

A Late Permian flora with *Dicroidium* from the Dead Sea region, Jordan

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Abstract

Three new species of *Dicroidium*, *D. irnensis*, *D. jordanensis* and *D. robustum*, are described from the Um Irna Formation (Upper Permian) of the Dead Sea region, Jordan. The plant remains are preserved as compressions with excellent cuticles. These are the earliest unequivocal records of *Dicroidium*, a genus that is typical for the Triassic of Gondwana. It is also the northernmost occurrence of this genus that apparently originated in the Permian in the palaeotropics. Middle and Late Permian floras from the Arabian Peninsula and adjacent regions show a remarkable mixture of elements from different floral provinces, i.e. Euramerica, Cathaysia and Gondwana. The climatic amelioration in the Early Triassic apparently enabled *Dicroidium* to migrate southward and eventually colonise the entire Gondwana region. *Dicroidium* is one of the very few megaplant genera not affected by the end-Permian biotic crisis, the largest Phanerozoic extinction event.

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1. Introduction

Palaeozoic floral provincialization began in the Early Carboniferous and reached its maximum in the Permian (DiMichele and Hook, 1992; Wnuk, 1996). Four distinct global floral provinces are recognised. These provinces are the southern Gondwanan Province, the northern Angaran Province, and the (sub) equatorial Euramerian and Cathaysian provinces, the latter two are sometimes regarded as a single province, the Amerosinian Province (Cleal and Wang Ziqiang, 2002). The Permian was a time of global climatic change with the transition from an icehouse to a greenhouse world. Atmospheric CO₂ concentrations are estimated to have reached about five times the present level (Berner, 2006a,b), although major fluctuations have been reported for the Permian (Montañez et al., 2007). The end-Permian extinction event, which affected marine and terrestrial floras and faunas, is often regarded as the most profound biotic crisis of the Phanerozoic (Erwin, 1993, 1999). Approximately

85% of the marine species disappeared (Erwin, 1999), and locally, 95% of peat-forming plants became extinct (Retallack, 1995; Michaelsen, 2002). However, it has been argued that in continental environments, the scale and timing of effects varied markedly between different regions (McLoughlin et al., 1997; Kozur, 1998; Rees, 2002). Several authors recognised a stepwise extinction pattern (e.g., Lindström and McLoughlin, 2007). Several plant groups became extinct across the Permian–Triassic boundary, whereas others, including most gymnosperms, suffered a marked decline in number of species. Only very few taxa, mainly lower vascular plants, survived the Permian–Triassic biotic crisis. Therefore, the recent discovery of an Upper Permian flora from the Dead Sea region in Jordan with abundant, well-preserved foliage assignable to the Southern Hemisphere pteridosperm genus *Dicroidium*, which is often regarded as typical for the Triassic of Gondwana (e.g., Anderson et al., 1999), is of particular interest. This flora, which is here called the Wadi Himara flora, has yielded several species of *Dicroidium*.

Two species occur abundantly and can be characterised on the basis of gross morphology, including the typical forked fronds,

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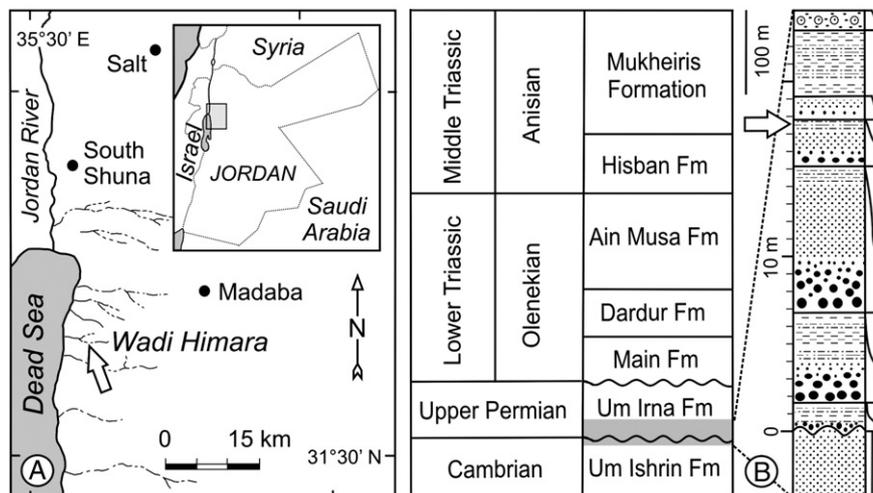


Fig. 1. A: Geographical position of the Wadi Himara locality (arrow). B: Stratigraphic subdivision of the Palaeozoic at the eastern side of the Dead Sea according to [Bandel and Khoury \(1981\)](#) with a schematic section of the lower part of the Um Irna Formation (right) and the position of the plant-bearing bed (arrow).

and cuticles. These two species are new and have provisionally been referred to as *Dicroidium* sp. A and *D.* sp. B ([Kerp et al., 2006](#)). They are formally described here as *Dicroidium jordanensis* and *D. irnensis*. A few frond fragments and several isolated pinnae of a third, much rarer species have been found. The pinnules of this species are morphologically most similar to those of *D. irnensis*, but they are much larger. The epidermal anatomy justifies its assignment to *Dicroidium*, but cuticles of this species clearly differ from those of other *Dicroidium* species. Even though we do not have complete fronds of this third form, it is here described as a new species: *Dicroidium robustum*. In addition, another form is informally described and illustrated as *Dicroidium* sp. Although this form clearly differs from the other three, we refrain from formally establishing a new taxon, because we feel that more material is needed.

The *Dicroidium* species from the Wadi Himara flora from the Late Permian Um Irna Formation in the Dead Sea region not only represent the earliest record of *Dicroidium*, but also by far the most northern occurrence of a taxon that became highly successful in the Middle and Late Triassic. These finds shed new light on the early history and distribution of the corystosperms, a group of seed ferns that has long been regarded as a typical Mesozoic group of pteridosperms.

This paper presents the description of the *Dicroidium* species from the Wadi Himara flora, based on macromorphology and on cuticles. Because of the excellent preservation it is possible to illustrate both the upper and lower surfaces of entire pinnules of two of the three species, showing every single cell. Such pinnules give important information on cell patterns and the distribution and density of stomata. However, these aspects will not be dealt with in this paper but the results of these investigations will be published separately. The Um Irna Formation has also yielded a well-preserved microflora that will also be described separately. The plant-bearing beds are also rich in charcoal. Two different types have been described, one of them could possibly belong to *Dicroidium* ([Uhl et al., 2007](#)).

In addition to *Dicroidium*, a small fragment of a taeniopterid leaf, identified as *Doratophyllum jordanicus* Mustafa, has been

found. It is just a small fragment, but with excellent cuticle. [Mustafa \(2003\)](#) originally illustrated a few, rather small cuticle fragments and he did not give a detailed description. We here describe and illustrate the cuticles of *D. jordanicus* in more detail.

2. Locality and source strata

The material was collected from a natural exposure in the lower part of the Um Irna Formation¹ at the northeastern rim of the Dead Sea, Jordan. The locality is situated at c. 2 km east from the main road that runs along the eastern shore of the Dead Sea, in the incised dry river valley named Wadi Himara. The outcrops of the Um Irna Formation are located c. 400 m upstream along the southern branch after the main bifurcation of Wadi Himara at 31° 37' 55.67" N and 35° 37' 15.69" E ([Fig. 1A](#)).

The Um Irna Formation was originally defined by [Bandel and Khoury \(1981\)](#) in Wadi Himara. In the type section from which the material described here was collected, the Um Irna Formation reaches a thickness of 67 m and unconformably overlies the Cambrian Um Ishrin Sandstone Formation. The Um Irna Formation is unconformably overlain by the Ma'in Formation but the two formations are separated by an erosional surface. The entire Um Irna Formation is developed in a continental facies. From the bottom to the top six sequences can be recognised, each beginning with a sandstone layer. [Makhlouf et al. \(1991\)](#) distinguished two sedimentary facies in the Um Irna Formation. The Lower Member (Facies 1) has a thickness of ca. 10 m and consists of sandstone and silty shale layers and lenses arranged in fining upward sequences. This facies, which corresponds with the first sequence of [Bandel and Khoury \(1981\)](#), has been interpreted as a distal braided fluvial deposit. The finer units sometimes show desiccation cracks indicating

¹ The name of this formation is sometimes spelled as Umm Irna Formation. Because the formation was originally described as Um Irna Formation, this spelling is retained here.

Plate I. *Dicroidium irnensis* nov. sp. Holotype. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 90)

1. Frond portion showing the bifurcation. Scale bar = 1 cm. Coll. No. PbO UmIr 3.

Plate II. *Dicroidium irnensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 91)

1. Portion of a frond with tongue-shaped pinna apices. Scale bar = 1 cm. Coll. No. PbO UmIr 4.
2. Portion of a frond showing the bifurcation. Scale bar = 1 cm. Coll. No. PbO UmIr 2.
3. Portion of a pinna faintly showing the venation. Scale bar = 5 mm. Coll. PbO UmIr 50.
4. Detail of Fig. 3. Scale bar = 2 mm.

Plate III. *Dicroidium irnensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 92)

- 1A–I. Macerated pinna apices showing the tongue-shaped terminal pinnules. A = Slide No. PbO LC1; B = Slide No. PbO LC2; C = Slide No. PbO LC3; D = Slide No. PbO LC4; E = Slide No. PbO LC5; F = Slide No. PbO LC1; G = Slide No. PbO LC6; H = Slide No. PbO LC7; J = Slide No. PbO LC8. Scale bar for A–I = 5 mm.
2. Detail of Fig. 1B faintly showing the venation. Scale bar = 5 mm.
- 3A–B. Upper (A = Slide No. LCU 21) and lower surface (B = Slide No. LCL 21) of a pinna apex showing stomata over the pinna rachis on the upper side and stomata on the pinnules lamina on the lower surface. Scale bar = 2 mm.

Plate IV. *Dicroidium irnensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 93)

- 1 + 4. Macerated pinnules showing the distribution of stomata within a single pinnule; rectangles indicate details shown of Figs. 2 and 3. 1 = Slide No. S11U; 2 = Slide No. S11L. Scale bars = 1 mm.
2. Detail of the cuticle of the upper pinnule surface of Fig. 1 showing the basal part of the pinnule with a few scattered stomata. Scale bar = 100 μ m.
3. Detail of the cuticle of the lower pinnule surface with very few stomata near the rachis (right) and abundant stomata on the rest of the pinnule surface. Same scale as Fig. 3.

Plate V. *Dicroidium irnensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 94)

Cuticle of the upper pinnules surface of a complete pinnule showing the distribution and orientation of the stomata. Slide No. UmIr201U+L. Scale bar = 500 μ m.

Plate VI. *Dicroidium irnensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 95)

Cuticle of the the lower pinnules surface of a complete pinnule showing the distribution and orientation of the stomata. Slide No. UmIr201U+L. Scale bar = 500 μ m.

Plate VII. *Dicroidium irnensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 96)

1. Cuticle of the lower surface showing the random distribution and orientation of the stomata. Slide No. UmIr201U+L Scale bar = 100 μ m.
2. Detail of the same specimen cuticle showing various types of stomata on the lower pinnule surface: the common type with two weakly cutinised lateral subsidiary cells and the rarer type with five normally cutinised subsidiary cells. Scale bar = 50 μ m.
3. Detail of the same specimen as in Fig. 1 showing various types of stomata of the lower pinnule surface. Scale bar = 50 μ m.

Plate VIII. *Dicroidium jordanensis* nov. sp. Holotype. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 97)

1. Most complete specimen showing the basal dichotomy of the frond. Because cuticles lift off very easily, part of the right side of the frond is missing. Coll. No. PbO UmIr 66. Scale bar = 1 cm.

Plate IX. *Dicroidium jordanensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 98)

1. Portion of a pinna showing the typical asymmetric pinnules. Coll. No. P/O 0152. Scale bar = 5 mm.
2. Basal part of a frond with the dichotomy of the frond rachis. Coll. No. PbO UmIr 8. Scale bar = 1 cm.
3. Portion of the right side of a frond. Note the shorter pinnae on the interior side of the frond (left). Coll. No. PbO UmIr 6. Scale bar = 1 cm.
4. Pinna apex showing the relatively small terminal pinnule and the strongly asymmetrical apical pinnules. Coll. No. PbO S38. Scale bar = 1 cm.

Plate X. *Dicroidium jordanensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 99)

1. Portion of a frond a frond in cuticular preservation. Slide No. PbO LC 20. Scale bar = 1 cm.
2. Portion of a pinna. Slide No. P/O 152. Scale bar = 5 mm.
- 3–8. Pinna apices showing the narrow, strongly asymmetrical pinnules and the slender terminal pinnules. 3: Slide No. PbO LC 14; 4: Slide No. PbO LC 13; 5: Slide No. PbO LC 12; 6: Slide No. PbO LC 14; 7: Slide No. PbO LC 11; 8: Slide No. No. PbO LC 16. All pinna apices at same magnification. Scale bar for all specimens = 5 mm.

Plate XI. *Dicroidium jordanensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 100)

Cuticle of the upper pinnules surface (Slide No. S31U/003b) of a complete pinnule from the lower to middle part of a pinna, showing the distribution and orientation of the stomata. Scale bar = 500 μ m.

Plate XII. *Dicroidium jordanensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 101)

Cuticle of the lower pinnules surface (Slide No. S7L/0007a) of a complete pinnule from the lower to middle part of a pinna, showing the distribution and orientation of the stomata.

Plate XIII. *Dicroidium jordanensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 102)

Cuticle of the upper pinnules surface (Plate XI; Slide S31U/0002b) of a complete pinnule from the apical part of a pinna, showing the distribution and orientation of the stomata. Scale bar = 500 μ m.

Plate XIV. *Dicroidium jordanensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 103)

Cuticle of the lower pinnules surface (Plate XII; Slide S31L/0002a.) of a complete pinnule from the apical part of a pinna, showing the distribution and orientation of the stomata.

Plate XV. *Dicroidium jordanensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 104)

1. Cuticle of the upper pinnule surface. Slide No. S31U/0003b. Scale bar = 100 μ m.
2. Cuticle of the lower surface of the same pinnule as Fig. 1 at the same magnification. Slide No. S31U/0003a. Scale bar = 100 μ m.
3. Cuticle of the lower pinnule surface with stomata. Slide No. B3L 0125. Scale bar = 100 μ m.

Plate XVI. *Dicroidium jordanensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 105)

1. Cuticle of the upper pinnule surface without papillae but with thickenings on the subsidiary cells. Slide XXX. Scale bar = 100 μ m.
2. Three stomata of the upper pinnule surface with prominent thickenings on subsidiary cells. Slide No. S31U/0115. Scale bar = 50 μ m.
- 3–4. Stomata of the upper leaf surface. Slide No. S8U/0006b. Scale bars = 50 μ m.
- 5–8. Stomata of the upper leaf surface: 6. Arrow = faintly visible wood lamellae; 8 = Stomatal complex without thickenings of the subsidiary cells. 5: Slide No. S31U/0115; 6: Slide No. S31U/0115; 7: Slide No. S31U/0115; 8: Slide No. S31U/007b. All scale bars = 25 μ m.
9. Sunken stomatal apparatus with very weakly cutinised subsidiary cells and guard cells. Slide No. S31UL/0109. Scale bar = 25 μ m.

Plate XVII. *Dicroidium jordanensis* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 106)

1. Cuticle of the upper pinnule surface with papillae. Slide No. S31UL/0109. Scale bar = 100 μ m.
2. Cuticle of the upper pinnule surface with papillae and a trichome (arrow). Slide No. S31UL/0109. Scale bar = 100 μ m.
3. Cuticle of the upper pinnule surface with two stomata and papillae. Slide No. S31UL/0109. Scale bar = 50 μ m.
4. Trichome base on the upper pinnule surface consisting of a number of radially arranged cells; the cells walls in the centre of the structure are thickened. Slide No. S31UL/0109. Scale bar = 50 μ m.
5. Trichome on the upper pinnule surface of which the uppermost part is apparently missing. Slide No. S31UL/0109. Scale bar = 25 μ m.
6. Complete trichome on the upper pinnule surface. Slide No. S31UL/0109. Scale bar = 50 μ m.
7. Cuticle of the upper pinnule surface with a stomatal apparatus and papillae. Slide No. S31UL/0109. Scale bar = 25 μ m.
8. Short, hollow papillae of the upper pinnule surface in sideview. Slide No. S31UL/0109. Scale bar = 25 μ m.
9. Cuticle of the upper pinnule surface with papillae. Note the radiating striae on the periclinal wall (arrow). Slide No. S31UL/0109. Scale bar = 25 μ m.
10. Cuticle of the upper pinnule surface with papillae and a trichome (arrow). Slide No. S31UL/0109. Scale bar = 25 μ m.

Plate XVIII. *Dicroidium jordanensis* nov. sp. (1–6, 8–9) and *D. irnensis* nov. sp. (7). Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 107)

1. Cuticle of the lower pinnule surface; overview with trichome (arrow). Slide No. UmIr 202L. Scale bar = 100 μ m.
2. Stomata on the lower pinnule surface. Slide No. UmIr 202L. Scale bar = 50 μ m.
3. Detail of Fig. 1: cuticle of the lower pinnule surface with stomata and a trichome. Scale bar = 50 μ m.
4. Cuticle of the lower pinnule surface with two stomata with different numbers of subsidiary cells. Slide XXX. Scale bar = 50 μ m.
5. Stoma on the lower pinnule surface. Slide No. UmIr 202L. Scale bar = 50 μ m.
6. Detail of Fig. 3 showing a trichome. Scale bar = 25 μ m.
7. A trichome of the lower pinnule surface of *Dicroidium irnensis*. Slide No. SU 141U+L/0001. Scale bar = 25 μ m.
- 8–9. Stomata on the lower pinnule surface. Slide No. UmIr 202L. Scale bars = 50 μ m.

Plate XIX. *Dicroidium robustum* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 108)

1. Holotype showing two axes with interior pinnules (lower half of the specimen) and fragments of larger pinnae (top). Coll. No. PbO S103. Scale bar = 1 cm.
2. Isolated pinna terminal. Coll. No. PbO S104. Scale bar = 1 cm.
- 3 + 4. Cuticle of a pinna portion from the same slab as the holotype. 3 = upper surface; 4 = lower surface. Slides No. S150U/001 and S150L/001. Scale bar = 1 cm.

Plate XX. *Dicroidium robustum* nov. sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan. (see page 109)

1. Cuticle of the upper pinnule surface. Slide S150U/001. Scale bar = 250 μ m.
2. Cuticle of the lower pinnule surface of the same specimen as Fig. 1. Slide S150L/001. Scale bar = 250 μ m.

periodic drying out of the depositional surface. The Upper Member of Makhlof et al. (1991) (Facies 2) consists of sandstone, silty sandstone and silty shale layers and comprises five fining upward sequences. These sediments show characteristics of both meandering and braided stream deposits; the environment is interpreted as a braided river in which deposition was largely controlled by periodic shifts of the active channel tracts (Makhlof et al., 1991). The silty layers were deposited in abandoned channels. In the entire Um Irna Formation, but especially in the middle and upper part, several palaeosols with ferruginous pisoliths (“iron-rich glaebules” *sensu* Makhlof et al., 1991) are developed. These palaeosols increase in thickness towards the top of the formation.

Dispersed plant cuticles occasionally occur in the organic- and sulphur-rich siltstones of the Lower Member. The plant remains described here from the Wadi Himara locality occur in organic-rich, grey to brownish silt and clay layers and lenses between 15.5 and 16.5 m above the base of the formation (Fig. 1B). Most of these beds yield numerous small cuticle fragments, but also larger specimens were found. In one layer plants remains are very abundant, and up to 25 cm long frond segments have been found. Apart from cuticles this layer has also yielded abundant charcoalfied wood remains (Uhl et al., 2007). In its type locality in Wadi Himara the uppermost part of the Um Irna Formation mainly consists of sandy deposits.

Although plant megafossils are abundant at the Wadi Himara locality, species diversity is low. The flora consists of three species of *Dicroidium*, which are formally described here. In addition, bulk macerations have yielded another, maybe two *Dicroidium* species. Because these are just isolated pinnules, they will not be described here in detail. A small fragment of *Doratophyllum jordanicus* Mustafa, a type of taeniopterid foliage, has been found. Although the specimen is too small to show the gross morphology, identification was possible because of the excellent preservation of the cuticles. Because these show much more detail than the specimens described by Mustafa (2003) they are described and illustrated here. The flora furthermore contains a few poorly preserved, unidentifiable axes and fern remains (cf. *Pecopteris*).

Bandel and Khoury (1981) attributed a Late Permian age to the Um Irna Formation on the basis of a preliminary analysis of the microflora. Also Makhlof et al. (1991) considered the Um Irna Formation to be Late Permian in age. A recent palynological study of the Um Irna Formation in its type section confirms a Late Permian age (Abu Hamad, 2004). The plant-bearing interval has yielded a rich and well-preserved microflora with *Lueckisporites virkkiae* Potonié et Klaus, *Klausipollenites schaubergeri* Potonié et Klaus and *Protohaploxylinus limpidus* (Balme et Hennelly) Hart. The palynological assem-

blages are dominated by bisaccate pollen grains, mainly various species of *Falcisporites* Leschik, including *F. zapfei* (Potonié et Klaus) Leschik and *F. stabilis* (de Jersey) Balme, which together may constitute over 50% of the associations. The high abundance of *Falcisporites* may at first glance seem unusual for the Upper Permian, but can easily be explained by the fact that this pollen type was produced by the pteridosperm *Dicroidium* (Balme, 1995), which is the most abundant megafloreal element in these beds. The Um Irna Formation is the terrestrial lateral equivalent of the Arqov Formation which has been deposited in a coastal marine environment (Weissbrod, 2005). The Arqov Formation is well dated as Late Permian with palynomorphs (e.g., Eshet and Cousminer, 1986; Eshet, 1990, 1992; Sandler et al., 2006) and foraminifera (e.g., Buchbinder et al., 1998; Orlov-Labkovsky, 2004).

Mustafa (2003) described a small megaflorea from an outcrop in the upper part of the Um Irna Formation near the main road along the eastern shore of the Dead Sea, at only a few kilometres from the Wadi Himara locality. This flora is dominated by *Doratophyllum jordanicus* Mustafa. Another common taxon is *Lobatannularia heianesis* (Kodaira) Kawasaki. Rarer elements are *Gigantonoclea* sp. and *Pecopteris* sp. *Lobatannularia* and *Gigantonoclea* are both typical Late Permian genera and became extinct at the Permian–Triassic boundary (Anderson et al., 1999). Unfortunately, samples from this latter locality did not yield identifiable palynomorphs.

The basal part of the unconformably overlying Ma'in Formation (Himara Member) has been dated as (?early) Scythian on the basis of poor palynological assemblages (Shawabekeh, 1998; Abu Hamad, 2004), and the second member of the Ma'in Formation has been dated as middle to late Scythian on the basis of bivalves (Cox, 1932) and conodonts (Huckriede and Stoppel, in Bender, 1968).

3. Materials and methods

The plant material from the Wadi Himara locality consists of mummified leaves and compressions with excellent cuticles, occurring in dull brownish to grey-black organic- and sulphur-rich silt- and claystones. Plant megafossils are abundant in the shaley and silty layers in the lower part of the Um Irna Formation, but only very few species have been recorded. One layer is extremely rich in cuticles. Complete pinnae are not rare. Bulk macerations of this cuticle-rich layer revealed that the vast majority of these cuticles belong to *Dicroidium*; few other taxa have been found among the dispersed cuticles, i.e., a few poorly preserved cuticles, most probably conifers. Most common are two new, here described species of *Dicroidium* [*D. irmensis* (Plates I–VII) and *D. jordanensis* (Plates VIII–XVII; Plate XVIII, 1–5, 7–9)], both

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3. Cuticle of the upper pinnule surface with randomly oriented stomata. Note the strongly cutinised ledges of the guard cells which are still present, even when the guard cells have disappeared. Slide S101U/001A. Scale bar = 100 µm.
 4. Detail of the cuticle of the upper pinnule surface with stomata. Note the very thin anticlinal walls. Slide S101U/001A. Scale bar = 100 µm.
 5. Stomata of the upper pinnule surface. Note that the lateral neighbouring cells are slightly weaker cutinised than the normal epidermal cells and often longer than the guard cells, thus giving the stomata a butterfly-like appearance. Wood lamellae are faintly visible. Slide S101U/001A. Scale bar = 50 µm.
 - 6 + 7. Stomata of the upper pinnule surface. Note the strongly cutinised ledges on the guard cells and the well-developed wood lamellae, especially in Fig. 7. Slide No. S101U/001A. Scale bar = 25 µm.



Plate 1 (see caption on page 87).

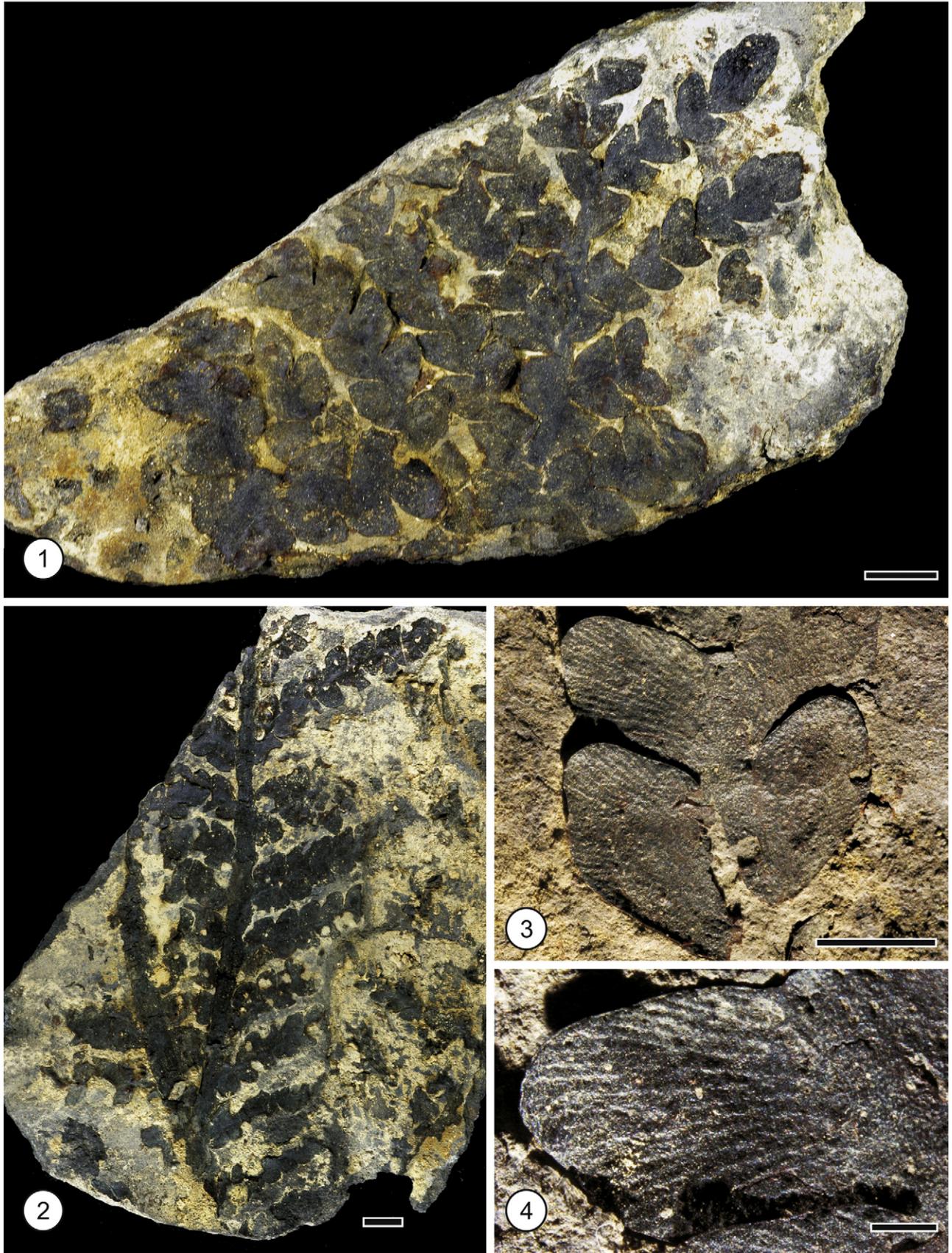


Plate II (see caption on page 87).

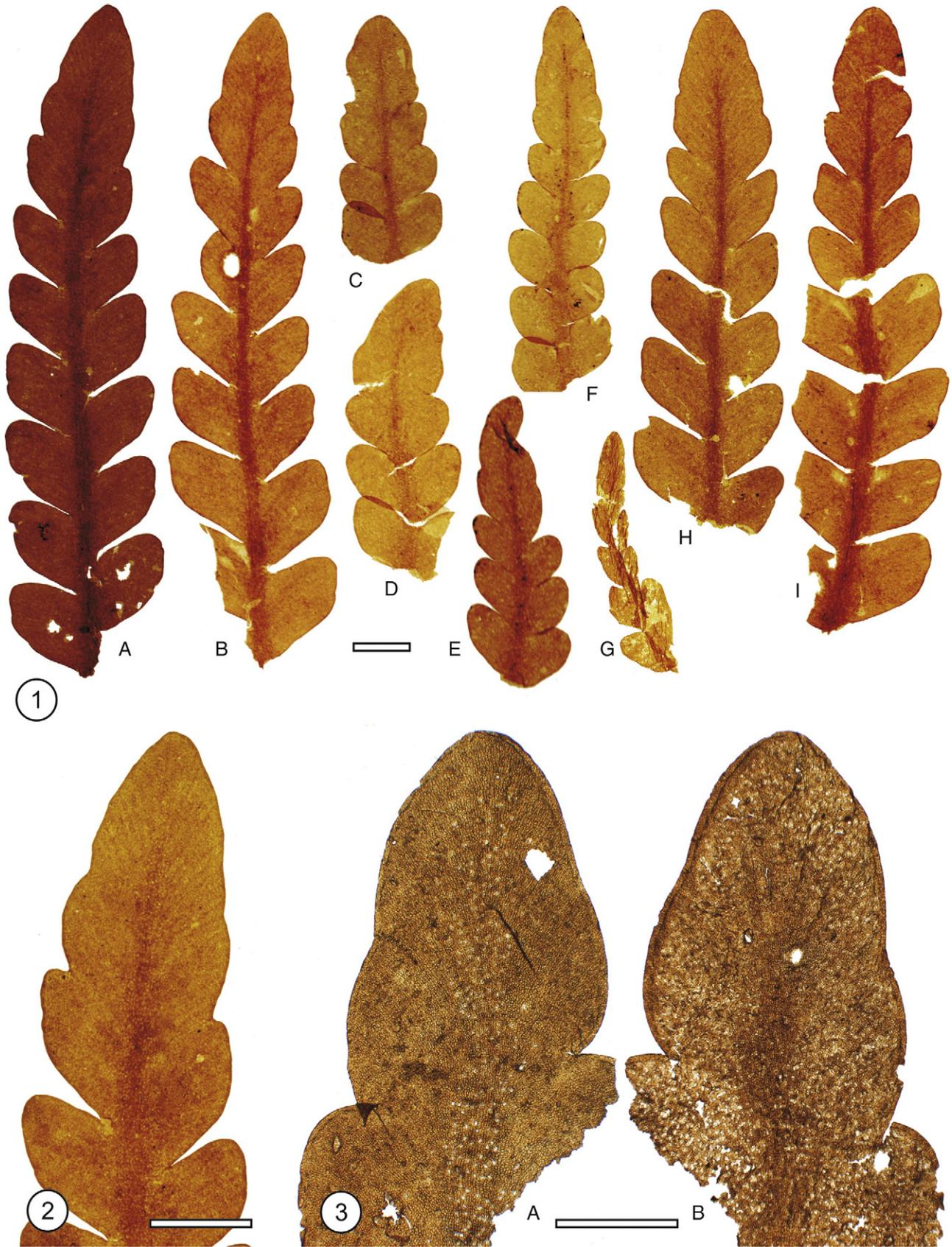


Plate III (see caption on page 87).

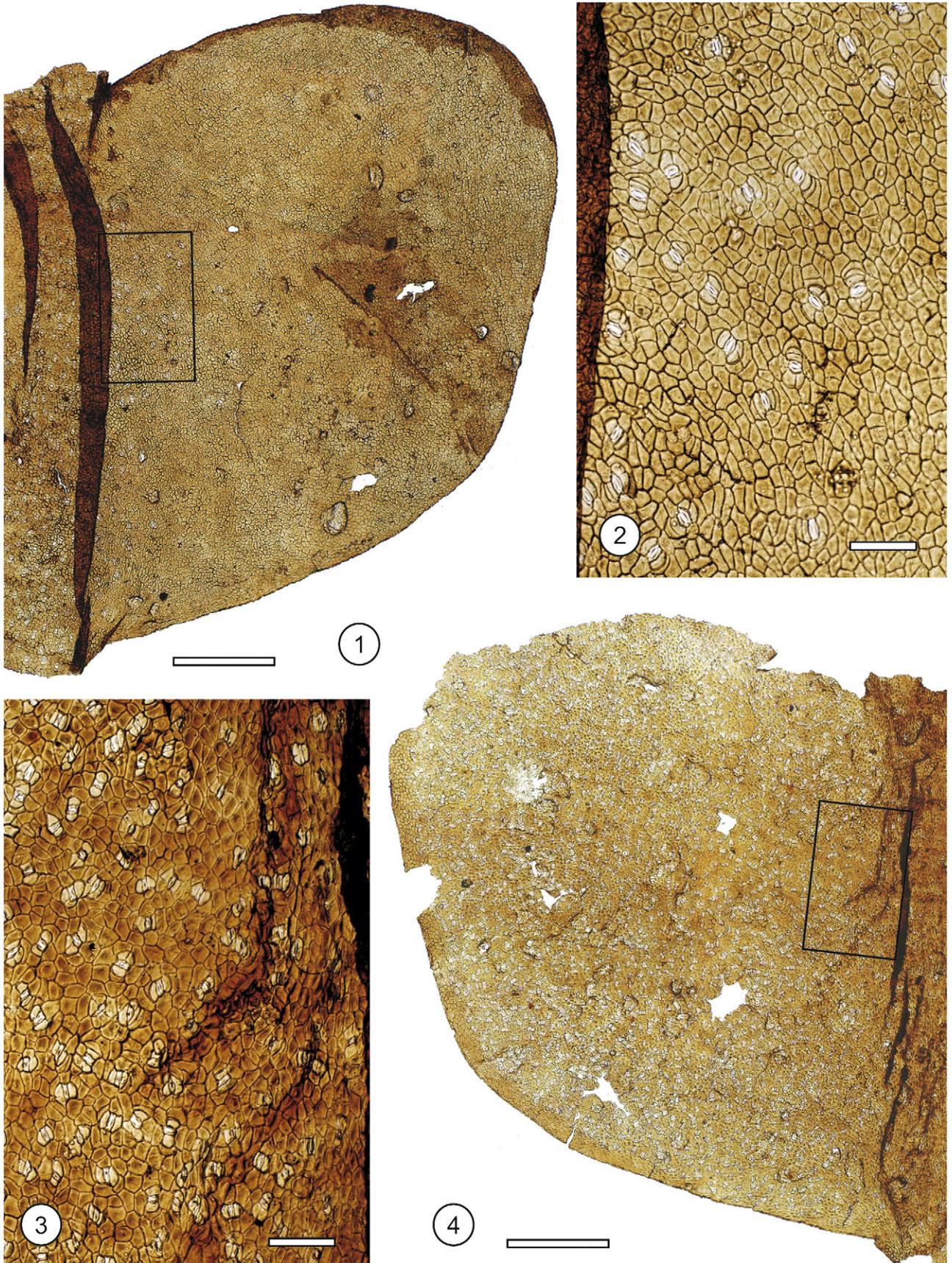


Plate IV (see caption on page 87).



Plates V (see caption on page 87).



Plate V1 (see caption on page 87).

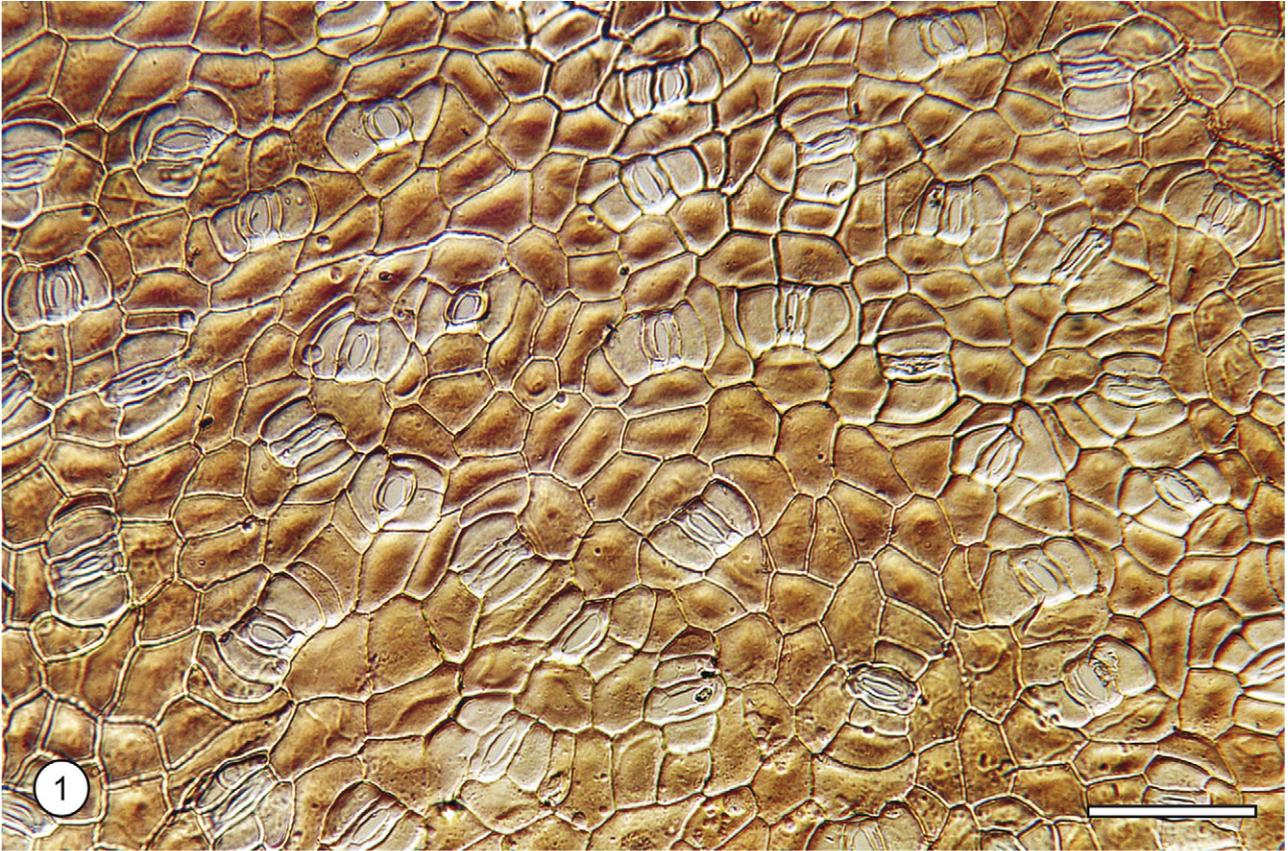


Plate VII (see caption on page 87).

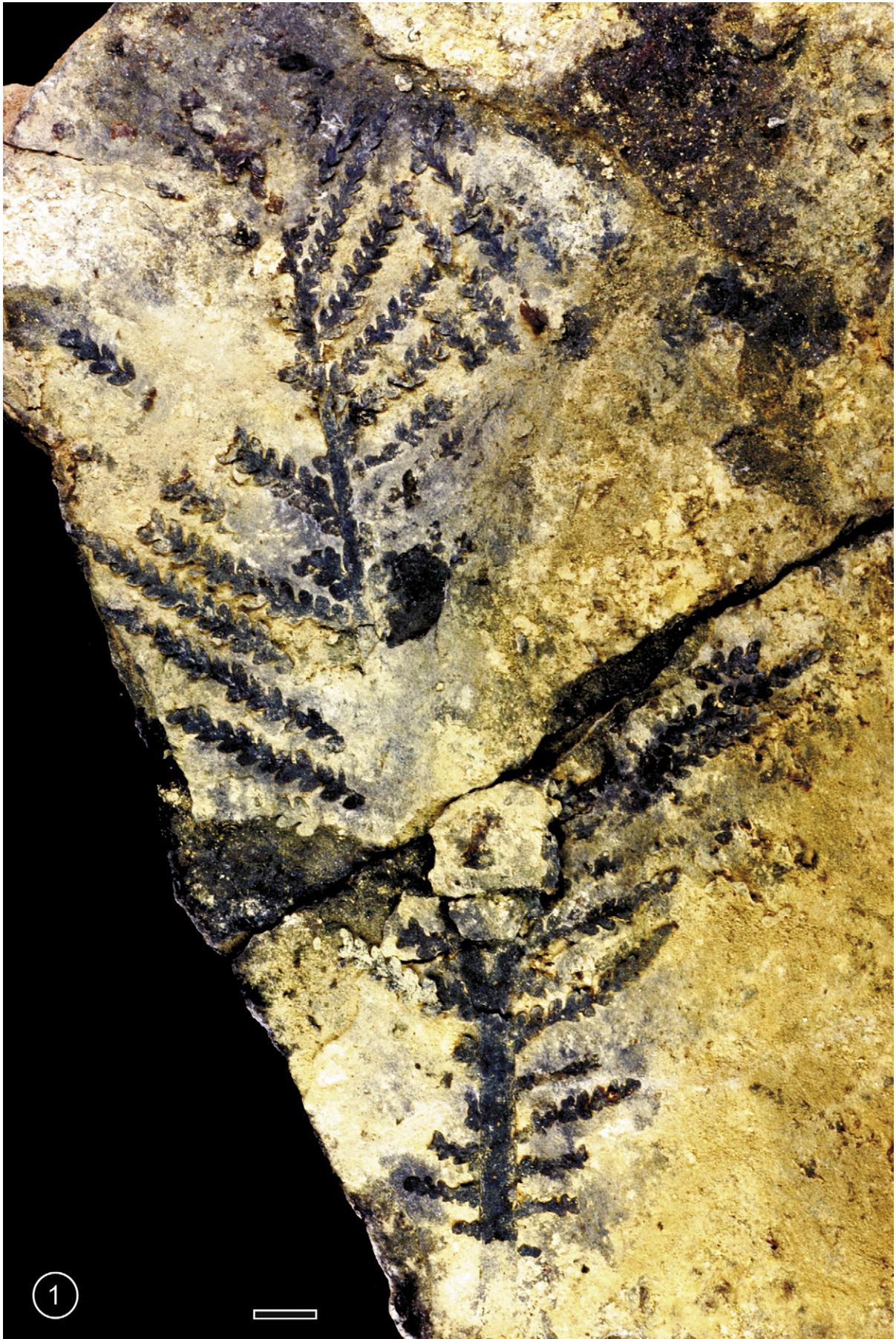


Plate VIII (see caption on page 87).

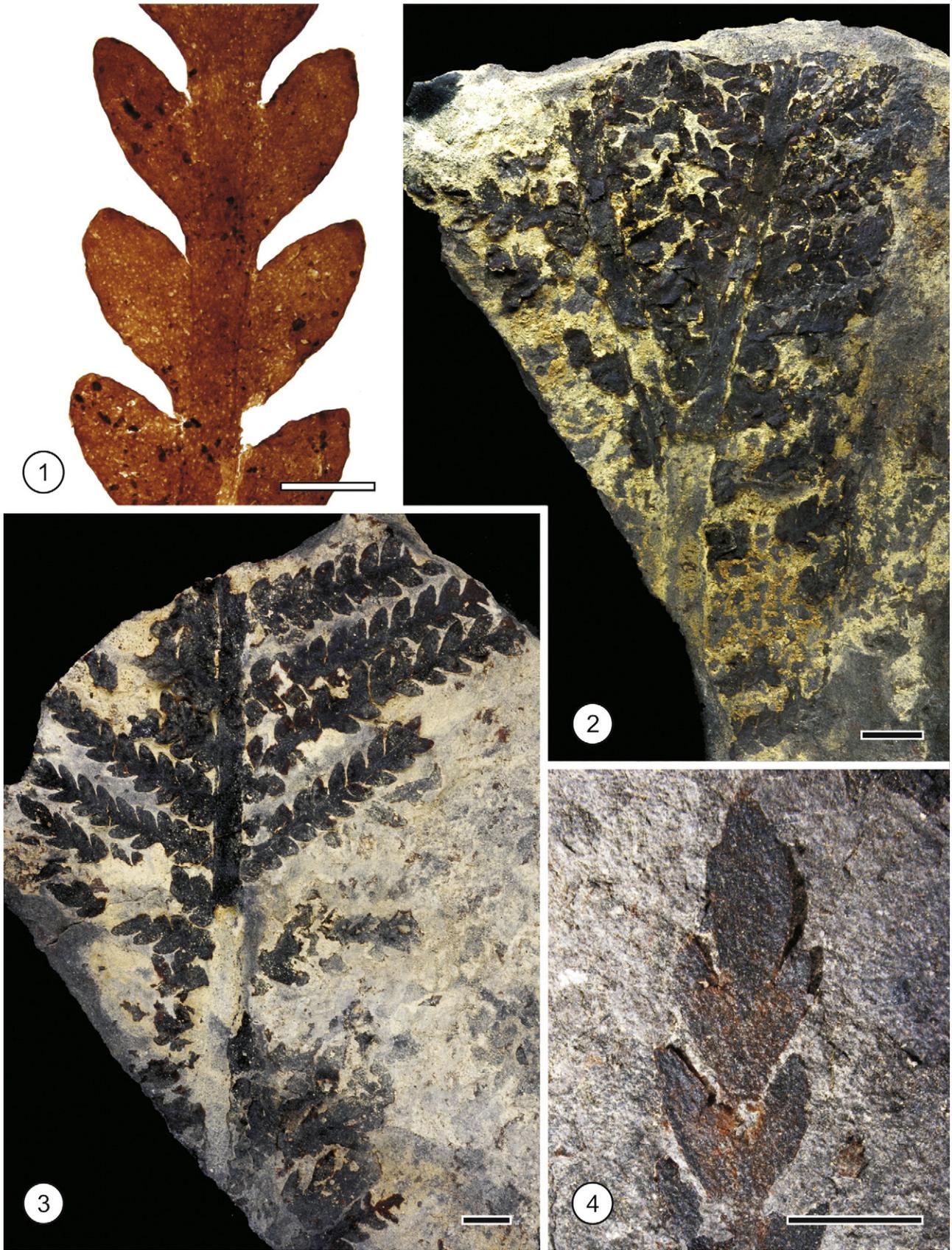


Plate 1X (see caption on page 87).



Plate X (see caption on page 87).

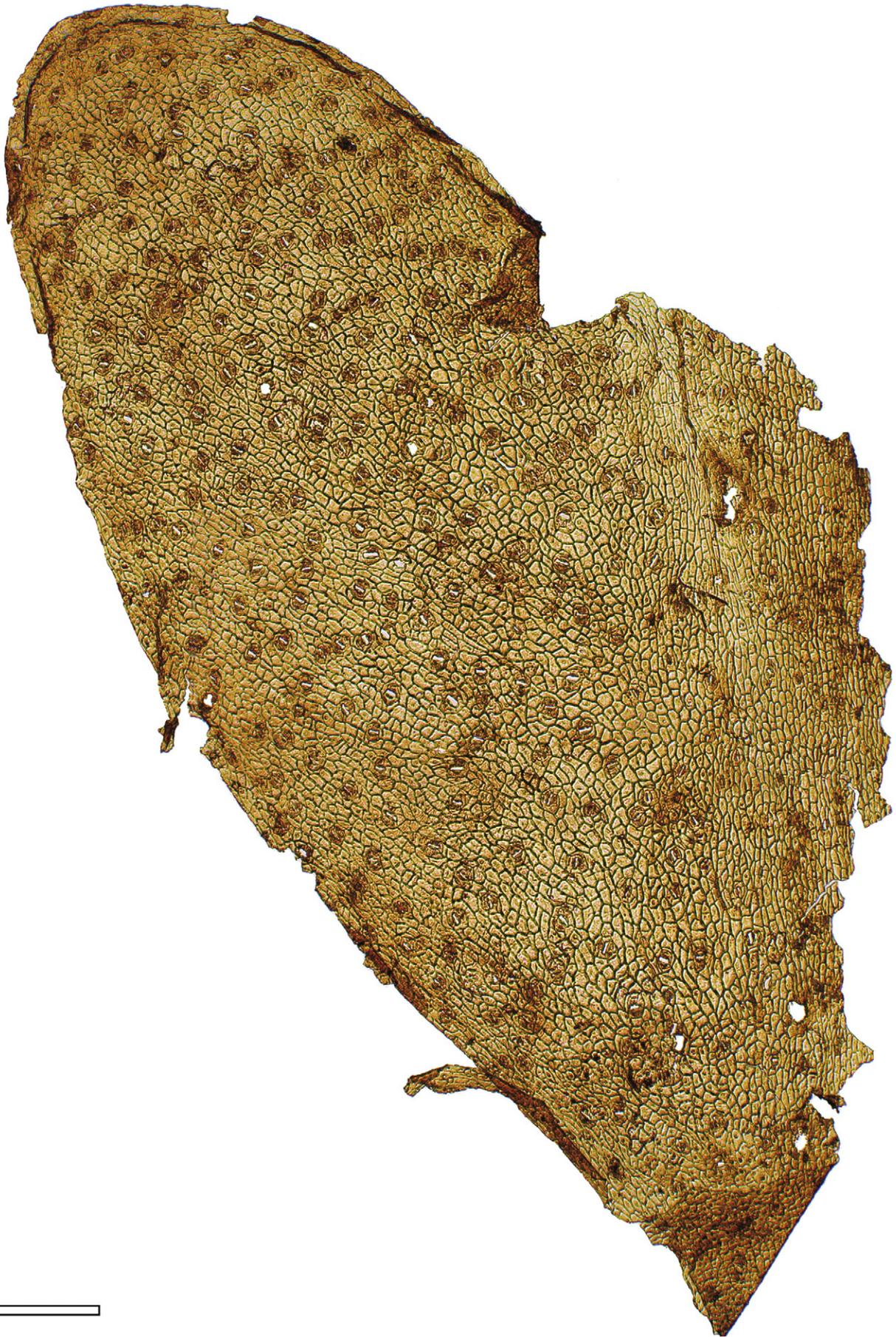


Plate XI (see caption on page 87).

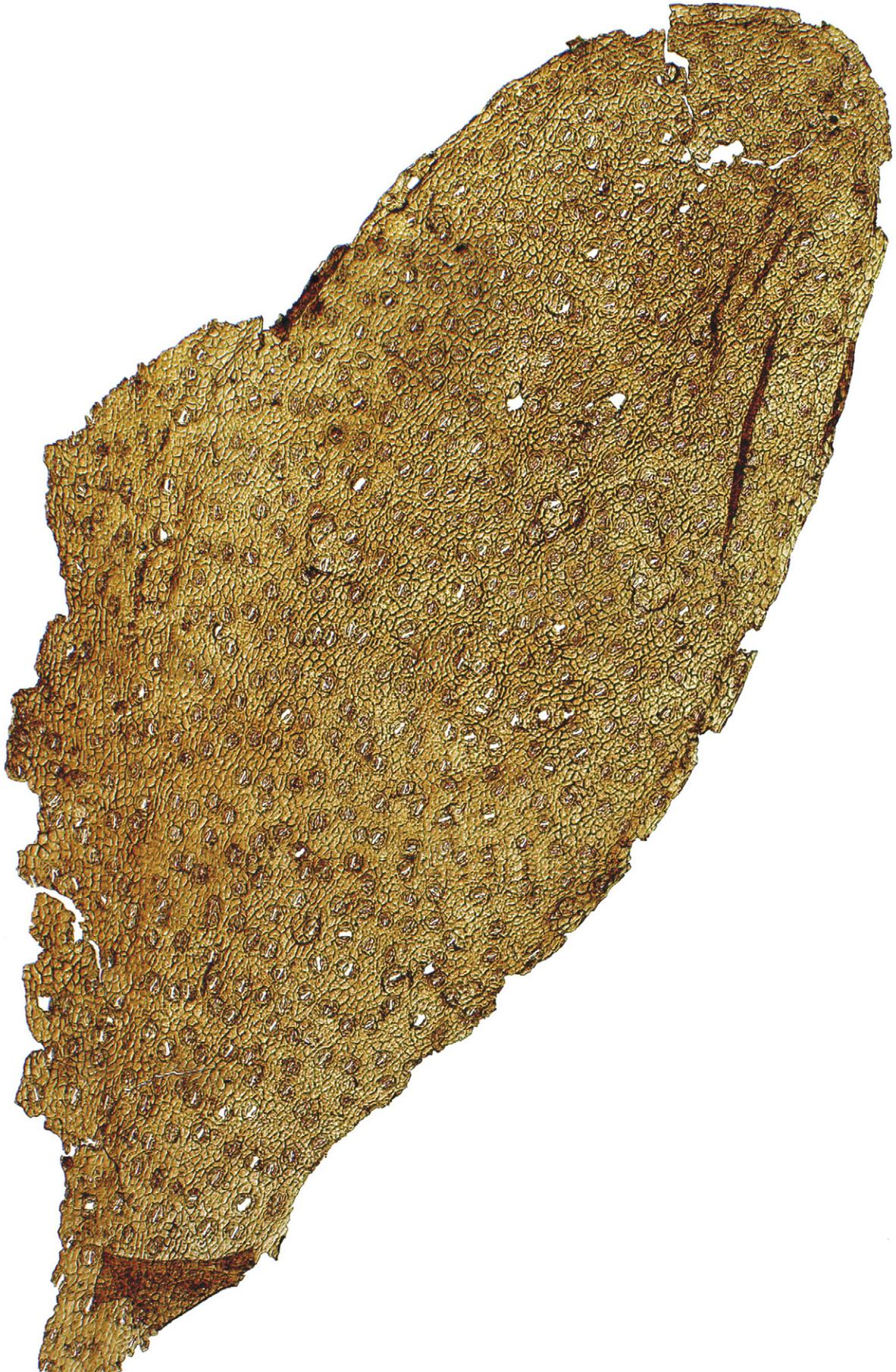


Plate XII (see caption on page 88).



Plate XIII (see caption on page 88).



Plate XIV (*see caption on page 88*).

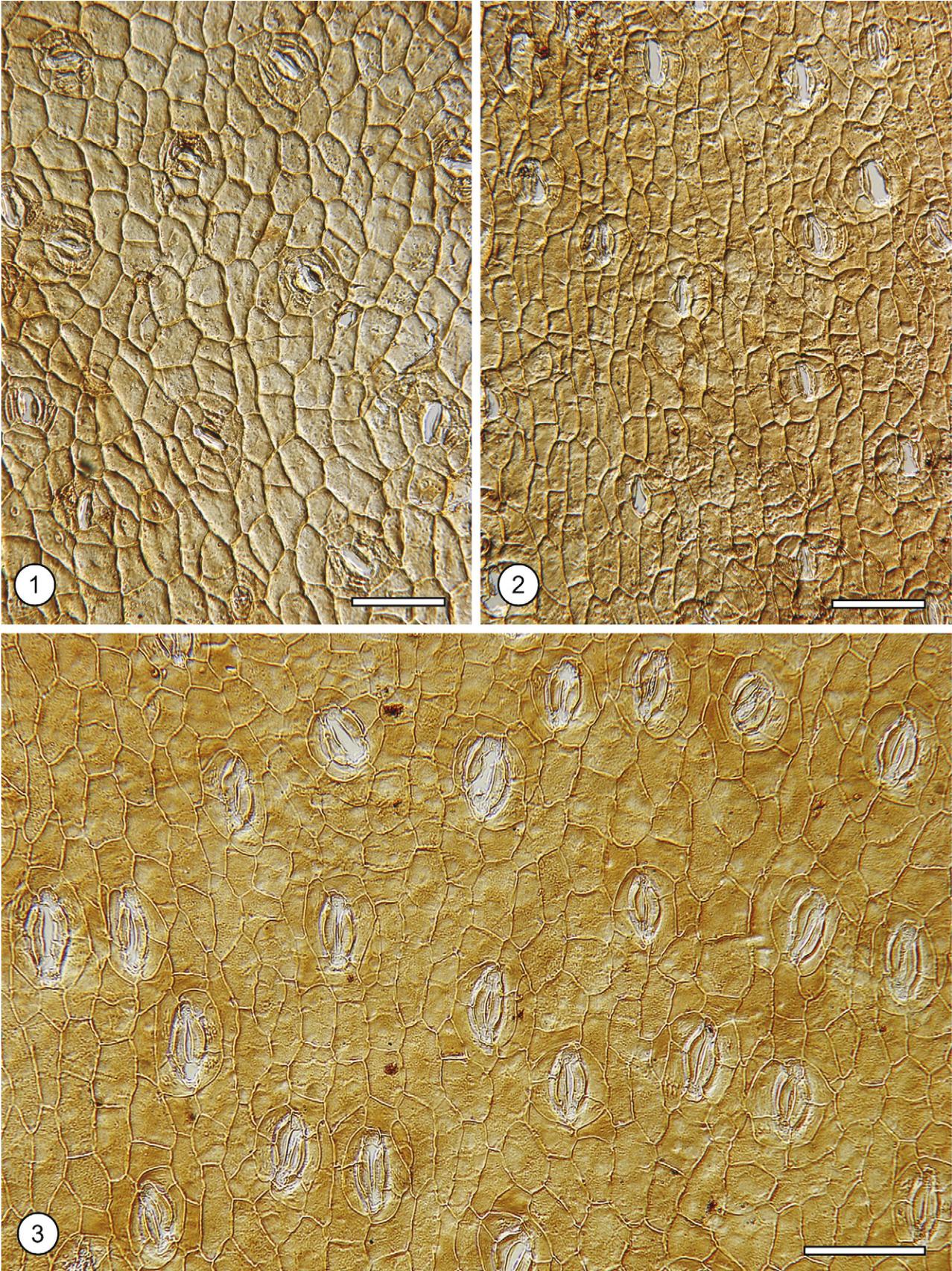


Plate XV (see caption on page 88).

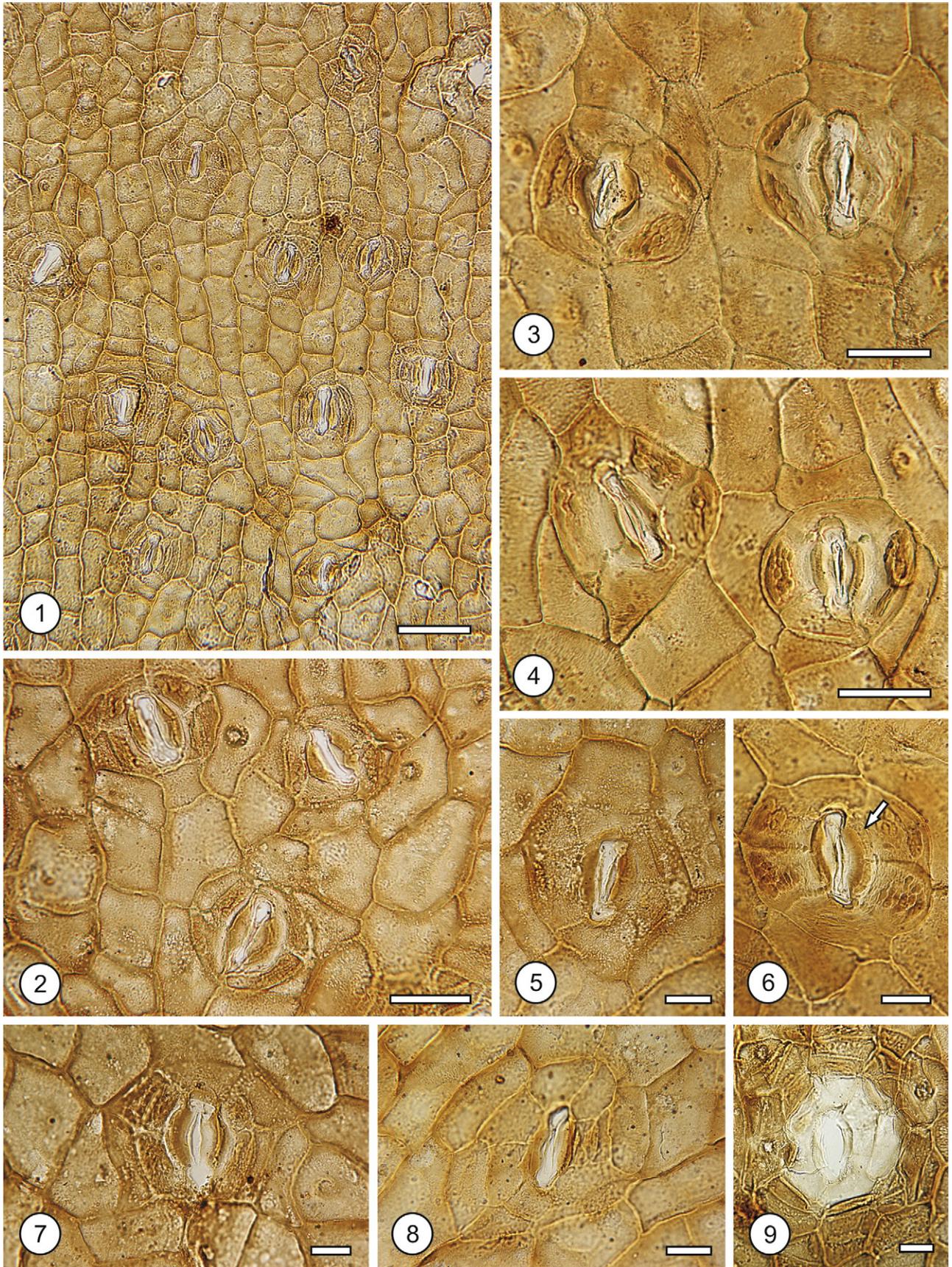


Plate XVI (see caption on page 88).

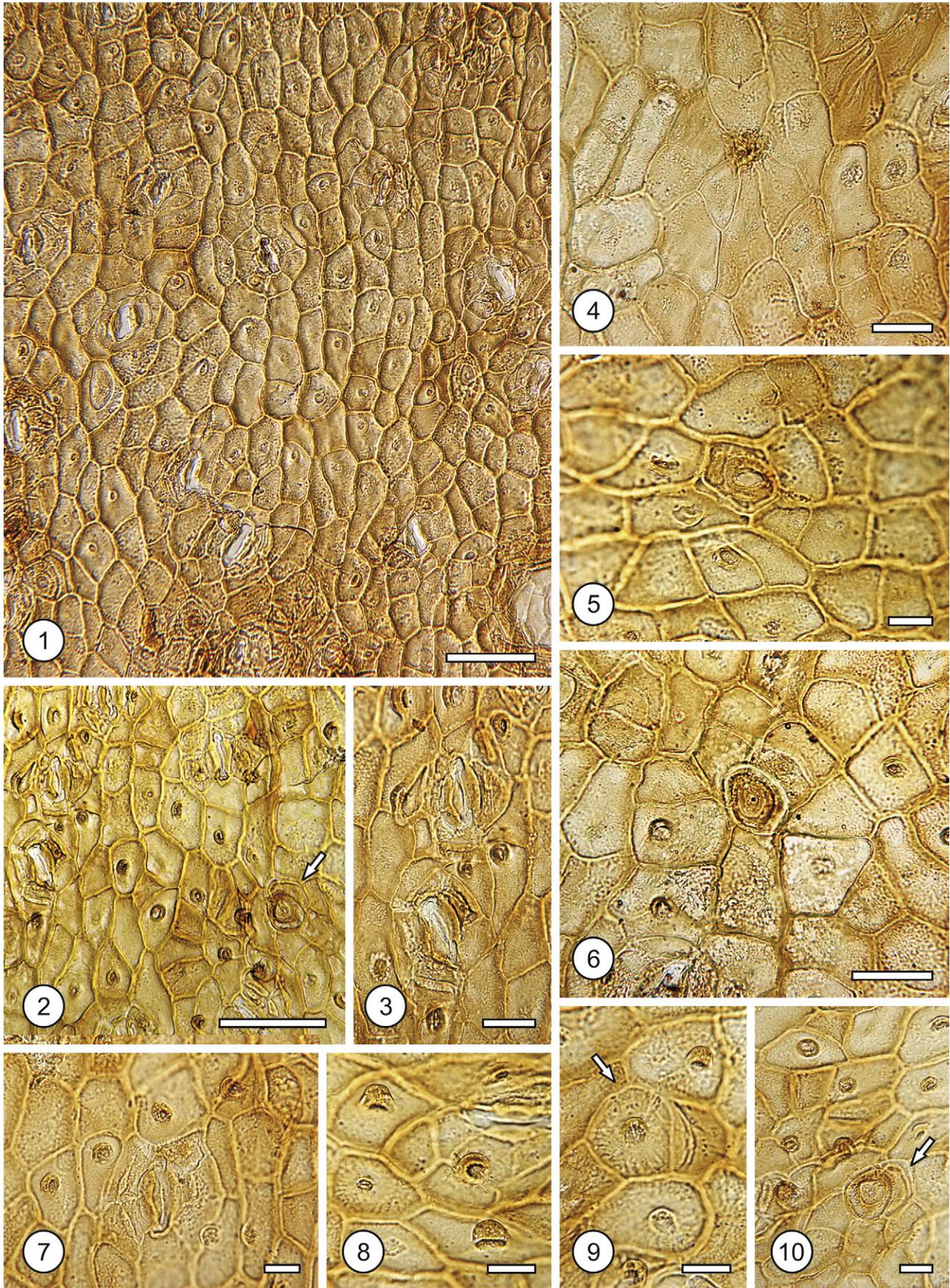


Plate XVII (see caption on page 88).

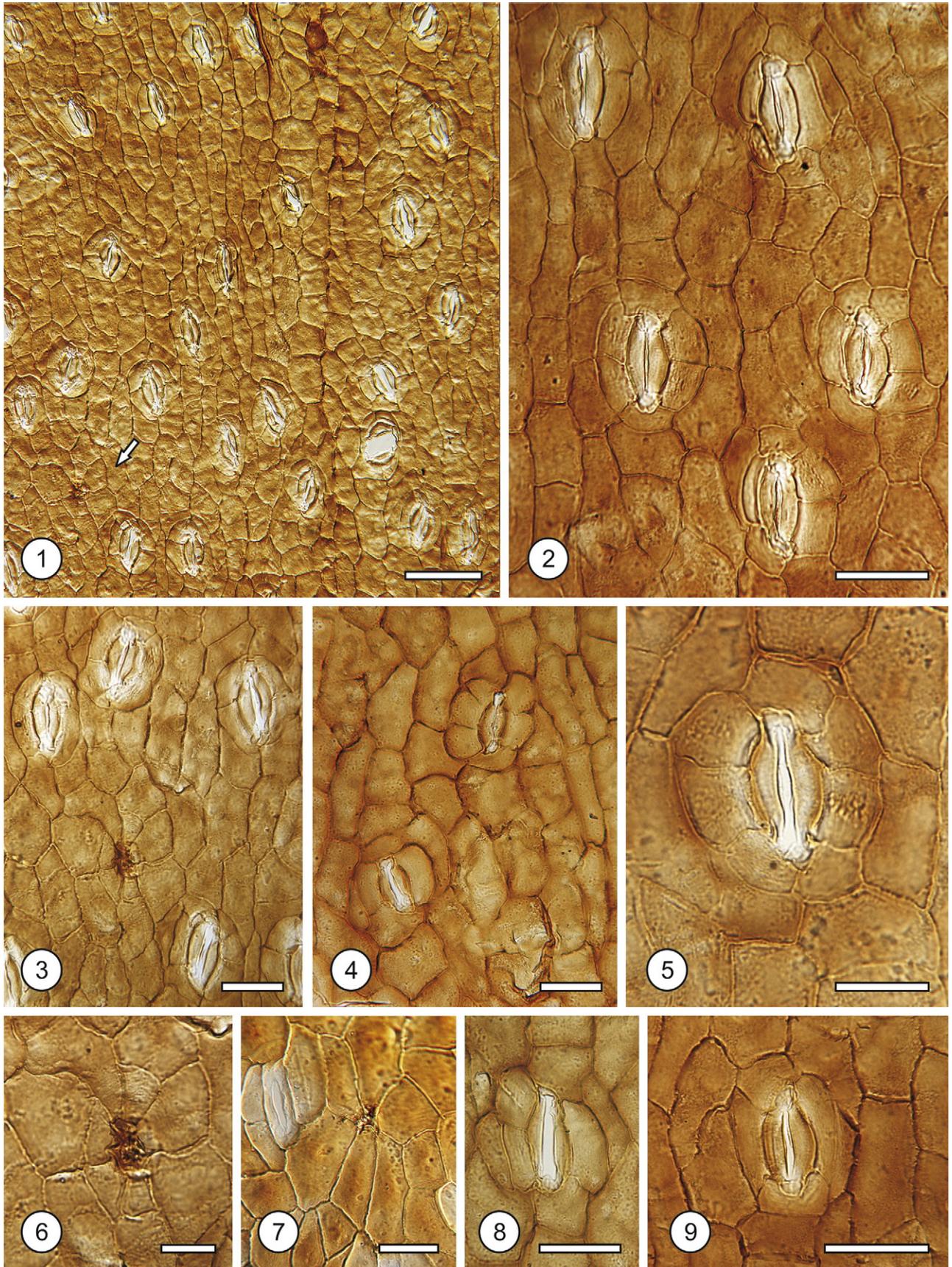


Plate XVIII (see caption on page 88).



1



2



3



4

Plate XIX (see caption on page 88).

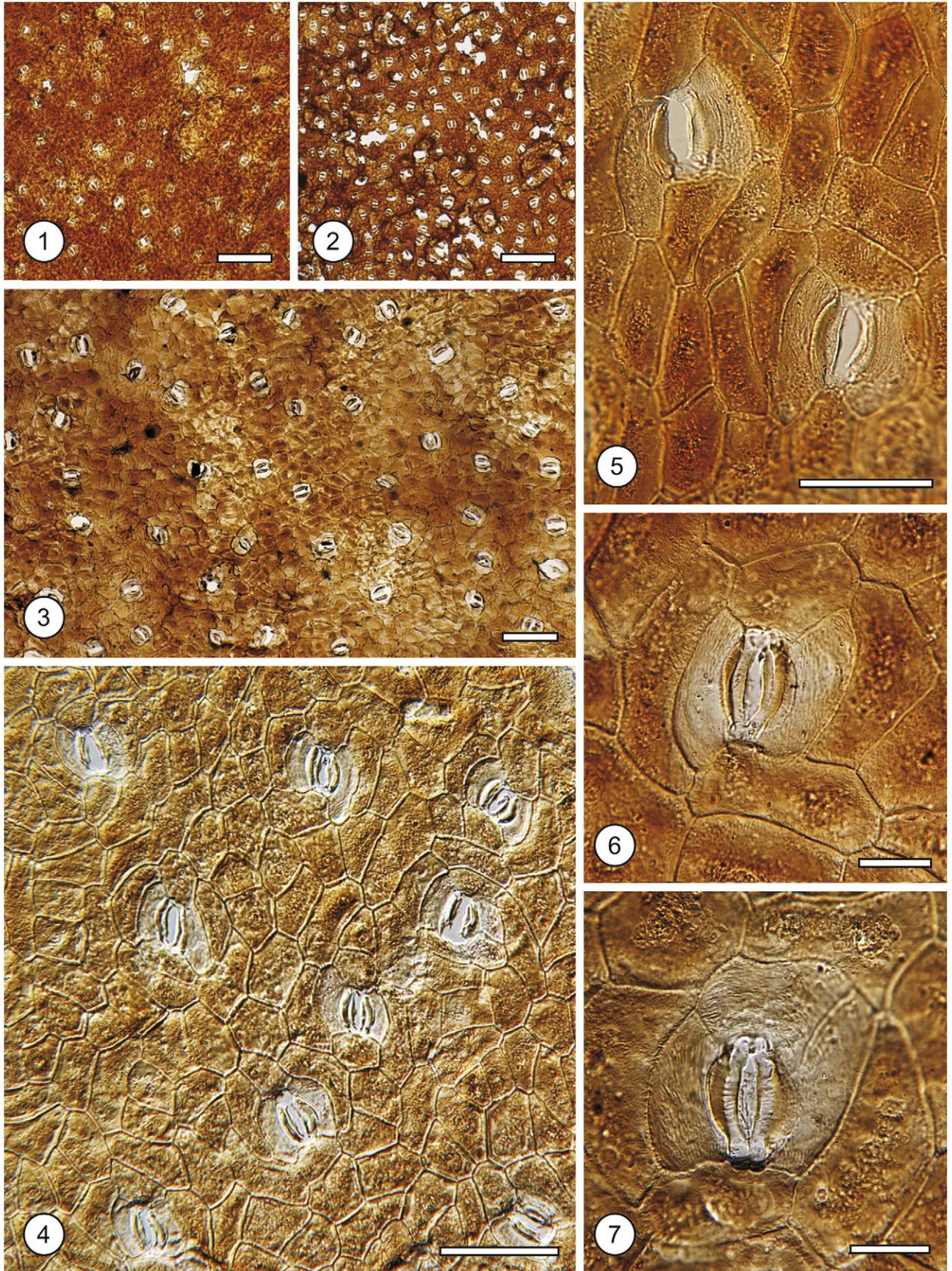


Plate XX (see caption on page 88).

having rather small pinnules. The third species [*D. robustum* (Plates XIX–XX)] is much rarer. Of the two former species a number of larger (up to 25 cm long) specimens have been found (e.g., Plate VIII), including several showing the typical frond architecture.

The light to medium brown-coloured mummified leaves very easily detach from the slabs. Unfortunately, when cuticles peel off, they do not leave a clear impression behind. Regarding the richness in sulphur, it seems most probable that the cuticles have been subjected to natural maceration by a reaction with sulphuric acid. A treatment with a 2% potassium hydroxide (KOH) solution usually suffices to clear the cuticles. Only the darkest specimens first have to be bleached a few minutes in a 4% sodium hypochlorite (NaClO) solution (= household bleach) and can then be treated with potassium hydroxide (Kerp, 1990; Kerp and Krings, 1999). After rinsing in water the cleared cuticles are dehydrated in pure glycerine for at least two days before they are mounted in glycerine jelly slides. Some cuticles were stained in Bismarck Brown (Vesuvium) to enhance the cell pattern (Lillie, 1977; Krings, 2000).

Bulk macerations were performed by dissolving the sediment with 43% hydrofluoric acid (HF) in order to isolate the cuticles from the rock. The cuticles were then bleached following the procedure outlined above. Complete pinnae are not uncommon; even up to 8 cm long rachides with several almost complete pinnules still attached (Plate X, 1) have been obtained by bulk maceration. Upper and lower cuticles can be separated with dissecting needles, thus enabling the study of the upper and lower cuticles of individual pinnules (Plate III; Plates IV–VI; Plates XI–XIV; Plate XV, 1–2). Several thousand cuticle slides have been prepared for this study, including more than a hundred “opened” pinnules, altogether giving a very good idea about the epidermal morphology and the variation within the three species that are formally described here. Such complete pinnules showing the distribution of the stomata are also ideal for determining possible variations in stomatal density and stomatal index. Such studies have been combined with isotope geochemical studies. These results will be presented and discussed in a separate paper. Although large amounts of material have been processed, no convincing examples of fertile organs have been found to date.

Hand specimens were photographed with a Nikon D100 digital camera using polarised light to enhance the contrast. Micrographs were made with an Olympus Vanox AH-2 Microscope (2.5–40× magnifications) and a Leitz Diaplan microscope with Nomarski interference contrast (100–1000× magnifications) with Leica DFC 480 and Nikon DS-5M-L1 digital camera systems. The photographs of the complete pinnules on Plates V–VI and Plates XI–XIV are composite pictures, each consisting of up to 40 photographs. Even though pinnules are complete and well preserved, single photographs of an entire pinnule do often not show enough details. Individual photographs were made with an Olympus Vanox AH-2 microscope equipped with a Nikon DS-5M-L1 digital camera system at magnifications of 10–40× and compositions were mounted using standard graphics software (Corel Photo-Paint, Adobe Photoshop).

Epidermal cells and stomata were measured with a Leica DM LB2 microscope equipped with a digital Leica DFC 480 camera and a Leica QWin V3 image analysis system; all average values given in the descriptions are based on 50 measurements each.

4. The genus *Dicroidium* Gothan 1912

The genus *Dicroidium* was established by Gothan (1912) for pinnate to bipinnate fronds with odontopteroid pinnules and a characteristic basal bifurcation. The four species recognised by Gothan were originally assigned to *Thinnfeldia* Ettingshausen 1852. Apart from the differences in frond architecture and epidermal anatomy, there appeared to be striking differences in the geographical distribution of *Dicroidium* and *Thinnfeldia*. *Dicroidium* is a typical Southern Hemisphere plant, whereas the occurrence of *Thinnfeldia* is restricted to the Northern Hemisphere, except for India which was in the Southern Hemisphere during the early Mesozoic. Although some subsequent authors questioned the criteria on the basis of which Gothan had established *Dicroidium* (e.g., Antevs, 1914), or even rejected the genus, it became generally accepted. Based on frond architecture and pinnule morphology Frenguelli (1943) distinguished four genera, i.e., *Dicroidium* Gothan, 1912, *Zuberia* Frenguelli, 1943, *Johnstonia* Walkom 1925 and *Diplasiophyllum* Frenguelli, 1943. Several authors, including Townrow (1957), Bonetti (1966), Archangelsky (1968), and Anderson and Anderson (1983), Kustatscher and Van Konijnenburg-van Cittert (2007), regarded the latter three genera as synonyms of *Dicroidium*. However, others still retain these genera (e.g., Petriella, 1979, 1981; Gnaedinger and Herbst, 2001; Zamuner et al., 2001; D’Angelo, 2006). The genus *Dicroidium* was emended by Townrow (1957), who also described cuticles of several additional species and transferred some species previously assigned to other genera to *Dicroidium*. More recent systematic studies of *Dicroidium* were published by Retallack (1977), who distinguished a large number of species and varieties, and by Anderson and Anderson (1983) who published a monograph on the genus *Dicroidium* based on material from the Late Triassic Molteno Group, South Africa. The number of taxa recognised by these latter authors is less than by other authors, especially on the infrageneric level. Anderson and Anderson (1983) recognised approximately 30 well-defined species and subspecies. The genus *Dicroidium* is used here in the sense of the latter authors, who have published the most complete account on the group.

Dicroidium belongs to the family Corystospermaceae. This family was instituted by Thomas (1933), who first described the ovuliferous and pollen organs as *Umkomasia* and *Pteruchus*. Correlations between foliage and reproductive organs were based on repeated associations and similarities in epidermal anatomy. Although these correlations were never questioned, there was some debate about the organization and interpretation of the fertile organs. *Umkomasia* is a cupulate organ with lateral axes that appear to be arranged in a single plane. The entire *Umkomasia* cupulate organ is a branching system, and each cupule represents an individual megasporophyll. Thomas (1933) considered the pollen organs to be organised in a similar

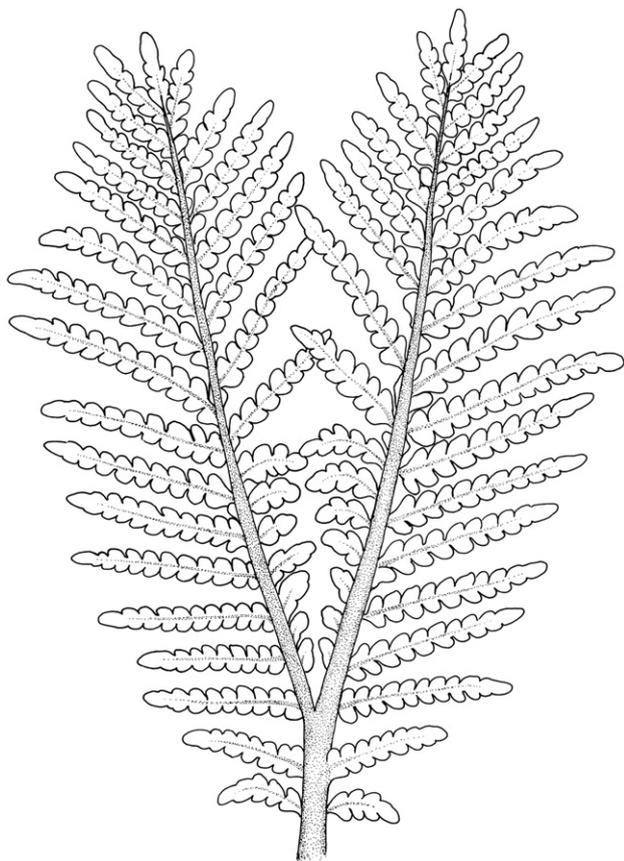


Fig. 2. Tentative reconstruction of a *Dicroidium irnensis* frond.

way, i.e. the ultimate flattened structures bearing the pollen sacs would be individual microsporophylls borne on a branch. This view was challenged by Townrow (1962), who held the opinion that the entire pollen organ described as *Pteruchus* was a single compound sporophyll. Axsmith et al. (2000) described new material from the Antarctic and they could confirm the correctness of Thomas' original interpretation. Moreover, they were the first to demonstrate an organic connection between cupulate organs and foliage-bearing axes. They also concluded that one foliage morphotype might have belonged to two different natural species. An up-to-date review of the reproductive biology of the Corystospermaceae can be found in Taylor et al. (2006).

Not only the taxonomy, but also the growth form of the *Dicroidium* plant has been a matter of debate. Archangelsky (1968) suggested that the *Dicroidium* plant might have had a liana-like growth habit. Later authors (e.g., Meyer-Berthaud et al., 1993; Taylor, 1996) could not find proof for a liana-like growth habit. Petriella (1981) reconstructed *Dicroidium* as an unbranched medium-sized tree with an apical crown of closely spaced fronds similar to a tree fern or palm tree. The most complete material currently known, described by Axsmith et al. (2000), suggests that the *Umkomasia uniramia*–*Dicroidium odontopteroides* plant from the Antarctic had an arborescent growth form similar to that of the extant *Ginkgo biloba*. Artabe et al. (2007) recently described an in situ preserved fossil corystosperm forest. They concluded that the trees, which grew

in monospecific stands, were evergreen gymnosperms, between 5 and 27 m high, with a palm-like growth habit. Based on growth ring patterns they concluded that the forest community colonised stressed environments.

The systematic position of the corystosperms is still not entirely clear. Some authors have suggested that the corystosperms could include angiosperm ancestors (Frohlich and Parker, 2000), but this is considered to be highly unlikely by others (e.g., Axsmith et al., 2000). A close relationship to the peltasperms, another group of Late Palaeozoic–Early Mesozoic seed ferns, is generally accepted (see e.g., Meyen, 1984; Crane, 1985; Nixon et al., 1994; Serbet and Rothwell, 1994; Doyle, 1996, 2006; Hilton and Bateman, 2006).

5. Systematic descriptions

Dicroidium irnensis Abu Hamad et Kerp nov. sp. (Plates I–VII; Plate XVIII, 7; Figs. 2 and 3))

Dicroidium nov. sp. B, Kerp, Abu Hamad, Bandel, Vöding, *Geology* 34, 266, fig. 2 D–F

Holotype: Specimen PbO UmIr 3, illustrated on Plate I.

Repository: Forschungsstelle für Paläobotanik, Geologisch-Paläontologisches Institut, Westfälische Wilhelms-Universität, Münster, Germany.

Type locality: Wadi Himara, in the incised river valley, ca. 400 m upstream along the southern branch after the main bifurcation at 31° 37' 55.67" N and 35° 37' 15.69" E.

Stratigraphic horizon: Silt and clay layers and lenses, 15.5–16.5 m above the base of the Um Irna Formation, Upper Permian.

Etymology: The name refers to the Um Irna Formation in which the fossils have been found. Um Irna is the mountain between Wadi Himara and Wadi Zarqa Ma'in.

Diagnosis:

Fronds small, bifurcated, bipinnate. Primary axis very robust and smooth, bifurcating with an angle of approximately 25° with at least two pairs of pinnae below the bifurcation; frond portions above the bifurcation more or less ovate in outline, tapering towards the apices and with their greatest width in the middle. Pinnae alternating to suboppositely attached, at angles between 45° and 70°, with up to 14 pinnules at each side.

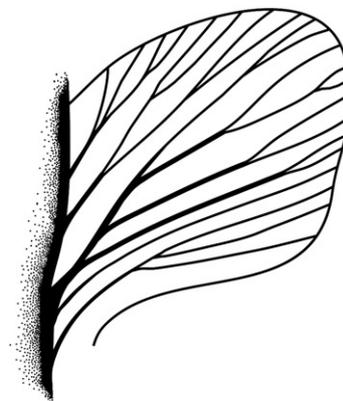


Fig. 3. Presumed venation pattern of a *Dicroidium irnensis* pinnule.

Pinnules densely spaced, sometimes overlapping, in alternating or subopposite position; pinnules obliquely attached with their entire basis, asymmetrical, outline tongue-shaped to rhomboidal with rounded apices. Basisopic pinnules more obliquely attached than acroscopic pinnules; basal basisopic pinnules occasionally continuing along the primary rachis. Pinnae ending in elongated, tongue-shaped pinnules and usually consisting of 3–5 strongly fused pinnules. Intercalary pinnules present, asymmetrically triangular to rhomboidal. Venation odontopteroid, lacking a clear midvein, with several veins entering the pinnule; veins rather densely spaced, bifurcating one or two times.

Leaves amphistomatic, stomata far more numerous on the lower side. Epidermal cells and stomata of the upper surfaces larger than those of the lower surfaces. Stomata of the upper side mainly restricted to the pinna rachides and basal parts of the pinnules, particularly over the veins, but very rare to absent on the more distal parts of the pinnules. Stomata very abundant on the lower leaf side, occurring all over the pinnule surface but rare or absent under the pinna axes. Stomata of the lower pinnule surfaces normally randomly distributed. Stomata commonly with four subsidiary cells, the lateral ones less strongly cutinised than the polar ones; stomata with a ring of five or six subsidiary cells occur occasionally. Papillae rare, mainly restricted to the lower pinnule surfaces.

5.1. Additional observations

The frond of *Dicroidium irnensis* is small. The most complete specimen is c. 12 cm long (Plate I). The primary rachis bifurcates with an angle of approximately 25°; five specimens showing the basal bifurcation have been collected (e.g., Plate I; Plate II, 2). The primary rachis is smooth and remarkably robust, 3–12 mm wide below the bifurcation and 2–6 mm above. At least two pairs of pinnae are inserted below the bifurcation (Plate II, 2). The maximum pinna length is unknown because virtually all longer attached pinnae are incomplete. Only a single complete attached pinna is known which measures 10 cm in length. The pinnae below the bifurcation are up to 4.5 cm long (Plate I).

The densely positioned pinnules are very broad, sometimes wider than long. They are usually 4.5–6 mm long but the smallest ones measure only 2.5 mm, whereas the longest ones reach a length of 9 mm. The average width is 4–6 mm, the smallest being only 2 mm and the largest up to 6.5 mm wide. Pinnule size ranges have been determined on the basis of measurements of over 50 hand specimens and are confirmed by many hundreds of larger pinna portions and complete pinnules obtained by bulk maceration. The average sizes are considered to represent pinnules from full-grown fronds. The broadly tongue-shaped pinna terminals (Plate II, 1; Plate III), consisting of 3–5 strongly fused pinnules are 12–20 mm long and 6.5–9.0 mm wide. The first pinnae in the interior of the bifurcation are undifferentiated; individual pinnules are not developed (Plate I). The venation (Plate II, 2–3) is often obscured by the cuticles and coalified mesophyll; up to eight, usually five veins enter each pinnule (Fig. 3). In weakly macerated cuticles the venation is sometimes still faintly visible (Plate III, 2–3).

Cuticles of the frond and pinna axes are thick, with elongated rectangular to isodiametric polygonal cells, arranged in longitudinal rows. The cells of the lower surface of the pinna axes are smaller than those of the upper surface of the pinna axes. The normal cells of the upper side of the pinna axis are 62–120 µm (average 80 µm) long and 20–44 µm (average 30 µm) wide, and those of the lower side are 32–72 µm long and 20–32 µm wide. The anticlinal walls are thick, straight to slightly bent. Stomata are common on the upper surfaces of pinna axes and arranged in longitudinal rows; they are rare on the lower surfaces of the pinna axes. Multicellular trichomes and papillae are rather common on the frond axis but far less common on the pinna axes.

The cuticles of the pinnules are thinner than those of the pinna axes, and the cuticle of the lower pinnule surface is much thinner than that of the upper pinnule surface. There is a gradual transition from the pinna axis into the pinnules. Stomata are frequent to very frequent over the upper surfaces of the pinna axes, where they are often more or less longitudinally oriented, rare in the basal one third of the pinnules, where they occur over the veins only, and virtually absent in the rest of the pinnules (Plate IV, 1; Plate V). Stomata are virtually absent on the lower surfaces of the pinna axes but very abundant over the entire lower pinnule surface (Plate IV, 3; Plate VI).

The normal epidermal cells of the upper pinnule surfaces (Plate IV, 1; Plate V) are isodiametric polygonal to slightly elongated, randomly oriented, 56–100 µm long and 25–50 µm wide, and those of the lower pinnule surfaces are 28–79 µm (average 46 µm) long and 16–47 µm (average 28 µm) wide. The stomata on the lower pinnule surfaces are randomly oriented and the guard cells are very narrow, weakly cutinised, 3–4 µm wide, and 28–44 µm long. The most common type of stomatal apparatus (>90% of all stomata) has four subsidiary cells, two lateral ones and two polar ones, the relatively wide lateral subsidiary cells are less strongly cutinised than the polar ones (Plate VII). These lateral subsidiary cells are 28–64 µm (average 40 µm) long and 16–28 µm (average 20 µm) wide. Lateral subsidiary cells occasionally divide and stomata with three to six subsidiary cells occur occasionally (Plate VII, 2–3); stomatal apparatuses are sometimes incomplete dicyclic. When more than two lateral subsidiary cells are present, these are often normally cutinised and they are of the same colour as the polar subsidiary cells (Plate VII, 2–3). Papillae are rare and when present, restricted to the lower pinnule surfaces, notably in the basal portions of the pinnules (Plate IV, 3). Multicellular trichomes (Plate XVIII, 7) occur but are not common; they are restricted to the lower pinnule surfaces.

Weakly macerated specimens of both the upper and lower cuticles sometimes show the presence of a second cutinised layer below the epidermis. The cells of this layer are much smaller than the cells of the epidermis, about one third to one fourth of the size of the epidermal cells.

5.1.1. Comparisons with other taxa

In its general appearance *Dicroidium irnensis* (Fig. 2) is most similar to *D. zuberi* (Szajnocha) Archangelsky, with regard to the general morphology of the frond as well as to the shape of the pinnules. *Dicroidium zuberi* first appears in the

lower Olenekian of Australia (Retallack, 1977) and it occurs throughout the Triassic (Anderson and Anderson, 1983). It is definitely the most widespread *Dicroidium* species and has been recorded from South America (e.g., partly as *Zuberia zuberi*: Frenguelli, 1943, 1944; Bonetti, 1966; Archangelsky, 1968; Petriella, 1979, 1981; Guerra-Sommer et al., 1999a; Gnaedinger and Herbst, 2001), South Africa (e.g., Anderson and Anderson, 1983), India (e.g., as *Thinnfeldia sahnii*, Seward, 1933; as *Dicroidium feistmantelii*: Jacob and Jacob, 1950), Australia (e.g., Retallack, 1977), New Zealand (e.g., Retallack, 1980), and the Antarctic (e.g., Retallack and Krull, 1999). For the synonymy of *Dicroidium zuberi* see the microfiche supplement to Retallack (1977), and Anderson and Anderson (1983); the latter authors also give a range chart and a palaeogeographic map showing the distribution. It is also one of the larger and most variable species. The pinnules of *D. irnensis* are strongly reminiscent of those of *D. zuberi*, except for the terminal pinnules. Another striking difference is the size. Pinnules of *D. zuberi* can, according to Frenguelli (1944), be 11–14 mm long and some authors have figured even much larger ones, e.g., Townrow (1957, Plate II, b–c: figured under the name *Hoegia papillata*) and Anderson and Anderson (1983, plate 36, 8–9). *Dicroidium zuberi* pinnules are normally about twice as large than those of *D. irnensis*. The neotype of *D. zuberi*, selected by Archangelsky (1968) and originally figured by Frenguelli (1944, plate 4), is a juvenile frond. Some of the pinnules of this specimen are about the same size as, but most are even larger than those of full-grown *D. irnensis* fronds. The shape of the terminal pinnae in *D. irnensis* and *D. zuberi* is very different. In *D. zuberi* the pinnae gradually taper towards the apex and end in a relatively small and narrow terminal pinnule, whereas the pinnae of *D. irnensis* hardly reduce in width towards the pinna apex and end in a long and broadly rounded terminal pinnule.

Also the cuticles of *Dicroidium irnensis* and *D. zuberi* differ considerably. *Dicroidium irnensis* has amphistomatic leaves, whereas those of *D. zuberi* are hypostomatic. However, it should be noted that on the upper leaf surface of *D. irnensis* stomata occur only over the pinna axes and in the basal parts of the pinnules. Anderson and Anderson (1983, p. 196) mentioned a single specimen (Slab 1351) from South Africa identified as *D. zuberi* having amphistomatic leaves, but they did not illustrate cuticles of this specimen. A clear difference is in the shape of the anticlinal walls. In *Dicroidium zuberi* the anticlinal walls of the upper and lower pinnule surfaces are straight but possess prominent anticlinal projections (= buttressed cell walls *sensu* Anderson and Anderson, 1983). Sometimes these projections are so well developed that the anticlinal walls may have a strongly sinuous appearance (Anderson and Anderson, 1983, plate 101, 6, plate 102, 1). Such anticlinal projections are absent in *D. irnensis*, which usually has straight to slightly bent anticlinal walls, without any thickenings or projections. *Dicroidium zuberi* has stomata with four to five very strongly cutinised subsidiary cells forming a ring, whereas in *D. irnensis* stomata usually have two lateral subsidiary cells that are very weakly cutinised and two polar cells that are normally cutinised.

At first glance *Dicroidium irnensis* also shows some superficial similarities with *D. jordanensis*. However, the

pinnule morphology and the cuticles are clearly different. These differences will be further discussed under *D. jordanensis* (p. xxx) and are listed in Table 1. Comparisons with other early (Early Triassic) *Dicroidium* species are presented in a separate paragraph and in Table 2.

5.1.2. Discussion

Although no complete fronds of *Dicroidium irnensis* have been found, the specimens at hand give a pretty good idea about the size and shape of the frond (Fig. 2). The frond looked rather similar to the juvenile frond of *D. zuberi* that has been illustrated by Frenguelli (1944, plate 4), although it must have been slightly smaller, attaining a length of ca. 20–25 cm. The angle of bifurcation is relatively small (25°). The lowermost interior pinnae are not well developed but the other pinnae in the interior part of the frond are normally developed and the pinnae from both sides overlapped each other like in many other *Dicroidium* species with bipinnate fronds.

The frond and pinnule morphologies justify the classification of this species to the genus *Dicroidium*. Although cuticles of the various *Dicroidium* species show considerable variation, notably in the shape of the stomata, these further substantiate the generic assignment. Stomata usually have two weakly cutinised lateral subsidiary cells and are of the same type as in *D. longifolium* which has been illustrated by Jacob and Jacob (1950). This latter species, however, has a very different pinnule morphology. Furthermore, the distribution of stomata is remarkable in *D. irnensis*; the leaves are amphistomatic, but the distribution of stomata on the upper and lower leaf surfaces is very uneven. On the upper leaf surface the stomata are almost completely restricted to the pinna rachises and basal parts of the pinnules; most of the pinnule lamina does not show any stomata (Plate IV, 1; Plate V). The cuticle of the lower pinnule surface is completely different, lacking stomata on the pinna axes, whereas the cuticles of the lower pinnule surfaces have numerous stomata. Stomata are evenly distributed over the entire pinnule surface (Plate IV, 3; Plate VI).

The fact that stomata on the upper leaf surfaces are restricted to the pinna axes and the basal parts of the veins may either suggest that (1) they might have had a function for evapotranspiration, or, (2) more likely, they were formed when the pinnules were not still fully differentiated and the lamina had not spread.

Dicroidium jordanensis Abu Hamad et Kerp nov. sp. (Plates VIII–XVII; Plate XVIII, 1–6, 8–9)

Dicroidium nov. sp. A, Kerp, Abu Hamad, Bandel, Vöding, *Geology* 34, 266, fig. 2 A–C

Holotype: Specimen PbO UmIr 66, illustrated on Plate VIII, 1.

Repository: Forschungsstelle für Paläobotanik, Geologisch-Paläontologisches Institut, Westfälische Wilhelms-Universität, Münster, Germany.

Type locality: Wadi Himara, in the incised river valley, ca. 400 m upstream along the southern branch after the main bifurcation at 31° 37' 55.67" N and 35° 37' 15.69" E.

Stratigraphic horizon: Silt and clay layers and lenses, 15.5–16.5 m above the base of the Um Irna Formation, Upper Permian.

Etymology: The name refers to the Jordan Valley, the rift structure of which the Dead Sea is a part.

Table 1
A comparison between *Dicroidium irnensis*, *D. jordanensis* and *D. robustum*

	<i>Dicroidium irnensis</i>	<i>Dicroidium jordanensis</i>	<i>Dicroidium robustum</i>
Position of the pinnules	Densely spaced, sometimes overlapping	Densely spaced only in the lower pinnae and towards the pinna apices	Densely spaced, sometimes almost overlapping
Shape of the pinnules	Broad, trapezoid with rounded apex; broadly attached, not decurrent	Asymmetrically tongue-shaped to triangular, often slightly constricted just above the pinnule base, apex obtuse to acute; decurrent	Broad, trapezoid with rounded apex; broadly attached, not decurrent
Size of the pinnules	2.5–9 mm, usually 4–6 mm long 2–6.5 mm wide	4–7.5 mm, usually 4–5 mm long 1.7–4.5 mm wide	5–15 mm long Up to 10 mm wide
Shape of the pinna terminals	Large, broadly tongue-shaped, consisting of 3–5 fused pinnules	Relatively small, usually rather narrow, sometimes even lanceolate	Very large, broadly tongue-shaped, consisting of 5–6 fused pinnules
Length and width of the pinna terminals	12–20 mm long 6.5–9 mm wide	Up to 7 mm long 1.5–3 mm wide	Up to 40 mm long Up to 14 mm wide
Distribution of stomata	Leaves amphistomatic, but stomata mainly on the lower cuticle; stomata on the upper surface are restricted to the pinna axes and the pinnule bases; most of the upper pinnule surface lacks stomata	Leaves amphistomatic; although stomata are less frequent on the upper than on the lower pinnule surface, they occur over the entire upper and lower pinnule surfaces and the pinna axes	Leaves amphistomatic, stomata common on both sides and scattered all over the pinnule lamina but more frequent on lower pinnule surface
Orientation of the stomata on the lower pinnule surfaces	Randomly oriented	Stomatal pores more or less aligned in the same direction, evenly distributed	Randomly oriented
Shape of the stomata	Mostly with 4–5 subsidiary cells, the polar ones are more strongly cutinised than the lateral ones; stomata with a ring of 5–6 subsidiary cells occur also, but are less frequent; incompletely dicyclic stomata occasionally present; subsidiary cells often strongly cutinised, especially on the upper pinnule surface	Stomata usually with a ring of 4–7 (average 5); stomata with 4 subsidiary cells often have 2 lateral ones at each side??; all epidermal cells equally strongly cutinised	Mostly with 4 subsidiary cells, the polar ones are more strongly cutinised than the lateral ones; stomata with a ring of 4–6 subsidiary cells occur very rarely; each guard cell bearing a very prominent longitudinal ledge
Papillae	Present but rare and small, mainly restricted to the lower pinnule surfaces, randomly distributed	Present on the upper pinnule surface, but small; mostly lacking	Very rare
Trichomes	Rather common on the frond axis but far less common on the pinna axes, very rare on the lower pinnule surface, randomly distributed	Present, mostly restricted to the rachis, pinna axes and the basal and marginal parts of the pinnules; more common on the upper pinnule surfaces	Relatively common

Diagnosis:

Fronds small, bifurcated, bipinnate. Primary axis robust and smooth, bifurcating with an angle of approximately 25°. At least

two pairs of pinnae are inserted below the bifurcation; frond portions above bifurcation more-or-less ovate in outline, tapering towards the apices and with their greatest width in

Table 2
Morphological comparison between the three species from the Dead Sea region and Early Triassic *Dicroidium* species

	Frond	Pinnules
<i>D. hughesii</i>	Pinnate, occasionally bipinnatifid	Alethopteroid, very large
<i>D. irnensis</i> *	Bipinnate	Odontopteroid, small
<i>D. jordanensis</i> *	Bipinnate	Odontopteroid, small
<i>D. narrabeenense</i> *	Pinnate to bipinnatifid	Alethopteroid, elongate, narrow with acute apex, bipinnatifid forms with strongly fused pinnules
<i>D. nidpurensis</i> *	Bipinnate (without basal bifurcation?)	Alethopteroid, lateral margins crenulate
<i>D. pinnis-distantibus</i>	Pinnate	Alethopteroid, very long and narrow, widely spaced
<i>D. robustum</i> *	Bipinnate	Odontopteroid, large and broad
<i>D. voiseyi</i>	Pinnate	Alethopteroid, very long and narrow
<i>D. zuberi</i> *	Bipinnate	Odontopteroid; large and broad, rhomboid

Taxa which can be further differentiated on the basis of epidermal characters are marked with an asterisk (*). For a detailed comparison of *D. irnensis*, *D. jordanensis* and *D. robustum* see Table 1.

the middle. Pinnae alternating to suboppositely attached, at angles of between 30° and 70°, bearing up to 17 pinnules at each side. Pinnules normally widely spaced but sometimes overlapping, in alternating or subopposite position; pinnules broadly attached, decurrent, asymmetrical, tongue-shaped to triangular in outline with rounded-to-acute apices pointing towards pinna apices. Basiscopic pinnules more obliquely attached than acroscopic pinnules; basal basiscopic pinnule semi-circular in outline. Pinnae ending in elongated, narrow terminal pinnules usually consisting of 2–3 strongly fused pinnules. Intercalary pinnules occasionally present, asymmetrically triangular and smaller than normal pinnules.

Leaves amphistomatic; stomata more abundant on lower than on upper leaf surface. Cells of upper leaf surface up to twice as large as those on lower surface. Normal epidermal cells isodiametric to elongated, rectangular. Stomatal complexes with two slightly sunken guard cells, partly underlying the adjacent subsidiary cells. Stomatal apparatus monocyclic to incomplete dicyclic with a ring of four to seven subsidiary cells; subsidiary cells similarly cutinised as normal cells.

5.2. Additional observations

The frond axis of *Dicroidium jordanensis* is narrower than that of *D. irnensis*, being 2–8 mm wide below the bifurcation and 4, occasionally up to 6 mm wide above the bifurcation. The pinnae are up to at least 9 cm long. Several, up to six pinnae may be present below the bifurcation (Plate VIII). The lower ones largely consist of strongly fused pinnules, whereas the ones just below the bifurcation show well differentiated pinnules. The lower pinnules in the interior of the frond strongly resemble the lower ones below the bifurcation (Plate IX, 2).

Pinnules are usually longer than wide, with a length-width ratio from 2:1 to 3:2. Pinnules are normally 4–5 mm long, but pinnules up to 7.5 mm long have occasionally been found. The width varies from 1.7 to 4.5 mm. Basal pinnules are often trapezoid to tongue-shaped and rounded (Plate IX, 2–3; Plate X, 1–2), those in the middle pinna portions asymmetrical trapezoid to triangular with more or less acute apices (Plate IX, 1; Plate X, 1–2; Plates XI–XII), and those of the apical frond portions rather narrow, triangular, inserted at a very low angle and pointing towards the pinna apices (Plate IX, 4; Plate X, 3–9; Plates XIII–XIV). Terminal pinnules are relatively narrow and ca. 7 mm long and 1.5 to 3 mm wide (Plate IX, 4; Plate X, 3–8).

The cells of the lower pinnule surfaces and pinna axes are smaller than those of the upper pinnule surfaces and pinna axes (cf. Plates XI–XII and Plates XIII–XIV). The normal cells of the upper side of the pinna axis are 36–108 μm (average 67 μm) long and 12–37 μm (average 24 μm) wide, and those of the lower side are 33–70 μm (average 52 μm) long and 10–30 μm (average 23 μm) wide. The normal epidermal cells of the upper pinnule surfaces are 38–72 μm (average 56 μm) long and 25–37 μm (average 32 μm) wide, and those of the lower pinnule surfaces are 32–58 μm (average 46 μm) long and 21–32 μm (average 28 μm) wide. Small, short, hollow, papillae, being up to 20 μm wide and high, may be present on the cells of the upper leaf surface (Plate XVII, 1–3. 7–9). Papillae are usually

positioned in the centre of a cell; papilla-bearing cells occasionally show vague striae radiating from the centre of the cell. Papillae are absent on the lower leaf surface. Less than 20% of the several thousand pinnules obtained by bulk maceration bear papillae, most of them only have papillae on the pinna rachides and in the basal parts of the pinnules.

Stomata on the upper pinnules surface are rather regularly distributed, near the pinnule margins and apex often in bands parallel to the pinnule margins (Plate XI; Plate XIII), occasionally also more or less arranged in longitudinal rows. Stomata on the lower pinnule surfaces are evenly distributed (Plate XII; Plate XIV). The most common type of stomatal apparatus has four to seven (usually five) subsidiary cells, encircling the stoma (Plate XV, 1; Plate XVI, 1–8). In internal view the guard cells are wide with faintly developed wood lamellae and each guard cell bears an outward projected, strongly cutinised longitudinal ridge or flange along the margin. The guard cells of the stomata are narrow in external view. Those of the upper pinnule surface are 4–7 μm wide and 26–66 μm (average 43 μm) long and those of the lower pinnule surface are 23–70 μm (average 49 μm) long. The lateral subsidiary cells are relatively wide. These subsidiary cells are 7–18 μm (average 12 μm) long and 8–15 μm (average 11 μm) wide. Subsidiary cells, particularly those of the stomata of the upper pinnule surface, may bear variably sized, irregularly shaped, often somewhat granular thickenings on the periclinal walls (Plate XVI, 1–7). Although most pinnules show such irregular thickenings, they are most prominently developed in pinnules with rather thick anticlinal walls and (abundant) papillae (Plate XVI, 1, 2, 4, 7). Such irregular thickenings rarely are present on the lower pinnule surfaces, but most stomatal complexes of the lower pinnule surface do not show such thickenings, and, if present, they are always less prominent than on the corresponding upper pinnule surface. One cuticle with rather thick anticlinal walls and strongly cutinised subsidiary cells shows an aberrant stomatal apparatus consisting of one or two (incomplete) rings of strongly cutinised neighbouring cells, encircling a ring of very weakly cutinised subsidiary cells and two weakly cutinised guard cells (Plate XVI, 9).

Trichomes (Plate XVI, 2, 4–6, 10; Plate XVIII, 1, 3, 6) are quite rare and mainly restricted to the frond rachis, the pinna axes and the basal and marginal parts of the pinnules; they occur on both the upper and lower pinnule surfaces, although they are more common on the upper surfaces. Trichome bases consist of four to seven radially arranged cells; the anticlinal walls in the interior part of the structure are usually more strongly cutinised. The trichome bases bear a (single?) globular cell (Plate XVII, 2, 5–6, 10), which is sometimes missing (Plate XVII, 4; Plate XVIII, 1, 3, 6). The presence of trichomes is apparently related to the presence of papillae, the thickness of anticlinal walls, and the degree of cutinisation of the subsidiary cells; trichomes are most common in pinnules with abundant papillae, thick-walled cells, and strongly cutinised subsidiary cells.

5.2.1. Discussion

Dicroidium jordanensis is a much more delicate form than *D. irnensis*, with thinner frond and pinna axes and more slender

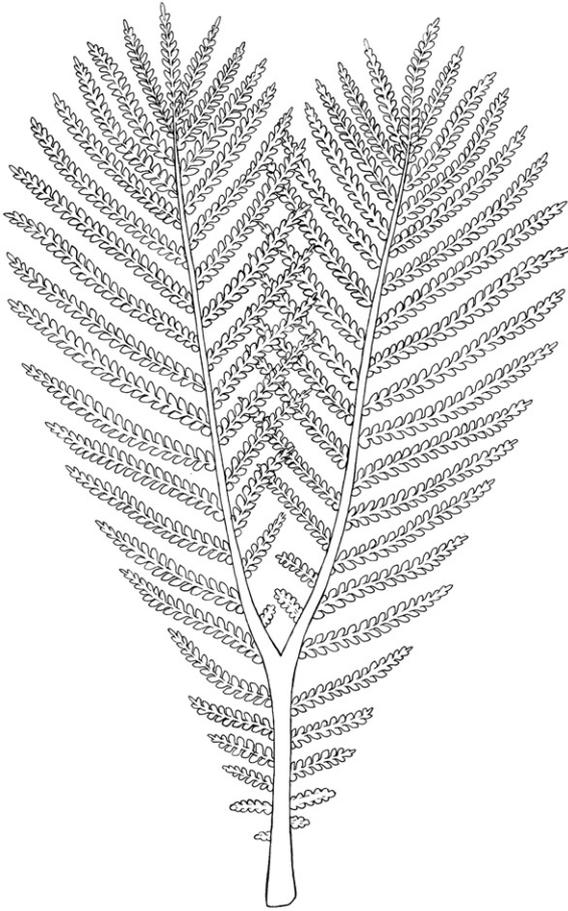


Fig. 4. Tentative reconstruction of a *Dicroidium jordanensis* frond.

pinnules. The entire full-grown frond (Fig. 4) was probably not longer than 30 cm. A specimen showing a widened frond base (Plate VIII, 1) suggests that an abscission tissue was present and that complete fronds were dropped. The largest specimen, which has been selected as the holotype, was probably a complete frond, but because cuticles have peeled off, the right part of the fork and the apical parts of the frond are not preserved. The venation of *D. jordanensis* is not known. Only very few compression specimens show some very faint veins, suggesting that the venation was odontopteroid, however, the number of veins seems to have been less than in *D. irnensis*; cuticles do not show a clear differentiation into costal and intercostal fields and therefore give no information on the venation.

Although the guard cells are partly underlying the subsidiary cells, they are not strongly sunken. The presence of stomata over the entire upper leaf surface, the relatively thin cuticles and the virtual absence of papillae in most of the specimens studied suggests that *Dicroidium jordanensis* grew in rather humid environments.

Dicroidium jordanensis is less common than *D. irnensis*, although it is still very well represented. Larger specimens of both species are often found on the same slab, suggesting that they grew together and preferred the same habitat.

5.2.2. Comparisons with other taxa

As stated before *Dicroidium jordanensis* shows some superficial similarities with *D. irnensis*. The main differences

are the shape of the pinnules. Pinnules of *D. jordanensis* are narrower than those of *D. irnensis*. In the middle portions of the pinnae, pinnules of *D. jordanensis* are asymmetrically trapezoid but otherwise they are asymmetrically triangular. Even more striking is the difference in shape of the terminal pinnules. The pinna terminals of *D. irnensis* are large, broad, trapezoid and obtuse, whereas those of *D. jordanensis* are asymmetrically triangular and much narrower. Also, the spacing of the pinnules differs in the two species; pinnules are densely spaced, often even overlapping in *D. irnensis*, whereas they are rather loosely positioned in *D. jordanensis*. Another clear difference is the shape of the pinna terminals, which are much larger in *D. irnensis*. Even more striking are the differences in the cuticles. In *D. irnensis* the upper cuticles of the pinnules hardly have any stomata, only a few at the pinnule bases, whereas stomata occur over the entire upper pinnule surface of *D. jordanensis*. Also the shape of the stomata differs considerably. In *D. jordanensis* stomata usually have a ring of 5–6 subsidiary cells, whereas the stomata of *D. irnensis* usually have two lateral, weakly cutinised subsidiary cells and two normally cutinised polar ones. Therefore, dispersed, fragmentary cuticle remains can easily be identified. The main differences between the two species are summarised in Table 1.

In its gross morphology *Dicroidium jordanensis* also shows some superficial resemblances with *D. superbum* f. *townrowii* (Retallack) Anderson et Anderson. This taxon was first described from the Ladinian of Australia and has also been recorded from the Carnian of South Africa. Although these taxa are morphologically quite similar, they differ considerably in their epidermal anatomy. *Dicroidium jordanensis* does not show the differentiation into coastal and intercostal fields that is typical for *D. superbum*. Moreover, the stomata of *D. superbum* are very different from those *D. jordanensis*. In the latter species, stomata are not sunken and subsidiary cells are not strongly cutinised as in *D. superbum*. The stomata of *D. jordanensis* are much more similar to those of species like *D. elongatum* (Carruthers) Archangelsky (cf. Anderson and Anderson, 1983, plate 103, figs. 3–4, 7–8) and *Dicroidium narrabeenense* (Dun in Walkom) Jacob et Jacob (cf. Jacob and Jacob, 1950, figs. 8A and 9). However, *D. elongatum* and *D. narrabeenense* have a very different gross morphology. *Dicroidium elongatum* has pinnate fronds with long, very narrow, lanceolate to sphenopteroid pinnules. *Dicroidium narrabeenense* has pinnate fronds with narrow pinnules to bipinnate fronds with narrow, largely fused (pinnatifid) pinnules [= *D. dubium* var. *australe* (Jacob et Jacob) Retallack].

Dicroidium robustum Kerp et Vörding nov. sp. (Plates XIX–XX)

Holotype: Specimen PbO S103, illustrated on Plate XIX, 1.

Repository: Forschungsstelle für Paläobotanik, Geologisch-Paläontologisches Institut, Westfälische Wilhelms-Universität, Münster, Germany.

Type locality: Wadi Himara, in the incised river valley, ca. 400 m upstream along the southern branch after the main bifurcation at 31° 37' 55.67" N and 35° 37' 15.69" E.

Stratigraphic horizon: Silt and clay layers and lenses, 15.5–16.5 m above the base of the Um Irna Formation, Upper Permian.

Etymology: The epithet refers to the very robust pinnules.

Diagnosis:

Bifurcated(?) fronds, bipinnate, with very large pinnules. Pinnules densely spaced, broadly tongue-shaped to rhomboidal apices rounded. Pinna terminals large, tongue-shaped, consisting of several fused pinnules.

Leaves amphistomatic; stomata randomly distributed on upper and lower pinnule surface, abundant on upper pinnule surface and comparatively more abundant on lower pinnule surface. Epidermal cells of upper pinnule surface larger than those of lower pinnule surface. Anticlinal walls very thin. No differentiation into costal and intercostal fields. Stomata randomly distributed and oriented. Guard cells with very prominent stomatal ledges and wood lamellae. Stomatal complexes usually with four subsidiary cells, usually two lateral, slightly weaker cutinised subsidiary cells and two normally cutinised polar cells; lateral neighbouring cells usually longer than guard cells.

5.3. Additional observations

The pinnules of *D. robustum* are much larger than those of *D. irnensis* and *D. jordanensis*. The pinnae are relatively short and bear a small number of up to 0.5–1.5 cm long and 1 up to 1 cm wide asymmetrically trapezoid pinnules and a large, up to 4 cm long and 1.4 cm wide tongue-shaped terminal pinnule (Plate XIX, 2). In addition, single pinnules are occasionally encountered in bulk macerations.

The leaves are amphistomatic with abundant stomata on the upper pinnule surface (Plate XX, 1) and even more on the lower surface (Plate XX, 2). The cells of the upper pinnule surface are larger than those of the lower pinnule surface. The cells of the upper pinnule surface are 40–85 μm (average 59 μm) long and 17–50 μm (average 36 μm) wide. The stomata are somewhat similar to those of *Dicroidium irnensis*, in having two thinner cutinised lateral subsidiary cells and two normal polar subsidiary cells (Pl XX, 4–7), although also here stomatal complexes with more than four (usually up to six) subsidiary cells occur occasionally. The stomatal pores on the upper pinnule surface are 25–50 μm (average 36 μm) long. The lateral subsidiary cells of *D. robustum* are often longer than the guard cells, usually 1.5 times as long (Plate XX, 4–7). Often a set of lateral neighbouring cells is present (Plate XX, 6). Sometimes the stomata seem to be slightly sunken, especially on the lower pinnule surface. The guard cells each bear a well developed, thick longitudinal ledge (Plate XX, 4–7) and they show very prominent wood lamellae (e.g., Plate XX, 7). In the few specimens that are available the guard cells are often damaged, but those that are intact are remarkably large. Only few examples of cuticles of lower pinnule surfaces were available for study. The epidermal cells of the lower pinnule surface are 25–80 μm (average 56 μm) long and 17–50 μm (average 34 μm) wide. The stomata of the lower pinnule surface are of the same type as on the upper pinnule surface, but slightly smaller and even still more numerous and stomatal complexes with more than four guard cells are more frequent; stomatal pores are 20–50 μm (average 36 μm) long. The stomata are slightly sunken on the lower pinnule surface.

5.3.1. Discussion and comparisons with other taxa

Only a few megafossils of *Dicroidium robustum* have been collected. The preservation of this material is much more fragmentary than that of the two previously described species. The specimens are very difficult to photograph because cuticles started to peel off soon after the plant-bearing surfaces were exposed, not leaving a clear impression behind. Moreover, pinnules rapidly broke up into smaller parts. The largest specimen shows parts of two rachides lying at an angle of c. 25°, strongly suggesting that they formed part of a bifurcated frond.

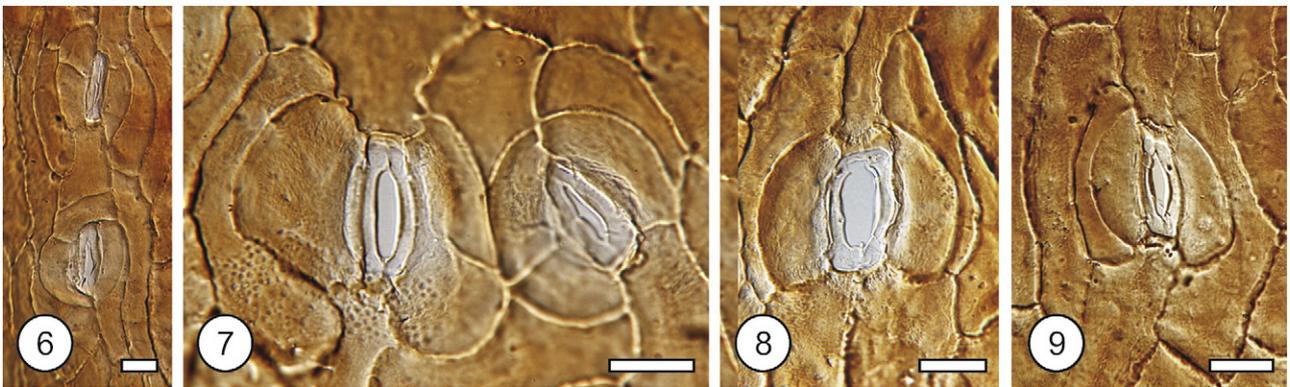
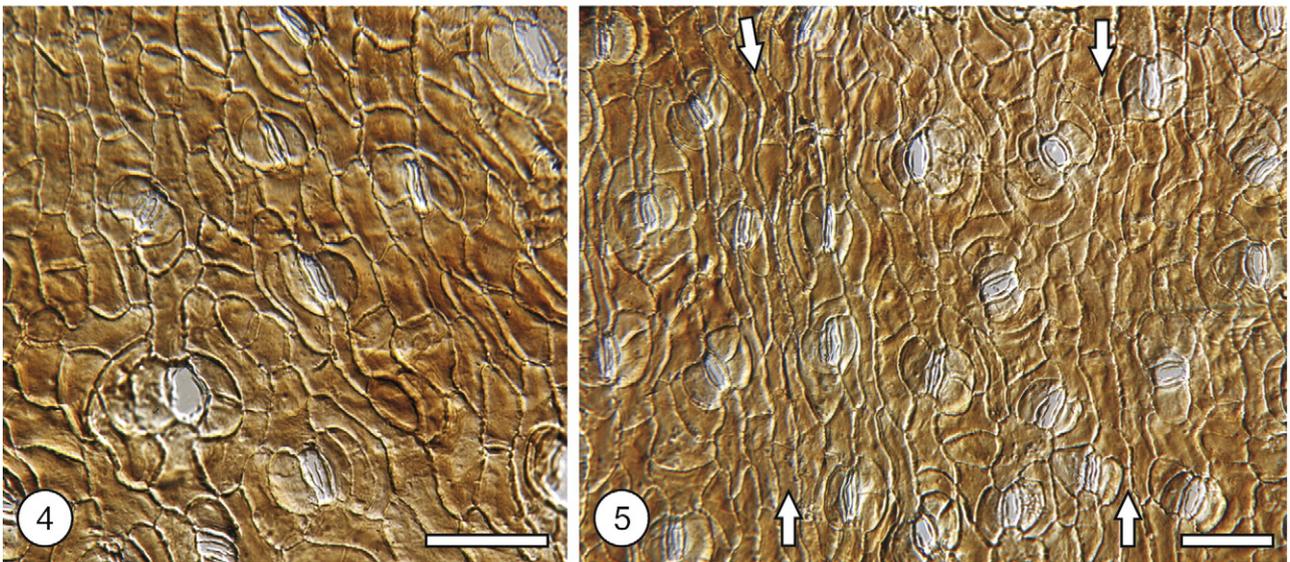
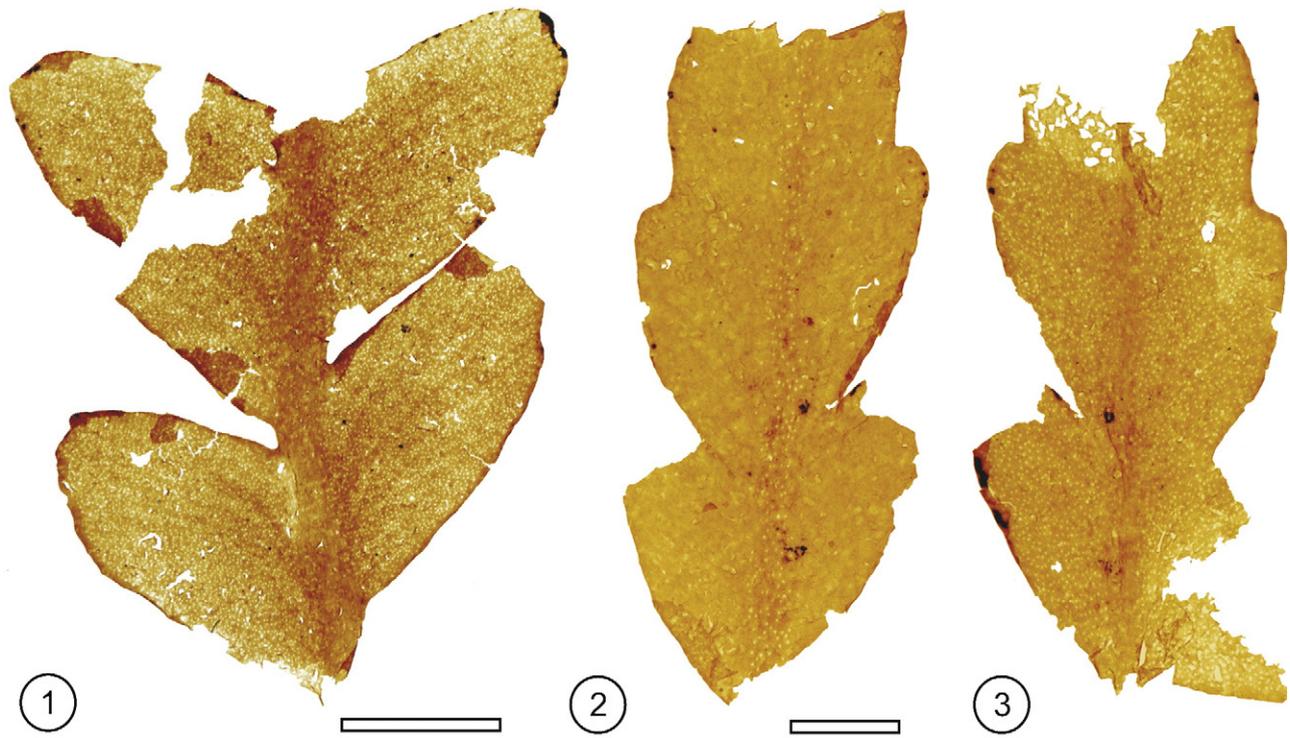
None of the other *Dicroidium* species with amphistomatic leaves (see Anderson and Anderson, 1983, p. 195–198) have such large pinnules and these species have pinnate fronds. The cuticle of *Dicroidium robustum* shows some superficial similarities with *D. irnensis* with regard to the shape of the pinnules and the epidermal anatomy. The normal pinnules of *D. robustum* have more or less the same shape as those of *D. irnensis* but they are at least twice as large. *D. robustum* differs from *D. irnensis* in having many stomata on the entire upper pinnule surfaces, whereas in *D. irnensis* stomata occur on the upper surface only over the pinna rachides and in the basal parts of the pinnules. Moreover, the stomata of *D. robustum* have a more irregular appearance and the most striking difference is the presence of very well developed, strongly cutinised stomatal ledges and prominent wood lamellae, which are both lacking in *D. irnensis*.

5.4. *Dicroidium* sp. (Plate XXI; Fig. 5)

In addition to the three *Dicroidium* species described above, another species has been encountered, here informally referred to as *Dicroidium* sp. Two specimens of a species superficially resembling *Dicroidium irnensis*, but having larger pinnules, apparently lacking the large tongue-shaped terminal pinnules and clearly showing a different epidermal anatomy, have been obtained by bulk maceration. One fragment, of which only the lower pinnule surface is preserved, shows two complete and two incomplete pinnules (Plate XXI, 1). In this specimen the venation is relatively well recognisable. The second fragment is a relatively narrow part of a pinna with strongly asymmetrical, largely fused, relatively narrow pinnules (Plate XXI, 2–3). Of this second specimen, cuticles of both the upper and lower pinnule surface are preserved.

The pinnules are up to 12 mm long and 7 mm wide, broadly tongue-shaped, asymmetrical and have a rounded apex. The venation is odontopteroid with up to five veins entering each pinnule; a clear midvein is lacking but the one or two veins entering the pinnule in the middle are more prominent than the others (Fig. 5). The veins bifurcate up to three times.

The leaves are amphistomatic but on the upper leaf surface stomata are restricted to the pinna rachides and the basal parts of the pinnules; they are lacking on the rest of the pinnule surface. Stomata are very common on the lower pinnule surfaces but very rare over the pinna rachides. Both the upper and lower pinnule surfaces show a differentiation into costal and intercostal fields, although this is much better developed on the lower pinnule surfaces.



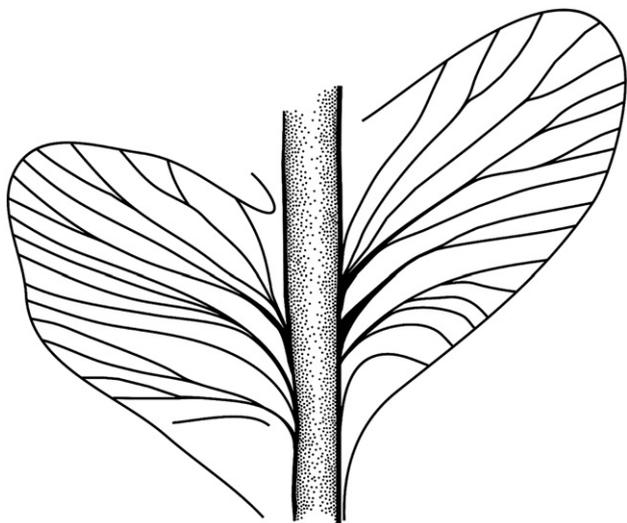


Fig. 5. Presumed venation pattern of *Dicroidium* nov. sp.

Cells of the upper pinnule surface are 26–73 μm (average 45 μm) long and 12–26 μm (average 19 μm) wide. Costal fields of the lower pinnule surface (Plate XXI, 4–5) are up to five cells wide and cells of the costal fields are 28–108 μm (average 52 μm) long and 8–27 μm (average 14 μm) wide; cells of the intercostal fields are 21–64 μm (average 37 μm) long and 9–29 μm (average 18 μm) wide. Cell walls are often slightly bent to sinuous; anticlinal walls often show small, irregular thickenings. Stomata occur in the costal and in the intercostal fields; the stomatal pores are often oriented parallel to the veins or perpendicular to the veins, rarely randomly oriented. Stomatal pores are 13–24 μm (average 18 μm) long. Stomata (Plate XXI, 4–7) have 4–6 subsidiary cells (average number: 4.68), with a lateral subsidiary cell at each side, and one or two cells at the polar sides; lateral subsidiary cells are very rarely transversely subdivided, but longitudinal cell divisions have often resulted in an incomplete double ring of subsidiary cells (Plate XXI, 8–9). All subsidiary cells are normally cutinised.

Although *Dicroidium* sp. shows some superficial similarities to *D. irnensis*, the differences between the two species are obvious. The former species has much larger pinnules, which are more pointed, and pinna terminals are much more slender. Moreover, there are a number of striking differences in epidermal anatomy. The lower pinnule surface of *D. sp.* shows a very clear differentiation into costal and intercostal

fields, which is completely lacking in *D. irnensis*. Stomata are not randomly oriented and all subsidiary cells are normally cutinised in *D. sp.*, whereas they are randomly oriented with two weaker cutinised lateral subsidiary cells in *D. irnensis*. Nevertheless, one may wonder whether *D. sp.* is not a full-grown form of *D. irnensis*. We feel that this option can be excluded because we bulk-macerated several kilos of sediment, which yielded thousands of complete pinnules, all of them being rather small but for two larger pinnules, showing the typical characteristics of *D. sp.* If *D. sp.* were a full-grown form of *D. irnensis*, one would have expected to find a series of intermediate forms showing a gradual transition between them. The cuticles clearly show that the material here assigned to *Dicroidium* sp. belongs to a fifth, still undescribed *Dicroidium* species. We refrain from formally establishing a new species because we feel that more material is needed for an adequate characterisation and to understand its natural variability.

5.5. Other plant remains from the Um Irna locality

Some other plant remains have been recorded from the Um Irna locality. Most common are charcoal fragments. These are described in a separate paper (Uhl et al., 2007). Furthermore, a few unidentifiable axis fragments, some pectopterid fern pinnules, and a fragment of taeniopterid foliage have been found. Because the latter has excellent cuticular preservation which enables an emendation of the diagnosis of the species that has been found in another locality in the Um Irna Formation, it is described in more detail.

Doratophyllum jordanicus Mustafa emend. Kerp et Vöröding (Plate XXII)

Doratophyllum jordanicus Mustafa 2003, N. Jb. Geol. Paläont. Mh., 2003(1), p. 40–44, figs. 3–10.

Original diagnosis (Mustafa, 2003, p. 40–42)

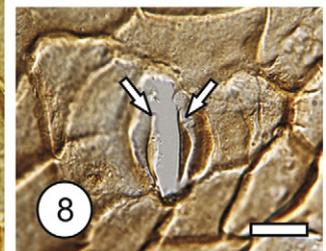
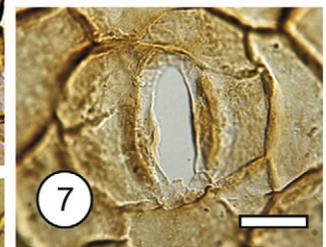
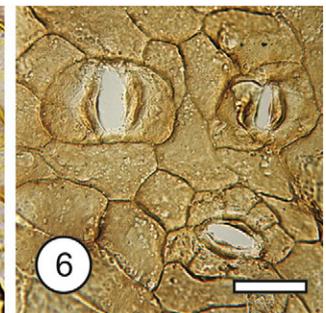
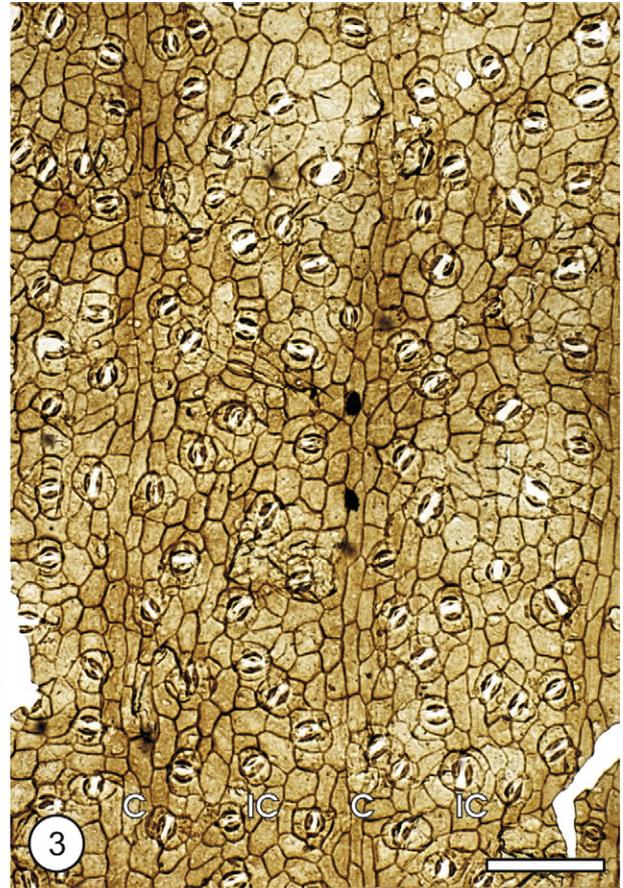
“Lanceolate leaves up to more than 30 cm long and 7 cm wide, with midrib 1–9 mm thick and more or less perpendicular lateral veins of about 26–40 mm per 10 mm. Leaf and lamina margins entire, stomata of haplocheilic type, subsidiary cells 3–6 arranged as a ring around the guard cells.”

5.6. Emendation of the specific diagnosis

The specific diagnosis given by Mustafa (2003, p. 40–42) can be emended by adding information on the epidermal anatomy:

Plate XXI. *Dicroidium* sp. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan.

1. Cuticle of the lower surface of a pinna with four pinnules showing the venation. Slide No. S53L/0002. Scale bar = 5 mm.
- 2 + 3. Cuticles of the apical portion of a pinna with short pinnules. 2 = Upper pinnule surface with stomata largely restricted to the pinna rachis. 3 = Lower pinnule surface with stomata all over the pinnule but rare over the pinna rachis. Slide No. S53L+U/0001. Scale bar = 2 mm.
4. Cuticle of the lower pinnule surface. Slide No. S53L+U/0001. Scale bar = 100 μm .
5. Cuticle of the lower pinnule surface with costal fields characterised by elongate cells (between arrows). Slide No. S53L+U/0001. Scale bar = 100 μm .
6. Cuticle of the lower pinnule surface with two stomata in a costal field. Note the very long, narrow cells adjacent to the stomata. Slide No. S53L+U/0001. Scale bar = 25 μm .
7. Cuticle of the lower pinnule surface with two stomata in an intercostal field. Slide No. S53L+U/0001. Scale bar = 25 μm .
- 8 + 9. Stomata of intercostal fields. Note the long, sometimes crescent-shaped cells largely surrounding the lateral neighbouring cells. Slide No. S53L+U/0001. Scale bars = 25 μm .



Leaves amphistomatic. Epidermis of upper leaf surface clearly differentiated into costal and intercostal fields. Costal fields of upper leaf surface 1–6 (usually 3–4) cells wide; cells of costal fields elongated trapezoid–polygonal to rectangular. Intercostal fields 4–12 cells wide; cells usually shorter to isodiametric. Stomata restricted to costal fields, irregularly distributed and oriented; stomatal complexes usually monocyclic to incomplete dicyclic; guard cells with small flap-like ledges; 4–8 subsidiary cells per stomatal complex. Epidermis of lower leaf surface with narrower costal fields, 1–5 cells wide; intercostal fields up to 10 cells wide. Stomata more frequent on lower leaf surface, restricted to costal fields, more-or-less evenly distributed and randomly oriented. Stomata on lower leaf surface similar to those of upper leaf surface; stomata vary in shape, including monocyclic, incomplete dicyclic, and stomata without well-developed neighbouring cells.

5.7. Additional description

Cells of the costal fields of the upper leaf surface (Plate XXII, 1, 2) are 22–133 μm (average 76 μm) long and 21–72 μm (average 38 μm) wide, whereas those of the intercostal fields are 25–106 μm (average 62 μm) long and 21–65 μm (average 41 μm) wide. The guard cells are 44–69 μm (average 58 μm) long and 3–6 μm wide.

On the lower leaf surface (Plate XXII, 3), the cells of the costal fields are 42–148 μm (average 91 μm) long and 18–46 μm (average 28 μm) wide, and those of the intercostal fields are 15–71 μm (average 42 μm) long and 21–78 μm (average 45 μm) wide. The guard cells of the stomata are 24–45 μm (average 34 μm) long and 3–5 μm wide.

5.8. Discussion

Although only a single fragment has been found, its assignment to *Doratophyllum jordanicus* is clear, particularly when the cuticles are compared to those illustrated by Mustafa (2003), even though the latter are much more fragmentary. Our small hand specimen shows a c. 2 cm² piece of cuticle on which the parallel veins are clearly marked. The cuticle, which peels off very easily, is excellently preserved. This species was originally described from the upper part of the Um Irna Formation, where it is one of the most common taxa, and this find shows that, even though it is very rare, the species is also present in the lower part of the Um

Irna Formation. The original diagnosis only mentioned the shape of the stomatal complexes, thus, the emendation is given above.

6. General discussion

The occurrence of several *Dicroidium* species in the Upper Permian of Jordan is remarkable because these are the oldest unequivocal records of a genus that is generally considered to be typical for the Triassic of Gondwana. Therefore, comparisons of the Wadi Himara species with other early representatives of *Dicroidium* are of special interest. Also the stratigraphic occurrence and the palaeogeographical distribution of *Dicroidium* needs to be discussed. This is particularly the case in relation to other Permian floras from the Arabian Peninsula and adjacent regions, which are often characterised by a mixture of elements from different floral provinces. These factors also must be considered in relation to the end-Permian mass extinction and the subsequent global distribution of typical Mesozoic floras.

6.1. Comparisons of the Wadi Himara *Dicroidium* species with Early Triassic *Dicroidium* species

The age of the Wadi Himara material is critical and a comparison with early representatives of *Dicroidium* is of particular interest. Apart from *Dicroidium zuberi* and *D. narrabeenense*, which have already been discussed, several other *Dicroidium* species have been reported from the Lower Triassic (Olenekian). These are traditionally considered to be the earliest representatives of the genus. The species are *D. hughesii* (Feistmantel) Lele, *D. nidpurensis* Bose et Srivastava, *D. pinnis-distantibus* (Kurtz) Frenguelli, and *D. voiseyi* Holmes et Ash. Some of these forms show different frond morphology, having usually pinnate instead of bipinnate fronds like in *Dicroidium irnensis* and *D. jordanensis*. *Dicroidium pinnis-distantibus* has very narrow, extremely widely spaced pinnules. *Dicroidium nidpurensis* has bipinnate fronds. The pinnules are entire-margined to slightly wavy. The lower cuticle shows a very clear differentiation into costal and intercostal fields, unlike the two species from the Um Irna Formation. It should be noted that the typical bifurcation has not been demonstrated for *D. nidpurensis*. Also regarding its alethopteroid venation it may be questioned whether this species could not better be accommodated in *Thinnfeldia* or *Pachypteris*. *Dicroidium voiseyi* has very long,

Plate XXII. *Doratophyllum jordanicus* Mustafa emend Kerp & Vörding. Um Irna Formation, Upper Permian; Wadi Himara, Dead Sea Region, Jordan.

1. Cuticle of the upper leaf surface. 1. Slide S102U/001; scale bar = 500 μm .
2. Cuticle of the upper leaf surface showing the clear differentiation into costal (= C) and intercostal fields (= IC), and the random orientation of the stomata. Slide S102U/001; scale bar = 200 μm .
3. Cuticle of the lower leaf surface showing the clear differentiation into costal (= C) and intercostal fields (= IC), and the random orientation of the stomata. Slide S102U+L/002; scale bar = 200 μm .
4. Cuticle of the upper leaf surface with stoma showing a small flap-like ledge on each guard cell. Slide S102U/001; scale bar = 50 μm .
5. Stoma of the upper leaf surface. Slide S102U/001; scale bar = 25 μm .
6. Cuticle of the lower leaf surface with three stomata. Note the variation in stomatal morphology, varying from stomata with two subsidiary cells (left above) to stomata with a ring of six subsidiary cells (right below). Slide S102U+L/002; scale bar = 50 μm .
7. Stoma of the upper leaf surface. Slide S102U/001; scale bar = 25 μm .
8. Stoma of the upper leaf surface with well-developed flap-like ledges on the guard cells. Slide 102U/001; scale bar = 25 μm .

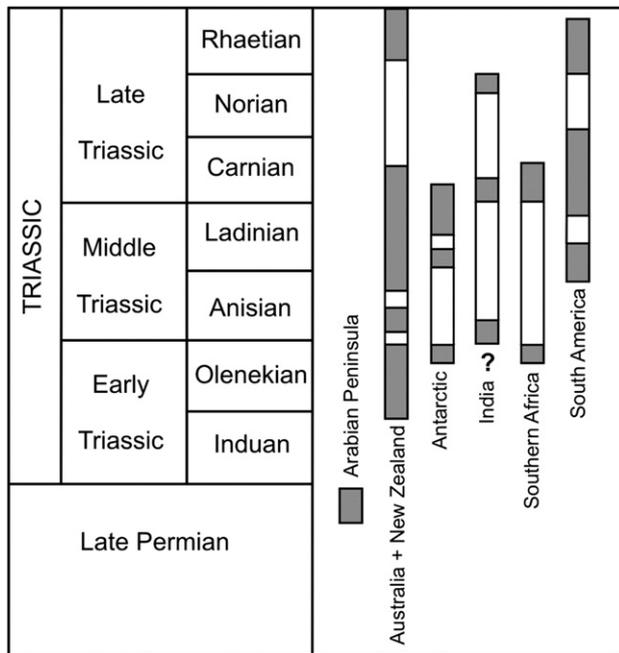


Fig. 6. Stratigraphic ranges of the genus *Dicroidium* in the Middle East and various parts of Gondwana. Ranges based on Anderson and Anderson (1983) and more recent literature.

narrow pinnules. The main gross morphological differences are summarised in Table 2.

6.2. Climatic and ecological considerations on *Dicroidium* from Wadi Himara

The palaeogeographical position of the Dead Sea region at c. 15°S (see e.g., Baud et al., 1993; Ziegler et al., 1997; Stampfli and Borel, 2001) indicates that the Wadi Himara flora grew in a (sub) tropical lowland area. The lithology of the Um Inna Formation and the cuticles provide further information on the climate and ecology of the Wadi Himara flora. Soils with pisolithes similar to those in the

middle and upper part of the Um Inna Formation, are typically formed in hot and humid climates with a high annual rainfall and a short dry season (Driessen et al., 2001). Also the epidermal features of the three *Dicroidium* species suggest humid conditions. The cuticles are not extraordinarily thick and leaves are amphistomatic. Stomata are very abundant, even when they are as in *Dicroidium irnensis*, mainly restricted to the lower pinnule surface. Moreover, the stomata are not sunken and the guard and subsidiary cells not thickened. Papillae are rare or even completely absent. The mass occurrence of *Dicroidium* in fluvial sediments, including larger, rather delicate frond segments, excludes long-distance transport. Therefore, we conclude that these plants grew along rivers and streams and around abandoned river channels. Recent observations that corystosperm vegetation was not very diverse (Artabe et al., 2007) seem to be confirmed by the Wadi Himara flora.

6.3. The stratigraphic and geographic distribution of *Dicroidium*

As has been outlined above, several *Dicroidium* species have been recorded from the Olenekian (Lower Triassic), but the genus is most common in the Middle and Upper Triassic. *Dicroidium callipteroides* has been considered as the earliest representative of the genus. The species is known from the basal part of the Narrabeen Group in the southern coalfield and western margin of the Sydney Basin (New South Wales, Australia), which is Early Triassic in age. The species has lent its name to the *Dicroidium callipteroides* Oppel Zone, the lowermost floral zone of the Triassic (Retallack, 1977, 1995). However, based on cuticular studies and associated fructifications, it was recently demonstrated that *D. callipteroides* does not belong to the corystosperms, but is a member of the peltasperms. Hence, this species could no longer be accommodated in *Dicroidium* and was transferred to *Lepidopteris* (Retallack, 2002). The oldest unequivocal representatives of *Dicroidium* (e.g., *D. narrabeenense*, *D. zuberi*) appear higher in the Narrabeen Group, i.e. in the upper Bulgo Sandstone and the Newport Formation, which are of early Olenekian (Smithian) age. The last occurrences of *Dicroidium*

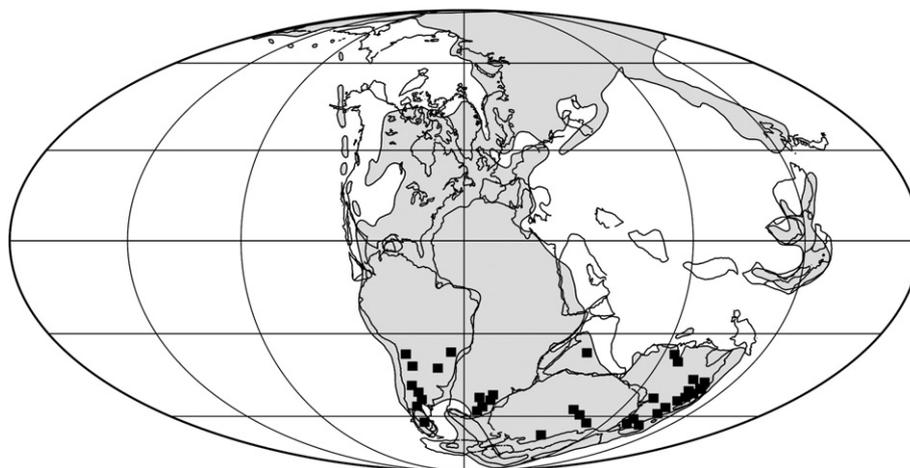


Fig. 7. The geographical distribution of *Dicroidium* in the Triassic. Map modified after Scotese (2002). Distribution of *Dicroidium* according to Anderson and Anderson (1983) and more recent literature.

have been reported from the Rhaetian (Retallack, 1977). The stratigraphic ranges of the genus *Dicroidium* in the various parts of Gondwana are shown in Fig. 6.

Dicroidium is a typical Gondwana taxon. It has been described from localities found at palaeolatitudes higher than 35°S in South Africa, Australia, New Zealand, India, Chile, Argentina and Antarctica (Anderson and Anderson, 1983). More recently the genus has also been recorded from other localities in Chile (e.g., Mohr and Schöner, 1985; Gnaedinger and Herbst, 2001), southern Brazil (e.g., Guerra-Sommer et al., 1999a,b), and the Antarctic (e.g., Pigg, 1990; Boucher et al., 1993; Meyer-Berthaud et al., 1993; Axsmith et al., 2000). There are two reports of *Dicroidium* from the Northern Hemisphere. Wagner (1962) illustrated a specimen from the uppermost Permian of Hazro (SE Turkey) as “? *Dicroidium* vel ? *Thinnfeldia*”. This specimen was later identified as *Botrychiopsis* sp. (Archangelsky and Wagner, 1983). Lejal Nicol and Klitzsch (1975) reported two species of *Dicroidium* from the Jurassic of the Murzuk Basin (Libya). They mentioned the occurrence of *Dicroidium odontopteroides* (Morris) Gothan, but this species was not illustrated. The figured specimen of *D. nidpurensis* is very fragmentary, showing only a few pinnules with an alethopteroid venation. Neither the specimen illustrated from Libya nor the type material from Nidpur (Madhya Pradesh, India; Bose and Srivasta, 1971) shows a bifurcation of the frond, which is typical for *Dicroidium*. It can therefore be concluded that the material from the Dead Sea region is the first unequivocal report from the Northern Hemisphere. The geographical distribution of *Dicroidium* during the Triassic is shown in Fig. 7. This map shows that the Dead Sea occurrence is located at least 25° further north than the northern limit of its distribution area during the Triassic.

6.4. Middle and Late Permian from the Arabian Peninsula and adjacent regions

In the Late Permian, the Arabian Plate was connected to the northeastern part of the African Plate, and the Dead Sea region was a lowland area located at c. 15°S, well within the equatorial belt [Baud et al., 1993; Ziegler et al., 1997 (Fig. 9); Golonka and Ford, 2000; Dercourt et al., 2000; Stampfli and Borel, 2001 (Fig. 8)]. Comparisons of the Wadi Himara micro- and macroflora with Middle to Late Permian floras from the Palaeo- and Neotethys regions are of special interest with regard to considerations as to the palaeophytogeographical and palaeoecological significance of the Dead Sea plant fossils. Middle to Late Permian floras from this region include the Southern Alps (northern Italy), the Hazro flora from eastern Turkey, the Ga'ara flora from northwestern Iraq, several floras from Saudi Arabia and the Gharif flora from central Oman (Fig. 8).

The Late Permian floras from the Southern Alps (northern Italy) are generally dominated by conifers; *Ortiseia* Florin, *Majonica* Clement-Westerhof, *Pseudovoltzia* Florin, *Dolomitia* Clement-Westerhof, *Quadrocladus* Mädlar, and *Ullmannia* Göppert are the most common genera (Clement-Westerhof, 1984, 1987). Additional floral elements include peltasperms

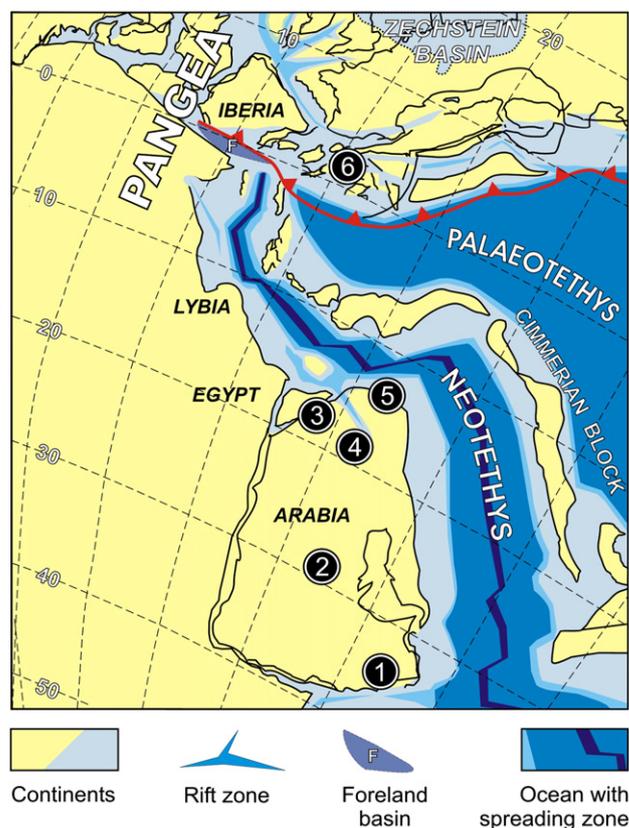


Fig. 8. Localities of Middle and Late Permian in the Tethyan Region: 1 = Oman: Euramerian, cathaysian and gondwanan elements (Middle Permian); 2 = Saudi Arabia: Euramerian, cathaysian and gondwanan elements (Late Permian); 3 = Um Irna Formation, Jordan: cathaysian and gondwanan elements (Late Permian); 4 = Western Iraq: Cathaysian elements (Late Permian); 5 = Eastern Anatolia: Euramerian, cathaysian and gondwanan elements (Late Permian); 6 = Southern Alps: Euramerian (and gondwanan?) elements. Map modified after Stampfli and Borel (2001).

(Poort and Kerp, 1990) and ginkgophytes. Virtually all gymnosperm taxa from the Southern Alps display xeromorphic features, including a thick cuticle, often with prominent papillae, and frequently in combination with strongly sunken stomata and heavily cutinised subsidiary cells. Moreover, most of the plants had thick fleshy leaves, and in some conifers, e.g., *Ortiseia*, the leaves were covered with closely spaced hairs (Clement-Westerhof, 1984). The floras of the Southern Alps probably represent xeric hinterland vegetation. Some genera from the Southern Alps are also known from the Germanic Zechstein, i.e., *Pseudovoltzia*, *Quadrocladus*, and *Ullmannia* (see e.g., Schweitzer, 1986). However, the microfloras of the Southern Alps differ from those of the Germanic Zechstein, but these differences are quantitative rather than qualitative (Kerp, 1996, 2000). The conifers, which are abundant in the floras from the Southern Alps, were apparently also present in the Arabian region. This is evidenced by the occurrence in the Wadi Himara microflora of (pre)pollen such as *Lueckisporites virkkiae* Potonié et Klaus, *Jugasporites delasaucei* (Potonié et Klaus) Leschik and *Nuskosporites dulhuntyi* Potonié et Klaus, which have been attributed to conifers (Looy et al., 1999; 2001). In the Um Irna Formation, these forms are relatively rare,

suggesting that these plants did not grow in the immediate vicinity of the area of deposition, but further away, probably in drier habitats.

A completely different flora has been described from the uppermost Permian of Hazro, eastern Anatolia, Turkey (Wagner, 1962; Archangelsky and Wagner, 1983). The composition of this flora, which includes numerous sphenopsids and several pectopterids, suggests a warm and humid environment. The flora contains several typical cathaysian taxa, i.e., *Lobatannularia heianensis* (Kodaira) Kawasaki, *Sphenophyllum* cf. *koboense* Kobatake, *Bicoemleptopteris hallei* Asama, *Fasciapteris hallei* (Kawasaki) Gu et Zhi, *Cladophlebis tenuicostata* (Halle) Archangelsky et Wagner, and *Pseudomariopteris hallei* (Stockmans et Mathieu) Wagner, but also gondwanan elements such as *Glossopteris anatolica* Archangelsky et Wagner and *Botrychiopsis* sp. Palaeogeographical reconstructions show that the Hazro flora was more or less equatorial (Dercourt et al., 2000). Cathaysian elements have also been recorded from Iraq, Saudi Arabia, and Oman.

A small flora, exclusively consisting of cathaysian elements, has been described from the Ga'ara region, western Iraq (Čtyroký, 1973). Although the age of this flora is not very well constrained, it can be regarded as Middle to Late Permian. This flora contains the typical cathaysian taxa *Lobatannularia heiansensis* and *Plagiozamites oblongifolius* Halle, together with *Pectopteris* sp., *Taeniopteris* sp. and *Protoblechnum* sp. The composition of this flora suggests a warm and humid environment.

Floral assemblages have been described from two members of the Middle Permian to Lower Triassic Khuff Formation in Qasim Province, Saudi Arabia (El-Khayal et al., 1980; Lemoigne, 1981a,b; Hill and El-Khayal, 1983; El-Khayal and Wagner, 1985; Hill et al., 1985; Wagner et al., 1985; Berthelin, 2002). According to Le Nindre et al. (1990) the Khuff Formation can be subdivided into five members. Plant fossils have been described from the Unayzah and Midnab members, which are both Late Permian in age. The flora from the Unayzah Member is dominated by several pectopterids and *Lobatannularia lingulata* (Halle) Kawasaki, the latter being a typical cathaysian form. Other cathaysian elements are *Fasciapteris hallei* (Kawasaki) Gu et Zhi and *Gigantonoclea* sp. This flora furthermore encompasses *Cladophlebis*, sphenopterids and a cordaite. An early marattialean fern was described as *Quasimia schijfsmae* (Hill et al., 1985). Based on the abundance of ferns and sphenophytes, the climate has been interpreted as warm and humid. The somewhat younger flora from the Midnab Member contains *Pseudovoltzia liebeana* (Geinitz) Florin, *Culmitzschia* sp., *Wattia texana* Mamay, *Discinites orientalis* Gu et Zhi and pectopterids (Hill and El-Khayal, 1983). Berthelin (2002; Broutin et al., work in progress) also mentions *Ullmannia bronni* Göppert, *Phyllothea australis* Brongniart, *Lobatannularia heianensis*, *L. multifolia* Kon'no et Asama, *Glossopteris formosa* Feistmantel, *G. decipiens* Feistmantel and *Arberia* sp. The flora from the Midnab Member represents a mixture of European-type conifers (*Pseudovoltzia*, *Ullmannia*, *Culmitzschia*), cathaysian forms (*Lobatannularia*, *Discinites*) and gondwanan elements (*Glossopteris*, *Arberia*, *Phyllothea*). The conifers were adapted to drier habitats, whereas the

sphenopsids indicate humid conditions. It may therefore be concluded that this association constitutes a mixture from different environments.

Another mixed flora has been reported from the Gharif Formation (Wordian) of central Oman, where rich macrofloras with a mixture of euramerican, cathaysian and gondwanan taxa have been found (Broutin et al., 1995; Berthelin, 2002; Berthelin et al., 2003, 2006). Typically European forms are *Otoviccia hypnoides* (Brongniart) Kerp et al., *Sigillaria brardii* Brongniart and *Calamites gigas* Brongniart and its fructification *Metacalamostachys dumasii* (Zeiller) Barthel. Cathaysian elements include *Gigantopteris* sp., *Gigantonoclea lagrellii* (Halle) Koidzumi, *Cathaysiopteris whitei* (Halle) Koidzumi, *Tingia* sp., *Tingiostachya* sp., *Lepidodendron acutangulata* (Halle) Stockmans et Mathieu, and *Sphenophyllum sino-coreanum* Yabe. Gondwanan taxa include seven species of glossopterids, i.e., *Glossopteris anatolica* Archangelsky et Wagner, *G. occidentalis* White, *G. damudica* Feistmantel, *G. taeniopteroides* Feistmantel, *G. angustifolia* Brongniart, *G. clamarginata* Anderson et Anderson, and *G. browniana* Brongniart. Several types of glossopterid fructifications have been found. *Sphenophyllum speciosum* (Royle) McClelland is another species that is widely distributed in Gondwana but that has also been reported from China and Korea. A new undescribed genus of comioid plant, originally found in north-central Texas (Chaney et al., 2007), is another remarkable genus from the Gharif flora. Also silicified wood remains and the palynoflora also show a mixture of elements from different floral provinces (Broutin et al., 1995; Berthelin et al., 2003).

Middle and Late Permian floras from the Arabian Plate thus often show a mixture of elements from several floral provinces. These mixed floras are explained as the result of the expansion and migration of taxa from other floral provinces to the Arabian region. A northward expansion of gondwanan elements is easily imaginable because, during the Permian, the Arabian Plate was still connected to the African Plate. During the Permian this block moved northwards and a number of typical gondwanan elements apparently adapted to gradually changing climatic conditions. The westward migration of cathaysian elements is more difficult to explain, because Cathaysia consists of a number of isolated blocks in the eastern part of the Tethys. Several palaeogeographical reconstructions have been proposed for the Middle–Late Permian (Baud et al., 1993; Scotese and Langford, 1995; Ziegler et al., 1997; Golonka and Ford, 2000; Dercourt et al., 2000; Stampfli and Borel, 2001; Crasquin-Soleau et al., 2001). One of the main differences between these palaeogeographical reconstructions is the position of Cathaysia (Fig. 9). The Ziegler et al. (1997) map is one of the few palaeogeographical reconstructions in which the Dead Sea region is not shown as marine but as a land mass.

It has been suggested that the migration of cathaysian plants into the Arabian region was primarily determined by the evolution of climatic and palaeogeographic conditions (Fluteau et al., 2001a,b). Cathaysian elements first settled in the Arabian region during the Wordian, when the Arabian plate had moved northward to a latitude of 20°S. Cathaysian plants thrived in warm and humid flood plains, whereas the seasonally dry,

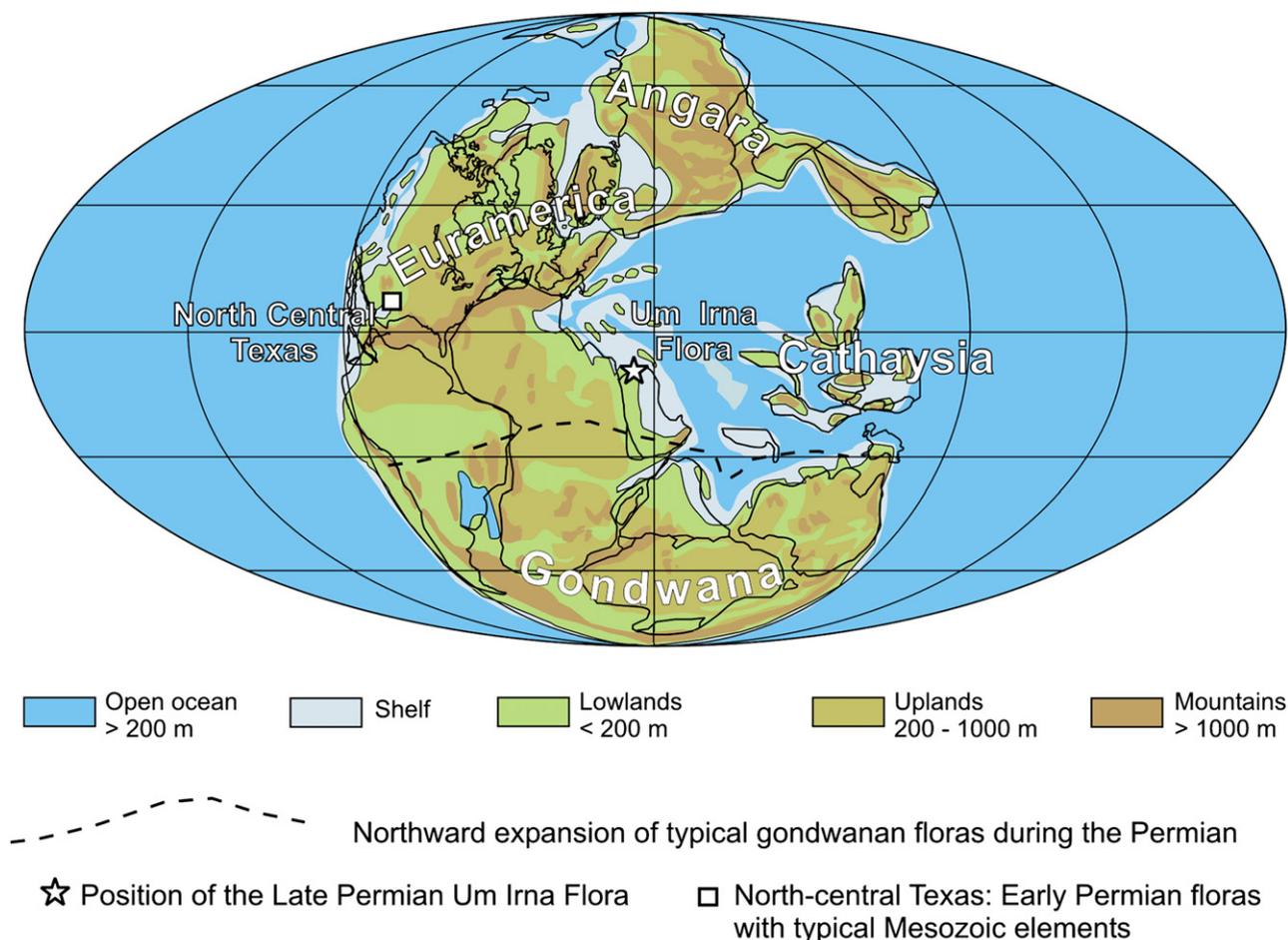


Fig. 9. Palaeogeographic map of the Late Permian with position of the Wadi Himara flora, the position of the north-central Texas flora described by DiMichele et al. (2001). Map modified after Ziegler et al. (1997).

slightly elevated areas of this same region were apparently inhabited by European-type conifers. However, not only cathaysian elements reached the limits of their geographical distribution in the Arabian Plate, but also gondwanan taxa such as the glossopterids. Gondwanan Late Permian glossopterid-dominated floras usually are considered to have been adapted to cool-to-cold climate and seasonally moist habitats (McLoughlin et al., 1997). The glossopterids from the Arabian Plate (Broutin et al., 1995; Berthelin et al., 2006), Turkey (Archangelsky and Wagner, 1983) and Morocco (Broutin et al., 1998) were apparently adapted to warmer conditions than the typical gondwanan forms.

Some typical gondwanan taxa migrated northward during the Permian, and *Dicroidium*, which seems to have originated in the palaeotropics, later migrated southward. The palaeogeographic position of the Dead Sea locality with *Dicroidium* indicates a warm and humid climate.

6.5. The Permian–Triassic transition and the subsequent southward migration of *Dicroidium*

The Permian–Triassic biotic crisis, probably the largest mass extinction in Earth history, led to a large-scale extinction of both marine and terrestrial organisms (Erwin, 1993; 1999; Retallack,

1995). Among the plant groups that became extinct were some of the typical cathaysian taxa, such as the gigantopterids, *Tingia* and *Lobatannularia*. Other groups strongly diminished and eventually also perished, e.g., the glossopterids in Gondwana. Only a few Triassic floras with *Dicroidium* and glossopterids have been described (Thomas, 1952, 1958; Anderson and Anderson, 1983, 1985; Bose et al., 1990; Holmes, 1992). Conifers are well represented in the Late Permian and Triassic, but the mega- and the microfossil record suggest that hardly any of the genera known from the Permian persisted into the Triassic (Eshet, 1983; Gall et al., 1998; DiMichele et al., 2001; Looy et al., 1999, 2001). Four discrete successive recovery stages have been recognised after the Permian–Triassic extinction, comprising most of the Early Triassic (Eshet et al., 1995).

In Gondwana, the Permian–Triassic transition is characterised by a shift from cold temperate to cool temperate conditions (Retallack and Krull, 1999). In Gondwana, the earliest Triassic is considered to have been significantly warmer and more seasonally dry than the latest Permian based on sedimentological, palaeopedological, and palaeobotanical evidence (McLoughlin et al., 1997; Retallack and Krull, 1999; Ward et al., 2000; Michaelsen, 2002). The Early Triassic vegetation of Gondwana was not diverse and was dominated by lycopsids and voltzialean conifers; highly diverse, *Dicroidium*-dominated floras are not known prior to the

Middle Triassic (Retallack, 1995). In the Northern Hemisphere, Early Triassic floras were dominated by lycopsids; conifers did not reappear before the transition from the Early to the Middle Triassic (Looy et al., 1999; Grauvogel-Stamm and Ash, 2005). The Early Triassic floras from Cathaysia are characterised by a dominance of lycopsids (e.g., Wang, 1996).

It appears that some pteridosperm groups were not affected by the biotic crisis at the Permian–Triassic transition. *Dicroidium* is one of the very few genera that survived the biotic crisis at the Permian–Triassic transition, although it should be noted that there are no unequivocal records of this genus from the earliest Triassic. This, however, might be due to the fact that in general only very few floras from the lowermost Triassic are known. During the Early Triassic, as the climate became increasingly favourable, *Dicroidium* apparently migrated southward, whereas the Arabian Plate moved further northward. The corystosperms fully expanded during the Middle Triassic where they reached their maximum diversity and inhabited large parts of Gondwana. Not only *Dicroidium* migrated southward but also the peltasperms (Retallack, 2002). This group of rather small, probably shrubby, mesic to xeric plants, which was once considered to be an exclusively Mesozoic group, originated in the tropics during the latest Carboniferous (*Autunia* and *Peltaspermum*: Kerp, 1988). This small group was widespread during the Permian and apparently was not provincialised, given that peltasperms have been reported from all floral provinces, except for Gondwana. The peltasperms survived the Permian–Triassic biotic crisis and migrated southward during the Early Triassic with *Lepidopteris callipteroides* as the earliest gondwanan representative (Retallack, 2002). Similar migration patterns have also been observed for palynomorph taxa (Lindström and McLoughlin, 2007). *Triplexisporites playfordii* and *Playfordiaspora cancellosa* first appeared during the Middle and Late Permian at palaeolatitudes of c. 20°S and they later migrated southwards and became characteristic elements of Australian gondwanan microfloras. This is ascribed to an intense global warming that already had begun during the Permian (Lindström and McLoughlin, 2007).

Possible causes for the end-Permian biotic crisis still remain a matter of debate. Global warming resulted in an expansion of the tropical belt, a pole-ward shift of adjacent climate zones, and a contraction of the more temperate and cool zones at higher latitudes. A further complication for the Permo-Triassic is that, in time, continents moved northward through climatic belts. Future studies should focus on the palaeotropics, where effects of climatic changes were probably less severe than elsewhere. Unfortunately, very little is known about Late Permian and Early Triassic tropical floras. However, it is interesting to note that plants with Mesozoic affinities, primarily Northern Hemisphere conifers and cycads (e.g., *Swedenborgia*, *Dioonitocarpidium*), have been described from the Lower Permian of north-central Texas (DiMichele et al., 2001). During the Permian, Texas was a lowland area positioned at a similar latitude as Jordan, but north of the equator, and separated from the Southern Hemisphere by a mountain chain (Fig. 9), the altitude of which is still a matter of debate (Fluteau et al., 2001b). The occurrences of typical Mesozoic conifers and cycads in Texas, and of *Dicroidium* in

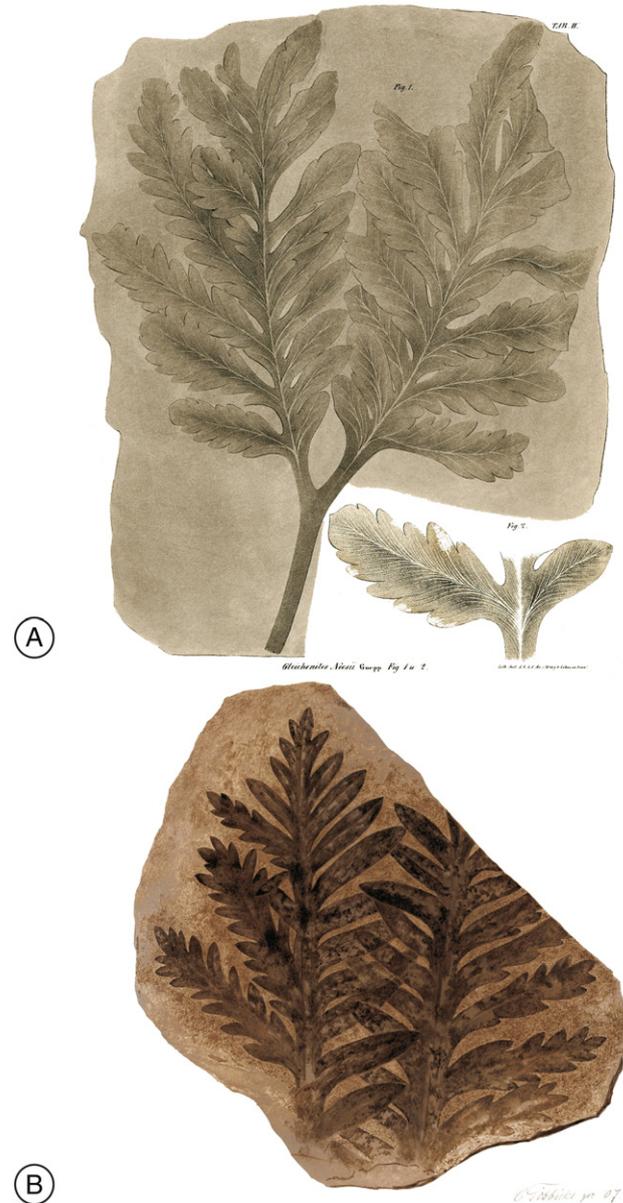


Fig. 10. *Dicroidium*-like foliage from the Lower Permian of Otovice (Czech Republic). A. The specimen originally illustrated as *Gleichenites neesii* by Göppert (1836, Plate II, 1–2). Reprinted with permission of the Deutsche Akademie für Naturforscher Leopoldina, Halle/Saale. B. An illustration of a specimen from the collection of the Museum für Naturkunde, Berlin, made for W. Gothan (1907).

Jordan suggest that, during the Permian, the tropics might have been a radiation centre for “Mesozoic” gymnosperms. With the climatic amelioration in the Early Triassic, *Dicroidium* migrated southward and became a dominant constituent of many Gondwana floras, whereas conifers and cycads expanded northward to colonise large parts of the Northern Hemisphere.

6.6. Speculations on the earliest corystosperms

The corystosperms are often considered to be closely related to the peltasperms (e.g., Crane, 1985; Meyen, 1988; Doyle, 1996). *Dicroidium* has often been compared with *Supaia* from the Middle Permian, which has fronds showing a similar

bifurcate architecture (e.g., Schopf, 1973). *Supaia* was originally described from the Hermit Shale of Arizona and was long considered to be endemic to the American Southwest. However, the genus has also been recorded from southern France (Doubinger and Kruseman, 1965) and northern Spain (Gand et al., 1997). *Supaia* has been interpreted as a peltasperm (Wang, 1997). However, it should be noted that both groups are considered to be closely related.

The presence of not less than four *Dicroidium* species in a single locality in the palaeotropics strongly suggests that this group had evolved much earlier. Unfortunately, the type of settings in which such early forms could be expected is rarely preserved. However, a very intriguing type of foliage has been described and illustrated from the Otovice Limestone (Lower Permian; Bohemia, Czech Republic) under the name *Gleichenites neesii* (Göppert, 1836, Plate II, 1–2). The Otovice (formerly known as Ottendorf) flora is dominated by callipterids but also contains several rare, extrabasinal elements that have hardly ever been reported from other localities. *Autunia conferta* is one of the most common taxa. In Otovice, *A. conferta* fronds are often not very regularly developed, in that they commonly show profound overtopping in their upper part with strongly prolonged pinnules (Kerp, 1988); the specimen illustrated by Göppert (1864–65, Plate XIII, 1) as *C. affinis* is another nice example of such a strongly overtopping *A. conferta* frond. However, the specimen originally illustrated as *Gleichenites neesii* (Göppert, 1836, which is reproduced here as Fig. 10A) looks entirely different and shows an almost complete, bipinnate frond with a very well-developed basal dichotomy. The frond is asymmetrical because the pinnae of the left interior side are less well differentiated as those on the right side, but also the basal ones at the right side are hardly differentiated. The other pinnae bear pinnules that are somewhat reminiscent of those of *Dicroidium jordanensis* but pinnules are basally fused. Pinna terminals are large and are formed by three or more strongly fused pinnules. The venation is rather loose, odontopteroid, like in *D. irnensis*. Unfortunately, this specimen could not be found during a recent visit to the original Göppert collection in Wrocław, Poland (pers. comm., R. Rößler, Chemnitz, 2006). Another, less complete but similar specimen from Otovice is kept in the collection of the Museum für Naturkunde, Humboldt University Berlin. This specimen is broken and does not show the basal bifurcation. However, the position of the two pinnate frond portions strongly suggests that the frond architecture was the same. Because the Otovice material is very difficult to photograph, we here illustrate a still unpublished drawing of the Berlin specimen commissioned by W. Gothan in 1907 (Fig. 10B). These two specimens look very similar to *Dicroidium*, but definite proof cannot be given due the lack of cuticle. Even though it is still highly speculative, the *Dicroidium*-like fossils from the Lower Permian of Otovice seem to indicate that the origin of the corystosperms, or at least the first occurrence of typical corystosperm-like foliage, might even be traced back to the Early Permian.

7. Concluding remarks

The Wadi Himara flora described here represents the earliest and most northern occurrence of a genus that apparently

originated during the Late Permian and survived the Permian–Triassic biotic crises. Although no megafloral data were previously available, the pollen record suggests that *Dicroidium* may have occurred already by Late Permian times. The pollen attributed to *Dicroidium* has been described as *Falcisporites* (Balme, 1995), a taxon that first appeared in the Upper Permian and was originally described from the German Zechstein (Leschik, 1956). The high abundance of *Falcisporites* in the Late Permian Wadi Himara palynoflora is not surprising because these grains were produced by *Dicroidium*, the dominant floral element in this hypautochthonous megaflora. The range of *Dicroidium*, which is traditionally regarded as a typical Triassic genus, can now be extended into the Permian. This is the first unequivocal record of the Corystospermales from the Permian. Four species of *Dicroidium* are known from the Upper Permian of Jordan. Therefore, it may be assumed that the Corystospermales developed earlier than is commonly thought. The geographical distribution of *Dicroidium* was not restricted to Gondwana. The genus apparently evolved in the palaeotropics. With the climatic amelioration in the Early Triassic (e.g., Kidder and Worsley 2004) the genus migrated southward and finally colonised the entire Gondwana region, where in the Middle and Late Triassic, it became one of the dominant floral elements. The early representatives of *Dicroidium* grew in hot but at least temporarily humid, extrabasinal environments. During the Triassic the genus adapted to drier habitats.

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