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RESEARCH ARTICLE

Evidence of profuse bark shedding in *Dicroidium* seed ferns (Umkomasiales) from the Triassic of Antarctica

Philipp Hiller,[1] Michael Krings,[2,3] Hans Kerp,[1] Zhuo Feng[4,5] & Benjamin Bomfleur[1]

[1]Institute for Geology and Palaeontology, Palaeobotany Research Group, University of Münster, Münster, Germany; [2]Bavarian Natural History Collections—Bavarian State Collection for Palaeontology and Geology, Munich, Germany; [3]Department of Earth and Environmental Sciences, Palaeontology & Geobiology, Ludwig- Maximilians-Universität München, Munich, Germany; [4]Institute of Palaeontology, Yunnan Key Laboratory of Earth System Science, Yunnan University, Kunming, China; [5]Southwest United Graduate School, Kunming, China

Abstract

During the 11th German Antarctic North Victoria Land Expedition in 2015/16, exceptionally well-preserved permineralized *Kykloxylon* stems—the wood of the iconic *Dicroidium* plants of the Gondwanan Triassic—were collected from the Middle to Upper Triassic Helliwell Formation in north Victoria Land, Transantarctic Mountains, Antarctica. Some of these logs show large borings and cavities that are partly filled with multi-layered periderm. This periderm is identical in cell shape and dimensions to isolated flakes of tissue that are superabundant in bulk macerations of *Dicroidium*-bearing rock samples from different coeval locations in the Transantarctic Mountains. These flakes are interpreted as shed bark fragments of *Dicroidium*-bearing umkomasialean trees. Various hypotheses on the adaptive advantages of bark shedding are discussed, including the reduction of epiphyte load. Palynological data document an abundance of potentially epiphytic cryptogams (spikemosses and bryophytes) in the environments in which the *Dicroidium* trees grew, and modern ecosystems with a climate comparable to that of the Late Triassic in Antarctica are in many cases also characterized by a lush epiphyte vegetation. Another advantage could lie in the reduction of infections by phytopathogenic microorganisms, as abundant fungal remains in both the wound periderm and the dispersed periderm flakes indicate.

Keywords
Epiphytes; fossil wood; palaeoecology; periderm; Transantarctic Mountains; Gondwana

Correspondence
Philipp Hiller, Institute for Geology and Palaeontology, Palaeobotany Research Group, University of Münster, Heisenbergstraße 2, D-48149 Münster, Germany. E-mail: philipp.hiller@uni-muenster.de

Abbreviations
GANOVEX: German Antarctic North Victoria Land Expedition

Introduction

Named after their characteristic bipartite fronds, *Dicroidium* seed ferns (Umkomasiales, also referred to as Corystospermales) are the most iconic plant group of the Triassic vegetation in southern Gondwana. They are reconstructed as tall trees (Petriella 1977; Meyer-Berthaud et al. 1992; Bomfleur, Decombeix et al. 2014), which formed the dominant canopy taxa in the warm, humid Triassic polar forest biome (Taylor & Taylor 1990; Escapa et al. 2011; Cantrill & Poole 2012). Abundant impression/compression fossils of numerous *Dicroidium* foliage taxa have been described from localities throughout Gondwana (Anderson et al. 2020), including many assemblages that have yielded detailed information on cuticle micromorphology and epidermal anatomy (Gothan 1912; Thomas 1933; Townrow 1957; Archangelsky 1968; Anderson & Anderson 1983; Blomenkemper et al. 2018; Drovandi et al. 2022; Unverfärth et al. 2022). Particularly rich and diverse *Dicroidium* assemblages, some in cuticle preservation, come from sites in the Transantarctic Mountains (Boucher et al. 1993; Bomfleur & Kerp 2010; Escapa et al. 2011). Moreover, several permineralized peat deposits in Antarctica have yielded structurally preserved umkomasialean fossils, including *Dicroidium* leaves (Pigg 1990), *Pteruchus* pollen organs (Yao et al. 1995), the characteristic *Umkomasia* ovuliferous organs (Klavins et al. 2002) and abundant roots and wood of the *Kykloxylon* type (Meyer-Berthaud et al. 1993; Decombeix et al. 2014), as well as examples of associations of *Dicroidium* plants with different types of microorganisms (e.g., Harper et al. 2020). The fossil assemblages from Antarctica are today widely regarded as a unique source of new information about the systematic classification, biology and ecology of the Umkomasiales of the Gondwana Triassic. Ongoing palaeontological exploration of the Transantarctic Mountains continues to unearth new fossils and fossil sites that further deepen our understanding of these plants and the Triassic polar forest biome in which they thrived.

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In addition to fronds and reproductive organs, permineralized stems can also be of great importance when ecological features of fossil plants are examined. Woody stems not only yield information on the growth habit and growth rate but may also contain evidence of associations with arthropods and microorganisms (e.g., Feng et al. 2017). The widespread gymnosperm wood type *Kykloxylon* was first described from Fremouw Peak in the central Transantarctic Mountains and was demonstrated to belong to the same plant as *Dicroidium* foliage (Meyer-Berthaud et al. 1993). *Kykloxylon* wood is pycnoxylic and characterized by a small pith, a variably lobed secondary xylem cylinder and paired vascular traces extending into the lateral organs (Decombeix et al. 2014). Although many well-preserved *Kykloxylon* axes from different localities in the Transantarctic Mountains are known (Meyer-Berthaud et al. 1993; Decombeix et al. 2014; Oh et al. 2016), a detailed description of its extraxylary tissues, including periderm structure and production, is lacking. Periderm plays an important role in protecting inner plant tissues and also appears as wound tissue in many seed plants (Serra et al. 2022; Lalica & Tomescu 2024). Fossil periderm, which is quite rare compared with the high abundance of fossil wood, is therefore an excellent source of information about the ecology of fossil plants.

Here, we present permineralized *Kykloxylon* stems from several Upper Triassic deposits in the Helliwell Hills (north Victoria Land) of East Antarctica. Some of the specimens represent fluted trunk bases, which exhibit irregular cavities and putative arthropod borings that are all lined with a massive, multi-layered periderm. The periderm is very similar, if not identical with regard to cell shapes, dimensions and arrangement, to isolated flakes of tissue that frequently occur in bulk-maceration residues of *Dicroidium*-rich rocks from elsewhere in the Transantarctic Mountains. This discovery suggests that profuse bark shedding in *Dicroidium* trees may have been an adaptation to certain conditions of the habitat.

Material and methods

More than 200 specimens of permineralized wood and silicified peat were collected from the type section of the Middle to Upper Triassic Helliwell Formation in the Helliwell Hills (71°44′2″S, 161°21′36″E; Bomfleur et al. 2021; Fig. 1), Rennick Glacier area, north Victoria Land, Antarctica, during GANOVEX XI, in 2015/16.

The Helliwell Formation is a sedimentary succession consisting mainly of dark grey to blackish carbonaceous mudstones, locally with thin coal seams and with intercalations of greenish ripple-laminated volcanoclastic silt- and fine-grained sandstone. Two cliff-forming intercalations of fine- to medium-grained volcanoclastic sandstone—55 m and 27 m thick, respectively—occur in the upper part of the formation (Bomfleur et al. 2021). Individual mudstone

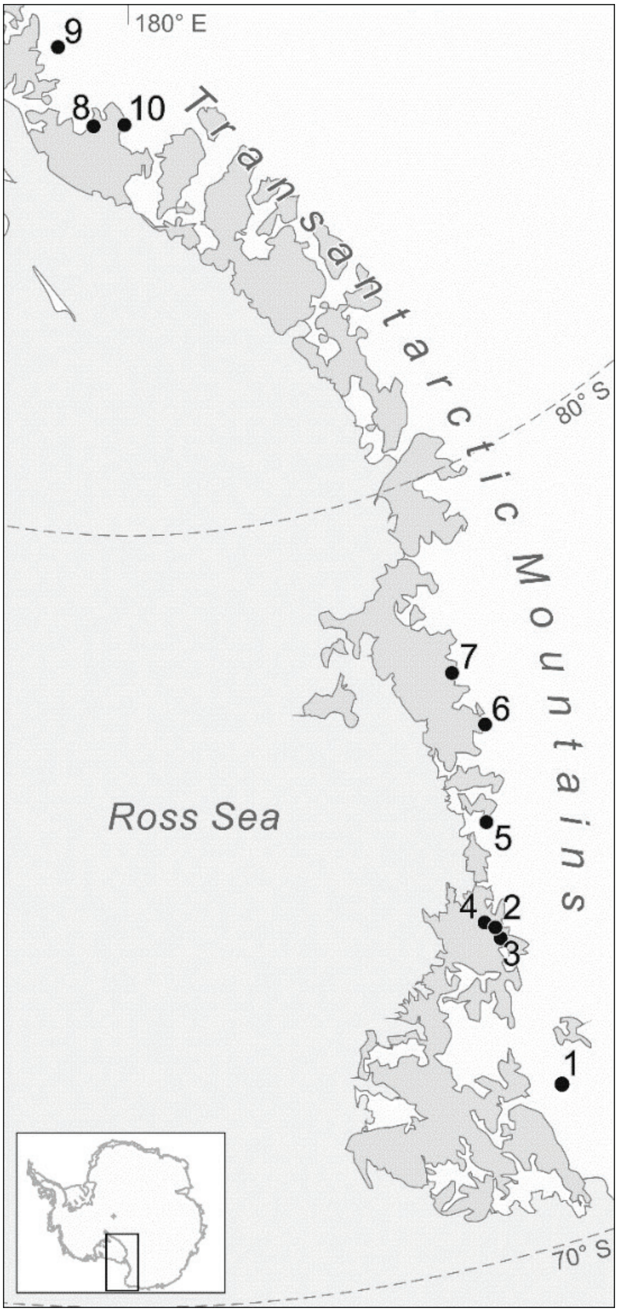

Fig. 1 Map of the Transantarctic Mountains, illustrating where *Kykloxylon* bark tissue has been found. Literature data is referring to occurrences *of Litothallus ganovex*. Locations in northern Victoria Land: (1) Helliwell Hills (this study), (2) Timber Peak, (3) “Timber Peak West,” (4) “southeast of Timber Peak” (this study and Bomfleur et al. 2009). Locations in southern Victoria Land: (5) Ricker Hills area, near Benson Knob (this study), (6) Allan Hills, (7) Shapeless Mountain (Escapa et al. 2011). Locations in the Central Transantarctic Mountains: (8) “Alfies Elbow” (Bomfleur et al. 2009), (9) Mt. Wisting (10) Misery Peak (Escapa et al. 2011). Base map from https://lima.usgs.gov.

beds in the formation also contain occasional leaf adpression fossils of lycopsids, sphenophytes, several different seed ferns and conifers (Bomfleur et al. 2021), in addition to putative conchostracan valves (BB, pers. obs.) and a single archosaur footprint (Mörs et al. 2019).

The depositional environment has been interpreted as a fluviolacustrine setting transitional between a meandering-stream system with extensive floodplains and a sand-dominated braided stream system. In agreement with previous studies of other Antarctic sites (Collinson 1997; Cúneo et al. 2003), the abundance of plant fossils, peat and coal are used to suggest humid and highly favourable climatic conditions during the Middle and Late Triassic (Bomfleur et al. 2021).

Thin sections of a permineralized stem (specimen number GXI-HCSE-089) and silicified peat (specimen numbers GXI-HCNW-block01 and GXI-HCNW-block02) were made following the method outlined by Hass & Rowe (1999). For comparison, we analysed bulk-macerate residues of *Dicroidium*-bearing rock samples from three sites in the Upper Triassic lower Section Peak Formation, namely Timber Peak (74°11′0″S, 162°23′–0″E; Norris 1965; Bomfleur & Kerp 2010), an unnamed nunatak west of Timber Peak (74°8′23″S, 162°12′48″E) and the escarpment of the Polar Plateau halfway between Timber Peak and Eskimo Point (74°13′16″S, 162°28′13″E). An additional specimen comes from as-yet unnamed Middle or Upper Triassic deposits near Benson Knob, southern Prince Albert Mountains (75°44′50″S, 159°17′53″E; Fig. 1). The samples were collected during the GANOVEX IX (2005/06), GANOVEX XI (2015/16) and GANOVEX XIII (2018/19) expeditions.

Bulk maceration for dispersed cuticles followed the standard procedures described by Kerp & Krings (1999) and Bomfleur & Kerp (2010). Specimens were photographed using a Canon EOS 5D mark IV digital camera. Slides and thin sections were analysed and photographed using a Leica MZ16 stereo microscope equipped with a Leica DFC 450 digital camera. Minor photographic adjustments were made using Corel Photo Paint 2021 and Affinity Photo. All specimens, offcuts, thin sections and microscope slides are stored in the collection of the Palaeobotany Group, Institute for Geology and Palaeontology, University of Münster in Münster, Germany, under accession numbers GIX-TI13/5-063a–g, 064, 071a(001–010), 073–084, GXI-HCSE-001–088, GXI-HCSE-089-ts01–20, GXI-HCNW-block01-ts01, GXI-HCNW-block02-ts01–04, GXIII-TiW-001-S1–4, GXIII-RHBN-001-s1–2, GXIII-RHBN-002-s1 and GXIII-SETI-13-s1.

Results

The vast majority of permineralized wood and smaller woody axes from the Helliwell Formation are assigned to the fossil genus *Kykloxylon* based on the presence of a very small pith (less than 5 mm in diameter), a massive, pycnoxylic and variably lobed secondary xylem cylinder and characteristically paired vascular traces extending into the lateral organs (Decombeix et al. 2014). Several specimens give evidence of arthropod activities in the form of borings, and other physical damage of unknown origin and show signs of fungal-induced decay (Stubblefield & Taylor 1986), all of which are often visible even before preparation (Fig. 2a, b). Thin sections of specimen GXI-HCSE-089, which is particularly well-preserved and therefore informative, indicate that large parts of the stem core have eroded and hollowed out (Fig. 2c). The centre of the resulting cavity is densely packed with clumps of xylem fragments, each 100–200 µm in diameter (Fig. 2d), and abundant ovoidal coprolites (Fig. 2e), which are about 60–80 µm long and 40–50 µm wide. In the periphery of the cavity there is a layer of periderm (up to 2.5 mm thick) that lines the cavity inwards along the boundary to the intact wood (Fig. 2c–e). In transverse view, this periderm appears as a tissue comprising densely packed rectangular (sometimes almost isodiametric, but more often about half as wide as long) cells approximately 25 µm wide and 25–50 µm long. Cell contents or remnants thereof are not normally preserved, except for a few cases in which cells contain an inclusion of amorphous, black or brown matter. Layers of cells that are very similar in size and shape to the cavity periderm have also been found surrounding several *Kykloxylon* axes preserved in silicified peat (Fig. 2f). These layers are interpreted as representing the stem's regular periderm formation around the xylem during stem dilatation.

Inside the cavity of stem specimen GXI-HCSE-089, pieces of the periderm also occur in the form of detached flakes preserved in varying orientations (Fig. 3a). In the paradermal view, the periderm flakes reveal that they consist of continuous sheets of polygonal (usually four-, six- or eight-sided) cells, which are almost isodiametric (ca. 50 µm in diameter) to approximately two times longer than wide (Fig. 3c). Lateral views of the flakes show that the flakes may consist of one to several layers of these cells. Most of the cells are empty and translucent, but some contain an inclusion of dark, homogeneous material. In some areas, the periderm cell sheets contain masses of fungal hyphae up to 2.5 µm in diameter (Fig. 3f).

Dispersed tissue fragments displaying a cell pattern coinciding with that of the flakes described above are very abundant in the organic residues of bulk-macerated *Dicroidium*-bearing rocks from four different locations in the Transantarctic Mountains. These dispersed remains are easily fragmented and therefore typically small (about 1 mm maximum; Fig. 3b). Like the in situ flakes of

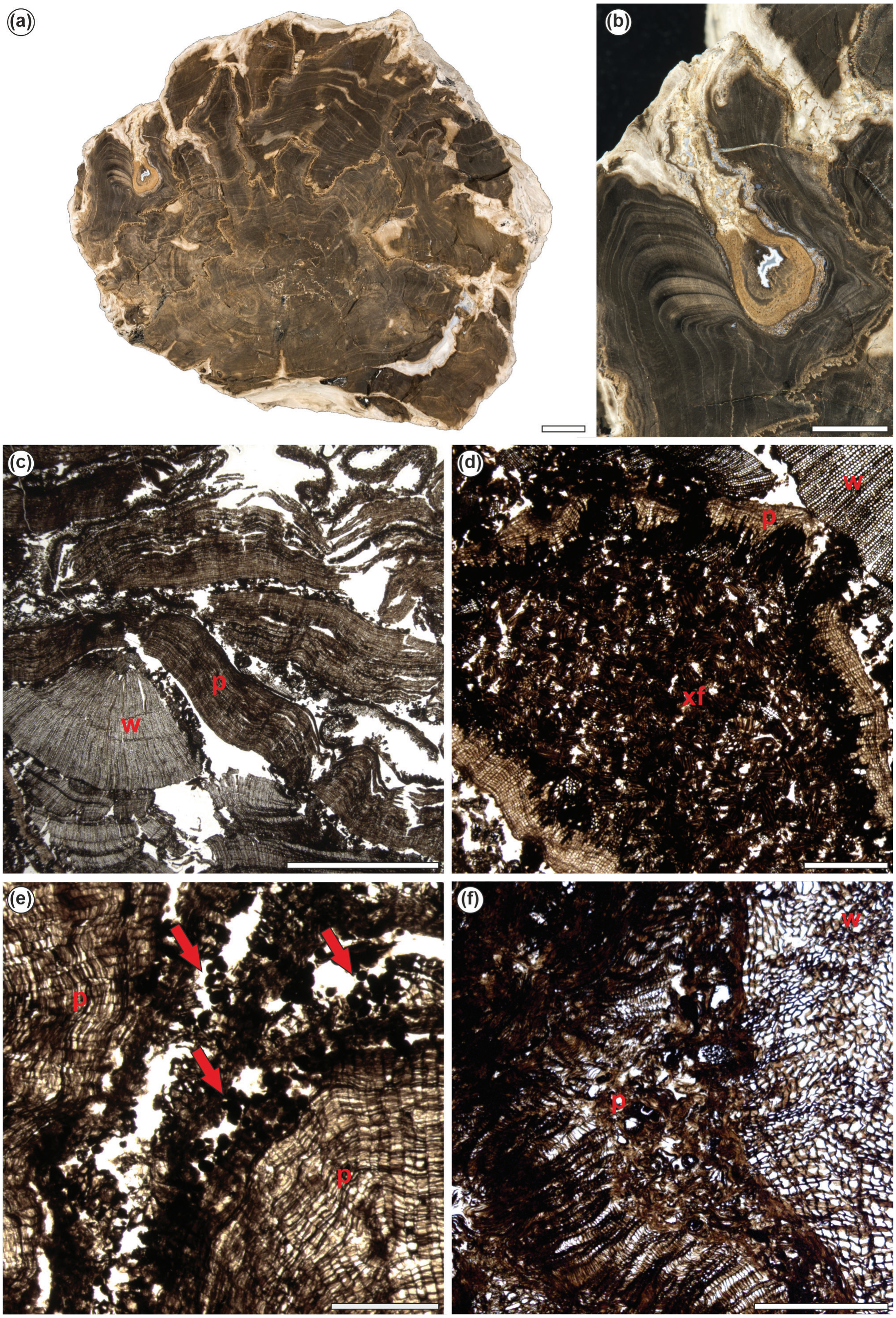

Fig. 2 Permineralized *Kykloxylon* stems from the Upper Triassic of Antarctica. (a) a *Kykloxylon* stem from Helliwell Hills (specimen GXI-HCSE-076), showing a fluted trunk structure. (b) Detail of (a), showing sinuous bark inside of a wounding structure. (c) Cross-section of a *Kykloxylon* stem (thin section GXI-HCSE-089-ts03) showing a cavity filled with xylem (w) and periderm (p) tissue. (d) Cross-section of a *Kykloxylon* stem (thin section GXI-HCSE-089-ts04) showing cavity inside of wood (w) lined with periderm (p) and filled with xylem fragments (xf). (e) Cross-section of a *Kykloxylon* stem (thin section GXI-HCSE-089-ts04) showing coprolites (arrows) between thick periderm layers (p). (f) Tissue detail of a *Kykloxylon* axis from silicified peat (thin section GXI-HCNW-block02-ts01), showing the secondary xylem (w) surrounded by periderm (p). Scale bars: (a) 1 cm; (b), (c) 5 mm; (d) 1 mm; (e), (f) 500 µm.

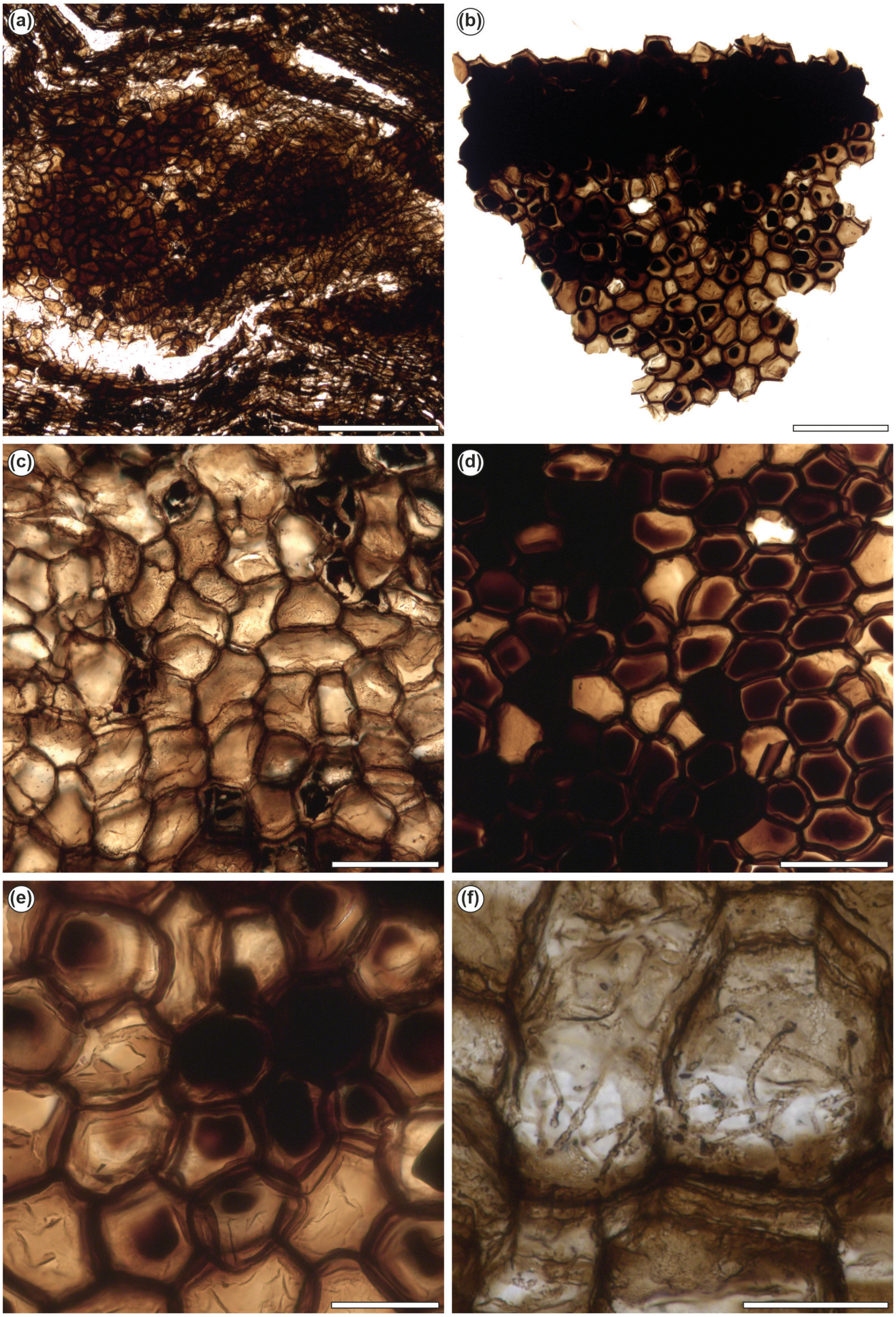

Fig. 3 Periderm tissues from the Upper Triassic of Antarctica. (a) Detached flake of periderm inside of a cavity in a *Kykloxylon* stem (thin section GXI-HCSE-089-ts01) in paradermal view. (b) Isolated periderm flake from bulk maceration residues from Timber Peak, whose upper part slightly indicates the originally multi-layered character of these flakes, compared to Plate III of Bomfleur et al. 2009 (slide GIX-TI13/5-071a-03-sl1). (c) Detail of a detached flake of periderm inside of a cavity in a *Kykloxylon* stem (thin section GXI-HCSE-089-ts02) in paradermal view. (d) Flake of periderm from bulk maceration residue from Timber Peak (slide GIX-TI13/5-071a-01-sl1). (e) Cell detail of periderm flake from bulk maceration residue from Timber Peak (slide GIX-TI13/5-071a-03-sl1). (f) Fungal hyphae in periderm cells (thin section GXI-HCSE-089-ts02). Scale bars: (a), (b) 500 µm; (c), (d) 100 µm; (e), (f) 50 µm.

Fig. 4 Trees heavily loaded with epiphytes in the Hoh Rainforest, Olympic Peninsula, Washington state, USA. (Photo by B. Bomfleur.)

periderm described above, they consist of one to several contiguous layers of polygonal, four-, five-, six- or eight-sided cells of ca. 15–60 µm in diameter (Fig. 3d, e). Cells are empty or have opaque black fillings; some may also contain remains of collapsed cell walls and fungal hyphae.

Discussion

Permineralized *Kykloxylon* stems, as well as smaller *Kykloxylon* axes preserved in silicified peat, from the Helliwell Hills provide evidence of the presence of a prominent periderm, which is exquisitely preserved, allowing a detailed description of its structure and composition. Furthermore, flakes of detached periderm are part of the cavity infill in damaged *Kykloxylon* wood. The periderm that surrounds the woody axes from the silicified peat is interpreted as bark, whereas the detached flakes of periderm in the cavities are interpreted as belonging to wound tissue that formed in response to arthropod damage. These detached flakes are identical in every observable structural feature—for instance, cell size, shape and arrangement, as well as vertical organization in stacks of contiguous layers—to a particular type of dispersed mesofossil recovered from bulk-macerations. Dispersed fossils of this type of mesofossil have previously been described under the name *Litothallus ganovex* Bomfleur et al. (2009) and interpreted tentatively as remains of a non-mineralized freshwater macroalga similar to certain present-day species of the order Hildenbrandiales (Bomfleur et al. 2009; Bomfleur et al. 2010).

The *Kykloxylon* fossils with in situ periderm presented here demonstrate that the compression fossils and isolated sheets of cells described previously as *Litothallus ganovex* from multiple sites in the Transantarctic Mountains (Bomfleur et al. 2009; Bomfleur et al. 2010; Escapa et al. 2011; Fig. 1), are actually fragments of shed bark of *Kykloxylon* trees, rather than the remains of some thalloid organism. The fact that these tissue fragments appear in abundance in assemblages rich in *Dicroidium* leaf litter adds support to this conclusion, as *Dicroidium* is the foliage attributed to *Kykloxylon* wood, and the *Dicroidium* plant has been interpreted as a deciduous tree (Meyer-Berthaud et al. 1993; Taylor 1996; Cúneo et al. 2003). Our data is evidence that the *Dicroidium* trees of the Antarctic Middle and Late Triassic were characterized by profuse bark shedding.

Present-day plants profusely shed bark (exfoliation) for different reasons. For example, trees like *Platanus* shed their bark continuously in the process of stem growth and also during drought-induced stem shrinkage (Kozlowski & Pallardy 1997). Moreover, bark shedding may promote stem photosynthesis, which particularly occurs in younger stems and twigs (Pfanz & Aschan 2001) and may indicate that the plant can reproduce with the aid of fire, as is known in many species of the bark-shedding tree *Eucalyptus*. *Eucalyptus* is well-adapted to wildfires and is able to reproduce after fire damage because of branching of epicormic shoots produced in the vascular cambium (Burrows 2002). Some of the plant remains in silicified peat from the Helliwell Hills appear opaque black and exhibit a pattern of fracturing that is typical for charcoal, possibly indicating wildfire activity. However, the sure identification of these remains as charcoal would require further chemical or petrological analyses. In addition, Decombeix et al. (2018) described epicormic shoots from the Triassic of the Beardmore Glacier area, Antarctica; however, they did not find evidence that the production of these shoots was related to wildfires. Furthermore, the climatic reconstruction for the depositional environment of the Middle to Upper Triassic Helliwell Formation—a humid, peat-forming environment—renders the regular occurrence of wildfires rather unlikely.

Yet another function of bark exfoliation is to get rid of climbers and epiphytes, which may reduce the fitness, growth, fertility and general survival rate of the trees (Putz 1984; Stevens 1987; Givnish 1992, 1995; Ladwig & Meiners 2009; van der Heijden & Phillips 2008; Ingwell et al. 2010; Milks et al. 2017; Cabal et al. 2020). Epiphytes and climbing plants are potential competitors for nutrients and water (Milks et al. 2017) and may mechanically damage the host stem (Schimper 1888; Lutz 1943; Putz 1984). In extant trees, bark exfoliation is regarded as one of several strategies to reduce epiphyte load (Sfair et al. 2016). Humid climates are known to be conducive to the growth of epiphytic plants (Oliver 1930; Benzing 1990). A prominent example is the temperate Hoh Rainforest in the state of Washington, north-western USA (Fig. 4). A comparably humid and temperate climate has been suggested for the Late Triassic of Antarctica (Collinson 1997; Cúneo et al. 2003).

There is no direct macrofossil evidence as yet for epiphytes associated with *Kykloxylon* from the Upper Triassic of Antarctica. However, palynomorph assemblages from Timber Peak (Bomfleur, Schöner et al. 2014) contain abundant *Uvaesporites* and *Neoraistrickia* spores, with *U. verrucosus* alone accounting for 15.2% of the spore assemblage (BB, pers. obs.); these spores were produced by spikemosses (Looy et al. 2005). The Timber Peak data also show a diversity of bryophytes (Bomfleur, Schöner et al. 2014). These two groups of plants form a major component of epiphyte communities in temperate rainforests today (Zotz 2005). The absence of spikemosses and the scarcity of bryophytes in the Upper Triassic macrofossil record of the Transantarctic Mountains—despite their predominance in the palynological record—can be generally explained by the lower fossilization potential of these delicate plants (see Bomfleur, Klymiuk et al. 2014; Tomescu et al. 2018) but may also reflect epiphytic growth as an important factor reducing preservation potential (see Pšenička & Opluštil 2013).

Finally, bark shedding could also have reduced or even prevented infections by phytopathogenic microorganisms. The *Kykloxylon* periderm seems to have been quite easily accessible to fungi, as fungal remains, such as hyphae and conidia, are found in abundance not only in the cells of both the wound tissue of the large logs (Fig. 3f) and the in situ bark preserved in silicified peat, but also in the isolated periderm flakes obtained through bulk-maceration. It is therefore conceivable that fungi and other harmful microorganisms were continuously removed from the outer surfaces and peripheral tissue layers of stems and branches by frequent shedding of the bark. On the other hand, the fact that the bark is commonly colonized by fungi indicates that profuse bark shedding by *Dicroidium* trees could also have played an important ecological role in the forest ecosystems in which these trees grew. In this scenario, the shed bark and the abundant abscised *Dicroidium* leaves would have formed litter layers that were decomposed by fungi and could, therefore, have been important contributors to soil formation.

Conclusions

Kykloxylon fossils from the Helliwell Hills in the Transantarctic Mountains contribute to our understanding of umkomasialean tree ecology. Considerable amounts of periderm that formed in cavities interpreted as injuries are indicative of the ability of these trees to seal and heal damages inflicted by arthropods or by other physical and biological forces. Moreover, the *Kykloxylon* in situ periderm is very similar to dispersed flakes of tissue found alongside *Dicroidium* foliage cuticles in bulk macerations from different Upper Triassic locations in the Transantarctic Mountains. The flakes are therefore interpreted as exfoliated bark of the *Dicroidium* trees.

The innumerable periderm flakes in all samples strongly suggest that *Dicroidium* plants produced, and eventually shed, large amounts of bark during their lifetime. One possible function of this process could be to lessen the epiphyte load, as epiphytic plants were probably quite common in the Late Triassic temperate rainforest-like ecosystem. Another possible explanation is defence against phytopathogenic microorganisms. Decomposition of the bark by fungi may have contributed to soil formation.

We anticipate that continued investigation of permineralized plant fossils from Antarctica will give additional insights into the very special ecology of the *Dicroidium*-dominated high latitude Antarctic forest ecosystems of the Triassic.

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Disclosure statement

The authors report no conflict of interest.

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