NEW INSIGHTS INTO 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 using computed tomography, providing new information on their internal anatomy and external morphology. *Weichselia reticulata* has a unique anatomy, distinct from all other extant or fossil ferns. Stem external morphology

suggests adaptations to stressful environments, due to the 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. Although these new results do not settle the question of the systematic affinities of *Weichselia*, 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.

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 developed a wide range of morphologies and anatomies through time (Tidwell & Ash 1994). After a first evolutionary radiation in the Palaeozoic, the Mesozoic is a key period for the group that sees the rise of most modern families (Niklas *et al.* 1983; Lehtonen *et al.* 2017).

Weichselia reticulata (Stokes & 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 & Webb, 1824), based on small charred fragments of vegetative fronds that are the most frequent type of remains of this fern (Fig. 1C). Unambiguous stem material is very

scarce, and it is known only from a few specimens coming from the Cran du Nord locality (Bernissart colliery, Négresse mineshaft, Belgium). This material was first studied by Bommer (1910) but it is Alvin (1971) who 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 organization of the leaves (Bommer 1910; Alvin 1968; Alvin 1971; Van Konijnenburg-Van Cittert 1993; Sender *et al.* 2015). However, based on the work of Bommer (1910) and focussing on anatomical characters only, Edwards (1933) suggested a close relationship with *Paradoxopteris* Hirmer from the Early and early Late Cretaceous of North Africa (Hirmer 1927; Edwards 1933; Koeniguer 1966; El Afty *et al.* 2020), which is close to Marattiaceae. A few authors also suggest a connection to this
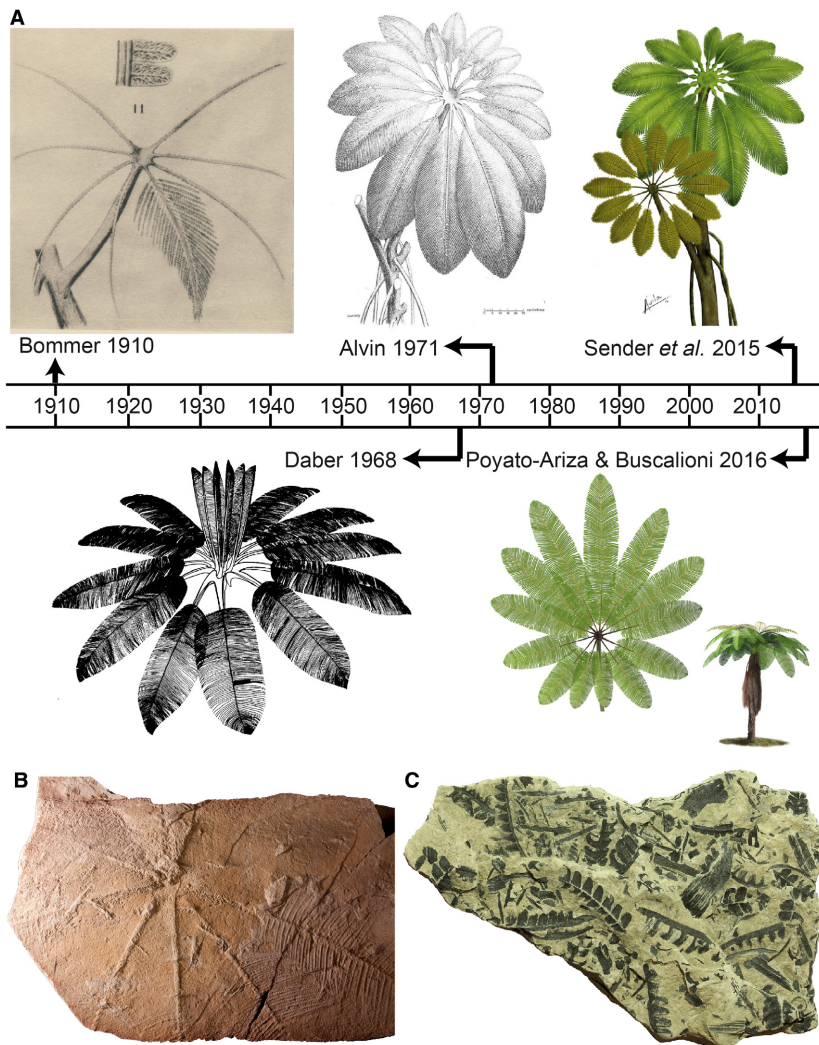
FIG. 1. A, representation of all the reconstructions of *Weichselia reticulata* to date. B, fragment of a pedate frond (MCCM-LH 17327) preserved as an impression from the locality of Las Hoyas (upper Barremian of Cuenca, Spain). C, hand specimen from the locality of Tilgate Forest (Valanginian of England) with numerous fragments of secondary pinnae (NHMUK PB V 51405).

family based on anatomy and fertile structures (Zeiller 1914; Silantieva & Krassilov 2006).

Weichselia has been recovered from freshwater deposits such as lakes or rivers (Seward 1900; Carpentier 1927; Daber 1968; Barthel & Boettcher 1978; Barale 1979; Harris 1981; Aguirrezabala *et al.* 1985; Ross & Cook 1995; Batten 1998; Diéguez & 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 & Bandel 1998; Barale & Ouaja 2001; Lyon *et al.* 2001; Gomez *et al.* 2002; Barale & Azar 2004; Almendros *et al.* 2005; Diez *et al.* 2005; Silantieva & 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 that 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 that 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 & 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 micro-computed tomography (μCT), 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. 2A). This basin corresponds to an east–west subsiding zone where Meso-Cenozoic sediments accumulated. Rather small, the subsiding area (40 × 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 (Quinif & Licour 2012; Spagna *et al.* 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 last 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, using 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. The gallery was started from pit no. 1 (called Négresse) towards the north. The gallery entered the sinkhole on its southern side 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 southern margin of the sinkhole (Cornet 1927; Delmer & Van Wichelen 1980). The exact position of the specimens is unknown but they appear to originate from lithological unit δ (Fig. 2C), which 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, which is interpreted as lacustrine (Van den Broeck 1898) or lacustrine to swampy (Yans *et al.* 2012; Schnyder *et al.* 2009; Spagna *et al.* 2012).

MATERIAL AND METHOD

The material studied consists of stems, petioles and rachises preserved as lignite that were assigned to *W. reticulata*. The examined specimens were collected in the Cran du Nord locality (Bernissart Colliery, Négresse mineshaft, Belgium) and are housed in the Royal Belgian Institute of Natural Sciences (RBINS) in Brussels, Belgium (IRSNB b 0229, 8424, 8425, 8426, 8427; RBINS-PBOT-935, 936, 955, 976, 1073, 06846-0024). 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.

Additional comparative material

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 & Turner (2017); *Platycerium aethyopicum* Hook. material figured by Allison (1913); *Psaronius* Cotta material figured by Morgan (1959), and Rothwell & Blickle (1982).

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

CT 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 on μCT at the RBINS (Brussels, Belgium). Scanning was completed using an RX EasyTom 150, with copper filter. For IRSNB b 8424, images were generated at a voltage of
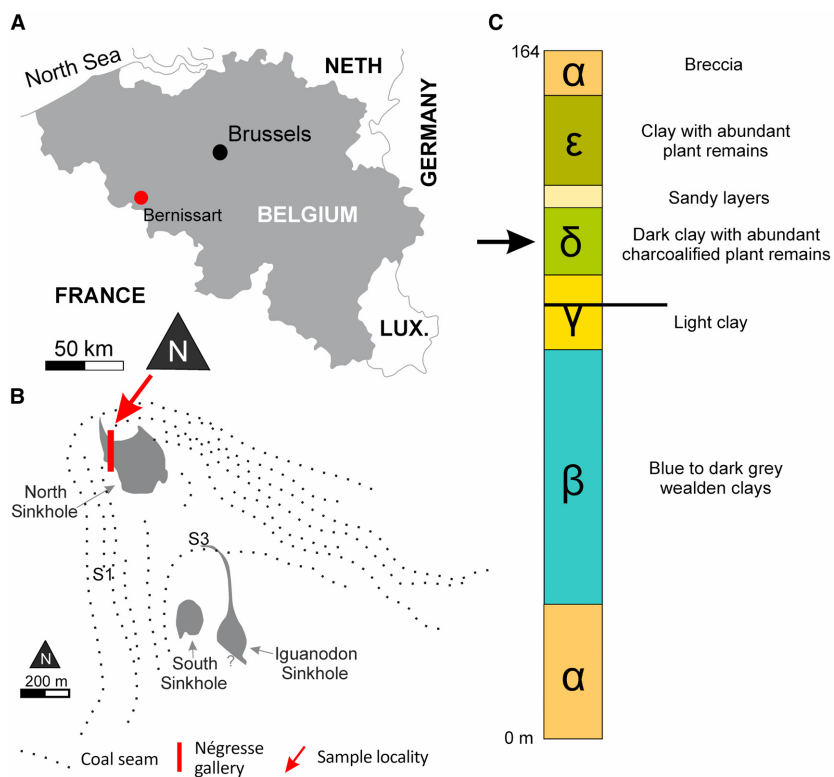
FIG. 2. Position of the Bernissart locality. A, map of Belgium marking the Mons Basin. B, detailed subsurface mining map of the locality including the different sinkholes, with intersecting coal seams, and the location of the Négresse connecting gallery (coordinates 50°28′60″N 3°38′33.2″E); S1, *puits 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 γ marks the point where the orientation of the layers changes; the arrow marks the position of the samples studied herein.

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 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 using 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 to better identify the organ insertions. Posteriorly, the models were uploaded in Meshlab (Cignoni *et al.* 2008) and 3D-Slicer (Fedorov *et al.* 2012), where sectioning of the models was performed.

Despite the obvious advantages of μCT 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 in 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 used for reconstruction and comparison*

Stem diameter, bundle size and cortex thickness were measured on the listed specimens, except for *Angiopteris evecta*, which was obtained from Blomquist (1922), and *Psaronius* from Rothwell & Blickle (1982). The largest measurement was recorded for each category. General information on the anatomy and morphology was collected from observations of the listed specimens, 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 genus (not species) level.

Three variables with biomechanical implications for and of interest in 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 LMA was calculated following Peppe *et al.* (2014):

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

The petiole width must be measured at the base of the lamina (Peppe *et al.* 2014). In this case the width was measured as that immediately under the petiole heads collected from Bernissart. These specimens are
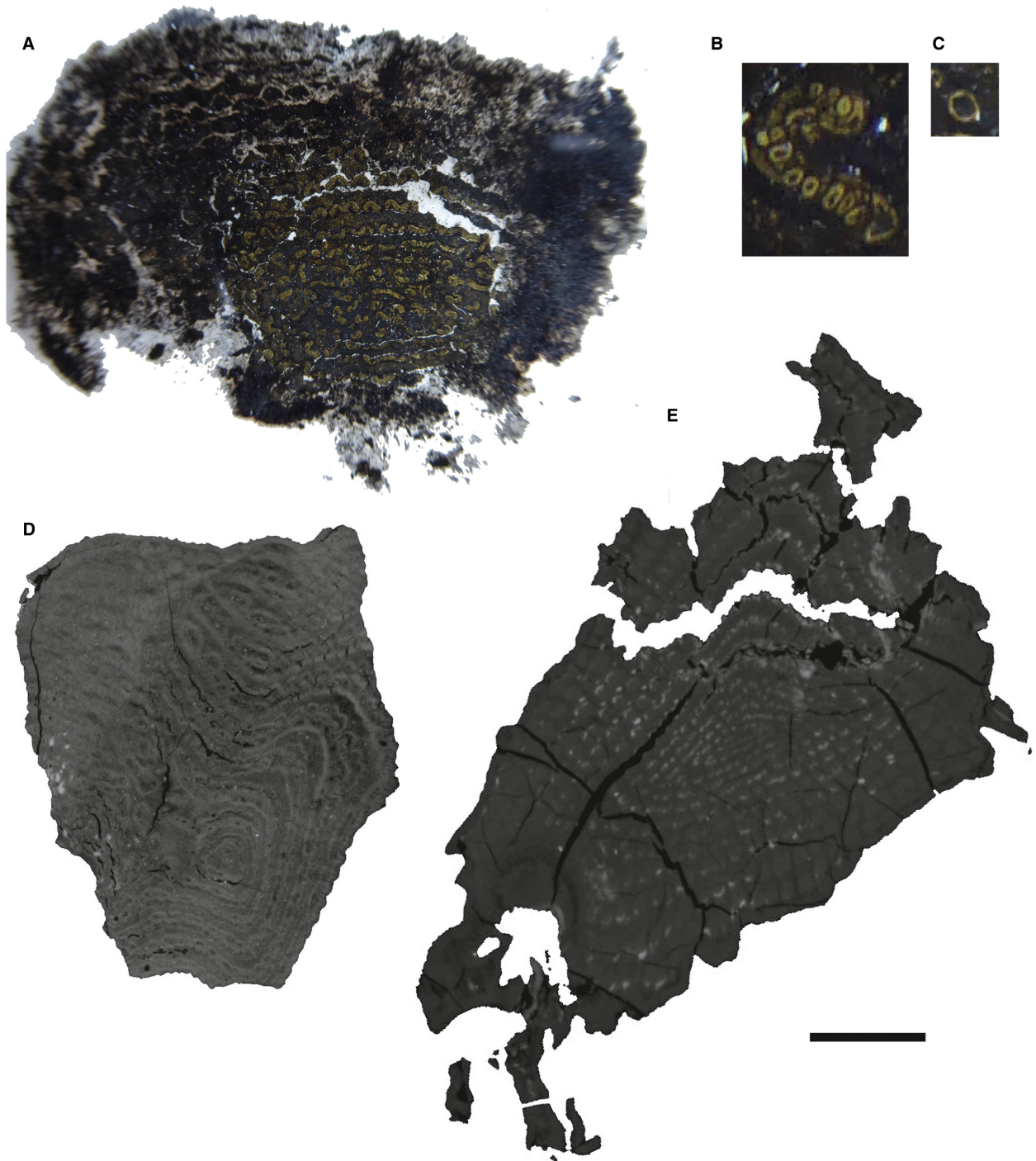
FIG. 3. Sections of stems. A–C, thin section of specimen IRSNB b 0229 housed at the RBINS and figured by Alvin (1971): A, whole section; B–C, enlargements of A (magnification, ×7.5): B, one bundle, C, secretory canal. D–E, Y slices of μCT scans of: D, IRSNB b 8424; E, IRSNB b 8425. Scale bar represents 1 cm.

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

	Weichselia	Paradoxopteris	Matonia	Danaea	Angiopteris	Osmunda	Cyathea	Platycerium	Psaronius
Stem diameter (cm)	7.14	15.83	0.45	1.4	2	0.41	5.53	1.27	43
Bundle size (cm)	0.2	0.53	0.24	0.15	0.15	0.04	3.42	0.13	0.45–6.6
Bundle/stem	0.03	0.03	0.54	0.11	0.08	0.1	0.62	0.1	0.57
Type of stele	Dictyostele	Dictyostele	Solenostele	Dictyostele	Dictyostele	Dictyostele	Dictyostele	Dictyostele	Dictyostele
Polycyclic	Yes	Yes	Yes	Yes	Yes	No	No	Yes	Yes
No. strands supporting leaf	Many	Np	One	Two	Many	One	Many	Many	Many
Accessory strands	?	Yes	No	No	No	No	Yes	Yes, arising from original dictyostele	No
Roots from central strand	Yes	?	No	Yes	Yes	No	No	No	Rarely
Secretory canals	?	No	No	Yes	Yes	No	No	No	Yes
Endodermis	?	?	Yes	No	No	Yes	Yes	Yes	No
Cortex/stem diameter	Np	Np	0.07	0.1	Np	Np	0.03	0.03	0.23
Growth habit*	?	?	Terrestrial	Terrestrial	Terrestrial	Terrestrial	Arborescent	Epiphytic	Arborescent
Position of rhizome	?	?	Creeping	Erect or creeping	Erect	Erect	Erect	Creeping	Erect
Branching	?	Np	Yes	No branching	No branching	Yes	Rare	Lateral bud	No branching
Equal branching?	?	Np	Yes	No	No	Yes	Yes	No	No
Stem curved?	Yes	Np	Yes	No	No	?	No	?	No
Petiole/stem	0.66	Np	0.75	1.17†	0.25†	0.71	0.62	0.63	1.2 or 0.2
Leaf	Pedate frond, and bipinnate	Np	Pedate frond, and once pinnate	Once pinnate	Bipinnate	Bipinnate	Once to many times pinnate	Bifurcately branched	Pinnate
Leaf area (cm²)	41 902	Np	229	20.9	13.7	81.8	25 587	?	?
LMA (g/m²)	352.5*	Np	165	50	150	225	158	?	?
Rhizome length (cm)	857‡	2515‡	13	200	100?	?	1000	?	1500

LMA, leaf mass per area; Np, not present in the specimen studied.

*Following Peppe et al. (2014).

†Calculated approximately, from data that are not general or from the same plant (source of data: Rolleri 2002 and Rolleri 2004).

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

slightly compressed, therefore not only was the measured value used, but a smaller value was calculated supposing a maximum width increase of the original specimen by 10% after compression as proposed by Niklas (1978).

2. The maximum height of *W. reticulata* was calculated following Niklas (1994), who proposed a model for the estimation of height in fossil plants. In order to compare the results of the model with observed heights in ferns, this value was also calculated for some extant genera. It must be noted that the estimates calculated with this model are first order of magnitude approximations.

$$\log(\text{Height}) = 2.51 + 1.41 \times \log(\text{Diameter of stem})$$
$$+0.03 \times \log(\text{Diameter of stem})^2$$

3. The number of fronds that could be supported by each node of the stem in *W. reticulata* was constrained using Corner's rule, based on the existence of a correlation between the primary diameter of the stem and the leaf borne by it. It must be noted that one internode must also support the leaves borne on internodes distal to it (Brouat *et al.* 1998). We followed Brouat *et al.* (1998), who proposed a simple method to calculate the maximum area of foliage that can be borne on a stem of a certain size based on Corner's rules:

$$\log(y) = \log(b) + a \times \log(x)$$
$$y = bx^a$$

where y is the cross-sectional area of the stem, x is the area of the leaf, b is the intercept at y (we use -4.21), and a is the slope (we use 1.1).

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, therefore we applied the method to other fern taxa with sufficient 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, 6A). Alvin (1971) observed five 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 μCT information, 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°–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 10 concentric rings present in IRSNB b 8425 (Fig. 4A).
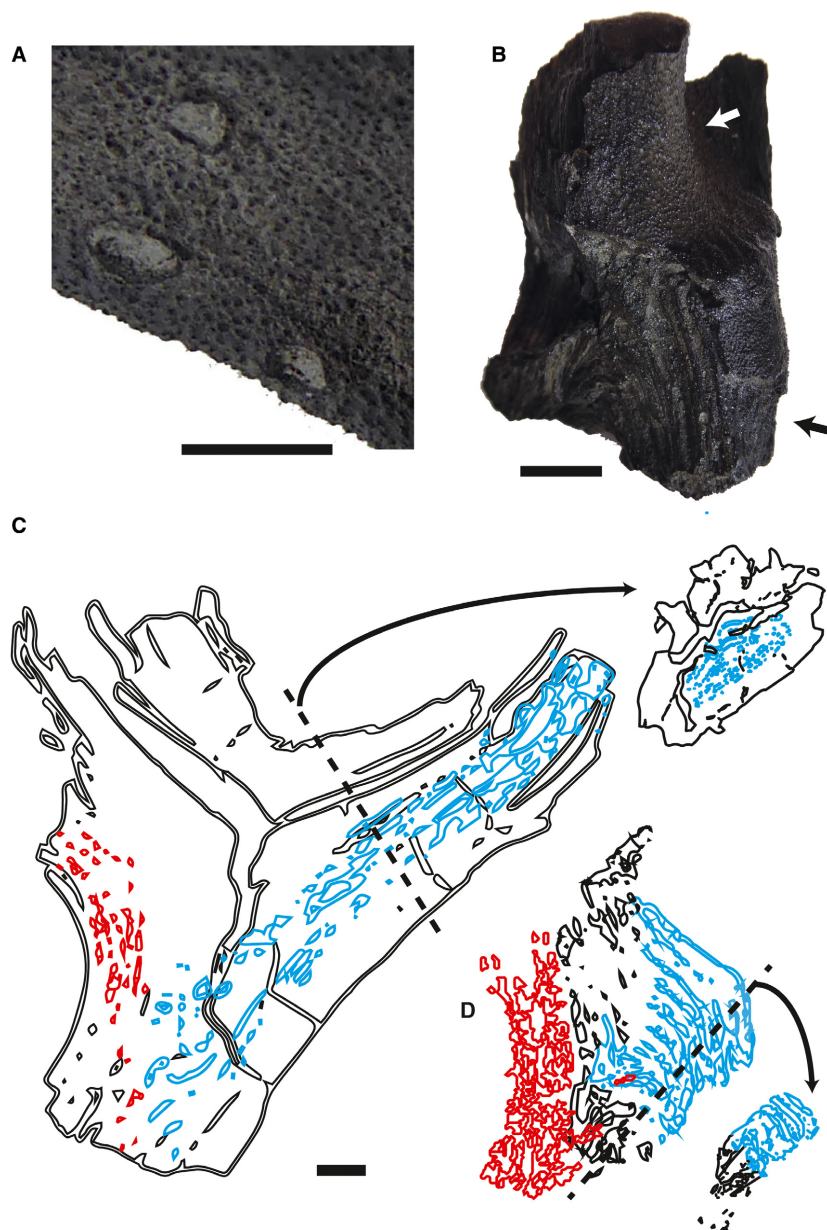
Radicular organs

Material: IRSNB b 8424.

The anatomy of specimen IRSNB b 8424 shows some strands that are orientated in a 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 with 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 are 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

FIG. 4. Scars on the stem. A, specimen IRSNB b 8426 showing crater-like marks and tubercles. 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. Scale bars represent: 0.5 cm (A); 1 cm (B–D).

specimens without creases, but are also present in very irregular, creased ones. They are millimetric, but variable in size and shape. When imaged on μCT they present the same density as the rest of the surface.

Crater-like marks

Material: IRSNB b 8426.

These structures have been observed only on one specimen already figured by Alvin (1971, pl. 2, fig. 2). 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 from 0.19 × 0.17 to 0.34 × 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
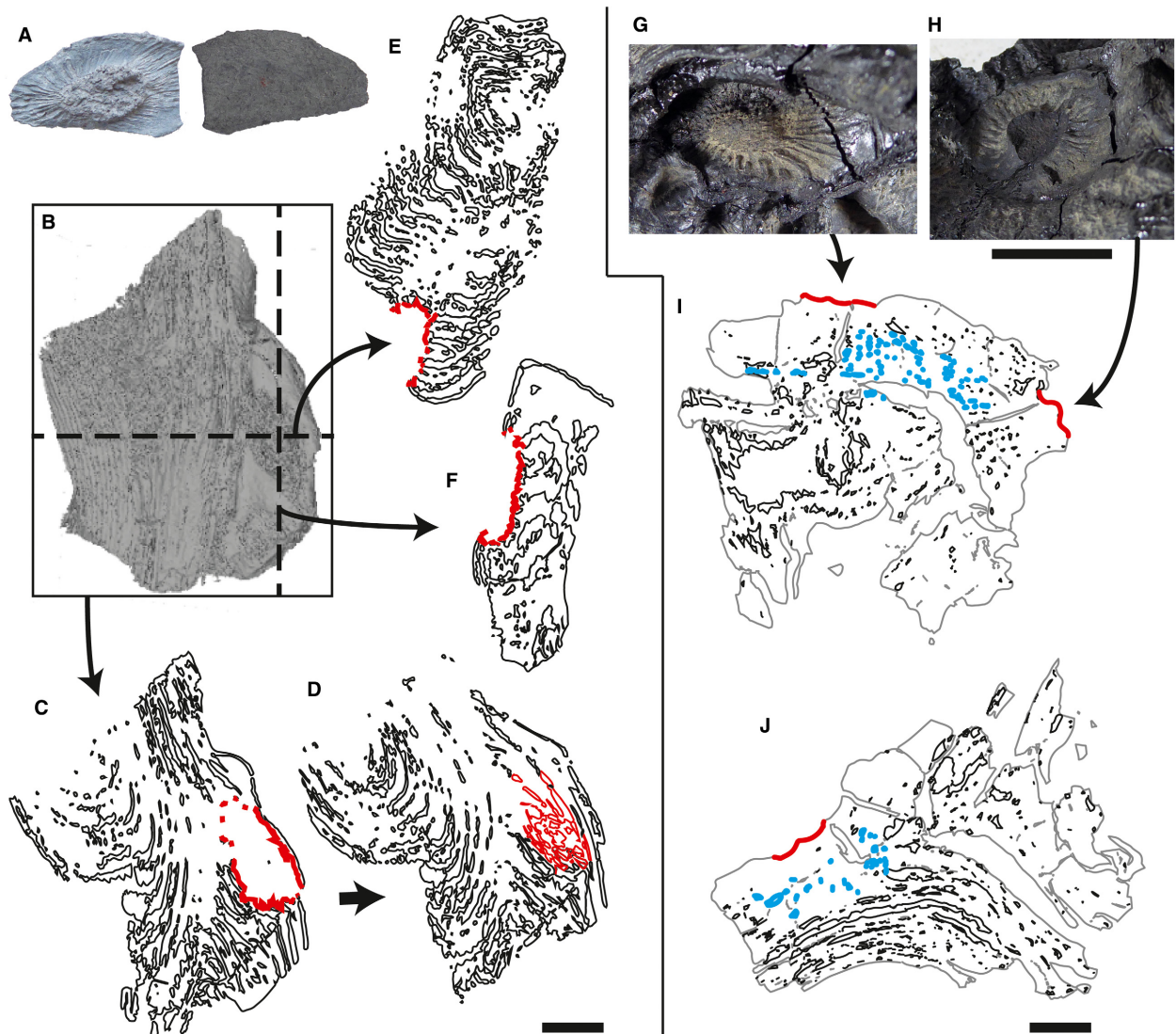
FIG. 5. Elliptical scars. A, isolated elliptical scar in specimen IRSNB b 8427: left, external view; right, internal view. B–F, vascular tissue at an elliptical scar in specimen IRSNB b 8424: B, reconstruction of vascular tissue in 3D; C–D, subsequent sections of the frontal view: C, absence of vascular tissue; 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 represent 1 cm.

the collection (Fig. 5A, G, H). Their outline is clearly defined, and they are slightly depressed in relation to the rest of the stem; they measure 0.64–2.8 cm × 0.73–1.54 cm. Two differentiated zones can be observed: a central elliptical to circular rugose protruding area measuring 0.49–1.49 cm × 0.862–0.35 cm; 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, 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, I, J).
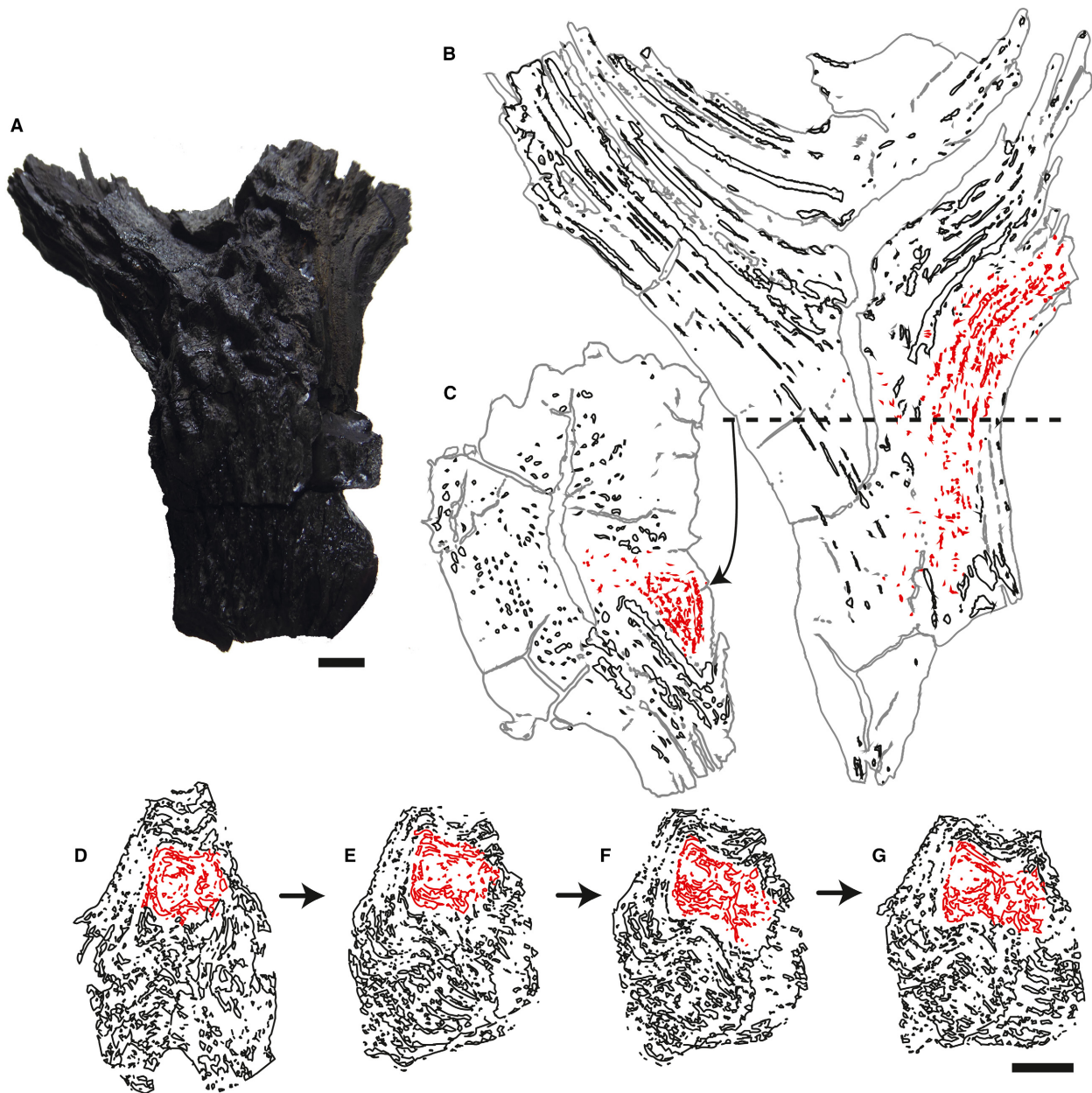
FIG. 6. Stems. A, IRSNB b 8425. B–G, vascular system of specimens IRSNB b 8424 and 8425 obtained from segmentation of μCT scans: B–C, IRSNB b 8425: B, lateral section; C, transverse section at area where the petiole emerges; D–G, sequential transverse sections of IRSNB b 8424 at possible branching area; red, central vascular bundles; black, other bundles. Scale bars represent 1 cm.

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 (Figs 4C, D, 6B). No branching has been directly observed, but at the apicalmost 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 nine concentric rings of irregularly shaped vascular bundles, which are generally C shaped, and measure 0.15–0.22 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 *W. reticulata*, alternating with the bundles. These structures were observed in the thin sections but are not clearly identified on µCT 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 of 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, therefore the phyllotaxy cannot be inferred.

Calculations for reconstruction

In order to attempt a reconstruction of the whole plant, certain characters associated with the morphology, architecture, and anatomy of *Weichselia reticulata* have to be analysed (Table 1). Important variables for plant reconstruction can then be 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 317.2–352.5 g/m^2, calculated following Peppe *et al.* (2014) based on measurements of the specimens published in Blanco-Moreno *et al.* (2019). This could be an overestimate, given that fronds with a large ratio of petiole width to 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 to pinnate fronds (Niklas 1991), and the results in Peppe *et al.* (2014) show that the largest LMA correspond to palmate or simple fronds.

Plant height. 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 those recorded for each taxon in the literature (Table 3). The number of leaves estimated for *Weichselia*

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).
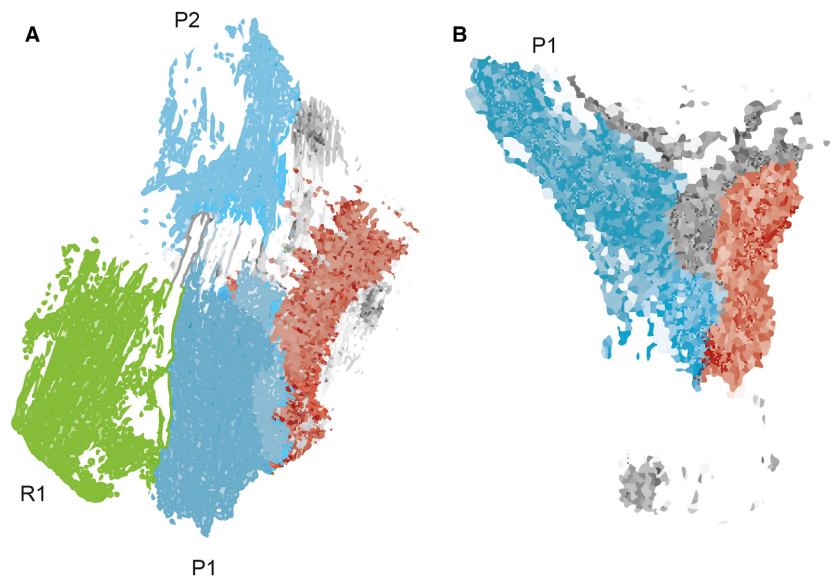
by this method is therefore accepted as a valid estimate until more information can be obtained, and is given as 1 to 2 leaves (Table 3).

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 & Krassilov (2006); and (3) Matoniaceae, which is the most accepted sister group to *Weichselia* (Alvin 1971; Sender *et al.* 2015). We also include two other genera: *Cyathea* (Cyatheaceae), for a comparison with an arborescent fern with a tall upright stem, as has been suggested for *Weichselia* in some reconstructions (Poyato-Ariza & Buscalioni 2016); and *Platycerium* Desv. (Polypodiaceae), which was found to be the only fern with a stele organization more or less comparable to the specimen studied herein.

External morphology and scars

The herein 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 made possible only by the presence of small lenticel-like tubercles filled with spongy tissue that act as pneumathodes (Bower 1923). Another

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

	Calculated height	Maximum height*
Weichselia	857	?
Danaea	99	200
Cyathea	567	2400
Psaronius min.	345†	1500
Psaronius max.	2170†	1500

Danaea, Rolleri (2004); *Cyathea*, Bower (1926); *Psaronius*, Morgan (1959).
†Calculated from Rothwell & Blickle (1982).

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

	Max. stem area (cm²)	Max. foliage area (cm²)	No. leaves obs.	No. leaves possible
Weichselia	25.57*	41 902	?	1–2*
Matonia	0.16	211*	1	1 small*
Matonia max.	0.48	633*	1	2*
Cyathea	24.02	39 272*	1–3	2*
Psaronius	50.27	236 527*	5–8	7*
Psaronius max.	158.36	671 381*	5–8	19*

*Obtained from the formula. Other values 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 Kato (1993); *Cyathea*, from Table 1, Tanner (1983), and Durand & Goldstein (2001); *Psaronius*, most frequent stem diameter measurement in Rothwell & Blickle (1982); and *Psaronius* max., from Table 1 and Rothwell & Blickle (1982).

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 instead 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 have similar surface features to the ones observed in *Weichselia*. *Angiopteris* Hoffm. and *Danaea* present scales associated with 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 present only in one specimen and do not 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 organization is like that of some aquatic and wetland plant roots with radial lysigeny and wheel-shaped 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

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).

aerophores, sometimes termed pneumathodes, and non-linear 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 non-linear 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 & 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, for example 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, figs 161, 162; Bower 1926, fig. 560). In contrast, in *Weichselia* they only create gaps in the vascular system directly below them, and they do not seem to be related to involutions in the petiole or the putative roots (Fig. 5E, 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 & Turner 2012). In such structures, the vascular tissues do not enter the gland (White & 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 & 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 (Halle 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. Comparison of the Belgian material with a selection of fern taxa is summarized in Table 1, and Figures 9 and 10. First, 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 lie in the size of the vascular bundles and in the presence of auxiliary strands with round morphology that alternate with the C-shaped meristeles in *Paradoxopteris* (Fig. 9G). Koeniguer (1966) separated *Paradoxopteris stromeri* Hirmer into two varieties: one with large vascular bundles that are more than 2.5-fold larger than in *Weichselia*, and a second with smaller bundles that have a mean size of 0.22–0.28 cm, which fits within the size range of the bundles in *Weichselia*. However, although not clearly visible in the μCT 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 organization, 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 six 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 (Fig. 9B, 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 stelar anatomy among known fossil and extant ferns.

Systematic affinities

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

On the one hand, they have 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 organization 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 organizations (Blanco-Moreno *et al.* 2019). Their anatomy, however, is different: *Weichselia* has a polycyclic stele while Matoniaceae have solenostelic steles. However, Allison (1913) studying *Platycerium* argued that its polycyclic dictyostele could derive from the fragmentation of a polycyclic
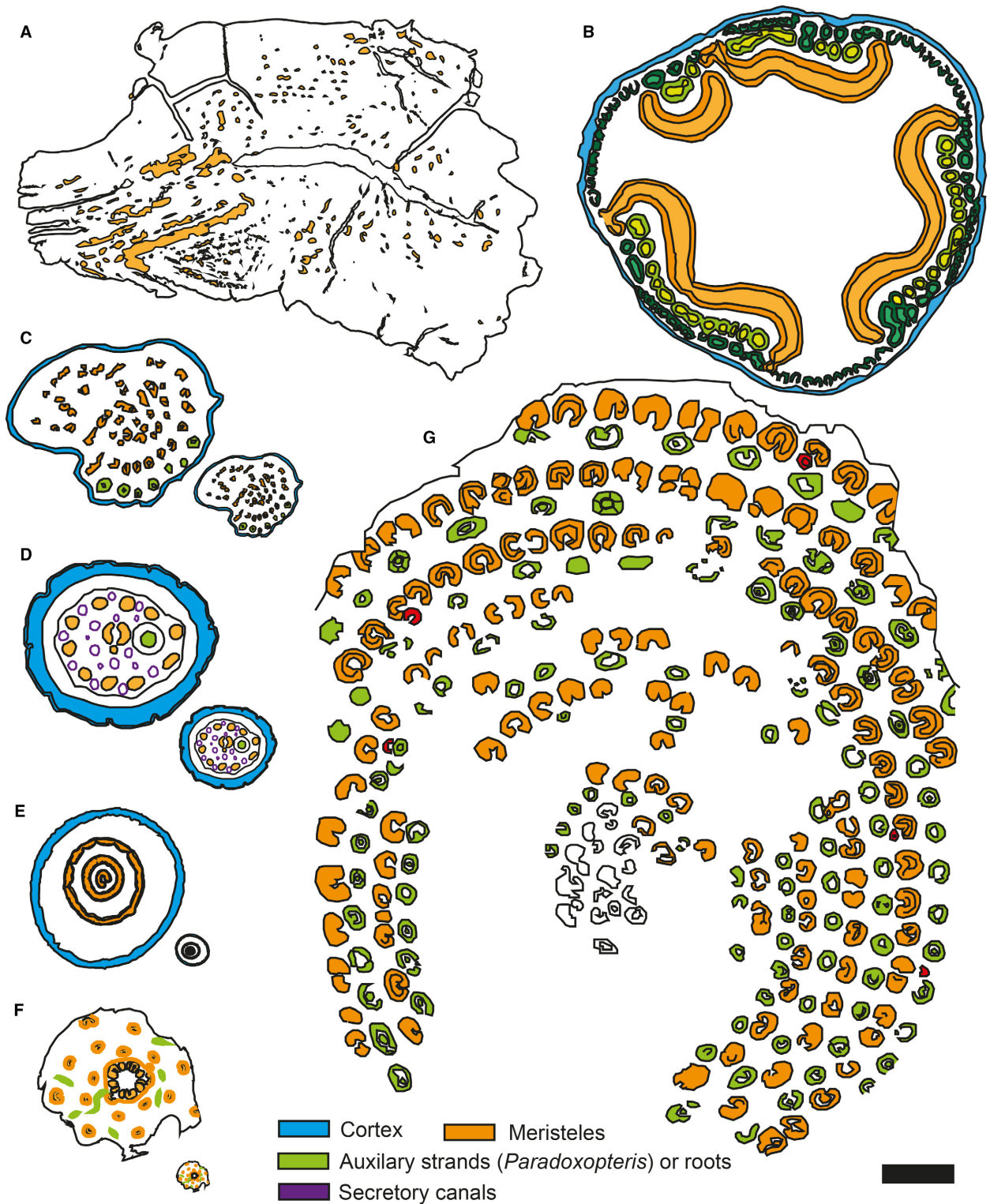
FIG. 9. Comparison of the anatomy between fern species; all shown in transverse section. A, *Weichselia reticulata* (IRSNB b 8425). B, *Cyathea trichiata* Domin drawn after White & Turner (2017). C, *Platycerium aethyopicum* drawn after Allison (1913). D, *Danaea moritziana* Rosenst. drawn after Rolleri (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).

solenostele such as the one present in *Matonia*. Moreover, their size is not comparable, because 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 organization of *Weichselia* renders comparison with other extant or fossil ferns difficult. The present results unfortunately do not allow for a definite systematic assignation. Even if, at the end of this comparison, an association with the Marattiaceae and Psaroniaceae seems 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 into the possible autecology of *Weichselia reticulata*. First, the presence of large elliptical scars at the base of the petioles, if interpreted as aerophores, indicates that the stem and petiole were 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 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 they might have had the function of a temporary aerophore. The presence of possible mucilage canals and the large size of the fronds further justify the need for 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, in contrast, 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 & Smith 1998; Koptur *et al.* 2013). The fact that ants most probably appeared in the Albian, *c.* 110 Ma (Grimaldi & Agosti 2000), would rule out an 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 & 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 byproducts without an excessive loss of water in xerophytes. *Weichselia* has previously been interpreted as a xerophyte (Alvin 1974; Watson & Alvin 1996).

High LMA is found in plants under high irradiance (Poorter *et al.* 2009), and the position of the fronds in *Weichselia* suggests that the sun would have fallen directly upon the leaves (Blanco-Moreno *et al.* 2019). Fern fronds live around 2–3 years at most (literature cited by Karst & Lechowicz 2007), and a high LMA generally indicates that the fronds were especially long-lived (Tanner 1983; Karst & Lechowicz 2007). This suggests that *Weichselia* fronds were not shed regularly and grew at a lower relative rate (Poorter *et al.* 2009). This strategy is not 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 & Alvin 1996). *Weichselia* was most
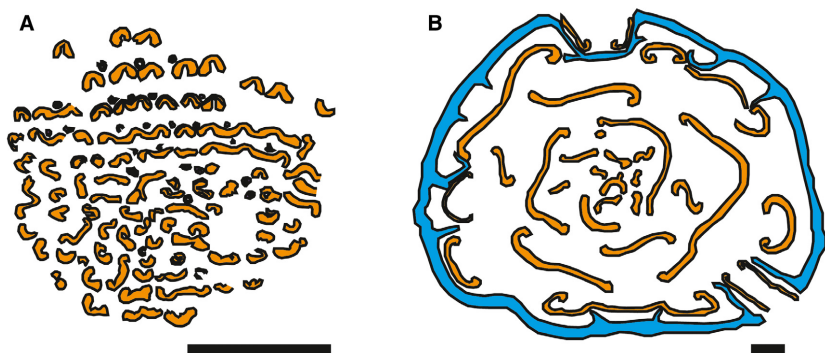
FIG. 10. A, central strands of thin section of *Weichselia reticulata* (IRSNB b 0229). B, anatomy of *Psaronius magnificus* (Herzer) Rothwell & Blickle, 1982 without the roots. Scale bars represent 1 cm.

probably a re-sprouter like *Pteridium* Gleditsch, as suggested by Scott *et al.* (2000), and like some tree-ferns that are fire tolerant and re-sprout from buds in their fibrous trunks after a fire (Ough & Murphy 2004).

The environmental conditions of the habitat of *Weichselia reticulata* have been much discussed. Some authors have suggested that 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 have suggested that 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 a trophophyte in coastal wet ground that dried periodically (Daber 1968). This study does not provide keys to the environment where *Weichselia* grew, but 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 with 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*, is related to protection from high insolation and not to aridity (Kessler *et al.* 2007).

Guidelines for reconstruction

We consider that the present data on the morphology, anatomy, and architecture of *Weichselia reticulata* do not allow for a complete reconstruction of the habit of the whole plant with confidence. However, they do shed new light on existing reconstructions and allow discussion of which aspects are accurate.

Previous reconstructions of *W. reticulata* (Bommer 1910; 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 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 present analyses nevertheless do not provide direct evidence for the stem being upright. Both specimens studied on µCT 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; and (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 organization of the petiole vascularization that does not arise directly from the central strands and is perpendicular to the stem (Figs 6B, 7B, 11A). In this plant, the perpendicular vascular strands act like 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 has been previously suggested (Blanco-Moreno *et al.* 2019),

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 (A) petiole and (B) ramification.
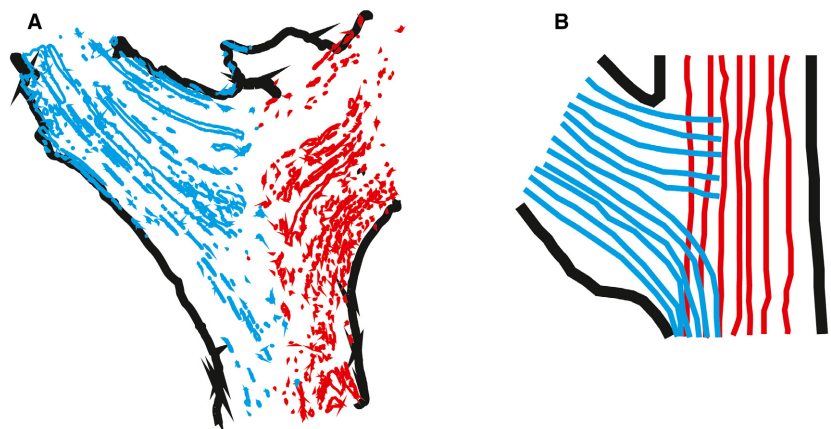
on an upright stem the vasculature of the petiole bases could similarly act like tensile cables. Fronds were large and most probably heavy (according to high LMA) and would need a good mechanical support at the petiole insertion. The asymmetric disposition of the tensile cable-like vascularization in 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 the Niklas (1994) formula (see results section).

Roots are present in all reconstructions, but their organization does not fit what is seen in the specimens. Root insertions are always too small. They are inserted at very large angles compared with the possible rooting organ observed in specimen IRSNB b 8424. Bommer (1910) and Sender *et al.* (2015) drew them in a different position than that observed in this study.

Petioles, although inserted at an excessively large angle, are correctly proportioned in Bommer (1910). This is also the case in Alvin (1971). They are too small in relation to the stem width in Poyato-Ariza & Buscalioni (2016). Sender *et al.* (2015) suggested in their reconstruction that the fronds occur at the end of branches. Setting aside that a possible branching of the stem has been described; petioles have definitely been observed, and the pedate heads are thus not borne directly as the termination of branches. Finally, the Cycas-like reconstruction by Daber (1968) does not fit any of the results discussed herein and is considered to be the least 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 that there could be up to two fronds per node, possibly ruling out the complete helix disposition. In contrast, 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*.

CONCLUSION

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 from 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 of thin sections of this and other material is 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 into 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 allow for further interpretations of the autecology of this cosmopolitan fern.

DATA ARCHIVING STATEMENT

Images and models 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.natura lsciences.be/virtual-collections/paleontology/paleobotany/weichselia

Access to the raw CT data archived in the collection can be requested from the curator of the RBINS Collections of Palaeontology, from the RBINS Scientific Survey of Heritage, currently Annelise Folie (annelise.folie@naturalsciences.be).

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REFERENCES

AGUIRREZABALA, L. M., TORRES, J. A. and VIERA, L. I. 1985. El Weald de Igea (Cameros-La Rioja). Sedimentología, bioestratigrafía y paleoicnología de grandes reptiles (dinosaurios). *Munibe Ciencias Naturales*, **37**, 111–138.

ALLISON, H. E. 1913. On the vascular anatomy of the rhizome of *Platycerium*. *New Phytologist*, **12**, 311–321.

ALMENDROS, G., ZANCADA, M. C., GONZÁLEZ-VILA, F. J., LESIAK, M. A. and ÁLVAREZ-RAMIS, C. 2005. Molecular features of fossil organic matter in remains of the Lower Cretaceous fern *Weichselia reticulata* from Przenosza basement (Poland). *Organic Geochemistry*, **36**, 1108–1115.

ALVIN, K. L. 1968. The spore-bearing organs of the Cretaceous fern *Weichselia* Stiehler. *Botanical Journal of the Linnean Society*, **61**, 87–92.

—— 1971. *Weichselia reticulata* (Stokes et Webb) Fontaine from the Wealden of Belgium. *Mémoire de L'Institut Royal des Sciences Naturelles de Belgique*, **166**, 1–33.

—— 1974. Leaf anatomy of *Weichselia* based on fusainized material. *Palaeontology*, **17**, 587–598.

ARENS, N. C. 1997. Responses of leaf anatomy to light environment in the tree fern *Cyathea caracasana* (Cyatheaceae) and its application to some ancient seed ferns. *Palaios*, **12**, 84–94.

—— and SMITH, A. R. 1998. *Cyathea planadae*, a remarkable new creeping tree fern from Colombia, South America. *American Fern Journal*, **88**, 49–59.

BAELE, J. M., GODEFROIT, P., SPAGNA, P. and DUPUIS, C. 2012. A short introduction to the geology of the Mons Basin and the Iguanodon Sinkhole, Belgium. 35–42. *In* GODEFROIT, P. (ed.) *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, 629 pp.

BARALE, G. 1979. Découverte de *Weichselia reticulata* (Stokes & Webb) Fontaine emend. Alvin, filicinée leptosporangiée, dans le Crétacé Inférieur de la province de Lérida (Espagne): implications stratigraphiques et paléoécologiques. *Geobios*, **12**, 313–319.

—— and AZAR, D. 2004. Cuticules végétales dans le Crétacé inférieur du Sud du Liban. *Comptes Rendus Palevol*, **3**, 119–124.

—— and OUAJA, M. 2001. Découverte de nouvelles flores avec des restes à affinités angiospermiennes dans le Crétacé inférieur du Sud tunisien. *Cretaceous Research*, **22**, 131–143.

BARRAL, A., GOMEZ, B., ZORRILLA, J. M., SERRANO, J. M., YANS, J., CAZEDEBAT, M., DAVIERO-GOMEZ, V., EWIN, T. A. M. and LECUYER, C. 2016. Local-scale analysis of plant community from the Early Cretaceous riparian ecosystem of Hautrage, Belgium. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **443**, 107–122.

BARTHEL, K. W. and BOETTCHER, R. 1978. Abu Ballas Formation (Tithonian/Berriasian; Southwestern Desert, Egypt) a significant lithostratigraphic unit of the former 'Nubian Series'. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, **18**, 153–166.

BATTEN, D. J. 1974. Wealden palaeoecology from the distribution of plant fossils. *Proceedings of the Geologists' Association*, **85**, 433–458.

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

BIERHORST, D.W. 1971. *Morphology of vascular plants*. Macmillan, 560 pp.

BLANCO-MORENO, C., GOMEZ, B. and BUSCALIONI, A. D. 2018. Palaeobiogeographic and metric analysis of the Mesozoic fern *Weichselia*. *Geobios*, **51**, 571–578.

—— —— MARUGÁN-LOBÓN, J., DAVIERO-GOMEZ, V. and BUSCALIONI, A. D. 2019. A novel approach for the metric analysis of fern fronds: growth and architecture of the Mesozoic fern *Weichselia reticulata* in the light of modern ferns. *PLoS One*, **14**, e0219192.

BLOMQUIST, H. L. 1922. Vascular anatomy of *Angiopteris evecta*. *Botanical Gazette*, **73**, 181–199.

BOMMER, C. 1910. Contribution à l'étude du genre *Weichselia*. *Bulletin de la Société Royale de Botanique de Belgique*, **3**, 296–304.

BOWER, F. O. 1923. *The ferns (Filicales): Analytical examination of the criteria of comparison*. Vol. **1**. Cambridge University Press, 359 pp.

—— 1926. *The ferns (Filicales): The Eusporangiatae and other relatively primitive ferns*. Vol. **2**. Cambridge University Press, 344 pp.

BROUAT, C., GIBERNAU, M., AMSELLEM, L. and McKEY, D. 1998. Corner's rules revisited: ontogenetic and interspecific patterns in leaf–stem allometry. *The New Phytologist*, **139**, 459–470.

CARPENTIER, A. 1927. La flore wealdienne de Féron-Glageon (Nord). *Mémoires de la Société Géologique du Nord*, **1**, 1–151.

CIGNONI, P., CALLIERI, M., CORSINI, M., DELLEPIANE, M., GANOVELLI, F. and RANZUGLIA, G. 2008. Meshlab: an open-source mesh processing tool. 129–136. *In* SCARANO, V., DE CHIARA, R. and ERRA, U. (eds). *Eurographics Italian Chapter Conference*. The Eurographics Association.

CORNET, J. 1927. L'époque wealdienne dans le Hainaut. *Annales de la Société Géologique de Belgique, Tome L.*, 161–164.

—— and SCHMITZ, G. 1898. Les puits naturels du terrain houiller du Hainaut. *Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie*, **12**, 301–318.

DABER, R. 1968. A *Weichselia–Stiehleria*–Matoniaceae community within the Quedlinburg Estuary of Lower Cretaceous age. *Botanical Journal of the Linnean Society*, **61**, 75–85.

DAVIES, K. L. 1991. A brief comparative survey of aerophore structure within the Filicopsida. *Botanical Journal of the Linnean Society*, **107**, 115–137.

DEJAX, J., PONS, D. and YANS, J. 2007. Palynology of the dinosaur-bearing Wealden facies in the natural pit of Bernissart (Belgium). *Review of Palaeobotany & Palynology*, **144**, 25–38.

DELCLÒS, X. and SORIANO, C. 2016. Insecta. 70–88. *In* POYATO-ARIZA, F. J. and BUSCALIONI, A. (eds). *Las Hoyas: A Cretaceous wetland.* Verlag Dr Friedrich Pfeil, 262 pp.

DELMER, A. and VAN WICHELEN, P. 1980. Répertoire des puits naturels connus en terrain houiller du Hainaut. *Geological Survey of Belgium Professional Papers*, **172**, 1–234.

DIÉGUEZ, M. C. and MELÉNDEZ, N. 2000. Early Cretaceous ferns from lacustrine limestones at Las Hoyas, Cuenca province, Spain. *Palaeontology*, **43**, 1113–1141.

DIEZ, J., SENDER, L., VILLANUEVA-AMADOZ, U., FERRER, J. and RUBIO, C. 2005. New data regarding *Weichselia reticulata*: soral clusters and the spore developmental process. *Review of Palaeobotany & Palynology*, **135**, 99–107.

DURAND, L. Z. and GOLDSTEIN, G. 2001. Growth, leaf characteristics, and spore production in native and invasive tree ferns in Hawaii. *American Fern Journal*, **91**, 25–36.

EDWARDS, W. N. 1933. On the Cretaceous fern *Paradoxopteris* and its connexion with *Weichselia. Annals of Botany*, **47**, 317–341.

EL ATFY, H., JASPER, A. and UHL, D. 2020. A new record of *Paradoxopteris stromeri* Hirmer 1927 (Monilophyta, incertae sedis) from the Cenomanian of Sinai, Egypt. *Review of Palaeobotany & Palynology*, **273**, 104148.

EL-KHAYAL, A. 1985. Occurrence of a characteristic Wealden fern (*Weichselia reticulata*) in the Wasia Formation, central Saudi Arabia. *Scrypta Geologica*, **79**, 75–88.

EVERT, R. F. 2006. *Esau's plant anatomy: Meristems, cells, and tissues of the plant body: Their structure, function, and development.* John Wiley & Sons, Hoboken, NJ, 600 pp.

FEDOROV, A., BEICHEL, R., KALPATHY-CRAMER, J., FINET, J., FILLION-ROBIN, J. C., PUJOL, S., BAUER, C., JENNINGS, D., FENNESSY, F., SONKA, M. and BUATTI, J. 2012. 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging*, **30**, 1323–1341.

GODEFROIT, P. 2012. *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems.* Indiana University Press, 629 pp.

GOMEZ, B., THÉVENARD, F., FANTIN, M. and GIUSBERTI, L. 2002. Late Cretaceous plants from the Bonarelli level of the Venetian Alps, northeastern Italy. *Cretaceous Research*, **23**, 671–685.

—— GILLOT, T., DAVIERO-GOMEZ, V., SPAGNA, P. and YANS, J. 2008. Paleoflora from the Wealden facies strata of Belgium: mega-and meso-fossils of Hautrage (Mons Basin). *Memoirs of the Geological Survey*, **55**, 53–60.

GRIMALDI, D. and AGOSTI, D. 2000. A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. *Proceedings of the National Academy of Sciences*, **97**, 13678–13683.

HALLE, F. 1965. Les stolons de la fougère arborescente *Cyathea manniana* Hooker. *Comptes Rendus de L'Académie des Sciences*, **261**, 2935–2938.

—— 1966. Étude de la ramification du tronc chez quelques fougères arborescentes. *Adansonia*, **6**, 405–424.

HARRIS, T. M. 1981. Burnt ferns from the English Wealden. *Proceedings of the Geologists' Association*, **92**, 47–58.

HAUSHAHN, T., SPECK, T. and MASSELTER, T. 2014. Branching morphology of decapitated arborescent monocotyledons with secondary growth. *American Journal of Botany*, **101**, 754–763.

HEIL, M. 2015. Extrafloral nectar at the plant-insect interface: a spotlight on chemical ecology, phenotypic plasticity, and food webs. *Annual Review of Entomology*, **60**, 213–232.

HESSE, L., MASSELTER, T., LEUPOLD, J., SPENGLER, N., SPECK, T. and KORVINK, J. G. 2016. Magnetic resonance imaging reveals functional anatomy and biomechanics of a living dragon tree. *Scientific Reports*, **6**, 32685.

HIRMER, M. 1927. *Handbuch der Paláobotanik.* R. Oldenbourg, Berlin, 708 pp.

JUNG, J., LEE, S. C. and CHOI, H. 2008. Anatomical patterns of aerenchyma in aquatic and wetland plants. *Journal of Plant Biology*, **51**, 428–439.

KARST, A. L. and LECHOWICZ, M. J. 2007. Are correlations among foliar traits in ferns consistent with those in the seed plants? *New Phytologist*, **173**, 306–312.

KATO, M. 1993. A taxonomic study of the genus *Matonia* (Matoniaceae). *Blumea: Biodiversity, Evolution & Biogeography of Plants*, **38**, 167–172.

KESSLER, M., SIORAK, Y., WUNDERLICH, M. and WEGNER, C. 2007. Patterns of morphological leaf traits among pteridophytes along humidity and temperature gradients in the Bolivian Andes. *Functional Plant Biology*, **34**, 963–971.

KOENIGUER, J. C. 1966. Étude paléophytogéographique du Continental Intercalaire de l'Afrique Nord-Équatoriale. Sur de nouveaux échantillons du genre *Paradoxopteris. Mémoires de la Société Géologique de France*, **105**, 100–112.

KOPTUR, S., SMITH, A. R. and BAKER, I. 1982. Nectaries in some neotropical species of *Polypodium* (Polypodiaceae): preliminary observations and analyses. *Biotropica*, **14**, 108–113.

—— PALACIOS-RIOS, M., DÍAZ-CASTELAZO, C., MACKAY, W. P. and RICO-GRAY, V. 2013. Nectar secretion on fern fronds associated with lower levels of herbivore damage: field experiments with a widespread epiphyte of Mexican cloud forest remnants. *Annals of Botany*, **111**, 1277–1283.

KRAMER, K. U. 1990. Matoniaceae. 183–185. *In* KRAMER, K. U. and GREEN, P. S. (eds). *Pteridophytes and gymnosperms.* Springer, 404 pp.

LEHTONEN, S., SILVESTRO, D., KARGER, D. N., SCOTESE, C., TUOMISTO, H., KESSLER, M., PEÑA, C., WAHLBERG, N. and ANTONELLI, A. 2017. Environmentally driven extinction and opportunistic origination explain fern diversification patterns. *Scientific Reports*, **7**, 1–12.

LYON, M. A., JOHNSON, K., WING, S., NICHOLAS, D., LACOVARA, K. and SMITH, J. 2001. Late Cretaceous equatorial coastal vegetation: new megaflora associated with

dinosaur finds in the Bahariya oasis, Egypt. *Geological Society of America Abstracts With Programs*, **33**, 1179.

MORGAN, E. J. 1959. The morphology and anatomy of American species of the genus *Psaronius*. *Illinois Biological Monographs*, **27**, 1–108.

NIKLAS, K. J. 1978. Morphometric relationships and rates of evolution among Paleozoic vascular plants. *Evolutionary Biology*, **11**, 509–543.

—— 1991. Flexural stiffness allometries of angiosperm and fern petioles and rachises: evidence for biomechanical convergence. *Evolution*, **45**, 734–750.

—— 1994. Predicting the height of fossil plant remains: an allometric approach to an old problem. *American Journal of Botany*, **81**, 1235–1242.

—— TIFFNEY, B. H. and KNOLL, A. H. 1983. Patterns in vascular land plant diversification. *Nature*, **303**, 614–616.

OUGH, K. and MURPHY, A. 2004. Decline in tree-fern abundance after clearfell harvesting. *Forest Ecology & Management*, **199**, 153–163.

PEPPE, D. J., LEMONS, C. R., ROYER, D. L., WING, S. L., WRIGHT, I. J., LUSK, C. H. and RHODEN, C. H. 2014. Biomechanical and leaf–climate relationships: a comparison of ferns and seed plants. *American Journal of Botany*, **101**, 338–347.

POORTER, H., NIINEMETS, U., POORTER, L., WRIGHT, I. J. and VILLAR, R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, **182**, 565–588.

POYATO-ARIZA, F. J. and BUSCALIONI, A. D. 2016. *Las Hoyas: A Cretaceous wetland*. Verlag Dr Friedrich Pfeil, 262 pp.

PPG I 2016. A community-derived classification for extant lycophytes and ferns. *Journal of Systematics & Evolution*, **54**, 563–603.

QUINIF, Y. and LICOURT, L. 2012. The karstic phenomenon of the Iguanodon Sinkhole and the geomorphological situation of the Mons Basin during the Early Cretaceous. 51–61. *In* GODEFROIT, P. (ed.) *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, 629 pp.

ROLLERI, C. H. 2002. Caracteres diagnósticos y taxonomía en el género *Angiopteris* Hoffm. (Marattiaceae Bercht. & JS Presl): I, los caracteres. *Revista del Museo de La Plata*, **15**, 23–49.

—— 2004. Revisión del género *Danaea* (Marattiaceae-Pteridophyta). *Darwiniana, Nueva Serie*, **42**, 217–301.

ROMÁN GÓMEZ, P. 1986. Nota sobre la macroflora del Cretácico inferior de la Cuenca de Préjano (LaRioja). *Coloquios de Paleontología*, **41**, 35–40.

ROSS, A. J. and COOK, E. 1995. The stratigraphy and palaeontology of the Upper Weald Clay (Barremian) at Smokejacks Brickworks, Ockley, Surrey, England. *Cretaceous Research*, **16**, 705–716.

ROTHWELL, G. W. and BLICKLE, A. H. 1982. *Psaronius magnificus* n. comb., a marattialean fern from the Upper Pennsylvanian of North America. *Journal of Paleontology*, **56**, 459–468.

SCHNEIDER, C. A., RASBAND, W. S. and ELICERI, K. W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, **9**, 671.

SCHNYDER, J., DEJAX, J., KEPPENS, E., TU, T. T. N., SPAGNA, P., BOULILA, S., GALBRUN, B., RIBOULLEAU, A., THSIBANGU, J. P. and YANS, J. 2009. An Early Cretaceous lacustrine record: organic matter and organic carbon isotopes at Bernissart (Mons Basin, Belgium). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **281**, 79–91.

SCOTT, A. C., CRIPPS, J. A., COLLINSON, M. E. and NICHOLS, G. J. 2000. The taphonomy of charcoal following a recent heathland fire and some implications for the interpretation of fossil charcoal deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **164**, 1–31.

SENDER, L. M., VILLANUEVA-AMADOZ, U., PONS, D., DIEZ, J. B., GARCÍA-ÁVILA, M. and FERRER, J. 2015. New reconstruction of *Weichselia reticulata* (Stokes et Webb) Fontaine in Ward emend. Alvin, 1971 based on fertile remains from the middle Albian of Spain. *Historical Biology*, **27**, 460–468.

SEWARD, A. C. 1900. La flore wealdienne de Bernissart. *Mémoire du Muséum D'Histoire Naturelle de Belgique*, **1**, 1–37.

SHINAQ, R. and BANDEL, K. 1998. The flora of an estuarine channel margin in the Early Cretaceous of Jordan. *Freiberger Forschungshefte C 474, Paläontologie, Stratigraphie, Fazies*, **6**, 39–57.

SILANTIEVA, N. and KRASSILOV, V. 2006. *Weichselia* Stiehler from Lower Cretaceous of Makhtesh Ramon, Israel: new morphological interpretation and taxonomical affinities. *Acta Palaeobotanica Krakow*, **46**, 119–135.

SMITH, A. R., PRYER, K. M., SCHETTPELZ, E., KORALL, P., SCHNEIDER, H. and WOLF, P. G. 2006. A classification for extant ferns. *Taxon*, **55**, 705–731.

SPAGNA, P., YANS, J., SCHNYDER, J. and DUPUIS, C. 2012. The palaeoenvironment of the Bernissart iguanodons: sedimentological analysis of the Lower Cretaceous Wealden facies in the Bernissart area. 87–96. *In* GODEFROIT, P. (ed.) *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, 629 pp.

STOKES, C. and WEBB, P. B. 1824. Description of some fossil vegetables of the Tilgate Forest in Sussex. *Transactions of the Geological Society of London, Series 2*, **1**, 421–424.

TANNER, E. V. J. 1983. Leaf demography and growth of the tree-fern *Cyathea pubescens* Mett. ex Kuhn in Jamaica. *Botanical Journal of the Linnean Society*, **87**, 213–227.

TIDWELL, W. D. and ASH, S. R. 1994. A review of selected Triassic to Early Cretaceous ferns. *Journal of Plant Research*, **107**, 417–442.

VAN DEN BROECK, E. 1898. Les coupes du gisement de Bernissart. Caractères et dispositions sedimentaires de l'argile ossifere du cran aux Iguanodons. *Bulletin de la Societé Belge de Géologie de Paleontologie et de Hydrologie*, **12**, 216–243.

VAN KONIJNENBURG-VAN CITTERT, J. H. A. 1993. A review of the Matoniaceae based on in situ spores. *Review of Palaeobotany & Palynology*, **7**, 235–267.

WATSON, J. and ALVIN, K. L. 1996. An English Wealden floral list, with comments on possible environmental indicators. *Cretaceous Research*, **17**, 5–26.

WEST, C. 1915. On the structure and development of the secretory tissues of the Marattiaceae. *Annals of Botany*, **29**, 409–422.

WHITE, R. A. and TURNER, M. D. 2012. The anatomy and occurrence of foliar nectaries in *Cyathea* (Cyatheaceae). *American Fern Journal*, **102**, 91–114.

—— —— 2017. The comparative anatomy of *Hymenophyllopsis* and *Cyathea* (Cyatheaceae): a striking case of heterochrony in fern evolution. *American Fern Journal*, **107**, 30–57.

YANS, J., ROBASZYNSKI, F. and MASURE, E. 2012. Biostratigraphy of the Cretaceous sediments overlying the Wealden facies in the Iguanodon sinkhole at Bernissart. 87–96. *In* GODEFROIT, P. (ed.) *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, 629 pp.

ZEILLER, R. 1914. Sur quelques plantes wealdiennes recueillies au Pérou par M. le Capitaine Berthon. *Revue Générale de Botanique*, **25**, 647–674.