Mummified *Dicroidium* (Umkomasiales) leaves and reproductive organs from the Upper Triassic of South Australia

Jan Unverfärth[1]*, Stephen McLoughlin[2], and Benjamin Bomfleur[1]*

[1] Palaeobotany Research Group, Institute of Geology and Palaeontology, Westfälische Wilhelms-Universität Münster, Heisenbergstrasse 2, D–48149 Münster, Germany
[2] Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden

*corresponding author: *jan.un@uni-muenster.de*

Abstract:

The Leigh Creek Coal Measures incorporate unusually low-rank coals from the Upper Triassic of South Australia. Associated fluvio-lacustrine deposits contain well-preserved, partly mummified plant remains dominated by corystosperm seed ferns. The assemblage comprises seven species of *Dicroidium*, including *D. odontopteroides*, *D. lineatum*, *D. dubium*, *D. zuberi*, and *Dicroidium* spp. A, B and C, and associated reproductive organs, including various fragments of cupulate structures (*Umkomasia* sp. cf. *U. quadripartita* and *Fanerotheca* sp. cf. *F. waldeckiformis*) and pollen organs (*Pteruchus africanus*), all having excellent cuticle preservation. Based on a comprehensive analysis of more than 550 individual specimens, we (1) document diagnostic epidermal and cuticular features for foliage and reproductive organs, (2) provide an identification key for the *Dicroidium* species present, and (3) infer affiliations between reproductive organs and particular leaf species based on correspondence in epidermal anatomy and cuticle micromorphology and on mutual-occurrence data. Collectively, the Leigh Creek material contributes towards a more robust and realistic systematic classification of Umkomasiaceae, offers a rare chance for whole-plant reassembly of individual species, and refines reconstruction of the *Dicroidium*-dominated forest ecosystems in the middle to high latitudes of the Late Triassic greenhouse world.

Keywords: Corystosperms, *Umkomasia*, *Fanerotheca*, *Pteruchus*, cuticle analysis, whole-plant reconstruction, Gondwana.

Table of contents

1 Introduction

Umkomasiales Doweld 2001 (Corystospermales Němejc 1968) is an extinct order of seed plants whose characteristic bifurcate leaves have been known from the fossil record for more than 150 years (Morris 1845). The taxon was established based on leaf compressions and associated reproductive organs from the Carnian of South Africa (Thomas 1933) and was soon recognized as the most iconic and characteristic plant group of the Gondwanan Triassic. Fossils attributed to this group have been employed extensively for biostratigraphic subdivision and correlation of Triassic strata (e.g., Retallack 1977; Retallack 1980a), biogeographic evaluation of the Gondwanan flora (e.g., Gothan 1912; Anderson & Anderson 1983), palaeoecological reconstructions of the austral vegetation (Retallack 1977), analyses of plant-arthropod interactions in deep time (SCOTT et al. 2004; MCLOUGHLIN 2011; LABANDEIRA 2013; LABANDEIRA et al. 2018; CARIGLINO et al. 2021), and they have been the topic of popular science articles relating to plant diversification and mass extinction (MAYS & MCLOUGHLIN 2019). The distinctive bipartite *Dicroidium* GOTHAN 1912 leaves are among the most widespread, diverse, and abundant Triassic plant fossils from continental lowland habitats in middle to high southern palaeolatitudes (ANDERSON & ANDERSON 1983). They define a distinct Triassic Gondwanan phytogeographic province generally called the '*Dicroidium* flora' (HIRMER 1936; TOWNROW 1957; MCLOUGHLIN 2001). *Dicroidium* encompasses simple to tripinnate, bipartite leaves with a basal bifurcation (GOTHAN 1912) and with epidermal features typically including butterfly-shaped stomata with only lateral subsidiary cells (TOWNROW 1957; "pseudosyndetocheilic stomata" of RETALLACK 1977). Reproductive organs of these Gondwanan corystosperms comprise ovuliferous organs with recurved, usually uni-ovulate cupules (including *Umkomasia* H.H.THOMAS 1933, *Fanerotheca* FRENG. 1944a, and *Axsmithia* H.M.ANDERSON 2019) and simple forked to multi-pinnate pollen organs (*Pteruchus* H.H.THOMAS 1933) with circular to strongly elongate (linear) microsporophylls bearing dense clusters of pollen sacs over the entire abaxial surface. In addition, several types of permineralized and petrified wood have been associated with these various compression fossils, including unusual manoxylic stems with abundant parenchyma and wedge-shaped xylem segments (*Rhexoxylon* N.BANCROFT 1913) and pycnoxylic stems with prominent growth rings (e.g., *Kykloxylon* MEYER-BERTH. 1993; DECOMBEIX et al. 2014).

Given the long history of research on this group, the abundant and widespread fossil occurrences, and the rich curated collections—some with very well-preserved material—it is surprising that a consistent and universally accepted systematic classification of these typical Gondwanan corystosperms has not been established. Today, two broad taxonomic approaches are applied to the group. One approach argues that various leaves with an overall similar bauplan and epidermal features but with different pinna or pinnule morphologies should be assigned to separate genera, including *Johnstonia* WALKOM 1925b, *Harringtonia* FRENG. 1942, *Dicroidiopsis* FRENG. 1943, *Diplasiophyllum* FRENG. 1943, *Xylopteris* FRENG. 1943, *Zuberia* FRENG. 1943, *Tetraptilon* FRENG. 1950, or *Hoegia* TOWNROW 1957 (see, e.g., FRENGUELLI 1942, 1943; ARTABE 1990; BARBONI et al. 2016; ANDERSON et al. 2019b). The second approach is to unite all such leaf forms under a single genus (*Dicroidium*) based on their consistent association with *Umkomasia*- and *Pteruchus*-type reproductive structures.

This issue is complicated by the uncertain diagnostic significance of macro- versus micromorphological features in those cases in which cuticles are preserved (see, e.g., THOMAS 1933; JONES & DE JERSEY 1947; JACOB & JACOB 1950; TOWNROW 1957; ARCHANGELSKY 1968; ANDERSON & ANDERSON 1983; BOMFLEUR & KERP 2010; PATTEMORE 2016; MARTÍNEZ et al. 2020; DROVANDI et al. *in press*), and also by several cases of apparent hybridization between taxa (ANDERSON & ANDERSON 1983). Moreover, a well-resolved understanding of the biology and ecology of these plants has been hampered by the fact that almost all organs are preserved in isolation, in many cases in the form of mats of abundant abscised leaves interspersed with detached reproductive organs. Discoveries of different plant parts in organic connection are exceedingly rare, with less than a handful of cases preserving leaves in attachment to axes (ANDERSON et al. 2008; ANDERSON & ANDERSON 1983; AXSMITH et al. 2000). An especially informative occurrence of this fossil group is preserved in the silicified peat of the Fremouw Formation in the Transantarctic Mountains, which has yielded permineralized pollen organs, ovuliferous organs, leaves and stems (PIGG 1990; MEYER-BERTHAUD et al. 1993; YAO et al. 1995; KLAVINS et al. 2002; DECOMBEIX et al. 2014). Nevertheless, the anatomical data obtained from this deposit are difficult to integrate systematically into the group's impression/compression fossil record. There have been only rare attempts to reconstruct umkomasialean plants as a whole (RETALLACK 1977; CRANE 1985; RETALLACK & DILCHER 1988; TAYLOR et al. 2006; BLOMENKEMPER et al. 2020).

This rather diffuse knowledge about the typically Triassic Gondwanan Umkomasiaceae is beginning to gain greater significance with the increasing awareness that corystosperms were much more diverse, widespread, and longer-ranging in the stratigraphic record than previously thought. Recently, Umkomasiales have been described from uppermost Permian strata of Jordan and Pakistan (ABU HAMAD et al. 2008; SCHNEEBELI-HERMANN et al. 2014; BLOMENKEMPER et al. 2020) and the Jurassic of Antarctica, revealing a remarkable pattern of a tropical "cradle" and polar refugia for this group (BOMFLEUR et al. 2018). Furthermore, possible descendants have also been described from the Cretaceous of Mongolia (SHI et al. 2016, 2019). Various other predominantly Gondwanan genera (e.g., *Komlopteris* BARBACKA 1994, *Rintoulia* MCLOUGHLIN et NAGALINGUM 2002) of Jurassic to Eocene age have unforked but otherwise similar leaf forms, venation and cuticle morphology (MAHESHWARI 1986; MCLOUGHLIN et al. 2002, 2008), collectively attesting to a much greater stratigraphic range and significance of Umkomasiales in the Mesozoic vegetation than appreciated previously.

Moreover, there is mounting evidence that Umkomasiaceae are central to our understanding of seed-plant relationships and perhaps even the origin of angiosperms (SHI et al. 2016, 2019). Therefore, it is of crucial importance to resolve the taxonomic delimitation, the diagnostic value of macro- and micromorphological features, and the organ affiliations of this group to advance their application in phylogenetic analyses.

Here, we present the first detailed cuticle analysis of a diverse assemblage of *Dicroidium* leaves and associated reproductive organs from South Australia. The exceptional preservation of fine details prompted us to apply novel preparation procedures with newly adapted laboratory methods. The systematic survey of hundreds of cuticle specimens investigated at the cellular level provided a robust basis to evaluate the diagnostic significance of macro- and micromorphological features in the group, which finally allowed us to distinguish seven *Dicroidium* species in the studied succession. In addition, the cuticle characters enabled us to link various leaf and reproductive organs into probable biological affiliations.

2 Geological setting

[*half-column Text-fig. 1*]

The Leigh Creek Coal Measures, predominantly Late Triassic in age, are distributed across five small, isolated intramontane basins, lying within the Adelaide Geosyncline in the Flinders Ranges, 550 km north of Adelaide, South Australia (Text-figs 1.1, 1.2). The sedimentary basins at Leigh Creek subsided against reactivated Neoproterozoic basement faults (TOWNSEND 1979) during a phase of extensional tectonism affecting much of eastern Australia in the Late Triassic. A coeval plant-rich deposit occurs in the small Springfield Basin around 180 km south of Leigh Creek (JOHNSON 1960; AMTSBERG 1969). Several additional coal- and plant-bearing continental sedimentary units accumulated at this time along the eastern margin of Australia, e.g., in the Callide, Tarong, and Ipswich basins of Queensland and New South Wales (STAINES et al. 1985; JELL 2013; JELL & MCKELLAR 2013) and in the Tasmania Basin, Tasmania (BACON 1995). Western Australian Triassic strata have been sparsely surveyed for Upper Triassic plant remains (MCLOUGHLIN & HILL 1996; PEYROT et al. 2019), but a few records of *Dicroidium* have been noted in the epicratonic Canning Basin (ANTEVS 1913; WHITE & YEATES 1976), and coeval strata in the rifted depressions of the Perth and Carnarvon basins are potentially prospective for floras of this age (COCKBAIN 1990; HOCKING 1990). During the

Triassic, South Australia was located at around 55° South, landlocked, with a low-relief topography and an alternating wet to dry climate, which led to widespread subaerial weathering and pedogenesis, and the accumulation of continental (freshwater) deposits at Leigh Creek and Springfield (ANDERSON & ANDERSON 1983; KRIEG 1995; SCOTESE 2001).

The Telford Basin (also known locally as Lobe B) is by far the largest of the five basins in the Leigh Creek area. It is asymmetrically elliptical in plan view, covers an area of 34 km² and contains up to 1000 m of continental strata laid down during three depositional phases (Text-figs 1.2, 1.3, 2.1). The Triassic mud-, silt- and sandstones lie unconformably on Proterozoic Adelaide Fold Belt units (KWITKO 1995). The Triassic strata contain several coal seams, informally grouped into the 'lower', 'middle' and 'upper series' coals (PARKIN 1953), which were mined by open-cut methods from 1943 to 2015 (Text-figs 2.2, 2.3). The Triassic succession is locally overlain unconformably by a thin succession of basal Jurassic mudstones and siltstones (PLAYFORD & DETTMANN 1965; PARKER 1987, see also Text-figs 1.2, 1.3). The Leigh Creek Coal Measures have been interpreted as the deposits of swamp-, lake- and associated river systems laid down in a relatively warm and moist climate (KWITKO 1995). Rapid changes in these conditions are also documented by abundant siderite hard bands and fossils in siderite concretions (Text-figs 2.4, 2.5), which formed after rapid flooding that resulted in elevated water table and anoxic conditions (BOJANOWSKI et al. 2016). Freshwater conditions are also indicated by a modest fossil fauna of non-marine molluscs (LUDBROOK 1961), fish (WADE 1953; PLEDGE & BAULCH 2013; BERRELL et al. 2020), and amphibians (PLEDGE 2013). The Upper Triassic and Lower Jurassic strata were subject to subsequent gentle deformation and erosion (TOWNSEND 1979), resulting in the current bowl-shaped synclinal architecture of the basins, which probably represent remnants of a once more extensive Triassic sedimentary cover across the region (KWITKO 1995). Locally, the Leigh Creek Coal Measures and associated Jurassic strata are overlain unconformably by a thin veneer of Quaternary alluvial-plain deposits.

The Leigh Creek Coalfield was discovered during railway construction in 1888 (BROWN 1891). The first descriptions of fossil plants from these deposits were made by ETHERIDGE (1891, 1895). More comprehensive studies of fossil plants from the coal measures, originally collected by Dr Georgina Sweet, were described by CHAPMAN & COOKSON (1926) and partly revised by AMTSBERG (1969), including additional new findings. The most recent palaeobotanical fieldwork, conducted in 1997 (BARONE-NUGENT et al. 1997), resulted in a publication on the morphology and cuticular characters of the petriellalean foliage *Rochipteris* R.HERBST, TRONCOSO et GNAEDINGER 2001 (BARONE-NUGENT et al. 2003). Fossil leaf cuticle from the Telford Basin was also used in the refinement of techniques for quantitative phase-amplitude optical microscopy (BARONE-NUGENT et al. 2002). Fossil plants are distributed throughout the Triassic deposits of the Telford Basin (BARONE-NUGENT et al. 2003). The extensive set of matted leaf accumulations recovered in 1997 probably represents the last productive palaeontological fieldwork in the basin, as mining operations declined in the early 21st Century and ceased in 2015 (FLINDERS POWER PARTNERSHIP 2017). At the time of writing, the only current extractive activity in the Telford Basin involves a pilot plant for in situ coal gasification and urea production operated by Leigh Creek Energy Limited.

3 Material and methods

[*full page Text-fig. 2*] [*howsoever it fits Text-fig. 3*]

The material was collected during fieldwork in the formerly active open-pit mine of the Telford Basin, in 1997. Samples were taken from 14 stratigraphic levels at 22 individual sampling sites (see Table 1; Text-fig. 1.2, 2.1, 3). Eleven sample sites occur in a 60-m-thick profile through the 'upper series' in the centre of the Telford Basin mine (Text-fig. 3), at pit U26 of the local mine plan. Sample LC-21 also derives from the 'upper series' but from the uppermost carbonaceous siltstone exposed on the northwestern access ramp to pit U27 (Text-fig. 1.2). Additional samples from the 'middle' and 'lower series' were collected from pits M13 and L7, respectively, of the local mine plan (Text-fig. 1.2). The material consists of mummified plant remains with well-preserved cuticles and charcoal layers in unconsolidated to weakly lithified mudstones and siltstones (Text-figs 2.6-2.16). The organic material is preserved at an overall very low-grade coal rank (lignite A to sub-bituminous C: SPRINGBETT et al. 1995).

Macroscopic images were obtained using a Canon EOS 5D Mark IV camera with an oblique light source for untreated specimens and a light table for specimens fixed to permanent slides. Plant material was extracted from the sediment using a modification of the acid-free palynological processing method, including the use of sodium hexametaphosphate $(NaPO_3)_6$ (e.g., RIDING & KYFFIN-HUGHES 2004, 2011). Bulk samples (mainly mudstones) were submerged in a beaker with a 10% saturated solution of water and sodium hexametaphosphate and heated below the cooking temperature for a few hours on a hot plate in order to deflocculate the clay matrix. Afterwards, the softened sediment could be sieved to extract plant material. This acid-free approach provided a much faster, cheaper, eco-friendly and less toxic extraction method enabling recovery of cuticles within hours. Disintegrated rock samples were first filtered using commercial sieves to recover all macrofossils from the sediment. Residues were then sieved using >250 µm nylon mesh to recover all mesofossil contents. If necessary, additional adhering sediment was removed by submerging extracted plant material in 40% hydrofluoric acid (HF) for about 24 hours. Prior to the acid extraction, some samples needed treatment with 40% hydrochloric acid (HCl) for 48 h to remove adhering crusts of siderite and prevent the formation of potassium fluoride. Coalified mesophyll was removed using 25% nitric acid (HNO_3) and potassium chlorate ($KClO_3$) (Schulze's reagent) for 72 hours with additional subsequent potassium hydroxide solution (KOH; 10%) treatment for up to 20 minutes (see KERP 1990). Depending on the opacity of the cuticles, additional bleaching was undertaken using a commercial chlorine detergent for a few minutes. Cuticles were mounted in glycerine jelly on slides for light microscopic (LM) analysis and were studied either with transmitted light (TL) or with epifluorescence light (RL) using a Leica DM5500 B. Photos of microscopic cuticle details were obtained using either the Leica DM5500 B or a Leica Diaplan microscope with Nomarski interference contrast, with a mounted Nikon DS-5M digital camera; many of the images were stacked and/or stitched from individual images taken at different focal planes to increase resolution and image quality (see, e.g., KERP & BOMFLEUR 2011). Selected cuticles were dehydrated in ethanol, mounted on aluminium stubs and coated with gold or iridium for scanning electron microscopy (SEM) images, using JEOL 6610/6510 LA microscopes. The material is housed in the collections of the Palaeobiology Department of the Swedish Museum of Natural History, Stockholm, Sweden, under the registration numbers NRM S089761–S089782.

With respect to terminology, we aim to differentiate as clearly as possible between idiocuticular features—i.e., those related to the cuticular sheet itself (such as solid papillae or 'leaf lenses')—and epidermal features reflected in the cuticular morphology, such as cellular architecture of the stomata.

[*full column Table 1*]

4 Systematic Palaeontology

Order Umkomasiales DOWELD 2001 (Corystospermales NĚMEJC 1968)

Family Umkomasiaceae PETRIELLA 1981

Genus *Dicroidium* GOTHAN 1912

Type species: Dicroidium odontopteroides (MORRIS 1845) GOTHAN 1912

Type: original material of MORRIS (1845) reportedly lost (TOWNROW 1957); lectotype designated by TOWNROW (1966) is specimen no. 81932 in the collections of the Geology Department of the University of Tasmania, Hobart, (Tasmania, Australia), collected from the bank of the Coal River about one kilometer E of Lowdina Homestead, Campania, Tasmania (presumed by Townrow to be the type locality also for Morris' original material).

[*half-column text-fig. 4*]

Genera here considered synonymous:

(=) *Johnstonia* WALKOM, Pap. Proc. Royal Soc. Tasmania 1924: 79. 2 Mar 1925.

(=) *Harringtonia* FRENG., Notas Mus. La Plata 7: 271. 30 Dec 1942.

(=) *Dicroidiopsis* FRENG., Revista Mus. La Plata, Secc. Paleontol., Ser. 2, 2: 289. 30 Sep 1943.

(=) *Diplasiophyllum* FRENG., Revista Mus. La Plata, Secc. Paleontol., Ser. 2, 2: 299. 30 Sep 1943.

(=) *Zuberia* FRENG., Revista Mus. La Plata, Secc. Paleontol., Ser. 2, 2: 308. 30 Sep 1943.

(=) *Xylopteris* FRENG., Revista Mus. La Plata, Secc. Paleontol., Ser. 2, 2: 324. 30 Sep 1943.

(=) *Tetraptilon* FRENG., Revista Asoc. Geol. Argent. 5(1): 15. 1950.

(=) *Hoegia* TOWNROW, Trans. Geol. Soc. South Africa 60: 47. 1957.

(=) *Jordaniopteris* H.M.ANDERSON, Alcheringa 44: 75. 10 July 2019.

General description of the genus as circumscribed here.—Forked leaves with an acute bifurcation in basal third, with entire, pinnate, bipinnatifid to bipinnate or tripartite architecture and more or less obcordate outline (Text-fig. 4). Leaves small (<10 cm), medium (10–25 cm), large (25–50 cm) to very large (>50 cm, up to around 100 cm) long (see, e.g., ANDERSON & ANDERSON 1983). Pinnae opposite to subopposite with largest and most complex pinnae in central portion of the leaf. Petiole base commonly with modified foliar basal elements, in many cases strongly lobed and differentiated from succeeding pinnules (BOMFLEUR et al. 2012). Below leaf bifurcation, pinnae simpler and clearly separated; towards apices of segments above bifurcation, pinnules become closer and more broadly attached to rachis. Pinnae shortened on inner leaf above furcation. Near the leaf apex, pinnae simpler and gradually fuse adjacent to rachis, until reaching the apex, where commonly three to five pinnae fuse together. Pinnae and pinnules contracted or broadly attached with obtuse apices. Pinna venation commonly pinnate-sphenopteroid, in pinnules typically odontopteroid, arising from the basiscopic portion of the leaflet, or alethopteroid (see Text-fig. 5, on the left).

Most leaves amphistomatic, with uneven stomatal density and orientation on adaxial versus abaxial surface and costal versus intercostal areas. Cuticles varying from thin and relatively featureless to thick and heavily modified (Text-fig. 5, to the right). Costal areas and rachis commonly with cells elongated and aligned parallel to vein course and with stomatal pores orientated mainly longitudinally or transversely; intercostal areas usually with cells more isodiametric and more irregularly arranged and with stomatal pores less clearly orientated. Most stomata orientated either longitudinally or transversely, with only lateral subsidiary cells clearly differentiated (typical ‘butterfly-shapes’), or irregularly orientated and with a complete or once-interrupted ring of subsidiary cells (see Fig. 5 of BOMFLEUR & KERP 2010). Anticlinal cuticle flanges variable, ranging from smooth to granular to variably thickened or buttressed. Periclinal cuticle with variable cuticular features, including simple, solid or hollow papillae and more or less diffuse, lens-shaped thickenings of cuticle layer proper (see cuticle cross-section details in Text-fig. 5 and ‘leaf-lenses’ in BOMFLEUR & KERP 2010). Some species with common bases of multicellular trichomes.

Comparison & Remarks.—We follow the lines of arguments brought forward by, e.g., TOWNROW (1957), BONETTI (1966), ARCHANGELSKY (1968), ANDERSON & ANDERSON (1983, 2003) and BLOMENKEMPER et al. (2020), and regard the multiple leaf genera listed in the synonymy to be congeneric with *Dicroidium*. We cannot identify macro- or micromorphological characters that would consistently differentiate them at the generic level.

In Australia, the stratigraphically lowest occurrence of *Dicroidium* is in the Lower Triassic, a short interval above the end-Permian extinction horizon (FIELDING et al. 2019; MAYS et al.

2020). The genus becomes a common element of fossil assemblages in Spathian strata (RETALLACK 1977; HOLMES & ASH 1979) and dominates floras in succeeding strata up to the – end-Triassic extinction horizon (BALME et al. 1995). *Dicroidium* has its centre of distribution in the middle and high palaeolatitudes of Gondwana, with particularly large collections described from the Middle to Upper Triassic of South Africa (DU TOIT 1927; THOMAS 1933; ANDERSON & ANDERSON 1983), South America (FRENGUELLI 1943, 1944b; BORTOLUZZI & BARBERENA 1967; ARCHANGELSKY 1968; PETRIELLA 1981; GUERRA-SOMMER & CAZZULO KLEPZIG 2000), Antarctica (TOWNROW 1967; BOUCHER et al. 1993; BOMFLEUR & KERP 2010; ESCAPA et al. 2011; BOMFLEUR et al. 2012), India (e.g., FEISTMANTEL 1879a; PAL et al. 2014; RAO & LELE 1962; SEWARD 1932), Australia (e.g., WALKOM 1917, 1925a, 1928; JONES & DE JERSEY 1947; TOWNROW 1957; HOLMES & ANDERSON 2005; PATTEMORE 2016), and New Zealand (e.g., ARBER 1913, 1917; RETALLACK 1980b). More recently, however, *Dicroidium* has also been described from the uppermost Permian of the palaeoequatorial regions (KERP et al. 2006; ABU HAMAD et al. 2008; SCHNEEBELI-HERMANN et al. 2014; BLOMENKEMPER et al. 2020) and from the Jurassic of Antarctica (REES & CLEAL 2004; BOMFLEUR et al. 2018).

The occurrence of brachyparacytic, “butterfly-shaped” stomatal complexes with lateral subsidiary cells only (“pseudosyndetocheilic stomata” of RETALLACK 1977) is a typical feature of the genus. It is, however, not exclusive to *Dicroidium*; some cuticles of the superficially similar, yet unforked fronds of *Kurtziana* FRENG. 1942, for instance, have been described as having similar stomata (PETRIELLA & ARRONDO 1982; ARTABE et al. 1991), as do those of several other, typically Paleozoic seed-fern groups, including lyginopterids and medullosans (see, e.g., BARTHEL 1962).

Dicroidium odontopteroides **(MORRIS 1845) GOTHAN 1912**

Text-fig. 5.1, Pls 1–3

Stratigraphic levels: LC-4, LC-5, LC-5/6, LC-9, LC-11, LC-12, LC-13, LC-14, U26 Highwall.

Basionym: Pecopteris odontopteroides MORRIS 1845 in STRZELECKI, p. 249, pl. 6, figs 2–4.

Selected references and synonyms:

1912 *Dicroidium odontopteroides* (MORRIS) GOTHAN 1912, p. 75, pl. 15, fig. 4, pl. 16, fig. 5.

1917 *Thinnfeldia odontopteroides* (MORRIS) WALKOM, p. 19, pl. 3, fig 1.

1957 *Dicroidium odontopteroides* (MORRIS) GOTHAN – TOWNROW, figs 3, 4, 5.

1979 *Dicroidium odontopteroides* (MORRIS) GOTHAN – PETRIELLA, pl. I, 6, 9, pl. II, 1–2.

1983 *Dicroidium odontopteroides* subsp. *orbiculoides* ANDERSON et ANDERSON, p. 98, p. 207, figs 1–6, p. 209, figs 1–6.

2010 *Dicroidium odontopteroides* (MORRIS) GOTHAN – BOMFLEUR & KERP, figs 1–6, p. 74, figs 1–3, p. 75, figs 1–9.

2011a *Dicroidium odontopteroides* (MORRIS) GOTHAN – BOMFLEUR et al., fig. 4a, b.

2018 *Dicroidium odontopteroides* (MORRIS) GOTHAN – BOMFLEUR et al., figs 1–12.

Description.—Leaves bipartite (forked at 34–38°), small to medium in length (c. 10 cm), pinnate, with elongate obcordate outline (Pl. 1, Figs 1, 7). Pinnule size and shape highly variable between and within individual leaves (Pl. 1, Figs 1–4, 7, 8). Modified basal elements as long as wide, circular and finely lobed several times (Pl. 1, Fig. 5). Pinnules in proximal leaf portion attached oppositely, 5 mm long, equidimensional (square) to slightly trapezoid (Pl. 1, Fig. 3), constricted towards petiole, with odontopteroid venation. Pinnules above bifurcation attached in increasingly subopposite arrangement, rhombic (Pl. 1, Fig. 1) to elongate-triangular (Pl. 1, Fig. 7), with shorter obovate to triangular pinnules in the inner portion of the bifurcation being slightly constricted or broadly attached at their base, with odontopteroid venation and acute to obtuse apices. Largest, most complex pinnae occurring in the central outer leaf portion, with trapezoid to elongate triangular pinnules (Pl. 1, Figs 2, 4); more proximal pinnules short triangular with odontopteroid venation; more distal pinnules elongate-triangular with more alethopteroid venation (Pl. 1, Figs 2, 4). Apical pinnules broadly attached, strongly fused (Pl. 1, Figs 6, 9), subopposite, either short-triangular (Pl. 1, Fig. 8) or obovate (Pl. 1, Fig. 9).

Adaxial cuticle usually thicker than abaxial cuticle (Pl. 2, Figs 1, 2; Pl. 3, Figs 1, 2). Epidermal cell outlines square to rectangular, usually slightly (1.15 times) longer than wide, and slightly larger on the abaxial surface (av. 50 x 40 µm) than adaxial surface (av. 40 x 35 µm). Epidermal cell pattern on both surfaces relatively uniform, without clear differentiation into costal and intercostal fields (Pl. 2, Figs 1, 2), except for the rachis (Pl. 3, Fig. 1). Periclinal cuticle wall thick, typically with 2–4 diffuse lens-like thickenings per cell (Pl. 3, Figs 2, 3).

Anticlinal wall flanges thick, straight, to slightly curved, with granular to buttressed ornamentation (Pl. 3, Fig. 3). Leaves amphistomatic, with densely, almost evenly distributed stomata on both surfaces; on upper surface, stomata slightly more numerous over rachis and primary veins (Pl. 2; Pl. 3, Fig. 1). Most stomata orientated parallel or transverse to venation (Pl. 2), paracytic or laterocytic, with 2–4 lateral subsidiary cells (Pl. 3, Figs 1, 2). Subsidiary-cell periclinal wall more weakly cutinized than that of regular epidermal cells (see, e.g., Pl. 3, Fig. 1), bearing concentric wrinkled ornamentation but lacking lens-like thickenings or papillae (Pl. 3, Figs 2–4), with straight polar wall flanges and convex lateral wall flange, thickened in distal portion (Pl. 3, Figs 6, 8). Guard cells flat, only slightly sunken, feebly cutinized, with distinct proximal thickening delimiting pore, lacking anticlinal wall flanges (Pl. 3, Figs 6–8). Hair bases not evident. Mesophyll containing oblate resin bodies (usually c. 70 µm in diameter) distributed evenly within the pinnules (see Pl. 1, Figs 7, 8; Pl. 3, Fig. 5).

Comparison and Remarks.—This species can be clearly delimited and identified based on a characteristic combination of macromorphological and cuticular features. *Dicroidium odontopteroides* has widely variable gross morphology and especially pinna shapes (see Pl. 1). This is also reflected in the complicated and inconsistent classification approaches applied to material from other localities. Whereas some authors recognise up to six intraspecific taxa (subspecies, varieties or formae; e.g., ANDERSON & ANDERSON 1983; RETALLACK 1977) within *D. odontopteroides*, others assign some forms to separate species (e.g., ANDERSON et al. 2019b), and yet others use only a single, very broadly circumscribed species (e.g., PATTEMORE 2016) or species complex (HOLMES & ANDERSON 2005). All Leigh Creek specimens share a consistent combination of epidermal and cuticular features. Of special importance for the delimitation of (in a few cases) superficially similar leaves of *D. lineatum* (TEN.-WOODS) J.M.ANDERSON et H.M.ANDERSON 2003 is the occurrence of granular to buttressed anticlinal walls, of typically two to four lens-like thickenings, and of only slightly sunken guard cells.

The cuticular morphology and epidermal anatomy of the studied material closely match those specimens described from other occurrences of the species in South Africa (GOTHAN 1912; TOWNROW 1957; *D. odontopteroides* forma *orbiculoides* in ANDERSON & ANDERSON 1983), India (LELE 1962), Australia (TOWNROW 1966; see fig. 8A of PATTEMORE 2016), and Antarctica

(BOMFLEUR & KERP 2010; BOMFLEUR et al. 2018), which provides robust support for the diagnostic value of these features. With respect to the broad macromorphological circumscription of the species as applied by some authors, our material is most similar in pinna shape and venation to *D. odontopteroides* forma *orbiculoides* and with short-leafed forms of *D. odontopteroides* forma *odontopteroides* of ANDERSON & ANDERSON (1983).

***Dicroidium lineatum* (TEN.-WOODS 1883) H.M.ANDERSON et J.M.ANDERSON 1970 emend.**

Text-fig. 5.2, Pls 4, 5

Stratigraphic levels: LC-4, LC-5, LC-5/6, LC-6, LC-9, LC-11, LC-12, LC-13, LC-14, U26 Highwall.

Basionym: Gleichenia lineata TEN.-WOODS 1883, p. 130, pl. 3, fig. 6, pl. 8, fig. 2.

Selected references and synonyms:

1898 *Thinnfeldia indica* var. *falcata* SHIRLEY, p. 21, pl. 7, fig. 2.

1917 *Thinnfeldia acuta* WALKOM, p. 23, pl. 3, fig. 4.

1970 *Dicroidium lineatum* (TEN.-WOODS) H.M.ANDERSON et J.M.ANDERSON, chart 9.

1977 *Dicroidium lancifolium* var. *lineatum* (TEN.-WOODS) RETALLACK, microfiche frame H17.

1983 *Dicroidium odontopteroides* subsp. *lineatum* (TEN.-WOODS) J.M.ANDERSON et H.M.ANDERSON, p. 101, pl. 64, figs 12–29, pl. 65, figs 1–3, pl. 79, figs 4, 6, pl. 108, fig. 1.

1985 *Dicroidium lancifolium* var. *lineatum* (TEN.-WOODS) RETALLACK – ARTABE, pl. 3, fig. 5.

1992 *Dicroidium lancifolium* (MORRIS) GOTHAN – TAYLOR et al., fig. 2.

2001 *Dicroidium lancifolium* var. *lineatum*, GNAEDINGER & HERBST, fig. 2, A–E, fig. 3L.

2005 ‘*Dicroidium lineatum* complex’ W.B.K.HOLMES & H.M.ANDERSON, p. 7, figs 10B, C; 11A, B, D; 12A–C.

2011 *Dicroidium lineatum* (TEN.-WOODS) H.M.ANDERSON et J.M.ANDERSON – LUTZ et al., p. 574, figs 3.6, 5.7.

Diagnosis (here emended).—Leaves of intermediate length (typically in the range of 10–20 cm), pinnate, bipartite. Pinnules mostly separate. Fully developed pinnules in central leaf portion strongly elongate and narrow--triangular to lanceolate, typically about five times longer than wide. Venation alethopteroid; primary vein straight, extending up to near pinnule apex; secondary veins dense, simple or dichotomising once. Periclinal cuticle with a single, central, diffuse lens-like thickening per cell. Anticlinal wall flanges straight to slightly curved and smooth. Leaves amphistomatic, with stomata distributed evenly across abaxial cuticle but concentrated mainly on primary and basal secondary veins on the adaxial cuticle. Subsidiary-cell cuticle similar to or slightly thinner than that of regular epidermal cells, smooth, lacking lens-like thickenings or papillae.

Description.—Leaves of intermediate length (<15 cm), pinnate, bipartite with obcordate outline (Pl. 4, Figs 1, 2, 6). Pinnules in proximal leaf portion (sub-)opposite, clearly separate and attached at about right angles to rachis (Pl. 4, Figs 2, 5), distally becoming increasingly subopposite to alternate, more closely set to abutting, and attached at more acute angles (Pl. 4, Figs 1, 3). Leaf tips consisting of up to five increasingly fused pinnules (Pl. 4, Figs 4, 7). In central portion of frond (Pl. 4, Fig. 1), pinnules broadly attached, slightly constricted at base, lanceolate, typically about five times longer than wide (av. 30 x 6 mm); simpler pinnules near leaf base and on inner side immediately above bifurcation short, triangular to semicircular (Pl. 4, Figs 2, 3). Modified basal elements at petiole base roughly circular (as long as wide), three or more times lobed (Pl. 4, Fig. 8). Venation dense, alethopteroid; primary vein straight, extending to near the pinnule apex; secondary veins given off at 20–40°, simple or dichotomising once before reaching the leaf margin (see, e.g., Pl. 4, Figs 1, 5, 6).

Adaxial and abaxial cuticle about equally thick (Pl. 5, Figs. 1, 2). Epidermal cells usually elongate-rectangular, orientated parallel to venation (c. 30 x 26 µm). Costal fields with longitudinally aligned and more strongly elongate cells compared to intercostal fields (Pl. 5, Figs 1, 2, 7). Periclinal cuticle with a single, central, diffuse lens-like thickening per cell (see, e.g., Pl. 5, Figs 2, 5). Anticlinal wall flanges straight to slightly curved and smooth (see, e.g., Pl. 5, Figs 1, 5, 7). Rachis with rectangular epidermal cells, orientated in growth direction (Pl. 5, Fig. 3). Leaves amphistomatic, with stomata distributed evenly across abaxial cuticle but concentrated mainly on primary and basal secondary veins on the adaxial cuticle (see, e.g., Pl. 5, Figs 1, 2, 7). Stomata orientated usually parallel or transverse to venation, paracytic or laterocytic, with 2–4 lateral subsidiary cells and typically without polar subsidiary cells (Pl. 5, Figs 1, 5). Subsidiary-cell cuticle similar to or slightly thinner than that of regular epidermal cells, smooth, lacking lens-like thickenings or papillae, with straight polar wall flanges and with convex lateral wall flange, being thickened distally. Guard cells sunken, feebly cutinized, with crescentic anticlinal flanges and distinct proximal thickening delimiting the pore (Pl. 5, Figs 5, 8). Mesophyll containing oblate resin bodies (about 100 µm in diameter) that are evenly distributed in the intercostal leaf areas (Pl. 4, Fig. 1; Pl. 5, Fig. 4).

Comparison and Remarks.—This species is readily delimited from all co-occurring species based on the combination of strongly elongate, entire-margined pinnae, alethopteroid venation with acute-angled, simple or once-dichotomizing secondary veins, and the characteristic occurrence of just a single, diffuse lens-like thickening per regular epidermal cell.

Based on macromorphology alone, leaf fragments may appear similar to other pinnate *Dicroidium* leaves with long, alethopteroid pinnae. Such leaf forms have been referred to various species and subspecies, including *Dicroidium odontopteroides* forma *koningifolium* J.M.ANDERSON et H.M.ANDERSON 1983 and *D. odontopteroides* subsp. *hlatimbifolium* J.M.ANDERSON et H.M.ANDERSON 1983 (ANDERSON & ANDERSON 1983), *Dicroidium lancifolium* (GOTHAN 1912; BOUCHER et al. 1993), *Dicroidium dubium* (FEISTM.) GOTHAN 1912 (e.g., ANDERSON & ANDERSON 1983) and *Dicroidium pinnis-distantibus* (KURTZ) FRENG. 1943 (see RETALLACK 1977). However, *Dicroidium lineatum*, as defined here, is unique among these forms in having closely set, relatively narrow (usually 2–4 mm wide), entire-margined pinnae with acute apices and with acute-angled, simple to once-forked secondary veins. In addition, the species has diagnostic epidermal and cuticular features that easily distinguish it from superficially similar forms, including the occurrence of just a single, diffuse, lens-like thickening per regular epidermal cell (unlike 2–4 in *D. odontopteroides* or 1–2 in *D. dubium*); the smooth and straight anticlinal walls (unlike the granular to buttressed walls in *D. odontopteroides*); and the lack of subsidiary-cell papillae (unlike *D. dubium*).

Dicroidium dubium **(FEISTM. 1878) GOTHAN 1912**

Text-fig. 5.3, Pls 6, 7.

Stratigraphic level: LC-1, LC-2, LC-4, LC-5, LC-6, LC-9, U26 Highwall.

Basionym: Gleichenia dubia FEISTM. 1878, p. 106, pl. 15, fig. 8.

Selected references and synonyms:

1912 *Dicroidium dubium* (Feistm.) Gothan, p. 78, pl. 15, fig. 3.

1947 *Sphenopteris bergina* O.A.Jones et de Jersey, p. 31, pl. 4, figs 2–3, pl. 5, fig. 5, text-fig. 20.

1977 *Dicroidium dubium* var. *dubium* Retallack, frame H9.

1983 *Dicroidium dubium* subsp. *dubium* J.M.Anderson & H.M.Anderson, pl. 32, pl. 53, figs 15–22, pl. 58, pl. 59, pl. 60, figs 1–5, pl. 99, pl. 108, fig. 2.

1995 *Dicroidium dubium* (Feistm.) Gothan – Boucher, figs 37–40.

2005 *Dicroidium dubium* (Feistm.) Gothan – Holmes & Anderson, figs 13 A–C, 14 A–E.

2012 *Dicroidium dubium* (Feistm.) Gothan – Bomfleur et al., pl. III.

2016 *Dicroidium dubium* (Feistm.) Gothan – Pattemore, figs 9, 10.

Description.—Fragments of medium-sized, bifurcate, bipinnatifid to incompletely bipinnate leaves (Pl. 6). Pinnule size and shape varying greatly within frond; smallest pinnules in proximal leaf portion and on inner sides above bifurcation <5 mm long and roughly equidimensional, rounded triangular to trapezoid, with odontopteroid venation (Pl. 6, Figs 1, 2); larger pinnules more elongate lanceolate with alethopteroid venation (Pl. 6, Fig. 1); largest and most complex pinnules on outer side of central leaf portions narrowly lanceolate, about 5 mm broad and up to 35 mm long, with constricted base, distinctly dissected to lobed basal portion grading into narrow tongue-shaped pinnule apex, and with distinct midrib persisting near to pinnule apex giving off acute-angled, usually once- or twice-forked secondary veins that may form odontopteroid vein bundles in basal pinna lobes (Pl. 6, Figs 1, 4, 5). Modified basal elements bipartite, basiscopic portion rounded triangular (similar basal leaf pinnules), separated by deep lobe from the acroscopic portion, which is strongly elongated and lobed at least once (Pl. 6, Fig. 3).

Adaxial cuticle slightly thicker than abaxial cuticle. Cuticle on midrib thicker, both adaxially and abaxially. Adaxial pinna and pinnule lamina with weakly differentiated epidermal cells; abaxial pinna and pinnule lamina differentiated into more strongly cutinized costal fields with more elongate (50 x 20 µm), longitudinally aligned epidermal cells and thinner intercostal fields with shorter (35 x 25 µm), more randomly orientated cells (Pl. 7, Figs 1–3, 7). Periclinal cuticle smooth, usually with two (1–4) lens-like thickenings/papillae per cell (Pl. 7, Figs 1–4). Anticlinal wall flanges thin, slightly thicker on lower leaf surface, slightly curved and with uneven “knobby” texture (see, e.g., Pl. 7, Figs 4, 7, 8).

Leaves amphistomatic, with stomata distributed almost evenly over costal and intercostal areas on both leaf surfaces (Pl. 7, Figs. 1, 2), but with fewer stomata in costal fields of abaxial surface (Pl. 7, Figs 2, 3). Stomata orientated irregularly, usually with 2–4 lateral subsidiary cells. Subsidiary-cell cuticle similar to or slightly more strongly cutinized than regular epidermal cells, with granular lens-like thickening (Pl. 7, Fig. 4); on abaxial leaf surface sporadically forming a single, more or less pronounced solid lappet covering part of the stomatal pit (Pl. 7, Fig. 6). Guard cells sunken (Pl. 7, Fig. 5, 7), feebly cutinized (Pl. 7, Fig. 4), with more strongly cutinized crescentic anticlinal wall flanges and with distinct rounded proximal thickening delimiting the pore (Pl. 7, Figs 4, 8). Stomatal pore straight to spindle-shaped. Mesophyll containing abundant oblate resin bodies distributed evenly throughout the leaf.

Comparison and Remarks.—Apart from the characteristic bipinnatifid to incompletely bipinnate architecture, *D. dubium* is easily separated from co-occurring *Dicroidium* species by the presence of a solid, more or less pronounced thickening or lappet on the subsidiary-cell cuticle. Isolated medium-sized pinnules may appear superficially similar to large pinnules of *D. lineatum*, but can be distinguished based on the typical number of lens-shaped thickenings per cell (usually two in *D. dubium* versus one in *D. lineatum*), the knobbly structure of the anticlinal-wall flanges, and the papillate subsidiary cells. These same features also serve to distinguish isolated short pinnules of *D. dubium* from those of *D. odontopteroides*.

Dicroidium dubium was first described by FEISTMANTEL (1878) based on material from the Sydney Basin, New South Wales. Broadly similar bipinnatifid *Dicroidium* leaves vary widely in size and pinna and pinnule morphology, which has led some authors to distinguish either several intraspecific taxa (ANDERSON & ANDERSON 1983) or up to five species (ANDERSON et al. 2019b) for such material. The present specimens, however, are concordant with the most typical leaf morphology—assigned either to *D. dubium* subsp. *dubium* (RETALLACK 1977; ANDERSON & ANDERSON 1983) or simply to *D. dubium* (ANDERSON et al. 2019b)—that are widespread throughout the Gondwanan Triassic (e.g., see RETALLACK 1977; FEISTMANTEL 1878; ANDERSON & ANDERSON 1983; HOLMES & ANDERSON 2005; BOMFLEUR et al. 2012; PATTEMORE 2016).

Specimens having the typical cuticle structure of the species (i.e., with the characteristic subsidiary-cell thickenings and papillae) were first described by JONES AND DE JERSEY (1947) under the name *Sphenopteris bergina* from the Carnian Ipswich Coal Measures, Australia. ANDERSON AND ANDERSON (1983) illustrated cuticles of two subspecies from the Molteno Formation, South Africa; their *D. dubium* subsp. *dubium* specimens provided only poorly preserved, thin cuticles, but they clearly possess the typical subsidiary-cell papillae arching over the stomatal pore (see Pl. 7, Figs 3, 5). The cuticles of *D. dubium* subsp. *switzifolium* J.M.ANDERSON et H.M.ANDERSON 1983—later considered to be a separate species by ANDERSON et al. (2019b)—appear very similar to those of the present specimens except for the much deeper pinnule dissection, the more buttressed anticlinal-wall flanges, and the common trichomes in the former (ANDERSON & ANDERSON 1983). BOUCHER (1995) also mentioned subsidiary-cell papillae as a diagnostic feature of this species.

BOMFLEUR and KERP (2010) included leaves with similar-sized but essentially entire-margined pinnules in *D. dubium*. However, based on macromorphological and micromorphological features, including the lack of subsidiary-cell papillae, these ought to remain assigned to a separate species, *D. lancifolium* (see also BOUCHER et al. 1993; BOMFLEUR et al. 2011b).

Dicroidium zuberi **(SZAJNOCHA 1888) S.ARCHANG. 1968**

Text-fig. 5.4, Pls 8, 9

Stratigraphic levels: LC-1, LC-17, LC-18, Pit M13.

Basionym: Cardiopteris zuberi SZAJNOCHA 1888, p. 233–234, pl. 2, fig. 1.

Selected references and synonyms:

1879a *Thinnfeldia odontopteroides* pro parte, FEISTMANTEL, pp. 165–169, pl. XI, fig. 1a, b.

1888 (=) *Cardiopteris zuberi* SZAJNOCHA, pp. 233–234, pl. 2, fig. 1.

1894 (=) *Thinnfeldia feistmantelli* [sic] R.M.JOHNST., p. 175.

1912 (=) *Dicroidium feistmanteli* GOTHAN non (R.M.JOHNST.) GOTHAN, p. 78., pl. 16, fig. 1.

1926 (=) *Thinnfeldia feistmanteli* R.M.JOHNST. – CHAPMAN & COOKSON, pp. 167–168, pl. 20, fig. 9, pl. 21, fig. 10.

1933 *Dicroidium* sp. cf. *D. feistmanteli* (R.M.JOHNST.) GOTHAN – THOMAS, figs 50, 52(b).

1943 (=) *Zuberia zuberi* (SZAJNOCHA) FRENG., pp. 300–310.

1944b (=) *Zuberia feistmanteli* (R.M.JOHNST.) FRENG., pp. 3–9, Lámina I–III.

1944b *Zuberia zuberi* (SZAJNOCHA) FRENG. – FRENGUELLI, pp. 9–19, Lámina IV–IX.

1957 (=) *Dicroidium feistmanteli* (R.M.JOHNST.) GOTHAN – TOWNROW, pp. 42–48.

1968 *Dicroidium zuberi* (SZAJNOCHA) S.ARCHANG., pp. 502–504, Plate 98, figs 1–2, text-figs 1a, 2d, e.

1983 *Dicroidium zuberi* (SZAJNOCHA) S.ARCHANG. – ANDERSON & ANDERSON, p. 108, pl. 61, 62, 101, 102.

2014 *Dicroidium zuberi* (SZAJNOCHA) S.ARCHANG. – PAL et al., p. 142–143, pl. 1, 3–6.

Description.—Fragments of presumably large (>25 cm), bifurcate, bipinnate leaves (Text-fig. 2.6). Largest primary pinnae in central leaf portion oblong to linear, up to c. 8 cm long and c. 2 cm wide, tapering gently towards apex (Pl. 8, Figs 1, 3, 5, 7, 8), attached at angles of 80° to <45° with angles decreasing towards leaf apex. Pinnules arranged suboppositely, almost touching, broadly attached to rachis at about right angles, sporadically with slightly constricted bases, becoming progressively fused only in terminal portion of leaf (see, e.g., Pl. 8, Fig. 8). Pinnules comparatively large, on average broader than 5 mm and stout (shorter than wide) to about equidimensional, of variable shape; some specimens with short, more or less rounded rectangular to rhombic pinnules (Pl. 8, Figs 1, 3), others with more equidimensional, rounded-triangular to tongue-shaped pinnules.

Pinnule venation odontopteroid, with many evenly sized veins entering pinnule base, each dichotomizing up to twice and running nearly straight to leaf margins, collectively forming dense, near-parallel venation roughly perpendicular to pinna rachis (Pl. 8, Fig. 6, 7).

Leigh Creek leaves represented by two distinct types of cuticle, each with a characteristic, consistent combination of cuticular and epidermal features. Cuticle type 1 (from sampling sites LC 17 and LC 18) very thick on both leaf surfaces, with strongly thickened anticlinal wall flanges (Pl. 8, Figs 2, 4; Pl. 9, Figs 1, 2). Most (c. 80%) epidermal cells slightly elongated parallel to venation (c. 50 x 35 µm); costal fields in larger pinnules well-differentiated (Pl. 9, Figs 1, 2), with strongly elongated epidermal cells, especially on abaxial surface (c. 120 x 50 µm compared to c. 55 x 35 µm on the adaxial surface). Periclinal walls bearing one to four (usually two) distinct papillae with fine radiating striae (Pl. 9, Figs 1, 5, 6, 8); periclinal cuticle unevenly thick across lamina, forming mosaic of more strongly and weakly (c. 5%) cutinized cells (see, e.g., Pl. 8, Fig. 4). Anticlinal wall flanges relatively straight to slightly wavy and strongly buttressed, thicker over rachis (Pl. 9, Figs 7, 9). Leaves unequally amphistomatic, with stomata concentrated mainly in intercostal fields of abaxial surface and on rachis and costal fields of adaxial surface (Pl. 8, Figs, 2, 4). Stomata orientated randomly, typically surrounded by an incomplete or complete ring of subsidiary cells consisting of two or more lateral subsidiary cells and up to two polar subsidiary cells (Pl. 9, Figs 7, 8, 9). Subsidiary cells more thinly cutinized than regular epidermal cells, lacking papillae, having concentric wrinkles parallel to stomatal pore, sporadically with a distinct thickening along the distal anticlinal wall (Pl. 9, Fig. 8). Anticlinal wall flanges of subsidiary cells straight, smooth, weakly cutinized, and lacking buttressed thickening. Guard cells exposed or slightly sunken, feebly cutinized, with thickened lip surrounding the pore (Pl. 9, Figs 7–9). Mesophyll containing oblate resin bodies (c. 80 µm in diameter, see Pl. 9, Fig. 10). Trichome bases rare (Pl. 9, Fig. 11).

Cuticle type 2 (from sampling levels LC22–24 in the ‘middle series’ of Pit M13, and LC 1 and LC 17 in the ‘upper series’ of pit U26) with thick adaxial cuticle and very thin abaxial cuticle (Pl. 9, Figs 3, 4). Most epidermal cells (c. 60%) slightly elongated parallel to venation (50 x 33 µm), generally smaller on the abaxial cuticle (42 x 27 µm). Periclinal walls usually smooth with one diffuse, lens-like thickening (Pl. 9, Fig. 3). Anticlinal wall flanges rather straight to slightly wavy and delicately buttressed, thicker on rachis. Leaves mostly hypostomatic, with stomata distributed evenly across rachis and lamina on abaxial leaf surface but restricted to rachis on adaxial surface (i.e., upper lamina surface lacking stomata). Stomata randomly orientated, typically surrounded by an incomplete or complete ring of subsidiary cells consisting of two or more lateral cells and up to two polar cells (Pl. 9, Fig. 4). Subsidiary cells slightly more thickly cutinized than regular epidermal cells, with straight and smooth anticlinal wall flanges lacking buttressed thickenings. Guard cells exposed or slightly sunken, weakly cutinized. Abaxial epidermis with scattered hair bases (25 µm in diameter, see Pl. 9, Fig. 4). Mesophyll containing oblate resin bodies (c. 80 µm in diameter).

Comparison and Remarks.—Dicroidium zuberi differs from the other co-occurring *Dicroidium* species in the combination of large bipinnate leaves with separate, short-triangular to square pinnules, strongly buttressed anticlinal cell-wall flanges and minimally sunken stomata. The type 1 cuticle has greater similarity to that of *D. odontopteroides* in its superficial stomata and anticlinal wall ornamentation but has much more distinct hollow papillae and has many fewer stomata on the adaxial leaf surface. The type-2 cuticle has superficial similarities to cuticles of *D. lineatum* in possessing a single lens-like thickening per cell but differs in its strongly buttressed anticlinal walls and in lacking papillae/lens-like thickenings on the adaxial lamina surface.

The large to very large bipinnate-bifurcate leaves of this type now recognized to belong to Umkomasiaceae have been known from the Triassic of Gondwana for more than a century (FEISTMANTEL 1879b; SZAJNOCHA 1888). Overall, these leaves can be highly variable in size, shape, pinnule morphology, and also epidermal details. As a result, their systematic classification and species delimitation remain problematic (DROVANDI et al. *in press*). Some authors emphasize differences in leaf architecture and morphology and recognize these leaves as belonging to the separate genus *Zuberia* with up to six species (ARTABE 1990). Others assign all such leaves to *Dicroidium* (BONETTI 1966; RETALLACK 1977), some to just a single, highly variable species *D. zuberi* (ARCHANGELSKY 1968; ANDERSON & ANDERSON 1983; ANDERSON et al. 2019b), which is also followed here. We note, however, that this broadly defined concept encompasses a great variety of leaves with contrasting sizes and shapes (FRENGUELLI 1944b), pinnule morphologies (e.g., SEWARD 1932; ARTABE 1990), and epidermal details (see, e.g., TOWNROW 1957; ANDERSON & ANDERSON 1983; MARTINEZ et al. 2020; DROVANDI et al. *in press*).

In general, the morphological diversity apparent within *D. zuberi* is akin to the intraspecific variation evident in the dissected foliage of many extant dicot angiosperms, especially among large tree species where leaf form varies according to tree maturity, hydraulic resistance, and exposure to sunlight, among other environmental variables (JENSEN 1990; KLEINSCHMIT 1993; VISCOSI et al. 2012; RAMIREZ et al. 2020). Nevertheless, our observations of the epidermal and cuticular features lead us to suspect that there are, in fact, at least two separate forms within *Dicroidium zuberi* that should probably be resolved into separate species. Unfortunately, many of the earlier, potentially typifying descriptions of superficially similar (FEISTMANTEL 1879b; SZAJNOCHA 1888), large and bipartite leaves are inconsistent or incompatible with observed or illustrated macromorphological features (DROVANDI et al. *in press*), and it remains impossible at present to resolve this issue. Notably, ANDERSON & ANDERSON (1983) likewise observed two distinctive cuticle types (similar to the Leigh Creek types 1 and 2) in their material of *Dicroidum zuberi* from South Africa. One of those types was described as being multi-papillate and amphistomatic (from assemblage Hla211) and the other as being unipapillate and hypostomatic (from assemblage Lit111), which the authors interpreted to reflect ecologically driven phenotypes of the same species. As with other taxa in the Leigh Creek material (e.g., *Dicroidium odontopteroides* and *Dicroidium lineatum*), we assume that two species may be represented among these specimens based on the very clear differentiation into two distinct cuticle types. By analogy, the similarly bipinnate *Dicroidium* leaves from the Permian of Jordan proved to be easily separable into three species based on macroscopic and microscopic characters (BLOMENKEMPER et al. 2020), and consistent differences in epidermal and cuticular features are apparent also among the many examples of bipinnate *Dicroidium* fronds from South America (see ARCHANGELSKY 1968; MARTÍNEZ et al. 2020; DROVANDI et al. in press).

For reasons outlined above, and because the present material is strongly fragmented, we refrain from a more detailed formal taxonomic treatment for the moment. Future research should focus on two aspects for explicit species diagnoses of bipinnate-bifurcate specimens: comparison of large Early Triassic leaves (e.g., from Argentina) and small leaves from the Late Triassic (e.g., Australia, South Africa) applying detailed analyses of the leaf morphology, pinna sizes, shape and margins, and the cuticle structure with precise measurements of epidermal cell size, number and shape of papillae, and stomatal distribution on the adaxial and abaxial leaf surfaces.

In conclusion, some of the large bipartite *Dicroidium* leaves from the Gondwanan Triassic cannot yet be adequately separated into more than one species on the basis of existing diagnoses. As a result, we provisionally use the oldest valid name, *Dicroidium zuberi*, for large bipartite leaves in the Leigh Creek material.

Dicroidium sp. A

Text-fig. 5.5, Pls 10, 11

Stratigraphic level: LC-5, LC-14, LC-18.

Possible previous records:

1927 *Stenopteris densifolia* A.L.DU TOIT, p. 364, text-fig. 14 a, b.

1947 *Stenopteris spinifolia* (TEN.-WOODS) A.C.SEWARD – JONES & DE JERSEY, p. 28, text-figs 17, 18, pl. 3, figs 2–4.

1965 *Xylopteris spinifolia* (TEN.-WOODS) FRENG. – HILL, PLAYFORD & WOODS, p. 10, pl. 5, fig. 7.

1980 *Xylopteris spinifolia* (TEN.-WOODS) FRENG. – BALDONI, p. 150, fig. 2.

1983 *Dicroidium elongatum* forma *remotipinnulium* J.M.ANDERSON et H.M.ANDERSON, p. 117, pl. 48, figs 24–32.

1983 *Dicroidium elongatum* forma *rotundipinnulium* J.M.ANDERSON et H.M.ANDERSON, p. 115, pl. 38, figs 19–28, pl. 107, figs 5–8.

2006 *Xylopteris remotipinnulia* (J.M.ANDERSON et H.M.ANDERSON) OTTONE, p. 479, fig. 2A.

2016 *Xylopteris remotipinnulia* (J.M.ANDERSON et H.M.ANDERSON) OTTONE – BARBONI et al., p. 617, fig. 8, 4–5.

2016 *Xylopteris spinifolia* (TEN.-WOODS) FRENG. – BARBONI et al., p. 611, fig. 7, 1–4.

Description.—Leaves small (<10 cm long), bipartite, pinnate to bipinnate, with V-shaped outline. Bipinnate branching evident in proximal portion of the frond (Pl. 10, Fig. 6). Pinnae (sub-)opposite, distant, attached at about 45° to the rachis (Pl. 10, Figs 3, 6–8); becoming increasingly subopposite to alternate towards apex (Pl. 10, Fig. 6), attached at more acute angles, progressively fusing with rachis (see, e.g., Pl. 10, Fig. 7); apices formed by several (2–3) fused pinnae (Pl. 10, Fig. 4). Central pinnae broadly attached, 3–16 mm long, needle-like and of uniform (c. 0.8 mm) width (Pl. 10, Figs 3, 6, 7), shorter and more strongly fused pinnules (3–5) towards base (Pl. 10, Figs 1, 2), especially basal pinnules (Pl. 10, Fig. 8) and basal elements below furcation. Venation simple, single central veins in pinnules, covering central 25% of lamina, extending to apical margin (see, e.g., Pl. 10, Figs 4, 5).

Adaxial and abaxial cuticle of equal thickness (Pl. 10, Figs 1, 2; Pl. 11, Figs 1, 2). Epidermal cells usually rectangular (22 x 45 µm) and aligned parallel to veins. Costal fields on abaxial surface with more clearly elongate and slender (narrowly rectangular: 17 µm x 70 µm) cells (Pl. 11, Fig. 2, 3); adaxial leaf surface lacking differentiated costal and intercostal fields (Pl. 11, Fig. 1). Periclinal cuticle smooth and usually with two (up to four) diffuse lens-like thickenings per cell (see, e.g., Pl. 11, Figs 1, 5), in some cases associated with radial wrinkles. Anticlinal wall flanges straight to slightly wavy and clearly buttressed (Pl. 11, Figs 5, 8). Leaves amphistomatic; stomata distributed evenly on leaf, with slightly higher density on abaxial surface (Pl. 10, Figs 1, 2, Pl. 11, Figs 1, 2). Stomata usually orientated parallel or, more rarely, transverse to venation, usually with two to four lateral subsidiary cells and no clearly differentiated polar subsidiary cells. Subsidiary cells cutinized to same degree as regular epidermal cells; cuticle smooth, lacking periclinal ornamentation. Guard cells sunken (see Pl. 11, Fig. 5), strongly cutinized, with crescentic anticlinal wall flanges and striae orthogonal to pore (Pl. 11, Figs 5, 6, 8). Stomatal pit slightly sunken (Pl. 11, Fig. 7), weakly cutinized, with straight pore (10–15 µm) having strongly cutinized ledges (Pl. 11, Fig. 8). Mesophyll containing oblate resin bodies (c. 100 µm in diameter) evenly distributed in intercostal areas (Pl. 10, Figs 4, 5; Pl. 11, Fig. 4).

Comparison and Remarks.—Dicroidium sp. A is easily distinguishable from other species in the Leigh Creek assemblage by its needle-like pinnae, the intermediate cuticle thickness, amphistomatic cuticles with 2–4 lens-like thickenings, buttressed anticlinal epidermal walls, and the crescentic anticlinal wall flanges of the guard cells. Superficially, it is similar to *Dicroidium* sp. B, which also has fragmentary needle-like pinnules but has much higher variability in pinnule morphology and differs in its thicker cuticle with notably more deeply sunken and more complex stomatal apparatuses (see *Dicroidium* sp. B, Text-fig. 5). The cuticles of *Dicroidium* sp. A strongly resemble those of *Dicroidium odontopteroides*, having small epidermal cells bearing two or more lens-like thickenings and with slightly buttressed and wavy walls. However, *Dicroidium* sp. A differs by its more complex (crescentic anticlinal wall flanges) and more deeply sunken stomatal apparatuses (see Text-fig. 5).

Species assignment of these specimens remains problematic for several reasons. First, most pinnae have short, widely spaced pinnules that may be basally fused and bear multiple veins—features that are different from those of the more typical simple, needle-like and single-veined segments of *Dicroidium elongatum* (CARRUTH.) S.ARCHANG. 1968. Moreover, the cuticle of *D. elongatum* is thicker, has larger, more elongated and regularly orientated cells with simple, straight cell walls and with more strongly cutinized subsidiary cells (see, e.g., Jones & de Jersey 1947; Anderson & Anderson 1983; Bomfleur & Kerp 2010). Second, the leaf fragments of *Dicroidium* sp. A differ from the more complex leaves of *Dicroidium spinifolium* (Ten.-Woods) J.M.Anderson et H.M.Anderson 1983, which also has a much smoother cuticle lacking papillae/lens-like thickenings and has straight simple cell walls (Anderson & Anderson 1983; Bomfleur & Kerp 2010). Thirdly, *Dicroidium* sp. A. has distinctive cuticle features that are more congruent with those of particular leaves described as *D. elongatum* forma *rotundipinnulium* and *D. elongatum* forma *remotipinnulium* (Anderson & Anderson 1983) and simpler leaves described as *Xylopteris spinifolia* by Jones and de Jersey (1947) and Baldoni (1980). These findings highlight the divergent interpretations of needle-like Umkomasiales leaves—some authors splitting them into multiple species of *Xylopteris* (=*Dicroidium*) (e.g., Retallack 1977; Barboni et al. 2016), others merging them into one or only a few species with several forms or morphotypes (Anderson & Anderson 1983; Anderson et al. 2019b).

Based on differences in cuticle morphology, we assume that *Dicroidium* leaves with needle-like pinnules can be classified into at least three species: a second with larger, straight, particularly elongate leaves, strong cutinization, and elongate rectangular epidermal cells (*D. elongatum* type); one with architecturally more complex and more morphologically diverse leaves, with thinner cutinization, inverse amphistomatic (stomata confined to adaxial costal fields and abaxial intercostal fields) stomatal arrangement, and an absence of papillae/lens-like thickenings (*D. spinifolium* type); and a third type with intermediate pinna complexity, shorter pinnules, amphistomatic leaves with thin cuticle, isodiametric epidermal cells, and several lens-like thickenings per cell (*D. remotipinnulium*, *D. rotundipinnulium*, and *D. tripinnatum* (O.A.Jones et de Jersey) J.M.Anderson et H.M.Anderson 1970 type). *Dicroidium* sp. A appears to fit in this third category, but since the present material is fragmentary, we refrain from a formal assignment. Very similar material has been described from South Africa (e.g., du Toit 1927; Anderson & Anderson 1983), South America (e.g., Baldoni 1980; Barboni et al. 2016) and Australia (e.g., Jones & de Jersey 1947; Hill et al. 1965).

***Dicroidium* sp. B**

Text-fig. 5.6, Pl. 12, 13.

Stratigraphic level: LC-18, LC-19, LC-21.

Possible previous records:

1957 *Dicroidium superbum* (SHIRLEY) TOWNROW, p. 43, text-figs 7E–G; 8A, 10A, B.

1977 *Dicroidium townrovii* RETALLACK, frame I13.

1982 *Dicroidium shirleyi* W.B.K.HOLMES, pp. 11–12, figs 5E, 6B.

1983 *Dicroidium superbum* forma *townrovii* (RETALLACK) J.M.ANDERSON & H.M.ANDERSON, p. 110, pl. 50, 1–16.

1983 *Dicroidium superbum* forma *superbum* (SHIRLEY) TOWNROW – J.M.ANDERSON & H.M.ANDERSON, p. 111, pl. 49, 15–19, pl. 86, 11.

Description.—Only frond fragments recovered; however, fronds inferred to be bipartite based on pinna shape and orientation on rachis (Pl. 12). Two macroscopically different frond and pinna types recovered. Pinnule type one (Pl. 12, Figs 5–12) arranged suboppositely, clearly separated and attached broadly at almost right angles to rachis, typically as long as wide (c. 4.5 x 4.5 mm), trapezoid to square (Pl. 12, Figs 9, 10), with rounded apex; additional isolated pinnules oval with constricted base (Pl. 12, Figs 11, 12), possibly deriving from basal leaf portions; venation odontopteroid, with veins dichotomizing up to three times at acute angles, with lateral veins running straight and almost parallel towards margin. Pinnule type two (Pl. 12, Figs 1–4) narrow to needle-shaped (c. 1 x 2–10 mm), with rounded segment apices, oppositely to suboppositely arranged, clearly separated, broadly attached to rachis at acute angles (<45°); leaf apices consisting of three strongly fused segments; venation consisting of single central vein per segment.

Epidermal anatomy and cuticle micromorphology consistent among different pinnule forms (Pl. 13). Adaxial cuticle thicker than abaxial cuticle (Pl. 13, Figs 1, 2). Two thirds of the epidermal cells slightly elongated parallel to venation, other cells isodiametric. Costal fields with longitudinally aligned and narrower, strongly elongated cells (about 15 x 50 µm) compared to intercostal fields (around 22 x 40 µm). Periclinal cuticle with single discrete papilla per cell on the adaxial cuticle (Pl. 13, Figs 1, 4, 9) and much more diffuse thickening on the abaxial cuticle (Pl. 13, Figs 2, 3). Anticlinal wall flanges straight to slightly curved, thickly cutinized and strongly buttressed (Pl. 13, Figs 3–6). Leaves amphistomatic, with stomata distributed evenly in intercostal fields on adaxial and abaxial leaf surface (Pl. 13, Figs

1, 2). Stomata orientated mostly parallel to venation, with two to four lateral subsidiary cells (Pl. 13, Figs 3–6). Subsidiary-cell cuticle equivalent in thickness to that of regular epidermal cells but lacking papillae (Pl. 13, Figs 3, 4). Guard cells narrowly rectangular (Pl. 13, Figs 3–6), with thickly cutinized distal anticlinal flanges, sunken deeply in cuticle (Pl. 13, Fig. 9), covered by distinctly cutinized oval Florin ring, with long axis transverse to the pore's direction (Pl. 13, Figs 3, 4). Some leaves with moderately common trichomes (Pl. 13, Fig. 7). Mesophyll containing long resin canals (diameters c. 35 µm, see Pl. 13, Fig. 8) probably extending throughout the entire pinnule, but generally disintegrating during maceration (Pl. 13, Fig. 8).

Comparison and Remarks.—Based on gross morphology alone, type 1 pinnules of this species are very similar to those of *Dicroidium zuberi* and type 2 pinnae are similar to those of *Dicroidium* sp. A. The cuticles, however, can be clearly distinguished from the other species by their overall thickness and their thick, straight, slightly buttressed anticlinal walls, usually one papilla per cell, deeply sunken stomata and resin canals.

This complement of typical cuticular features also serves as our basis to assign these various frond and pinna morphologies to the same species. On balance, the spectrum of macromorphological features is somewhat reminiscent of relatively complex leaves with polymorphic pinnules of the *Dicroidium superbum* complex (see, e.g., TOWNROW 1957; RETALLACK 1977; HOLMES 1982; ANDERSON & ANDERSON 1983).

Cuticles similar to those described here as *Dicroidium* sp. B have been documented from the Ipswich Coal Measures (TOWNROW 1957). These were described as tough, with a thicker adaxial cuticle of isodiametric cells and a thinner abaxial cuticle having elongated (rectangular) cells in the costal fields, with straight to finely sinuous (probably buttressed) anticlinal walls and distinct small papillae. Stomata were said to be deeply sunken, with subsidiary cells covering parts of the guard cells (TOWNROW 1957).

***Dicroidium* sp. C**

Text-fig. 5.7, Pl. 14.

Stratigraphic level: LC-13.

Possible previous records:

1947 ?*Neuropteridium* sp. O.A.JONES et DE JERSEY, pp. 33–34, Text-figs 21, 22.

1967 *Johnstonia trilobita* (JOHNST.) O.A.JONES et DE JERSEY 1947 – TOWNROW, p. 466, Fig. 2D.

1983 *Dicroidium crassinerve* (GEINITZ) J.M.ANDERSON et H.M.ANDERSON forma *trilobitum* (JOHNST.) J.M.ANDERSON et H.M.ANDERSON pro parte, p. 95, pl. 85, figs 33, 38–40.

Description.—Fragments of pinnate fronds; pinnules attached suboppositely and clearly separated (Pl. 14, Figs 1–3). In proximal leaf portion, pinnules broadly attached at about right angles; towards apex becoming slightly constricted at base and attached at more acute angles (Pl. 14, Fig. 1). In central leaf portion, pinnules around two to three times longer than wide (c. 10 x 4 mm). Pinnules near leaf base and on the inner side immediately above the bifurcation short (Pl. 14, Figs 1, 2), triangular, and about as long as wide (3.5 x 3 mm). Pinnule margins shallowly and smoothly dentate to crenate throughout frond. Modified basal elements have not been recovered. Venation density moderate; in short pinnules odontopteroid (Pl. 14, Figs 2, 3), in elongate pinnules more alethopteroid with primary vein extending close to pinnule apex, but dichotomizing once before reaching apex (Pl. 14, Fig. 1). Secondary veins given off at 20–30°, dichotomizing once before reaching margin.

Adaxial and abaxial cuticles equally thin. Epidermal cells (Pl. 14, Figs 4, 5, 6) slightly elongated (rectangular) and typically either orientated parallel or transverse to venation (35 x 25 µm), less commonly square (30 x 30 µm). Epidermal cells of costal fields on abaxial leaf surface longitudinally aligned and more strongly elongated (15 x 55 µm). Cuticle over periclinal walls with one diffuse lens-like thickening per cell (Pl. 14, Figs 5, 6). Anticlinal walls thin, straight to very slightly curved and smooth. Leaves unevenly (inverse) amphistomatic with stomata distributed regularly across abaxial surface but located only on rachis of adaxial surface. Stomata orientated either parallel or transverse to venation (Pl. 14, Fig. 4), slightly sunken in lamina (Pl. 14, Fig. 6). Guard cells narrow, more thickly cutinized than subsidiaries, surrounding a straight pore (Pl. 14, Fig. 4). Mesophyll containing oblate resin bodies of varied size (50–120 µm in diameter) distributed evenly across pinnules (Pl. 14, Figs 1–4).

Comparison and Remarks.—Pinnules of this species closely resemble *Dicroidium lineatum* from Leigh Creek, in having a lanceolate shape, alethopteroid venation, and simple epidermal cells with straight anticlinal walls, one weak lens-like thickening and slightly sunken stomata. However, they are clearly differentiated based on their unequal (inverse) stomatal distribution on the adaxial and abaxial leaf surfaces, shallowly dentate to crenate leaf margins and much more weakly cutinized leaves. The pinnule dimensions are generally most similar to *D. odontopteroides*.

Only three incomplete leaf fragments were recovered. The species is similar to a specimen illustrated by ANDERSON & ANDERSON (1983) as *Dicroidium crassinerve* forma *trilobitum*, in having short rhombic, triangular or oblong pinnules with characteristic dentate to crenate pinnule margins. ANDERSON &ANDERSON (1983) included such specimens within a broader morphological spectrum encompassing also short and apically three-lobed pinnules (e.g., their pl. 68, figs 26–30), which have been described from various locations across southern Gondwana (FEISTMANTEL 1889; ANTEVS 1914; JONES & DE JERSEY 1947; TOWNROW 1966; BOUCHER et al. 1995; NIELSEN 2005). We regard these leaves with lobed and crenate to dentate pinnules illustrated by ANDERSON AND ANDERSON (1983) and the specimens here described from Leigh Creek as possibly belonging to a distinct species separate from the typical *D. crassinerve* in general and also from *D. trilobitum* (JOHNST.) ANTEVS 1914 in particular. JONES AND DE JERSEY (1947) described a similar forked leaf with rhombic to oblong pinnules and a lobed margin from the Ipswich Coal Measures (Australia) under the name *Neuropteridium* sp., but did not give any information about the cuticle.

The Leigh Creek species differs from *Dicroidium trilobitum* and from the various other forms of *D. crassinerve* (to which this leaf morphology has been referred) in having an extremely thin cuticle and in being mostly hypostomatic with only a few stomata on the upper leaf surface (TOWNROW 1966; ANDERSON & ANDERSON 1983; CANTRILL et al. 1995; BOMFLEUR & KERP 2010). These cuticle details, together with the typical crenate to dentate pinnule margin, may delimit a previously undescribed species, but owing to the sparse and incomplete material, we refrain from formally establishing a new taxon for these specimens.

Fertile organs

Residues of bulk-macerated shales and siltstones throughout the section have also yielded abundant fragments of Umkomasiaceae reproductive organs. In addition to the taxa described in detail below, most samples have also yielded small fragments of pollen sacs with bisaccate pollen but without any further diagnostic features.

Genus *Umkomasia* H.H.THOMAS 1933

Type species.—*Umkomasia macleanii* H.H.THOMAS 1933

Type: The holotype of *U. macleanii* is specimen V23360 (U11) in the collections of the Natural History Museum, London, collected from the Carnian Molteno Formation exposed at the Waterfall locality in Umkomaas Valley, Karoo Basin, South Africa (THOMAS 1933, p. 203, text-figs 1–4, pl. 23, fig. 56).

***Umkomasia* sp. cf. *U. quadripartita* J.M.ANDERSON et H.M.ANDERSON 2003**

Pl. 15–17.

Stratigraphic levels: LC-5, LC-20.

Reference

2003 *Umkomasia quadripartita* J.M.ANDERSON et H.M.ANDERSON, p. 247, pls 84, 85.

Description.—Isolated cupules ovoid, 7–9 mm long and 4–7 mm wide, preserved either in lateral or in dorsiventral compression, split open about halfway into two almost hemispherical lobes, with pedicel attached broadly along distal cupule surface, recurved and extending downwards from between lobes along dorsal cupule surface (Pl. 16, Figs 1–7; Pl. 17, Figs 1, 2).

Proximal pedicel cylindrical, about 1 mm wide, and with similar cuticle thickness, epidermal cell pattern, and stomatal density over entire surface (Pl. 15, Fig. 1; Pl. 17, Figs 1, 2); distally (towards the cupule), pedicel becoming flattened, broadening to about 2.5 mm width (see, e.g., Pl. 16, Fig. 3; Pl. 17, Fig. 2), with epidermis becoming increasingly differentiated into abaxial pedicel surface similar to inner cupule surface (see Pl. 17, Figs 1, 5, compare to Pl. 15, Fig. 3) and adaxial pedicel surface more similar to outer cupule surface but with more strongly elongate cells (Pl. 16, Fig. 3; Pl. 17, Figs 2, 3).

Outer cupule surface with isodiametric cells (c. 27 µm in diameter), thick and evenly cutinized periclinal surface and anticlinal wall flanges, and evenly distributed stomata (Pl. 15, Figs 2, 4, 6, 7; Pl. 17, Figs 4, 6); inner cupule surface with elongate, longitudinally aligned cells (about 45 µm long and 20 µm wide), with thin periclinal and anticlinal wall cuticle, and lacking stomata or hair bases (Pl. 15, Figs 2, 3, 5). Stomata orientated randomly (see Pl. 16), typically with two to four subsidiary cells and lacking polar subsidiary cells (Pl. 15, Figs 6, 7). Subsidiary cells with concentric wrinkles and commonly with more or less distinct papilla-like thickening on periclinal surface. Guard cells slightly sunken (see Pl. 17, Fig. 6), surrounded by strongly cutinized walls forming an almost circular pit around the pore; pore delimited by thickened lips.

Comparison and Remarks.—Incorporating observations of diverse epidermal (cuticle) features, THOMAS (1933) established three genera with fourteen species to contain the various types of cupulate organs associated with *Dicroidium* foliage from the Triassic Molteno Formation, South Africa. However, since cuticle features of the genus have only rarely been studied since then, all these species were later placed into synonymy of just a single species, *Umkomasia macleanii* (e.g., ANDERSON & ANDERSON 2003; ANDERSON et al. 2019c). The isolated cupules described here are assigned to *Umkomasia* based on the characteristic epidermal architecture together with the size, the recurved orientation, and the deep median splitting of the cupule into two hemispherical halves (see, e.g., ANDERSON & ANDERSON 2003). They are, however, significantly larger (about twice the diameter) of any specimens described in Thomas' original publication. In size, shape, and lobing, the cupules conform with two species from the Molteno Formation that have medium-sized cupules split into two lobes, i.e., *U. bracteolata* J.M.Anderson et H.M.Anderson 2003 and *U. quadripartita* J.M.Anderson et H.M.Anderson 2003 (ANDERSON et al. 2019c). The two species are distinguished from one another primarily by the average number of cupules per megasporophyll unit—a feature that cannot be resolved in our fragmented material. We note, however, that the likely affiliation with *Dicroidium dubium* (see discussion) provides circumstantial evidence for an at least tentative assignment to *U*. sp. cf. *U. quadripartita*; the reference assemblage for *U. quadripartita* (Mat111 in the Molteno Formation) is dominated by this leaf species (see ANDERSON & ANDERSON 1983, 2003).

Genus *Fanerotheca* Freng. 1944a emend. J.M.Anderson et H.M.Anderson 2003

Type species: *Fanerotheca exstans* FRENG. 1944a emend. Bodnar, Morel, Coturel et Ganuza 2020

Type: FRENGUELLI (1944a) did not designate a holotype for the type species; recently, BODNAR et al. (2020) proposed specimen no. LPPB 10258, 10259 (counterpart) from Frenguelli's original material to serve as lectotype, housed in the palaeobotanical collections the Museo de La Plata, La Plata, Argentina, collected from the type bed EPI, of the upper section of the

Carnian Potrerillos Formation, exposed at Puesto Mínguez, Cacheuta Hill, in Mendoza Province, Argentina (Bodnar 2020, p. 7, Fig. 3 A & B).

Fanerotheca sp. cf. _F. waldeckiformis_ J.M.Anderson et H.M.Anderson 2003

Pl. 18, 19.

Stratigraphic levels: LC-5, LC-11, LC-13, U26 Highwall.

Possible previous records:

1927 *Sagenopteris* sp. du Toit, p. 399, pl. 29, fig. 3.

1944a *Fanerotheca exstans* Freng., p. 393, pl. 1, fig. 2, pl. 2, fig. 1.

1960 *Antevsia extans* (Freng.) Townrow, pp. 350–352, text-fig. 9G, pl. 9A–D.

2003 *Fanerotheca waldeckiformis* J.M.Anderson et H.M.Anderson, p. 276, pls 100–101.

2003 *Fanerotheca cruciformis* J.M.Anderson et H.M.Anderson, p. 277, pl. 102, figs 1–4.

Description.—Isolated cupules, split open and flattened symmetrically into cross-shaped structures with four even-sized, ovate or lanceolate to rounded-triangular lobes radiating out from cupule centre; lobes 3–5 mm long and 2–3 mm in maximum width, divided about 50–75% from tip to cupule centre (Pl. 18, Figs 1–4; Pl. 19, Figs 1–3), commonly with longitudinal folding along the free lateral margins (see, e.g., Pl. 18, Fig. 4; Pl. 19, Fig. 3). Pedicels about 500 µm wide, attached to centre of cupule base and arising in a way suggestive of originally right-angled attachment (i.e., not incurved or confluent with cupule surface; see, e.g., Pl. 19, Figs 1–3).

Cupule cuticle very thin throughout; outer surface of central cupule partly verrucose, shrivelled, more strongly cutinized (Pl. 19, Figs 1, 2); area of seed attachment in inner cupule centre without cuticle and instead commonly with remnants of coalified material (see, Pl. 18, Fig. 1; Pl. 19, Fig. 3).

Epidermal cells on outer surface of central cupule part near-isodiametric (about 30 µm in diameter, see Pl. 18, Fig. 6; Pl. 19, Fig. 4), towards margin and into lobes becoming more clearly elongate (c. 25 µm wide and c. 72 µm long, see Pl. 19, Figs 3, 5). Periclinal walls with subtle, diffuse central thickening (only visible under UV fluorescence, see Pl. 19); anticlinal walls thin, straight to slightly curved (Pl. 19, Figs 4–6). Cupules amphistomatic. Stomata orientated randomly, distributed mainly over central lamina and central parts of the individual lobes. Guard cells sunken more deeply into cuticle, anticlinal wall flanges more thickly cutinized, in some cases creating a ring around the pore (see Pl. 18, Fig. 7; Pl. 19, Figs 5, 6). Stomatal pore straight to spindle-shaped; ledges slightly thickened. Cupules bearing conspicuous oblate resin bodies 100–400 µm (av. 220 µm, see Pl. 18, Figs 5, 6) in diameter distributed evenly between cuticles, mainly in cupule centre and in basal and central portions of lobes (see Pl. 18, Figs 1–3).

Comparison and Remarks.—Although only isolated fragments have been recovered, the cupules can be readily assigned to *Fanerotheca* based on the straight, perpendicular attachment of the pedicel in the cupule centre (as opposed to the recurved orientation and confluent pedicel attachment in *Umkomasia* cupules), the deep splitting of the cupule into four even-sized lobes, and the characteristic epidermal architecture. The genus is apparently widespread and surprisingly common in the Triassic of Gondwana (ANDERSON & ANDERSON 2003). In addition to the systematic descriptions of *Fanerotheca* from South America (FRENGUELLI 1944a; BODNAR et al. 2020) and South Africa (ANDERSON & ANDERSON 2003), similar cupules have been reported under various names by other authors from South Africa (DU TOIT 1927; TOWNROW 1960), Australia (WALKOM 1915), Antarctica (BOMFLEUR et al. 2014), and South America (TOWNROW 1960; JAIN & DELEVORYAS 1967). Five species are currently recognized (BODNAR et al. 2020). Since many of the specific diagnostic characters relate to features of the cupule-bearing branching system, the isolated cupules reported here cannot be assigned to any particular species with certainty. We note, however, that in size and shape of the cupule lobes and in pedicel dimensions, our material is particularly similar to *Fanerotheca cruciformis* and *F. waldeckiformis* from the Molteno Formation of South Africa (ANDERSON & ANDERSON 2003); by analogy with the South African assemblages, similar co-occurrence and inferred affiliation with the same *Dicroidium* leaf type leads us to tentatively assign these specimens to *Fanerotheca* sp. cf. *F. waldeckiformis* (see discussion).

Dispersed Umkomasiaceae seeds

Text-fig. 2.8.

Stratigraphic levels: LC-4, LC-14, U26 Highwall.

Selected references:

1933 Isolated corystospermous seeds, THOMAS, fig. 33, pl. 24, figs 67–69.

2003 *Umkomasia monopartita* J.M.Anderson et H.M.Anderson pro parte (isolated seeds only), pl. 87, figs 10–13.

Description.—Isolated seeds were recovered from several beds, including two charcoalified specimens and several cuticle fragments. Seeds elongate cordate (2.5–4.5 mm long and 2–3.4 mm wide), with gently (c. 45°) curved, bifid micropylar extension (Text-fig. 2.8), central bifurcation covered with clusters of bisaccate *Alisporites* Daugherty 1941/*Falcisporites* Leschik 1956-type pollen. Seed bases slightly depressed. Cuticles thick; epidermal cells square to slightly rectangular with strongly cutinized periclinal and anticlinal walls. No stomata observed.

Remarks.—The curved, bifid micropylar extension of these seeds indicate affinities with Umkomasiaceae; the specimens most closely resemble the dispersed seeds of *Umkomasia* organs (see, e.g., Thomas 1933: figs 67–69) since they lack the prominent wing typical of *Feruglioa* Freng. 1944a, the seed type produced in *Fanerotheca* (e.g., Anderson & Anderson 2003; Bodnar et al. 2020).

Genus *Pteruchus* H.H.Thomas 1933 emend. H.M.Anderson 2019

Type species: *Pteruchus africanus* H.H.Thomas 1933 emend. H.M.Anderson 2019

Type: Holotype of the type species is specimen V23384 (U244) in the collections of the Natural History Museum, London, collected from the Carnian Molteno Formation exposed at the Waterfall locality in Umkomaas Valley, Karoo Basin, South Africa (Thomas 1933, p. 212, text-figs 34, 35, pl. 24, figs 71, 72).

***Pteruchus africanus* H.H.Thomas 1933 emend. H.M.Anderson 2019**

Pl. 20.

Stratigraphic levels: LC-12, LC-13.

Selected references and synonyms:

1933 *Pteruchus africanus* H.H.Thomas, p. 212, text-figs 34, 35, pl. 24, figs 71, 72.

1933 (=) *Pteruchus papillatus* H.H.Thomas, p. 237, text-figs 36, 37.

1933 (=) *Pteruchus peltatus* H.H.Thomas, p. 238, text-figs 38, 39.

1933 (=) *Pteruchus hoegi* H.H.THOMAS, p. 239, text-figs 40, 41, pl. 24, fig. 75.

1933 (=) *Pteruchus stormbergensis* H.H.THOMAS, p. 241, text-fig. 43.

1933 (=) *Pteruchus dubius* H.H.THOMAS, p. 241, text-figs 44, 45.

1933 (=) *Pteruchus minor* H.H.THOMAS, p. 242, text-figs 46, pl. 24, fig. 76.

1962 *Pteruchus africanus* H.H.THOMAS – TOWNROW, fig. 1A–D, F, fig. 2D–G, fig. 8B, C, fig. 9A–D, pl. 24, fig. 4, pl. 25, figs 1, 2.

Description.—Only incomplete fructifications recovered; microsporophylls consisting of a slender (700 µm wide) stalk terminating in simple, dorsiventral microsporophyll lamina (Pl. 20, Figs 1, 2). Microsporophyll lamina oval (c. 6 x 4.5 mm); margin finely sinuate forming about ten even-sized lobules (Pl. 20, Fig. 1), covering pollen sacs almost entirely except for c. 0.5-mm-wide fringe of protruding pollen-sac apices (overall dimensions including protruding microsporangia up to 7 x 5.5 mm). Abaxial lamina surface bearing 14–24 fusiform, straight to slightly twisted pollen sacs, each about 1500 µm long and 600–650 µm wide, broadly attached, arising more or less perpendicular to lamina surface, and showing fine, gently helical longitudinal striations (Pl. 20, Figs 2, 3, 7).

Cuticle of adaxial microsporophyll lamina thick. Epidermal cells in central lamina portion roughly isodiametric (30–40 µm long) and irregularly orientated (Pl. 20, Figs 4–6); periclinal cell walls with 2–4 small papillae, anticlinal walls straight and slightly buttressed. Towards lamina margin, epidermal cells becoming more elongate (30 µm wide, 44 µm long) perpendicular to margin; periclinal walls thinner and lacking papillae; anticlinal walls thin and straight. Stomata orientated randomly on adaxial surface, usually with two (to four) lateral subsidiary cells (see, e.g., Pl. 20, Fig. 6). Subsidiary cells less cutinized than regular epidermal cells, lacking papillae. Guard cells simple, faintly cutinized and flush with epidermis.

Pollen sacs with simple, narrowly rectangular epidermal cells (c. 135 µm long and 40 µm wide, see Pl. 20, Fig. 3), orientated longitudinally; periclinal walls thin and lacking ornamentation; anticlinal walls thin and straight (Pl. 20, Fig. 7). Most sacs containing masses of bisaccate non-taeniate pollen grains of *Alisporites*/*Falcisporites* type (Pl. 20, Figs 8, 9).

Comparison and Remarks.—These pollen organs can be placed with certainty into the broadly defined species *Pteruchus africanus* as emended by H.M. Anderson in H.M. ANDERSON et al. (2019a), based on the size, shape, and lobate margin of the microsporophyll lamina, the number of pollen sacs, and the distinctive stomatal architecture (see also TOWNROW 1962; ANDERSON & ANDERSON 2003). Cuticle details of *Pteruchus* were originally described by THOMAS (1933) from the Molteno Formation, South Africa, but these related mainly to the rather uniform and meagerly informative cuticle of the stalk instead of the microsporophyll lamina. TOWNROW (1962) described the cuticles of the lamina as bearing irregular lumps (compare Pl. 20, Figs 1, 3, 5) with obtusely to non-buttressed anticlinal walls and only slightly sunken stomata with exposed pits, which agrees with our findings. Slightly helical organization of cells in the pollen sac wall is common in several other extinct gymnosperm groups—e.g., in *Antevsia* (Peltaspermales: ANDERSON & ANDERSON 2003, pl. 48), *Arberiella* (Glossopteridales: MCLOUGHLIN & PREVEC 2021, fig. 3D), and *Stachyopitys* (Hamshawviales: ANDERSON & ANDERSON 2003, pl. 74, fig. 13). This cell organization might represent an adaptation to torsional splitting with hydration/desiccation to facilitate pollen release.

5 Discussion

Although plant fossils have been recorded from the Leigh Creek Coal Measures for more than 100 years (ETHERIDGE 1891), the richness, diversity and quality of the fossil material has never been fully explored. The low degree of compaction and weak cementation of the host deposits, coupled with the limited alteration and low coalification rank of the buried organic matter, provides an exceptional source of new information for palaeobotanical investigations. The exquisite preservation state allowed us to modify conventional processing methods to obtain large sample volumes and optimal preparation results in a short time and at low laboratory costs. Moreover, the individually adapted workflow enabled us to obtain particular states of preservation for specific scientific questions. The minimal alteration of the cuticles offered a unique opportunity to critically evaluate the significance of cuticle features for species delimitation and whole-plant re-assembly in Umkomasiales. The composition of distinct taphocoenoses also provides an exceptionally detailed insight into the palaeoecology of *Dicroidium* plants and the continental middle- to high-latitude palaeoenvironments of Triassic Gondwana.

Comments on chemical extraction and preparation procedures

The diverse forms of plant-fossil preservation in the Leigh Creek Coal Measures include mummified lignitic remains (most with well-preserved cuticle and leaf resins, some with preserved vascular bundles and even the remains of mesophyll tissues), charcoalified fragments, and variable types of naturally macerated specimens, all in varying degrees of fragmentation that range from mats of near-complete leaves to accumulations of strongly comminuted debris. Some associated woody stems are preserved by siliceous and sideritic permineralization. Since most fossils in these deposits are preserved in weakly consolidated mudstone and siltstone, we adapted various traditional and novel methods of extraction and preparation for the study of the material. The use of sodium hexametaphosphate for sediment disaggregation enabled us to obtain large quantities of plant material in a very short time and without the application of harmful chemicals. This method is limited to weakly or unconsolidated sediments and only separates mineral matter from the organic material; it does not chemically dissolve the sediment, resulting in less pristinely cleaned samples compared to HF treatment, which is still needed for SEM preparation. After extraction of the fossils, it was necessary to undertake detailed screening of the material, using a stereo microscope and fluorescence microscope, to recover fossils that would otherwise be disintegrated in the following chemical preparation. Carbonized plant fragments (seeds, bark, reproductive organs) and naturally macerated leaves were isolated to observe the venation and distribution of resin bodies or evidence of plant-insect interactions (e.g., galling, mining, leaf-margin feeding). Subsequent chemical maceration was undertaken either for bulk assemblages or isolated specimens; iteratively, the concentration of 25% cold nitric acid for several days was found to be most effective—depending on the degree of prior natural maceration of the fossils. A second bulk material screening was carried out to recover all new and unusual fossils for further microscopic analysis, including additional cuticles, material with cellular preservation (vascular bundles, mesophyll), charcoalified fossils, and arthropod remains. Subsequently, additional oxidation of the fossils was carried out when necessary using chlorine-bleach to remove amorphous mesophyll from between the cuticles or to further bleach very opaque cuticles for optimal observation using light microscopy or SEM. Following this workflow enabled us to recover the maximum information from these uniquely well preserved matted leaf layers, containing diverse and detailed macro-, meso-, and microfossil taphocoenoses.

Cuticular analysis as a tool in corystosperm taxonomy

The value of cuticle analysis for the taxonomy of fossil seed plants had already been recognized in the 19th century (e.g., WESSEL & WEBER 1855; BORNEMANN 1856). Epidermal and cuticular features have proven especially useful for the discrimination of pteridosperm foliage at various taxonomic ranks (e.g., GOTHAN 1916; HARRIS 1932a, b; FLORIN 1933; BARTHEL 1961, 1962; KRINGS 1997; KERP & KRINGS 2003). Umkomasiaceae in particular have early on been recognized as having distinctive epidermal anatomy (GOTHAN 1912; THOMAS 1933; TOWNROW 1957; ARCHANGELSKY 1968), but the taxonomic significance of cuticle features in the group has also been questioned (e.g., ANTEVS 1914; PATTEMORE 2016).

Our results clearly demonstrate cuticular analysis to be a highly useful tool for the identification and delimitation of Umkomasiaceae fossils. Almost every *Dicroidium* species in the assemblage can be characterized by a consistent set of diagnostic cuticular and epidermal features, except for the few poorly preserved fragments of *Dicroidium* sp. C. The diagnostic significance of such features can be assessed (1) due to the large sample size (>550 microscopic slides with many more samples observed without mounting); (2) in the consistency with which they occur across several stratigraphic levels and within laterally correlative assemblages (i.e., LC12–14); and (3) from the comprehensive observations via various analytical techniques (see methods; LM, TM, SEM).

Our results also highlight, however, that the taxonomic utility of cuticle features should be evaluated critically for the studied plant group (see, e.g., BARCLAY et al. 2007; BOMFLEUR & KERP 2010). The material should provide information both on macroscopic and on microscopic features in order to render taxonomic results that are applicable to material lacking preserved cuticles. Moreover, sufficient quantities of material are required to account for the intraspecific variability in each taxon. Ideally, material from different beds or from laterally separate samples is needed to exclude site-specific environmental influences on cuticular morphology (see, e.g., BARCLAY et al. 2007). The observation of details from the central lamina, on both adaxial and abaxial surfaces, and in both costal and intercostal fields is required to effectively circumscribe each taxon. The cuticles of the petiole, rachis and lamina margins commonly show fewer features and are less differentiated—and thus less informative—for *Dicroidium* species demarcation.

Features that proved to be most diagnostic for the delimitation of *Dicroidium* species were (1) stomatal distribution, (2) anticlinal wall course and ornamentation; (3) periclinal wall thickness and structure; (4) the differentiation of subsidiary cells compared to regular epidermal cells; and (5) regular epidermal cell size, shape and orientation. Numbers and configuration of subsidiary cells and the resulting overall structure of the stomatal apparatus, by contrast, proved to be remarkably consistent across most species observed (see also BOMFLEUR & KERP 2010). A notable exception is the more common occurrence of cyclocytic stomata with a complete ring of subsidiary cells in *Dicroidium zuberi*, as observed by previous authors (see also, e.g., TOWNROW 1957; ANDERSON & ANDERSON 1983). Based on the results of our analysis, we provide an identification key for *Dicroidium* species from Leigh Creek that we anticipate will prove applicable to other *Dicroidium* cuticle assemblages (Text-fig. 5). If a large number of cuticle specimens is available, micromorphological details offer a very important source of information for precise species circumscription. This is especially crucial in cases where evidence from gross morphology alone is ambiguous, either because two species appear similar in macromorphology—as the two distinct cuticle types of *Dicroidium zuberi*-like fronds reported here might indicate—or because a single species has highly variable frond morphology (see *Dicroidium* sp. A).

Whole-plant reconstruction

Given the ubiquity and abundance of corystosperm fossils in the Triassic of Gondwana, it is surprising how few affiliations between species of leaves and reproductive organs have been established thus far (BLOMENKEMPER et al. 2020). The extraordinary preservation of the Leigh Creek material offers a rare opportunity to contribute towards reconstructing whole-plant species of *Dicroidium*. Based on mutual-occurrence data (Table 1) and similarities in epidermal and cuticle features, all identified taxa of reproductive organs, including *Umkomasia* sp. cf. *U. quadripartita*, *Fanerotheca* sp. cf. *F. waldeckiformis*, and *Pteruchus africanus*, can be linked to particular *Dicroidium* foliage species.

The complement of cuticle features of *Umkomasia* sp. cf. *U. quadripartita* is fully consistent with that observed in *Dicroidium dubium*. Of particular importance is the differentiation of subsidiary cells with the sporadic occurrence of a single solid thickening or papilla in *Umkomasia* sp. cf. *U. quadripartita*; among the studied leaf species, this feature is unique to *Dicroidium dubium*, which strongly favours its affiliation with the aforementioned reproductive organ. Additional evidence comes from co-occurrence data in that the common occurrence of isolated *Umkomasia* sp. cf. *U. quadripartita* cupules is restricted to a single bed in which *D. dubium* is also common (Table 1). Notably, the type material of *Umkomasia quadripartita* in the Molteno Formation (ANDERSON & ANDERSON 2003) derives from an assemblage that is also dominated by (and served as the reference assemblage for) *Dicroidium dubium* (ANDERSON & ANDERSON 1983).

The ovule-bearing *Fanerotheca*, associated with *Dicroidium* foliage at many localities (FRENGUELLI 1944a; TOWNROW 1962; ANDERSON & ANDERSON 2003; ANDERSON et al. 2019c; BODNAR et al. 2020), can be correlated with the leaf species *D. lineatum* based on corresponding cuticle features (see systematic description). In addition, *Fanerotheca* occurs in assemblages in which *D. lineatum* is abundant or even dominant (Table 1). In South Africa, the various species of *Fanerotheca* co-occur with several species of *Dicroidium* foliage, mainly *D. crassinerve*, *D. odontopteroides*, *D. elongatum* and *D. lineatum* (ANDERSON & ANDERSON 1983, 2003). Particularly informative is assemblage Wal111, where *Dicroidium lineatum* (there classified as *D. odontopteroides* subsp. *lineatum*) is the only *Dicroidium* species present, makes up more than 90% of the recovered fossils, and is associated with abundant reproductive organs securely referable to *Fanerotheca waldeckiformis*.

The pollen organ *Pteruchus africanus* can be linked to *Dicroidium odontopteroides*. Based on cuticle features, the central lamina of *Pteruchus africanus* resembles that of *D. zuberi* and *D. odontopteroides* in having small, sub-isodiametric epidermal cells, shallow stomatal complexes without the deeper crescentic anticlinal wall flanges of the guard cells, and the 2–4 papillae or lens-like thickenings per cell. Compared to these two foliage species, it is especially similar to *D. odontopteroides* in having rather smooth (as opposed to strongly buttressed) anticlinal flanges and in showing mostly laterocytic stomata with only lateral subsidiary cells. Moreover, well-preserved *Pteruchus africanus* specimens have been recovered from only two assemblages, both of which contain *D. odontopteroides* as common or dominant elements and in which *D. zuberi* is absent (Table 1). There is strong evidence to suggest that at least some of the small-laminar *Pteruchus africanus* pollen organs were borne on plants with *D. odontopteroides* foliage. This is supported by co-occurrence data from South Africa (TOWNROW 1962; RETALLACK & DILCHER 1988; ANDERSON & ANDERSON 2003), Australia (TOWNROW 1962) and Antarctica (AXSMITH et al. 2000). However, macromorphologically similar *Pteruchus* organs also occur with other *Dicroidium* species, including narrow-leafed *D. elongatum*-like forms (e.g., TOWNROW 1962). We suggest that future studies should aim to resolve the broadly defined *Pteruchus africanus* as emended by Anderson (ANDERSON et al. 2019c) into more narrowly circumscribed species (see THOMAS 1933, TOWNROW 1962). However, this should be informed especially by studying the diagnostic cuticle features of the microsporophyll lamina, which appear to be most informative for organ affiliation (BLOMENKEMPER et al. 2020; this study).

Collectively, our results highlight the significance of cuticular analyses as a tool for whole plant reconstruction in Umkomasiales (see BLOMENKEMPER et al. 2020), whereby we link *Fanerotheca* sp. to *Dicroidium lineatum*, *Umkomasia* sp. cf. *U. quadripartita* to *D. dubium* and *Pteruchus africanus* to *D. odontopteroides* based on their strong resemblances in cuticular features.

Palaeoenvironment/Palaeoecology of the Leigh Creek Flora

In the Late Triassic, Leigh Creek was situated at around 55° South, in a perhumid climate with warm summers and mild, frost-free winters during a period of globally elevated temperatures (ANDERSON & ANDERSON 1983; SCOTESE et al. 1999, 2001, 2021). In the Leigh Creek area, the flora thrived under humid conditions, documented by swamp-, lake- and river- deposits with thick peat accumulations (TOWNSEND 1979; KWITKO 1995; Text-figs 2, 3). No detailed sedimentary facies analysis has been carried out on the Leigh Creek Coal Measures. However, representative measured sections in mine pits exposing the ‘middle and upper series’ coals (see Text-fig 2, 3) and embracing the intervals sampled for this study reveal predominantly mudrock-dominated lithologies bracketing coals and sparse, thin sheet-like sandstones. The representative sedimentary structures (flat and wavy laminations) generally indicate low-energy conditions. Numerous sideritic and pyritic concretions indicate regularly anoxic reducing conditions. Various root-rich and burrowed layers also attest to periodic exposure and immature palaeosol development. The preservation of freshwater molluscs and fish in the ‘lower series’ indicates episodic development of more oxygen-rich environments during deposition of that interval (WADE 1953; LUDBROOK 1961; PLEDGE & BAULCH 2013; BERRELL et al. 2020). Algal palynomorphs recovered from the succession also attest to oxygenated surface waters (PLAYFORD AND DETTMANN 1965; MAYS et al., 2021). Collectively, the sedimentological and palaeontological features of the succession indicate deposition within predominantly lacustrine and paludal environments with only minor contributions of fluvially transported sands.

The Leigh Creek fossil assemblages record typical diversity levels of *Dicroidium*-dominated plant communities from Upper Triassic strata of southern Gondwana (RETALLACK 1977, 1980b; ANDERSON & ANDERSON 1983, 2003; PAL 1984; GUERRA-SOMMER & CAZZULO KLEPZIG 2000; ESCAPA et al. 2011; HOLMES & ANDERSON 2013; PATTEMORE 2016). Altogether, the recorded *Dicroidium* species all seem to be common and widely distributed representatives of the genus. This applies most obviously to the type species *D. odontopteroides* and the other well-known species *D. zuberi* and *D. dubium* (ANDERSON & ANDERSON 1983); however, the narrow-leafed forms that we distinguish as a separate species *D. lineatum* are also rather common throughout Gondwana, and even the three unassigned species (D. sp. A, D. sp. B and D. sp. C) have macromorphological features that correspond superficially to those of other widely distributed forms, including *D. elongatum*, *D. spinifolium*, *D. superbum* and *D. crassinerve* (see, e.g., ANDERSON & ANDERSON 1983).

Notably, the species compositions of the individual *Dicroidium* assemblages from particular sampled layers are very distinct (Table 1). Most assemblages contain only two or three *Dicroidium* species; this low diversity is remarkable given that the analysed sample material from each bed usually comprised hundreds of cuticle fragments derived from multiple hand specimens, some of these taken from within metre-thick intervals and over lateral distances of several meters (compare, e.g., positions of samples levels LC12-14 in Text-Fig. 3). Together with abundant rooting structures and overall intact preservation of leaves, this consistently low diversity indicates more-or-less autochthonous deposition with negligible transport and mixing. Therefore, we interpret the taxonomic composition of the individual *Dicroidium* assemblages to accurately reflect the original species composition of the local vegetation. As a result, we recognise three different types of *Dicroidium* assemblages; (1) an assemblage type from the lower series (samples LC-17–20) dominated by *D. zuberi*; (2) one from the upper series (LC-1–9) characterized by common to dominant *D. dubium*; and (3) a third from the upper series (LC-11–14) composed almost entirely of *D. odontopteroides* and *D. lineatum*.

Similar *Dicroidium* communities, especially a local dominance of either *D. odontopteroides* and *D. lineatum* versus *D. zuberi*, have also been reported from the Upper Triassic of South Africa (ANDERSON & ANDERSON 1983), Australia (RETALLACK 1977; HOLMES &

ANDERSON 2005), and Argentina (see, e.g., ARTABE et al. 2001). These different species compositions likely reflect local gradients in site-specific habitat conditions, such as water availability and soil parameters. *Dicroidium zuberi*, for instance, is commonly interpreted to have grown preferably on better-drained and more exposed sites (see, e.g., RETALLACK 1977; DROVANDI et al. *in press*). *Dicroidium dubium*, by contrast, apparently preferred more water-logged conditions in peat-forming overbank environments; in the present collections, occurrences of this species are closely associated with coal deposits (Text-fig. 3), and the corresponding permineralized taxon *D. fremouwense* is dominant in silicified peat deposits from Antarctica (PIGG 1990). Taken together, we interpret these different *Dicroidium* assemblages from the various stratigraphic levels to reflect a mosaic of heterogenous plant communities in a well-structured environment at a given time, rather than evolutionary changes to plant lineages or significant changes in the climatic regime.

In general, approximately 95% of the Leigh Creek fossil plant assemblage consists of umkomasialean plants fragments, which have been reconstructed as tree stratum components of the ecosystem (RETALLACK 1977; PETRIELLA 1978; CÚNEO et al. 2003). Large sideritized logs and stumps (Text-fig. 2.4) are co-preserved with the *Dicroidium*-dominated leaf beds at Leigh Creek. These are accompanied by conifer trees, denoted by *Heidiphyllum elongatum* and *Rissikia media* (CHAPMAN & COOKSON 1926; BARONE-NUGENT et al. 2003). The herbaceous stratum of the palaeovegetation was composed of equisetaleans (CHAPMAN & COOKSON 1926), some Petriellales (BARONE-NUGENT et al. 2003), and several fern species of Dipterideaceae and Cyatheales that are preserved in cuticle and charcoal macerates (Text-fig. 2.14—2.16). This is supported by a diverse array of dispersed spores of ferns, lycopsids and bryophytes (PLAYFORD & DETTMANN 1965). Ground-cover species of isoetaleans have been identified by the abundant occurrence of megaspores in palynological assemblages (DETTMANN 1961). In addition, we observed sporadic cuticles of less well-documented gymnosperms belonging to *Kurtziana* and *Sphenobaiera*, for which whole-plant reconstructions are not yet available but which possibly belonged to the tree canopy layer. Altogether, the Leigh Creek Lagerstätte derives from well-stratified forest vegetation, with umkomasialeans being the dominant floral component in the canopy layer. This accords with reconstructions of Gondwanan Triassic peat-forming vegetation by others (e.g., RETALLACK 1977; RETALLACK & DILCHER 1988; BOMFLEUR et al. 2014: fig. 7). The common occurrence of umkomasialean leaf mats (Text-fig. 2.13) at Leigh Creek supports the inferred deciduous habit of this group and its adaptation to seasonality and dark winters in higher latitudes (MEYER-BERTHAUD et al. 1993; BOMFLEUR & KERP 2010).

This environmental setting is also reflected in functional-morphological features of the *Dicroidium* cuticles. Thin amphistomatic leaves with densely distributed, superficial or little-sunken stomata on both sides indicate high conductance to CO_2 and H_2O and strong photosynthetic capacity (PARKHURST 1978; MOTT et al. 1982) under negligible limitations in the water supply. Among extant plants, such a complement of features is further indicative of short leaf-lifespan (ONODA et al. 2012 and references therein), consistent with the inferred seasonal deciduousness of *Dicroidium* plants (MCLOUGHLIN 2001; BOMFLEUR & KERP 2010; BOMFLEUR et al. 2012). Another characteristic feature of *Dicroidium* cuticles that may have aided photosynthetic performance is the lens-shaped thickenings of the periclinal cuticle layer. Unlike the more typical leaf papillae, which project from the cuticle exterior and are generally thought to increase the protective leaf boundary layer, these lens-shaped thickenings are more or less diffuse and form only low topography on the cuticle surface. It can further be expected that these structures in themselves are too large to have had any major effect on water-repellence properties, as has been suspected for certain microreliefs on fossil cuticles (e.g., POTT et al. 2007). We suspect that these structures instead functioned as leaf 'lenses' that collect and direct light into chloroplast-rich tissue to maximize light harvest (HABERLANDT 1905, 1914; MARTIN & JUNIPER 1970; see also BOMFLEUR & KERP 2010).

At Leigh Creek, all investigated *Dicroidium* species and the *Fanerotheca* species feature oblate resin bodies or resin channels between the veins, so far documented only as secretory structures in permineralized umkomasialeans from Antarctica (PIGG 1990; YAO et al. 1995; KLAVINS et al. 2002). Although these findings might be due to the exceptional preservation of the material, comparable amounts of resin bodies have not been observed in cuticular analyses of corystosperms elsewhere (e.g., JONES & DE JERSEY 1947; JACOB & JACOB 1950; ANDERSON & ANDERSON 1983; ABU HAMAD et al. 2008; BOMFLEUR & KERP 2010). In modern plants, such resin bodies result from sequestration of secondary metabolites and are considered to provide defences against herbivory, reduce transpirational water loss, and aid wound healing (FAHN 1988; KRINGS 2000 and references therein). KLAVINS et al. (2002) hypothesized the large number of secretory structures to be a by-product of the higher metabolic rates that corystosperms in Antarctica required to proliferate in the short growing seasons at high latitudes and to provide defence against herbivores that foraged more intensely in those short seasons. Detailed analysis of *Dicroidium* cuticles from the Triassic of Timber Peak in Antarctica, however, did not identify any resin bodies, despite the occurrence of *D. odontopteroides* cuticles conforming in all other respects precisely to those found in this study (see BOMFLEUR & KERP 2010). Among the Leigh Creek specimens, we observed extensive herbivory (approximately 5–10% of specimens), including leaf margin feeding, leaf mining, and piercing and sucking (see Text-figs 2.11, 2.12), indicating that herbivory was a strong, prevalent stressor to plant growth in this environment; enhanced resin production could thus be a response against arthropod herbivores. It is notable, however, that leaves of other gymnosperm groups at Leigh Creek also contain abundant resin products, including resin canals in *Heidiphyllum*, *Kurtziana* and ginkgophyte leaves (UNVERFÄRTH, personal observation 2021) and individual secretory cells in *Rochipteris* leaves (BARONE-NUGENT et al. 2003; UNVERFÄRTH, personal observation 2021). Regardless of the botanical affinity of the individual plants, this seemingly ubiquitous resin production may instead indicate a different cause for elevated stress in the vegetation. A recent review of the occurrence of Late Triassic amber linked resin production to environmental stress during the Carnian Pluvial Event, including wetter conditions, increased CO_2, acid rain and frequent wildfires (see SEYFULLAH et al. 2018 and references therein). Evidence for regular wildfire activity, in particular, is the presence of prominent charcoal layers at Leigh Creek with well-preserved fern-fragments (Text-figs 2.14, 2.15, 2.16), indicating recurring understory forest fires. Charcoal bands have also been reported from other Upper Triassic southern Gondwanan deposits (see ABU HAMAD et al. 2012 and reference herein), but quantitative evaluation of charcoal occurrences from the fossil record for the interpretation of wildfire frequency is notoriously difficult (BATTEN 1998; FIGUEIRAL & WILLCOX 1999; MAYS & MCLOUGHLIN, in press) so whether this interval experienced an elevated fire regime remains uncertain. Further geochemical investigation of the resin might shed light on its purpose.

6 Summary

We describe the first cuticle details of umkomasialeans (corystosperms) from the Leigh Creek Coal Measures, South Australia, including seven foliage species (*Dicroidium*), two ovuliferous organs (*Umkomasia* and *Fanerotheca*) and one pollen organ (*Pteruchus*). We adapted novel extraction methods for the weakly compacted mudrocks with exceptionally well preserved, mummified plant preservation (lignite A to sub-bituminous C rank coals), which can easily be performed in other studies with similar preservation. Our material facilitated detailed analysis of an extensive assemblage of plant remains, which led to a deeper understanding of cuticle features, diagnostic characters for recognising umkomasialean species, and the intraspecific variability of the leaves. Although cuticles may not be preserved in every fossil deposit containing Umkomasiales, the detailed analysis of the Leigh Creek material provides an essential benchmark for validating existing species diagnoses and highlighting shortcomings in existing species concepts. We identified diagnostic cuticle traits and defined areas of the cuticle that are suitable for robust species delimitation. The excellent cuticle preservation and co-occurrence of taxa based on isolated organs provides an important tool to link dispersed foliage and reproductive structures at the species level and contributes to whole-plant reconstructions. Beyond its contribution towards more precise species and generic circumscriptions and for whole-plant re-assembly, we anticipate that cuticular analysis of corystosperm foliage and reproductive organs will also prove informative for inferring broader phylogenetic relationships among seed plants, which are still not satisfactorily resolved (see CRANE 1985; COIRO et al. 2018 and references therein).

The Leigh Creek flora is dominated by umkomasialean species that are typical of Late Triassic assemblages of middle- to high-latitude Gondwana. The assemblages are mainly dominated by smaller, architecturally complex leaves with shorter, elliptical pollen organs. The common mass accumulation of well-preserved leaves into mats, the presence of resin bodies, plant-insect interactions (feeding, mining, piercing and sucking) and the micromorphological characters (paracytic stomata, predominantly amphistomatic distribution, common papillae and lenticular thickenings on epidermal cells) give important insights into these peat-forming wetland ecosystems that developed under strongly seasonal climates that prevailed throughout the Triassic at high southern latitudes.

Acknowledgements

This work was supported by the German Science Foundation (DFG Emmy Noether grant BO3131/1–1 ‘Latitudinal Patterns in Plant Evolution’ to B.B.) and a grant from the Swedish Research Council (VR grant number 2018-04527) to S.M. Initial collection of the studied material was carried out in collaboration with Andrew Drinnan and Eroia Barone-Nugent (University of Melbourne) in 1997. We wish to thank; Heidi and Keith Holmes

(Dorrigo) and John Anderson (Pretoria) for fruitful discussion and for their generous literature donation; Arno Rohrbach (Münster) for kind assistance with SEM analysis and imaging; Anne Niehus (Münster) for skilful help with chemical preparation; Dora Schilling (Münster) for the illustrations in Text-Fig. 4; and Michael Krings (München), Lutz Kunzmann (Dresden) and Ronny Rößler (Chemnitz) for constructive criticism on an earlier version of our manuscript.

Reference list

Abu Hamad, A., Jasper, A., & Uhl, D. (2012). The record of Triassic charcoal and other evidence for palaeo-wildfires: Signal for atmospheric oxygen levels, taphonomic biases or lack of fuel? *International Journal of Coal Geology, 96-97*, 60–71. doi:https://doi.org/10.1016/j.coal.2012.03.006

Abu Hamad, A., Kerp, H., Vörding, B., & Bandel, K. (2008). A Late Permian flora with *Dicroidium* from the Dead Sea region, Jordan. *Review of Palaeobotany and Palynology, 149*, 85–130.

Amtsberg, H. (1969). A contribution to the mesophytic flora of South Australia (Springfield and Leigh Creek). *Transactions of the Royal Society of South Australia, 93*, 79–86.

Anderson, H. M. & Anderson, J. M. (1970). A preliminary Review of the Biostratigraphy of the uppermost Permian, Triassic and Lowermost Jurassic of Gondwanaland. *Palaeontologica Africana, 13*, 1-21.

Anderson, H. M., Barbacka, M., Bamford, M. K., Holmes, W. B. K., & Anderson, J. M. (2019a). *Pteruchus* (microsporophyll): part 2 of a reassessment of Gondwana Triassic plant genera and a reclassification of some previously attributed. *Alcheringa, 43*, 540–562.

Anderson, H. M., Barbacka, M. K., Bamford, M. K., Holmes, W. B. K., & Anderson, J. M. (2019b). *Dicroidium* (foliage) and affiliated wood Part 3 of a reassessment of Gondwana Triassic plant genera and a reclassification of some previously attributed. *Alcheringa, 44*, 64–92.

Anderson, H. M., Barbacka, M. K., Bamford, M. K., Holmes, W. B. K., & Anderson, J. M. (2019c). *Umkomasia* (megasporophyll): part 1 of a reassessment of Gondwana Triassic plant genera and reclassification of some previously attributed. *Alcheringa, 43*(1), 43–70.

ANDERSON, H. M., HOLMES, W. B. K., & FITNESS, L. A. (2008). Stems with attached *Dicroidium* leaves from the Ipswich Coal Measures, Queensland, Australia. *Memoirs of the Queensland Museum, 52*(2), 1–12.

ANDERSON, J. M., & ANDERSON, H. M. (1983). *Palaeoflora of southern Africa - Molteno Formation (Triassic). Vol. 1. Part 1. Introduction / Part 2. Dicroidium. Balkema*. Rotterdam.

ANDERSON, J. M., & ANDERSON, H. M. (2003). *Heyday of the Gymnosperms: systematics and biodiversity of the Late Triassic Molteno fructifications*. Pretoria: Strelitzia.

ANTEVS, E. (1913). Results of Dr. E. Mjöbergs Swedish Scientific Expedition to Australia 1910-1913. V. Some Mesozoic Plants. *Kungliga Svenska Vetenskapsakademiens Handlingar, 52*(5), 1–5.

ANTEVS, E. (1914). Die Gattungen *Thinnfeldia*, Ett. und *Dicroidium*, Goth. *Kongl. svenska Vetenskaps Academien Handlingar, 51*(6), 1–71.

ARBER, E. A. N. (1913). A preliminary note on the fossil plants of the Mount Potts Beds, New Zealand, Collected by Mr. D. G. Lillie, biologist to Captain Scott´s Antarctic Expedition in the "Terra Nova". *Proceedings of the Royal Society B, 86*, 344–347.

ARBER, E. A. N. (1917). The earlier Mesozoic floras of New Zealand. *New Zealand Geological Survey, Palaeontological Bulletin, 6*, 1–66.

ARCHANGELSKY, S. (1968). Studies on Triassic fossil plants from Argentina. IV. The leaf genus *Dicroidium* and its possible relation to *Rhexoxylon* stems. *Palaeontology, 11*(4), 500–512.

ARTABE, A. E. (1985). Estudio sistemático de la tafoflora triásica de Los Menucos, provincia de Río Negro, Argentina. Parte I. Sphenophyta, Filicophyta, Pteridospermophyta. *Ameghiniana, 22*(1-2), 3–22.

ARTABE, A. E. (1990). Revalidación del género triásico *Zuberia* Frenguelli 1943, familia Corystospermaceae. *Revista del Museo de la Plata (N.S.), Sec. Paleont., 9*, 145–155.

ARTABE, A. E., ZAMUNER, A. B., & ARCHANGELSKY, S. (1991). Estudios cuticulares en cycadopsidas fosiles. El genero *Kurtziana* Frenguelli 1942. *Ameghiniana, 28*(3–4), 365–374.

ARTABE, A. E., MOREL, E. M., & SPALLETTI, L. A. (2001). Paleoecología de las floras triásicas argentinas. In A. E. Artabe, E. M. Morel, & A. B. Zamuner (Eds.), *El Sistema Triásico en la Argentina*(199–225). La Plata: Fundación del Museo de La Plata “Francisco Pascasio Moreno”.

AXSMITH, B. J., TAYLOR, E. L., TAYLOR, T. N., & CÚNEO, N. R. (2000). New perspectives on the Mesozoic seed fern order Corystospermales based on attached organs from the Triassic Antarctica. *American Journal of Botany, 87*, 757–768.

BACON, C. A. (1995). Tasmanian Basin. In C. R. WARD, C. W. MALLETT, & J. W. BEESTON (Eds.), *Geology of Australian Coal Basins* (Vol. 1, pp. 441–453). Sydney: Geological Society of Australia, Coal Geology Group.

BALDONI, A. M. (1980). Revision de las especies del genero *Xylopteris* (Corystospermaceae) en el Triasico de Argentina, Australia y Sudafrica. *Ameghiniana, 17*(2), 135–155.

BALME, B. E., KERSHAW, A. P., WEBB, J. A. (1995). Floras of Australian coal measures, with notes on their associated Mesozoic faunas. In C.R. WARD, H. J. HARRINGTON, C. W. MALLETT, & J. W. BEESTON (Eds.), *Geology of Australian Coal Basins. Geological Society of Australia Coal Geology Group Special Publication 1* (pp. 41–62). Sydney.

BARBONI, R., DUTRA, T. L., & FACCINI, U. F. (2016). *Xylopteris* (Frenguelli) Stipanicic & Bonetti in the Middle–Upper Triassic (Santa Maria Formation) of Brazil. *Ameghiniana, 53*, 599–622.

BARCLAY, R., MCELWAIN, J., DILCHER, D., & SAGEMAN, B. (2007). The Cuticle Database: Developing an interactive tool for taxonomic and paleoenvironmental study of the fossil cuticle record. *Courier Forschungsinstitut Senckenberg, 258*, 39–55.

BARONE-NUGENT, E. D., DRINNAN, A. N., & MCLOUGHLIN, S. (1997). Late Triassic flora of the Leigh Creek Coal Measures, South Australia. *Geological Society of Australia Abstracts, 48*, 92.

BARONE-NUGENT, E. D., BARTY, A., & NUGENT, K. A. (2002). Quantitative phase-amplitude microscopy I: optical microscopy. *Journal of Microscopy, 206,* 194–203.

BARONE-NUGENT, E. D., MCLOUGHLIN, S., & DRINNAN, A. N. (2003). New species of *Rochipteris* from the Upper Triassic of Australia. *Review of Palaeobotany and Palynology, 123*(3–4), 273–287.

BARTHEL, M. (1961). Der Epidermisbau einiger oberkarbonischer Pteridospermen. *Geologie, 10(7)*, 828–849.

BARTHEL, M. (1962). Epidermisuntersuchungen an einigen inkohlten Pteridospermenblättern des Oberkarbons und Perms. *Geologie*, *11, Beiheft 33*, 1–140.

BATTEN, D. J. (1998). Palaeoenvironmental implications of plant, insect and other organic-walled microfossils in the Weald Clay Formation (Lower Cretaceous) of southeast England. *Cretaceous Research*, *19*, 279–315.

BERRELL, R. W., BOISVERT, C., TRINAJSTIC, K., SIVERSSON, M., ALVARADO-ORTEGA, J., CAVIN, L., SALISBURY, S. W., & KEMP, A. (2020). A review of Australia's Mesozoic fishes. *Alcheringa*, *44*, 286–311.

BLOMENKEMPER, P., KERP, H., ABU HAMAD, A., & BOMFLEUR, B. (2020). Contributions towards whole-plant reconstructions of *Dicroidium* plants (Umkomasiaceae) from the Permian of Jordan. *Review of Palaeobotany and Palynology, 278*, 104210.

BODNAR, J., MOREL, E. M., COTUREL, E. P., & GANUZA, D. G. (2020). New plant fossil records and biostratigraphic analysis from the Uspallata Group (Late Triassic) at Cacheuta Hill, Cuyo Basin, west-central Argentina. *Geobios, 60*, 3–27. https://doi.org/10.1016/j.geobios.2020.04.002

BOJANOWSKI, M. J., JAROSZEWICZ, E., KOŠIR, A., ŁOZIŃSKI, M., MARYNOWSKI, L., WYSOCKA, A., & DERKOWSKI, A. (2016). Root-related rhodochrosite and concretionary siderite formation in oxygen-deficient conditions induced by a ground-water table rise. *Sedimentology, 63*(3), 523–551. https://doi.org/10.1111/sed.12227

BOMFLEUR, B., BLOMENKEMPER, P., KERP, H., & MCLOUGHLIN, S. (2018). Polar regions of the Mesozoic–Paleogene greenhouse world as refugia for relict plant groups. In M. KRINGS, C. J. HARPER, N. R. CÚNEO, & G. W. ROTHWELL (Eds.), *Transformative Paleobotany Papers to Commemorate the Life and Legacy of Thomas N. Taylor* (Vol. 24, pp. 593–611): Academic Press, Elsevier Inc.

BOMFLEUR, B., ESCAPA, I. H., TAYLOR, E. L., & TAYLOR, T. N. (2012). Modified basal elements in *Dicroidium* fronds (Corystospermales). *Review of Palaeobotany and Palynology, 170*, 15–26.

BOMFLEUR, B., & KERP, H. (2010). *Dicroidium* diversity in the Upper Triassic of north Victoria Land, East Antarctica. *Review of Palaeobotany and Palynology, 160*, 67–101.

BOMFLEUR, B., KLYMIUK, A. A., TAYLOR, E. L., TAYLOR, T. N., GULBRANSON, E. L., & ISBELL, J. L. (2014). Diverse bryophyte mesofossils from the Triassic of Antarctica. *Lethaia, 47*(1), 120–132.

BOMFLEUR, B., SCHNEIDER, J. W., SCHÖNER, R., VIERECK-GÖTTE, L., & KERP, H. (2011a). Fossil sites in the continental Victoria and Ferrar groups (Triassic-Jurassic) of North Victoria Land, Antarctica. *Polarforschung, 80*, 88–90.

BOMFLEUR, B., TAYLOR, E. L., TAYLOR, T. N., SERBET, R., KRINGS, M., & KERP, H. (2011b). Systematics and paleoecology of a new peltaspermalean seed fern from the Triassic polar vegetation of Gondwana. *International Journal of Plant Sciences, 172*, 807–835.

BONETTI, M. I. R. (1966). Consideraciones sobre algunos representantes de la Familia "Corystospermaceae". *Ameghiniana, 10*(4), 389–395.

BORNEMANN, J. G. (1856). Über organische Reste der Lettenkohlengruppe Thüringens: Ein Beitrag zur Fauna und Flora dieser Formation, besonders über fossile Cycadeen, nebst vergleichenden Untersuchungen über die Blattstruktur der jetztweltlichen Cycadeen-Gattungen. Leipzig: Engelmann, W.

BORTOLUZZI, C. A., & BARBERENA, M. C. (1967). The Santa Maria beds in Rio Grande do Sul (Brazil). In J. J. BINGARELLA, R. D. BECKER, & I. D. Pinto (Eds.), *Problems in Gondwana Geology* (pp. 169–196). Curitiba: Universidade Federal do Paraná.

BOUCHER, L. D. (1995). *Morphometric and paleobiogeographic analyses of Dicroidium from the Triassic of Gondwana.* PhD thesis, The Ohio State University, Ann Arbor.

BOUCHER, L. D., TAYLOR, E. L., & TAYLOR, T. N. (1993). *Dicroidium* from the Triassic of Antarctica. *New Mexico Museum of Natural History and Science Bulletin, 3*, 39–46.

BOUCHER, L. D., TAYLOR, E. L., TAYLOR, T. N., CÚNEO, N. R., & OSBORN, J. M. (1995). *Dicroidium* compression floras from southern Victoria Land. *Antarctic Journal*, *30*, 40–41.

BROWN, H. Y. L. (1891). Report on coal bearing area in neighbourhood of Leigh Creek. *South Australian Parliamentary Papers, 158*, 1–14.

CARIGLINO, B., MOISAN, P., & LARA, M. B. (2021). The fossil record of plant-insect interactions and associated entomofaunas in Permian and Triassic floras from southwestern Gondwana: A review and future prospects. *Journal of South American Earth Sciences, 111*, 1–22.

CANTRILL, D., DRINNAN, A. N., & WEBB, J. A. (1995). Late Triassic plant fossils from the Prince Charles Mountains, East Antarctica. *Antarctic Science, 7*(1), 51–62.

CHAPMAN, F., & COOKSON, I. C. (1926). A revision of the "Sweet" collection of Triassic plant remains from Leigh Creek, South Australia. *Transactions of the Royal Society of South Australia, 50*, 163–178.

COCKBAIN, A. E. (1990). Perth Basin. In A. F. TRENDALL (Ed.), *Geology and Mineral Resources of Western Australia:* (Vol. 3, pp. 495–524). Perth: Western Australia Geological Survey, Memoir.

COIRO, M., CHOMICKI, G., & DOYLE, J. A. (2018). Experimental signal dissection and method sensitivity analyses reaffirm the potential of fossils and morphology in the resolution of the relationship of angiosperms and Gnetales. *Paleobiology, 44*(3), 490–510.

CRANE, P. R. (1985). Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals of the Missouri Botanical Garden, 72*, 716–793.

CÚNEO, N. R., TAYLOR, E. L., TAYLOR, T. N., & KRINGS, M. (2003). In situ fossil forest from the upper Fremouw Formation (Triassic) of Antarctica: paleoenvironmental setting and paleoclimate analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology, 197*, 239–261.

DECOMBEIX, A.-L., BOMFLEUR, B., TAYLOR, E. L., & TAYLOR, T. N. (2014). New insights into the anatomy, development, and affinities of corystosperm trees from the Triassic of Antarctica. *Review of Palaeobotany and Palynology, 203*, 22–34.

DETTMANN, M. E. (1961). Lower Mesozoic megaspores from Tasmania and South Australia. *Micropaleontology*, *7*(1), 71–86. doi:10.2307/1484144

DROVANDI, J. M., CORREA, G. A., COLOMBI, C. E., & CÉSARI, S. N. (*in press*): *Dicroidium (Zuberia) zuberi* (Szajnocha) Archangelsky from exceptional Carnian leaf litters of the Ischigualasto Formation, westernmost Gondwana. *Historical Biolog*y. https://doi.org/10.1080/08912963.2021.1974017

DU TOIT, A. L. (1927). The fossil flora of Upper Karroo Beds. *Annals of the South African Museum, 22*, 289–420.

ESCAPA, I. H., TAYLOR, E. L., CÚNEO, N. R., BOMFLEUR, B., BERGENE, J., SERBET, R., & TAYLOR, T. N. (2011). Triassic floras of Antarctica: Plant diversity and distribution in high paleolatitude communities. *Palaios, 26*(9), 522–544. doi:10.2110/palo.2010.p10-122r

ETHERIDGE, R. (1891). Description of some South Australian Silurian and Mesozoic fossils. In H. Y. L. BROWN (Ed.), *Reports on the coal-bearing area in neighbourhood of Leigh's Creek* (pp. 9–14).

ETHERIDGE, R. (1895). Additional plant-remains from the Leigh Creek Coal-field, central Australia. *Transactions of the Royal Society of South Australia, 19*, 138–145.

FAHN, A. (1988). Secretory tissues in vascular plants. *New Phytologist, 108*(3), 229–257. doi:https://doi.org/10.1111/j.1469-8137.1988.tb04159.x

FEISTMANTEL, O. (1878). Palaeozoische und mesozoische Flora des östlichen Australiens. *Palaeontographica, Suppl., 3*(3,2), 55–130.

FEISTMANTEL, O. (1879a). The fossil Flora of the Gondwana System Vol. III (Lower Gondwana). *Palaeontologia Indica, XII*.

FEISTMANTEL, O. (1879b). *Palaeontologische Beiträge: Palaeozoische und mesozoische Flora des östlichen Australiens* (2 ed. Vol. 2). Cassel: Fischer, T.

FEISTMANTEL, O. (1889). *Übersichtliche Darstellung der geologisch-palaeontologischen Verhältnisse Süd-Afrikas. 1. Theil. Die Karoo-Formation und die dieselbe unterlagernden Schichten.* (Vol. 7). Prag: Königl. böhm. Gesellschaft der Wissenschaften.

FIELDING, C. R., FRANK, T. D., MCLOUGHLIN, S., VAJDA, V., MAYS, C., TEVYAW, A. P., WINGUTH, A., WINGUTH, C., NICOLL, R. S., BOCKING, M., & CROWLEY, J. L. (2019). Age and pattern of the southern high-latitude continental end-Permian extinction constrained by multiproxy analysis. *Nature Communications, 10*, 385–397.

FIGUEIRAL, I., & WILLCOX, G. (1999). Archaeobotany and sub-fossils: collecting and analytical techniques. In T.P. JONES and N.P. ROWE (Eds.), Fossil Plants and Spores, Modern Techniques (p. 290–294). Geological Society of London, London.

FLINDERS POWER PARTNERSHIP (2017). *Mine closure plan for the Leigh Creek coalfield, PEPR 415204*. Department of the Premier and Cabinet, South Australia, Adelaide. https://sarigbasis.pir.sa.gov.au/WebtopEw/ws/samref/sarig1/image/DDD/PEPR415204.pdf

FLORIN, R. (1933). Studien Über die Cycadales des Mesozoikums nebst Erörterungen über die Spaltöffnungsapparate der Bennettitales. *Kungligar Svenska Vetenskapsakademien Handlingar*, *12(5)*, 1–34.

FRENGUELLI, J. (1942). Contribuciones al conocimiento de la flora del Gondwana superior en la Argentina. I. *Harringtonia argentinica* (Arber) n. gen. *Notas del Museo de La Plata, Paleontología, 7*(42), 265–273.

FRENGUELLI, J. (1943). Reseña crítica de los géneros atribuidos a la Serie de *Thinnfeldia*. *Revista del Museo de La Plata, Sección Paleontología, 2*(2), 225–342.

FRENGUELLI, J. (1944a). Contribuciones al conocimiento de la flora del Gondwana superior en la Argentina XVIII. *Notas del Museo de La Plata, Sección Paleontología, 9*(66), 393–402.

FRENGUELLI, J. (1944b). Las especies del género "*Zuberia*" en la Argentina. *Anales del Museo de la Plata, Nueva Serie, Paleontología: Seccion B, 2*(1), 1–30.

FRENGUELLI, J. (1950). Addenda a la Flora del Gondwana Superior en la Argentina. *Revista de la Asociación Geológica Argentina, 5*(1), 15–30.

GNAEDINGER, S., & HERBST, R. (2001). Pteridospermas triásicas del Norte Chico de Chile. *Ameghiniana, 38*(3), 281–298.

GOTHAN, W. (1912). Über die Gattung *Thinnfeldia* Ettinghausen. *Abhandlungen der Naturforschenden Gesellschaft zu Nürnberg, 19*, 67–80.

GOTHAN, W. (1916). Über die Epidermis einiger Neuropteriden des Karbons. *Jahrbuch der königlichen preussischen geologischen Landesanstalt*, *35*, 373–381.

GUERRA-SOMMER, M., & CAZZULO KLEPZIG, M. (2000). The Triassic taphoflora from Parana Basin, southern Brazil: An overview. *Revista Brasileira de Geociências, 30*, 481–485.

HABERLANDT, G. (1905). Die Lichtsinnesorgane der Laubblätter. Wilhelm Engelmann, Leipzig, 142 pp.

HABERLANDT, G. (1914). Physiological Plant Anatomy. Macmillan and Company, limited, London. 777 pp.

HARRIS, T.M. (1932a). The fossil flora of Scoresby Sound. Part 2. Description of seed plants incertae sedis together with a discussion of certain cycadophyte cuticles. *Meddelelser om Grønland*, *85(3)*, 1–114.

HARRIS, T.M. (1932b). The fossil flora of Scoresby Sound. Part 3. Caytoniales and Bennettitales. *Meddelelser om Grønland*, *85(5)*, 1–133.

HILL, D., PLAYFORD, G., & WOODS, J. T. (1965). Triassic fossils of Queensland. *Queensland Palaeontological Society*, 32 pp.

HIRMER, M. (1936). Paläobotanik. In: F. VON WETTSTEIN (Ed.), Fortschritte der Botanik, Fünfter Band (pp. 72–103). Berlin: Julius Springer.

HOCKING, R. M. (1990). Carnarvon Basin. In A. F. TRENDALL (Ed.), *Geology and mineral resources of Western Australia* (Vol. 3, pp. 457–494). Perth: Western Australian Geological Survey Memoir.

Holmes, W. B. K. (1982). The Middle Triassic flora from Benolong, near Dubbo, central-western New South Wales. *Alcheringa, 6*(1), 1–33. doi:10.1080/03115518208565416

Holmes, W. B. K., & Anderson, H. M. (2005). The Middle Triassic megafossil flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 4. Umkomasiaceae. *Dicroidium* and affiliated fructifications. *Proceedings of the Linnean Society of New South Wales, 126*, 1–37.

Holmes, W. B. K., & Anderson, W. H. (2013). A synthesis of the rich Gondwana Triassic megafossil flora from Nymboida, Australia. *The Triassic System, New Mexico Museum of Natural History and Science Bulletin, 61*, 296–305.

Holmes, W.B.K., & Ash, S.R. (1979). An Early Triassic megafossil flora from the Lorne Basin, New South Wales. *Proceedings of the Linnean Society of N.S.W., 103*, 47–70.

Jacob, K., & Jacob, C. (1950). A preliminary account of the structure of the cuticles of *Dicroidium* (*Thinnfeldia*) fronds from the Mesozoic of Australia. *Proceedings of the National Institute of Sciences of India, 16*(2), 101–126.

Jain, R. K., & Delevoryas, T. (1967). A Middle Triassic flora from the Cacheuta Formation, Minas de Petroleo, Argentina. *Palaeontology, 10*, 564.

Jell, P. A. (2013). Tarong Basin. In P. A. Jell (Ed.), *Geology of Queensland* (pp. 396–397). Brisbane: Geological Survey of Queensland.

Jell, P. A., & McKellar, J. L. (2013). Callide Basin. In P. A. Jell (Ed.), *Geology of Queensland* (pp. 398). Brisbane: Geological Survey of Queensland.

Jensen, R. J. (1990). Detecting shape variation in oak leaf morphology: a comparison of rotational-fit methods. *American Journal of Botany, 77*, 1279–1293.

Johnson, W. (1960). *Exploration for coal: Springfield Basin in the Hundred of Cudla-Mudla, Gordon-Cradock district* (Vol. 16). Adelaide: Department of Mines, South Australian Geological Survey.

Johnston, R. M. (1894). Further contributions to the fossil flora of Tasmania. *Papers and proceedings of the Royal Society of Tasmania, 1893*, 170–178.

Jones, O. A., & de Jersey, N. J. (1947). The flora of the Ipswich Coal Measures - Morphology and floral succession. *Department of Geology Queensland Papers, 3*(3/4), 1–102.

Kerp, H. (1990). The study of gymnosperms by means of cuticular analysis. *Palaios, 5*, 548–569.

Kerp, H., Abu Hamad, A., Vörding, B., & Bandel, K. (2006). Typical Triassic Gondwanan floral elements in the Upper Permian of the paleotropics. *Geology, 34*, 265–268.

Kerp, H., & Bomfleur, B. (2011). Photography of plant fossils - New techniques, old tricks. *Review of Palaeobotany and Palynology, 166*, 117–151.

Kerp, H. & Krings, M. (2003). Kutikularanalytische Befunde zur Abgrenzung des *Odontopteroides minor* f. *zeilleri* Potonié von *Odontopteroides reichiana* Gutbier. *Courier Forschungsinstitut Senckenberg, 241*, 31–42.

Klavins, S. D., Taylor, T. N., & Taylor, E. L. (2002). Anatomy of Umkomasia (Corystospermales) from the Triassic of Antarctica. *American Journal of Botany, 89*(4), 664–676.

Kleinschmit, J., (1993). Intraspecific variation of growth and adaptive traits in European oak species. *Annals of Forest Science, 50* (suppl. 1), 166s–185s.

Krieg, G. W. (1995). Mesozoic. In J. F. Drexel & W. V. Preiss (Eds.), *The Geology of South Australia* (Bulletin 54 ed., Vol. 2, pp. 93–150): Geological Survey of South Australia.

Krings, M. (1997). Möglichkeiten und Grenzen der Kutikularanalyse - das Beispiel der Samenfarne aus dem Stefan (Oberkarbon) von Blanzy-Montceau (Zentralmassiv, Frankreich). *Veröffenlichungen Museum für Naturkunde Chemnitz, 20,* 57–70.

Krings, M. (2000). Remains of secretory cavities in Stephanian pteridosperms from Montceau (Central France): a comparative study. *Botanical Journal of the Linnean Society, 132*, 369–383.

Kwitko, G. (1995). Triassic intramontane basins. In J. F. Drexel & W. V. Preiss (Eds.), *The Geology of South Australia* (54 ed., Vol. 2, pp. 98–101). Adelaide: South Australia Geological Survey Bulletin.

Labandeira, C. C. (2013). Deep-time patterns of tissue consumption by terrestrial arthropod herbivores. *Naturwissenschaften, 100*(4), 355–364. doi:10.1007/s00114-013-1035-4

Labandeira, C. C., Anderson, J. M., & Anderson, H. M. (2018). Expansion of arthropod herbivory in Late Triassic South Africa: The Molteno Biota, Aasvoëlberg 411 Site and developmental biology of a gall. In L. H. Tanner (Ed.), *The Late Triassic World: Earth in a Time of Transition* (pp. 623–719). Cham: Springer International Publishing.

Lele, K. M. (1962). Studies on Indian Middle Gondwana Flora: 1 On *Dicroidium* from the South Rewa Gondwana Basin. *The Palaeobotanist, 10*(1, 2), 48–68.

Ludbrook, N. H. (1961). Mesozoic non-marine Mollusca (Pelecypoda: Unionidae) from the north of South Australia. *Transactions of the Royal Society of South Australia, 84*, 139–147.

Lutz, A., Gnaedinger, S., Mancuso, A., & Crisafulli, A. (2011). Paleoflora de la Formación los Rastros (Triásico Medio), Provincia de San Juan, Argentina. Consideraciones Taxonómicas y Tafonómicas. *Ameghiniana, 48*(4), 568–588, 521.

Maheshwari, H. K. (1986). *Thinnfeldia indica* Feistmantel and associated plant fossils from Tiruchirapalli District, Tamil Nadu. *Palaeobotanist, 35*, 13–21.

Martin, J. T., & Juniper, B. E. (1970). *The Cuticles of Plants.* London: Edward Arnold Publishers. 347 pp.

Martinez, L. C. A., Artabe, A. E., & Archangelsky, S. (2020). Studies of the leaf cuticle fine structure of *Zuberia papillata* (Townrow) Artabe 1990 from Hoyada de Ischigualasto (Upper Triassic), San Juan Province, Argentina. *Review of Palaeobotany and Palynology, 281*, 104272.

Mays, C., & McLoughlin, S. (2019). Caught between mass extinctions - the rise and fall of *Dicroidium*. *Deposits Magazine, 59*, 43–47.

Mays, C., & McLoughlin, S. (in press). End-Permian burnout: The role of Permian-Triassic wildfires in extinction, carbon cycling and environmental change in eastern Gondwana. *Palaios XX,* xxx–xxx. doi:https://doi.org/10.2110/palo.2021.051

Mays, C., Vajda, V., Frank, T. D., Fielding, C. R., Nicoll, R. S., Tevyaw, A. P., & McLoughlin, S. (2020). Refined Permian–Triassic floristic timeline reveals early collapse and delayed recovery of south polar terrestrial ecosystems. *Geological Society of America Bulletin*, *132*, 1489–1513.

Mays, C., Vajda, V., & McLoughlin, S., 2021. Permian–Triassic non-marine algae of Gondwana—distributions, natural affinities and ecological implications. *Earth-Science Reviews, 212*, 103382. doi:https://doi.org/10.1016/j.earscirev.2020.103382

McLoughlin. S., (2001). The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany, 49*, 271–300.

McLoughlin, S. (2011). New records of leaf galls and arthropod oviposition scars in Permian–Triassic Gondwanan gymnosperms. *Australian Journal of Botany, 59*, 156–169.

McLoughlin, S., Carpenter, R. J., Jordan, G. J., & Hill, R. S. (2008). Seed ferns survived the end-Cretaceous mass-extinction in Tasmania. *American Journal of Botany, 95*, 465–471.

McLoughlin, S., & Hill, R. S. (1996). The succession of Western Australian Phanerozoic terrestrial floras. In, S. D. Hopper, J. A. Chappill, M. S. Harvey, & A. S. George (Eds), *Gondwanan Heritage: Past, Present and Future of the Western Australian Biota* (Proceedings of the Conference on Systematics, Evolution and Conservation of the Western Australian Biota, Perth, 1993) (pp. 61–80). Sydney: Surrey Beatty.

McLoughlin, S., & Prevec, R. (2021). The reproductive biology of glossopterid gymnosperms — A review. *Review of Palaeobotany and Palynology* 295, 104527.

McLoughlin, S., Tosolini, A. M. P., Nagalingum, N. S., & Drinnan, A. N. (2002). *Early Cretaceous (Neocomian) flora and fauna of the Lower Strzelecki Group, Gippsland Basin, Victoria, Australia* (Vol. 26). *Association of Australasian Palaeontologists Memoirs*, Canberra.

Meyer-Berthaud, B., Taylor, T. N., & Taylor, E. L. (1993). Petrified stems bearing *Dicroidium* leaves from the Triassic of Antarctica. *Paleontology, 36*(2), 337–356.

Morris, J. (1845). Fossil flora. In P. E. De Strezlecki (Ed.), *Physical description of New South Wales and Van Diemans Land* (pp. 245–254). London: Longman, Brown & Green.

Mott, K. A., Gibson, A. C., & O'Leary, J. W. (1982). The adaptive significance of amphistomatic leaves. *Plant, Cell & Environment, 5*(6), 455–460. doi:https://doi.org/10.1111/1365-3040.ep11611750

Nielsen, S. N. (2005). The Triassic Santa Juana Formation at the lower Biobío River, south central Chile. *Journal of South American Earth Sciences, 19*(4), 547. doi:10.1016/j.jsames.2005.06.002

Onoda, Y., Richards, L., & Westoby, M. (2012). The importance of leaf cuticle for carbon economy and mechanical strength. *New Phytologist, 196*(2), 441–447. doi:https://doi.org/10.1111/j.1469-8137.2012.04263.x

Ottone, E. G. (2006). Plantas triásicas del Grupo Rincón Blanco, provincia de San Juan, Argentina. *Ameghiniana, 43*(2), 477–486.

Pal, P. K. (1984). Triassic plant megafossils from the Tiki Formation, South Rewa Gondwana basin, India. *The Palaeobotanist, 32*(3), 253–309.

Pal, P. K., Ghosh, A. K., Kar, R., Singh, R. S., Sarkar, M., & Chatterjee, R. (2014). Reappraisal of the genus *Dicroidium* Gothan from the Triassic sediments of India. *The Palaeobotanist, 63*(2), 127–155.

Parker, F. M. (1987). *Leigh Creek Coal Measures study. Palynology of selected core and outcrop samples.* Electricity Trust of South Australia Report (unpublished).

PARKHURST, D. F. (1978). The adaptive significance of stomatal occurrence on one or both surfaces of leaves. *Journal of Ecology, 66*(2), 367–383. doi:10.2307/2259142

PARKIN, L. W. (1953). The Leigh Creek Coalfield. *Geological Survey of South Australia Bulletin*, *31*, 1–74.

PATTEMORE, G. A. (2016). Megaflora of the Australian Triassic–Jurassic: a taxonomic revision. *Acta Palaeobotanica, 56*(2), 121–182.

PETRIELLA, B. (1978). La reconstruccion de *Dicroidium* (Pteridospermopsida, Corystospermaceae). *Obra del Centenario del Museo de La Plata, 5*, 107–110.

PETRIELLA, B. (1979). Sinopsis de las Corystospermaceae (Corystospermales, Pteridospermophyta) de Argentina. I. Hojas. *Revista de la Asociación Paleontológica Argentina, 16*, 81–102.

PETRIELLA, B. (1981). Sistematica y Vinculaciones de las Corystospermaceae H. Thomas. *Revista de la Asociación Paleontológica Argentina, 18*, 221–234.

PETRIELLA, B., & ARRONDO, O. G. (1982). El genero *Kurtziana* Frenguelli: Su morfologia y vinculaciones. *Ameghiniana, 19*(3–4), 209–215.

PEYROT, D., PLAYFORD, G., MANTLE, D. J., BACKHOUSE, J., MILNE, L. A., CARPENTER, R. J., Foster, C., Mory, A. J., McLoughlin, S., Vitacca, J., Scibiorski, J., & BEVAN, J. (2019). The greening of Western Australian landscapes: the Phanerozoic plant record. *Journal of the Royal Society of Western Australia, 102*, 52–82.

PIGG, K. B. (1990). Anatomically preserved *Dicroidium* foliage from the central Transantarctic mountains. *Review of Palaeobotany and Palynology, 66*(1–2), 129–145.

PLAYFORD, G., & DETTMANN, M. E. (1965). Rhaeto-Liassic plant microfossils from the Leigh Creek Coal Measures, South Australia. *Senckenbergiana Lethaea, 46*, 127–181.

PLEDGE, N. S. (2013). First South Australian labyrinthodont: A possible chigutisaurid stereospondyl amphibian from the Late Triassic at Leigh Creek. *Transactions of the Royal Society of South Australia, 137*(1), 127–134.

PLEDGE, N. S., & BAULCH, J. C. (2013). New fish from the Late Triassic Leigh Creek Coal Measures, South Australia. *Transactions of the Royal Society of South Australia, 137*(1), 90–96.

POTT, C., KRINGS, M., & KERP, H. (2007). A surface microrelief on the leaves of *Glossophyllum florinii* (? Ginkgoales) from the Upper Triassic of Lunz, Austria. *Botanical Journal of the Linnean Society*, *153*(1), 87–95.

RAMIREZ, H.-L., IVEY, C. T., WRIGHT, J. W., MACDONALD, B. W. S., & SORK, V. L. (2020). Variation in leaf shape in a *Quercus lobata* common garden: tests for adaptation to climate and physiological consequences. *Madroño*, *67*, 77–84.

RAO, A. R., & LELE, K. M. (1962). On the cuticle of *Dicroidium* (*Thinnfeldia*) *sahnii* (Seward) with some observations on the genera *Thinnfeldia* and *Dicroidium*. *Palaeobotanist, 11*(1–2), 7–12.

REES, P. M., & CLEAL, C. J. (2004). Lower Jurassic floras from Hope Bay and Botany Bay, Antarctica. *Special Papers in Palaeontology, 72*, 1–90.

RETALLACK, G. J. (1977). Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Alcheringa, 1*(3), 247–278, incl. microfiche supplement.

RETALLACK, G. J. (1980a). Late Carboniferous to Middle Triassic megafossil floras from the Sydney Basin. In C. HERBERT & R. J. HELBY (Eds.), *A Guide to the Sydney Basin* (Vol. 26, pp. 384–430). Sydney: Geological Survey of New South Wales Bulletin.

RETALLACK, G. J. (1980b). Middle Triassic megafossil plants and trace fossils from Tank Gully, Canterbury, New Zealand. *Journal of the Royal Society of New Zealand, 10*(1), 31–63.

RETALLACK, G. J., & DILCHER, D. L. (1988). Reconstructions of selected seed ferns. *Annals of the Missouri Botanical Garden, 75*(3), 1010–1057.

RIDING, J. B., & KYFFIN-HUGHES, J. E. (2004). A review of the laboratory preparation of palynomorphs with a description of an effective non-acid technique. *Revista Brasileira de Paleontologia, 7*, 13–44.

RIDING, J. B., & KYFFIN-HUGHES, J. E. (2011). A direct comparison of three palynological preparation techniques. *Review of Palaeobotany and Palynology, 167*(3), 212–221.

SCHNEEBELI-HERMANN, E., KÜRSCHNER, W. M., KERP, H., BOMFLEUER, B., HOCHULI, P. A., BUCHER, H., WARE, D., & ROOHI, G. (2014). Vegetation history across the Permian-Triassic boundary in Pakistan (Amb section, Salt Range). *Gondwana Research, 27*(3), 911–924.

SCOTESE, C. R. (2001). *Atlas of Earth History* (Vol. 1). Arlington, Texas.

SCOTESE, C. R., BOUCOT, A. J., & MCKERROW, W. S. (1999). Gondwanan paleogeography and paleoclimatology. *Journal of African Earth Sciences*, *28*, 99–114.

SCOTESE, C. R., SONG, H., MILLS, B. J. W., & VAN DER MEER, D. G. (2021). Phanerozoic paleotemperatures: The Earth's changing climate during the last 540 million years.

Earth-Science Reviews, 215, 1–47. doi: https://doi.org/10.1016/j.earscirev.2021.103503

Scott, A. C., Anderson, J. M., & Anderson, H. M., (2004). Evidence of plant-insect interactions in the Upper Triassic Molteno Formation of South Africa. *Journal* of *the Geological Society, 161*, 401–410.

Seward, A. C. (1932). On some fossil plants from the Parsora Stage, Rewa. *Record of the Geological Survey of India, 66*, 235–243.

Seyfullah, L. J., Roghi, G., Corso, J. D., & Schmidt, A. R. (2018). The Carnian Pluvial Episode and the first global appearance of amber. *Journal of the Geological Society, 175*(6), 1012–1018. doi:10.1144/jgs2017-143

Shi, G., Crane, P. R., Herendeen, P. S., Ichinnorov, N., Takahashi, M., & Herrera, F. (2019). Diversity and homologies of corystosperm seed-bearing structures from the Early Cretaceous of Mongolia. *Journal of Systematic Palaeontology, 0*(0), 1–33.

Shi, G., Leslie, A. B., Herendeen, P. S., Herrera, F., Ichinnorov, N., Takahashi, M., Knopf, P., & Crane, P. R. (2016). Early Cretaceous Umkomasia from Mongolia: implications for homology of corystosperm cupules. *New Phytologist, 210*(4), 1418–1429.

Shirley, J. F. (1898). Additions to the fossil flora of Queensland, mainly from the Ipswich Formation. Trias-Jura System. *Geological Survey of Queensland Bulletin 7*, 1–25.

Springbett, G. M., Kremor, A. G., & Brennan, S. H. (1995). Leigh Creek Coalfield. In C. R. Ward, H. J. Harrington, C. W. Mallett, & J. W. Beeston (Eds.), *Geology of Australian Coal Basins.* Sydney: Geological Society of Australia Coal Geology Group Special Publication, 1, 513–524.

Staines, H. R. E., Faulkner, A. J., & Thornton, M. P. (1985). Ipswich Coalfield. In C. R. Ward, H. J. Harrington, C. W. Mallett, & J. W. Beeston (Eds.), *Geology of Australian Coal Basins*. Sydney: Geological Society of Australia, Coal Geology Group, Special Publication, 1, 455–464.

Szajnocha, L. (1888). Über fossile Pflanzenreste aus Cacheuta in der argentinischen Republik. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien - mathematisch-naturwissenschaftliche Klasse, 97*(1), 219–245.

Taylor, E. L., Boucher, L. D., & Taylor, T. N. (1992). *Dicroidium* foliage from Mount Falla, central Transantarctic Mountains. *Antarctic Journal 27*(5), 2–3.

TAYLOR, E. L., TAYLOR, T. N., KERP, H., & HERMSEN, E. J. (2006). Mesozoic seed ferns: Old paradigms, new discoveries. *Journal of the Torrey Botanical Society, 133*, 62–82.

TENISON-WOODS, J. E. (1883). On the fossil flora of the coal deposits of Australia. *Proceedings of the Linnean Society of New South Wales, 8*, 1–131.

THOMAS, H. H. (1933). VII. On some pteridospermous plants from the Mesozoic rocks of South Africa. *Philosophical Transactions of the Royal Society of London, Series B, 222*(483–493), 193–265.

TOWNROW, J. A. (1957). On *Dicroidium*, probably a pteridospermous leaf, and other leaves now removed from this genus. *South African Journal of Geology, 60*, 21–60.

TOWNROW, J. A. (1960). The Peltaspermaceae, a pteridosperm family of Permian and Triassic age. *Palaeontology, 3, Part 3*, 333.

TOWNROW, J. A. (1962). On *Pteruchus*, a microsporophyll of the Corystospermaceae. *British Museum (Natural History), 6*(2), 289–320.

TOWNROW, J. A. (1966). On *Dicroidium odontopteroides* and *D. obtusifolium* in Tasmania. *The Palaeobotanist, 14*, 128–136.

TOWNROW, J. A. (1967). Fossil plants from Allan and Carapace Nunataks, and from the upper Mill and Shackleton Glaciers, Antarctica. *New Zealand Journal of Geology and Geophysics, 10*(2), 456–473. doi:10.1080/00288306.1967.10426750

TOWNSEND, I. J. (1979). The correlation and depositional history of the Leigh Creek Coal Measures. *Geological Survey of South Australia Quartely Geological Notes, 70*, 5–10.

VISCOSI, V., ANTONECCHIA, G., LEPAIS, O., FORTINI, P., GERBER, S., & LOY, A. (2012). Leaf shape and size differentiation in white oaks: assessment of allometric relationships among three sympatric species and their hybrids. *International Journal of Plant Sciences*, *173*, 875–884.

WADE, R. T. (1953). Note on a Triassic fish fossil from Leigh Creek, South Australia. *Transactions of the Royal Society of South Australia, 76*, 80–81.

WALKOM, A. B. (1915). Mesozoic floras of Queensland. Part I. The Flora of the Ipswich and Walloon Series. (a.) Introdiction. (b.) Equisetales (Vol. 252). *Queensland Geological Survey Publication,* 252, 1–51.

WALKOM, A. B. (1917). Mesozoic Floras of Queensland. Part 1.-concluded. The flora of the Ipswich and Walloon Series. (d) Ginkgoales, (e) Cycadophyta, (f) Coniferales. *Queensland Geological Survey Publication, 259*, 1–49.

WALKOM, A. B. (1925a). Fossil plants from the Narrabeen Stage of the Hawkesbury Series. *Proceedings of the Linnean Society of N.S.W.*, *50*, 214–224.

WALKOM, A. B. (1925b). Notes on some Tasmanian Mesozoic plants. Part I. *Papers and Proceedings of the Royal Society of Tasmania*, 73–87.

WALKOM, A. B. (1928). Fossil plants from the Esk district, Queensland. *Proceedings of the Linnean Society of N.S.W.*, *53*, 458–468.

WESSEL, P., & WEBER O. (1855). Neuer Beitrag zur Tertiärflora der niederrheinischen Braunkohlenformation. *Palaeontographica*, *04* (*4*), 111–130.

WHITE, M. E., & YEATES, A. N. (1976). Plant fossils from the northeastern part of the Canning Basin, Western Australia. *Bureau of Mineral Resources, Geology and Geophysics, Record 1976, 18*, 1–32.

YAO, X., TAYLOR, T. N., & TAYLOR, E. L. (1995). The corystoperm pollen organ *Pteruchus* from the Triassic of Antarctica. *American Journal of Botany, 82*, 535–546.

Text-figure captions

Text-fig. 1 (half column) Geography and geology of the Leigh Creek Coal Measures (South Australia). 1 – Australia with major Mesozoic sedimentary basins and an asterisk marking the Leigh Creek basins. 2 – Leigh Creek sedimentary basins, with the studied Telford Basin (Lobe B) in the centre. Fieldwork sampling sites marked with flags. 3 – Geological profile of the sedimentary Leigh Creek succession with pollen zones (Text-figs 2 and 3 modified after KWITKO 1995).

Text-fig. 2 (full column) Photographic images of the Telford Basin and the modes of preservation of the fossil plants. 1 – Satellite image of the Telford basin (Lobe B) with the three sampling areas; A: Pit U26 and adjacent U27 (‘Upper Series’). B: Pit M13 (‘Middle Series’). C: Pit L7 (‘Lower Series’). 2 – Central Telford Basin excavation site of the Upper Series Coal looking eastward. 3 – Highwall profile outcrop with the Triassic–Cenozoic disconformity in the upper part. 4 – Sideritized tree trunk within the Upper Series. 5 – Siderized hardgrounds within the Upper Series. 6 – Large bipartite *Dicroidium zuberi* (SZAJNOCHA) S.ARCHANG. 1968 leaf fragment on mudstone from the pit M13. Scale bar = 5 cm.

7 – Thin and brittle fern foliage imprints on unconsolidated mudstone. Scale bar = 5 mm. 8 – Charcoalified *Umkomasia* H.H.THOMAS 1933 seeds from the Upper Series. Scale bars = 1 mm. 9 – *Dicroidium* GOTHAN 1912 leaf litter on unconsolidated mudstone from the Upper Series. Scale bar = 4 cm. 10 – Loose *Dicroidium* GOTHAN 1912 leaf litter from the Upper Series. Scale bar = 5 cm. 11 – Leaf margin feeding on *Dicroidium lineatum* (TEN.-WOODS) H.M.ANDERSON et J.M.ANDERSON 1970 leaf fragment. Scale bar = 1 cm. 12 – Leaf mining in a *Dicroidium* GOTHAN 1912 pinna fragment. Scale bar = 3 mm. 13 and 14 – Unconsolidated mudstone with leaf litter layers from the Upper series. 14 - 16 – Charcoalified fern fragments from the Upper Series. Scale bars = 1 mm.

Text-fig. 2 (as it fits) Lithological profile of the 'upper series' with the sampled (LC-) section in pit U26.

Text-fig. 3 (half column) General schematic *Dicroidium* GOTHAN 1912 leaf with terminology aspects.

Text-fig. 4 (half column) Schematic key to the *Dicroidium* GOTHAN 1912 taxa. On the left: shape and venation of the pinnules. On the right: Corresponding cuticle with diagnostic features on internal view and cross-section of the periclinal wall ornamentation (inset).

Table 1 Sampled stratigraphic levels with (co-)occurring foliage and fertile organs highlighted in light grey. +++ abundant, ++ common, + rare, +- very rare, ? uncertain findings. Samples LC-12, LC-13 and LC-14 are laterally correlative assemblages from the same stratigraphic level.

Plates 1-20 and explanations of plates

Plate 1 – Macroscopic images of *Dicroidium odontopteroides* (MORRIS) GOTHAN 1912 cuticles extracted from the Leigh Creek Coal Measures (South Australia), Upper Triassic. Figs 1–4 only cleaned from the sediment with no further chemical treatment. Figs 5–9 cleaned and macerated samples.

Fig. 1 Furcate frond, simple pinnate with rhombic, (sub-opposite) pinnules, shorter inner and larger outer pinnules above furcation, typical odontopteroid venation, non-macerated. NRMS089772-27. Scale bar = 5 mm.

Fig. 2 Pinnules attached to rachis with elongated triangular shape, mixed odontopteroid/alethopteroid venation and lobation in the middle of the lower leaf margin, resin bodies preserved between the nerves. NRMS089772-41. Scale bar = 5 mm.

Fig. 3 Basal leaf portion, widely spaced, rectangular and in the upper third lobed pinnules. NRMS089772-07. Scale bar = 5 mm.

Figs 4 Elongated triangular, minor lobed pinnules of more spacious outer leaf portions. NRMS089772-18. Scale bar = 5 mm.

Fig. 5 Modified basal element, rounded and strongly undulose margin. NRMS089772-133. Scale bar = 2 mm.

Figs 6, 9 Apical pinnules roundly fused, single cuticle layers. Fig. 7 apex probably still juvenile and with stronger fused lobes and meristem in the uppermost pinnule portion. NRMS089772-154, NRMS089772-135. Scale bars = 2 mm.

Figs 7, 8 Simple pinnate leaf portions with narrow triangular pinnules shapes and small resin bodies between upper and lower leaf’s cuticle. NRMS089772-128, scale bar = 3 mm. NRMS089772-127, scale bar = 5 mm.

Plate 2 – Upper and lower cuticle of *Dicroidium odontopteroides* (Morris) Gothan 1912 leaf portion. Scale bar = 1 mm

Fig. 1 Upper cuticle. NRMS089772-125.

Fig. 2 Lower cuticle. NRMS089772-125.

Plate 3 – Transmitted light micrographs of *Dicroidium odontopteroides* (Morris) Gothan 1912 cuticles from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Fig. 1 Epidermal cell pattern of intercostal field (left) and costal field (right). NRMS089772-125. Scale bar = 100 µm.

Fig. 2 Epidermal details of the cuticle with focus plane on the typical two to four lens-like papillae per regular epidermal cell. NRMS089771-48. Scale bar = 100 µm.

Fig. 3 Cuticle details with closer view on leaf lenses and slightly knobbed or "buttressed" anticlinal cell walls. NRMS089772-100. Scale bar = 50 µm.

Fig. 4 Cuticle details with strong Nomarski interference contrast, focussing on the buttressed anticlinal walls. NRMS089772-152. Scale bar = 50 µm.

Fig. 5 Detail of the spherical resin body, preserved in the mesophyll. NRMS089772-96. Scale bar = 50 µm.

Fig. 6 Stomata complex details with thin cutinized guard cells, shallow stomata and subsidiary cells with strong cutinized distal anticlinal walls. NRMS089771-60. Scale bar = 10 µm.

Fig. 7 Secondary electron microscopic (SEM) image with details of the slightly buttressed cells walls and the shallow stomata complex with the differently cutinized subsidiary cells. NRMS089772-175-01. Scale bar = 50 µm.

Fig. 8 SEM image with details of the stomata complex. Note the shallow and thin guard cells the thicker cutinized pore and the subsidiary cell's thick cutinized distal anticlinal walls. NRMS089772-176-02. Scale bar = 10 µm.

Plate 4 – Macroscopic images of *Dicroidium lineatum* (Ten.-Woods) H.M.Anderson et J.M.Anderson 1970 leaf fragments from the Leigh Creek Coal Measures (South Australia). Figs. 1-4 and 8 only cleaned from the sediment, figs. 6 and 7 also macerated. If not otherwise stated, scale bars = 5 mm.

Fig. 1 Two leaf portions above the bifurcation. Pinnules fully grown, spacious suboppositely attached with resin bodies covering the whole leaf. NRMS089773.

Fig. 2 Portion of a bifurcating leaf segment. Note the opposite attached pinnules below the furcation and the strongly reduced pinnules on the inner leaf above the furcation. NRMS089765.

Fig. 3 Leaf segment above the furcation, with short pinnules on the lower left. EBN5A.

Fig. 4 Apical leaf segment with three fused pinnules at the apex (probably with leaf margin feeding). NRMS089773.

Fig. 5 Leaf segment below the furcation with shorter pinnules and constricted bases. NRMS089773-11.

Fig. 6 Cuticle segment with furcation in the upper rachis. Note the top segment with upper cuticle removed. NRMS089772-159.

Fig. 7 Cuticle of a leaf apex, with three apical pinnules fused and resin bodies preserved in the lamina. NRMS089773-59.

Fig. 8 Basal pinnule with rectangular shape and lobation on the apical leaf margin. NRMS089765. Scale bar = 3 mm.

Plate 5 – Transmitted light micrographs of *Dicroidium lineatum* (Ten.-Woods) H.M.Anderson et J.M.Anderson 1970 cuticles from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Fig. 1 Lower cuticle with main nerve parallel to the lower image margin and sub-nerves running at 45° from lower left to upper right corner of the image. Note the single lens-like thickening per cell and the thinner cutinisation compared to Pl. 5, Fig 2. NRMS089765-59. Scale bar = 200 µm.

Fig. 2 Upper cuticle corresponding to Pl. 5, Fig .1 and with identical orientation. NRMS089765-59. Scale bar = 200 µm.

Fig. 3 Cuticle of the rachis. Note the rectangular cells orientated in rows with relative thick cutinized anticlinal walls. NRMS089772-159. Scale bar = 100 µm.

Fig. 4 Details of the spherical resin bodies preserved between *D. lineatum* cuticles. NRMS089771-65. Scale bar = 50 µm.

Fig. 5 Cuticle details with strong Nomarski interference contrast, highlighting the relief, the shallow lens-like papillae, the slightly sunken stomata and the more or less straight and smooth anticlinal walls. EBN5-B15. Scale bar = 50 µm.

Fig. 6 Stomatal details displayed with Nomarski interference contrast. Note the slightly sunken pore and the batwing-shaped anticlinal wall flanges of the guard cells. NRMS089765-59. Scale bar = 20 µm.

Fig. 7 SEM image of epidermal cell pattern with main nerve running from left to right in the upper half of the picture. NRMS089772-181. Scale bar = 100 µm.

Fig. 8 SEM image with stomatal details. Note the deeper sunken stomatal complex with the batwing-shaped anticlinal wall flanges. NRMS089772-181. Scale bar = 10 µm.

Plate 6 – Macroscopic images of non-macerated *Dicroidium dubium* (Feistm.) Gothan 1912 from the Upper Triassic Leigh Creek Coal Measures (South Australia). Scale bars = 2 mm.

Fig. 1	Leaf segment probably including the furcation, evident by the upper right short and trapezoid pinna, typical for the inner leaf above the furcation. NRMS089765.
Fig. 2	Short trapezoid pinnules with odontopteroid venation. NRMS089765.
Fig. 3	Basal pinna deeply lobed in two with alethopteroid venation in each segment. NRMS089765.
Figs 4, 5	Elongated pinnae with alethopteroid venation and lobed leaf margins. Both specimens show blotch mines and impressions of roots. NRMS089765.

Plate 7 – Microscopic images of macerated *Dicroidium dubium* (Feistm.) Gothan 1912 cuticles from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Figs 1, 2	Upper (1) and lower (2) cuticle, with undifferentiated costal and intercostal fields in the upper cuticle and more elongated and aligned costal fields in the lower cuticle. NRMS089761-12. Scale bars = 200 µm.
Fig. 3	Cuticle of the upper rachis, with differentiated costal fields and more strongly swollen papillae. NRMS089765-111. Scale bar = 200 µm.
Fig. 4	Stomatal details with usually two papillae per cell, straight to delicately undulose, the typical thickenings on the subsidiary cells and a thin thickening of the guard cells. NRMS089761-12. Scale bar = 50 µm.
Fig. 5	SEM image with papillate cuticle in external view (left) and smooth cuticle in internal view (right). Arrows indicating stomatal pits and stomatal complexes. NRMS089765-135-02. Scale bar = 200 µm.
Fig. 6	Details of a cuticle with strongly swollen papillae arching over the stomatal pit. NRMS089765-116. Scale bar = 25 µm.

Fig. 7	SEM image showing the inner surface of cuticle with aligned epidermal cells in costal area on the left and randomly orientated stomata in intercostal area on the right. NRMS089765-135-02. Scale bar = 100 µm.
Fig. 8	SEM image of internal cuticle surface showing a stomatal complex. NRMS089765-135-02. Scale bar = 20 µm.

Plate 8 – Transmitted light microscopic and macroscopic images of macerated *Dicroidium zuberi* (SZAJNOCHA) S.ARCHANG. 1968 leaves from the Upper Triassic Leigh Creek Coal Measures (South Australia). Scale bar of images = 2 mm, unless otherwise stated.

Fig. 1	Leaf fragment with short, trapezoid and slightly lobed pinnules. NRMS089776-09.
Figs 2, 4	Microscopic image of pinna with upper (2) and lower (4) cuticle type 1, with amphistomatic leaves. NRMS089776-04. Scale bar = 1 mm.
Fig. 3	Leaf fragment with larger pinnules, slightly lobed in the middle, with upper cuticle removed on the lower left pinnule. NRMS089776-07.
Fig. 5	Leaf fragment with elongated and rounded-trapezoid pinnules. NRMS089775-13.
Fig. 6	Non-macerated pinna fragment with parallel dichotomizing venation. NRMS089765-89.
Fig. 7	Large triangular to trapezoid leaf fragment with upper cuticle removed on the lower half. NRMS089776-07.
Fig. 8	Apical leaf fragment with three fused pinnules. NRMS089776-23.

Plate 9 – Transmitted light micrographs of *Dicroidium zuberi* (SZAJNOCHA) S.ARCHANG. 1968 from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Figs 1, 2	Upper (1) and lower (2) cuticle type 1, with fewer stomata on the more strongly cutinized upper cuticle. NRMS089775-09. Scale bars = 100 µm.

Figs 3, 4 Upper (3) and lower (4) cuticle type 2, without stomata on the more strongly cutinized cuticle, a faintly cutinized lower cuticle with stomata and trichome bases. NRMS089761-03. Scale bars = 100 µm.

Fig. 5 Enlargement of the distinct papillae in *D. zuberi*. NRMS089776-08. Scale bar = 50 µm.

Fig. 6 SEM image from the outer cuticle surface illustrating the papillae. NRMS089776-28. Scale bar = 50 µm.

Fig. 7 SEM image of the inner cuticle with strongly buttressed anticlinal cell walls. NRMS089776-28. Scale bar = 50 µm.

Fig. 8 Stomatal details with non-papillate, non-buttressed anticlinal walls and with striated subsidiary cells, and with more thinly cutinized and shallow guard cells. NRMS089775-15. Scale bar = 25 µm.

Fig. 9 SEM image of a stoma. NRMS089776-28. Scale bar = 25 µm.

Fig. 10 Cuticle with preserved spherical resin bodies. NRMS089775-15. Scale bar = 100 µm.

Fig. 11 Trichome base from the lower cuticle type 2. NRMS089775-09. Scale bar = 50 µm.

Plate 10 – Macroscopic images of *Dicroidium* sp. A cuticle fragments from the Upper Triassic Leigh Creek Coal Measures (South Australia). Scale bars = 2 mm if not stated otherwise.

Figs 1, 2 Upper (1) and lower (2) cuticle of a leaf segment with very short triangular pinnules. NRMS089773-66.

Fig. 3 Leaf segment with strongly elongated pinnules. NRMS089773-62.

Fig. 4 Apex with three strongly fused pinnules. NRMS089773-84. Scale bar = 1 mm.

Fig. 5 Non-macerated pinna fragment with clear main nerve and oblate resin bodies. NRMS089773-23.

Fig. 6 Pinnate leaf segment connecting to the rachis at the base, with gradually shortened and more strongly fused pinnules. NRMS089773-64.

Fig. 7 Apical leaf segment with slightly longer finite pinnule segments. NRMS089773.

Fig. 8 Leaf segment with short, triangular and strongly fused pinnules. NRMS089773.

Plate 11 – Transmitted light micrographs of *Dicroidium* sp. A from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Figs 1, 2 Upper (1) and lower (2) cuticles of an elongated pinna segment. Note the elongated and aligned cells in the central costal fields and the 2–4 lens-like thickenings per cell. EBN14-B14. Scale bars = 200 µm.

Fig. 3 Cuticular details of the rachis from the specimen figured on Pl. 1 Fig. 1. Note the costal field in the centre of the image. NRMS089773-59. Scale bar = 200 µm.

Fig. 4 Non-macerated pinna (Plate 8, Fig. 4) with details of the coalified nerve in the centre and two spherical resin bodies to the left and right. NRMS089773-23. Scale bar = 200 µm.

Fig. 5 Cuticle details with slightly buttressed cell walls, lens-like periclinal wall thickenings and crescent-shaped anticlinal walls of the stomatal guard cells. NRMS089773-66. Scale bar = 50 µm.

Fig. 6 Cuticular details of the stomatal complex with a ring of four subsidiary cells and concentric striae on the guard cells around the spindle-shaped pore. NRMS089773-68. Scale bar = 20 µm.

Fig. 7 SEM image of the outer (lower image) and inner cuticle (upper image). Note the outer cuticle with papillate surface and the arrows, pointing to the stomata pits. Note the inner cuticle with buttressed cell walls, the papillae markings on the periclinal walls and the distinct anticlinal walls of the guard cells. NRMS089773-88-01. Scale bar = 100 µm.

Fig. 8 SEM image of the stomatal complex with crescentic guard cells and thicker cutinisation around the pore. NRMS089773-88-02. Scale bar = 10 µm.

Plate 12 – Macroscopic and transmitted-light microscopic images of *Dicroidium* sp. B from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Figs 1, 2 Adaxial (1) and abaxial (2) cuticle of a leaf segment with very short and slender pinnules. NRMS089779-13. Scale bar = 1 mm.

Figs 3, 4 Adaxial (3) and abaxial (4) cuticle of an elongate pinna fragment. NRMS089779-21. Scale bar = 2 mm.

Figs 5, 6 Adaxial (5) and abaxial (6) cuticle of a short and oval pinna fragment. NRMS089779-02. Scale bar = 5 mm.

Figs 7, 8 Adaxial (1) and abaxial (2) cuticle of a leaf fragment with oval pinna. NRMS089779-17. Scale bar = 2 mm.

Figs 9, 10 Adaxial (9) and abaxial (10) cuticle of a leaf fragment with two sub-opposite rectangular to rhombic pinnules. NRMS089779-01. Scale bar = 2 mm.

Figs 11, 12 Adaxial (11) and abaxial (12) cuticle of a round pinnules. NRMS089779-03. Scale bar = 2 mm.

Plate 13 – Microscopic images of *Dicroidium* sp. B from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Figs 1, 2 Adaxial (1) and abaxial (2) cuticle with dichotomizing costal fields in the centre. NRMS089779-01. Scale bar = 100 µm.

Fig. 3 Cuticle details with deeply sunken stomatal complexes, orientated in growth direction. NRMS089779-01. Scale bar = 50 µm.

Fig. 4 Stomatal details with strongly cutinized florin ring. NRMS089779-08. Scale bar = 25 µm.

Fig. 5 SEM image of the internal cuticle with thick anticlinal walls and large and deeply sunken guard cells. NRMS089779-29. Scale bar = 50 µm.

Fig. 6 SEM image of the stomatal complex with the large and broad guard cells. NRMS089779-29. Scale bar = 20 µm.

Fig. 7 Cuticle with elongate oval trichomes. NRMS089779-02. Scale bar = 50 µm.

Fig. 8 Disintegrated resin channels within the cuticles. NRMS089779-08. Scale bar = 100 µm.

Fig. 9 SEM image with the outer (left) and inner (right) cuticle surface. Note the papillate surface and the arrows, indicating the stomatal pits. NRMS089779-28. Scale bar = 100 µm.

Plate 14 – Macroscopic and microscopic images of non-macerated *Dicroidium* sp. C specimen from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Fig. 1 Leaf fragment with short triangular pinnules with odontopteroid venation at the base and oblong pinnules with alethopteroid venation at the top. Note the dentate to crenate leaf margins and the small oblate resin bodies within the leaves. NRMS089772-26. Scale bar = 2 mm.

Fig. 2 Leaf fragment with leaf damage on the two pinnules at the lower left. NRMS089772-24. Scale bar = 2 mm.

Fig. 3 Leaf fragment with triangular pinna. NRMS089772-25. Scale bar = 2 mm.

Fig. 4 Transmitted light micrograph with rachis to the right and resin bodies in the central upper half of the image. Note the strongly cutinized anticlinal walls of the guard cells. NRMS089772-24. Scale bar = 200 µm.

Fig. 5 Fluorescence microscopic image of the cuticle exterior, showing epidermal cells with straight anticlinal walls, one lens-like thickening per cell and slightly sunken stomata with strongly cutinized guard cells. NRMS089772-25. Scale bar = 100 µm.

Fig. 6	External fluorescence microscopic image of a stoma. NRMS089772-24. Scale bar = 50 µm.

Plate 15 – Micrographs of *Umkomasia* sp. cf. *U. quadripartita* J.M.ANDERSON et H.M.ANDERSON 2003 from the Upper Triassic Leigh Creek Coal Measures (South Australia). NRMS089765-122.

Fig. 1	Complete cupule with petiole attached, inner cuticle partly removed. Scale bar = 1 mm.
Fig. 2	Detail of the inner cuticle with epidermal cells in rows and lacking any stomata. Scale bar = 200 µm.
Fig. 3	Cupule margin with inner cuticle still attached on the left-hand side of the image. Scale bar = 200 µm.
Fig. 4	Details of the outer cuticle with randomly and isodiametric epidermal cells and numerous stomata in random orientation. Scale bar = 200 µm.
Fig. 5	Inner cupule with rows of epidermal cells, with thick anticlinal walls. Scale bar = 100 µm.
Figs 6, 7	Inner cuticle with details of the stomata. Note the strongly cutinized guard cells and the papillate subsidiary cells. Scale bars = 50 µm.

Plate 16 – Fluorescence micrographs of cupules of *Umkomasia* sp. cf. *U. quadripartita* J.M.ANDERSON et H.M.ANDERSON 2003 from the Upper Triassic Leigh Creek Coal Measures (South Australia). Scale bars = 1 mm.

Figs 1, 2	Cupule in lateral view with the two hemispherical halves. NRMS089765.
Figs 3, 4	Cupule in dorsal (3) and ventral (4) view. Note the petiole merging in the upper part with the cupule. NRMS089765.

Fig. 5	Cupule in ventral view. NRMS089765.
Fig. 6	Cupule in lateral view. NRMS089765.
Fig. 7	Cupule in lateral view. NRMS089765.

Plate 17 – Fluorescence micrographs of an *Umkomasia* sp. cf. *U. quadripartita* J.M.ANDERSON et H.M.ANDERSON 2003 cupule from the Upper Triassic Leigh Creek Coal Measures (South Australia). NRMS089765, if not stated otherwise.

Figs 1, 2	One hemisphere of a cupule with dorsal (1) and ventral (2) view. Scale bars = 100 µm.
Fig. 3	Outer petiole epidermal cell details. Scale bar = 200 µm.
Fig. 4	Central cupule lamina surface in external view. Scale bar = 200 µm.
Fig. 5	Inner petiole epidermal details. Scale bar = 200 µm.
Fig. 6	Central cupule epidermal details from inside. NRMS089765-122. Scale bar = 200 µm.

Plate 18 – Macroscopic and microscopic images of *Fanerotheca* sp. cf. *F. waldeckiformis* J.M.ANDERSON et H.M.ANDERSON 2003 from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Fig. 1	Cupule, opened and with pedicel attached, partly disintegrated. NRMS089772-57. Scale bar = 1 mm.
Fig. 2	Closed cupule with numerous resin bodies preserved. NRMS089765. Scale bar = 1 mm.
Fig. 3	Cupule, macerated, opened and attached with the pedicel attached to the peduncle. Note the large resin bodies. NRMS089772-162. Scale bar = 1 mm.
Fig. 4	Cupule fragment. NRMS089770. Scale bar = 1 mm.

Fig. 5 Resin bodies preserved between the cuticle of the specimen in Fig. 5. NRMS089772-32. Scale bar = 200 µm.

Fig. 6 Cuticle of a macerated cupule with oblate resin bodies in the top and collapsed and partly folded lamina. NRMS089765-123. Scale bar = 200 µm.

Fig. 7 Stomatal details with thick anticlinal wall flanges of the guard cells and slightly sunken stoma. NRMS089772-162. Scale bar = 20 µm.

Plate 19 – Fluorescence microscopic images of *Fanerotheca* sp. cf. *F. waldeckiformis* J.M.ANDERSON et H.M.ANDERSON 2003 from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Fig. 1 Complete cupule with four lobes. Note the strongly cutinized and wrinkled central lamina attached to the petiole. NRMS089770. Scale bar = 1 mm.

Figs 2, 3 Open cupule in dorsal (2) and ventral (3) view. Note the petiole in the central lamina pointing upwards and the coaly remains of the seeds' vascular supply in ventral view. NRMS089770. Scale bars = 1 mm.

Fig. 4 Cuticle details of the central lamina. Note the isodiametric cell outlines, the single thickening per cell and the slightly sunken stomata. NRMS089770. Scale bar = 100 µm.

Fig. 5 Cuticle of the apical lobes. Note the elongated epidermal cells. NRMS089770. Scale bar = 100 µm.

Fig. 6 Stomatal details. NRMS089770. Scale bar = 50 µm.

Plate 20 – Fluorescence micrographs of *Pteruchus africanus* H.H.THOMAS 1933 emend. H.M.ANDERSON 2019 from the Upper Triassic Leigh Creek Coal Measures (South Australia).

Figs 1, 2 Fertile head in dorsal (1) and ventral (2) view. Note the lobed and strongly cutinized lamina in dorsal view and the pedicel at the base. NRMS089772. Scale bar = 1 mm.

Fig. 3 Fertile head laterally flattened and pollen sacci facing to the top. NRMS089772. Scale bar = 500 µm.

Fig. 4 Central lamina cuticle. NRMS089772. Scale bar = 200 µm.

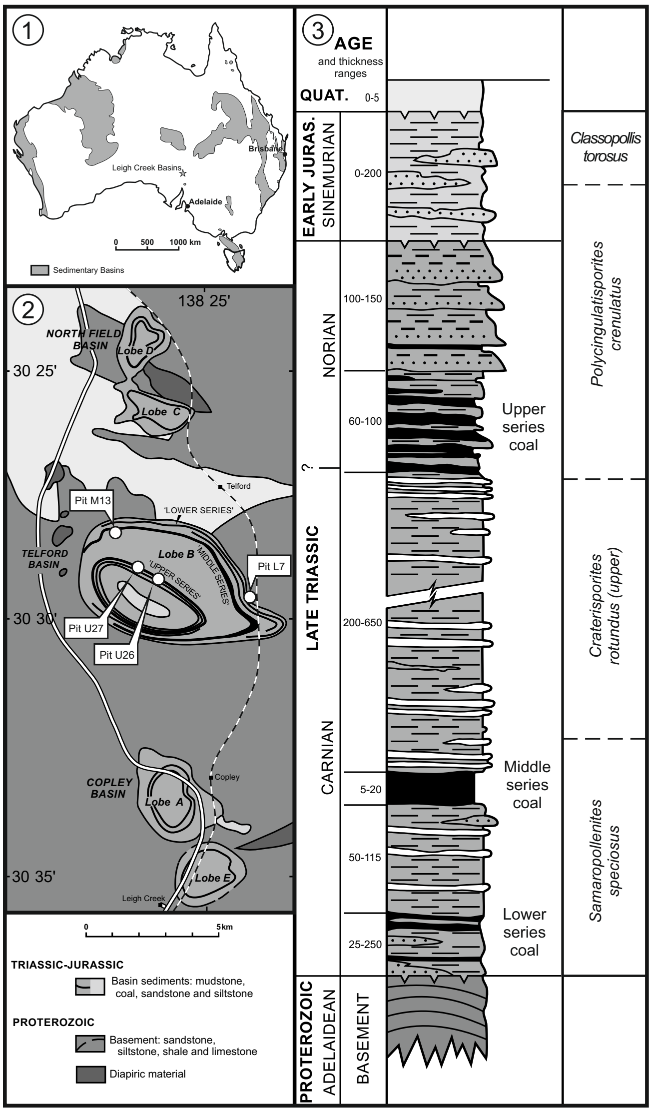
Fig. 5 Central lamina details. Note the several discrete papillae per epidermal cell. EBN13A-P2D. Scale bar = 200 µm.

Fig. 6 Central lamina cuticle details with sunken stomata. NRMS089772. Scale bar = 100 µm.

Fig. 7 Pollen sac with bisaccate pollen grains inside. NRMS089771-69. Scale bar = 500 µm.

Fig. 8 Light microscopic image inside a pollen sac with bisaccate pollen. NRMS089771-69. Scale bar = 50 µm.

Fig. 9 Light microscopic image of a bisaccate *Alisporites*/*Falcisporites* pollen grain. NRMS089771-69. Scale bar = 20 µm.

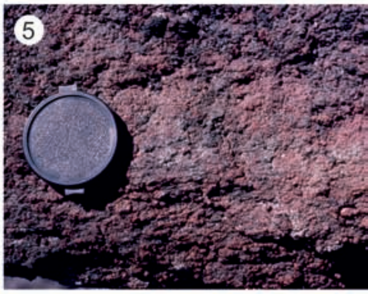

1
Leigh Creek Basins
Brisbane
Adelaide
0 500 1000 km
Sedimentary Basins
2
138 25'
NORTH FIELD BASIN
Lobe D
30 25'
Lobe C
Telford
Pit M13
'LOWER SERIES'
TELFORD BASIN
Lobe B
'MIDDLE SERIES'
'UPPER SERIES'
Pit L7
30 30'
Pit U27
Pit U26
COPLEY BASIN
Copley
Lobe A
30 35'
Lobe E
Leigh Creek
0 5km
TRIASSIC-JURASSIC
Basin sediments: mudstone, coal, sandstone and siltstone
PROTEROZOIC
Basement: sandstone, siltstone, shale and limestone
Diapiric material
3
AGE
and thickness ranges
QUAT. 0-5
EARLY JURAS.
SINEMURIAN
0-200
Classopollis torosus
LATE TRIASSIC
NORIAN
100-150
60-100
?
Upper series coal
Polycingulatisporites crenulatus
CARNIAN
200-650
Craterisporites rotundus (upper)
5-20
Middle series coal
50-115
25-250
Lower series coal
Samaropollenites speciosus
PROTEROZOIC
ADELAIDEAN
BASEMENT

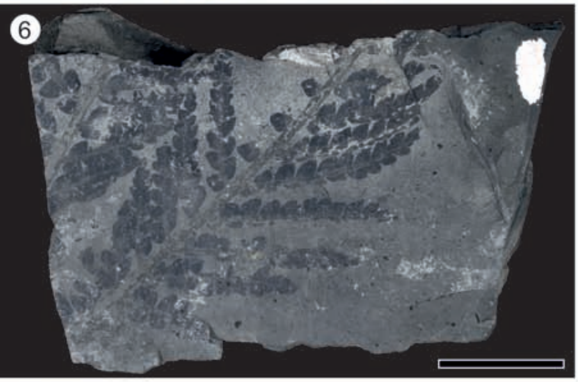

1
N
B
A
C

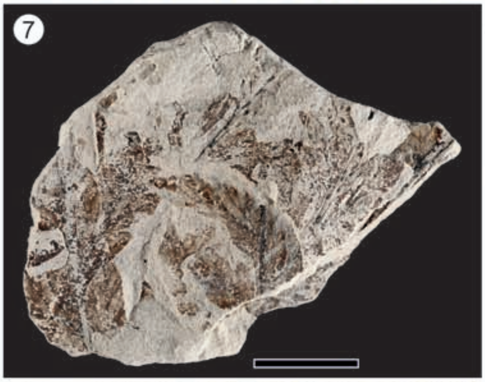

2


3


4

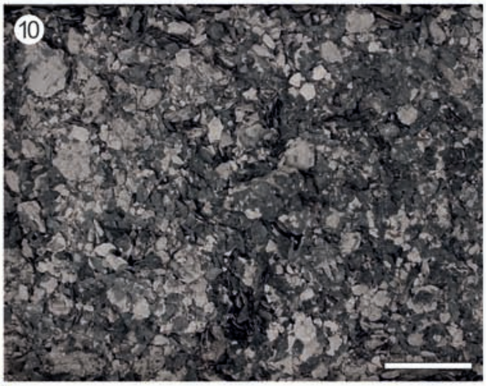

5


6


7

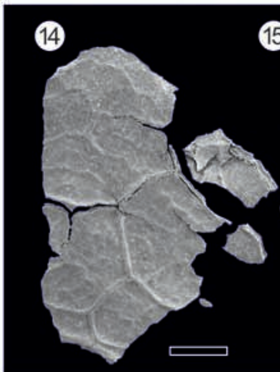

8

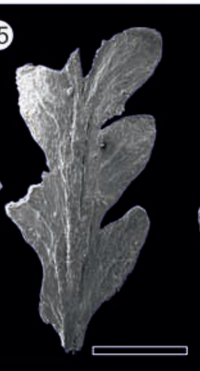

9


10

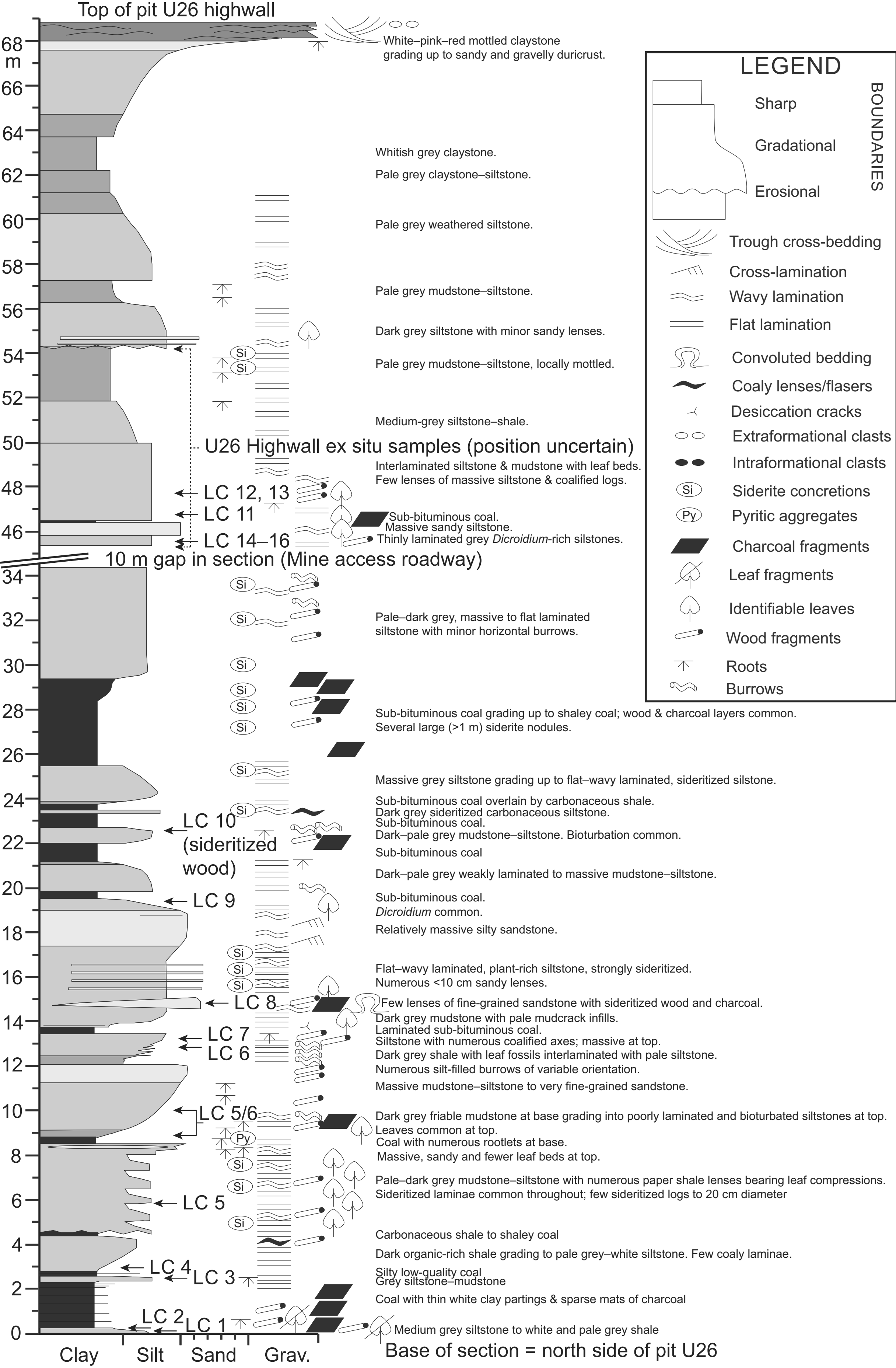

11
12

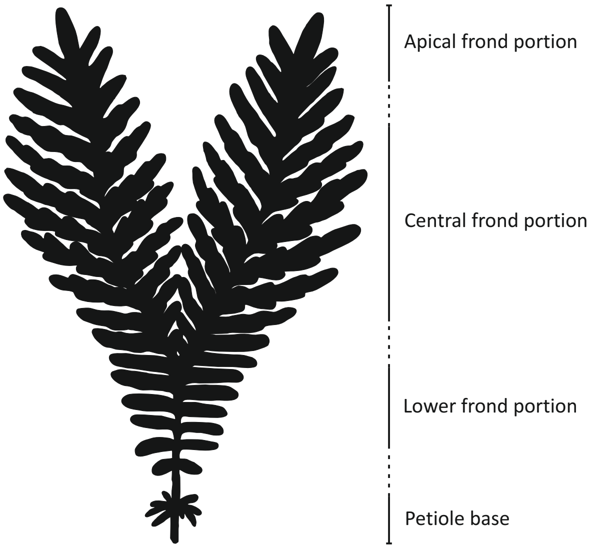

13

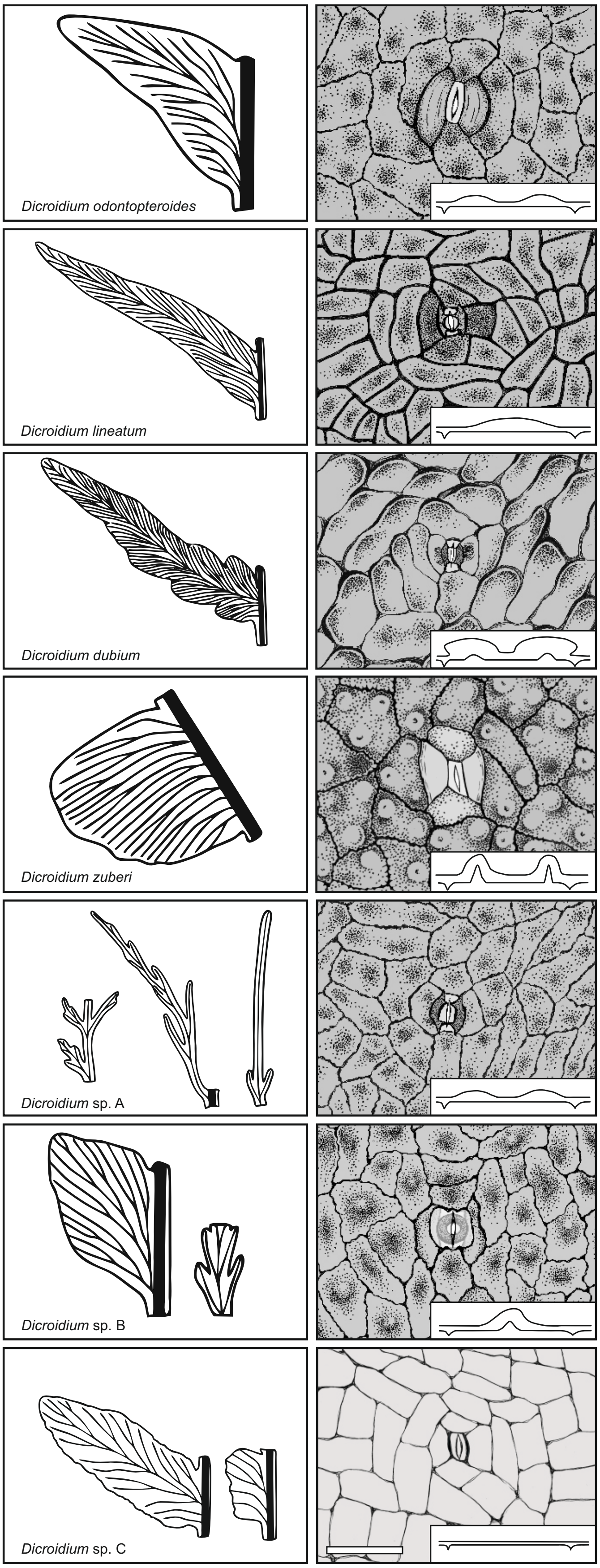

14


15


16


Top of pit U26 highwall
White–pink–red mottled claystone grading up to sandy and gravelly duricrust.
Whitish grey claystone.
Pale grey claystone–siltstone.
Pale grey weathered siltstone.
Pale grey mudstone–siltstone.
Dark grey siltstone with minor sandy lenses.
Pale grey mudstone–siltstone, locally mottled.
Medium-grey siltstone–shale.
U26 Highwall ex situ samples (position uncertain)
Interlaminated siltstone & mudstone with leaf beds.
Few lenses of massive siltstone & coalified logs.
LC 12, 13
LC 11
Sub-bituminous coal.
Massive sandy siltstone.
LC 14–16
Thinly laminated grey *Dicroidium*-rich silstones.
10 m gap in section (Mine access roadway)
Pale–dark grey, massive to flat laminated siltstone with minor horizontal burrows.
Sub-bituminous coal grading up to shaley coal; wood & charcoal layers common.
Several large (>1 m) siderite nodules.
Massive grey siltstone grading up to flat–wavy laminated, sideritized silstone.
Sub-bituminous coal overlain by carbonaceous shale.
Dark grey sideritized carbonaceous siltstone.
Sub-bituminous coal.
Dark–pale grey mudstone–siltstone. Bioturbation common.
LC 10 (sideritized wood)
Sub-bituminous coal
Dark–pale grey weakly laminated to massive mudstone–siltstone.
LC 9
Sub-bituminous coal.
Dicroidium common.
Relatively massive silty sandstone.
Flat–wavy laminated, plant-rich siltstone, strongly sideritized.
Numerous <10 cm sandy lenses.
LC 8
Few lenses of fine-grained sandstone with sideritized wood and charcoal.
Dark grey mudstone with pale mudcrack infills.
Laminated sub-bituminous coal.
LC 7
Siltstone with numerous coalified axes; massive at top.
LC 6
Dark grey shale with leaf fossils interlaminated with pale siltstone.
Numerous silt-filled burrows of variable orientation.
Massive mudstone–siltstone to very fine-grained sandstone.
LC 5/6
Dark grey friable mudstone at base grading into poorly laminated and bioturbated siltstones at top.
Leaves common at top.
Coal with numerous rootlets at base.
Massive, sandy and fewer leaf beds at top.
Pale–dark grey mudstone–siltstone with numerous paper shale lenses bearing leaf compressions.
Sideritized laminae common throughout; few sideritized logs to 20 cm diameter
LC 5
Carbonaceous shale to shaley coal
Dark organic-rich shale grading to pale grey–white siltstone. Few coaly laminae.
LC 4
LC 3
Silty low-quality coal
Grey siltstone–mudstone
Coal with thin white clay partings & sparse mats of charcoal
LC 2
LC 1
Medium grey siltstone to white and pale grey shale
Base of section = north side of pit U26
Si
Py
m
68
66
64
62
60
58
56
54
52
50
48
46
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
Clay
Silt
Sand
Grav.
LEGEND
BOUNDARIES
Sharp
Gradational
Erosional
Trough cross-bedding
Cross-lamination
Wavy lamination
Flat lamination
Convoluted bedding
Coaly lenses/flasers
Desiccation cracks
Extraformational clasts
Intraformational clasts
Siderite concretions
Pyritic aggregates
Charcoal fragments
Leaf fragments
Identifiable leaves
Wood fragments
Roots
Burrows


Apical frond portion
Central frond portion
Lower frond portion
Petiole base

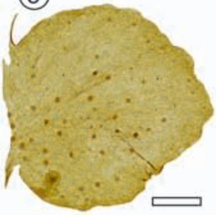

Dicroidium odontopteroides
Dicroidium lineatum
Dicroidium dubium
Dicroidium zuberi
Dicroidium sp. A
Dicroidium sp. B
Dicroidium sp. C


①


②


③


④


⑤


⑥

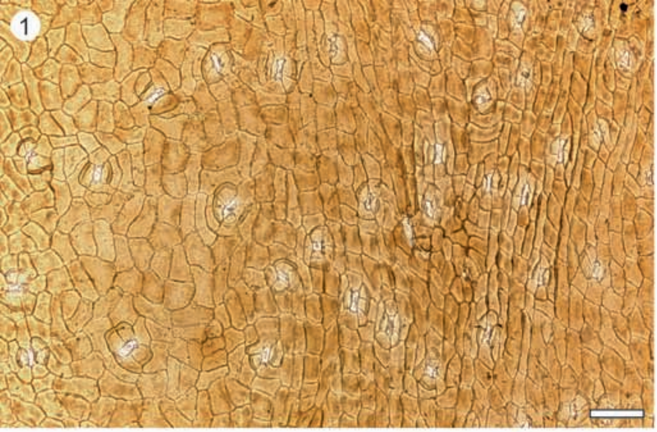

⑦

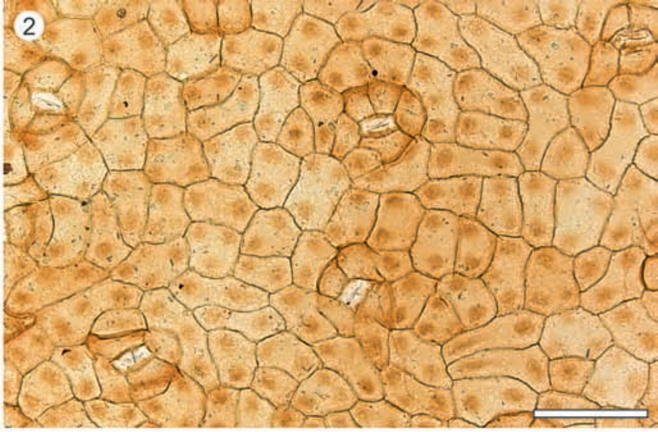

⑧


⑨

①

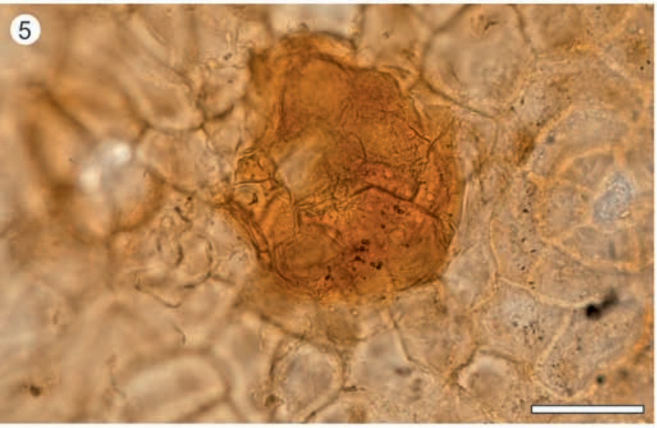
②

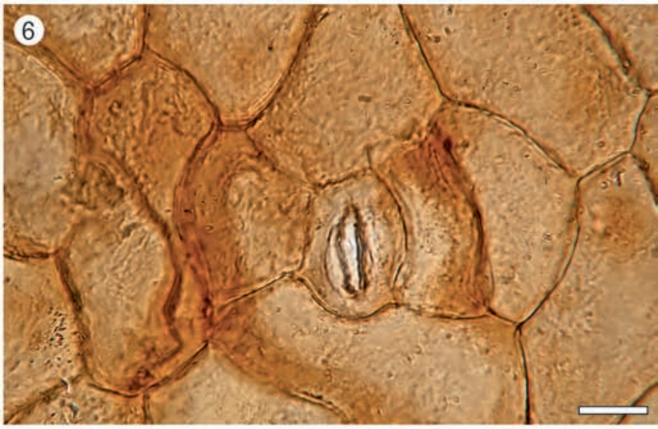

1

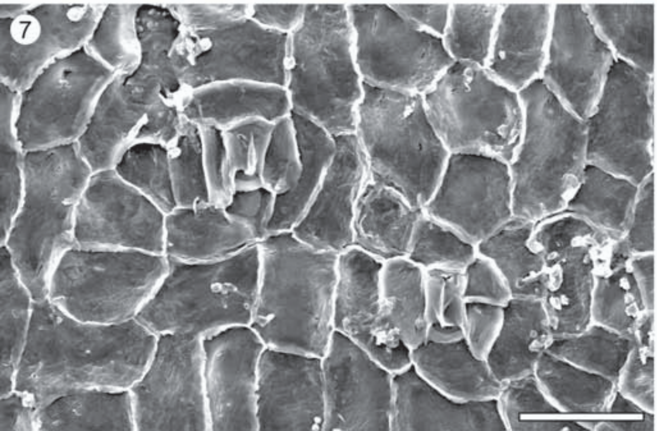

2

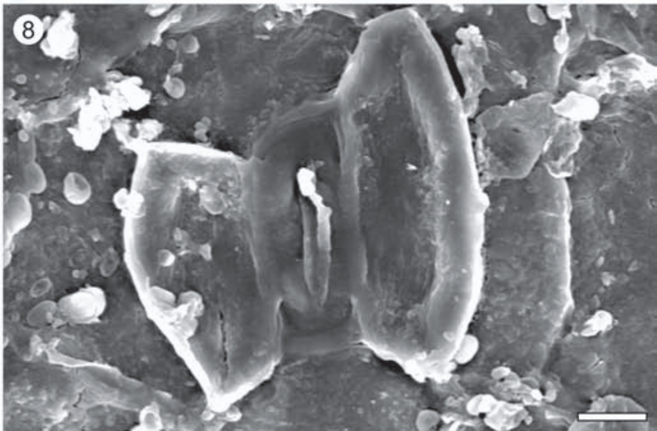

3


4

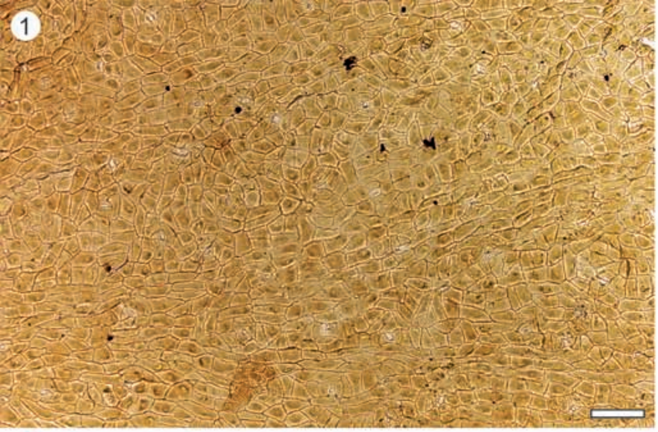

5

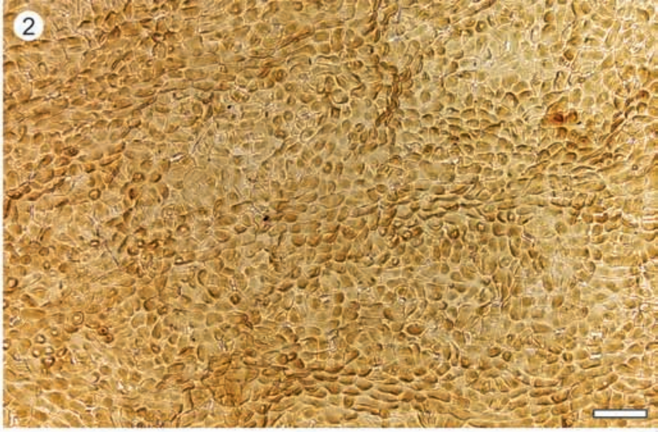

6

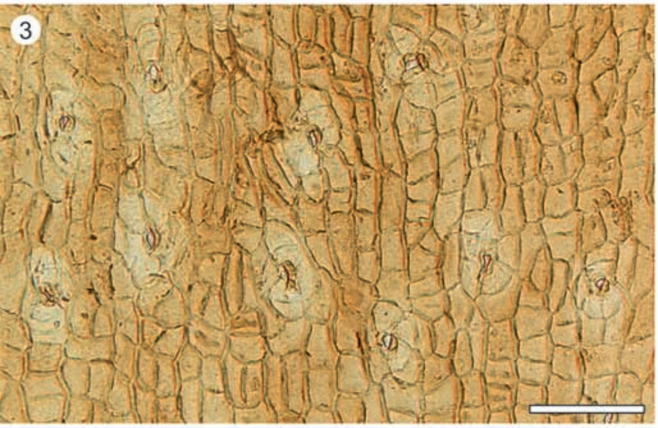

7

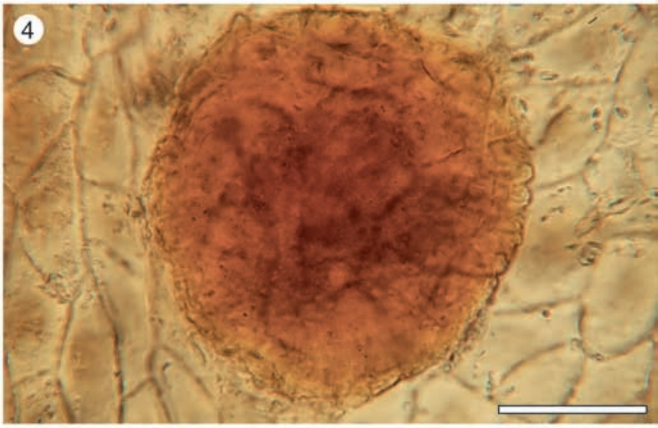

8


①
②
③
④
⑤
⑥
⑦
⑧


1

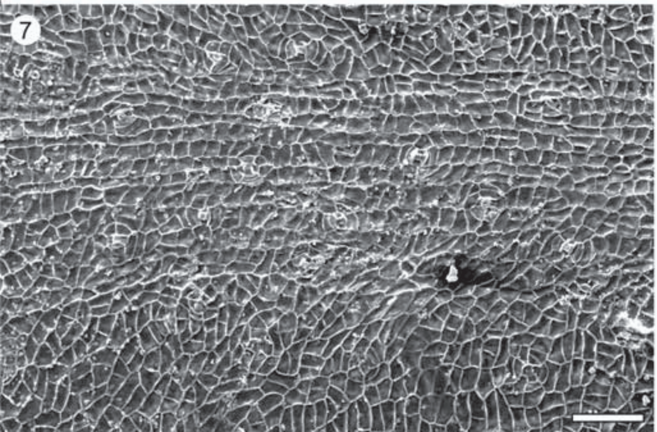

2

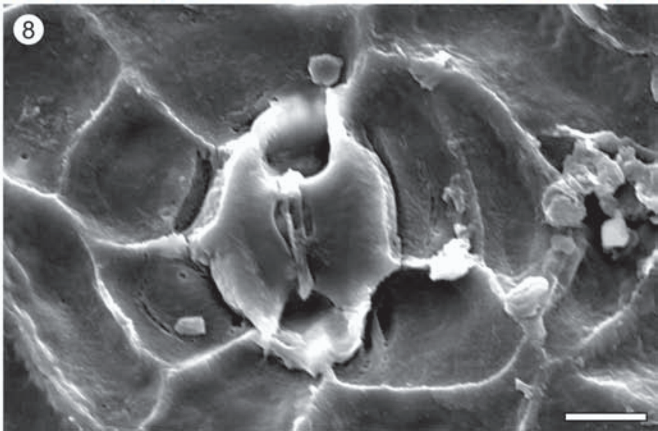

3

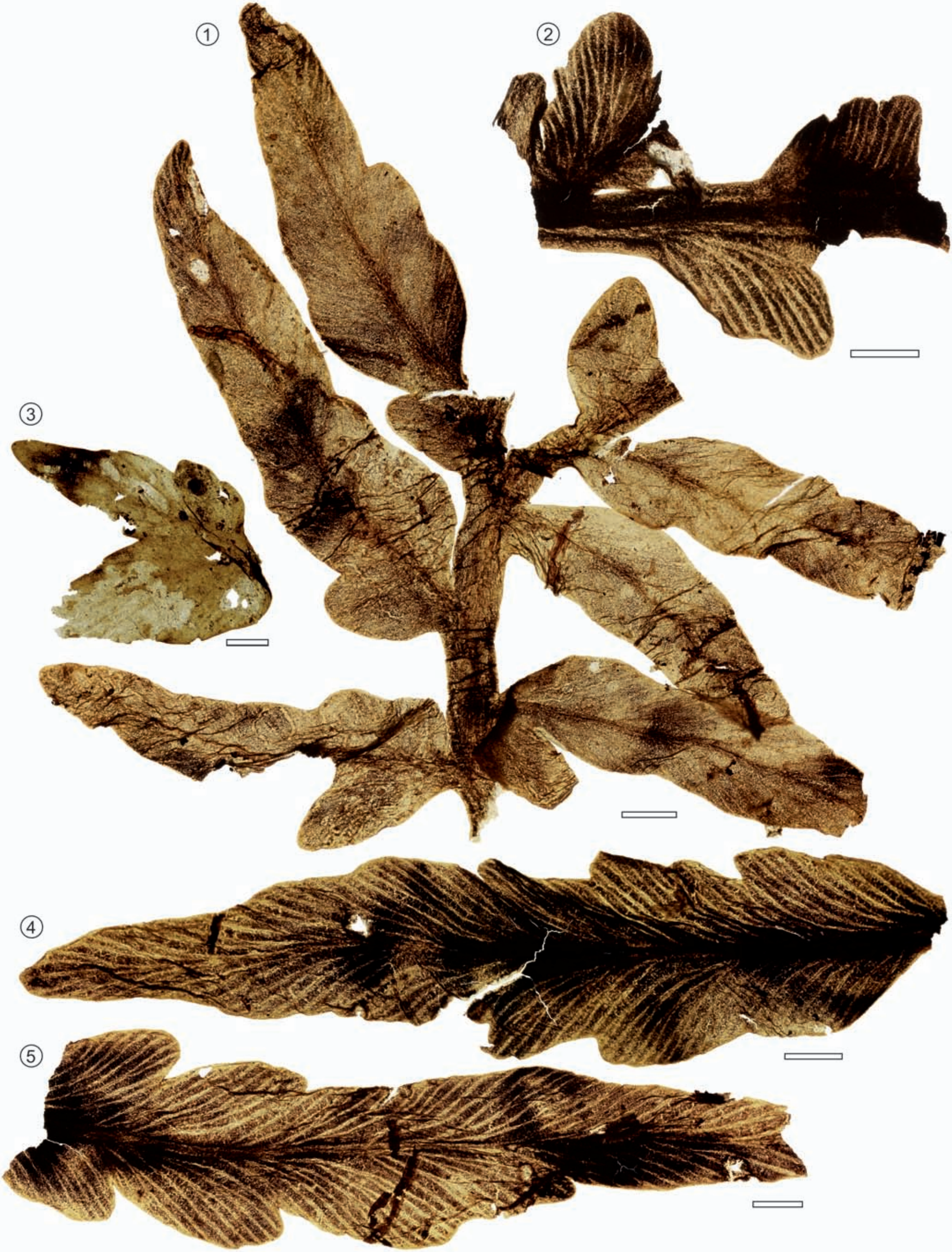

4

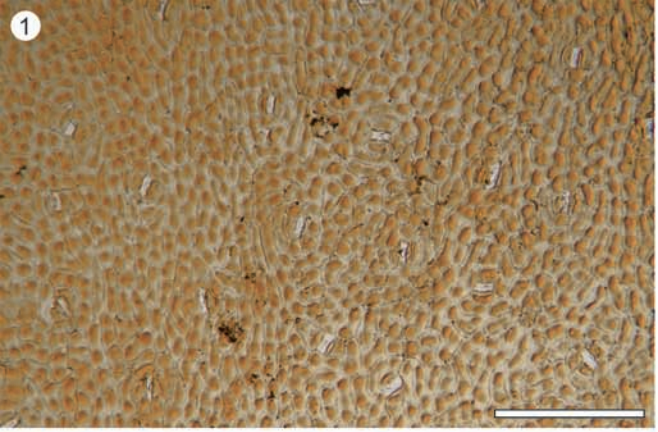

5

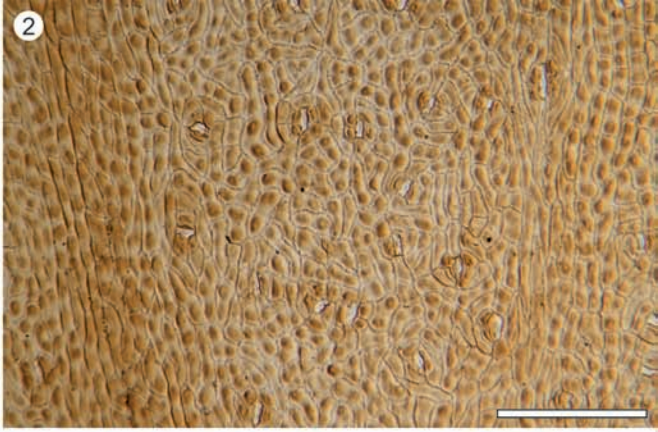

6

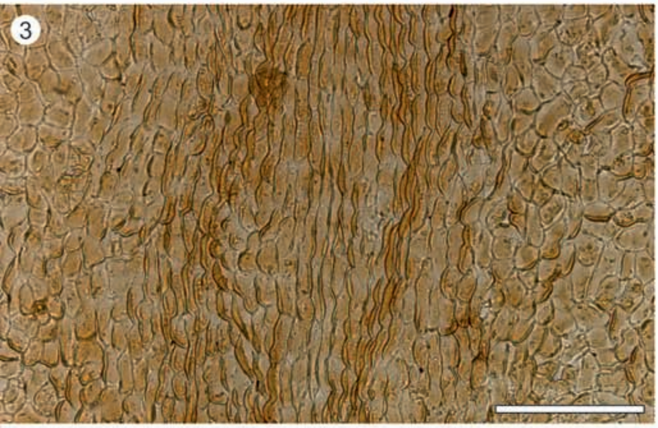

7

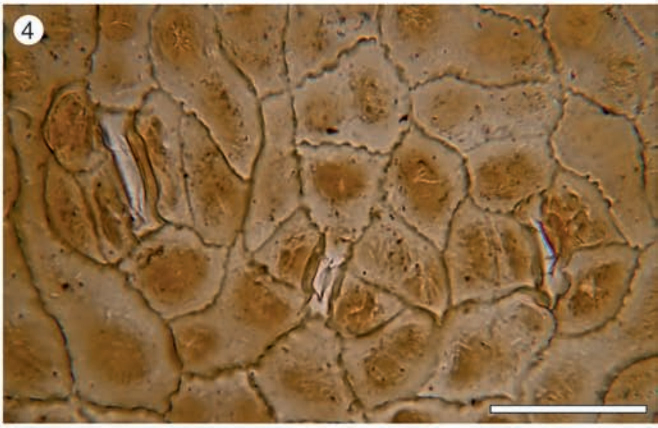

8

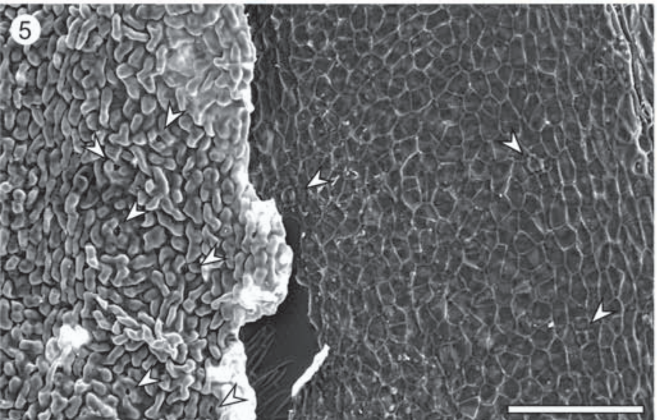

①
②
③
④
⑤

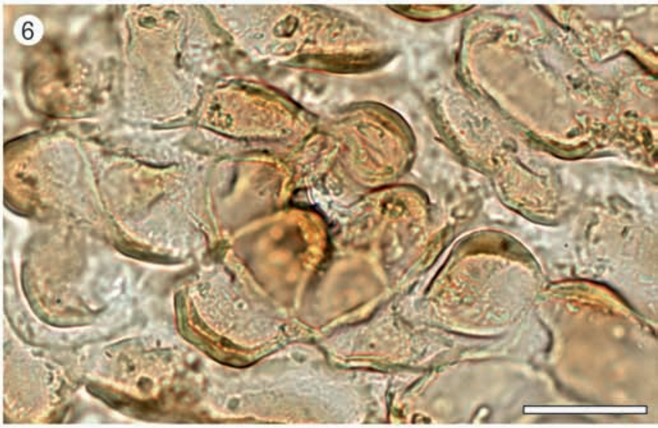

1

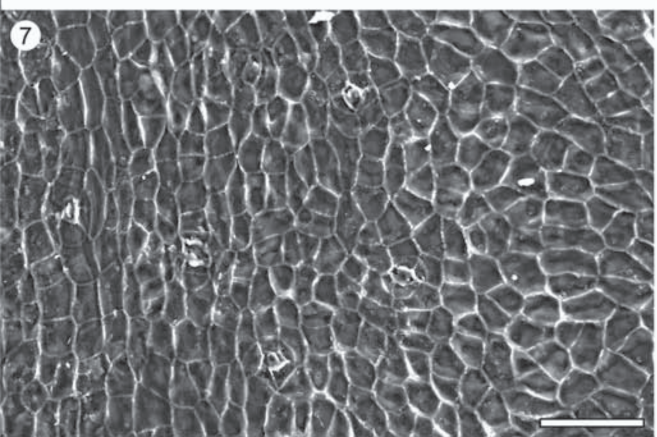

2

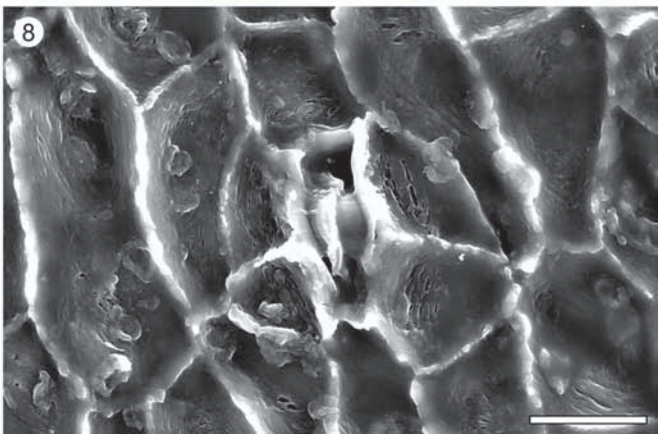

3


4

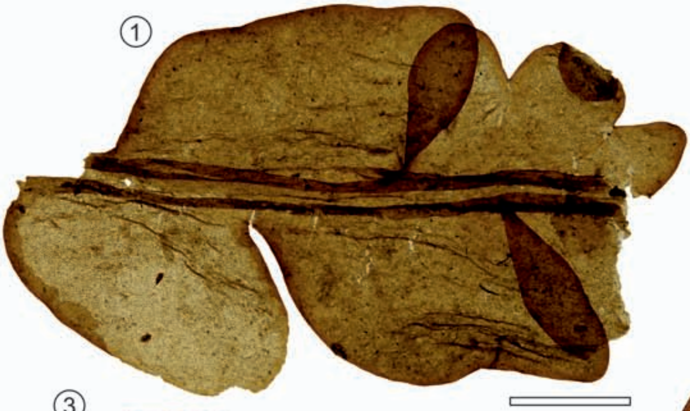

5


6


7

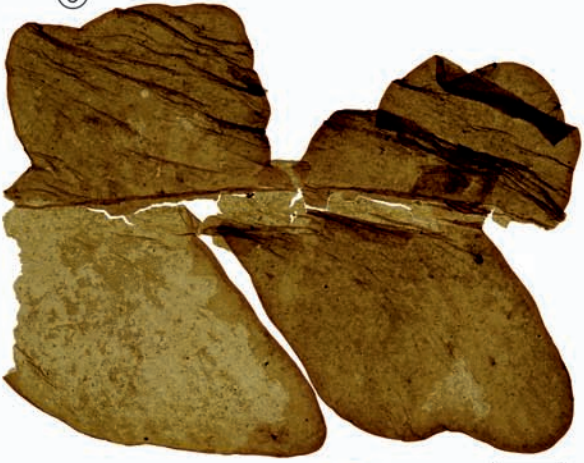

8

①



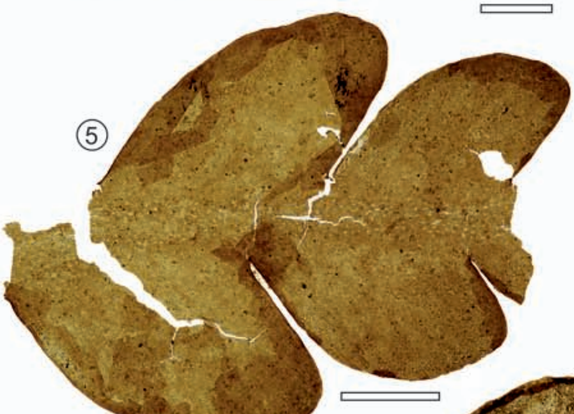
②

③



④

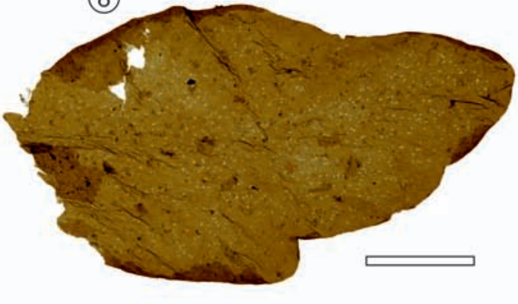
⑤

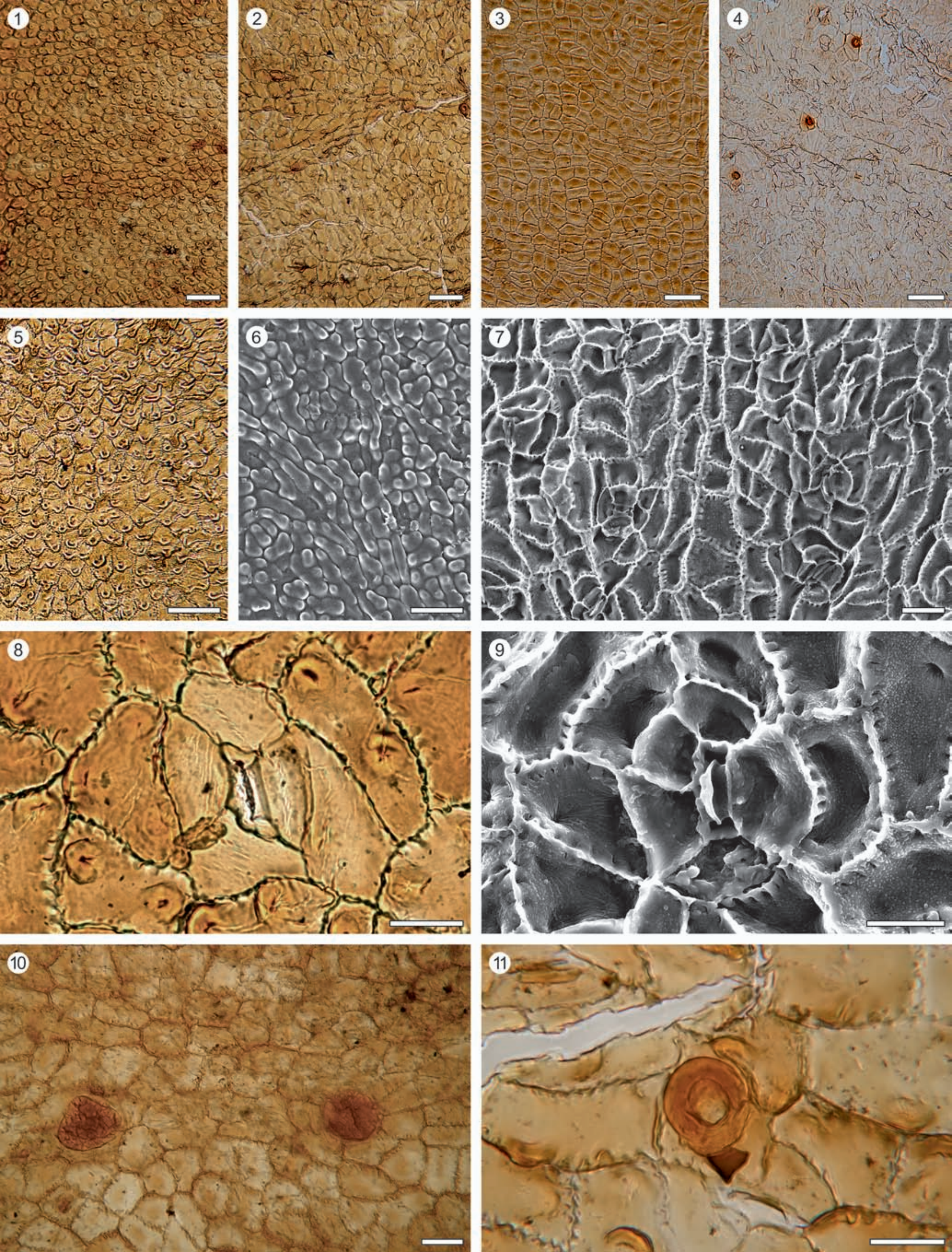


⑥

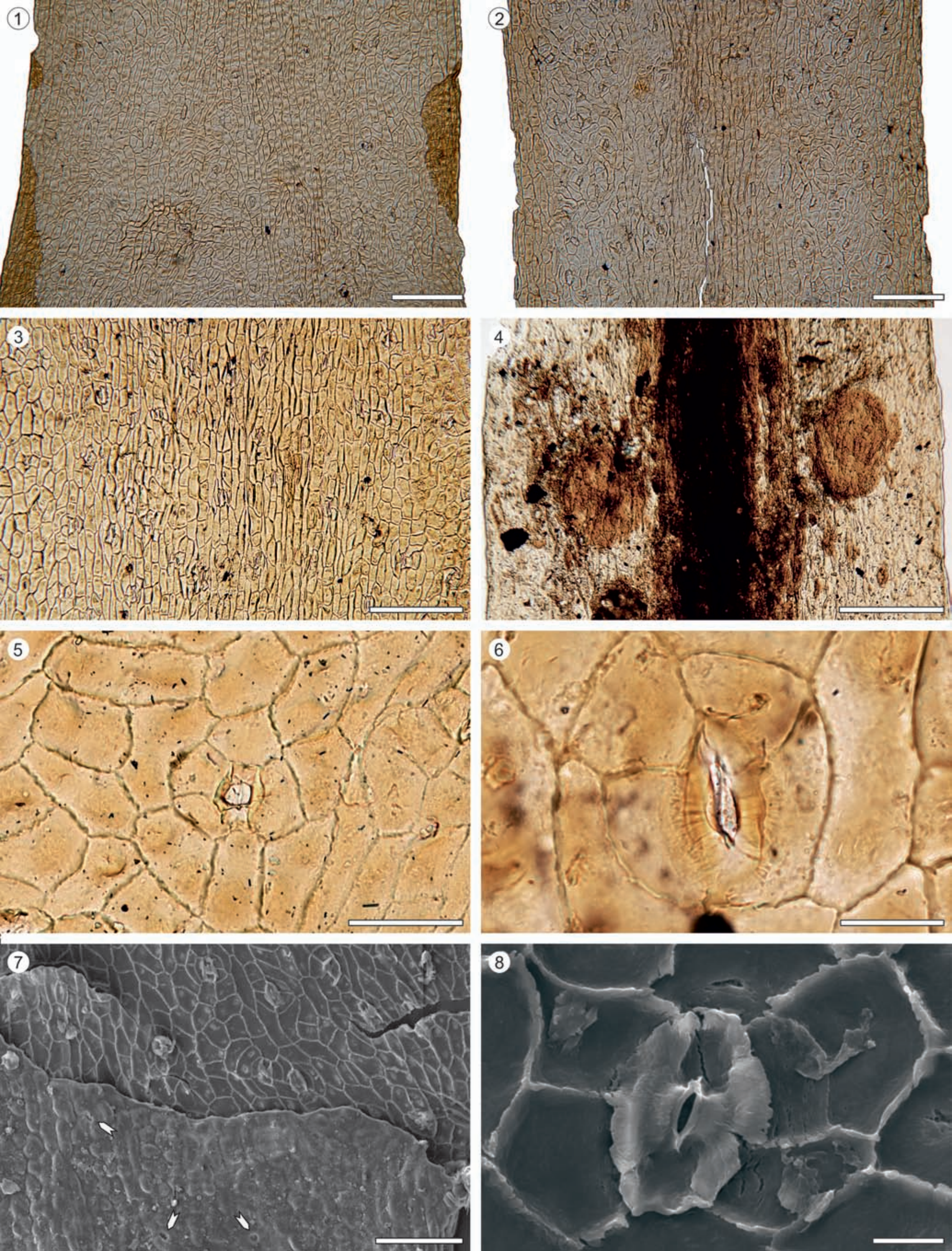
⑦

⑧

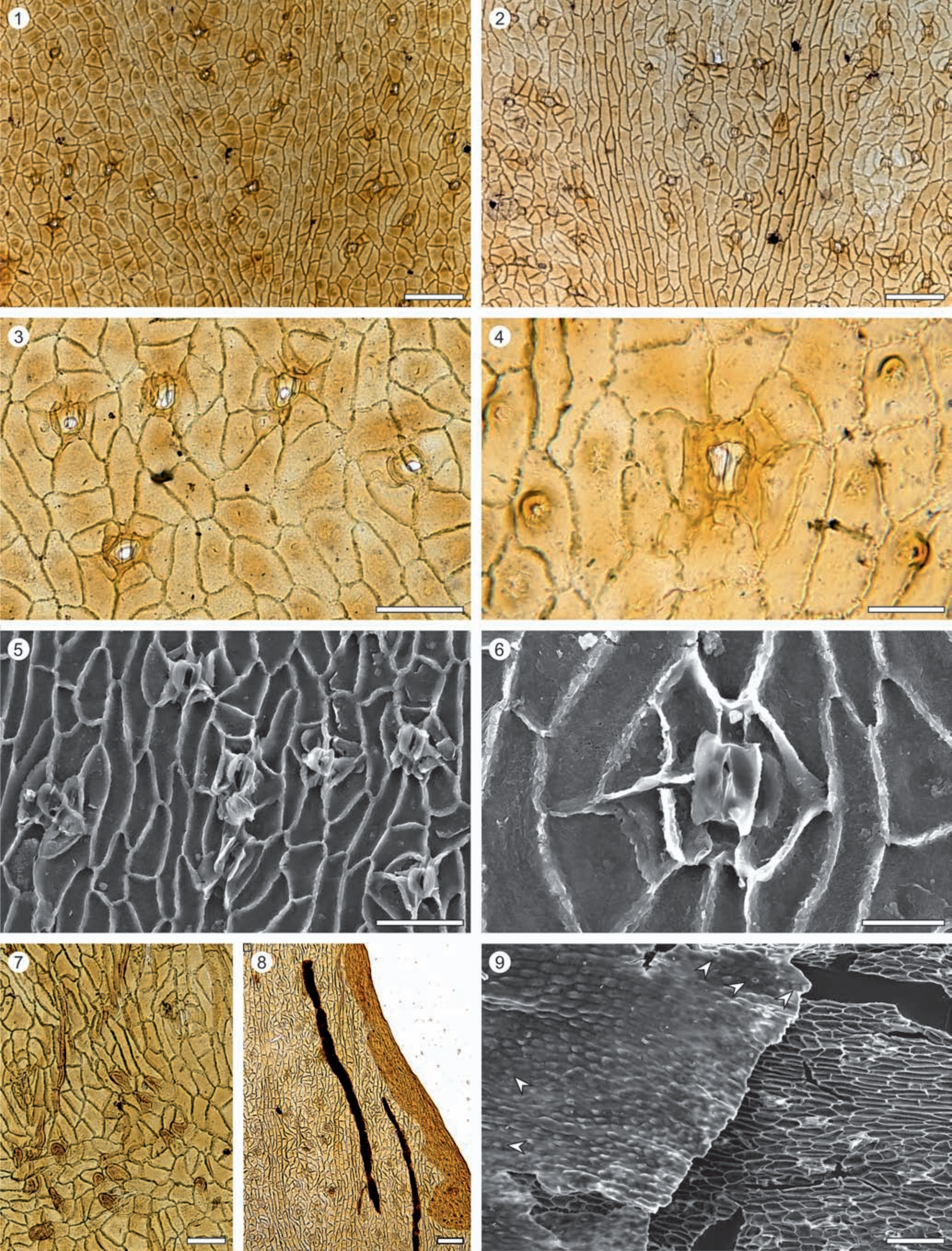



1
2
3
4
5
6
7
8
9
10
11

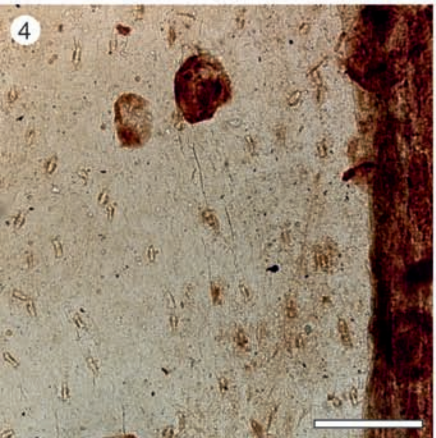

①
②
③
④
⑤
⑥
⑦
⑧

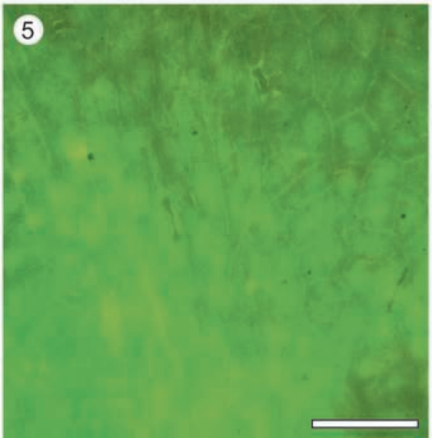

1
2
3
4
5
6
7
8

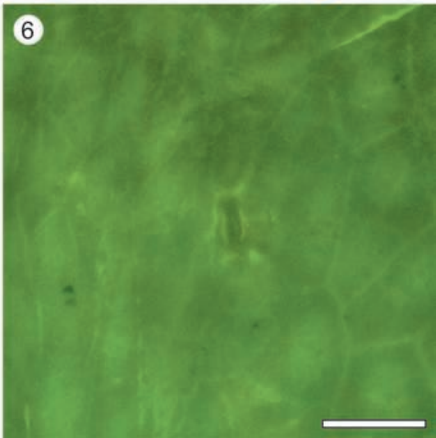

①
②
③
④
⑤
⑥
⑦
⑧
⑨
⑩
⑪
⑫

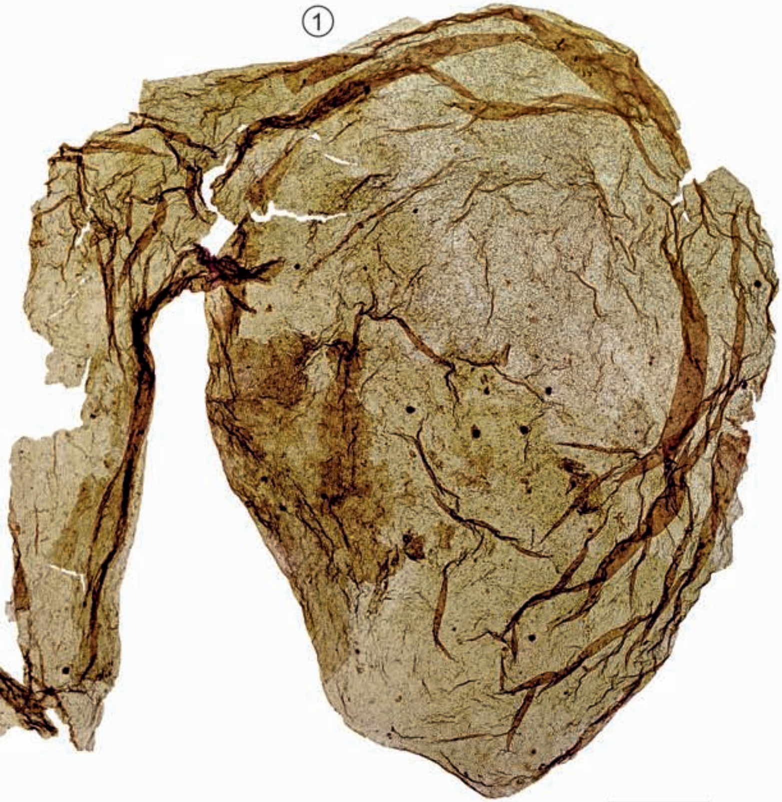

1
2
3
4
5
6
7
8
9

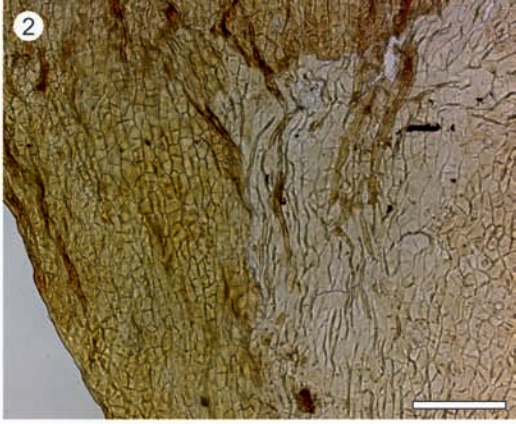

①
②
③


4

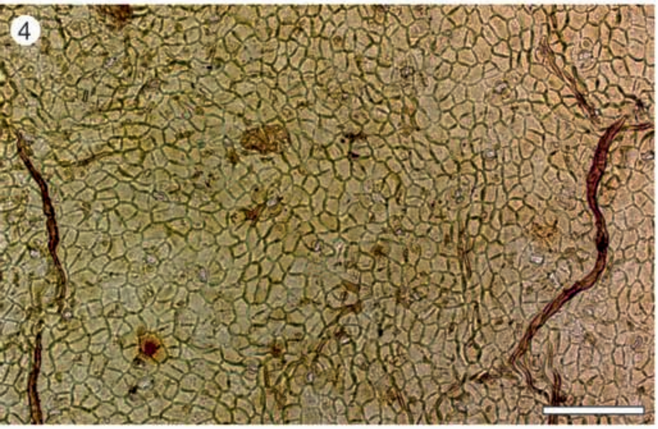

5

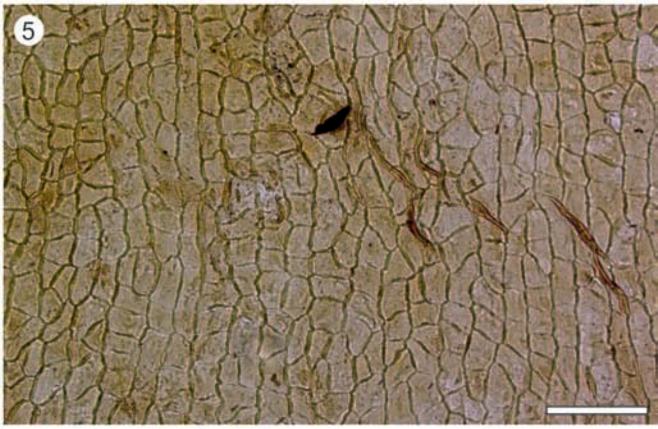

6

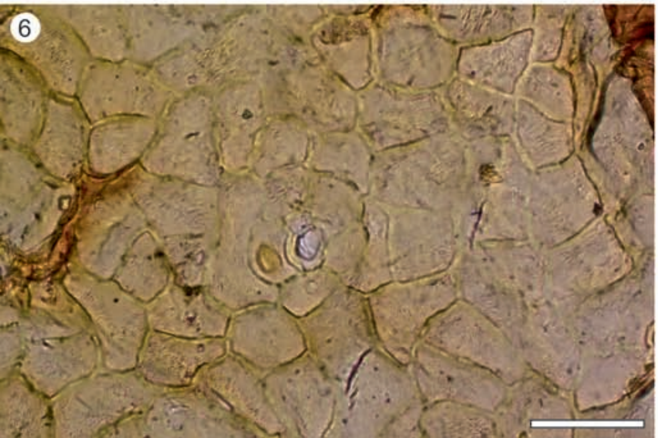

①

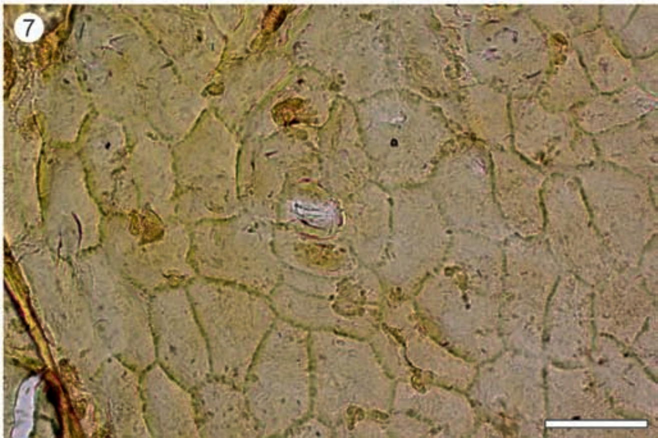

2

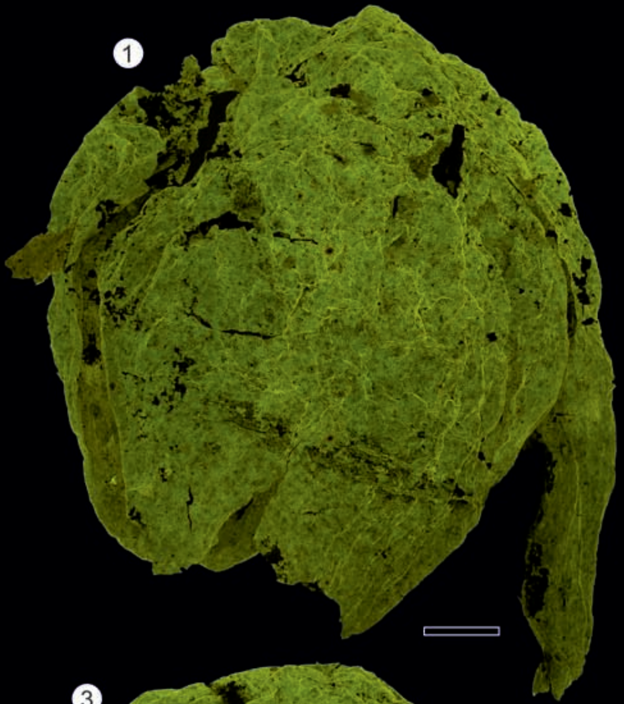

3


4

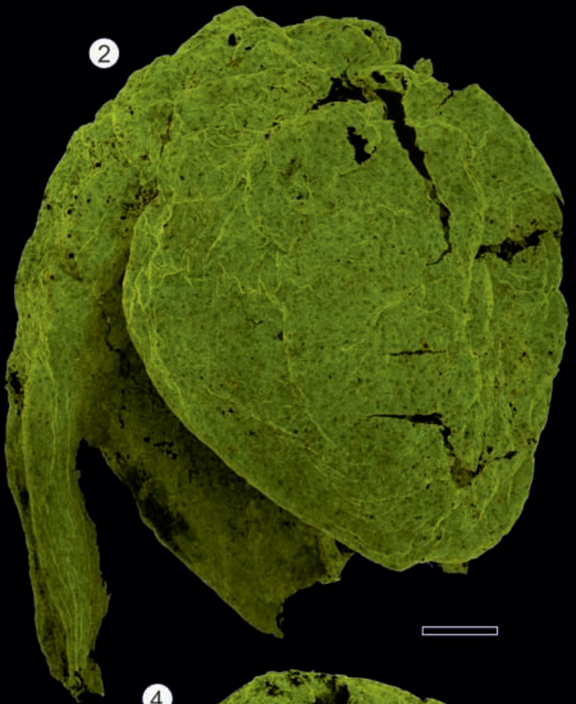

5


6

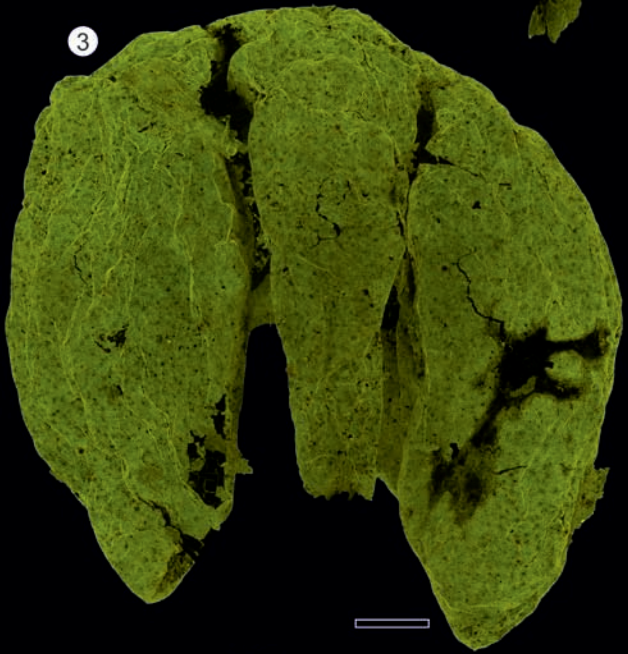

7



①

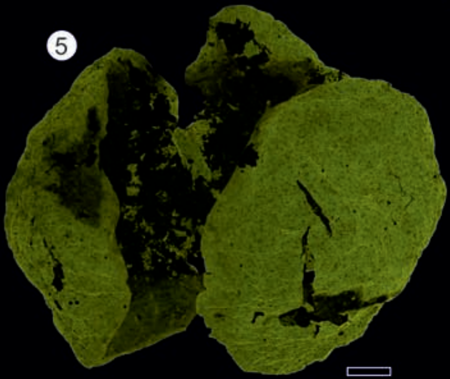


②

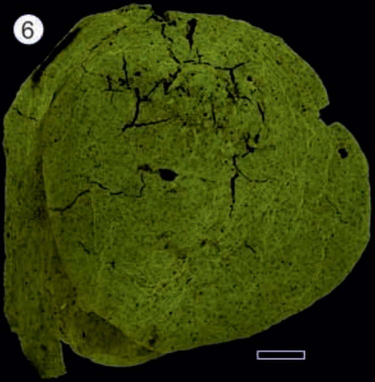


③

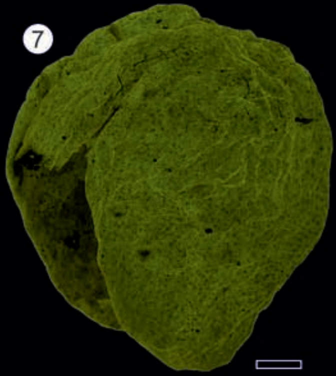
④



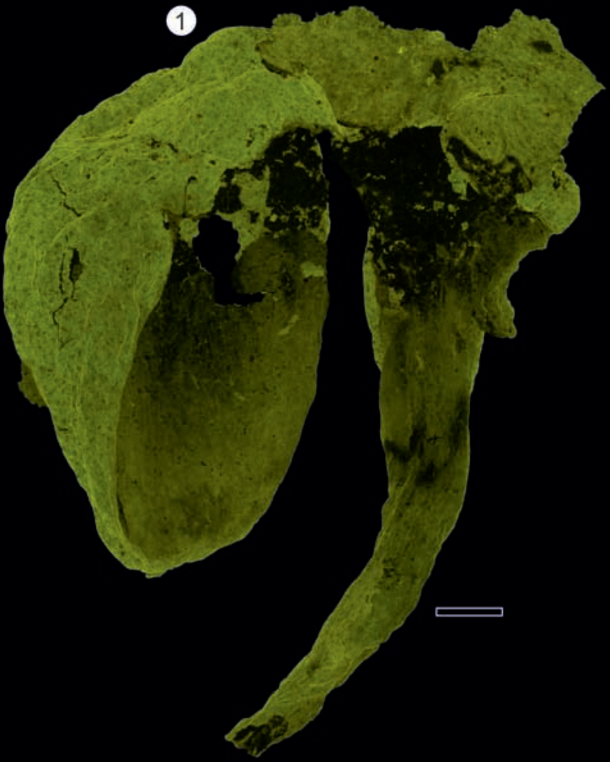
⑤

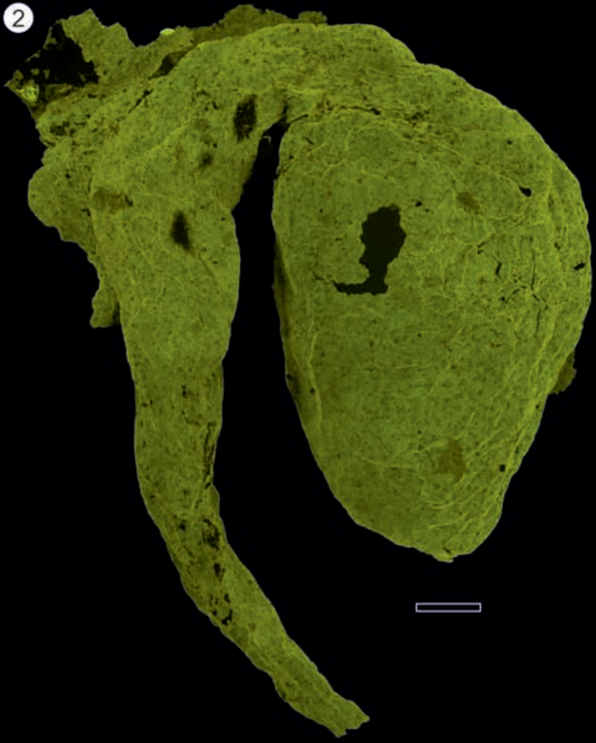


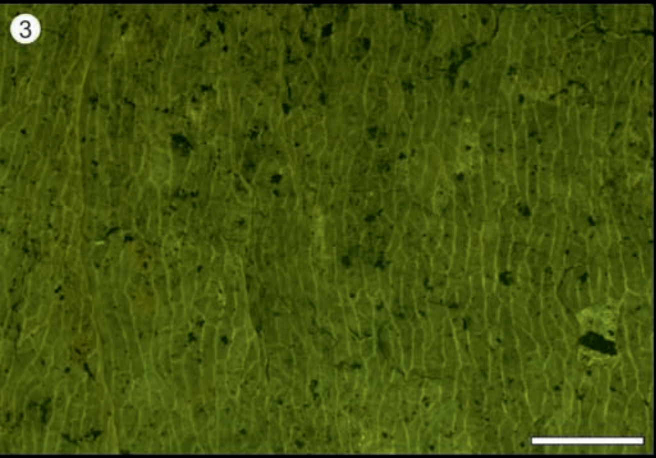
⑥

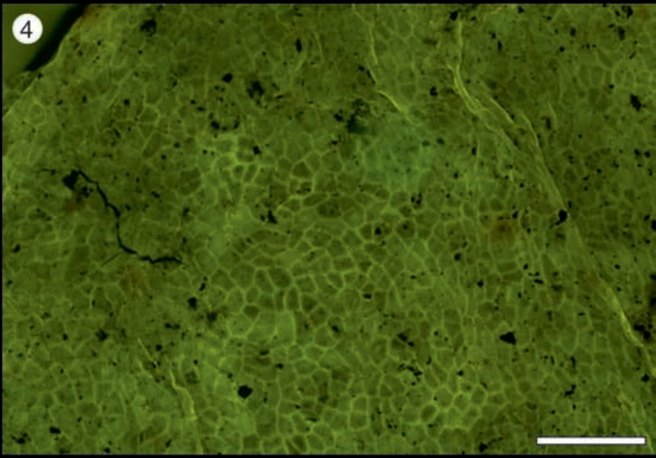


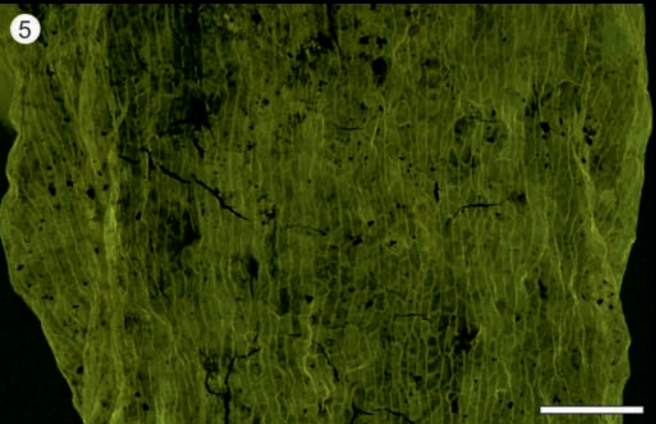
⑦

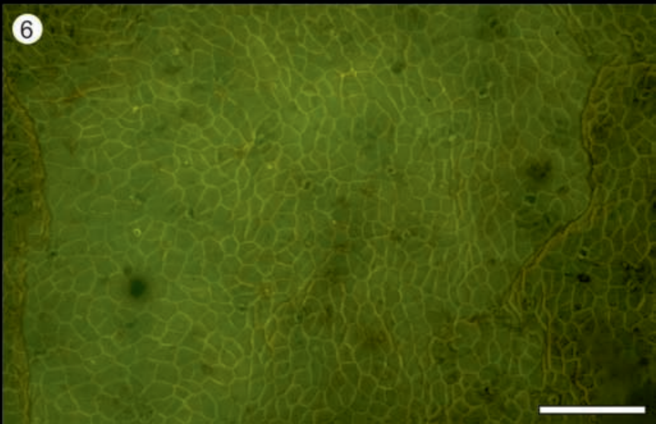

1

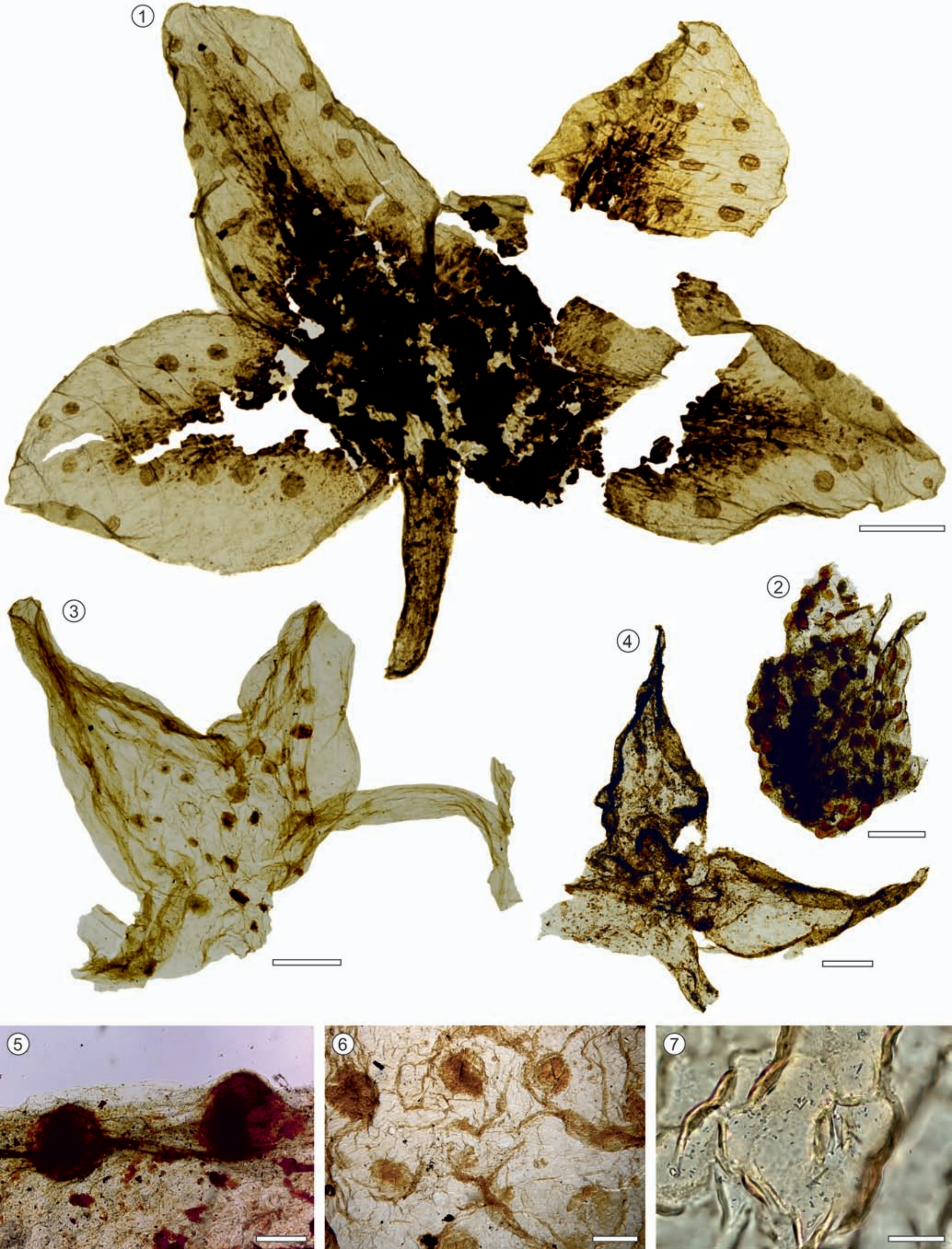

2

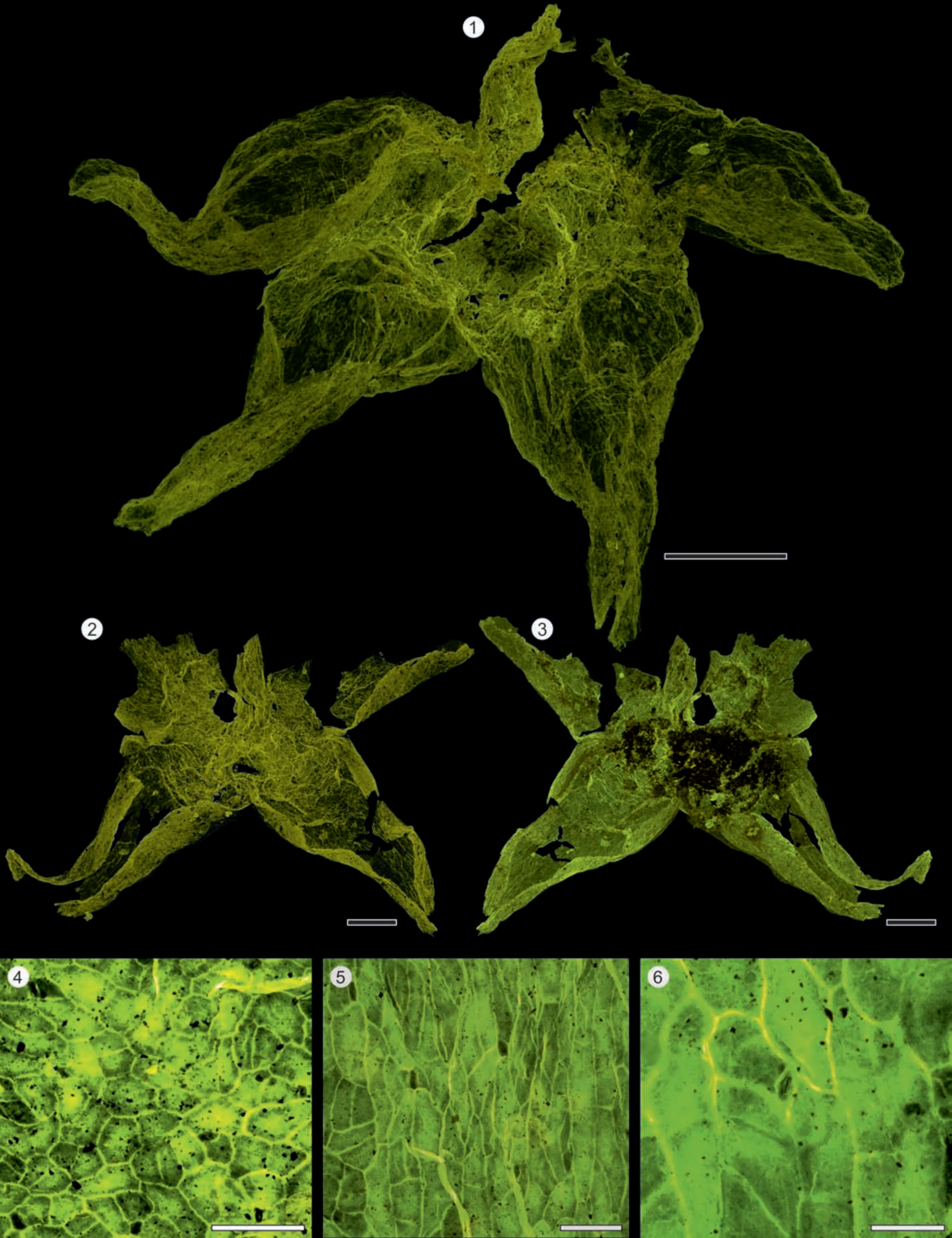

3

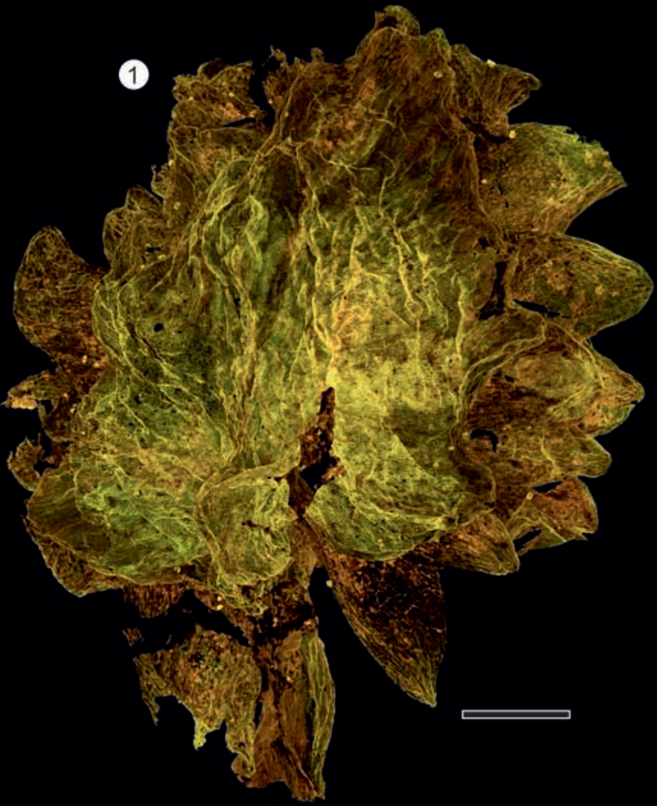

4

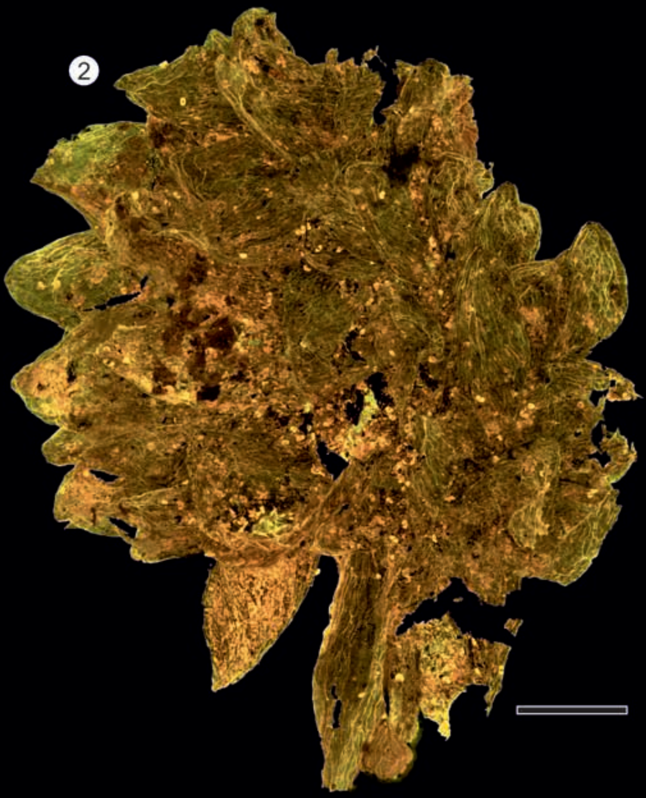

5

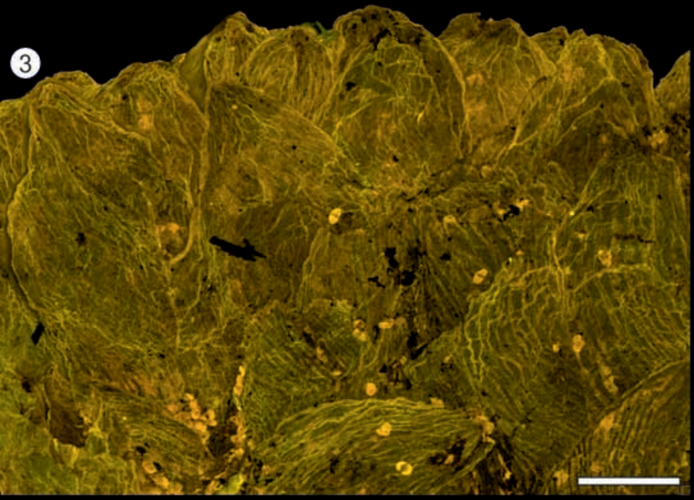

6

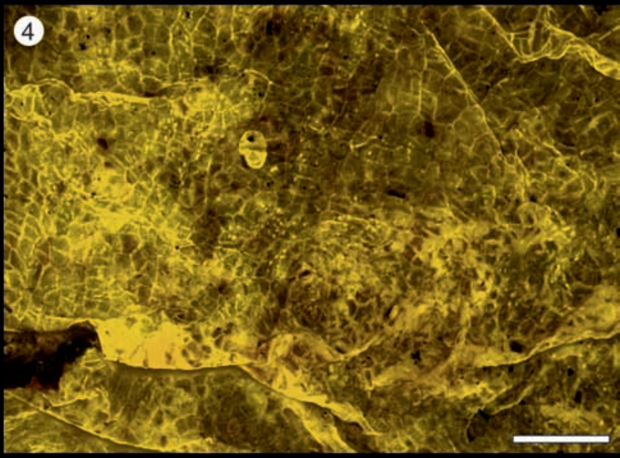

①
②
③
④
⑤
⑥
⑦

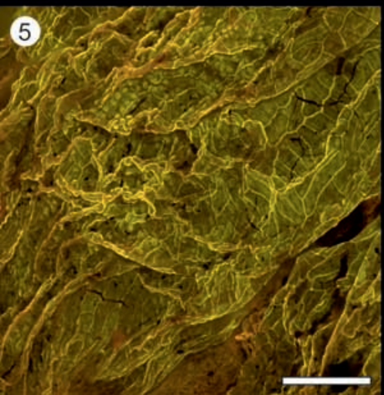

①
②
③
④
⑤
⑥

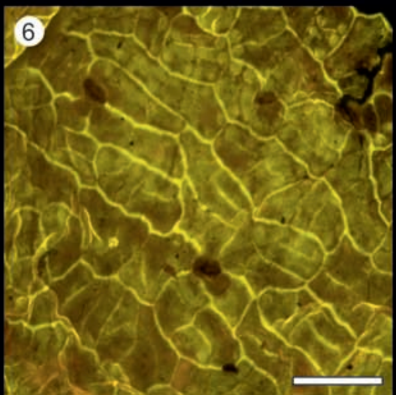

①

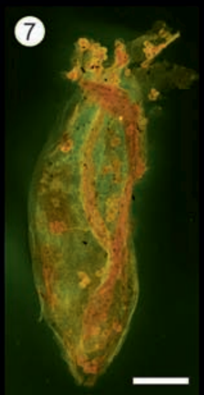

②

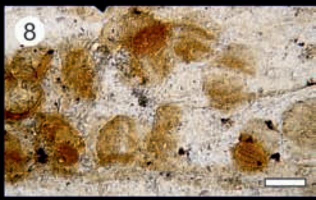

③


④


⑤


⑥


⑦


⑧


⑨

Field number		Foliage type							Fertile organs		
		Dicroidium lineatum	*D. odontopteroides*	*D. dubium*	*D. zuberi*	*D.* sp. A	*D.* sp. B	*D.* sp. C	*Umkomasia sp. cf. U. quadripartita*	*Fanerotheca* sp. cf. *F. waldeckiformis*	*Pteruchus africanus*
LC-21 (Pit U26)	Upper Series						+				
U26 Highwall (Pit U26)	Upper Series	**+++**	+	+	?					+	
LC-14 (Pit U26)	Upper Series	**+++**	+			+					
LC-13 (Pit U26)	Upper Series	++	**+++**					+		+-	+
LC-12 (Pit U26)	Upper Series	++	++								+
LC-11 (Pit U26)	Upper Series	**+++**	+							+-	
LC-9 (Pit U26)	Upper Series	+	+	++							
LC-6 (Pit U26)	Upper Series	+		++							
LC-5/6 (Pit U26)	Upper Series	+	+	?							
LC-5 (Pit U26)	Upper Series	++	++	++		+			+	+-	
LC-4 (Pit U26)	Upper Series	++	+	++							
LC-2 (Pit U26)	Upper Series			**+++**							
LC-1 (Pit U26)	Upper Series			++	++						
Floor of Pit (Pit M13)	?Middle Series				+						
LC-17 (Pit L7)	Lower Series				++	?					?
LC-18 (Pit L7)	Lower Series				++	+	++				
LC-19 (Pit L7)	Lower Series						**+++**				
LC-20 (Pit L7)	Lower Series								+-		