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Archaeopteris trees at high southern latitudes in the late Devonian

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ABSTRACT

During the Devonian Period plants first reached forest stature, impacting chemical weathering of rocks, fluvial systems, atmospheric composition and possibly aquatic eutrophication. Hypothetically these factors contributed to increasing climatic instability culminating in the End Devonian Mass Extinction Event. Understanding the timing of the spread of forests is however a prerequisite to correlation with its proposed consequences. Though evidence for forests at low palaeolatitudes demonstrates their emergence by the mid Devonian, sparse high-palaeolatitude records almost entirely comprise herbaceous lycopods. By the Famennian forest ecosystems are widely evidenced at low palaeolatitudes, however high latitude palaeofloras are almost exclusively represented by a single locality, the Waterloo Farm lagerstätte from South Africa (approximate palaeolatitude, 70°S). Understanding climatic and ecological conditions at this locality is doubly important as it also hosts diverse vertebrate taxa, including the only high latitude Devonian tetrapods. *Archaeopteris*, the quintessential Late Devonian woody tree, has previously been identified at this locality on the basis of leafy branch system fragments, though some uncertainty has remained as to whether these represent tree sized organisms. Here we present co-occurring large axes, including a trunk base, attributable to *Archaeopteris* trees inferred to be in excess of 20 m height, the first demonstration of forest stature at high latitudes in the Devonian. This possibly reflects high latitude climatic amelioration, resultant from warm ocean currents circulating southwards in response to progressive closure of the Iapetus Sea. As such, changing continental configurations may have indirectly facilitated the spread of forest ecosystems and helped to drive climatic instability and ultimately extinctions towards the end of the Devonian.

1. Introduction

The Devonian was a time of significant evolution of plant life, with the establishment of forest stature vegetation for the first time in Earth history. This development is believed to have had massive permanent repercussions; enhancing the chemical weathering of rocks, changing the nature of fluvial systems, affecting global atmospheric conditions, precipitating widespread eutrophication of water bodies, and hypothetically contributing to increasing climatic instability towards the end of the Period (eg. Algeo et al., 2001; Smart et al., 2023). These effects have been argued to have culminated in the End Devonian Mass Extinction Event (EDMEE) (Algeo et al., 1995, Algeo and Shen, 2024), one of the greatest Mass Extinctions to have affected life history (Sallan and Coates, 2010). Understanding the timing and extent of the spread of forest species is critical in attempts to correlate their spread with its theoretical repercussions. However, the record of plant fossils is heavily biased in favour of low latitudes. During the Middle Devonian, when the first cladoxylopsid, *Archaeopteris* and lycopod forests were being established in equatorial and low latitudes (Davies et al., 2024; Giesen and Berry, 2013; Stein et al., 2012, 2020; Berry and Marshall, 2015), the sparse fossil record from high latitudes is almost entirely comprised of herbaceous lycopsids recorded from Argentina (c. 70 degrees S) (Cingolani et al., 2002; di Pasquo et al., 2015), Brazil (Matsumura et al., 2015), and South Africa (~ 70–80 S (Torsvik and Cocks, 2013)) (Plumstead, 1977; Chaloner et al., 1980; Anderson and Anderson, 1985), though small bifurcating axes are also noted from South Africa (RG pers. comm.).

During the later parts of the Late Devonian, as *Archaeopteris* forests with woody trunks up to 30 m high may have become the dominant terrestrial vegetation in equatorial to warm temperate regions (Marshall, 1996), there are also records of forests made up of small lycopods with stigmarian root systems in equatorial latitudes of China (Wang et al., 2019). The only significant high latitude flora known at this time is from the late Famennian aged (Gess and Whitfield, 2020)

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Waterloo Farm locality in South Africa, where the latitude is believed to be approximately 70° S (Gess and Ahlberg, 2018), whilst some floral material has also been recovered from the nearby Coombs Hill locality (Harris et al., 2021a). At Waterloo Farm moderately sized (up to 85 mm diameter) monopodal lycopods with cormose rhizomorphs (Gess and Hiller, 1995; Prestianni and Gess, 2014), have previously been reported associated with *Archaeopteris* remains (Gess and Hiller, 1995). These latter comprised fragmentary 'fronds' with characteristic *Archaeopteris* leaves and a single fertile fragment (Gess and Hiller, 1995; Anderson et al., 1995). Most commonly, such leafy branch system fragments bear partially dissected webbed leaves diagnosed as *Archaeopteris notosaria* (Anderson et al., 1995). Rare remains of a second undescribed taxon with highly dissected unwebbed leaves have also been noted (Gess and Hiller, 1995). Leafy branch systems of *Archaeopteris notosaria* have subsequently also been recorded from the Coombs Hill locality within the Witpoort Formation of the Makhanda district (Harris et al., 2021b). Historical and near contemporary suggestions that *Archaeopteris* may have included small plants with fern-like habits (e.g. Chaloner, 1999), imply that the stature of Waterloo Farm *Archaeopteris* cannot be taken for granted. Indeed little is known of the way *Archaeopteris* would have lived at this palaeo-latitude, in terms of seasonality, deciduousness and physiology, partly because of the lack of anatomically preserved wood which might yield information in the form of growth rings (LeHir et al., 2011).

Ongoing excavations at Waterloo Farm, splitting of rock and collection of material exposed on site have subsequently revealed a tree stump, large woody axes and large near-complete *Archaeopteris* leafy branch systems. In this paper we briefly describe these large remains and demonstrate the presence of *Archaeopteris* trees at approximately 70° S palaeolatitude, probably in the Devonian south polar circle. This is an important step in the understanding of the environment at Waterloo Farm which hosts an important and diverse assemblage of fish and tetrapods as well as aquatic algae, invertebrates and terrestrial plants (Gess and Ahlberg, 2018, Gess and Whitfield, 2020 (and numerous refs therein), Miyashita et al., 2021, Scholze and Gess, 2021, Harris et al., 2021a, Gess and Prestianni, 2022, Gess and Ahlberg, 2023, Gess and Burrow, 2024). In addition it provides the first definite evidence that forest tree-sized species had populated high latitudes by the latest Devonian.

The diverse terrestrial flora of Waterloo Farm (Gess and Whitfield, 2020), ranging from trees (Anderson et al., 1995, herein) to shrubs (e.g. Gess and Prestianni, 2022) and herbs (e.g. Prestianni and Gess, 2018) demonstrates that despite its high latitude this part of Gondwana's coastline enjoyed a climate supportive of abundant flora.This possibly resulted from amelioration of water temperatures in response to changing continental configurations, as discussed below.

2. Materials and methods

All material was collected by RG from the Waterloo Farm lagerstätte, on the southern outskirts of Makhanda (formerly Grahamstown) in the Eastern Cape, South Africa, is accessioned into the collection of the Albany Museum in Makhanda (Grahamstown) and housed at the Albany Museum's Devonian Ecosystems Project building at 87 Beaufort Street. The Waterloo Farm lagerstätte comprises deposits from the upper portion of the Famennian aged Witpoort Formation (Witteberg Group, Cape Supergroup), exposed in a road cutting initiated in 1985. These include black mudstone horizons interpreted as estuarine in origin, including the MFL or Main Fish Lens (from which the majority of Waterloo Farm fossils have been recovered) and the plant-rich 'Blue Layer' as well as underlying channelised metasandstones and overlying sheet-like metasandstones. Channelised sandstones have been interpreted as back barrier tidal channels (Hiller and Taylor, 1992) however paucity of tidal indicators renders this interpretation equivocal and deposition on a coastal braidplain has been proposed as an alternate interpretation for similar facies in other sections (Harris and Gess, 2022). Sheetlike overlying sandstones have been interpreted as backbarrier tidal delta deposits (Hiller and Taylor, 1992). Red-stained horizons encountered within the upper portions of the MFL black shale (during excavations in the mid 90s) are congruent with regular alternate reddish bands regionally common within this facies. Preliminary geochemical analysis of a banded sequence at Coombs Hill suggests genesis related to cyclical salinity changes (Hoosen, 2019), possibly resultant from seasonal influx of glacial melt waters (Gess and Whitfield, 2020).

. Material herein described is recovered from all three portions of the Waterloo Farm section, with that in figure one recovered from a black-mud-chip containing horizon overlying the fossil-rich black mudstone layers and associated with *Leptophloem* axes, including one with an attached cormose root base. Material in Fig. 2a and b is recovered from lag deposits rich in reddish mud chips, which occur at intervals within the channelised sandstones underlying the black mudstone horizons. These latter deposits commonly contain (sometimes uprooted) *Leptophloem* axes and less commonly *Haplostigma* axes (Prestianni and Gess,

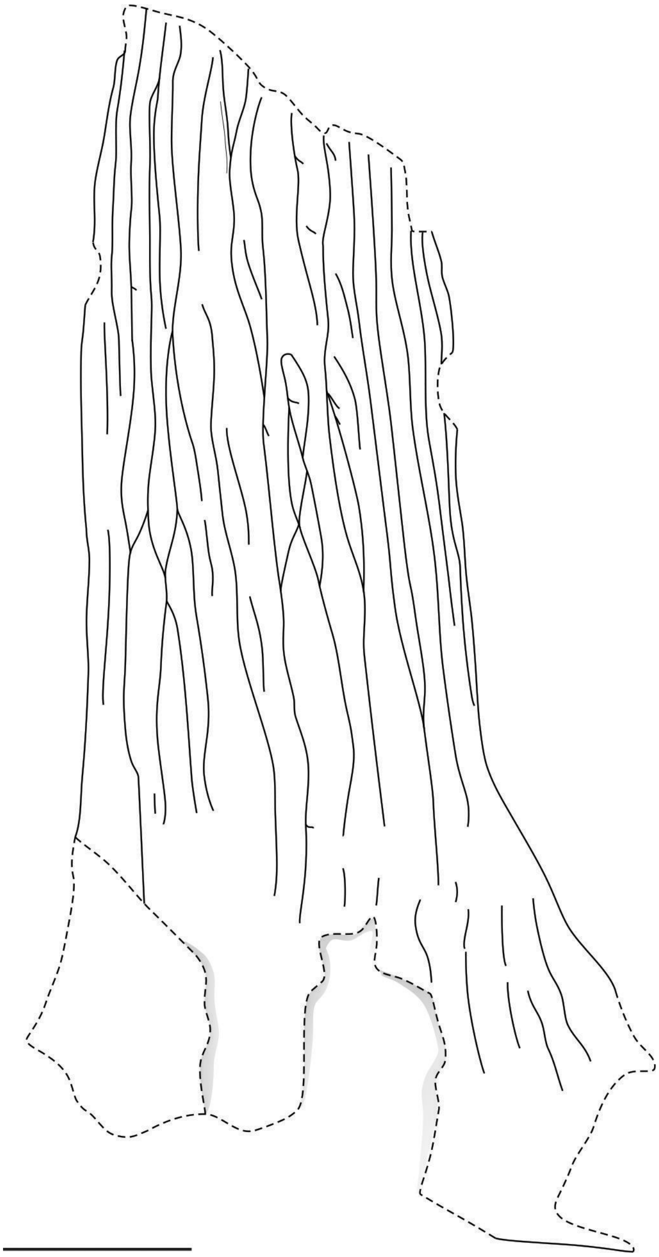

Fig. 2. Line drawing of the *Archaeopteris* stump (AM 18331) from Waterloo Farm – see Plate 1a. Scale bar = 10 cm.

2014). The axis in Fig. 2c and specimen in Fig. 3 were excavated from estuarine mudstones of the Blue Layer and MFL respectively.

The specimens in Plates 1 and 2c were photographed in a darkened room using a Nikon D800 camera and 60 mm macro lens using two LED array light sources with polarising filters and a circular polarising filter on the lens. Intensity and position of the light sources was controlled to emphasise surface features, as noted in the figure captions. Other specimens were photographed outdoors with natural light as mentioned

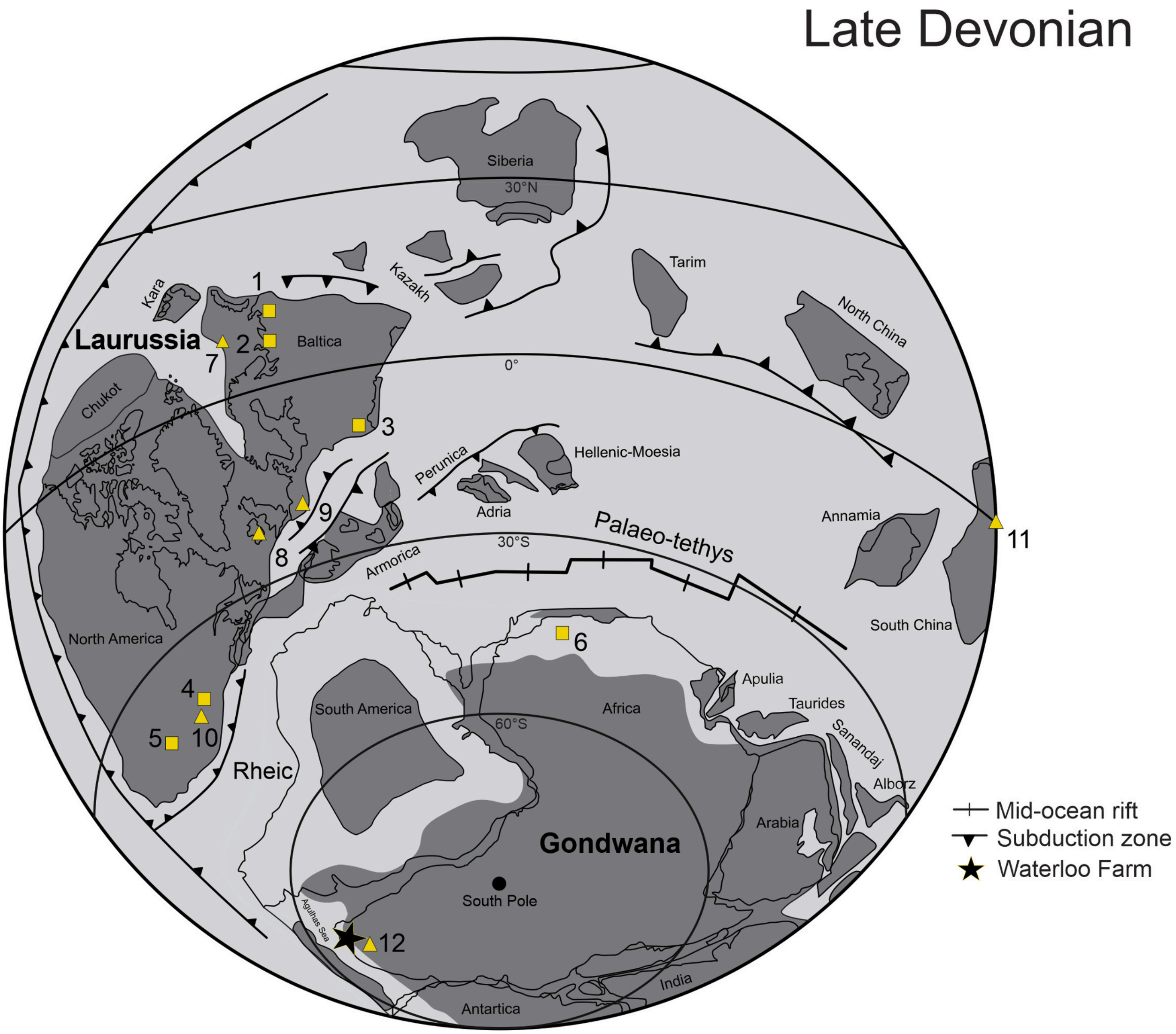

Fig. 3. Selected Famennian records of *Callixylon*, wood of *Archaeopteris*

1) Timone Mountains, Russia (Lemoigne et al., 1983)
2) Volonga River, Timan (Lyubarova and Snigirevsky, 2020)
3) Marioupoul, Ukraine (Lemoigne et al., 1983)
4) Numerous localities in Ohio, Indiana, West Virginia, New York, Kentucky, Tenessee (e.g. Chitaley and Cai, 2001)
5) Oklahoma (Trivett, 1993)
6) Morocco (Tanrattana et al., 2019)

Selected Famennian records of *Archaeopteris*

7) Bear Island (Schweitzer, 2006)
8) Ireland (e.g Veenma et al., 2023)
9) Belgium and Germany (e.g. Kenrick and Fairon-Demaret, 1991)
10) Pennsylvania (e.g. Cressler, 2006)
11) Anhui, China (Guo and Wang, 2009)
12) Waterloo Farm, South Africa (this paper)

Reconstruction based on Torsvik and Cocks, 2004, with Gondwanan coastline modified after Torsvik and Cocks, 2013 and Gess and Whitfield, 2020, and position of Amorica and related terrains modified after Blakey, 2016.

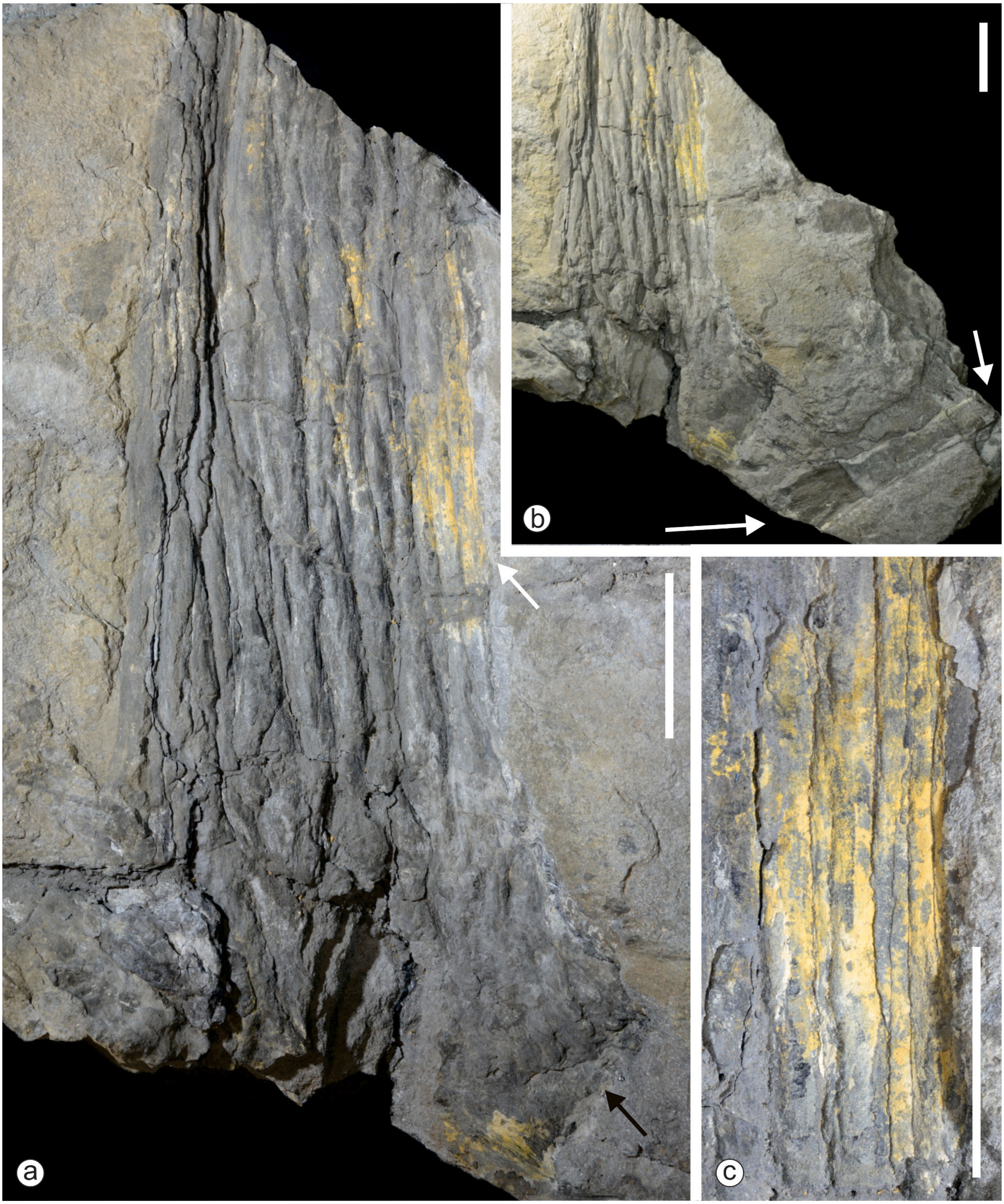

Plate 1.

a) General view of *Archaeopteris* stump (AM 18331) from Waterloo Farm. Lighting predominantly from top left. Black arrow shows the abrupt disappearance of the major lateral root into the sediment. White arrow shows the area enlarged in *c*. See also text-Fig. 1. Scale bar = 10 cm.
b) Wider view of the stump slab, showing basal part of *Leptophloeum* main axis (between arrows) with proximal parts of roots to bottom left, overlying major lateral root of *Archaeopteris*. Illumination dominantly from top left but with a greater amount of secondary light from in front of the slab to right of camera. Scale bar = 10 cm.
c) Close up of area of *Archaeopteris* trunk indicated by white arrow in a, showing corduroy texture. Illumination from right. Scale bar = 5 cm.

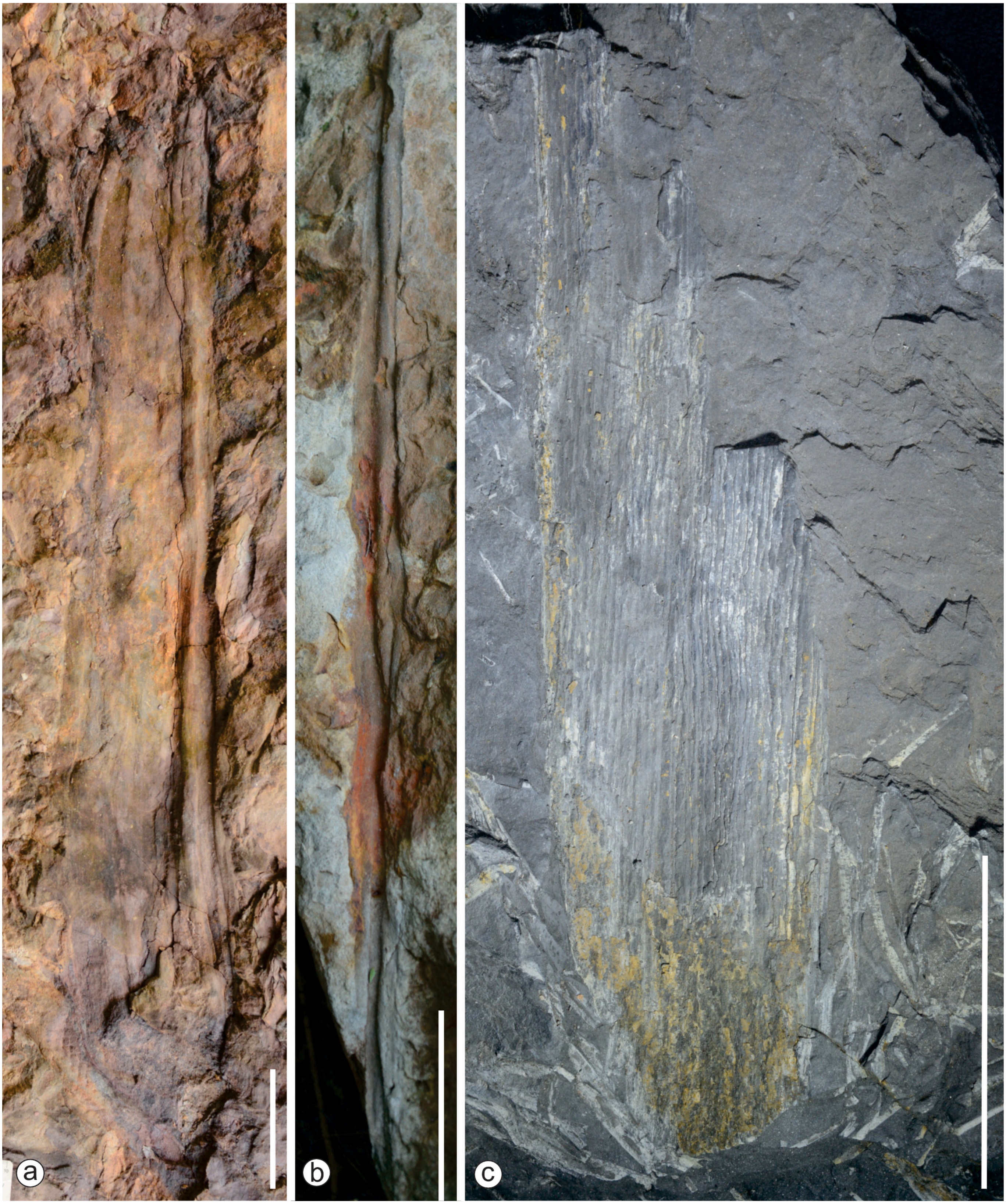

Plate 2.

a) Large axis with smooth surface found on sandstone slab with *Leptophloeum rhombicum* stems. Natural light.
b) Narrow axis with smooth surface on sandstone slab. Natural light.
c) Corduroy stem from shale levels (AM 5342). Cross polarised light.
d) All scale bars = 10 cm.

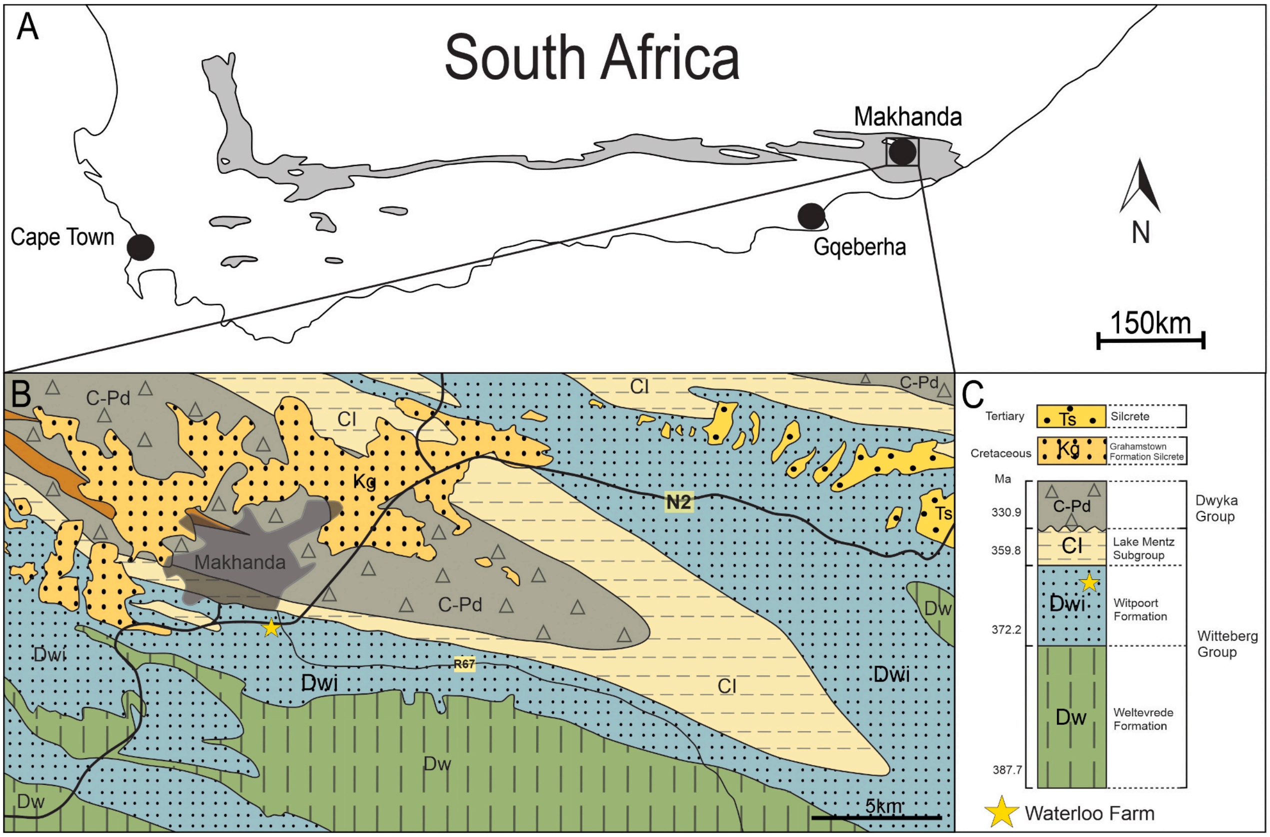

Fig. 1. A) Distribution of the outcrop of Witteberg Group rocks in South Africa, B) Geological map (based on Council for Geoscience sheet 3326, 1:250,000) showing position of the Waterloo Farm lagerstätte (star), C) Stratigraphic column of strata in the Makhanda area.

in figure captions. Photographs were assembled into plates using CorelDraw.

3. Description

3.1. *Stump slab*

A large stump (AM 18331) was recovered lying on the bedding plane of a large slab, currently a prominent display specimen in the Devonian Ecosystems Project gallery of Albany Museum, Markanda, South Africa (Plate 1, text-Fig. 2). The slab also displays a relatively poorly preserved base of the lycopsid *Leptophloem rhombicum* (Prestianni and Gess, 2014) in close association, lying just above the major root of the stump (Pl. Ib – arrows). This *Leptophloeum* is preserved over 33 cm length, is 45 mm wide at the top and 65 mm wide at the base. The proximal portions of the relatively large diameter rootlets can be seen at bottom left. This association effectively demonstrates the relative stature of the two plant types.

The stump is preserved over a maximum length of 67 cm. It principally comprises an impression from which a thin coalified compression has been largely removed by weathering. The bottom is only partly preserved, but a well-preserved base of a major root is preserved on the right-hand side, departing at an angle of about 35° below the estimated horizontal (125° clockwise from upright axis of stump). This root is 14 cm across and disappears into the matrix underneath the *Leptophloeum*. The root has slight longitudinal ribbing of the surface, the ribs being 10–15 mm wide. Depressions in the base of the specimen suggest other roots may have also been present going down into the slab. On the left hand side of the specimen the preservation of another large root is suggested but the margins cannot be well defined.

The basal trunk tapers distally. Measured at the top of the departing major root, the width of the trunk is 30 cm. 40 cm above this point the trunk has tapered gently to 20 cm, the uppermost part where the complete trunk is exposed.

The surface of the trunk is largely preserved as an impression displaying sub parallel to anastomosing depressions and ridges with an overall bark-like texture. The depressions are about 5 mm deep.

On the right hand side of the stem, a small area has a different texture, comprising narrow (3–5 mm wide) flattened carbonaceous strips with a small overlap (Plate 1 c). The orientation of the strips is parallel to the surface of the trunk. This texture is on top of, and therefore likely inside, the bark texture. This type of texture is sometimes referred to as a ‘corduroy texture’.

3.2. *Corduroy stems*

The collection contains 3 stems which display a corduroy texture as their principal character. These are each found in the dark grey mudstone of the Blue Layer. AM 5342, shown in Plate 2 c is 38 cm long and 85 mm in width. The corduroy stripes are 2–3 mm in width. It is hard to make out what is carbon and what is matrix, but some of the strips are covered by a thin layer of kaolinite that typically forms an external veneer to carbonised plant matter at the site. In places there is slight overlap of the strips which are parallel to the surface of the specimen.

A second corduroy axis (AM 18330) is 13 cm in width and 32 cm in length. In this specimen the strips are about 5 mm in width and the transverse section of some strips is slightly convex.

3.3. *Other substantial axes*

Two large axes are preserved from lag deposits in the channelised sandstone underlying the black mudstone horizons, and are preserved in a completely different way.

The largest (Plate 2a) is 66 cm long, 145 mm at the bottom and 105 mm at the top. It is largely smooth with one ridge close to the right hand side. There is no evidence of scars. It is associated in a lag with several axes of *L. rhombicum*.

The smaller (Plate 2 b) is 60 cm long, and 25–30 mm wide, smooth but with more pronounced ridges and also no scars.

These two large axes have smooth surfaces. This is consistent with a woody branch or trunk that has been stripped of its bark during transportation. If we assume that both the corduroy stems and the smooth stems are from the same plant, then it can be deduced that the corduroy pattern is likely part of the bark. In the large stump, an indication of the corduroy pattern is visible where a bark-like texture is also present (Plate 1 c).

3.4. *Archaeopteris* leafy branching systems

Although not being discussed in detail here, we note the presence of much larger *Archaeopteris* branching systems than previously described from this locality. For example, AM 18329 from the MFL horizon, (Plate 3) is a near complete penultimate branch on which are inserted both leaves and leafy ultimate branches. It preserves a length of 410 mm, is proximally 8.6 mm wide, and tapers distally to 2.4 mm in width. Proximal ultimate branches are up to 130 mm long, being 2.4 mm wide proximally and 0.5 mm wide distally. Distal ultimate branches are 40 mm long with a proximal width of 0.65 mm tapering to 0.4 mm distally. The leaves are moderately dissected and typical of *A. notosaria* from this locality. Conspecific leaf bearing axes have also been collected from the Blue Layer and thin interbeds in the underlying metasandstones.

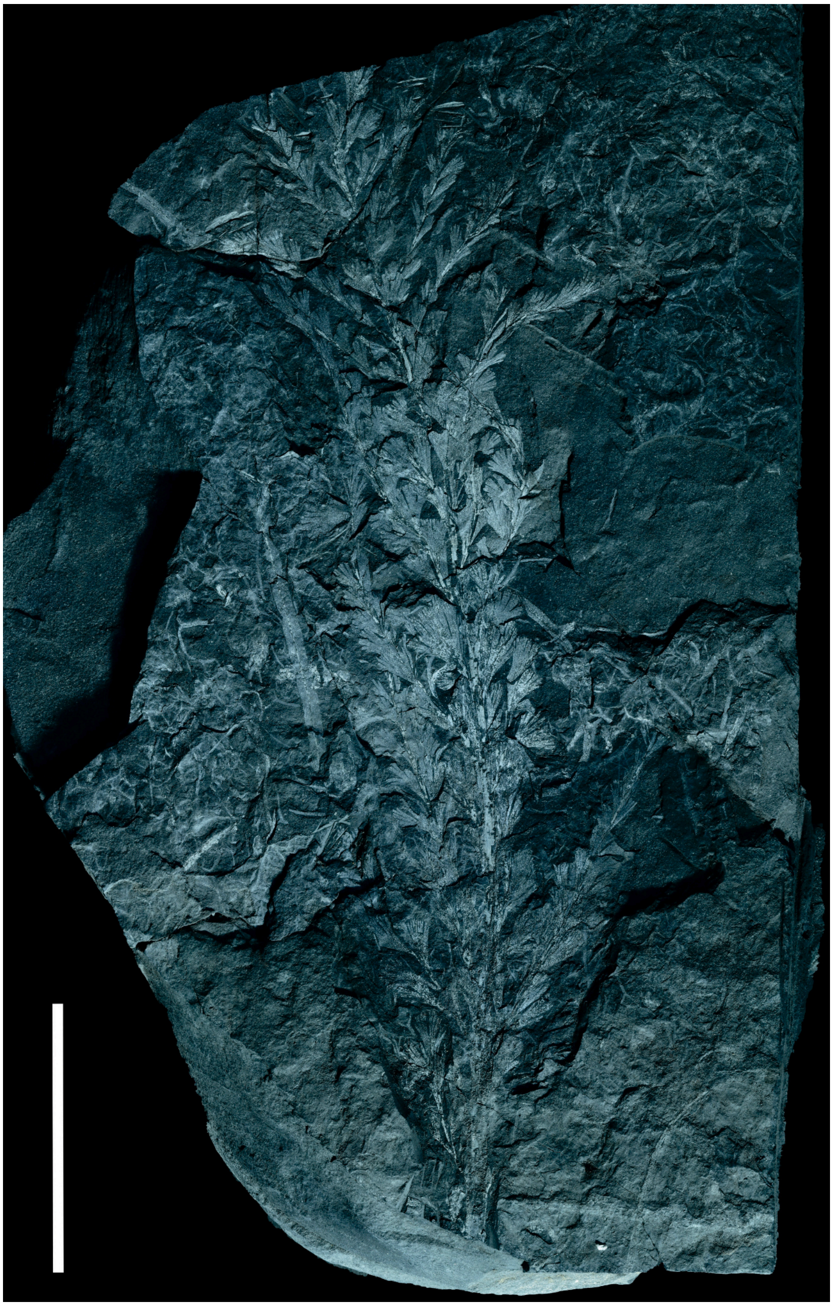

Plate 3.

a) Large leafy branch system of *Archaeopteris* (AM 18329) from Waterloo Farm, 410 mm in preserved length. Recovered from the MFL horizon. Scale bar = 10 cm.

4. Discusssion

4.1. Identity and comparison of the tree base

The co-occurrence of large tree bases and large leafy branch systems of *Archaeopteris* at Waterloo Farm is highly suggestive that they are parts of the same plant. As described below, previous reported occurrences of *Archaeopteris* trunk bases have similar morphology to that from Waterloo Farm. The only other reported trunks from Waterloo Farm are from lycopods, most commonly those of *Leptophloeum rhombicum*, which are up to 8.5 cm in diameter and for which the cormose base with small roots has already been described (Prestianni and Gess, 2014).

A *Callixylon* base from the Famennian of the Donbass described by Snigirevskaya (1994) is preserved in three dimensions in silica. It measures about 30 cm in diameter at the level where the roots are inserted, and tapers upwards over about 50 cm to a diameter of about 15 cm (CMB personal observations). At least 3 major roots about 10–12 cm in diameter, and some smaller ones, emerge from this base at about 45 degrees below the horizontal, but are only preserved for 30 cm or so. The most prominent shows a distinct taper and slight trend towards the horizontal. Identity as *Callixylon*, demonstrated by grouped pitting of radial cell walls amongst other characteristics, shows it to be the wood of the tree known as *Archaeopteris* (see e.g. Lemoigne et al., 1983). In size and shape, therefore, the compressed base of the Waterloo Farm specimen is entirely compatible with the Donbass specimen.

Much larger bases of apparent *Archaeopteris* trunks have been found in latest Devonian aged black shales of Indiana and neighbouring states. This includes a base 3 ft. wide, tapering to 18″ over the preserved 9 ft, with the remains of 2–3 large roots at the base (Arnold, 1931). Another fossil from Kentucky, identified only on the basis of its surface texture, tapering from 18 to 4″ over 20 ft, when joined with the base, suggested a total height of at least 29 ft, the trunk lacking obvious large branch bases (Arnold, 1931). While more recent publications describing the anatomy of long trunks of *Callixylon* demonstrate the presence of long-lived branches (Meyer-Berthaud et al., 2000) surprisingly little is known about the size of the lateral branches of *Archaeopteris* and therefore reconstructions remain speculative.

Older, Mid Devonian (mid Givetian) sediment moulds inferred to be *Archaeopteris* roots from Cairo, New York (Stein et al., 2020) suggest basal diameters of up to 45 cm. Primary root diameters of up to 15 cm adjacent to the base of the trees were matched with roots of up to 11 m length from the tree base. Primary roots observed in the Cairo palaeosoil are largely horizontal, suggesting that the roots continued to flatten out away from the trunk to form a large root plate.

Overall, the presence of a large tree base, with a small number of large roots tending towards the horizontal and a bark-like external texture is strongly suggestive of attribution to *Archaeopteris*, based on what is known from *Archaeopteris* at other localities.

4.2. Size of trees

Using allometry based on measurements of extant Norfolk Island Pines, Stein et al. (2020) estimated the height of *Archaeopteris* trees from the basal diameter and the diameter of the largest root. This methodology was adopted to avoid the measurement of diameter at breast height, which is a standard forestry technique but not applicable to fossil casts which only include the base or rooting systems of the plants.

For the Waterloo Farm specimen, based on a trunk base diameter of 30 cm, the Stein et al. method gives an estimated height of 24.70 m. Based on 14 cm root diameter, 25.30–26.50 m height is estimated.

4.3. Identity of the corduroy stems

The nature of corduroy stems associated with leafy branch systems of *Svalbardia* (Archaeopteridales) was discussed by Allen and Marshall (1986). They thought that the corduroy strips might relate to tangential rows of fibres within the bark or cortex of a stem. Such rows are now known from the secondary phloem of *Archaeopteris*, but on a small scale where demonstrated (Decombeix and Meyer-Berthaud, 2013) and need to be confirmed at a larger scale in anatomically preserved material. They can be distinguished from cladoxylopsid xylem strands because there is only one type and do not anastomose, and they are tangentially rather than radially aligned.

4.4. Palaeogeographical considerations

Selected Famennian occurrences of *Archaeopteris* and *Callixylon* are shown on a Late Devonian palaeogeographical reconstruction in text-Fig. 2. Maps of the distribution of *Archaeopteris* and *Callixylon*, averaged over the temporal range of *Archaeopteris* macrofossils (approximately mid Givetian – end Devonian = 25 Ma) – e.g. Bai et al., 2022, Meyer-Berthaud et al., 1997 – show a more or less global distribution, although data from central Gondwana is lacking. This distribution is little different in the Famennian alone (duration = 11 Ma). Geographical range of the known spores of *Archaeopteris*, *Geminospora lemurata* (microspore) and *Contagisporites optivus* (megaspore) is similar but with a bit more data from South America and Antarctica (Marshall, 1996). It is not, however, clear which megaspore relates to *Archaeopteris* in the Famennian and spore data from the Famennian (other than D/C boundary sections) is scarce (Marshall, pers. comm). Nonetheless, it does not seem unreasonable to infer that *Archaeopteris* was present in vegetation worldwide to at least 70 degrees south, and our stump strongly suggests that *Archaeopteris* was likely tree sized over that range.

Meyer-Berthaud et al. (2010, p. 68) noted that the large amount of living tissue in cladoxylopsid trees, including large amounts of parenchyma, likely meant that they required moisture in the growing season, and that they were unlikely to grow in areas with freezing temperatures. Although not forming such a large amount of the trunks, the extraordinarily large parenchymatous pith of *Archaeopteris* trunks, which may be found intact (Decombeix and Meyer-Berthaud, 2013), and likely largely of primary origin, suggests that *Archaeopteris* may not have been tolerant of extreme cold or dryness. This has implications for understanding the climatic conditions at Waterloo Farm in the late Famennian.

Amelioration of climatic conditions may have resulted from ocean currents bringing warm waters into high latitude coastal areas (Gess and Whitfield, 2020). This possibly resulted from development of cyclical movements within the Palaeopacific ocean in response to reduction or closure of the Rheic Ocean between Gondwana and Laurasia, towards the end of the Devonian (Streel et al., 2000). Significantly, putative glacial deposits within the Witpoort Formation are lenticular and consistent with valley glaciation rather than ice sheet development (Almond et al., 2002). This would be congruous with influx of warm water, which would result in increased snowfall in the cold, higher altitude interior (Streel et al., 2000) but an absence of snow or ice in the warmer coastal areas, as is demonstrated along the current west coast of southern New Zealand (Gess and Whitfield, 2020).

Similar effects are evident in contemporary ecosystems at 70 degrees latitude. In the Southern Hemisphere the Antarctic coastline is flanked by cold circumpolar currents and the Antarctic Peninsula, at 70 degrees south, supports a very limited flora including only two tracheophytes: an annual herb and a grass (Rudolph, 1965). By contrast, in the north, the warm Gulf Stream of equatorially derived water sweeps western Norway at 70 degrees and sheltered coastal areas such as Alta support forests of large birches and pines, with diverse understories (RG pers. obs.). The present position of the arctic tree line at around 70 degrees is variable around the Arctic Circle dependent on local climatic conditions, and also changes with global climatic influence over time (Payette and Lavoie, 1994). Similar to the probable position of Waterloo Farm within the Agulhas Sea, Alta is positioned away from open sea within a deep sheltered continental inlet, that is nonetheless influenced by the adjacent warm ocean current.

5. Conclusion

A substantial tree base from the Late Famennian Waterloo Farm lagerstätten is inferred to be the base of an *Archaeopteris* tree. Leafy branching systems of this tree have also been found. Estimated height of the tree is more than 20 m. This base, together with other substantial woody axes, indicate that there is little doubt that *Archaeopteris* was capable of forming true forests in high latitudes during the latest Devonian. The nature of the diverse flora, invertebrate and vertebrate assemblages suggest that the coastal climate was not polar, but day length was likely quite variable leading to strong seasonality.

Furthermore it is notable that, by the Famennian, potentially forested areas had extended south as far as the Antarctic circle. As evidence for their emergence during the mid Devonian is currently limited beyond palaeotropical areas (text-Fig. 2), this increase of their area of distribution will have plausibly contributed to the noted increase in climatic instability during the Famennian. High latitude climatic amelioration towards the end of the Devonian has previously been postulated to have resulted from changing ocean currents resultant from the progressive closure of the Rheic Ocean. It is therefore likely that changing continental configurations ultimately contributed to the End Devonian biotic crisis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

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