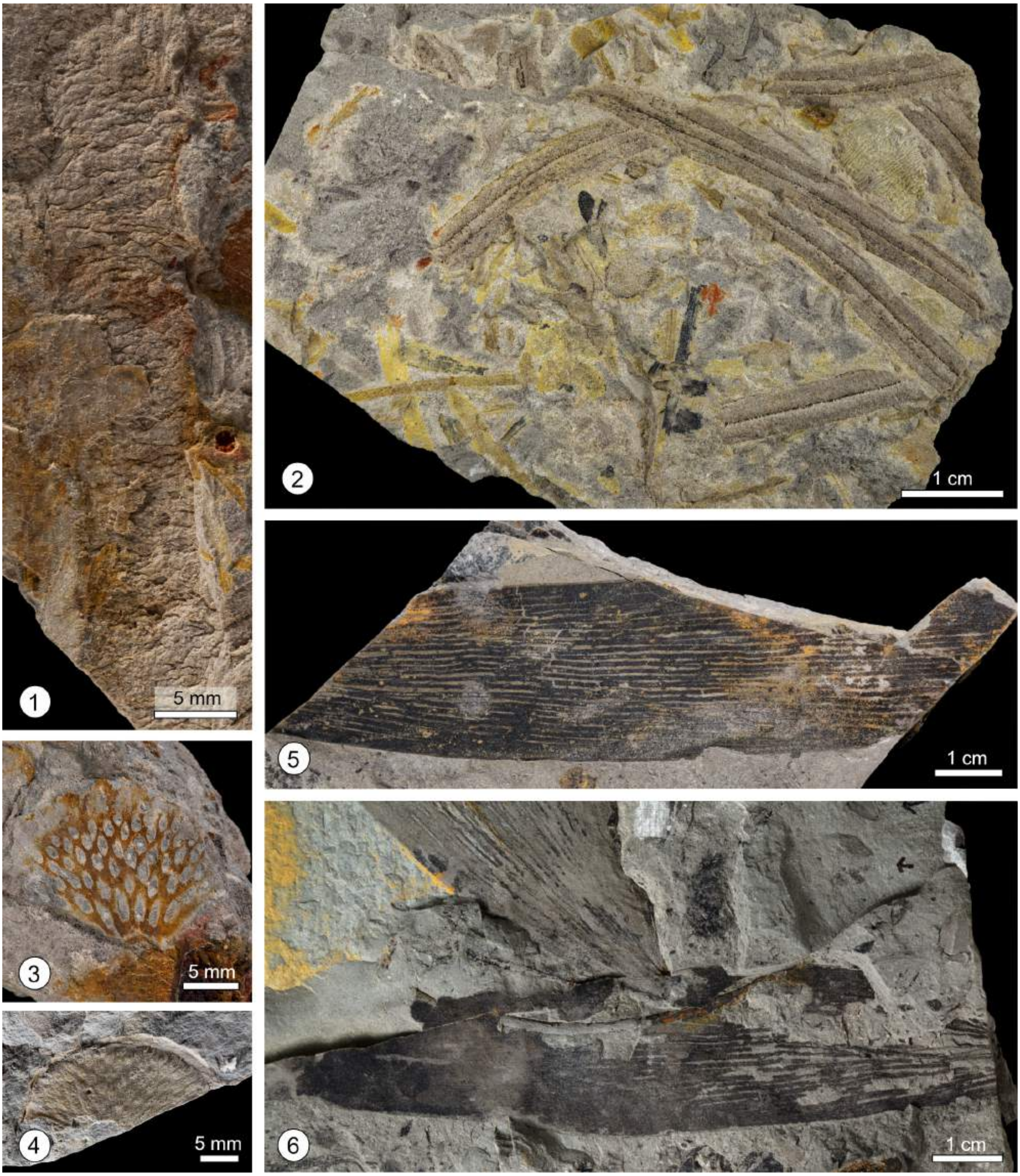


PLATE 2

Lycopsids and Noeggerathiales from the late Permian Umm Irna Formation, Jordan.

1. Corm of an isoetalean.
2. Amassment of dispersed fragments of isoetalean leaves.

3–4. *Discinites* sp., a noeggerathialean sporophyll.
5–6. *Tingia*–like leaf fragments.

the total thickness is difficult to determine, because close to the major Jordan Valley Fault rock successions are strongly affected by block faulting and complete sections are missing. Moreover, rapid facies changes, laterally as well as vertically, hamper direct bed–to–bed correlation where neither lower or upper boundary is exposed. For example, in the type section the basal 18 m of the Umm Irna Formation consist of whitish–yellowish sandstone intercalated with greyish to brownish clay–and siltstone containing abundant plant fossils. These beds are overlain by six fining–upward cycles of barren red sand–and siltstones, the top of each marked by a palaeosol. The occurrence of ferruginous pisolites in the uppermost clay beds (Bandel & Khoury, 1981) and the presence of deep, polygonal desiccation cracks in some of the palaeosols indicate a seasonally dry, tropical climate (Bandel & Khoury, 1981; Abu Hamad *et al.*, 2008; Stephenson & Powell, 2013). By contrast, six kilometres further south at the so–called Dyke Plateau (see Fig 2) the top of the formation consists of reddish–brown siltstone with abundant root remains and a several–metres–thick succession of yellowish–white sandstone, and grey, yellowish and red–brown silt–to pure claystone with abundant plant fossils. The depositional environment of the Umm Irna Formation has been interpreted as a distal braided–river system with common abandoned channels (Makhlouf *et al.*, 1991) and with extensive and heterogeneous floodplain environments (e.g. Stephenson & Powell, 2013). A composite section of the Umm Irna Formation was published by Stephenson and Powell (2013), who also gave a detailed interpretation of the sedimentological setting and studied palynomorphs of most of the outcrops dealt with in this paper.

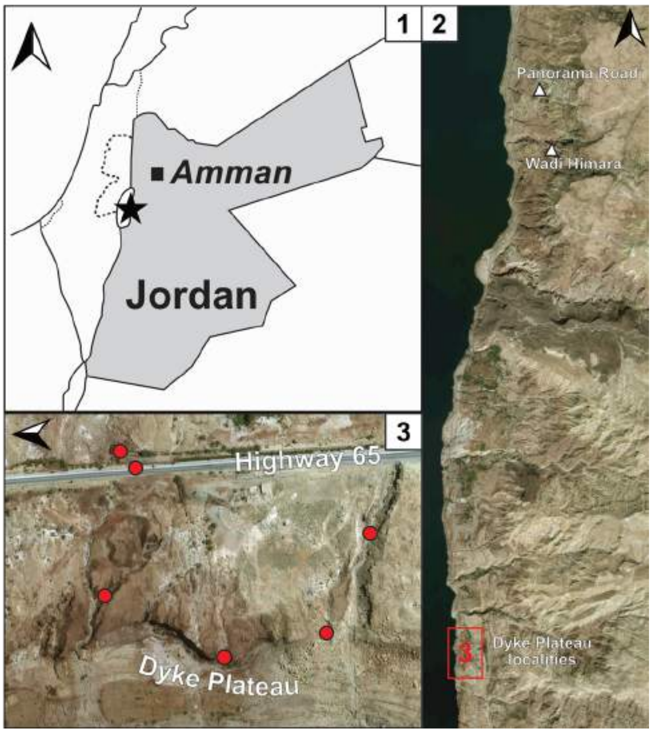


Fig. 2—Geographic map of the study area. (1) Geographic map of Jordan. Black star marks the study area. (2) Satellite image of the eastern coast of the Dead Sea. Red rectangle corresponds with (3). (3) Satellite image of the Dyke Plateau area. Red circles mark fossiliferous outcrops in the area.

Initially, the succession later defined as the Umm Irna Formation was mapped as Permo–Triassic (Bender, 1968). Multiple palynostratigraphic analyses of the Umm Irna Formation have consistently assigned a Permian age to the formation. Most of the earlier studies agree on a late Permian age (Brugman in Bandel & Khoury, 1981; Makhlouf *et al.*, 1991; Makhlouf, 1997; Abu Hamad, 2004; Bandel & Abu Hamad, 2013). The only previous reports indicating a possibly longer range from middle to late Permian (Stephenson & Powell, 2013, 2014) have recently been revised by the original authors in support of a late Permian age (Powell *et al.*, 2016, 2019). The overlying Ma'in Formation has been dated as Early Triassic with palynomorphs, foraminifera, conchostracans, and conodonts (e.g. Powell *et al.*, 2016, 2019; Scholze *et al.*, 2017). The lowermost fossiliferous beds near the base of the Nimra Member, c. 15 m above the top of the Umm Irna Formation, have been dated as mid–Induan (Powell *et al.*, 2019). The Umm Irna Formation exposed in Jordan can be correlated with the late Permian Arqov Formation in Israel (e.g. Eshet, 1990; Honigstein *et al.*, 2005; Orlova & Hirsch, 2005; Stephenson & Korngreen, 2020). Furthermore, the erosional basal unconformity of the overlying Ma'in Formation can, according to Powell *et al.* (2016), be correlated with the Arabian Plate transgression Tr 10 (Sharland *et al.*, 2001, 2004), coinciding with the supraregional Permian–Triassic boundary.

Plant macrofossils from the Umm Irna Formation were first mentioned by Bandel and Khoury (1981) in their description of the type section in Wadi Himara. Mustafa (2003) described a small flora of Cathaysian affinity with *Lobatannularia* and gigantopterids from a roadcut exposure along Highway 65 (Jordan Valley Highway). Abu Hamad (2004), Kerp *et al.* (2006) and Abu Hamad *et al.* (2008) described mummified leaves from the type section of the Umm Irna Formation in Wadi Himara with excellently preserved cuticles. In subsequent years additional plant–bearing localities in the Umm Irna Formation were found, which together yielded a very diverse flora, including the first occurrences of two other lineages of typical Mesozoic gymnosperms, the bennettitaleans and podocarpacean conifers (Blomenkemper *et al.*, 2018). Other groups present in the Umm Irna Formation include putative isoetaleans, sphenophytes, noeggerathialeans, marattialean ferns, taeniopterids, ginkgophytes, cycadophytes and various conifers, as well as a recently described enigmatic gymnosperm (Blomenkemper *et al.*, 2019). In the past 20

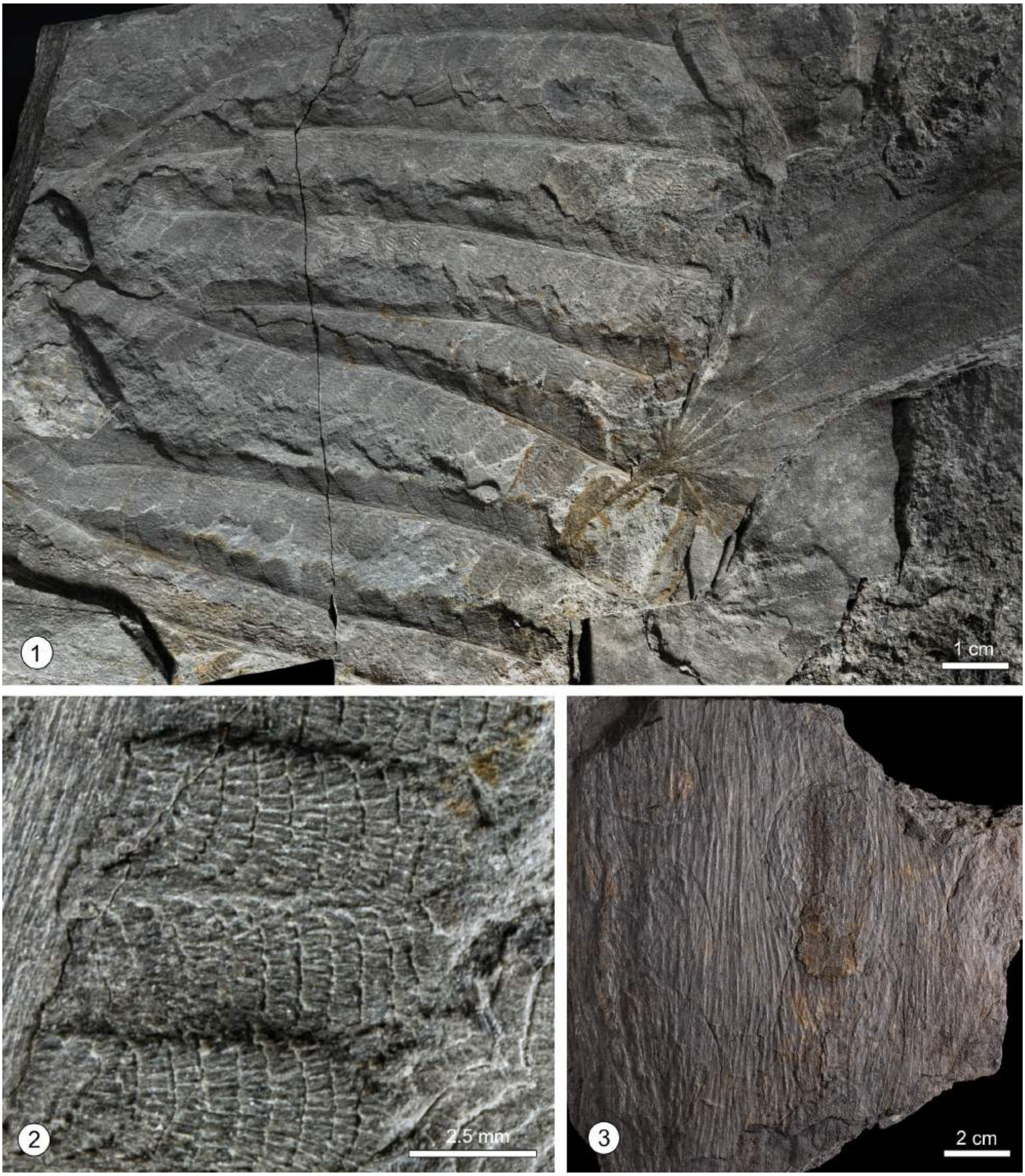


PLATE 3

Ferns from the late Permian Umm Irna Formation, Jordan.

1. *Qasimia schyfsmae* overlain by *Rhipidopsis brevicaulis*.
2. Detail of *Qasimia schyfsmae* showing the synangiae.
3. Portion of a *Caulopteris* sp. stem with leaf scars, partly overgrown by adventitious roots.

Table 1—Taxon list of the late Permian Umm Irna Formation (compiled after Abu Hamad *et al.*, 2008, 2017; Blomenkemper, 2020; Blomenkemper *et al.*, 2018, 2019, 2020, 2021).

Lycopsids
- *Isoetalean* corm and leaves

Sphenopsids
- *Calamites* sp.
- *Lobatannularia heianensis* (Kodaira, 1924) Kawasaki 1927
- *Lobatannularia spatulata* He 1986

Noeggerathiales
- *Discinites* cf. *orientalis* Gu & Zhi 1974
- *Discinites* sp.
- *Tingia* sp.

Ferns
- *Caulopteris* sp.
- *Pecopteris* cf. *arcuata* Halle 1927
- *Pecopteris* cf. *phegopteroides* (Feistmantel, 1878) Arber 1905
- *Pecopteris* sp.
- *Qasimia schyfsmae* (Lemoigne 1981) Hill *et al.* 1985
- *Gemellitheca* sp.

Lyginopteridales
- *Sphenopteris germanica* Weiss 1878

Nystroemiaceae
- *Saportaea salisburioides* Fontaine & White 1880
- *Nystroemia* sp.

Gigantopteridales
- *Gigantopteris nicotianaefolia* Schenk 1883
- *Gigantonoclea lagrelii* (Halle, 1927) Koidzumi 1936
- *Gigantonoclea* sp.

Glossopteridales
- *Glossopteris* cf. *formosa* Feistmantel 1881

Corystospermales
- *Dicroidium bandelii* Abu Hamad *et al.* 2017
- *Dicroidium hughesii* (Feistmantel, 1880) Lele 1962
- *Dicroidium irnense* Abu Hamad & Kerp 2008
- *Dicroidium jordanense* Abu Hamad & Kerp 2008
- *Dicroidium robustum* Kerp & Vörding 2008
- *Dicroidium* sp. A
- *Dicroidium* sp. B
- *Pteruchus frenguellii* Blomenkemper *et al.* 2020
- *Pteruchus lepidus* Blomenkemper *et al.* 2020
- *Pteruchus* sp.
- *Umkomasia aequatorialis* Blomenkemper *et al.*, 2020
- *Umkomasia* sp.

Cycadales
- *Ctenis* sp.
- *Doratophyllum jordanicus* Mustafa 2003
- *Plagiozamites* sp.
- *Pseudoctenis cornelii* Pott *et al.* 2007
- *Pseudoctenis* sp. 1
- *Pseudoctenis* sp. 2

Bennettitales
- *Pterophyllum pottii* Bomfleur & Kerp 2021
- *Nilssoniopteris jogiana* Blomenkemper & Abu Hamad 2021

Ginkgophytes
- *Sphenobaiera digitata* (Brongniart, 1828) Florin 1936
- *Sphenobaiera* sp.
- *Rhipidopsis brevicaulis* Kawasaki & Kon'no 1932
- *Rhipidopsis panii* Chow 1962

Conifers
- *Otovicia hypnoides* (Brongniart, 1828) Kerp *et al.* 1990
- *Elatocladus conferta* Halle 1913
- *Elatocladus* sp.
- *Rissikia* sp.
- *Quadrocladus* sp. 1
- *Quadrocladus* sp. 2
- *Ullmannia bronnii* Göppert 1850

Incertae sedis
- *Cryptokerpia sarlaccophora* Blomenkemper 2019
- *Taeniopteris multinervis* Weiss 1869
- *Taeniopteris* sp.

years a large collection of material comprising well over thousand specimens, including cuticle preparations, has been built up (Table 1). The number of taxa may, at first look, seem very high, but it should be noted that the Umm Irna Formation is characterized by rapid lateral and vertical facies changes and that each facies type is characterized by its own typical plant–fossil assemblage. Moreover, in some cases isolated parts of the same plant are described under different names.

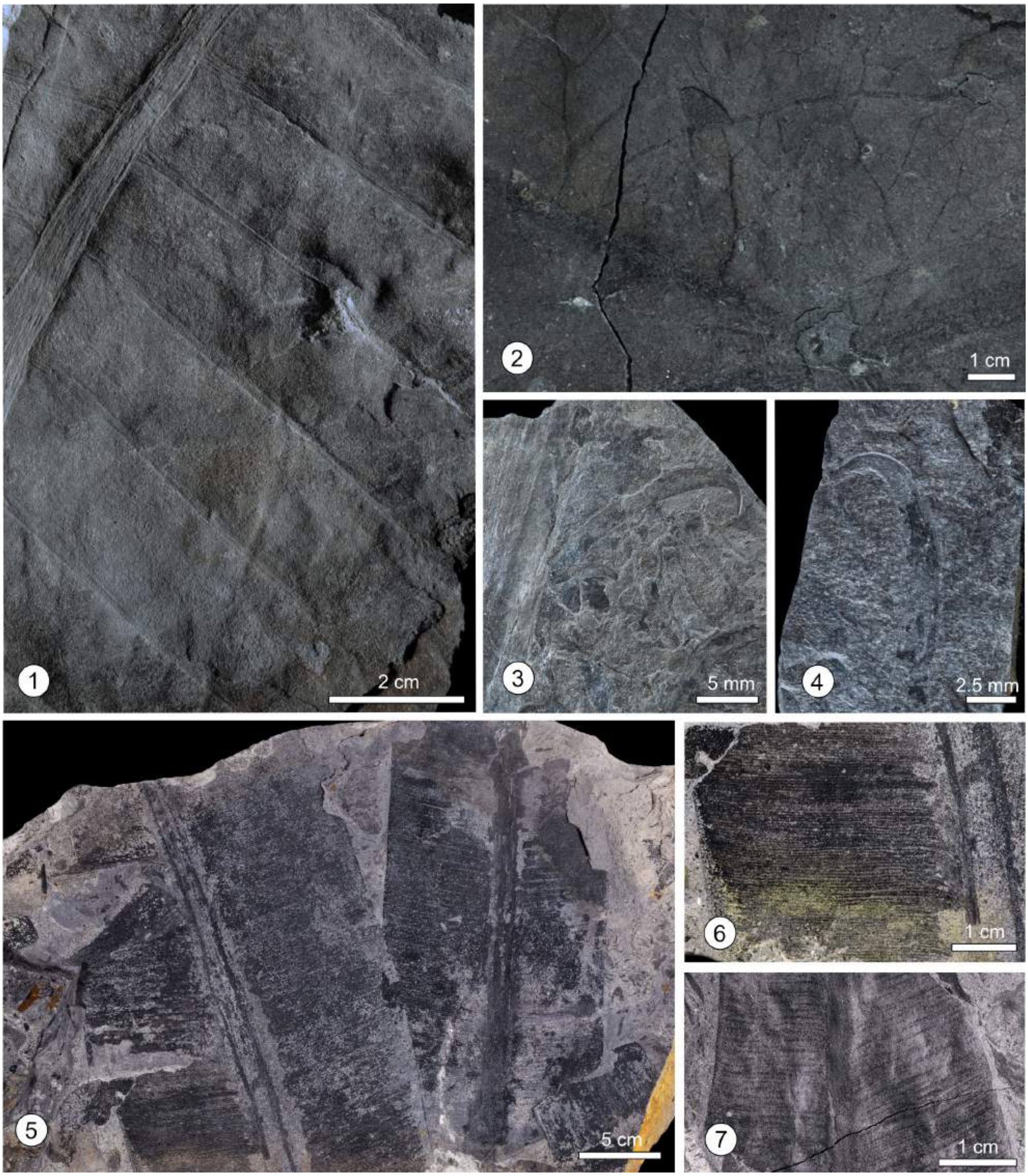


PLATE 4

Gigantopterids and *Taeniopteris* foliage from the late Permian Umm Irna Formation, Jordan.

1. Portion of a gigantopterid leaf.
2. Detail of *Gigantopteris nicotianaefolia* showing the venation pattern.

3–4. Gigantopterid climbing hooks.

5–6. *Taeniopteris multinervis*.

7. *Taeniopteris* sp.

THE FOSSIL FLORA OF THE UMM IRNA FORMATION

The fossil plant associations found in the outcrops of the Umm Irna Formation indicate habitats varying from permanently humid and swampy to dry. Altogether over 50 taxa are currently known from the Umm Irna Formation. This report is in many respects still preliminary. It presents the results of ongoing investigations. Some groups have already been studied in detail and results have been published, e.g. *Dicroidium* (Abu Hamad *et al.*, 2008, 2017; Blomenkemper *et al.*, 2020), the Bennettitales (Blomenkemper *et al.*, 2021), or the enigmatic *Saportaea* are currently in press (Kerp *et al.*, in press). Others, however, are still under investigation, e.g. conifers and cycads. Therefore, for a number of taxa identifications are at genus level only. Of conifers, only a number of distinct foliage types are illustrated. We expect that the diversity will further increase when cuticles and cones are studied in detail. Most of the material was collected during yearly fieldwork between 2015 and 2019. Collecting activities were interrupted by the Covid–19 pandemic, but we hope to go back in the field as soon as possible as some very promising localities have not been fully exploited. Nevertheless, we felt that a review of the late Permian flora of the Dead Sea is needed in order to clarify the importance of this flora, which comprises not only a mixture of elements from different floral provinces but also includes a number of typical Permian taxa combined with first occurrences of taxa so far only known from Mesozoic strata. The following paragraphs present a state–of–the–art review of the most important taxa from the Umm Irna Formation.

Sphenophytes

Calamitaleans occur in three localities of the Umm Irna Formation, but are overall rare. Two foliage types, *Lobatannularia heianensis* and *L. spatulata* (Pl. 1.4–5), have been recorded. Specimens are small and incomplete, yet well identifiable due to their characteristic shape. *Lobatannularia heianensis* has verticils with a broadly ovate outline, with leaves of unequal length, the ones directed to the foregoing whorls being shorter. In *L. spatulata* the individual leaves are fused forming wedge–shaped structures. Both species are common and widespread in Cathaysia. Further occurring are leafless *Calamites* stems (Pl. 1.1–3). Some of the ribs alternate at the nodes but others run through. Many of the ribs are conspicuously narrowed at the nodes but run through over the nodal lines (Pl. 1.3).

Lycopsids

Isoetaleans are known from a single locality only, where they are, however, very abundant (Pl. 2.1–2). A thin layer immediately underlying a bed with *Sphenobaiera digitata*, *Dicroidium irnense* and *Elatocladus conferta*, contains almost exclusively long, narrow, remarkably stiff leaves with a clear midvein that are similar to isoetalean leaves. The same layer also yielded several isoetalean corms (Pl. 2.1). Unfortunately, no organic material is preserved in this locality.

Noeggerathialeans

Several *Discinites* sporophylls were found in two different localities (Pl. 2.3–4). With their characteristic morphology they unmistakably represent members of the Noeggerathiales. However, noeggerathialean foliage is more difficult to identify. Isolated leaflets strongly reminiscent of *Tingia crassinervis* Halle 1927 were encountered (Pl. 2.5–6).

Ferns

Marattialean fern fronds (Pl. 3.1) were recorded from three localities, where they are abundant and co–occur with taeniopterids, sphenophytes, gigantopterids and *Rhipidopsis* (Pl. 3.1). In one locality, also a *Caulopteris* tree–fern stem was found (Pl. 3.3). Many of the fronds are fertile, and most of them can be preliminarily identified as a short–leaved form of *Qasimia* (Pl. 3.2). Others show synangia that are transversely oriented to pinna midribs, more reminiscent of *Gemellitheca* Wagner *et al.* 1985. In addition to fertile fronds, also various forms of sterile *Pecopteris* foliage are common in these assemblages.

Pteridosperms

Representatives of typical Paleozoic pteridosperm groups are extremely rare. One specimen of *Sphenopteris germanica* was found. Pollen organs supposed to belong to this type of foliage contain pollen with an ultrastructure typical for Lyginopteridales (Zavialova *et al.*, 2020). A systematic revision of *Sphenopteris germanica* is currently in press (DiMichele *et al.*, in press). Peltasperms, which are the most common seed ferns in Permian deposits in the Northern Hemisphere, are represented by just a single frond fragment with characteristic epidermal and cuticular features.

A few localities have yielded several types of gigantopterids (Pl. 4.1–4), a group typical for the Permian of Cathaysia. Although the preservation in the facies in which these leaf remains occur is rather meagre, at least one form could be identified as *Gigantopteris nicotianaefolia*. In additional to leaf remains, climber hooks (Pl. 4.1–4), as they also have been reported from China (Halle, 1927; Seyfullah *et al.*, 2014), were found in these same associations.

By far the most abundant and ubiquitous foliage type in the Umm Irna Formation is the corystosperm seed–fern frond *Dicroidium*. Gothan (1912) established the genus *Dicroidium* for pinnate to bipinnate fronds with a characteristic basal bifurcation and with odontopteroid or alethopteroid pinnules.

PLATE 5

Dicroidium fronds from the late Permian Umm Irna Formation, Jordan.

1. *Dicroidium robustum* frond with complete dichotomy of the frond axis.
2. *Dicroidium irnense*, almost complete frond with dichotomy of the frond axis.

3–4. *Dicroidium hughesii*.

4. detail of 3 showing the pinnules.

Based on frond architecture and pinnule morphology, some authors distinguish several additional frond genera, such as *Johnstonia* Walkom 1925, *Zuberia* Frenguelli 1943, *Diplasiophyllum* Frenguelli 1943, or *Xylopteris* Frenguelli 1943 (Petriella, 1979, 1981; Zamuner *et al*., 2001; D'Angelo *et al.,* 2011; Gnaedinger & Herbst, 2014; D'Angelo & Zodrow, 2018; D'Angelo, 2019; Martínez *et al*., 2020). Other authors regard some or all of these genera as synonyms of a more broadly defined genus *Dicroidium* (e.g. Townrow, 1957; Bonetti, 1966; Archangelsky, 1968; Anderson & Anderson, 1983; Abu Hamad *et al.,* 2008, 2017; Bomfleur & Kerp, 2010; Blomenkemper *et al*., 2020), which concept is also followed here. Five species of *Dicroidium–D. robustum* (Pl. 5.2)*, D. irnense* (Pl. 5.2; Pl. 6.1; Pl. 8.1–5)*, D. jordanense* (Pl. 7.1–5)*, D. bandelii* (Pl. 6.2)*, D. hughesii* (Pl. 5.3–4)– have been reported from the Umm Irna Formation (Abu Hamad *et al*., 2008, 2017; Blomenkemper *et al*., 2020; Pl. 5–8). The assignment of these fronds to *Dicroidium* based on morphology and epidermal architecture was, however, not universally accepted (e.g. Pattemore, 2016 a, b; Anderson *et al*., 2019a, b, c), given that the genus had before only been known from the Triassic of Gondwana (Anderson & Anderson, 1983; Anderson *et al*., 1999). Assignment to *Dicroidium* has gained further support with the recent description of the associated fertile organs. Two species of the pollen organ *Pteruchus*, *P. lepidus* and *P. frenguellii* (Pl. 6.4–7), and one species of the cupulate organ *Umkomasia* (Pl. 6.3) occur in the late Permian of Jordan (Blomenkemper *et al*., 2020). The former are both characterized by a long, strap–shaped lamina with abaxial, freely pending pollen sacs (Pl. 6.4–7); the latter is characterized by a delicate axis bearing at least three opposite pairs of cupules containing typical seeds with bifid micropyles (Pl. 6.3). Based on epidermal characteristics and co–occurrence data Blomenkemper *et al.* (2020) were also able to demonstrate that these organs were borne on specific *Dicroidium*–plants: *Pteruchus lepidus* and *Umkomasia aequatorialis* were produced by *Dicroidium robustum*–plants, whereas *P. frenguelli* was borne by *Dicroidium irnense*–plants. Altogether, these recent finds demonstrate that assignment of the foliage is fully justified. Finally, the presence of *Dicroidium hughesii* in Jordan, a taxon that was so far only known from the Triassic of Gondwana, is also the first evidence, that at least some Triassic species already occur in the latest Permian.

Conifers

At least six genera of conifers have been recorded from the Umm Irna Formation, including *Otovicia* (Pl. 9.1–2; Pl. 10.1), *Walchia, Quadrocladus* (Pl. 9.3–4; Pl. 10.1–2), *Ullmannia*, *Rissikia* (Pl. 10.4–6) and a *Podozamites*–like form (Pl. 10.3). In particular facies conifer remains are not rare, but–so far–*Elatocladus conferta* (Pl. 9.5–6) is the only species of which large specimens have been found. Of other species, only isolated twigs or very small branching systems were found. Most of the conifers are preserved with cuticles, except for *Elatocladus* that occurs in a single locality where no organic material is preserved. Apart from isolated twigs and a large number of isolated dwarf–shoots, many cones have been found, several of them still attached to twigs. First observations with the fluorescence microscope reveal that many male cones still contain *in situ* pollen. The conifers are currently under investigation and we expect to be able to provide more information in a forthcoming paper. Even though specimens are generally small, and detailed investigations are still ongoing, preliminary results show that that conifers were remarkably diverse and belong to several major groups. Noteworthy is that the association comprises forms typical for Euramerican Late Carboniferous–early Permian floras, like *Walchia* and *Otovicia*, genera well–known from upper Permian deposits the Northern Hemisphere, like *Ullmannia* and *Quadrocladus* (Pl. 9.3–4; Pl. 10.1–2), and taxa so far only described from Mesozoic strata, like *Rissikia*, a *Podozamites*–like conifer and *Elatocladus*.

The walchian conifer *Otovicia hypnoides* (Pl. 9.1–2; Pl. 10.1) from the uppermost part of the Umm Irna Formation exposed in the Dyke Plateau locality is the species with the longest stratigraphic range. The earliest *bona fide* records are from the middle and upper Stephanian of France (Langiaux, 1985) and the United States (e.g. Mapes & Rothwell, 1988). The species is common in the Cisuralian throughout Euramerica; and has also been reported from the Wordian of Oman (Berthelin *et al*., 2003). The occurrence of this small–leaved conifer in Jordan is the youngest that is known to date. The material consists of isolated twigs, small shoot systems, partly still attached pollen cones, and isolated dwarf shoots. The imbricate, mostly epistomatic leaves indicate drier habitats (Kerp *et al*., 1990). *Rissikia*, a *Podozamites*–like conifer and *Elatocladus* are three precocious taxa that have been described from Gondwana. These are the earliest records for these genera. Additionally, the find of isolated needles with well–preserved cuticles allowed the sound systematic placement of some of these remains into the Podocarpaceae, a family of conifers that is still living today (Blomenkemper *et al*., 2018).

Ginkgophytes

Ginkgophytes are regular components of the flora of the Umm Irna Formation. Most typical is *Sphenobaiera digitata* (Pl. 11.1), a well–known form from the lower Permian of Europe, which is also known from the European Zechstein. The genus *Sphenobaiera* has a very wide distribution and is known from both the Northern and Southern hemispheres. Also, smaller forms provisionally assignable to *Sphenobaiera* occur in Jordan. *Rhipidopsis* (Pl. 11.3–5) is a second type of foliage that is often assigned to the Ginkgoales, although no fructifications are known and compelling evidence is

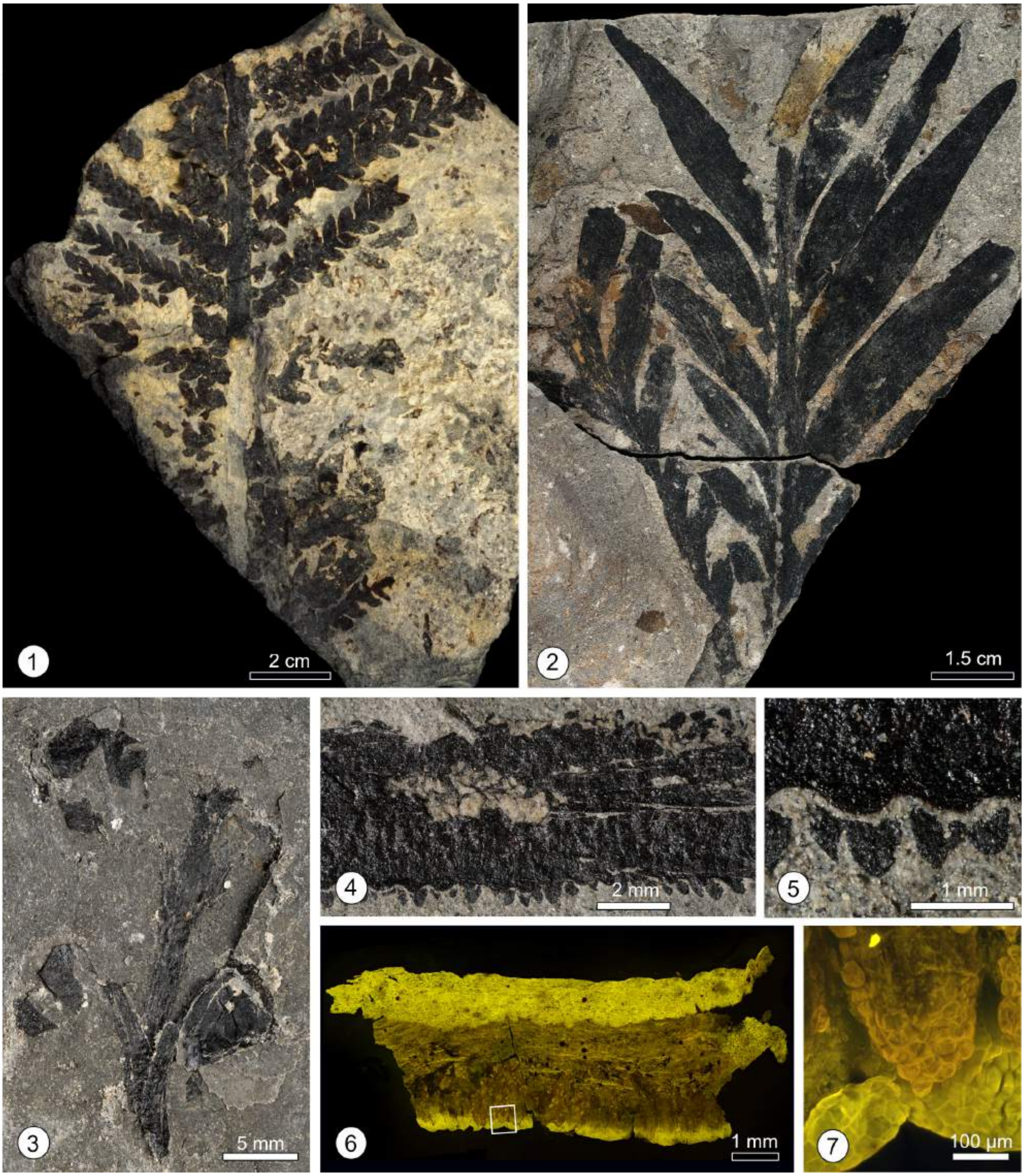


PLATE 6

Additional *Dicroidium* fronds and affiliated fertile organs from the late Permian Umm Irna Formation, Jordan.

1. *Dicroidium irnense*.
2. *Dicroidium bandelii*.
3. *Umkomasia aequatorialis*, note the remnants of cupules.

4–7. *Pteruchus lepidus*.

4. Detail of the sinuous lamina with protruding pollen sacs.
5. Detail of 4 showing the protruding pollen sacs below the lamina.
6. Epifluorescence picture of a dispersed fragment of *P. lepidus* with attached pollen sacs. White rectangle corresponds with 7.
7. Detail of 6 showing a pollen cluster of *in situ* bisaccate *Falcisporites* pollen.

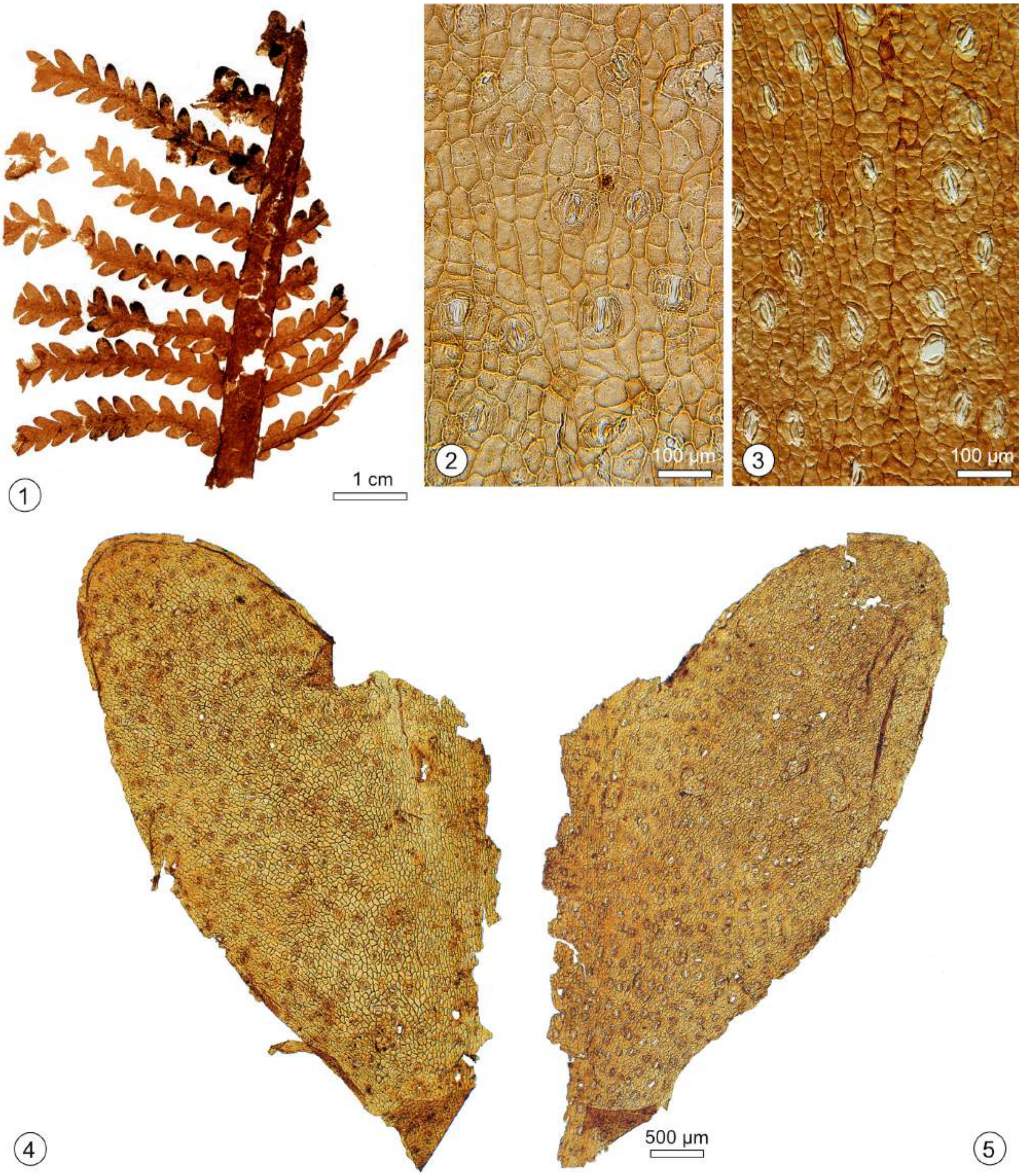


PLATE 7

Cuticles of *Dicroidium jordanense* from the late Permian Umm Irna Formation, Jordan.

1. Large frond fragment obtained by bulk maceration.
2. Detail of the upper surface.
3. Detail of the lower surface. Note the difference in stomatal density.
4. Upper surface of a complete pinnule.
5. Lower surface of a complete pinnule.

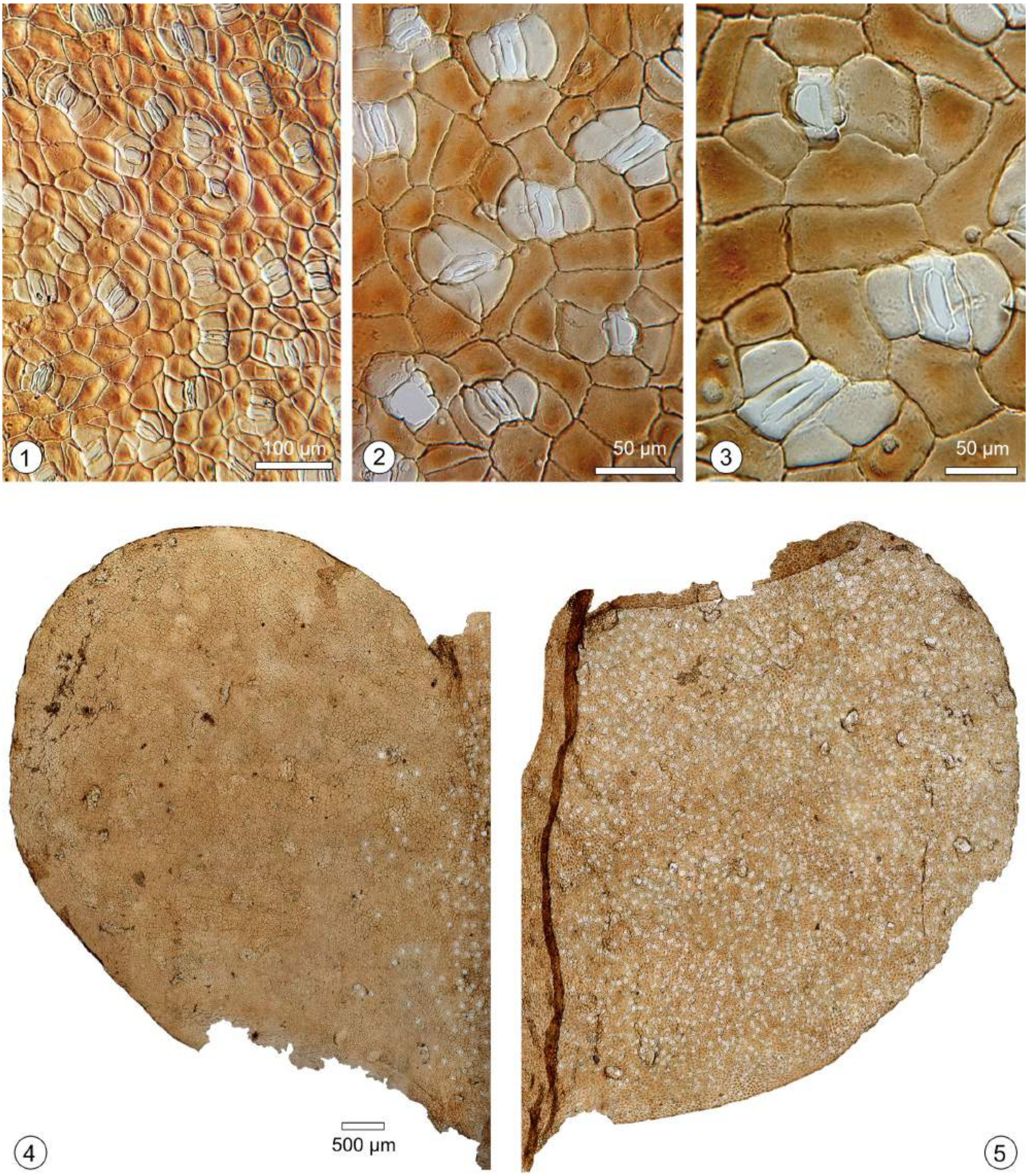


PLATE 8

Cuticles of *Dicroidium irnense* from the late Permian Umm Irna Formation, Jordan.

1–3. Overview of the lower leaf surface.
3–4. Detail of the lower surface showing the stomata.
4. Upper surface of a complete pinnule.
5. Lower surface of a complete pinnule.

missing. The genus *Rhipidopsis*, originally described by Schmalhausen (1879) from the Permian of Angara, has a very wide distribution. The two species reported here from Jordan, *R. brevicaulis* (Pl. 11.3–4) and *R. panii* (Pl. 11.5) were originally described from Cathaysia, where they appear to be quite common. Isolated leaf fragments consisting of (long), sometimes dichotomizing segments with parallel margins and a parallel venation are very difficult to identify without having information on the leaf architecture. In *Sphenobaiera* leaves are fan–shaped leaf without a real petiole, consisting of a series of repeatedly dichotomizing axes of more or less equal thickness. *Rhipidopsis* is a petiolate, palmate leaf with radiating lanceolate to oblong segments arising from a single point. *Saportaea* (Pl. 11.2), a genus that has also been found in the Umm Irna flora, is another taxon that has been assigned to the ginkgophytes, of which fragmentary remains can easily be confused with *Sphenobaiera*. *Saportaea* is a petiolate bipartite leaf with arcuate axes bearing either a broadly attached, reniform to flabellate lamina that may be incised into irregular segments, forms with regular parallel–margined elongate, bluntly ending segments that are fused only basally and sometimes dichotomize, and intermediate forms. All species have a well–developed parallel venation with veins that sometimes dichotomize. Recent finds in close association with ovule–bearing structures assignable to *Nystroemia* strongly suggest that *Saportaea* may belong to the gymnosperm family Nystroemiaceae (Kerp *et al.*, in press).

Cycads

Cycad–foliage, although occasionally preserved as large leaf fragment, is a rare component in the assemblages of the Umm Irna Formation and currently awaits formal description in an upcoming publication. At least two distinct types of foliage have been identified. Most common among these are simply segmented *Pseudoctenis*–like leaves (Pl. 12.1) with well–preserved cuticles (Pl. 12.2–4) that predominantly occur in the Dyke Plateau locality (see Fig. 1).

The second type has been assigned to *Ctenis* sp. (see Blomenkemper *et al.*, 2018) because of the overall elliptic to obtuse leaf morphology and anastomosing veins. Unfortunately, no specimens with well–preserved cuticles have been collected so far.

Bennettitales

Bennettitales are an iconic floral element of the Mesozoic and have often been affiliated with the so–called anthophyte clade or angiosperm precursors by some authors, partially due to their sophisticated method of reproduction (e.g. Friis *et al.*, 2007). However, due to strong morphological similarities with cycad foliage, sound systematic placement of sterile foliage without preserved cuticles has to be treated carefully.

From the upper Permian of Jordan, two distinct leaf type species, *Nilssoniopteris jogiana* and *Pterophyllum pottii* (Pl. 12.5–6), were recently formally described (Blomenkemper *et al.*, 2021). Both show syndetocheilic stomata that are diagnostic for the group. In addition to these, several types of dispersed cuticles from several localities, all showing syndetocheilic stomata, were described in the same publication (Pl. 12.7–9). Similar to cycads, Bennettitales are a rare element in these assemblages and only a few fragments of foliage with sufficiently well–preserved epidermal details have been collected. However, the presence of distinctive dispersed cuticles strongly indicates that the diversity of this peculiar plat group in the Paleozoic is underestimated and collection of additional material is needed.

Incertae sedis

Several species of *Taeniopteris* (Pl. 4.5–7) have been found. Most common is *Taeniopteris multinervis* (Pl. 4.5–6), a large broad–leaved taeniopterid. Taeniopterid foliage is known to have been produced by ferns, pteridosperms and cycads. Because in most cases we do not have cuticles and systematic affinities are unknown, this group is here classified under incertae sedis. Mustafa (2003) described a new species of *Doratophyllum*, *D. jordanicus*, and a reinvestigation of this species based on specimens with preserved cuticles is currently being carried out.

DISCUSSION

In several respects, the fossil flora of the Umm Irna Formation is remarkable and the combination of these makes this flora unique among late Permian floras:

- It is one of only very few highly diverse, latest Permian floras worldwide in a terrestrial facies;
- the flora contains–apart from some cosmopolitan taxa–a number of elements typical for either Euramerica, Cathaysia, or Gondwana;
- the flora includes some taxa of which the last occurrence appears to be (much) later than so far known. On the other hand, several other taxa recorded from the Umm Irna Formation were so far only known from the Mesozoic;
- eight localities with plant fossils have been found, representing several different facies types each with typical plant associations;
- Several of the localities have yielded material with excellently preserved cuticles.

Some of these points are briefly discussed below.

Highly diverse latest Permian floras are very rare worldwide (e.g. Bernardi *et al.*, 2017). The flora of the Umm Irna Formation comprises over 50 taxa (Table 1). However, it should be noted that the number of natural taxa is less, because different organs of the same plant may bear different

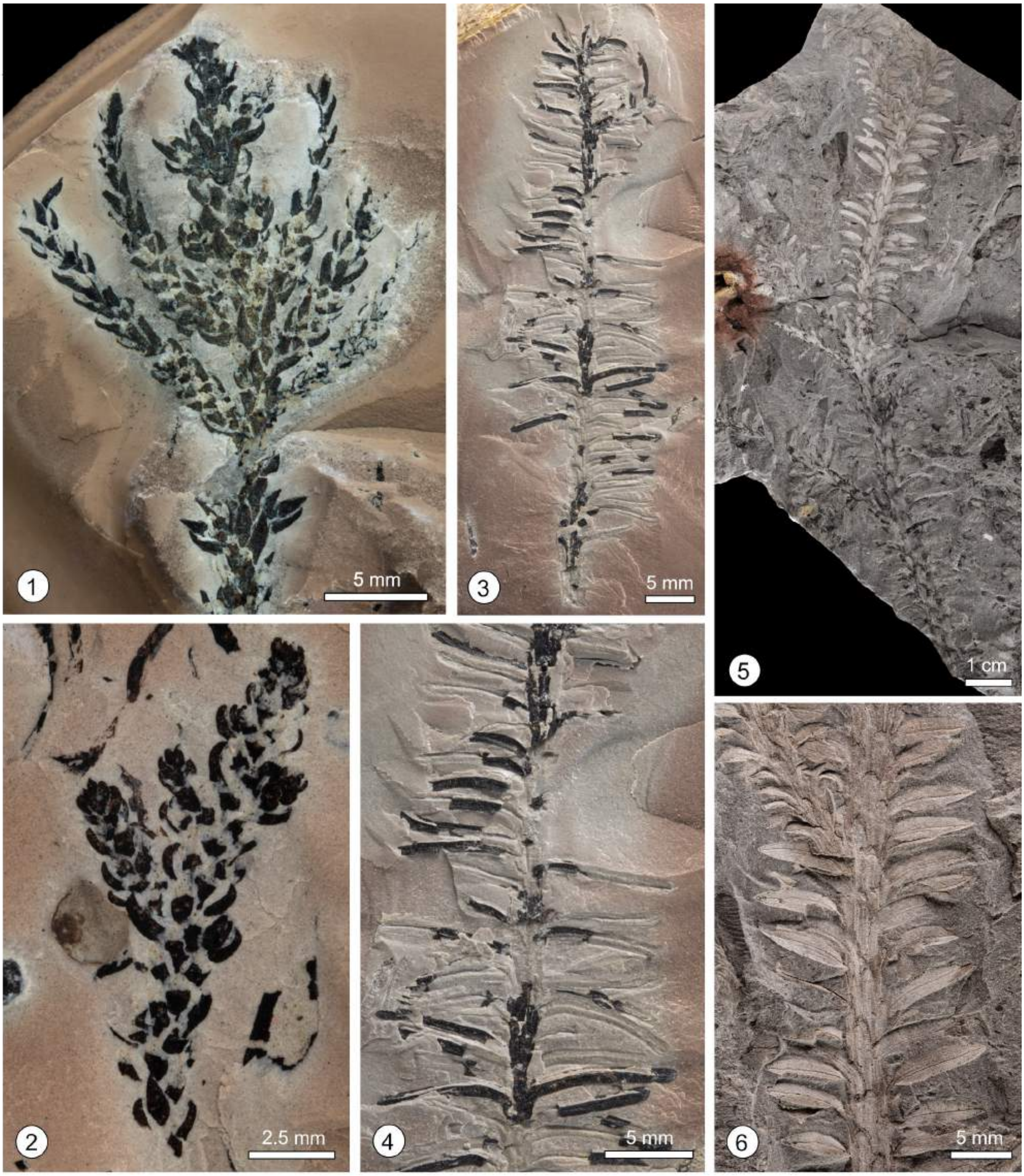


PLATE 9

Foliage fragments of conifers from the late Permian Umm Irna Formation, Jordan.

1–2. *Otovicia hypnoides*.
3–4. Long–leaved form of *Quadrocladus*.
4. Detail of 3.
5–6. *Elatocladus conferta*.
5. *E. conferta* showing the typical irregular branching.
6. Detail of *E. conferta* showing the prominent midvein of the leaves.

names. Nevertheless, the diversity is still high compared to the few other late Permian floras and we expect that detailed studies of particular groups that can be classified on the basis of cuticles and reproductive organs, such as conifers, will result in an even higher diversity.

The flora of the Umm Irna Formation is not only remarkable because of its high diversity but also with regard to the composition. It is a mixed flora that comprises taxa characteristic for different floral provinces, i.e. Euramerica, Cathaysia and Gondwana, and some cosmopolitan elements. This phenomenon alone is not exceptional, as several other Permian floras from the Near and Middle East comprise elements from two or more floral provinces (e.g. Wagner, 1962; Čtyroký, 1973; Berthelin *et al*., 2006a, b).

The Umm Irna Formation flora, however, also represents a peculiar mixture of taxa typical for different time periods. On one hand, it yields the last occurrences of several taxa so far only recorded from much older strata, so–called Lazarus taxa (Flessa & Jablonski, 1983; Jablonski, 1986). One example is *Otovicia hypnoides*, an easily identifiable walchian conifer of which foliage, pollen cones and ovuliferous dwarf–shoots have been found. *Otovicia* first appears in the latest Pennsylvanian and is common throughout the Cisuralian, and the last known occurrence recorded so far has been from the Wordian of Oman (Berthelin *et al.*, 2003). An additional example is *Sphenopteris germanica*, a species known from the uppermost Pennsylvanian and the lower Permian that co–occurs with a pollen organ of the *Schuetzia* type. A recent study of the *in situ* pollen demonstrated that the ultrastructure of the pollen wall is typical for Lyginopteridales (Zavialova *et al.*, 2020). *Sphenopteris germanica* has a long and complex taxonomic and nomenclatural history that is elucidated in an upcoming paper by DiMichele *et al.* It appears that this species is the last representative of the Lyginopteridales, a pteridosperm group that was very successful from the Mississippian to the Middle Pennsylvanian. Another remarkable taxon is *Saportaea salisburioides*, a type of gymnosperm foliage originally described from the latest Pennsylvanian of West Virginia and South–West Pennsylvania, U.S.A. (Fontaine & White, 1880). The material from Jordan is the second report of this particular species that appears to be long–ranging but very rare.

Other more common groups have one of their very late or even last occurrences in the Umm Irna Formation. The Gigantopteridales, a still enigmatic pteridosperm group from Cathaysia (e.g. Halle, 1927; Li & Yao, 1983; Yang *et al.*, 2006; Seyfullah *et al.*, 2014) and the southwestern United States (Mamay, 1986, 1988, 1989; DiMichele *et al.*, 2011) is often regarded as typical for the Permian, but some reports indicate that they may have persisted until the earliest Triassic (Chu *et al.*, 2016). The last representatives of the Noeggerathiales, a group of progymnosperms that first appeared in the Moscovian of Europe but is very typical for the Permian of Cathaysia, are here reported from Jordan.

It should be noted that peltasperms, the by far most common pteridosperms in Permian floras from the Northern Hemisphere (e.g. Gomankov & Meyen, 1986; Kerp, 1988; DiMichele *et al.*, 2005; Wang *et al.*, 2014) are almost completely missing in Jordan. Peltasperms evolved in the late Pennsylvanian in Euramerica and by the early Permian they had already spread over the entire Northern Hemisphere but they did not arrive in Gondwana until the Triassic (Retallack, 2002). Only a single specimen from the Umm Irna Formation that is currently still under investigation may possibly be assigned to this group.

On the other hand, a number of groups that are traditionally considered to be typical Mesozoic first appear in the Umm Irna Formation. One of the most common genera is the corystospermalean foliage *Dicroidium* of which five well–defined species have been described, some with fertile organs (Abu Hamad *et al.*, 2008, 2017; Blomenkemper *et al.*, 2020). One of these species, *D. hughesii*, is also known from the Triassic, whereas the other are so far only known from the upper Permian of Jordan. Among the conifers, forms like *Rissikia*, a *Podozamites*–like conifer, *Elatocladus* and isolated needles of Podocarpaceae can be classified as precocious appearances. Another typical Mesozoic group are the Bennettitaleans, a group that seemingly first appeared in the early Permian of China but is also present with two genera and six more types of dispersed cuticles (Blomenkemper *et al.*, 2018, 2021).

Not only is the precocious occurrence of these groups noteworthy in itself; also the high diversity within these groups, particularly the corystosperms and bennettitaleans, documents that these groups have an even earlier origin.

Several different facies types are recorded in the Umm Irna Formation, each yielding typical floral associations that range from wet–to more dry–adapted vegetation types. The mesic associations with abundant *Dicroidium* have yielded large to very large specimens including complete leaves that have been transported over very short distances only co–occurring with fertile organs, in some cases also with well–preserved cuticles. By contrast, the xeric vegetation dominated by conifers comprises mostly fragmentary specimens that have been transported over longer distance. A discussion of the different facies and floral associations is beyond the scope of this paper that intends to give a first systematic inventory of the fossil flora of the Umm Irna Formation. It is, however, already clear that the occurrences of precocious elements, so–called Methuselah taxa, are restricted to mesic and xeric vegetation types (Looy *et al.*, 2014), occurring in facies that generally have the lowest preservation potential.

Altogether, the Umm Irna Formation presents a unique window in vegetation types that are rarely preserved in the fossil record but is crucial for our understanding of plant evolution. Both the occurrences of representatives of rare but long–ranging taxa and the considerable diversity within the

PLATE 10

Conifer foliage and cuticles from the late Permian Umm Irna Formation, Jordan.

1. Small–leaved form of *Quadrocladus* sp. (Q) and *Otovicia hypnoides* (O).
2. Cuticle of *Quadrocladus* sp.
3. *Podozamites*–like conifer.

4–6. *Rissikia* sp.

6. Detail of a *Rissikia* sp. branch showing the leaves curved away from the axis and showing the basal torsion.

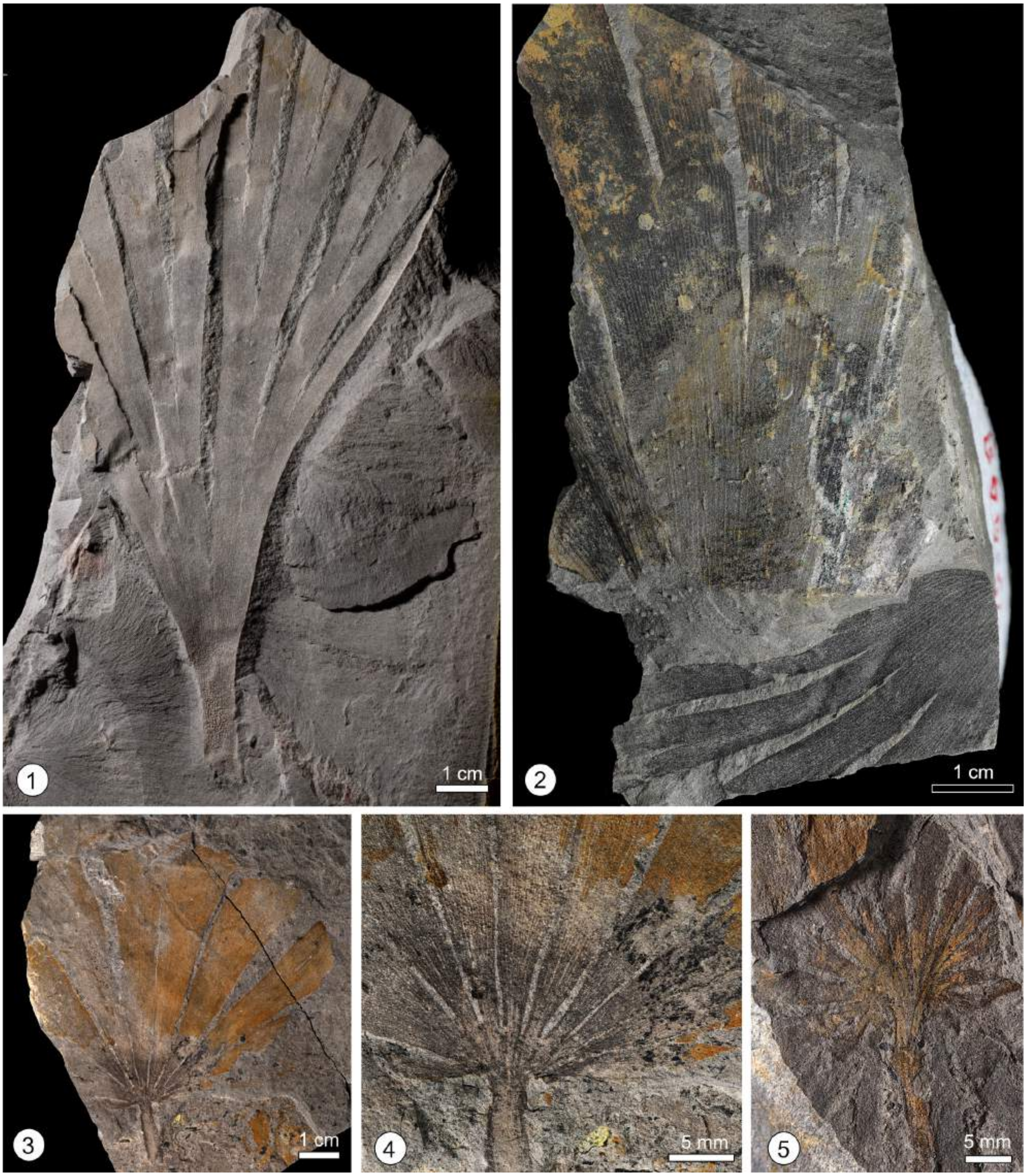


PLATE 11

Sphenobaiera, *Saportaea* and *Rhipidopsis* from the late Permian Umm Irna Formation, Jordan.

1. Nearly complete leaf of *Sphenobaiera digitata*.
2. Fragments of *Saportaea salisburioides*.
3–4. *Rhipidopsis brevicaulis.*
4. Detail of 3.
5. *Rhipidopsis panii*.

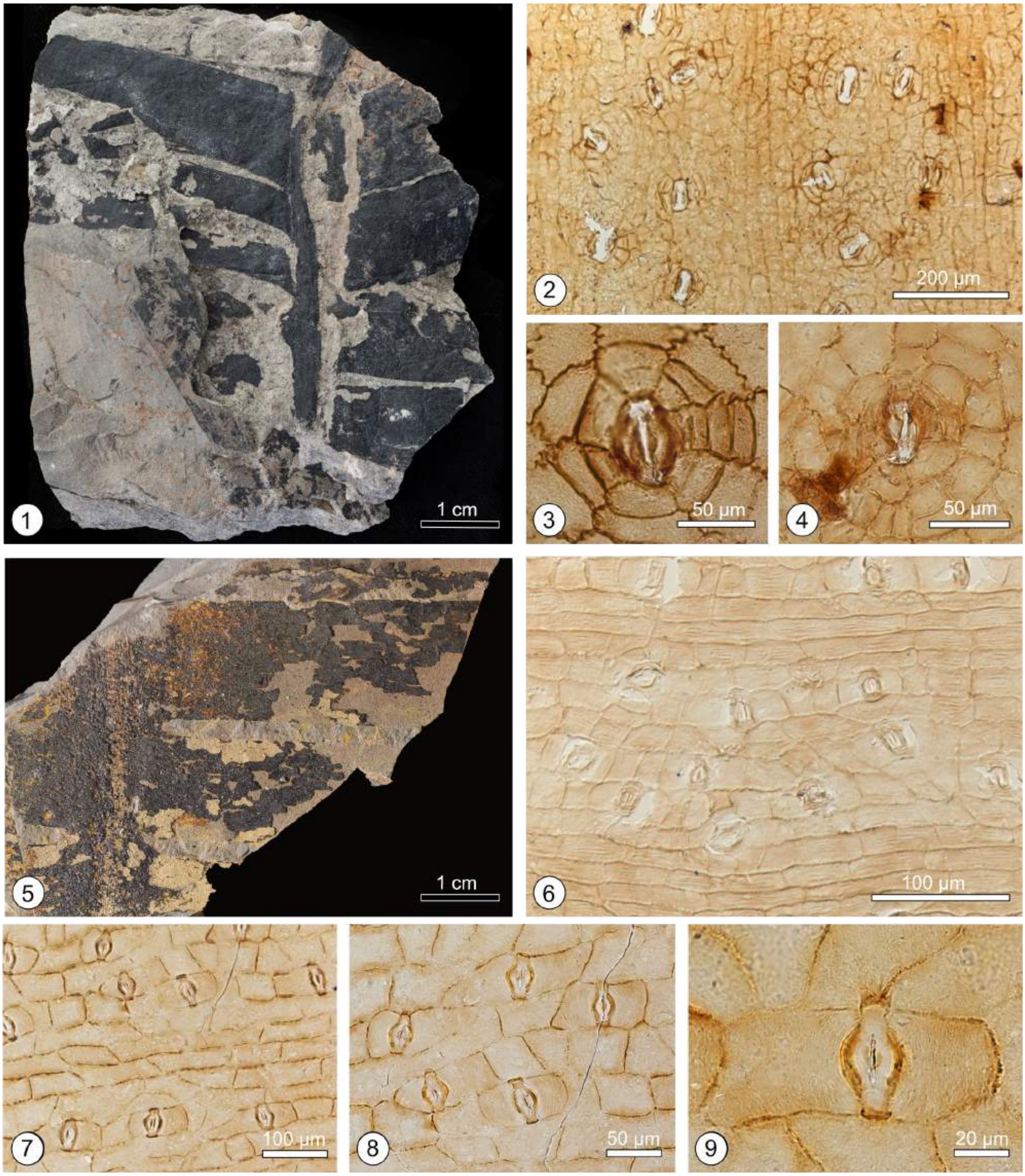


PLATE 12

Cycadophytes from the late Permian Umm Irna Formation, Jordan.

1. *Pseudoctenis* sp. 2
2–4. Cuticles of *Pseudoctenis* sp. 1.
2. Detail of the costal and intercostal fields of *Pseudoctenis* sp. 1.
3–4. Typical stomata of *Pseudoctenis* sp. 1.
5. *Pterophyllum pottii* a simply segmented bennettitalean leaf.
6. Lower surface of *P. pottii*. Note the distinct longitudinal striations on epidermal cells.
7–9. Bennettitalean cuticles obtained by bulk maceration.

more modern elements demonstrates that the terrestrial fossil record of plants is vastly incomplete.

Acknowledgements*—The authors wish to thank the University of Jordan (Amman) for support; Yahia S., Nidal S. and Haatem S. Badandi (Irbid, Jordan), Frank Scholze and Jörg W. Schneider (Freiberg, Germany), and Sebastian Voigt (Thallichtenberg, Germany) for field–work assistance. Funding: Financial support was provided by the German Science Foundation (DFG Emmy Noether grant BO3131/1–1 'Latitudinal Patterns in Plant Evolution' to B.B.; DFG grants KE584/11–1+2 and KE584/20–1 to H.K.). Abdalla Abu Hamad wishes to thank the DFG for his stay in Germany.*

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