Reinvestigating the fossil leaf *Welwitschiophyllum brasiliense* Dilcher et al., 2005, from the Lower Cretaceous Crato Formation of Brazil

Emily A. Roberts[1, 2*], Robert F. Loveridge[1], Jörg Weiß[3] David M. Martill[1] and Leyla J. Seyfullah[2]

[1]School of the Environment, Geography and Earth Sciences, University of Portsmouth, Burnaby Road, Portsmouth, PO1 3QL, UK

[2] Department of Palaeontology, University of Vienna, Althanstraße 14, 1090 Vienna, Austria

[3] Mikroskopisches Kollegium Bonn, Helene-Lange-Strasse 25, 53757 Sankt Augustin, Germany

*Corresponding author: Emily Roberts, emily.roberts@port.ac.uk

ABSTRACT

The Lower Cretaceous Crato Formation of north-east Brazil yields a diverse plant assemblage. It has yielded many macrofossils thought to be related to the enigmatic gymnosperm group Gnetales, including the long leaf *Welwitschiophyllum brasiliense* Dilcher et al., 2005. This fossil plant is considered to be related to the extant gnetalean *Welwitschia mirabilis* Hooker, 1863, despite lacking many gnetalean characteristics. Presently, this macrophyte fossil is known only from detached leaves and much anatomical information is currently unavailable. The reproductive structures assigned to the family Welwitschiaceae in the Crato Formation, as well as several key morphological features of the leaves are currently thought to relate fossil *Welwitschiophyllum* to extant *Welwitschia.* These leaf characters include: isobilateral leaf form, triangular elongated leaf shape with a wide base, longitudinal splitting from a frayed leaf apex, numerous parallel veins and possible thickening of the epidermis. However, many of these leaf characteristics also occur in many other macrophytes, perhaps as a result of convergence. Anatomical and morphological data described here from fossil *Welwitschiophyllum* leaves is compared with extant *Welwitschia*. Our results show that *Welwitschiophyllum* can only be placed tentatively in Gnetales, as many of the features we report are not diagnostic, and may have resulted from convergent evolution (e.g., gum). Fossils with better anatomical preservation and the

reconstruction of the whole plant are really needed to better understand the affinities of *Welwitschiophyllum*.

Keywords: Crato Formation, Lower Cretaceous, Gnetales, *Welwitschia, Welwitschiophyllum*

1. Introduction

Early Cretaceous floras typically have a higher abundance of gymnosperms than seen in many floras today, where angiosperms (flowering plants) have become dominant following the Cretaceous Terrestrial Revolution (Lloyd et al., 2008). One gymnosperm group in particular that flourished during the Mesozoic was the Gnetales (Crane, 1996), today represented only by three genera that vary significantly in morphological appearance and habitat. *Ephedra* Linnaeus 1753 is a plant with reduced leaves, usually shrubby, although a few are small trees and climbers, and it has 50 species distributed in subtropical, arid and temperate environments (Kubitzki, 1990). *Gnetum* Linnaeus 1767 has 39 species, mostly lianas, but includes trees and shrubs, which are all broad leaved with pinnate-reticulate venation, and inhabiting sub-tropical to tropical environments (Ickert-Bond and Renner, 2016). *Welwitschia mirabilis* Hooker 1863 is a plant with only two elongated, strap-like leaves on the woody caudex and a large taproot, and is restricted to the Namib Desert with only one species. *W. mirabilis* is sometimes divided into subspecies *W*. *mirabilis* ssp. *mirabilis* and *W*. *mirabilis* ssp. *namibiana* (Leuenberger, 2001).

The Gnetales of the Mesozoic display a rich diversity not reflected in the extant genera (Rydin et al., 2006; Crane, 1996). This diversity is well documented in the Lower Cretaceous Crato Formation of north-east Brazil, where eight genera have been erected to date, and many more plants identified as gnetalean, are yet to be described (Rydin et al., 2003; Dilcher et al., 2005; Martill et al., 2007; Kunzmann et al., 2009; Kunzmann et al., 2011; Ricardi-Branco et al., 2013; Löwe et al., 2013). Four of these Crato Formation plant fossils are considered to be relatives of *Welwitschia*; the seedling *Cratonia cotyledon* Rydin et al., 2003, young paired cotyledon *Priscowelwitschia austroamericana* Dilcher et al., 2005, male reproductive strobili *Welwitschiostrobus murili* Dilcher et al., 2005, and the leaf taxon

Welwitschiophyllum brasiliense Dilcher et al., 2005. The diversity of these *Welwitschia* associated macro-remains are of interest, as its history is chiefly represented by pollen in the fossil record.

Other Lower Cretaceous macro-remains with possible Welwitschiaceae affinities are known from the United States, China, Mongolia, Russia, and Europe. These fossils include the reproductive structures *Gurvanella dictyoptera* Krassilov, 1982 (=*Chaoyangia liangii* Duan, 1998; Rydin et al., 2006), *Heerala antiqua* (Heer) Krassilov and Bugdaeva, 1988, *Angarolepis odorata* Krassilov and Bugdaeva, 1988, *Eoantha zherikhinii* Krassilov, 1986, and the dispersed seeds, *Bicatia* Friis et al., 2014. *Drewria potomacensis* Crane and Upchurch, 1987 and *Conospermites hakeaefolius* Ettinghausen, 1867 are the only confirmed foliar remains of Welwitschiaceae found outside the Crato Formation.

Welwitschiophyllum is a rare occurrence of a non-cotyledonous foliar fossil assigned to Welwitschiaceae. They occur as distinctive detached leaves reaching up to ~850 mm in length. In order to better understand the relationship of this fossil taxon to *Welwitschia*, which previously was only based on morphological comparisons, we provide and review the *Welwitschiophyllum* anatomy based on thin sections and compare its histology to that of extant *Welwitschia.*

2. Geological setting

The Lower Cretaceous (~120 million years old) Crato Formation of north-east Brazil outcrops on the flanks of the Chapada do Araripe, in the Araripe Basin, mainly in the states of Ceará and Pernambuco (Batten, 2007; Martill, 2007) (Fig. 1). The best exposures are of anthropic origins (stone quarries) in the neighbourhood of Nova Olinda and Santana do Cariri in southern Ceará. All the fossils described here come from the quarries in this region. The formation comprises a heterolithic sequence of clays, silts and sands with conspicuous finely laminated limestones (Martill et al., 2007). The main fossil-bearing horizon, the Nova Olinda Member, is ~~a~~ composed of finely laminated limestone yielding a diverse and exceptionally preserved vertebrate, insect and plant assemblage (Martill et al., 2007). When found in the weathered limestone the plant fossils are preserved as orange-brown goethite compressions, but when found in the unweathered limestone they appear black; in both three-

dimensionality can be seen. The depositional environment is that of a saline lagoon with fresh water input with surrounding semi-arid to arid areas (Martill et al., 2007). Aridity is supported by the xeric adaptations of some of the flora (Mohr et al., 2006; Kunzmann et al., 2009; Mohr et al., 2015).

3. Materials and methods

Fossil repositories: The fossil material from the Crato Formation examined here comprises three isolated leaves of *W*. *brasiliense* Dilcher et al. 2005 (Specimens UERJ 13-P1, UERJ 14-P1, and UOP-PAL-MC0003). Specimens UERJ 13-P1, UERJ 14-P1 are accessioned at Rio Janeiro State University and UOP-PAL-MC0003 is accessioned at the University of Portsmouth.

CITES Permit: Analysis of extant *W*. *mirabilis* was performed on samples obtained on CITES permit No. 152606.

Petrographic thin sections: To examine the fossil plant histology three petrographic thin sections from specimens UERJ 13-P1, UERJ 14-P1, and UOP-PAL-MC0003 were made. To avoid damage in the initial cutting and grinding stages the specimens were painted with thin layers of EpoThin II resin. The initial layer of resin was applied whilst the sample was heated on a hotplate to 80ºC, it was then placed in a Struers Citovac vacuum chamber for 10 minutes and left overnight in a Heraeus Technomat pressure chamber to allow the resin to fully impregnate the material. Once the resin had cured the sample was cut using a Cutangrind saw made by Agate & General and a Buehler IsoMet Low Speed Precision Cutting Machine. Once cut, the surface was ground flat using 600 grade silicon carbide and water on a glass plate, and the sample was thoroughly dried then bonded with Epothin II to frosted glass using resin. Once the resin was cured, all excess material was cut away using a Buehler Petrothin machine leaving 0.5 mm thick sample attached to the glass, which was then carefully ground down to 35-40 µm. The slide was then further ground down to the finished 30 µm (using 600 grade silicon carbide and water on

104 a glass plate) whilst the mineralogy was being periodically checked using a petrological microscope to
105 ensure even thickness. These were examined using Leica DM750P and Zeiss Ax10 microscopes.
106
107 *Botanical thin sections:* Sections of *Welwitschia mirabilis* were fixed using AFE (Ethanol 70%,
108 Formaldehyde 36% and acetic acid 99% - 90:5:5), 50 µm sections with Jung cylinder microtome, staining
109 W3Asim II and examination with Leica DMLS microscope (Müller et al., 2011; Weiβ, 2015).
110
111 *Paraffin sections*: Sections of *Welwitschia mirabilis* were fixed using ethanol (50%), formaldehyde (10%)
112 glacial acetic acid (5%) and distilled water (35%) and then embedded in paraffin wax.
113
114 *Scanning electron microscopy*: SEM on fossil samples was undertaken on a Zeiss Evo Series NA10.
115 Extant *Welwitschia mirabilis* samples were examined under variable pressure.
116
117 *Fossil gum extraction and Spectroscopic analysis* : The fossil amber-coloured material (from
118 *Welwitschiophyllum* UERJ 13-P) was mechanically extracted from the matrix and the leaf fossil remains
119 using sterile scalpel blades and dental picks from leaf ducts using a Leica EZ4W stereomicroscope. The
120 extracted samples were washed in absolute alcohol to minimise contamination. The sample was then
121 ground into a fine powder using a pre-autoclaved and pre-sterilised glass micro-mortar and pestle. The
122 resulting powder was then further checked microscopically for any visible impurities, and none were
123 seen. Analysis on the sample (UERJ 13-P1) was performed using FTIR spectroscopy on a *PerkinElmer*
124 *'Spectrum 400'* spectrometer, fitted with an ATR sampling accessory (range 4000-550 cm^{-1}, 32
125 accumulations, 4 cm^{-1} resolution). For ATR analyses a small amount of the sample was placed in 0.5 ml
126 of water, which was heated to approximately 90°C for 10 minutes. A drop of the residual liquid was
127 placed on the ATR crystal, and the water allowed to evaporate, leaving a film of the extracted material
128 on the crystal surface. A spectrum was recorded (with 32 accumulations, to improve the quality of the
129 data, due to the very small amount of material under analysis) and peaks were normalised. Care was

taken to thoroughly clean the ATR crystal between sample measurements using warm water and pure ethanol and allowed to dry. Test spectra were made to ensure no cross contamination was occurring between the measurement scans. A baseline correction for both analyses with reference points at 3715 and 1800 cm^{-1} was performed. The spectrograph was visualised using SpectraGryph 1.2.10 software.

Image processing: Images were captured taken using Cannon EOS 80D and composed as combined figures using Inkscape. Fig. 1 was drawn in Inkscape. Fig. 2 is composed of single images taken and combined using Inkscape. Fig. 3A was stitched together to create an overview of the section, while Fig. 3B-3E were processed in Inkscape. Fig. 4A, B were stitched together to create an overview of the section. Fig. 4C, D were processed in Inkscape. Fig. 5. was visualised in SpectraGryph 1.2.10 software. Fig. 6A was processed in Inkscape, Fig. 6B was stacked using Zerene Stacker from 30 single images taken with a Panasonic GX7, whilst Fig. 6C (three images) and 6D (five images) were stacked using Helicon Focus.

4. Results comparing *Welwitschiophyllum* and *Welwitschia*

4.1. Morphology and anatomy of fossil Welwitschiophyllum *leaves*

Welwitschiophyllum brasiliense Dilcher et al., 2005 is a relatively common fossil leaf found in the Crato Formation. They are long (up to ~116 cm in length), lanceolate, detached leaves that taper to an acute apex and have a curved base (Fig. 2A). Where preserved, the leaves have a dense parallel venation (9-15 veins per cm). A single specimen comprising two apparently basally attached leaves that may be inferred as forming part of a rosette or other structure, was not available for study (Martill et al., 2007, pl. 27d). In some specimens the apex is frayed (Fig. 2B). *W*. *brasiliense* has also been recorded in association with the pterosaur *Ludodactylus*; it was first thought that the rigid and sharp leaf pierced the gular of the pterosaur leading to its eventual death (Frey et al., 2003; Martill et al., 2007, Fig. 17.4). An alternative theory is that this is in fact an abiotic association, due to the hyoid apparatus being preserved on top of the *Welwitschiophyllum* leaf, rather than wrapping around either side of the leaf

(Witton, 2017), which we deem less likely given the positioning of the leaf inside the mandibular apparatus.

Three specimens (Table 1, Fig. 2B–D) were available for detailed morphological and anatomical investigation for this study.

Table 1. A summary of the three examined *Welwitschiophyllum* specimens.

Specimen	Length	Maximum width	Apex	Preservation
UERJ 13-P1 (Fig. 2B)	279 mm	44 mm at its base	Frayed	Leaf colour - black (from unweathered limestone).
UERJ 14-P1 (Fig. 2C)	Leaf is incomplete (total length unknown). Length of remaining portion is 482 mm.	52.5 mm at its base	Missing	Leaf colour - black (from unweathered limestone). Leaf partly covered by limestone matrix.
UOP-PAL-MC0003 (Fig. 2D)	Leaf is incomplete (total length unknown). Length of remaining portion is 37 mm	32.5 mm	Missing	Leaf colour - red-brown (from weathered limestone). Leaf base is folded into the limestone.

As the whole plant is unknown for *Welwitschiophyllum*, and considerable information on leaf morphology and anatomy is information unavailable (e.g., for the epidermis, stomata, internal leaf tissues and their arrangement), adaxial and abaxial surfaces are inferred from the curvature of the leaf base. The inferred adaxial surface here is defined as the surface on the incurved side of the leaf and the abaxial the opposite surface. W*elwitschiophyllum* sections display differences between the inferred adaxial and abaxial surfaces (Fig. 3A, B). The abaxial surface possesses flask shaped pits at regular intervals with spacing of 380 µm, and depth of 125 µm. In UOP-PAL-MC0003, these pits are infilled, with sediment (Fig. 3A, B). Although no stomata are seen, these regular pits are interpreted as possible stomatal crypts on the basis of their size and regular distribution throughout the abaxial leaf surface. Between the stomatal crypts raised sections of the leaf are highly fibrous (Fig. 3B), however, in all cases the cuticle and upper epidermis is not preserved.

The adaxial leaf surface lacks the stomatal crypts seen in the abaxial surface, and has thick fibres in bundles throughout the surface (Fig. 3A, B). These are interpreted as hypodermal fibres due to

their positioning and thick (20 µm), fibrous nature. No definite vascular tissue have been identified in any of the specimens, but 250 µm wide voids (Fig. 3A, B) are here interpreted as the lacunae left by degraded vascular bundles. Neither accessory vascular bundles or lacunae of vascular bundles were identified.

Scanning electron microscopy (SEM) of the *Welwitschiophyllum* specimens revealed little detail as the leaf surfaces have been heavily mineralised and/or weathered away. However, one fossil leaf (UOP-PAL-MC0003) did retain some paradermal details (Fig. 3C, D). These include tube shaped structures that taper at the ends, connecting to each other (Fig. 3C, D) with holes perforating the structure (Fig. 3E). We interpret these structures as tracheids due to the tapering spindle shape of the connecting structures (Fig. 3C, D) and presence of pits present (Fig. 3E).

Transverse thin sections through the leaf show the variable amounts of anatomical details preserved in different leaves (Figs. 3A, 4A, 4B) and encroaching pyrite decay. Two thin sections of fossil *Welwitschiophyllum* leaves (UERJ 13-P1 and UERJ 14-P1) show adaxial amber-coloured ducts ranging in diameter from 75 µm to 200 µm wide (Fig. 4C, D). When analysed using FTIR and ATR they show a gum signal remarkably similar to that of extant *Welwitschia* gum (Fig. 5) (Roberts et al., 2020). In specimen UOP-PAL-MC0003 there are no remains of gum present, however, regular voids infilled with crystals towards the adaxial surface may represent ducts where the gum has been dissolved and infilled (Fig. 3B). The arrangement of these regular ducts indicates that these were constituent within the leaf.

4.2. Morphology and anatomy of leaves of extant Welwitschia

Despite *Welwitschia's* appearance of having many leaves it has only two perennial paired leaves (Fig. 6A) where the apices fray into 'thongs' (Hooker, 1863). The leaves are long, broad and coriaceous, and often split, giving the impression of separate leaves (Bornman et al., 1972). The parallel veined leaves can reach over 6 m in length (Hooker, 1863) and insert into a thick stem that has a robust corrugated periderm under the apex, which in mature specimens forms a distinctive 'terminal groove' (Hooker, 1863; Bornman et al., 1972). These two leaves are often strongly adaxially recurved. Below the

leaves the robust fibrous stem sits above the soil, and below it forms a massive root. *Welwitschia* is dioecious, where one plant bears either ovulate or staminate cones ~~or micro-strobuli~~. Usually, although not always, these are adaxial to the leaves developing from the stem meristem (Bornman et al., 1972).

When thin sectioned notable features of *Welwitschia* (Fig. 6B) leaves are sunken stomata, hypodermal fibres and sclerenchymous fibres, all appearing both adaxially and abaxially. Thin sections of *Welwitschia* investigated here did not reveal evidence of gum ducts, but paraffin sections show an orange-brown coloured amorphous mass that lacks any cellular detail (Fig. 6C, D). The only instance of gum in the thin sections was found in a callus, again seemingly amorphous (Fig. 6E). We interpret these instances as traumatic gum production formed lysigenously.

5. Discussion

Welwitschiophyllum was originally placed in the Welwitschiaceae based on the isobilateral form of the leaves, possible thickening of the epidermis, triangular elongated leaf shape with a wide base, parallel equidistant first-order veins that are convergent near the apex, with some veins disappearing into the margin, plus longitudinal splitting from a frayed leaf apex, and somewhat thickened or creased mid-leaf area (Dilcher et al., 2005). We observed some of these features but not any possible thickening of the epidermis, as the preservation did not allow this. We also could not observe any thickened or creased mid-leaf area. The folded leaf specimen (UOP-PAL-MC0003) may have folded that way into the sediment due to a creased mid leaf area, but this is not evident in the thin sections.

5.1. Comparative anatomy of Welwitschiophyllum *and* Welwitschia *leaves*

The general morphology of *Welwitschiophyllum* leaves differ from those of the extant *Welwitschia* in a number of respects, including smaller fossil leaves, a lanceolate outline and a concave leaf base. *Welwitschiophyllum* is only found as detached leaves, and thus it is not possible to determine the leaf arrangement for the fossil taxon and compare it to the rather unique two-leaf arrangement of *Welwitschia* (Fig. 2 and Fig. 6). It is possible that the *Welwitschiophyllum* leaves were abscised or, as

244 suggested by Dilcher et al. (2005), that they were wrapped around a stem. *Welwitschiophyllum* leaves
245 have distinct bases, whereas the very long, strap shaped, perennial leaves of *Welwitschia* originate
246 inside the stem and are not abscised. Despite these clear differences in general morphology the plants
247 do share some similarities in their long, thick leaves (growing to a considerable size) with first order
248 parallel venation.
249 The parallel venation of *Welwitschiophyllum* is not, however, a convincing character to assign
250 this fossil taxon leaf to Welwitschiaceae. Other fossil non-cotylendonous leaves (e.g. *Drewria* and
251 *Conospermites*) assigned to Welwitschiaceae display two vein orders, first order parallel veins, plus a
252 second order cross-venation with a chevron arrangement (Ettinghausen, 1867; Crane and Upchurch,
253 1987). This more typical welwitschioid leaf venation is highly conspicuous in *Drewria* and *Conospermites*
254 without the need for thin sectioning, unlike *Welwitschiophyllum* that clearly lacks accessory veins.
255 In the original description of *Welwitschiophyllum* the distinctive fraying of the leaf's apex was
256 also considered to ally this fossil leaf to the extant *Welwitschia*: (Dilcher et al., 2005) (Fig. 2B). Fraying of
257 the leaf in extant *Welwitschia* is often attributed to the wind (Bornman et al., 1972; Dilcher et al., 2005;
258 Maneveldt and Seydlitz, 2007), but the phenomenon also occurs in glasshouse cultivated specimens
259 where wind does not impact on the plant's development. Rather, it is thought that this fraying and
260 damaged apices is a result of sun damage (Martens, 1971; Norbert Lehrl, Vienna Palm House pers.
261 comm., 2019, pers. Obs., EAR, LJS). As discussed by Dilcher et al. (2005) fraying seen in the fossil
262 *Welwitschiophyllum* could have been a consequence of prolonged transport prior to deposition.
263 Additionally, many extant leaves with a similar elongate-lanceolate morphology also display fraying at
264 their apices e.g. *Yucca,* palms*, Cordyline* etc. Therefore, fraying of the leaf apex in *Welwitschiophyllum*
265 cannot be considered a reliable characteristic allying it with *Welwitschia*.
266
267 *5.2. Internal anatomy of* Welwitschiophyllum *and* Welwitschia *leaves*
268 Unlike *Welwitschia,* thin sections of *Welwitschiophyllum* display significant differences in
269 structure of the adaxial and abaxial surfaces, despite the limits of preservation shown in the prepared

materials presented here. *Welwitschia* has sunken stomata and bands of hypodermal fibres both adaxially and abaxially (Fig. 6B and Figures 1-2 of Rodin, 1958). *Welwitschiophyllum* has instead stomatal crypts abaxially, with gum ducts and bands of hypodermal fibres adaxially (Fig. 3B). These fibres have been interpreted as palisade cells by Biemann (2005). However, hypodermal fibres are more likely to be preserved than the palisade cells due to their dense fibrous nature that strengthens the leaf. The continuous fibres throughout the adaxial surface indicate that the leaf was quite rigid.

In Dilcher et al.'s (2005a) original discussion (but not their description) of *Welwitschiophyllum* it was suggested that the leaves may have had a thickened cuticle. No evidence for this is seen in our sections, but the epidermis and cuticle are not preserved in the specimens examined here.

In the sole transverse thin section illustrated by Biemann (2005, Figs. V.7, V.8, and V12a), it is clear that the specimens studied have a similar level of preservation as our specimen UOP-PAL-MC0003, due to their similar weathered appearance and the reduced level of anatomical detail preserved. Biemann (2005) interprets what we believe to be stomatal crypts as stomatal cavities, then later (Fig. V.12) marks one cavity as a bundle of hypodermic fibres. Biemann (2005) also interprets the placement of vascular bundles, epidermis, and mesophyll, however, these structures are not obvious in the section illustrated, so we do not consider that the interpretation is completely supported by the images presented (see Biemann, 2005: Figs. V.7, V8 and V.12a). Despite this, we do consider that the likely degraded remains of vascular bundles are in a similar position to the lacunae present in our in our sections, represented by what we interpret as degraded vascular bundles. Extant *Welwitschia* has numerous vascular bundles and accompanying accessory bundles inside the leaf tissue, (see here Fig. 6B and Rodin, 1958), these accessory bundles are not present in our specimens, nor those described by Biemann (2005).

There are, however, some similarities in structure between *Welwitschiophyllum* and *Welwitschia* in thin sections, including the hypodermal fibres, tracheids and sunken stomata. The comparisons are limited because clear vascular tissue is not preserved in our specimens, nor in the section illustrated by Biemann (2005).

296 *5.3. Gum inside* Welwitschiophyllum *and* Welwitschia *leaves*

297 Recently the first example of gum found preserved in the fossil record was discovered in the
298 leaves of *Welwitschiophyllum* (Roberts et al., 2020). FTIR analysis of this gum revealed it to be
299 remarkably similar to that present in leaves of *Welwitschia* (Roberts et al., 2020). The spectra generated
300 for the two gums are almost indistinguishable from each other and share key features in their spectra (a
301 very large hydroxyl peak at ~3400 cm^{-1}, peak absence at 1516 cm^{-1} and a very strong peak at 1077 cm^{-1}
302 (Fig. 5, Roberts et al., 2020). Further characterization of the gum is planned. Elongate, thin gum ducts
303 (lying parallel to the leaf axis) in *Welwitschiophyllum* are constituent within the leaf, i.e. they occur
304 regularly, and even have a principle and a secondary duct arrangement (Fig. 4D and Roberts et al.,
305 2020).

306 Gum, a water soluble polysaccharide, holds varying functional roles within plants, its
307 constituent presence in *Welwitschiophyllum* could be food storage, structural support, wound sealing
308 (to prevent water loss) or as a result of a pathology (e.g. fungal infection - gum ducts formed during
309 injury followed immediately by fungal infection can form several tangential rows: Nair et al., 1980;
310 Nussinovitch, 2010; BeMiller, 2014), although we regard the number of ducts more likely indicates a
311 structural, storage or sealing role. In cases of traumatic gum formation, the gum appears unstructured
312 and only very irregularly present (Fahn, 1988; Yamada, 2001). This is due to the different way the gum
313 is initiated. In traumatic gum formation (gummosis) the cell wall (which forms the gum) breaks down
314 and the subsequent amorphous gum appears at the point of the trauma. This is markedly different from
315 constituent gum that is instead found organised into consistently placed ducts.

316 Different types of *Welwitschia* leaf sections allowed us to visualise both the anatomy and any
317 potential gum. Our work shows that in all sections examined, regardless of sectioning/treatment
318 method, gum ducts are absent. The only potential example of any kind of leaf gum we found is
319 presented in Fig. 6C, which we have interpreted as a potential traumatic occurrence.

320 Historically, *Welwitschia* was thought to have constituent gum in both its leaves and stem
321 (Sykes, 1911; Rodin, 1958). However, published accounts reveal conflicting reports of leaf gum in

Welwitschia (Table 2. Bertrand, 1874; Sykes, 1911). It is clear from careful analysis of the images and text of the descriptions within these early studies that, in some cases, the likely erroneous interpretation from Sykes (1911) and perhaps a misunderstanding of the description in Bertrand (1874) was both accepted and propagated by subsequent authors (e.g. Takeda, 1913; Feustel, 1921; Rodin, 1958; Martens, 1971). Most illustrations and images of *Welwitschia* leaves lack gum ducts even when they are mentioned within the text (Table 2, and see Feustel, 1921; Rodin, 1958; Martens, 1971). The only two images detailing gum ducts are an incomplete drawing of a root with a 'resinous gland' half drawn at the edge of the section by Bertrand (1874, plate 1, fig. 2) and another in a leaf section by Sykes (1911, plate 17, fig. 1). We consider that the drawing by Sykes (1911, plate 17, fig. 1), is the source of this confusion. Sykes' illustration shows a cell-lined structure with the gum inside. However, we cannot verify the presence, neither from our sections nor from the remaining literature, of a secretory duct or blister in the leaves of *Welwitschia.* We believe that the interpretation of constituent gum in *Welwitschia* by Sykes (1911) could instead be due to sectioning through a bleb of traumatically-formed gum, and mistaking or assuming that the shape was contained within a cell-lined structure.

Table 2. Citations and descriptions in the literature regarding *Welwitschia* gum.

Literature	Terminology	Comments
Hooker (1863)	Gum	Lysigenous in the base (i.e. stem) and amorphous in the leaf. Gum not illustrated. See p. 12: 'The gum which exudes from the trunk, peduncles, and various parts of the inflorescence, and which is also found abundantly in small cavities of the parenchyma of the leaf and trunk, is formed by the collenchymatous swelling and subsequent deliquescence of the cellular tissue, as is shown at Plate XII. figs. 14,15 [our note the illustration is of the stem tissue]. Occasionally the spicular cells are involved in the forming collenchyma, and, being similarly acted upon, their superficial coat of crystals becomes mixed up with the mass. The gum is dry, transparent, pale yellow-brown, inodorous, and insipid. See also p. 18–19: Towards the middle of the leaf is a thicker layer of ordinary parenchyma) having cell-walls without markings, and almost empty cavities, with a few spicula, and occasionally groups of cells transformed into amorphous gum (collenchyma)' [our note: no gum illustrated].
Bertrand (1874)	Glandes résinifères	'Resiniferous glands' inside roots with illustration. See p. 7–8 and plate 1, fig. 2.

Literature	Terminology	Comments
De Bary (1884)	Mucilage sac	Doubts as to whether gum is constituent, but citing Hooker (1863). See fig. 187 [our note: an idealised *Welwitschia* section with possible sacs (labelled i, but not mentioned in caption)].
Sykes (1911)	Mucilage gland	Abaxial glands: see p. 181: a few mucilage glands occasionally appear on the lower side of the leaf. Only one illustration plate 17, fig. 1.
Takeda (1913)	Mucilage	Mentions mucilage canal presence. See p. 354–355: 'The Mucilage Canal. In the adult leaf one often notices the presence of mucilage canals. These occur between bundles, and always on the phloem side. They are round in transverse section and comparatively short, varying from a few millimetres to as much as 1 cm or more, and they run parallel to the long axis of the leaf. They arise lysigenously owing to deliquescence of certain mesophyll cells. Similar mucilage canals occur in all parts of plants, except in a very young seedling'. [our note: no gum illustrated].
Feustel (1921)	Schleimkanäle	Translated from p. 239: 'Mucous channels are often found in the adult leaf. Lies between bundles, always on the phloem [our note: abaxial] side. In cross section they show roundish diameter and are proportionate short, but varying from a few millimeters to 1 cm and more. They run parallel to the longitudinal axis of the leaf. Lysogenic origin'. [our note: no gum illustrated].
Rodin (1958)	Gum canals	Occasionally gum canals appear in the leaves mature plants. Also notes, gum canals always occur between vascular bundles on the lower side of the leaf adjacent to the phloem, as previously noted by Feustel (1921). Gum not illustrated.
Martens (1971)	Canaux lysigènes (gommes ou mucilages)	We translate p. 96: 'Secretory tissues are the products of lysogenic canals with gum or mucilage occurring between bundles, and always on the phloem side (Sykes, 1911)'. No gum illustrated.

5.4. Limits of preservation in Welwitschiophyllum

The preservation of *Welwitschiophyllum* impacts what can be observed. The best anatomical preservation comes counterintuitively from a weathered specimen UOP-PAL-MC0003, whereas the specimens (UERJ 13-P1 and UERJ 14- P1) that contain gum are found as unweathered specimens and appear to lack anatomical detail due to slight compaction and pyritisation. That gum is preserved in the unweathered material is more likely because it has undergone significantly less (or even none) meteoric weathering. Clearly, the unweathered specimens still had surrounding tissue intact protecting the highly water soluble gum. However, we cannot yet satisfactorily explain why the apparent better anatomical preservation occurs in weathered material, although we have been only permitted to section a few leaves.

The lack of vascular tissue present in the thin sections could be due to the high water content of the vessels, which are easily pyritised and thus the definition of the vascular tissue was lost due to mineral overgrowth. Conversely, hypodermal fibres are more likely to be preserved due to their dense fibrous nature. Despite the absence of xylem elements in thin sections under SEM, tracheids with pits can be seen (Fig. 3C, D and E). This preservation could be due to tracheids having a heavily lignified, three-layered secondary cell wall that is resistant to degradation, allowing their survival even though they are water conducting (Friedman and Cook, 2000).

5.5. Possible convergent features of Welwitschiophyllum *and* Welwitschia *leaves*

While *Welwitschiophyllum* shares some morphological and anatomical characteristics with *Welwitschia* leaves, these also occur in many other arid-adapted plants. In particular, stomatal crypts are often found in arid-adapted plants, where it is thought they facilitate diffusion of CO_2 from the abaxial surface to the adaxial surface in thicker leaves, and lessen the exposure of the stomata to environmental conditions (Hassiotou et al., 2009). *Welwitschiophyllum* was a coriaceous leaf and thought to have lived in an arid habitat, where stomatal crypts would be beneficial by reducing the distance of CO_2 diffusion to the adaxial surface of the leaf. Many plants with stomatal crypts carry them on the abaxial surface of the leaf (Hassitou et al., 2009; Roth-Nebelsick et al., 2009; Goldenberg et al., 2013), thus supporting our identification of abaxial and adaxial surfaces in *Welwitschiophyllum*.

Other features of *Welwitschiophyllum* that could be considered convergent include: coriaceous leaves, parallel venation, and a curved base. These can be seen in various fossil leaves: *Dracaena tayfunii* Denk et al., 2014, *Desmiophyllum gothanii* Florin, 1936, *Protoyucca shadishii* Tidwell and Parker, 1990, *Paracordyline* Conran and Christophel, 1998, *Pandanites* Tuzson, 1913, *Doryanthites* Berry, 1914, as well as numerous extant flora. The morphological similarity of *Welwitschiophyllum* to many other fossil leaves requires further investigation to determine botanical affinity.

Parallel leaf venation (without a midrib) as seen in *Welwitschiophyllum* is relatively common today in some monocots such as the Agavoidieae (e.g., *Agave*, *Yucca*) and across some Poales (which

includes the Bromeliaceae and Poaceae). Monocots are reported from the Crato Formation, but are quite distinct in their leaf shape and venation: *Spixiarum* Coiffard et al., 2013, *Cratolirion bognerianum* Coiffard et al., 2019, both having two vein orders.

Based on our new data we suggest that the affinity of the plant to which *Welwitschiophyllum* leaves belong is still unclear, since morphologically and anatomically many features observed could have resulted from convergence. There are some key differences including likely abscised, smaller fossil leaves, compared to perennial and ever-growing *Welwitschia* leaves and the differentiation between the abaxial and adaxial sides of the fossil leaf, but not in *Welwitschia* leaves. What is striking, however, is the presence of gum in both plants. However, even here there are clear differences. There are the regularly occurring gum ducts in *Welwitschiophyllum*, but possibly only traumatic gum blebs found in *Welwitschia* leaves. Based on the balance of the evidence so far, and until a whole plant can be fully reconstructed, we are still tentative with the definitive placement of *Welwitschiophyllum* in the Gnetales.

6. Conclusion

The original description (Dilcher et al., 2005) of *Welwitschiophyllum* related it to *Welwitschia* using the following characteristics: the isobilateral form of the leaves, possible thickening of the epidermis, triangular elongated leaf shape with a wide base, longitudinal splitting from a frayed leaf apex and numerous parallel veins. This study has shown that *Welwitschiophyllum* shares some key features with extant *Welwitschia*, i.e., having long, coriaceous, parallel veined leaves that produce gum and the presence of hypodermal fibres. However, there are some notable differences such as in the abaxial placement of stomatal crypts and solely adaxial hypodermal fibres seen in the fossil, whereas the extant plant has these on both sides of the leaf. There is no preserved evidence of epidermal thickening in the fossil leaves examined here, unlike that in *Welwitschia*. The method of gum production also differs between the two taxa, with *Welwitschiophyllum* having constituent gum ducts and *Welwitschia* amorphous traumatic gum formation. The frayed apex, present in many leaf species, is

not considered a dependable character. These characteristics used to define the botanical affinity of *Welwitschiophyllum* to *Welwitschia* must be used with caution, as they could be the result of convergence. Whilst the new anatomical data of *Welwitschiophyllum* revealed more detail than previously known and strengthening the likelihood of this plant belonging to an arid environment, it cannot yet definitively determine the relationship of *Welwitschiophyllum* to *Welwitschia*.

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Declaration of interest: None.

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562

563 **Figures**

564 

565 **Fig. 1.** Fig. 1. Locality map. (A) Map of South America with the location of the Crato Formation (north-east
566 Brazil) marked. (B) A detailed outline of the Chapada do Araripe, and the outcrop of the Araripe Group
567 (comprising of Ipubi, Crato and Rio da Batateiras formations), the Exu Formation and the Nova Olinda
568 Member (the fossil-bearing horizon of the Crato Formation). Labelled spots indicate towns.

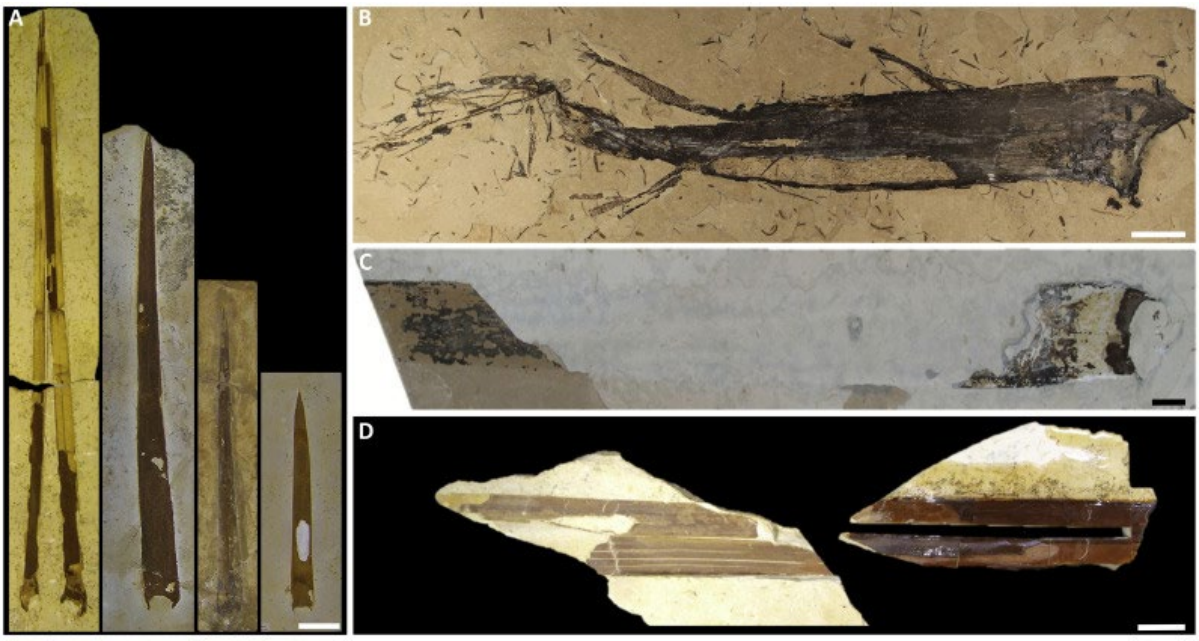
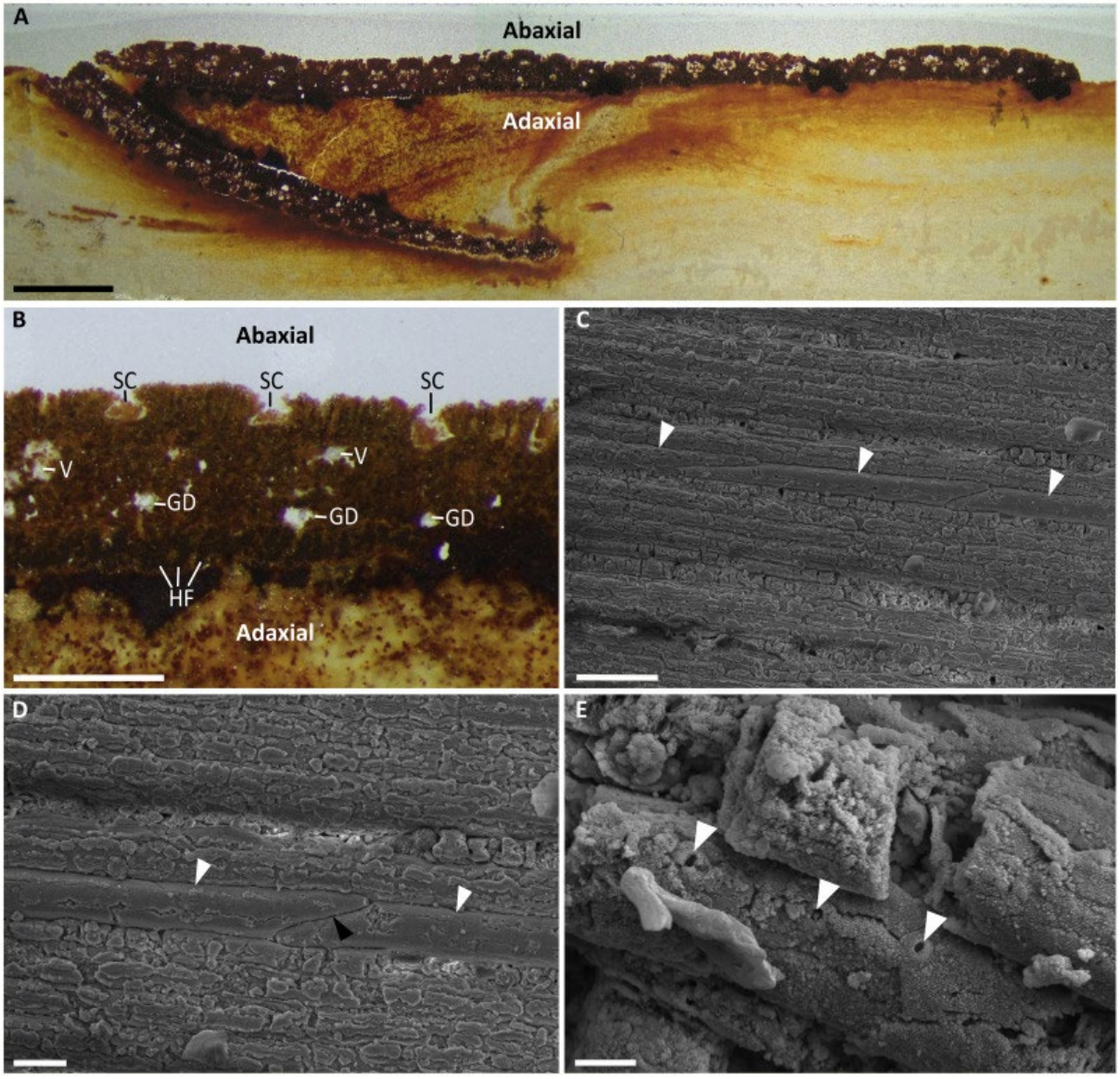
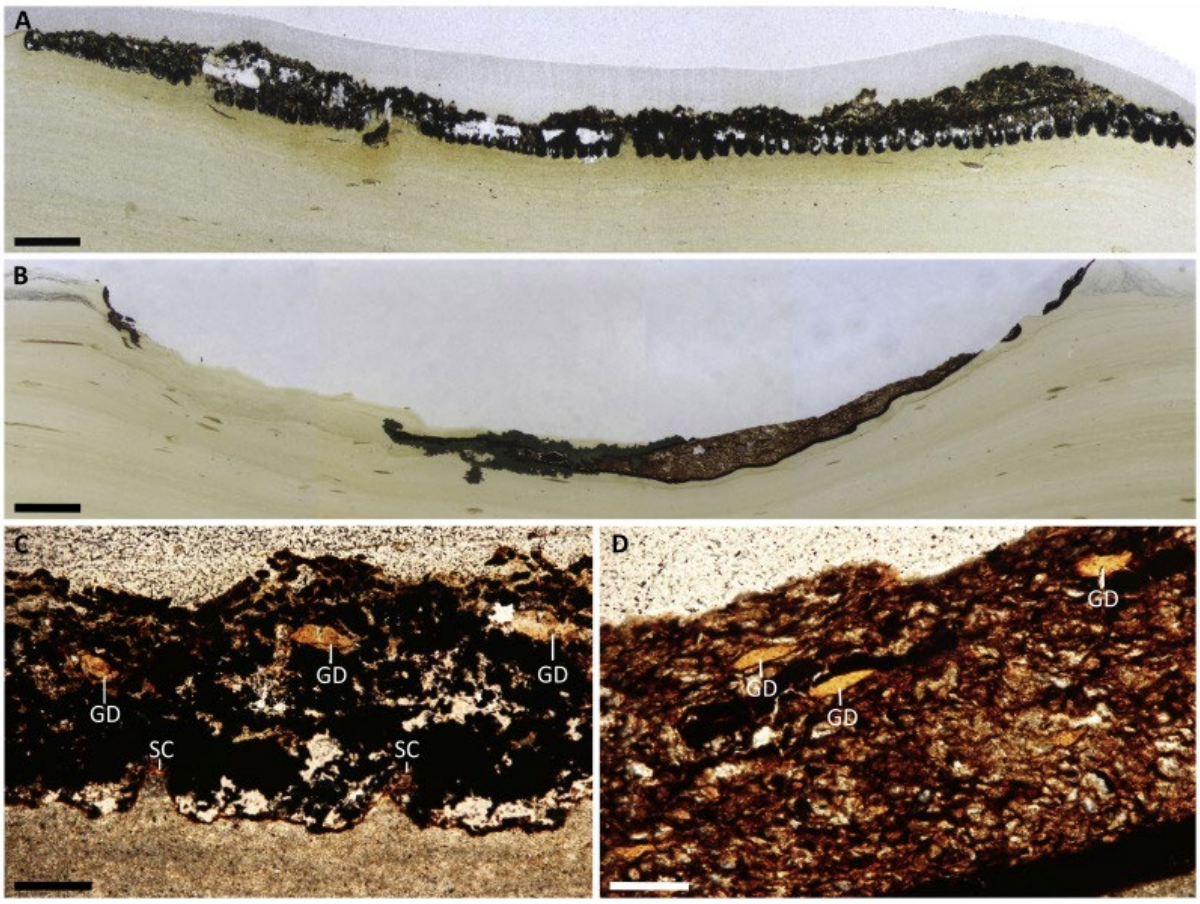


Fig. 2. The fossil leaf taxon *Welwitschiophyllum brasiliense*. (A) Specimens of *Welwitschiophyllum* leaves displaying a range of sizes. (B) Unweathered specimen with frayed apex (UERJ 13-P1). (C) An incomplete, unweathered specimen that has been partially covered in sediment (UERJ 14-P1). (D) Incomplete weathered specimen that has folded over in the sediment (UOP-PAL-MC0003). Scale bar represents 80 mm (A) and 20 mm (B, C, D).



575

576 **Fig. 3.** Thin section and SEM images from a folded *Welwitschiophyllum brasiliense* specimen (UOP-PAL-
577 MC0003). This specimen is orientated with the abaxial leaf surface uppermost. (A) Thin section
578 overview with abaxial and adaxial surfaces labelled (B) Thin section showing the anatomy preserved:
579 SC, stomatal crypts; V, degraded vascular tissue; GD, weathered out gum duct; HF, hypodermal fibres,
580 abaxial and adaxial surfaces labelled. (C) SEM image of connecting tracheids (tracheids indicated using
581 white arrow heads). (D) SEM image showing the typical way in which tracheids connect (tracheids
582 indicated using white arrow heads and the connection indicated using black arrow heads). (E) SEM of
583 the pits on a tracheid indicated using white arrow heads. Scale bars represent 2 mm (A), 500 µm (B),
584 100 µm (C), 30 µm (D), and 10 µm (E).



585

586 **Fig. 4.** Thin sections from two specimens of *Welwitschiophyllum* (UERJ 13-P1 and UERJ 14-P1). (A)

587 Overview thin section of UERJ 13-P1. (B) Overview thin section of UERJ 14-P1. (C) Detailed view of UERJ

588 13-P1 showing stomatal crypts (SC) and gum ducts with gum present inside (GD). (D) Detailed view of

589 UERJ 14-P1 gum ducts with gum still present inside. Scale bars represent 2 mm (A, B) and 200 µm (C, D).

590

591

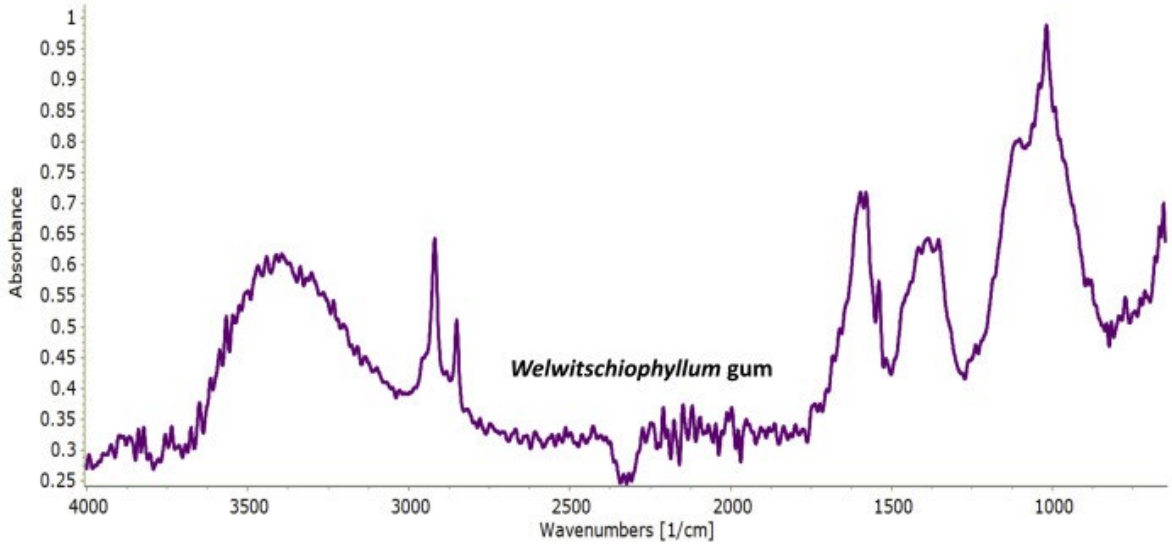


Fig. 5. ATR spectrum of gum recovered from fossil *Welwitschiophyllum* leaves (Specimen UERJ P1-13), see Roberts et al., 2020.

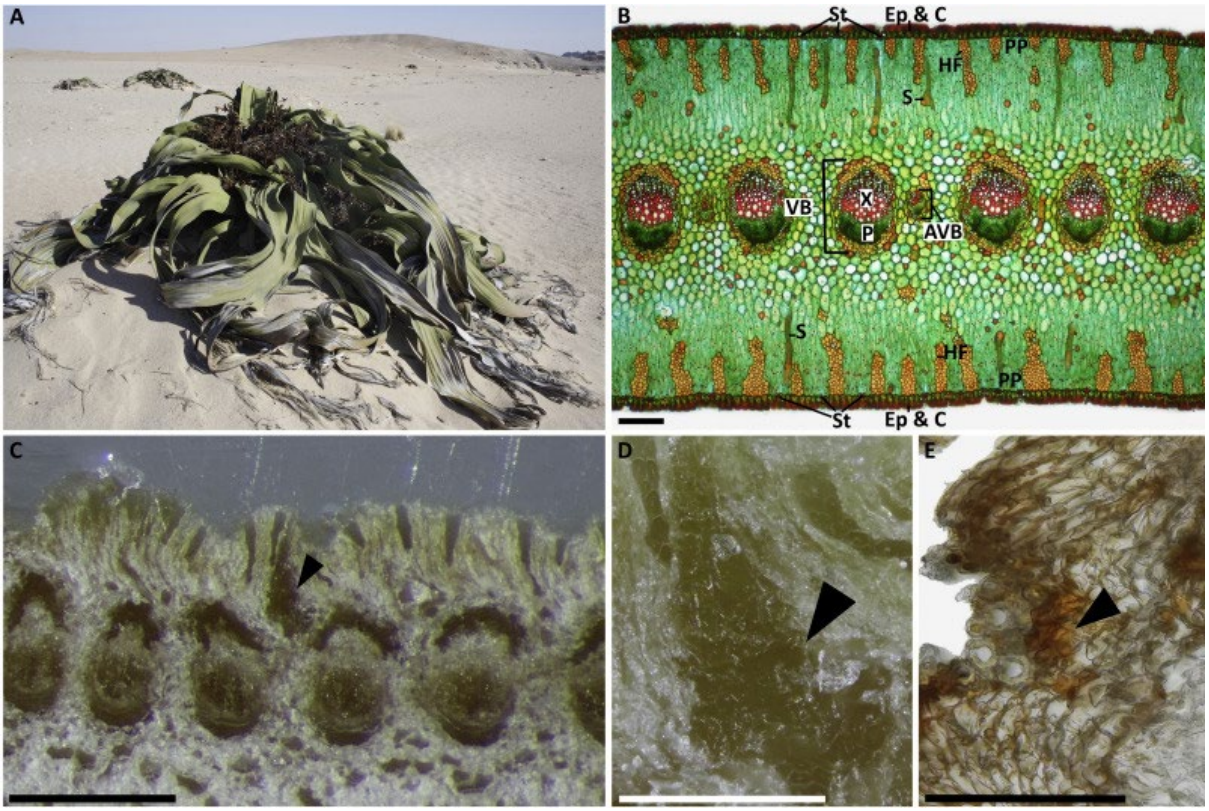


Fig. 6. *Welwitschia mirabilis* overview, thin sections and paraffin sections. (A) Plant in the Namib Desert (B) Stained thin section of a mature leaf showing anatomy: Ep & C, epidermis and cuticle; St, stomata; PP, palisade parenchyma; HF, hypodermal fibres; S, sclerids; VB, vascular bundle; AVB, accessory vascular bundle; X, xylem; P, phloem. (C) Paraffin section of mature leaf with black arrow indicating traumatic formation of gum. (D) Detailed view of (C) with black arrow head indicating of the traumatic gum showing its amorphous nature. (E) Traumatic gum formation indicated by a black arrow of a callus. Scale bars represent 200 µm (B), 500 µm (C) 100 µm (D) and 200 µm (E). Photo credit for 5A to Drs Christa Hofmann and Hugh Rice.