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New insights on the affinities, autoecology, and habit of the Mesozoic fern *Weichselia reticulata* based on the revision of stems from Bernissart (Mons Basin, Belgium)

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ABSTRACT

The Mesozoic is a key period in fern evolution, with the rise of most modern families. *Weichselia reticulata* is a widely distributed Jurassic-Cretaceous fern that has been suggested to belong to the Matoniaceae or possibly the Marattiaceae. The most accepted classic whole-plant reconstruction for this species is based on stem and foliage material from the Barremian/Aptian locality of Négresse (Bernissart, Mons Basin, Belgium). In this work, two of these stems are revised and analysed by CT-scan imaging, providing new information on their internal anatomy and external morphology. The results show that *Weichselia reticulata* has a unique anatomy, distinct from all other extant or fossil ferns. Stem external morphology suggests adaptations to stressful environments, as it presents scale insertions, and a thick cortex. Especially noteworthy is the presence of structures interpreted as aerophores or nectaries at the base of putative roots and petioles that could suggest a need for extra ventilation of the frond or interactions with animals. While these new results do not settle the question of the systematic affinities of *Weischelia*, they provide new information about its autoecology and allow us to test the validity of previous whole-plant reconstructions.

Key words: *Weichselia reticulata*, Bernissart, fern anatomy, Early Cretaceous, plant reconstruction, autecology.

INTRODUCTION

Today ferns represent the second largest group of vascular plants, with more than 300 genera and several thousand species (Bierhorst, 1971; PPG I, 2016). Particularly diversified, they have explored a wide range of morphologies and anatomies through time (Tidwell and Ash, 1994). After a first evolutionary radiation in the Paleozoic, the Mesozoic is a key period for the group that sees the rise of most modern families (e.g. Niklas et al., 1983; Lehtonen et al., 2017).

Weichselia reticulata (Stokes and Webb) Fontaine is a widespread Mesozoic fern, ranging in age from the Bathonian (Middle Jurassic) to the Cenomanian (Upper Cretaceous) and geographically from around 60°N to 60°S (Blanco-Moreno et al., 2018). It was first described from the English Weald as *Pecopteris reticulata* (Stokes and Webb, 1924), based on small charred fragments of vegetative fronds that are the most frequent type of remain of this fern (Fig. 1C). Unambiguous stem material is very scarce, and it is only known by a few specimens coming from the Cran du Nord locality (Bernissart colliery, Négresse mine shaft, Belgium). This material was first studied by Bommer (1910) but it is Alvin (1971) that provided its most detailed description.

Even though *W. reticulata* was widely distributed and is often very abundant in the localities where it is present, its systematic affinities remain unclear. It is often assigned to the Matoniaceae because of the organisation of the leaves (Bommer, 1910; Alvin, 1968; Alvin, 1971; Van Konijnenburg -Van Cittert, 1993; Sender, 2015). However, based on the work of Bommer (1910) and focussing on anatomical characters only, Edwards (1933) suggested a close relation with *Paradoxopteris* Hirmer from the Early and early-Late Cretaceous of North Africa (e.g. Hirmer, 1927; Edwards, 1933; Koeniguer, 1966; El Afty et al., 2019), which is close to Marattiaceae. A few authors also suggest a relation to this family based on anatomy and fertile structures (Zeiller, 1914; Silantieva and Krassilov, 2006).

Weichselia has been recovered from fresh water deposits such as lakes or rivers (Seward, 1900; Carpentier, 1927; Daber, 1968; Barthel and Boettcher, 1978; Barale, 1979 ;

Harris, 1981; Aguirrezabala et al., 1985; Ross and Cook, 1995; Batten, 1998; Diéguez and Meléndez, 2000; Gomez et al., 2008), as well as from brackish habitats such as marshes, deltas, estuaries or lagoons (Batten, 1974; El-Khayal, 1985; Román Gómez, 1986; Shinaq and Bandel, 1998; Barale and Ouaja, 2001; Lyon et al., 2001; Gomez et al., 2002; Barale and Azar, 2004; Almendros et al., 2005; Diez et al., 2005; Silantieva and Krassilov, 2006). Due to the xeromorphic traits observed in this genus (Alvin, 1974), some authors suggest that *Weichselia* inhabited dune regions in marine areas (El-Khayal, 1985), while others believe this fern was adapted to extreme drought conditions and attribute its presence in wet areas to transport from its natural habitat to fluvial ecosystems via flooding (Alvin, 1974). The high abundance of burnt remains of *Weichselia* in the fossil record has also led some authors to suggest it was an early successional plant (Barral et al., 2016).

To date there have been five main reconstructions of the general habit of *Weichselia reticulata* (Fig. 1A). Following the first reconstruction by Bommer (1910), Daber (1968) proposed a new one based on pedate petiole heads found in Quedlinburg (Barremian, Germany) that were interpreted as stems with a crown of radiating pinnate fronds. Alvin (1971) refuted this reconstruction and proposed the most accepted one to date. He described an upright stem with petioles that are spirally arranged and putative rooting organs produced in the opposite direction of the petioles. Sterile and fertile pinnae are separate and consist of radially disposed primary pinnae inserted in a pedate head. More recently, Sender et al. (2015) published a new reconstruction of this species based on a fertile pedate head from the Albian of Teruel (Spain). They represented a vegetative frond at the apical end of the stipe and a fertile frond at the end of a lateral ramification of the stem. Finally, Poyato-Ariza and Buscalioni (2016) suggested another reconstruction, based on material from Las Hoyas (upper Barremian, Cuenca, Spain). In this case, the general appearance of the plant is that of an extant tree fern, with a wide, tall, upright stem and a crown of fronds with petiole heads bearing radially disposed pinnae at the top.

To provide new information on *Weichselia*, we undertake here a revision of the external morphology and anatomy of the specimens studied by Alvin (1971) using µCT-scan imaging and we calculate parameters for the reconstruction of the plant's habit. A comparison with extant and fossil ferns allows us to propose (1) new insights about the possible systematic affinities of *Weichselia*, (2) additional clues about its autecology, and (3) guidelines for an accurate reconstruction of its habit.

GEOLOGICAL SETTING

Bernissart is located 25 km west of Mons, in southwestern Belgium, in the northern part of the Mons basin (Baele et al., 2012) (Fig. 2 A). This basin corresponds to an east–west subsiding zone where Meso-Cenozoic sediments accumulated. Rather small, the subsiding area (40 by 15 km) is mainly controlled by intrastratal dissolution of deep evaporite beds in the Mississippian (Carboniferous) basement. This dissolution process also led to the creation of several sinkholes, or natural pits (Spagna et al., 2012; Quinif & Licour, 2012). The natural pits acted as traps for the sediment, fauna, and flora present there at that time.

Three sinkholes have been recognized around Bernissart (Fig. 2B). They are the North, the South, and the Iguanodon sinkholes. The latter yielded the famous Bernissart Iguanodons. They were found in a Barremian/Aptian lacustrine clay, attributed to the Sainte-Barbe Clays Formation (Cornet & Schmitz, 1898; Cornet, 1927). The age of this formation has been determined based on palynologic data, based on sediments from the Iguanodon Sinkhole, as ranging from the middle Barremian to the earliest Aptian (Dejax et al., 2007).

The North Sinkhole was encountered in 1906 during the digging of a connecting gallery at a depth of 160 m. It started from the pit n°1 (called Négresse) in direction of the north. The gallery entered the sinkhole on its southern part and continued north for 164 m. The Wealden sediments are represented by dark grey to blue clays containing abundant charcoalified plant remains between 109 and 126 m from the south margin of the sinkhole (Cornet, 1927; Delmer and Van Wichelen, 1980). The exact position of the specimens is unknown but appear to originate from lithological unit δ (see arrow on Figure 2C) that corresponds to a dark clay with abundant charcoalified and lignified plant remains.

No detailed sedimentological analysis has been performed but the occurrence of sandy layers interbedding the clays as well as the occurrence of larger plant fragments could indicate a slightly more riverine environment than for the Iguanodon pit of Bernissart that is interpreted as lacustrine (Van den Broeck, 1898) or lacustrine to swampy (Yans, 2007; Schnyder et al., 2009; Spagna et al., 2012).

MATERIAL AND METHODS

Material

The material studied consists of stems, petioles, and rachises preserved as lignite that were assigned to *Weichselia reticulata*. They were collected in the Cran du Nord locality (Bernissart colliery, Négresse mine shaft, Belgium) and are housed in the Royal Belgian Institute of Natural Sciences (RBINS) in (Brussels, Belgium). In most cases, the specimens are only slightly compressed. We follow Alvin (1971) in his distinction between the different organs (stems, petioles, roots) and surface features (e.g. crater-like marks, tubercles) for these specimens.

Material examined: IRSNB b 0229, 8424, 8425, 8426, 8427; RBINS-PBOT-935, 936, 955, 976, 1073, 06846-0024.

Additional material used in the comparisons: *Paradoxopteris* material figured by Edwards (1933); *Matonia* R.Br. Ex Wall thin-sections from the Cornell University Plant Anatomy Collection; *Danaea* Sm. material figured by Rolleri (2004); *Angiopteris evecta* (Forst.) Hoffm. material figured by Blomquist (1922); *Osmunda cinnamomea* L. thin-sections from the Cornell University Plant Anatomy Collection; *Cyathea* Sm. material figured by White and Turner (2017);

Platycerium aethyopicum Hook. material figured by Allison (1913); *Psaronius* Cotta material figured by Morgan (1959), and Rothwell and Blickle (1982).

Institutional abbreviations: MCCM-LH, Las Hoyas collection housed at the Museo de Paleontología de Castilla-La Mancha (Cuenca, Spain); IRSNB b and RBINS-PBOT, Palaeobotany collection of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium); NHMUK PB V, Palaeobotany collection of the Natural History Museum (London, UK).

Methods

CT-Scan data acquisition and image processing. For the anatomical study of *Weichselia reticulata* two specimens of stems of this species collected from the locality of Négresse, IRSNB b 8424 and 8425, and housed at the RBINS, were imaged by µCT-scan at the RBINS (Brussels, Belgium). Scanning was completed using a RX EasyTom 150, with copper filter. For IRSNB b 8424, images were generated at a voltage of 145 kV and a current of 231 µA, with a set frame rate of 12.5 and 8 average frames per image. This generated 1440 images and a voxel size of 0.0609096 µm. For IRSNB b 8425, images were generated at a voltage of 139 kV and a current of 480 µA, with a set frame rate of 12.5 and 7 average frames per image. This generated 1440 images and a voxel size of 0.0816001 µm. Reconstructions, were performed using 3X-Act software from RX Solutions. The images obtained were reduced with the “binning” plugin in ImageJ 1.49v (Schneider et al., 2012). Segmentation, visualization and analysis were performed using Avizo software on the reduced images: 3D models were produced from the µCT images, and from these, models of the vascular system via segmentation by contrast thresholds. The central strands of the stem in both specimens, and the petiole in IRSNB b 8425, were isolated by further segmentation by hand in order to more clearly observe the course of the central strands, and better identify the organ insertions. Posteriorly, the models were uploaded in Meshlab (Cignoni et al., 2008) and 3D-Slicer (Fedorov et al., 2012) where sections of the models were performed.

Despite the obvious advantages of μCT-imaging in terms of non-destructive methods, several limitations may exist and are related to the preservation of the material and the actual contrast existing between different structures. The preservation of the material studied here was not always ideal for scanning, and the differences in contrast of the different tissues were sometimes very small, making it difficult to observe minute anatomical details (Fig. 3D). Additionally, the chosen resolution was not sufficient to study the bundle morphology and structure in detail (Fig. 3D-E). These details have been observed on existing historic thin sections (Fig. 3A-C; Alvin, 1971).

Variables for reconstruction and comparison with other ferns. Stem diameter, bundle size and cortex thickness were measured on the specimens mentioned in the material section, except for *Angiopteris evecta* which was obtained from Blomquist (1922), and *Psaronius* from Rothwell and Blickle (1982). The largest measurement was recorded for each category. General information on the anatomy and morphology was observed on the specimens mentioned in the materials section, and from the literature. Growth habit categories, leaf area, and leaf mass per area (LMA) were obtained from Peppe et al. (2014) except for Leaf area of *Cyathea* (from Arens, 1997). The largest measurement was recorded for each category and data were consulted at the generic (not specific) level.

Three variables with biomechanical implications and interest for the reconstruction of the plant habit were also calculated using the measurements obtained in Table 1 and in Blanco-Moreno et al., (2019):

1. The leaf mass per area (LMA) was calculated following Peppe et al. (2014):

$$\text{Log LMA frond} = 4.207 + 0.252 * \log(\text{Petiole width}^4/\text{Leaf area})$$

Once the maximum area of foliage the stem can bear is obtained, the number of possible leaves can be calculated based on the mean area of a single leaf (estimated in Blanco-Moreno et al., 2019).

The work by Brouat et al. (1998) is based on spermatophytes, so we applied the method to other fern taxa with enough information on the number of leaves per node (*Matonia*, *Cyathea* and *Psaronius)* in order to test it.

RESULTS

The stem surface is always covered with millimetric tubercles and is sometimes irregularly creased (Figs 4A-B, 5G-H, and 6A). Alvin (1971) observed 5 types of scars on the Belgian material of Négresse identified as: petiole bases, radicular organs, sclerenchymatous tubercles, crater like marks, and large elliptical scars (interpreted as aerophores). We here redescribe these structures with the help of the new information provided by the µCT-scan imaging, including their size and anatomy.

Petiole bases. Material. IRSNB b 8424, 8425; RBINS-PBOT-935

There is no difference between the surface of the stem and the petiole, they are all covered by the same creases and tubercles (Fig. 4B). The maximum width of the petiole ranges from 1.57 cm in RBINS-PBOT-935 up to 4.7 cm in IRSNB b 8425. Two petioles were observed on specimen IRSNB b 8424 measuring 2.4 and 2.3 cm in maximum width. Petioles depart at a 40° to 50° angle from the stem. This angle increases distally due to the curvature of the stem (Fig. 4C). Additionally, all specimens have elliptical scars associated with the base of the petiole that will be described in detail later.

Anatomically, petioles are formed by many meristeles from the stem's central rings. The meristeles in the petiole are placed in rows near the insertion (Fig. 6C) and become concentric distally, with up to of 10 concentric rings in IRSNB b 8425 (Fig. 4A).

Radicular organs. Material. IRSNB b 8424

The anatomy of specimen IRSNB b 8424 shows some strands that are orientated in the direction opposite to the petioles. This could be interpreted as a possible radicular organ (Fig. 4D). The preserved width is 3.5 cm and it is inserted at a 50° angle. Similarly to the petioles, the surface is ornamented and there is an elliptical scar associated to the base of the organ (Fig. 3B). The anatomy is also very similar and formed by many meristeles from the stem's central rings, with a semi-circular transverse section (Fig. 4D). The only difference between petioles and the putative rooting organ in IRSNB b 8424 is the direction of the vascular strands, which is opposite to each other.

Tubercles. Material. IRSNB b 8424, 8425, 8426, 8427, RBINS-PBOT-935, 936, 955, 976, 1073, 06846-0024.

Tubercles are present at the surface of most stems and petioles present in the collection (Fig. 4A-B). They cover the whole length of petioles up to the petiole heads, where they are especially found on the adaxial side. This ornamentation is also observed on the abaxial side of the broader primary rachises. When present, they completely cover the surface of the plant. They are clearly visible in specimens without creases, but are also present in very irregular, creased ones. They are millimetric, but variable in size and shape. When imaged by the µCT-scan they present the same density as the rest of the surface.

Crater like marks. Material. IRSNB b 8426.

These structures have only been observed on one specimen already figured by Alvin (Pl. II, fig. 2, 1971). The specimen is very deformed, and it is not possible to determine the part of the plant it belongs to. The surface is covered by tubercles, which are disrupted by these marks (Fig. 4A). They are slightly depressed in relation to the rest of the layer and are elliptical to more or less circular. The surface is smoother, lighter in colour, and shows no identifiable structures. They measure 0.19 by 0.17 to 0.34 by 0.15 cm.

Large elliptical scars. Material. IRSNB b 8424, 8425, 8427; RBINS-PBOT-935.

These structures have been observed on three stem fragments, and two disarticulated scars are present in the collection (Figs 5A and G-H). Their outline is clearly defined, and they are slightly depressed in relation to the rest of the stem, they measure 0.64 to 2.8 cm by 0.73 to 1.54 cm. Two differentiated zones can be observed: a central elliptical to circular rugose protruding area measuring 0.49 to 1.49 cm by 0.862 to 0.35; and a peripheral area that surrounds the central zone, which has more or less linear yet irregular marks that radiate from the central zone towards the margin of the scar (Fig. 5A, and G-H). The internal face of the scars, which can be observed in the disarticulated specimens, shows no signs of the two zones previously described. The surface is flat but rugose and covered by tubercles, their appearance is similar to the outer part of some of the stems but the tubercles are smaller (Fig. 5A). These structures are not connected to the vascular system. Indeed, where the scars are present the vascular tissue is cut off and there is an area with no vascular tissue at all just underneath these structures (Fig. 5B-E, and I-J).

These scars are present at the base of possible petioles and rooting organs, laterally oriented towards the abaxial side, only on one of the sides in specimens RBINS-PBOT-935 and IRSNB b 8424 (Fig. 5B), and one on each side in the case of the best preserved specimen (IRSNB b 8425, Fig. 5G-I). In specimens RBINS-PBOT-935 and IRSNB b 8425 a smaller scar is also present directly above (distally) the other scar mentioned.

Stem anatomy. Material. IRSNB b 0229, 8424 and 8425.

The preserved diameter of the stem is 7.14 cm in IRSNB b 8425, and 3.64 cm in IRSNB b 8424. The stems are curved in both specimens, at a 115° angle in IRSNB b 8425 and at a 145°

angle in IRSNB b 8424. The curvature in IRSNB b 8425 occurs at the level where a petiole is borne, and in IRSNB b 8424 where a possible root is borne (Fig. 4C-D and 6B). No branching has been directly observed, however, at the apical-most part of specimen IRSNB b 8424 the disposition of the vascular bundles could suggest dichotomous branching (Fig. 6D-G).

The internal anatomy of the plant consists of a highly dissected polycyclic dictyostele, organized in 9 concentric rings of irregularly shaped vascular bundles, which are generally C shaped, and measure 0.15 cm to 0.22 cm (Fig. 6). The density of vascular tissue is very high, bundles are present from the centre to the cortex. Alvin (1971) mentioned the presence of secretory canals in the stem of *Weichselia reticulata*, alternating with the bundles. These structures were observed in the thin sections but are not clearly identified in the µCT-scans due to the lack of resolution, although specimen IRSNB b 8424 does show some very dense spots in a similar position to the possible canals observed in the thin sections (Fig. 3D). The possible secretory canals observed in the thin sections consist on circular structures measuring up to 0.05 cm, with a single layer of cells in the periphery with a similar preservation to the vascular tissue of the plant, and a dark centre (Fig. 3C).

The disposition of petioles and putative roots in the specimens studied (Fig. 7) could be helicoidal or alternate in IRSNB b 8424. Lateral organ production observed in IRSNB b 8425 is less frequent, and there is only one petiole, so the phyllotaxy can not be inferred.

Calculations for reconstruction

In order to attempt a reconstruction of the whole plant, certain characters dealing with the morphology, architecture, and anatomy of *Weichselia reticulata* have to be analysed (Table 1). Important variables for plant reconstruction can be then calculated using approximations obtained from living plants: the leaf mass, and maximum height of the plant, and the number of fronds per node (constrained by Corner’s Rules).

Leaf mass. The LMA for *Weichselia* is 317.2g/m^2 to 352.5 g/m^2, calculated following Peppe et al. (2014) based on measurements on the specimens published in Blanco-Moreno et al. (2019). This value could be an overestimate, as fronds with a large relationship between petiole width and leaf area (PW^4/LA) have a lower LMA than expected by the model, and in the case of *Weichselia* PW^4/LA is larger than all other ferns in the sample from Peppe et al. (2014). However, it must be noted that the architecture of the *Weichselia* frond, with a pedate head, is mechanically more similar to palmate fronds than pinnate fronds (Niklas, 1991), and the results in Peppe et al., (2014) show that the largest LMA correspond to palmate or simple fronds.

Height of the plant. The results calculated from the model are within the maximum height measurements in the literature (Table 2), bearing in mind they are first order of magnitude approximations. This supports the validity of the model for the estimate of the height in *Weichselia*, which would be up to 8.57 m according to the model.

Phyllotaxy and number of leaves per node. Estimation of the number of fronds in the crown following Brouat et al. (1998) results in a possible number of leaves that is similar to the values recorded for each taxon in the literature (Table 3). The number of leaves estimated for *Weichselia* by this method is therefore accepted as a valid estimate until more information can be obtained and would be of 1 to 2 leaves (Table 3).

DISCUSSION

Morpho-anatomical comparison of Weichselia *with other ferns*

In order to better understand the affinities, autecology, and habit of *Weichselia reticulata*, the fossil material analysed here is compared with extant and fossil fern taxa selected because of previously suggested systematic affinities (Edwards, 1933). It includes (1) *Paradoxopteris* which was suggested by Edwards (1933) as the stem of *Weichselia reticulata*, (2) Marattiales due to the affinities proposed mainly by Edwards (1933) and Silantieva and Krassilov (2006), and (3) Matoniaceae which is the most accepted sister group to *Weichselia* (e.g. Alvin 1971; Sender et al., 2015). We also include two other genera: *Cyathea* (Cyatheaeceae), for a comparison with an arborescent fern with a tall upright stem as has been suggested for *Weichselia* in some reconstructions (e.g. Poyato Ariza et al., 2016), and *Platycerium* Desv. (Polypodiaceae), which was found to be the only fern with a stele organisation more or less comparable to the here studied specimens.

External morphology and scars

The here observed ornamentation of the stems of *Weichselia* is very similar to what is seen in the Cyatheaceae and some Marattiaceae. The stem surface of the Cyatheaceae is covered by a hard and impervious sclerotic cortex. The gas exchanges are only made possible by the presence of small lenticel like tubercles filled with spongy tissue that act as pneumatodes (Bower, 1923). Another characteristic feature of this family is the presence of scales borne upon sclerenchymatous outgrowths that cover leaves and stems while young. Although the scales tend to fall in later ontogenic stages, the sclerenchymatous outgrowths tend to remain and are responsible for the characteristic ornamentation of the stem (Fig. 8B). The tubercles observed on *Weichselia* are devoid of spongy tissue and rather appear as solid structures. They are nevertheless much smaller than the epidermal outgrowths of Cyatheaceae to which they do not compare favourably. Some fossil and extant Marattiaceae also present similar surface features to the ones observed in *Weichselia*. *Angiopteris* Hoffm. and *Danaea* present scales associated to persistent structures at the base of the petioles that resemble the tubercles here described, although they are more dispersed (Fig. 8A).

The crater-like marks are only present in one specimen and don’t have a set morphology or size. They were probably produced by an external agent that damaged the plant’s outermost layer.

In contrast, the elliptical scars have a constant morphology and a specific position in the stem. Similar structures have however been described in other fern taxa. Their organisation is like that of some aquatic and wetland plant roots with radial lysigeny and wheel-shaped type aerenchyma (Jung et al. 2008). The lack of vascular tissue in the area however led us to discard this possibility. Alvin (1971) discussed these scars and proposed that they could represent aerophores. In ferns, there are two types of aerating structures: linear aerophores, sometimes termed pneumathodes, and nonlinear aerophores, sometimes termed pneumatophores or lenticels in the Marattiaceae (Davies, 1991). In respect to this, the elliptical scars on *Weichselia* would rather be described as lenticels or nonlinear aerophores, which are also present in the Cyatheaceae (Bower, 1923) and the Marattiaceae (Smith et al., 2006). Lenticels are generally very simple in ferns (Fig. 8C-D) with some exceptions such as in *Cyathea horrida* (L.) Sm. (White and Turner, 2012). In this species lenticels are more complicated and are similar to the ones observed in *Weichselia*. Additionally, some lenticels found on spermatophytes, with filling tissue and closing layers (Evert, 2006) very much resemble the structure observed in *Weichselia*. The existence of gas exchanging structures at the base of the petioles is frequently observed in ferns e.g. Marattiaceae, Plagiogyraceae, Cyatheaceae or Thelypteridaceae. In all these cases, as observed in *Weichselia*, the hypodermis is not interrupted (Davies, 1991). Pneumathodes in Cyatheaceae and *Saccoloma* Spreng. (Dennstaedtiaceae) are related to involutions (i.e., curving of the vascular system towards the centre of the axis) in the leaf traces (Bower, 1923 fig. 161, 162; Bower 1926 fig. 560). By contrast, in *Weichselia* they only create gaps in the vascular system directly below them, and they don't seem to be related with involutions in the petiole or the putative roots (Fig. 5E and G). Another organ that can be found at the base of fern pinnae that somewhat resembles the elliptical scars observed in *Weichselia* are nectary glands, which are for example present in the Cyatheaceae, in *Angiopteris,* and in *Platycerium* (White and Turner, 2012). In such structures, the vascular tissues do not enter the gland (White and Turner, 2012), this corresponds to what is observed in *Weichselia*. Generally, nectary glands are found at the base of second or third order pinnae and pinnules and are recurrent in the different orders of ramification of the frond (White and Turner, 2012). No such disposition has been observed in *Weichselia*. Figure 8B shows a possible nectary or large protruding aerophore at the base of the petiole in *Sphaeropteris intermedia* (Mett.) R.M. Tryon, in a very similar position to the ones observed in *Weichselia*.

Large radicular organs are not very frequent in ferns, although the Marattiaceae have large roots (Bower, 1923). The anatomy of the putative root observed in *Weichselia reticulata* has not been observed in any other fern. Other structures with negative gravitropism that could be similar to those observed in *Weichselia* are lateral ramifications described in the Cyatheales that grow into stolons that stabilize the tall trunks and permit the vegetative reproduction of the plant (Hallé 1965, 1966). These buds are situated under the leaves in the Cyatheales, the same position of the putative root in *Weichselia*. Additionally, the scarce record of fertile remains of *Weichselia reticulata* could be related to a dominant vegetative reproduction of the plant.

Anatomy. The anatomy of *Weichselia reticulata* is particularly divergent and appears to be different to all ferns that have been published so far. The results of the comparison of the Belgian material with a selection of fern taxa are summarised in Table 1, and Figures 9 and 10. Firstly, the type of stele apart (which is a polycyclic dictyostele), it is clear that the anatomy of *Weichselia reticulata* is very different from that of *Paradoxopteris*. The main differences reside in the size of the vascular bundles and the presence of auxiliary strands with round morphology that are alternate with the C-shaped meristeles in *Paradoxopteris* (Fig. 9G). Koeniguer (1966) separates *Paradoxopteris stromeri* Hirmer into two varieties. One with large vascular bundles which are more than 2.5 times larger than in *Weichselia*. A second with smaller bundles that have a mean size of 0.22 to 0.28 cm, which fits within the size range of the bundles in *Weichselia*. However, although not clearly visible in the µCT-scan images of *Weichselia*, vascular strands are more or less C-shaped in all rings observed in the thin sections. There is thus no evidence of the auxiliary strands typical of *Paradoxopteris* (Fig. 3A).

While *Matonia* has a curved rhizome (Fig. 8E) that could be compared to the curved axes of specimens IRSNB b 8424 and 8425, it can be distinguished easily in terms of anatomy by its polycyclic solenostele. *Phanerosorus*, the second genus of the Matoniaceae, also presents a polycyclic solenostele (Kramer, 1990).

Marattiaceae in general is one of the groups that most resembles *Weichselia*. They share a similar stele organisation with small bundles and many strands arising from the central ones going to the petioles and putative roots (Fig. 9). The extinct genus *Psaronius*, related to the Marattiaceae, has a similar anatomy to *Weichselia* (Fig. 10). The polycyclic dictyostele is also very fragmented, and is spirally arranged, presenting up to 6 cycles. However, the bundles are much larger, and the external part of the stem of *Psaronius* is surrounded by a thick layer of adventitious roots. The secretory canals observed in *Weichselia* have a clear epithelium and are similar to the mucilage canals found in the petioles of *Angiopteris evecta* (West, 1915).

Osmunda L. and *Cyathea* are not polycyclic, and strands are larger than in *Weichselia* for both taxa (Figs 9B and F). Finally, the general appearance of the anatomy of *Platycerium* is similar to *Weichselia*, with a very fragmented polycyclic dictyostele and many strands forming the petiole (Fig. 9C). However, *Platycerium* roots are not produced by the central strands and the bundles are smaller than in *Weichselia*. It thus appears that *Weichselia* has a unique stellar anatomy among known fossil and extant ferns.

Systematic affinities

The systematic position of *Weichselia* has been discussed since its discovery. It is quite clear from the results herein obtained that it presents a unique combination of characters that could suggest a relation with groups as distinct as the Marattiales or the Matoniaceae.

On the one hand, they present characters that are considered exclusive to the Marattiales such as the roots originating from the central bundles, the possible secretory canals, the sclerenchymatous tubercles on the surface and the apparent absence of endodermis (it has not been observed in this work and was not identified by Alvin (1971)). However, Marattiales do not generally share the same stem and frond organisation as *Weichselia*. Stems are generally massive in the Marattiales whereas in *Weichselia* they are more elongated, and Marattiales do not present pedate fronds.

On the other hand, the similarities with the Matoniaceae are mostly architectural. They share similar curved stems, dichotomous branching and frond organisations (Blanco-Moreno et al., 2019). Their anatomy however is rather different, *Weichselia* presenting a polycyclic stele while Matoniaceae have solenostelic steles. However, Allison (1913) studying *Platycerium* has argued that its polycyclic dictyostele could derive from the fragmentation of a polycyclic solenostele such as the one present in *Matonia*. Moreover, their size is not comparable, as the stems of *Matonia* have a mean thickness of 0.6 cm (Kato, 1993) and pinnae measure around 35 cm, whereas the rhizome width of *Weichselia* is around 7 cm and pinnae can measure more than 100 cm.

The very peculiar organisation of *Weichselia* renders comparison with other extant or fossil ferns difficult. The here obtained results unfortunately do not allow for a definite systematic assignation. Even if, at the end of this comparison, a relation with the Marattiaceae and Psaroniaceae seem to be possible, we believe that the inclusion of *Weichselia* within the Marattiales would be very doubtful considering the many specimens of this plant that have been studied and published so far. A comprehensive analysis of all organs must be performed.

Autecology

The external morphology and the LMA provide some insights to the possible autecology of *Weichselia reticulata*. Firstly, the presence of large elliptical scars at the base of the petioles, if interpreted as aerophores, indicates that the stem and petiole was in need of extra ventilation. This could be seen as an indicator of a partially submerged plant. However, most ferns have aerophores (Davies, 1991). Large aerophores at the base of the petioles or stems in fact facilitate gaseous exchange when the epidermis is protected by a hard sclerotic layer (e.g. Cyatheaceae) and/or when the petioles of the juvenile fronds are covered by mucilage while they unfurl (e.g. Palgiogyraceae). In this case, when the fronds are mature, leaf stomata take over the gas exchanges and the aerophores cease to be functional (Davies, 1991). The morphology of the elliptical scars of *Weichselia*, similar to lenticels with closing layers, suggests that it might have had the function of a temporary aerophore. The presence of possible mucilage canals and the large size of the fronds further justify for the need of extra ventilation while the frond unfurled. The tubercles of the outer, probably sclerotic, layer of the stems, petioles and primary rachises of *Weichselia* are similar to those covering the Cyatheaceae. They indicate that the plant might have been covered by scales or hairs. This sclerotic outer layer might also be the cause of the presence of aerophores.

If, on the other hand, the elliptical scars are interpreted as nectaries, an association with insects in order to avoid herbivory can be suggested. Nectaries in ferns seem to indicate an association with ants, which protect the fronds against herbivores (Koptur et al., 1982; Arens and Smith, 1998; Koptur et al., 2013). The fact that ants most probably appeared in the Albian, ca 110 mya (Grimaldi and Agosti, 2000), would rule out the association with these animals, at least in the early records of *Weichselia*. However, others such as spiders, parasitoids, predatory wasps, beetles, mirids or mites also feed on extrafloral nectar (Heil, 2015). Insects from Bernissart have not been thoroughly studied, although they are present (Godefroit, 2012). Terrestrial Hemiptera, beetles, wasps, and dipterans were present in the Upper Barremian locality of Las Hoyas (Delclòs and Soriano, 2016), where *Weichselia* is the most common fern remain.

Another explanation for the existence of fern nectaries has been suggested by Koptur et al. (1982), related to the elimination of metabolic by-products without an excessive loss of water in xerophytes. *Weichselia* has previously been interpreted as a xerophyte (e.g. Alvin, 1974; Watson and Alvin, 1996).

High LMA is found in plants under high irradiance (Poorter et al., 2009), and the position of the fronds in *Weichselia* suggests the sun would have fallen directly upon the leaves (Blanco-Moreno et al., 2019). Fern fronds live around 2 to 3 years at most (literature cited by Karst and Lechowicz, 2007), and a high LMA generally indicates the fronds were especially long-lived (Tanner, 1983; Karst and Lechowicz, 2007). This suggests *Weichselia* fronds were not shed regularly and grew at a lower relative rate (Poorter et al., 2009). This strategy is not very concordant with the interpretation of *Weichselia* as an early successional plant (Barral et al., 2016), but more so to a plant tolerant to fire (Watson and Alvin, 1996). *Weichselia* was most probably a re-sprouter like *Pteridium* Gleditsch as suggested by Scott et al. (2000), and some tree-ferns that are fire-tolerant and re-sprout from buds in their fibrous trunks after a fire (Ough and Murphy, 2004).

The environmental conditions of the habitat of *Weichselia reticulata* have been much discussed. Some authors suggest this fern was adapted to extreme drought conditions and attribute its presence in aquatic environments to transport from its natural habitat to fluvial ecosystems via flooding (Alvin, 1974). Others suggest these adaptations are related to high salinity habitats, and that *Weichselia* inhabited dune regions in marine areas (El-Khayal, 1985), or even that it was trophophyte in coastal wet ground that dried periodically (Daber, 1968). This study does not provide keys to the environment where *Weichselia* grew, however, it must be noted that some of the traits traditionally interpreted as xeromorphic might not be so. For example, the thick cuticles in ferns do not correlate with low humidity, instead they seem to be associated to cold and nutrient-poor environments (Kessler et al., 2007). Also, the presence of scales or hairs discussed in this paper, which were probably covering the stem and rachis of *Weichselia*, are related to protection from high insolation and not to aridity (Kessler et al., 2007).

Guidelines for reconstruction

We consider that the data herein obtained on the morphology, anatomy, and architecture of *Weichselia reticulata* does not allow for a complete reconstruction of the habit of the whole plant with enough confidence. However, it does shed new light on existing reconstructions and allows us to discuss which aspects are accurate or not.

Previous reconstructions of *W. reticulata* (Bommer, 1911; Daber, 1968; Alvin, 1971; Sender et al., 2015; Poyato-Ariza & Buscalioni, 2016; Fig. 1A) are mainly based on the external morphology and on some thin sections of very fragmentary material. The CT-scan models herein analysed provide additional information on the anatomy and allow for a more accurate description of the stems. Although the illustrations provided in the previous reconstructions are artistic, if both these representations and the comments provided by the authors are analysed together, they can be discussed in the light of the new information obtained in this study.

The general habit of the plant, represented by the stem and organ insertions, differs from one reconstruction to another. The stem is however always represented straight, upright and aerial. The analyses here performed nevertheless do not provide direct evidence for the stem being upright. Both specimens studied by µCT-scan are incomplete and one side of the stem is in each case missing. However, the results allow us to conclude that: (1) It is not possible to know if the stem is dorsiventral or radial. (2) The presence of the elliptical scars, either if they are aerophores or nectaries, in the basalmost part of the petioles suggests that the stem was not buried. (3) The fact that both specimens show a curvature of the stem argues against an upright or tall stem.

There are however arguments supporting the reconstruction of *Weichselia* with an upright stem. These are: (1) the high density of the vascular system similar to the vascular system in monocots such as *Dracaena marginata* Aiton (Fig. 11; Haushahn et al., 2014; Hesse et al., 2016) and (2) the orientation and origin of the vascular system in the acroscopic part of the petiole of IRSNB b 8425. Indeed, the analogy with *Dracaena marginata* can be further applied to the organisation of the petiole vascularisation that does not arise directly from the central strands and is perpendicular to the stem (Fig. 6B, 7B, and 11A). In this plant, the perpendicular vascular strands act as “tensile cables” that transfer bending loads (Fig. 11B; Haushahn et al., 2014). If the large fronds of *Weichselia reticulata* are inserted in a plagiotropic position, as it has been previously suggested (Blanco-Moreno et al., 2019), on an upright stem the vasculature of the petiole bases could similarly act as “tensile cables”. Fronds were large and most probably heavy (according to high LMA) and would need a good mechanical support at the petiole insertion. The asymmetric disposition of the “tensile cable-like” vascularization in the petiole could support an upright position of the stem. Nevertheless, even if the stems were upright, the plant would not have reached the height of the highest arborescent ferns (Recent tree ferns and *Psaronius*) according to the calculations following Niklas’ formula (1994) (see results section).

Roots are present in all reconstructions, but their organisation does not fit what is seen on the specimens. Root insertions are always too small. They are inserted at very large angles in comparison to the possible rooting organ observed in specimen Pbot-00000-0127. Bommer (1910) and Sender et al. (2015) draw them in a different position than observed in this study.

Petioles, although inserted at an excessively large angle, show a correct proportion in Bommer (1910). This is also the case for Alvin (1971). They are too small in relation to the stem width in Poyato-Ariza and Buscalioni (2016). Sender et al. (2015) suggest in their reconstruction that the fronds occur at the end of branches. Set aside that a possible branching of the stem has been described, petioles have definitely been observed, the pedate heads are thus not borne directly as the termination of branches. Finally, the Cycas like reconstruction of Daber (1968) does not fit any of the here discussed results and is considered as the less accurate of all proposed reconstructions.

The exact disposition of the plant fronds could not be ascertained from the studied specimens. The fronds are not opposite and the anatomy shows that there could be two petioles close to each other, possibly three if the stem is interpreted as dorsiventral and the putative root as a petiole. It is however impossible to know whether they are disposed in a half helix arrangement (more plausible if the stem is dorsiventral) or in a complete helix. The calculations performed following Brouat et al. (1998) suggest there could be up to two fronds per node, possibly ruling out the complete helix disposition. On the other hand, the position of the putative radicular organ, alternating with the petioles, and apparently associated with the younger petiole in specimen IRSNB b 8424, is similar to the root disposition in upright stems with helicoidally disposed leaves of the Marattiaceae (Bower, 1926), especially of the genus *Danaea*.

CONCLUSIONS

The revision of the material from Négresse that provided the first whole plant reconstruction of the emblematic, yet mysterious fern *Weichselia reticulata*, has yielded interesting results. No evidence has been found to refute the assignation of the material to *Weichselia reticulata.* Although anatomically distinct to all consulted fossil and extant ferns, this study suggests some affinities with the Marattiales. This link is further supported by the surface morphology of the stem. Similarities with the Cyatheales are interpreted as evidencing similarities in their autecology. Further analysis including thin sections of this and other material are necessary in order to study the secretory canals, and corroborate the absence of endodermis, two characters that would more clearly link *Weichselia reticulata* to the Marattiales.

A whole plant reconstruction is not possible with the material at hand, but a more precise description of the external “scars” and stem anatomy has been obtained. Some of the inferences by Alvin (1971) have been corroborated, such as the presence of aerophores (or nectaries) and “rooting organs”. Additionally, the variables calculated for the reconstruction have provided some insights on the possible habit of *Weichselia*, which will be very valuable for future reconstructions based on more data and material. The new data obtained from the stems and fronds also allows for further interpretations of the autecology of this cosmopolitan fern.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Virtual Collections of the RBINS:

Specimen IRSNB b 8424: http://virtualcollections.naturalsciences.be/virtual-collections/paleontology/paleobotany/weichselia-sp

Specimen IRSNB b 8425: http://virtualcollections.naturalsciences.be/virtual-collections/paleontology/paleobotany/weichselia

The slides of the CT-scan must be requested to the curator of the RBINS Collections of Paleontology, from the RBINS Scientific Survey of Heritage, currently Annelise Folie (annelise.folie@naturalsciences.be).

[please note that the data for this paper are not yet published and these temporary links should not be shared without the express permission of the author]

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FIGURE AND TABLE CAPTIONS

FIG. 1. A, Representation of all the reconstructions of *Weichselia reticulata* to date. B, fragment of a pedate frond (MCCM-LH 17327) preserved as an impression from the locality of Las Hoyas (upper Barremian of Cuenca, Spain). C, hand specimen from the locality of Tilgate Forest (Valanginian of England) with numerous fragments of secondary pinnae (NHMUK PB V 51405).

FIG. 2. Localization of the locality of Bernissart. A, map of Belgium marking the Mons Basin. B, detailed map of the locality including the different sinkholes. The red line marks the Négresse connecting gallery (coordinates 50°28'60"N 3°38'33,2"E); S1, "puits Négresse" entrance leading to the North sinkhole; S3, "puits Sainte Barbe" entrance leading to the Iguanodon sinkhole. C, simplified log of the different lithological units encountered from south (0 m) to north (164 m) in the Négresse connecting gallery. The black line in the lithological unit Y marks the point where the orientation of the layers is changing. The arrow marks the position of the here studied samples.

FIG. 3. Sections of stems. A-B, Thin section housed at the RBINS and figured by Alvin (1971) IRSNB b 0229: A, whole section; B-C, enlargement of A x7.5; B, one bundle, C, secretory canal. D-E, Y slices of µCT-scans of: D, IRSNB b 8424; and E, IRSNB b 8425. Scale bar = 1 cm.

FIG. 4. Scars on the stem. A, Specimen IRSNB b 8426 showing crater-like marks and tubercles. Scale bar = 0.5 cm. B, Specimen IRSNB b 842497. White arrow, petiole insertion with tubercles; black arrow, possible radicular organ insertion. C, Longitudinal and transverse sections of the petiole in specimen IRSNB b 8425. Blue, central strands of the petiole; red, central strands of the

stem. D, Longitudinal and transverse sections of the possible radicular organ of specimen IRSNB b 8424. Blue, strands oriented in the opposite direction to the growth of the stem; red, central strands of the stem. B-D scale bars = 1 cm.

FIG. 5. Elliptical scars. A, isolated elliptical scar IRSNB b 8427) left, external view; right, internal view. B-F, Vascular tissue at an elliptical scar in specimen IRSNB b 8424. B, reconstruction of vascular tissue in 3D. C-D, subsequent sections of the frontal view: C, absence of vascular tissue and D, irregular disposition of bundles underneath. E, transverse section. F, longitudinal section, lateral view. G-J. Elliptical scars in specimen IRSNB b 8425. G-H. Photographs of the scars on the specimen. I-J. Diagrams of outer surface and the vascular system in relation to the elliptical scars. I. Transverse section, J. longitudinal section. Blue, central bundles of the petiole; red, elliptical scars; black, rest of bundles; grey, outer part of the specimen. Scale bars = 1 cm.

FIG. 6. Stems. A. IRSNB b 8425. B-G. Vascular system of specimens IRSNB b 8424 and 8425 obtained from segmentation of µCT-scans. B-C, IRSNB b 8425. B, lateral section. C, transversal section at area where the petiole emerges. D-G. Sequential transversal sections of IRSNB b 8424 at possible branching area. Red, central vascular bundles; black, other bundles. Scale bars = 1 cm.

FIG. 7. Models of the vascular system obtained from segmentation. The colouring of the different organs and stem centres is schematic, and was done posteriorly on the models. Red, central vascular strands of the stem; blue, vascular strands of the petiole (P1, oldest petiole in the specimen; P2, youngest petiole in the specimen); green, vascular strands of the rooting organ (R1, oldest rooting organ in the specimen).

FIG. 8. External morphology of Recent fern stems and petioles. A. Scales and tubercles in the bases of petioles in *Angiopteris palmatiformis*. B. Tubercles in the stem and petiole base of *Sphaeropteris intermedia*, there is a possible aerophore or nectary at the base of the petiole. C. Isolated aerophores or lenticels along a line in the petioles of *Sphaeropteris cooperi* (F.Muell.) R.M. Tryon. D. Isolated aerophores or lenticels in an irregular disposition in *Angiopteris evecta*. E. Curved rhizome of *Matonia pectinata* R. Br. (specimen K000407521 from Kew herbarium).

FIG. 9. Comparison of the anatomy between fern species; all shown in transverse section. A, *Weichselia reticulata* (IRSNB b 8425); B, *Cyathea trichiata* Domin drawn after White and Turner (2017); C, *Platycerium aethyopicum* drawn after Allison (1913); D, *Danaea moritziana* Rosenst. drawn after Rolleri (2004); E, *Matonia pectinata* drawn after image 9327 of the Cornell University Plant Anatomy Collection; F, *Osmunda cinnamomea* drawn after image 8798 of the Cornell University Plant Anatomy Collection; G, *Paradoxopteris stromeri* drawn after Edwards (1933). Scale bar represents 10 mm; C-F are shown at two magnifications: image on right is to scale; image on left: C–D, × 2 (scale bar represents 5 mm); E–F, × 5 (scale bar represents 2 mm).

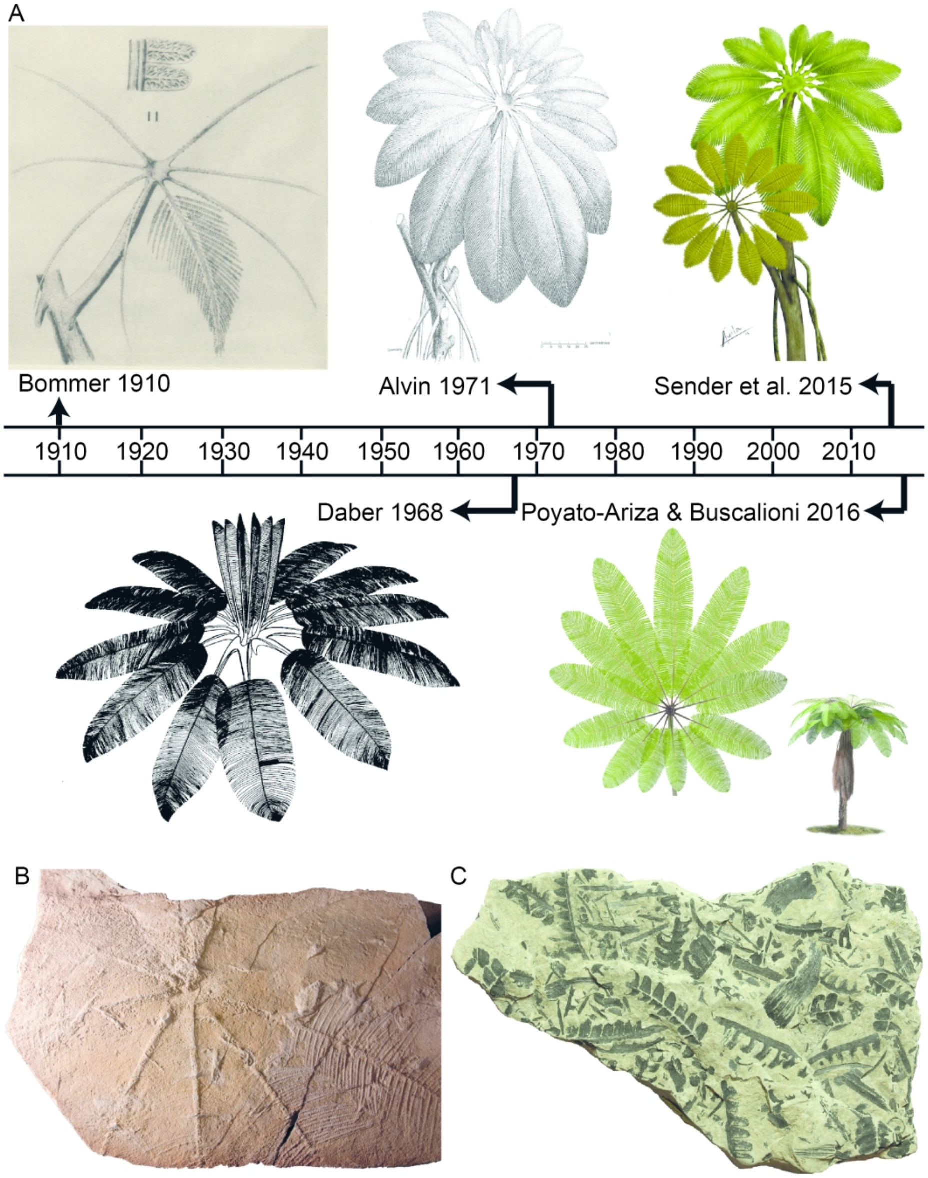
FIG. 10. A. Central strands of thin section of *Weichselia reticulata* (IRSNB b 0229) B. Anatomy of *Psaronius magnificus* (Herzer) Rothwell and Blickle without the roots (Rothwell and Blickle, 1982). Scale bars = 1cm.

FIG. 11. Vascular system comparison between A, *Weichselia reticulata* and B, *Dracaena marginata*, schematic diagram based on Haushahn et al. (2014). Red, central vascular strands of the stem; blue, vascular strands of the petiole in A and vascular strands of the ramification in B.

TABLE 1. Anatomical, morphological and architectural characters of *Weichselia reticulata* and other fern taxa.

TABLE 2. Calculated height following Niklas (1994) and maximum height from the literature.

TABLE 3. Variables used in the calculations of Corner's Rules following Brouat et al. (1998).



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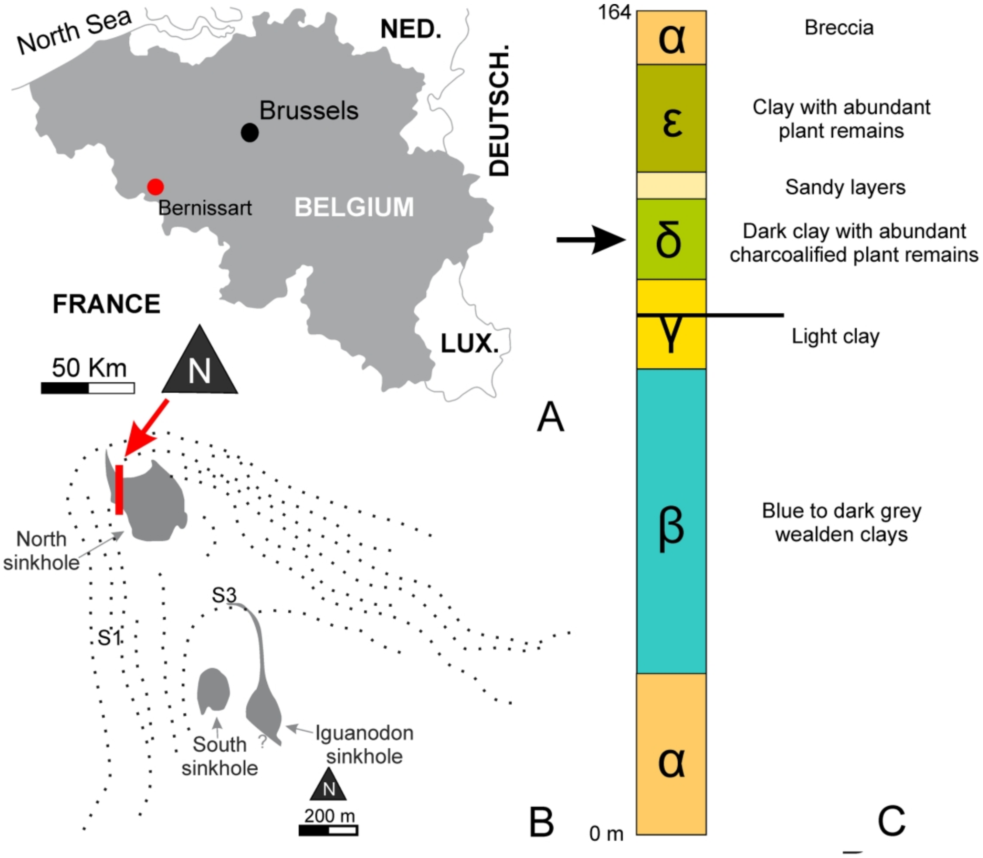

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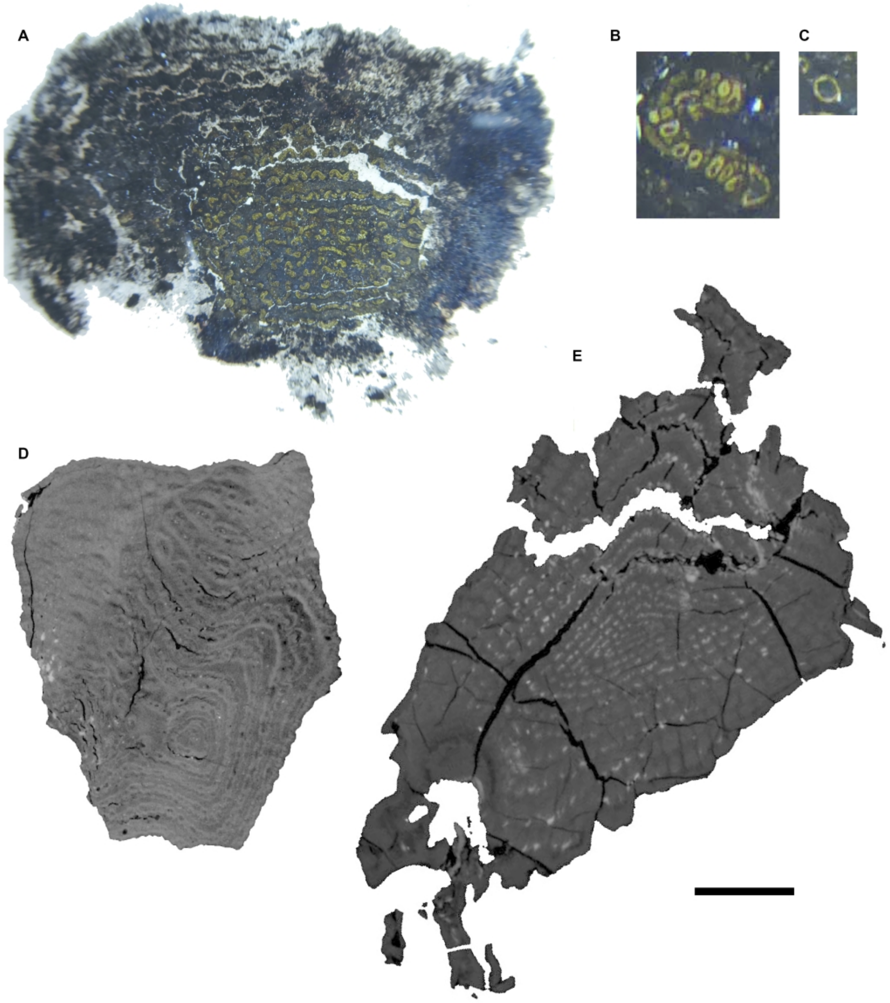

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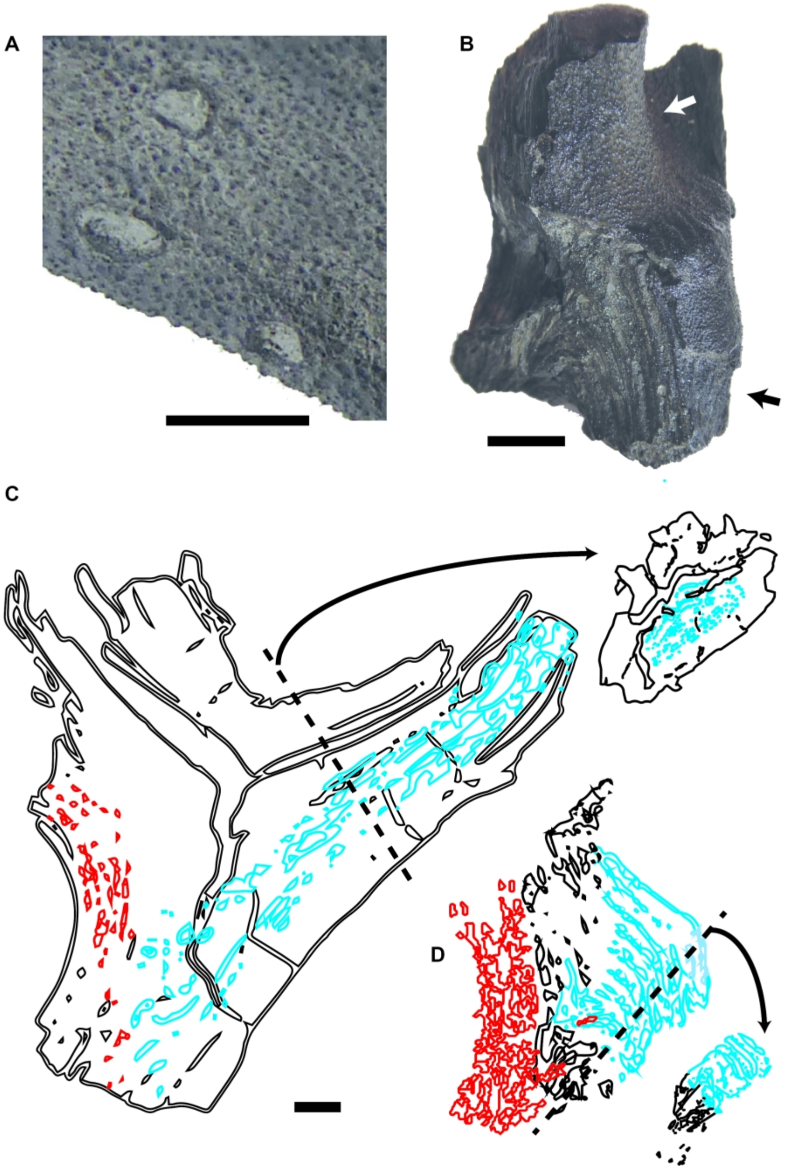

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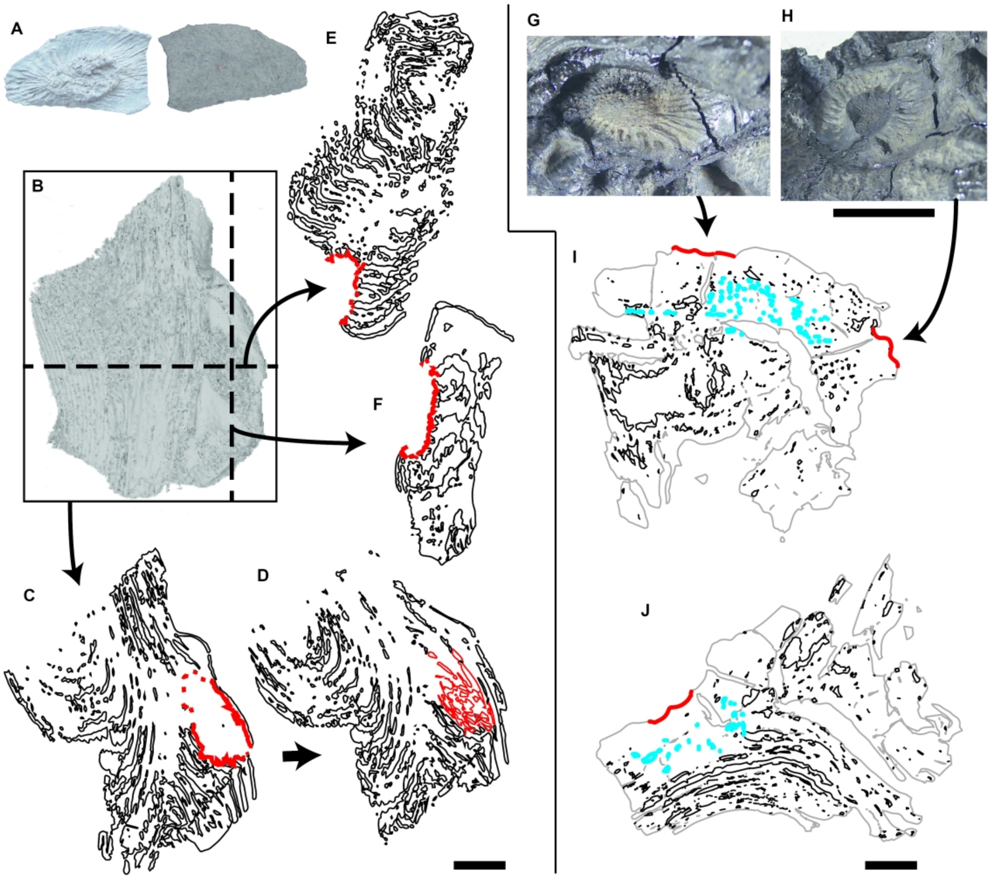

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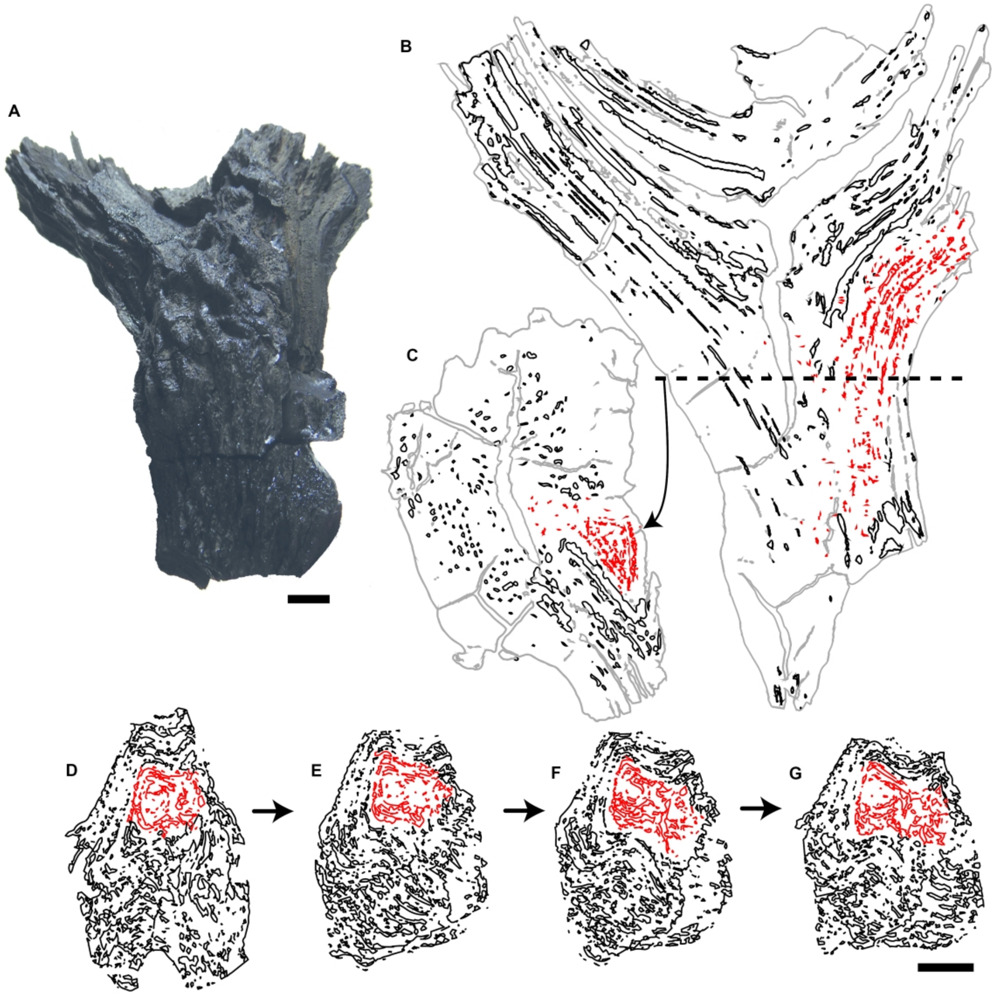

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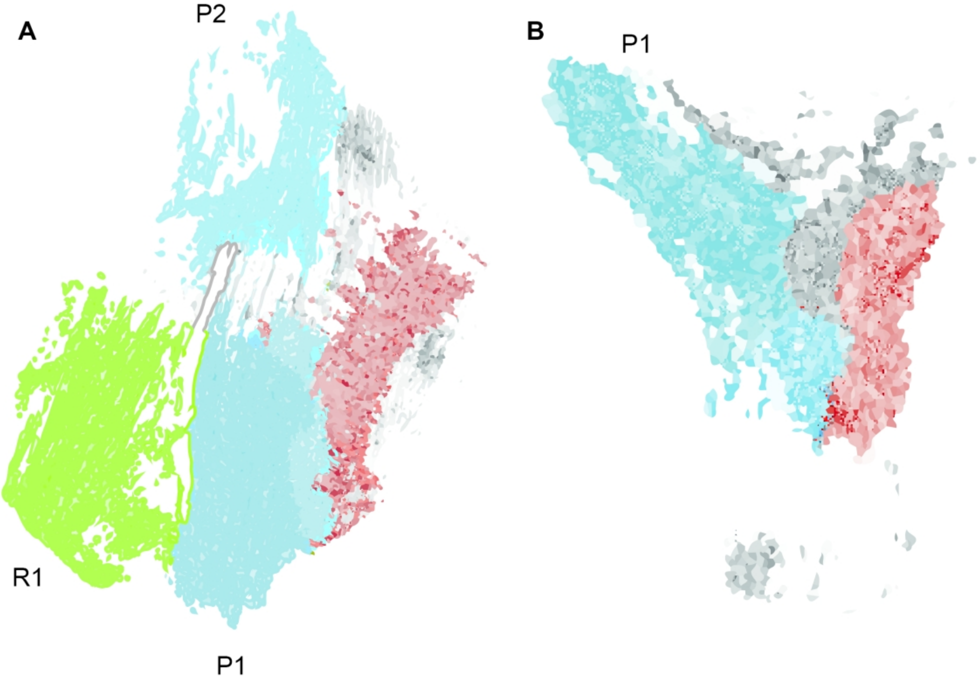

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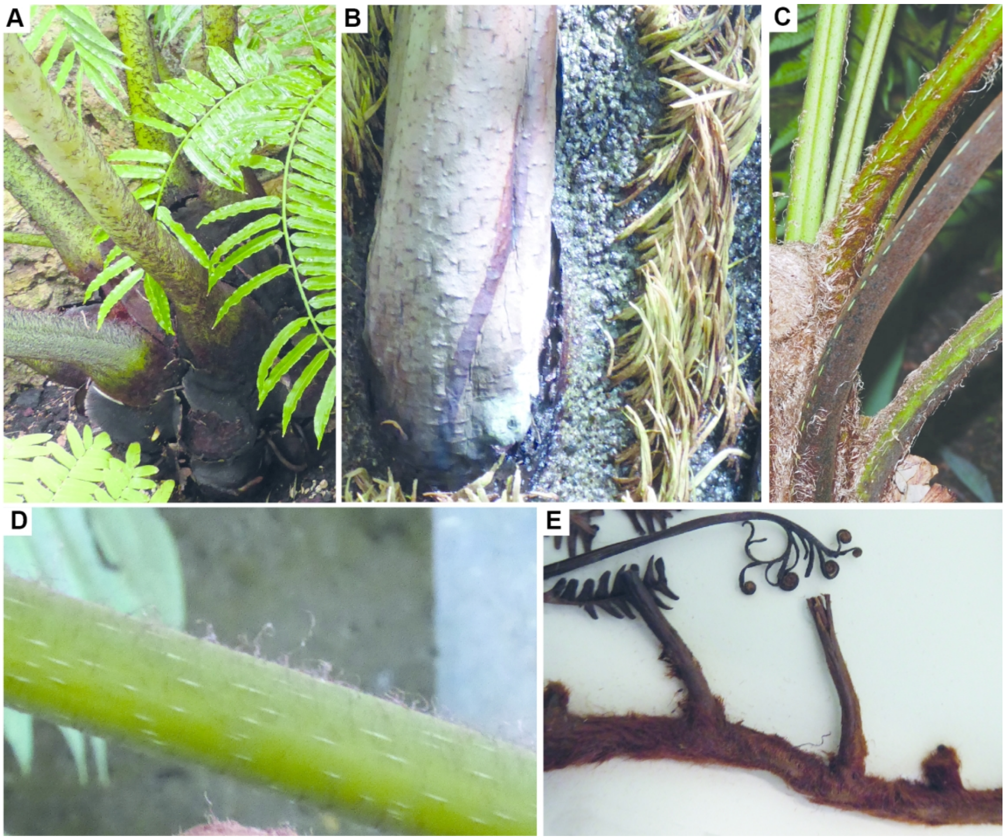

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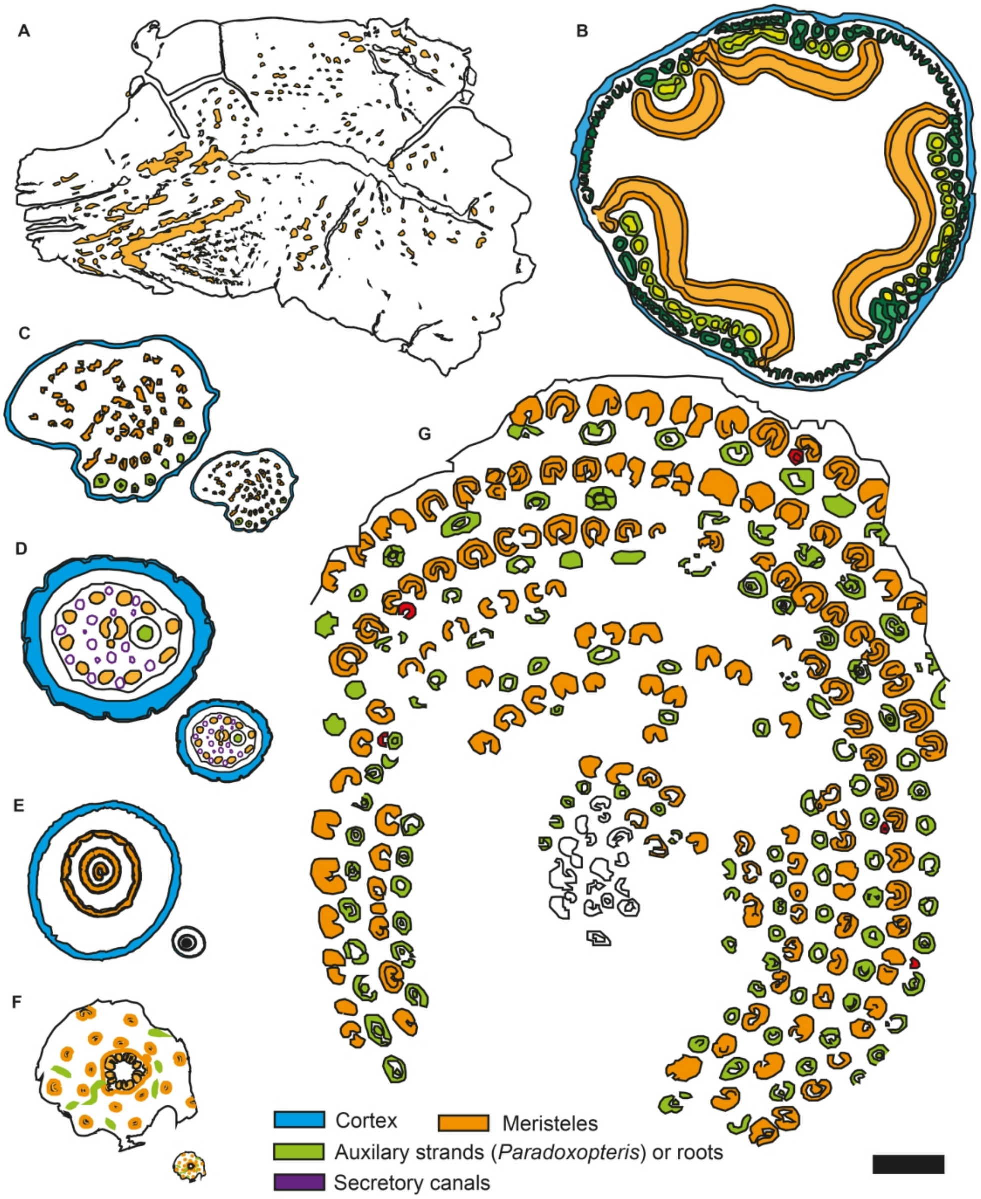

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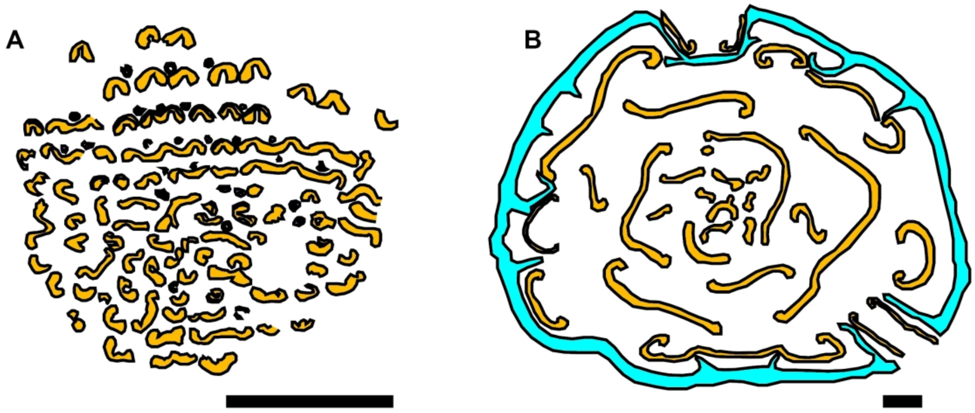

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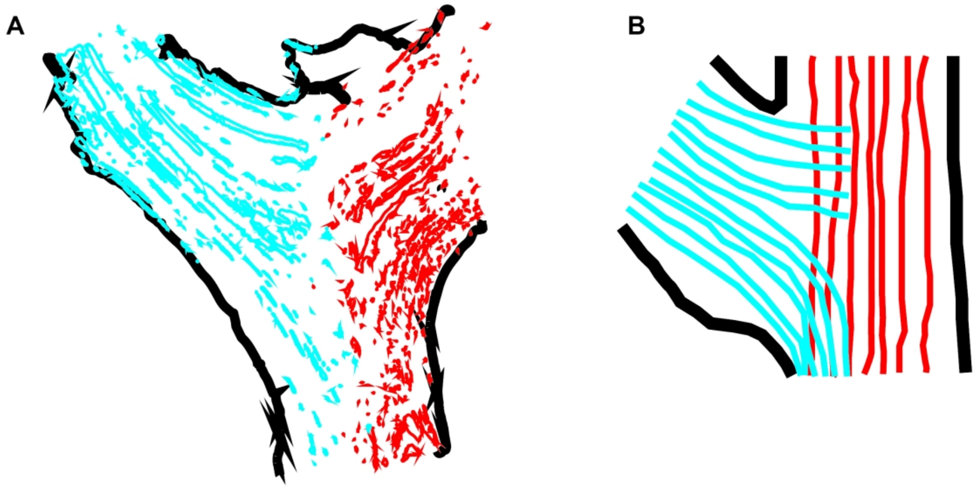

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	Weichselia	***Paradoxopteris***	***Matonia***
stem diameter (cm)	7.14	15.83	0.45
bundle size (cm)	0.2	0.53	0.24
bundle / stem	0.03	0.03	0.54
type of stele	Dictyostele	Dictyostele	Solenostele
Polycyclic	yes	yes	Yes
strands to leaf	many	Np	One
accessory strands	?	yes	No
roots from central strand	yes	?	No
secretory canals	?	no	No
endodermis	?	?	yes
Cortex /stem diameter	Np	Np	0.07
Growth habit[*]	?	?	Terrestrial
position of rhizome	?	?	Creeping
branching	?	Np	yes
Equal branching?	?	Np	yes
Stem curved?	yes	Np	yes
petiole/ stem	0.66	Np	0.75
Leaf	Pedate frond, and bipinnate	Np	Pedate frond, and once pinnate
Leaf area (cm^2)	41902	Np	229
LMA (g/m^2)	352.5*	Np	165
Rhizome length (cm)	857***	2515***	13

* Following Peppe et al. (2014)

** Calculated approximately, from data that are not general or from the same plant (source of data: Roll

***Calculated following Niklas (1994), maximum size if it is upright.

Danaea	***Angiopteris***	***Osmunda***	***Cyathea***	***Platycerium***
1.4	2	0.41	5.53	1.27
0.15	0.15	0.04	3.42	0.13
0.11	0.08	0.1	0.62	0.1
Dictyostele	Dictyostele	Dictyostele	Dictyostele	Dictyostele
yes	yes	no	no	yes
two	many	one	Many	many
no	no	no	Yes	yes, arising from original dictyostele
Yes	yes	no	no	no
yes	yes	no	no	no
no	no	yes	yes	yes
0.1	Np	Np	0.03	0.03
Terrestrial	Terrestrial	Terrestrial	Arborescent	Epiphytic
Erect or creeping	Erect	Erect	Erect	Creeping
No	no	yes	rare	Lateral bud
No branching	No branching	yes	yes	no
no	no	?	no	?
1.17**	0.25**	0.71	0.62	0.63
Once pinnate	Bipinnate	Bipinnate	Once to many times pinnate	Bifurcately branched
20.9	13.7	81.8	25587	?
50	150	225	158	?
200	100?	?	1000	?

leri, 2002 and Rolleri, 2004).

Psaronius
43
0.45 - 6.6
0.57
Dictyostele
yes
many
no
rarely
yes
no
0.23
Arborescent
Erect
no
No branching
no
1.2 or 0.2
pinnate
?
?
1500

	Calculated height	Maximum height (literature)
Weichselia	857	?
Danaea	99	200
Cyathea	567	2400
Psaronius min.	345	1500
Psaronius max.	2170	1500

Values in cm. *Danaea*, Rolleri (2004); *Cyathea*, Bower (1926); *Psaronius* Morgan (1959).

Psaronius min. and Psaronius max., are calculated from the minimum and maximum values from Rothwell and Blickle (1982) respectively.

	Max. stem area	Max. foliage area	Nº leaves obs.	Nº leaves possible
Weichselia	25.57*	41902	?	1 to 2*
Matonia	0.16	211*	1	1 small*
Matonia max.	0.48	633*	1	2*
Cyathea	24.02	39272*	1 to 3	2*
Psaronius	50.27	236527*	5 to 8	7*
Psaronius max.	158.36	671381*	5 to 8	19*

Max. stem area and Max. foliage area in cm^2. Variables obtained from the formula are marked with an asterisk. Other variables were obtained from the literature: *Weichselia*, from personal observation of specimens published in Blanco-Moreno et al. (2019); *Matonia*, from Table 1 and Kato (1993); *Matonia* max., from the maximum stem diameter in the literature (Kato, 1993); *Cyathea*, from Table 1, Tanner (1983), and Durand and Goldstein (2001); *Psaronius*, most frequent stem diameter measurement in Rothwell and Blickle (1982); and *Psaronius* max., from Table 1 and Rothwell and Blickle (1982).