Review of Palaeobotany and Palynology 297 (2022) 104585

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Flabellopteris lococannensis gen. et sp. nov.: A new fern-like plant from the Famennian of South Africa

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ARTICLE INFO

Article history:
Received 7 May 2021
Received in revised form 7 December 2021
Accepted 8 December 2021
Available online 13 December 2021

Keywords:
Euphyllophytes
Devonian
South Africa
Waterloo Farm
Witpoort Formation

ABSTRACT

A new fossil plant, *Flabellopteris lococannensis* Gess and Prestianni gen. et sp. nov., is described from the Famennian of South Africa. This plant is interpreted as monopodial in habit with a first order axis that only occasionally dichotomizes. The lateral organs (both branches and appendages) are borne spirally on all branching orders and a 1/3 organotaxy is suggested. The first order axes bear both second order axes and fertile appendages at the same nodes. Axes of the second and third branching orders bear appendages made of several isotomous dichotomies. Recurved paired sporangia are borne on dichotomizing appendages that are like the vegetative appendages. The plant bears some similarity to the Iridopteridales but also to the Late Devonian *Rhacophytales* and to the Lower Carboniferous fernlike plant *Chlidanophyton dublinensis*. The architecture of the plant is briefly discussed and its implication on the evolution of the frond is considered.

1. Introduction

The Devonian period is notably marked by the evolution and subsequent rapid diversification of the vascular plants among which the euphyllophytes occupy a peculiar position (Kenrick and Crane, 1997; Taylor et al., 2008). The rapidity of this diversification as well as its complexity contribute to our understanding of the phylogenetic relationships among basal euphyllophytes remaining highly problematic (Kenrick and Crane, 1997; Toledo et al., 2021, 2018; Xue et al., 2010). These problems can only be resolved by investigating the morphology and anatomy of additional basal euphyllophytes.

Plumstead (1967) described from the Howison's Poort locality a small dichotomous branching system bearing paired sporangia on recurved tips. She attributed this isolated specimen to the genus *Dutoitia* Hoeg as the new species *Dutoitia maraisia* Plumstead. Anderson and Anderson (1985) reported naked axes with alternate branching and a characteristic striation from the same locality and assigned them to a new taxon *Praeramunculus alternatiramus* Anderson and Anderson.

Gess and Hiller (1995), in a first account on the Late Devonian Waterloo Farm flora, illustrated and briefly described plant remains that they attributed to the progymnosperms. They recognised three branching orders bearing fertile appendages. They found rounded sporangia grouped in pairs and borne by small dichotomous branching systems. They also produced a partial reconstruction of the branching system and of the fertile parts. These authors recognised the similarity of these structures with those attributed to *Dutoitia* by Plumstead (1967) and based on their connection to several higher branching orders at Waterloo Farm, suggested that the plant represented by these structures should be excluded from the genus *Dutoitia*.

This study forms part of a systematic revision of the Famennian Waterloo Farm flora, based on extensive collections built over the last 25 years by RG (Gess and Hiller, 1995; Gess and Whitfield, 2020). It allows us to reassess the affinities of the plant described by Gess and Hiller (1995). We attribute it to a new taxon, *Flabellopteris lococannensis* Gess and Prestianni, gen. et sp. nov., which we describe here in detail and compare with similar taxa to address its systematic affinities.

2. Locality and geology

Specimens attributable to *Flabellopteris* have been collected by RG from the Waterloo Farm Lagerstätte, south of the city of Makhanda/Grahamstown (Eastern Cape, South Africa) (see Gess and Hiller, 1995; Gess and Whitfield, 2020). At this site plant fossils occur in a series of black shale lenses, interbedded within quartzitic strata of the Famennian (Late Devonian) aged Witpoort Formation (Witteberg Group, Cape Supergroup). These lenses comprise graphitic black shale interpreted as having been deposited as anaerobic mud in a back-barrier estuarine lagoonal environment adjacent to the Agulhas Sea (Gess and Hiller, 1995). Abundant fossil material is accumulated from both aquatic and

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https://doi.org/10.1016/j.revpalbo.2021.104585

adjacent terrestrial environments and includes both aquatic and terrestrial plants (Gess and Prestianni, 2018; Prestianni and Gess, 2019, 2014 and references therein), terrestrial (Gess, 2013) and aquatic invertebrates (Gess and Hiller, 1995; Scholze and Gess, 2017) and aquatic vertebrates (Gess and Whitfield, 2020 and references therein). Paleogeographic reconstructions indicate that the sequence exposed at the Waterloo Farm locality was deposited at high latitude, within 30° of the south pole (Torsvik and Cocks, 2011) or possibly at even higher latitude (Mitchell et al., 2012; Scotese and McKerrow, 1990; Scotese and Barrett, 1990). Material attributed to the taxon herein discussed has been recovered from the MFL (Main Fish Lens), from which most of the material so far described from Waterloo Farm has been recovered, as well as from the BL (Blue layer). This latter horizon is characterised by an almost total lack of animal remains and, in places, a high concentration of well preserved, relatively unfragmented plant remains. All the material herein described comes from a large, dislodged slab of rock derived from the BL and recovered by RG and N. Hiller in 1993.

3. Material and methods

The specimens are preserved as adpressions in a black, carbon rich, anaerobically derived metashale. In all specimens, organic material was replaced, during diagenesis, either by a silvery white phyllosilicate, which later altered to soft white kaolinite clay (Gess and Hiller, 1995), or a shiny coal. The material was originally exposed by splitting of the rock but the architecture of the axes was further explored through careful chiselling away of matrix with finer details being dégaged using triangular needles (Fairon-Demaret et al., 1999; Leclercq, 1960) or hand held porcupine quills. All material (figured and non-figured) is deposited in the Albany Museum Devonian Lab, 87 Beaufort Street, Makhanda/Grahamstown, Eastern Cape, South Africa. Some of this material was preliminarily illustrated in Gess and Hiller (1995).

4. Description

4.1. General observations

This description is based on an association of plant axes and fragments recovered from a single slab of rock (AM 5343) and possibly derived from a single plant. These include three large axes found aligned in parallel (Plate I, 1). All three axes are broken distally as well as proximally such that the base and the top of the first branching order are not recorded. Even though most appendages are not preserved, their morphology was possible to define. Fertile parts were recovered in attachment and are described hereafter. Additional material includes some in which all white mineralised material was removed by exposure to the rain (Plate II, 1) or has flaked off (Plate IV).

4.2. First-order axes

The plants are monopodial in overall appearance. The first order axis shows a slight and irregular undulation. First order axes up to 45 cm long are preserved and taper slightly from base to top, ranging from 7.5 to 9.0 mm wide at the base and from 5.6 to 6.8 mm wide at the top (Plate I).

The surface of the axes is devoid of spines. It is marked by deep parallel longitudinal ridges. Though not always visible on the “white” specimens (arrow R on Plate I and Plate II, 2), the ridges are particularly conspicuous on the “black” specimens in which the white mineral has been removed by weathering or has flaked off (Plate II, 1 and Plate IV). Up to 4 ridges per exposed face of the first order axis are observed. They measure between 1 and 2.5 mm in width and can easily be traced. Close to branching points, they seem to divide, and a part (often two) appear to follow the branches. The number of ridges tends to decrease with the branching order. Second order axes only show two to three ridges. In higher branching orders only one ridge can be traced. We interpret these ridges as marking the vascularisation.

At first sight, branching of the first order axis seems to occur helically (Plate I). In most cases, only one second order branch is observed per node. A close observation and preparation of selected nodes however reveals that several branches are produced simultaneously (see arrow N on Plate I, 1). We conclude that originally there were four second order axes originating at each node, arranged in two pairs (see below). Plate II, Figs. 2 and 3 show details of branching node N1 (Plate I, 1) revealed at two different stages of preparation. Three second order branches are visible (see 1–3 on Plate II, 3). They are produced opposite to the exposed face of the plant, seem to dip into the sediment and measure approximately 2 mm in width. Only two ridges can be seen on each of the second order branches. The branching node N2 (Plate I) is reproduced in detail in Plate II, 4. It clearly shows the ridges of the first order axis inflected towards the branching level. Two second order axes are clearly visible (3 and 4, Plate II, 4). At the base of axis “3”, two small, rounded structures are observed that are interpreted as the base of two additional axes marked 1 and 2 (Plate II, 4 see also bb1 and bb2 pl. III, 1). A detached portion of the slab best illustrates the branching pattern (Plate II, 6). This specimen shows a short 4.8 cm long first order axis distally ending at a branching point, beyond which the primary axis is broken away to reveal the full suite of branches. Four second order axes numbered from 1 to 4 are observed. They seem to be produced in pairs, branches 1 and 2 forming one pair and 3 and 4 a second pair. Branches 1 and 2 as well as 3 and 4 diverge at an angle of 35° from each other while 2 and 3 diverge at an angle of 40°. The whole second order branching system occupies approximately 110° of the axis circumference. A similar specimen is shown in Plate II, 5. We consider the plant to produce two pairs of second order axes at each node. In most specimens, a bulge is observed at the base of the second order axes giving to the whole stem an enlarged aspect at the node (Plate II, 4, 5 and 7).

In plant c, the first order axis is characterised by a peculiar division (arrow D1, Plate I, 1) which occurs 15 cm from the most proximally preserved point. It consists of a division of the first order axis into two more or less equivalent axes. One is 5.5 mm wide while the other is 6 mm wide. They both show the same organisation and tend to be straight and “vertical”. We interpret this division as a dichotomy though anatomical information would be necessary to confirm this. A similar situation is observed near the preserved tip of plant a (see D2, Plate I, 1). In the former case it coincides with the base of a short zone of condensed branching density (see S1 on Plate I, 1).

The three-dimensional organisation of the plant can be inferred from close observation of each branch insertion level. A detail of the apical part of the first order axis of plant c is shown in Plate III, 1. This specimen permits a clear understanding of the organotaxy of the first order branches (see interpretative drawing Fig. 1 a–c). At the first of the most apical preserved branching levels, second order axes are produced on the left side of the first order axis and slightly towards the observer as demonstrated by the presence of the broken branch bases (bb1, Plate III, 1). At the second level of branching, axes are produced on the right side of the stem with some also being produced towards the observer (see bb2, Plate III, 1). Finally, the third branching level is produced towards the left side of the first order axis, with only one branch visible on the plane of fracture and no additional branch bases observable. The remaining three axes are dipping into the sediment. An interpretative reconstruction of this plant fragment is proposed in Fig. 1. We suggest a 1/3 organotaxy for the first order axis as suggested by Fig. 1c with each set of branches being produced at 120° from those at the preceding level.

4.3. Second-order axes

Second-order axes are rarely well exposed. They are thinner measuring between 1.5 and 3.5 mm in width (Plate I, 1). They do not vary

Plate I. 1. General view of the rock slab showing the three aligned first order axes (a, b and c), showing occasional dichotomies (D1 and D2), the characteristic longitudinal ribbing of the axis (R) and regions of condensed growth (S1 and S2) and branching nodes (N1 and N2). Scale bar = 2 cm.

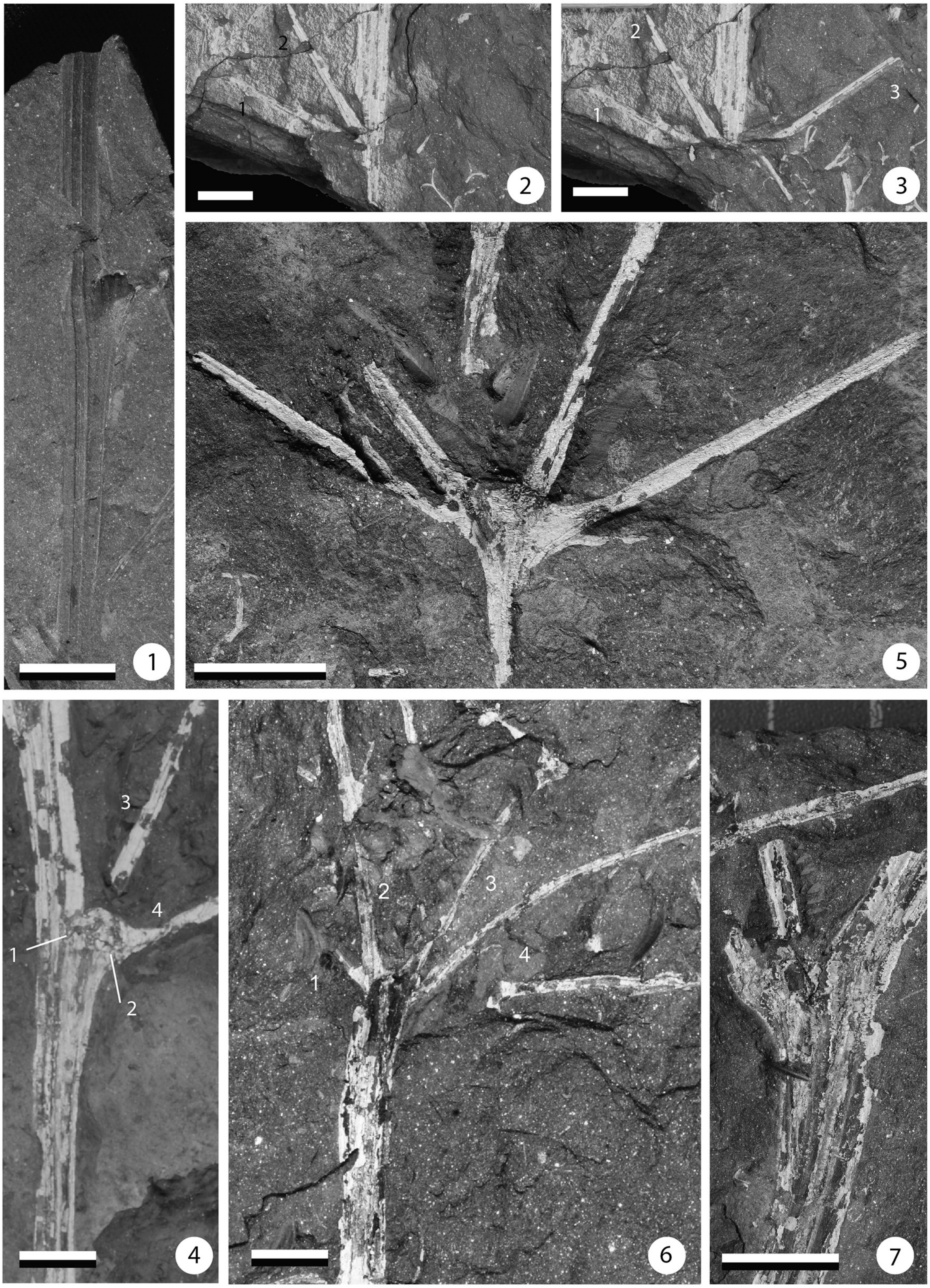

Plate II. 1. “Black” specimen showing the characteristic longitudinal ridging of the axes. Scale bar = 1 cm.
2. Detail of branching node N1 (Plate I, 1). Scale bar = 1 cm.
3. Detail of branching node N1 (Plate I, 1) with sediment partly removed revealing the base of three second order axes (1, 2 and 3). Scale bar = 1 cm.
4. Detail of branching node N2 (Plate I, 1) showing two second order axes (3 and 4) and the bases of two additional second order axes (1 and 2). Note the presence of an inflated base. Scale bar = 1 cm.
5. Detail of a branching node showing 4 second order axes departing from the same level. Scale bar = 1 cm.
6. Detail of a branching node showing 4 second order axes (1–4). Scale bar = 1 cm.
7. Detail of a first order axis at node showing the inflated base. Scale bar = 1 cm.

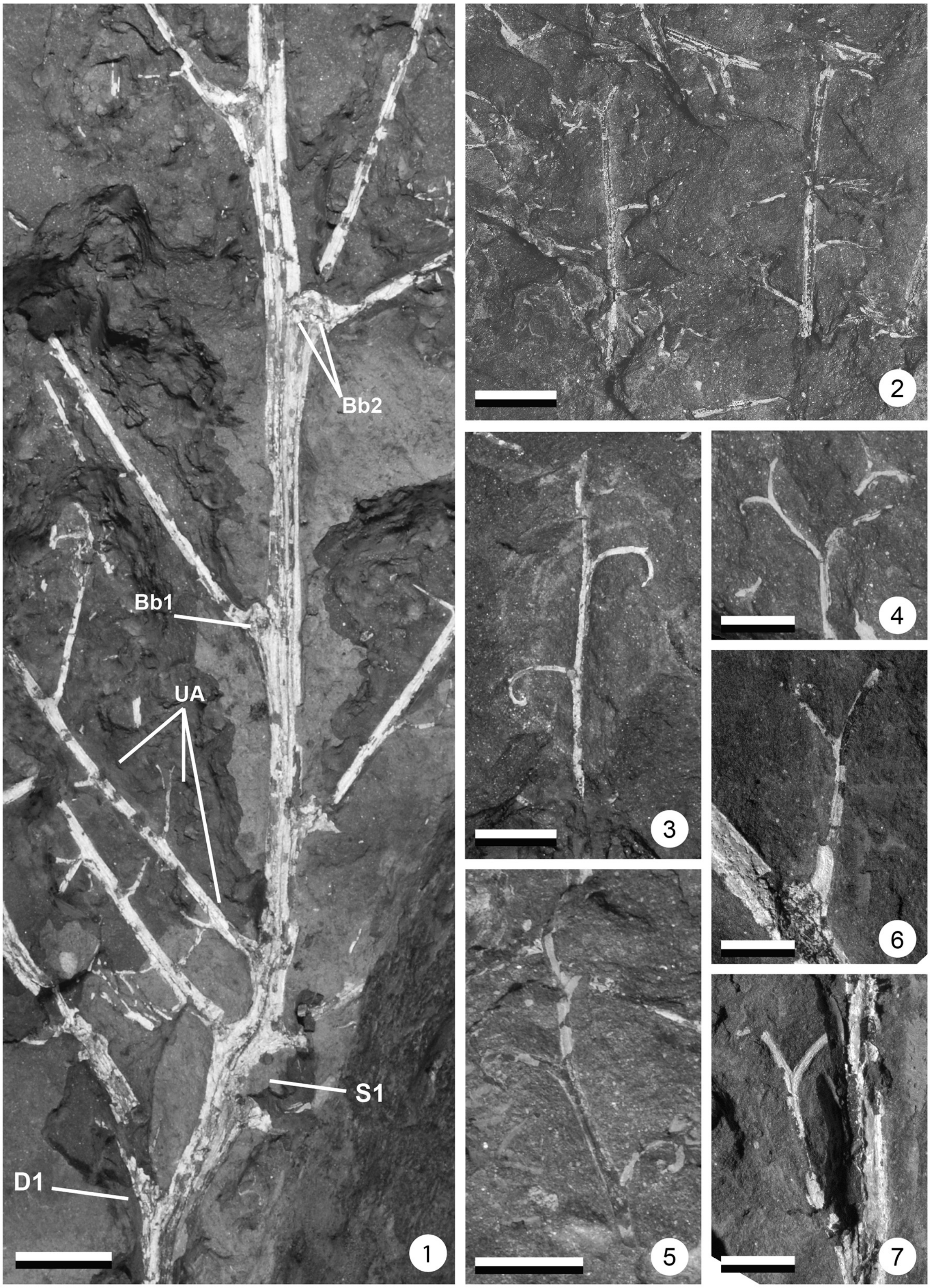

Plate III. 1. Detail of the upper portion of plant "c" (Plate I, 1) showing a dichotomy (D1), a zone of condensed growth (S1), several appendages on second order axes (UA) and several branch bases (Bb1 and Bb2). Scale bar = 1 cm.
2. Details of two isolated third order axes with appendages. Scale bar = 5 mm.
3. Detail of an isolated third order axis with appendages attached. Scale bar = 5 mm.
4. Isolated vegetative appendage. Scale bar = 5 mm.
5. Detail of third order axis near its tip. Scale bar = 5 mm.
6. Detail of an appendage attached to the proximal portion of a second order axis.
7. Detail of an appendage attached to the proximal portion of a second order axis.

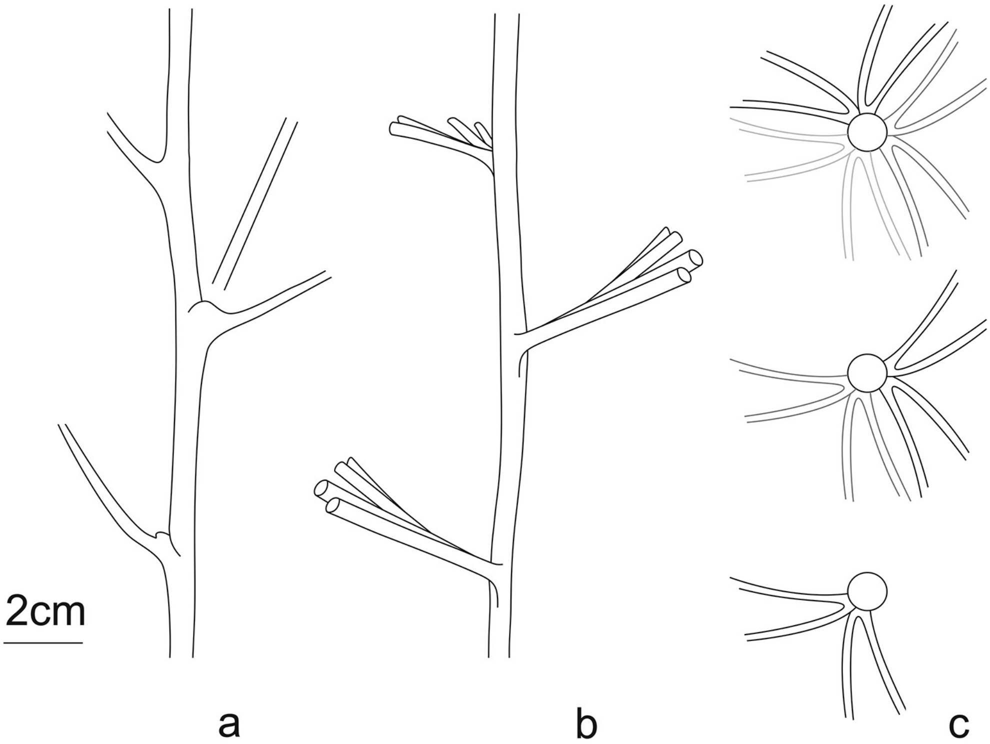

Fig. 1. Interpretation of first order axes organotaxy. (a) camera lucida drawing of the apical part of plant c (see Plate I, 1 and Plate III, 1). (b) interpretative three-dimensional reconstruction. (c) top view of reconstruction Fig. 1b, with three nodes of second-order axes.

significantly in width from base to top. Their length is difficult to assess reliably as no complete branch was recovered. The maximum recorded length is 20 cm. Their surface is also characterised by ridging though only one or two ridges are visible (Plate I, 1; Plate II, 2–6). The basal 7 to 9 cm of these axes seems in most case to be naked (Plate I, 1; Plate III, 1). However, the best-preserved specimens show them to bear appendages (UA) that are very likely not preserved in most cases (UA, Plate III, 1). Up to three appendages have been observed. They are helically arranged. The three UA correspond to one organotactic helix. After this first gyre of appendages, third order branches are produced (Plate I, 1; Plate III, 1). Second order axes thus produce both types of organs. They are inserted on the same helix, appendage occupying the first gyre and third order axes the remaining gyres.

4.4. Third-order branches

Only a few specimens allow good understanding of third order axes. They are small measuring between 1.0 and 1.5 mm in width (Plate III, 2–3, 5). They have a maximum measured length of 5 cm. Like the axes of all other branching orders, they are smooth and present ridges though very small and difficult to distinguish. They only bear appendages following the same 1/3 taxis as the rest of the plant.

4.5. Appendages

In most cases, it is difficult to ascertain whether the appendages are fertile or vegetative. Indeed, the tips are often incompletely preserved. So far, we consider vegetative appendages to consist of equally dichotomizing segments measuring less than 2 mm in maximum diameter. They appear to be fragile and are in most cases not preserved, or are incompletely preserved (Plate I, 1). Although the majority of appendages preserved appear to be fertile, including most or all of those in ultimate attachment to the first order axes studied, others located on branch fragments on the same slab appear to include vegetative examples, distinguished by termination in recurved pointed tips rather than sporangia. Their size and organisation vary according to their position on the plant (Plate I, 1; Plate III, 1–7). The appendages occurring on second order axes measure between 1.5 and 2 cm in length and 1.5 and 2 cm in width (Plate III, 6–7). They form an angle of approximately 75° with the axis (UA, Plate III, 1). They present three dichotomies (Plate III, 4). The first dichotomy occurs 0.6–0.8 cm from the base, the second 0.3–0.5 cm from the first, and the third 0.2 cm from the second. The last dichotomy in vegetative appendages produces a pair of small recurved pointed tips (Plate III, 4). The appendages occurring on third order axes measure between 0.5 and 1 cm in length and between 0.5 and 1 cm in width. They form an angle of approximately 45–90° with the axis. They present two dichotomies (Plate III, 2–3). The first dichotomy occurs after 0.3–0.5 cm and the second after 0.1 and 0.3 cm. The last dichotomy produces a pair of small recurved pointed tips if not fertile (Plate III, 2, 3 and 5).

Fertile appendages follow the same general organisation as the vegetative ones. They occur on first, second and third order axes. The organisation of the fertile appendages inserted on first order axes is best seen in Plate IV, 1–2 (Fig. 2, A–C) and Plate V, 2–4. Plate IV, 1,2 show part and counter part of the same fertile appendage. It rises from a first order axis at the same level as second order axes. Its exact position is however difficult to assess reliably. Indeed, the lack of anatomical details prevents us from understanding whether it is anatomically directly borne on the first order axis or produced very basally on the second order axis. The basal segment of the appendage seems to point slightly downwards. After 0.5 cm, a dichotomy occurs producing two segments that are clearly curved upwards giving to the whole fertile appendage an erect aspect (Plate IV, 1 and Fig. 2A). Two other dichotomies occur after 0.7–0.8 cm and 0.5–0.6 cm. The last dichotomy produces two recurved segments measuring 0.1–0.2 cm, each bearing a pair of elliptical sporangia (Plate IV 1,4 and Fig. 2B and C). The whole fertile appendage thus bears up to 16 sporangia (Fig. 2C). The sporangia are between 0.9 and 1.5 mm in length and 0.5–0.7 mm in width. Their surface in covered by a longitudinally elongated pattern here interpreted as cellular in

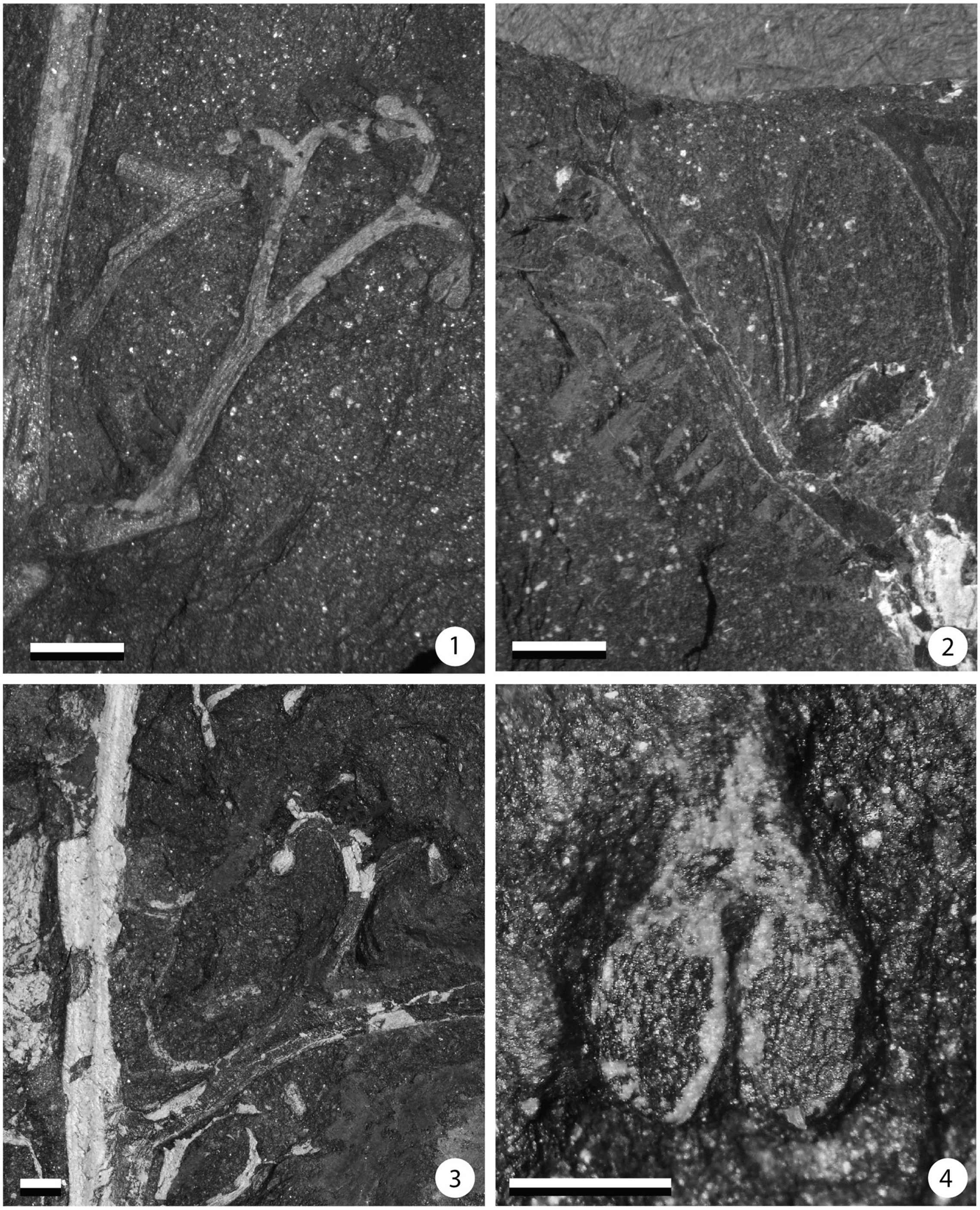

Plate IV. 1. Detail of a fertile appendage attached to a first order axis. Scale bar = 5 mm.
2. Counter part of specimen Plate IV, 1. Scale bar = 5 mm.
3. Fertile appendage attached to a third order axis. Scale bar = 2 mm.
4. Detail of a pair of sporangia showing cellular pattern of the epidermis. Scale bar = 1 mm.

origin. No obvious dehiscence structure is visible. Their tips are rounded. Multiple specimens corroborate these observations. The Plate V, 2 shows the insertion of the fertile appendage between two second order axes. It also clearly first goes down and then slightly curves up giving rise to a slightly erect fertile part. It seems to be inserted on an inflated structure. A similar inflated structure was observed in Plate V, 3. One node was further prepared allowing observation of two fertile appendages (Plate V, 4) suggesting that each pair of second order axes was associated with one fertile appendage (see Fig. 3). We have not been able to clearly decipher whether appendages on second order axes were fertile or vegetative. They are however slightly smaller than those on first order axes. Fertile appendages on third order axes are similar in structure though lacking one division of the axis they are equivalent to half of the structure observed on 1st and 2nd order axes, therefore producing only 8 terminal sporangia, and protruding about 5 mm from the 3rd order axis (Plate IV, 3).

The exact distribution of vegetative and fertile appendages throughout the plant is unknown. However, close observation of the preserved

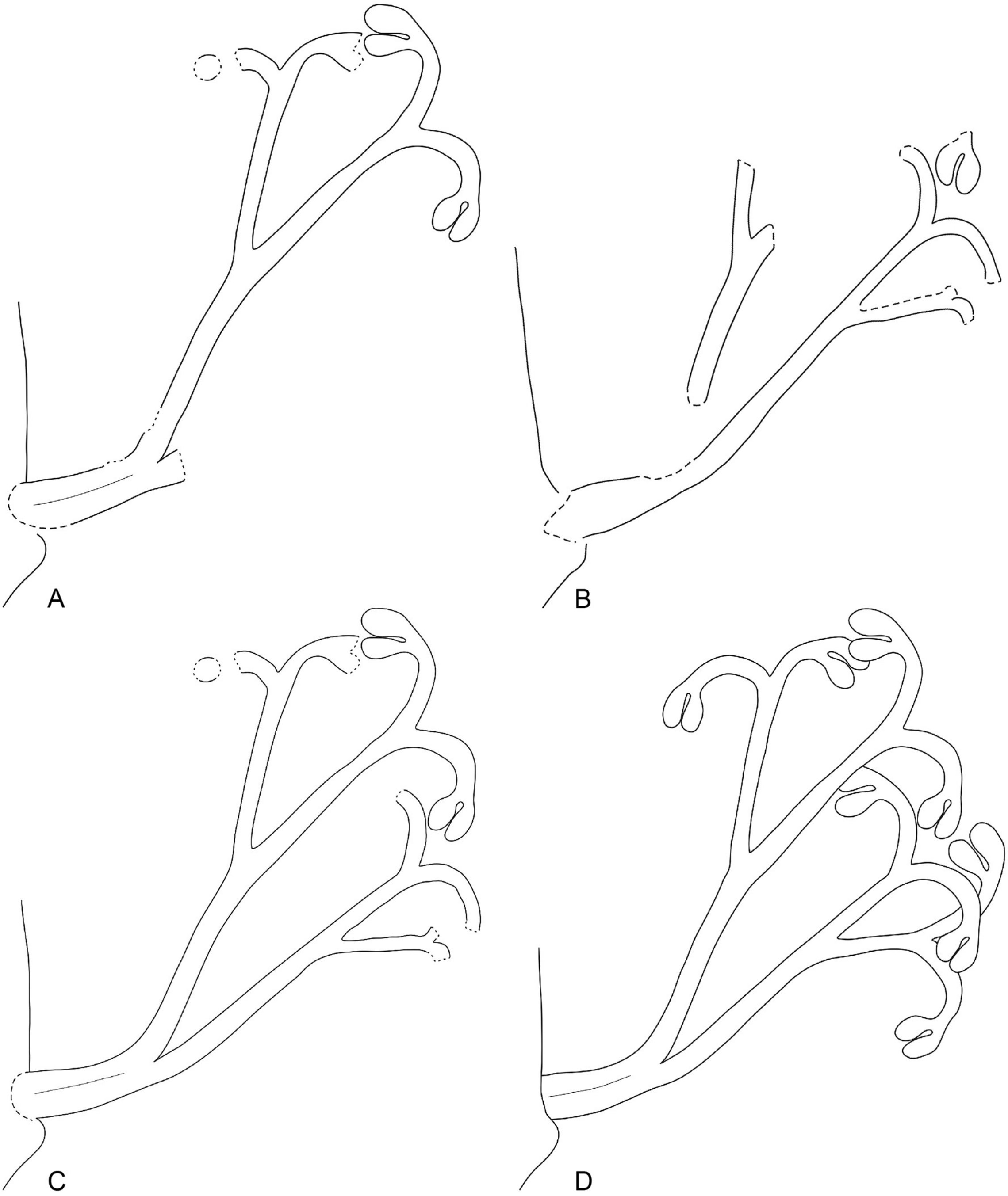

Fig. 2. Reconstruction of a fertile appendage at the base of second order axes. (a) Camera lucida drawing of specimen Plate IV, 1. (b) mirror image of camera lucida drawing of specimen Plate IV, 2. (c) superimposition of part and counterpart. (d) interpretative rendition.

appendages borne by third order axes tend to indicate that they are in most cases fertile.

4.6. Condensed regions

Internodes of the first order axes in all three specimens range from 29 to 51 mm long. On specimens a, b and c (Plate I, 1), in two zones respectively marked S2 and S1, a succession of particularly short internodes is observed. The S1 zone can be seen in greater detail Plate III, 1. It is comprised of 4 branching levels separated by internodes ranging from 0.5 to 1 cm in length. The S2 zone is reproduced in detail Plate VI, 1. It shows five branching levels separated by internodes ranging from 0.5 to 1 cm in length. In both zones attached second order axes seem to conform to other similar axes produced at other levels of the plants. In both cases, the condensed zones seem to be associated with levels where the first order axes dichotomize (see D1 and D2 on Plate I, 1). A third condensed zone (S3, Plate V, 1) is observed on an axis that apparently branches from plant b after dichotomy D3 (Plate I, 1).

4.7. Plant apices

Two isolated plant fragments show evidence of circination (Plate VI, 3–4). The specimen Plate VI, 2 (see also Plate I, between axes a,b) measures 9.7 cm long and 8.9 cm wide. Though relatively small, it is thought

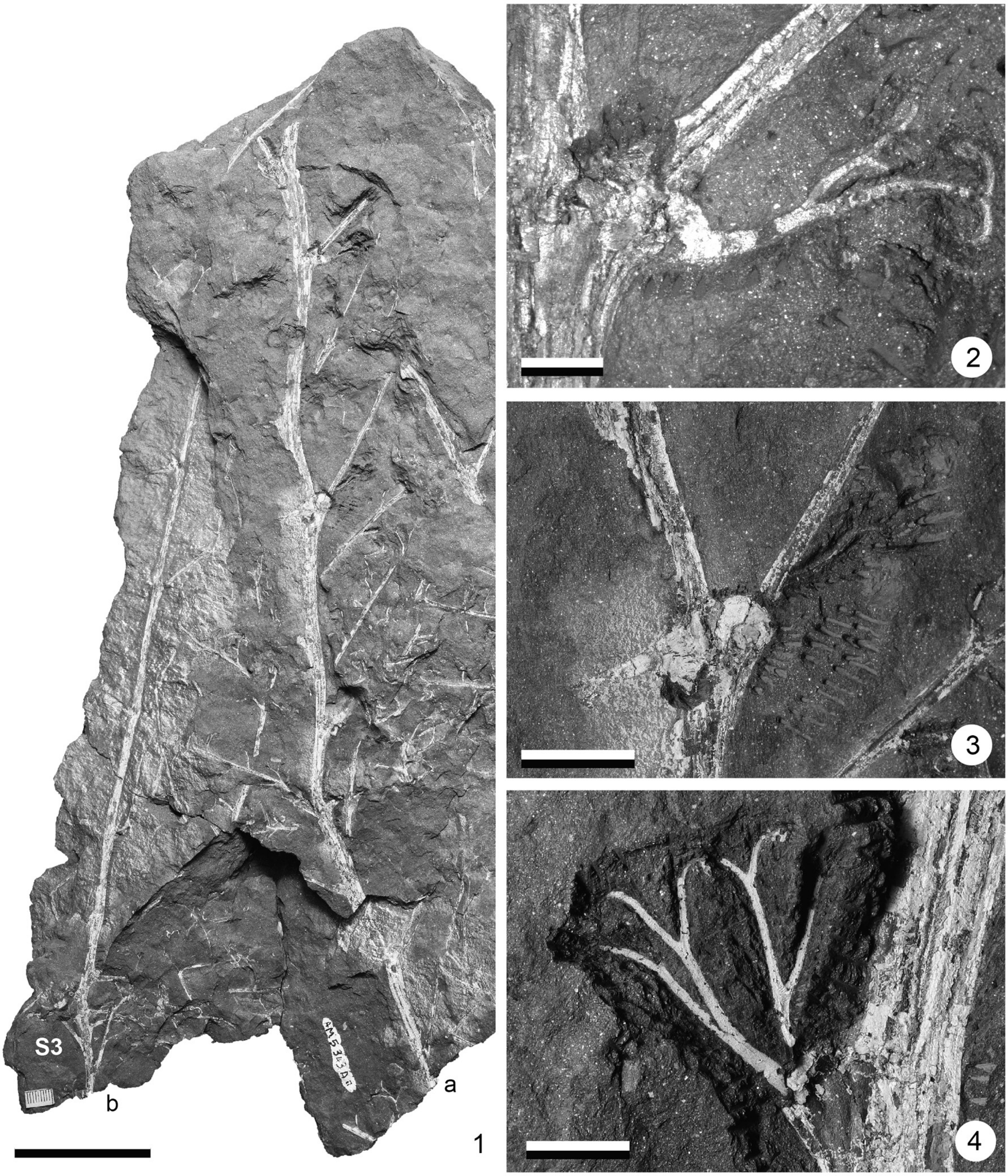

Plate V. 1. Counterparts of plants a and a part of branch of b (Plate I, 1), showing the occurrence of a condensed zone (S3) on plant b. Scale bar = 5 cm.
2. Detail of a node showing a fertile appendage with an inflated base. Scale bar = 5 mm.
3. Detail of a first order node showing the inflated base and the base of a fertile appendage. Scale bar = 5 mm.
4. Detail of a node showing two fertile appendages. Scale bar = 5 mm.

to represent the tip of a first order axis. The first order axis is 7.8 cm long and comprised of four nodes. The first node is situated 2.8 cm from the preserved base of the axis. The following internodes are respectively 2.9, 1.6 and 0.7 cm long. Only one second order axis is preserved for its entire length and measures 6.9 cm long. It displays the characteristic organisation comprised of a first organotactic helix of UAs followed by third order axes. The last branching level of the first order axis is occupied by an immature truss of axes and UAs. The whole specimen is interpreted as a developing tip. The circinate character of the growth is best seen in Plate VI, 4. This specimen consists of a 5 cm long fragment of a first order axis. At its base, the characteristic ridging is visible. Only two branching level are preserved. A first level, situated at 1.2 cm from the base of the specimen shows one second order axis and a very fragmentary UA. The second branching level is situated at 1.2 cm from the former. It shows a closely packed truss of axes and UA curved upwards and pressed against the first order axis. The upper part of this truss shows several UAs with circinate tips.

5. Interpretations and morphological characteristics

Though only represented by specimens found on a single slab of rock, the large size of the preserved plant fragments and their degree of

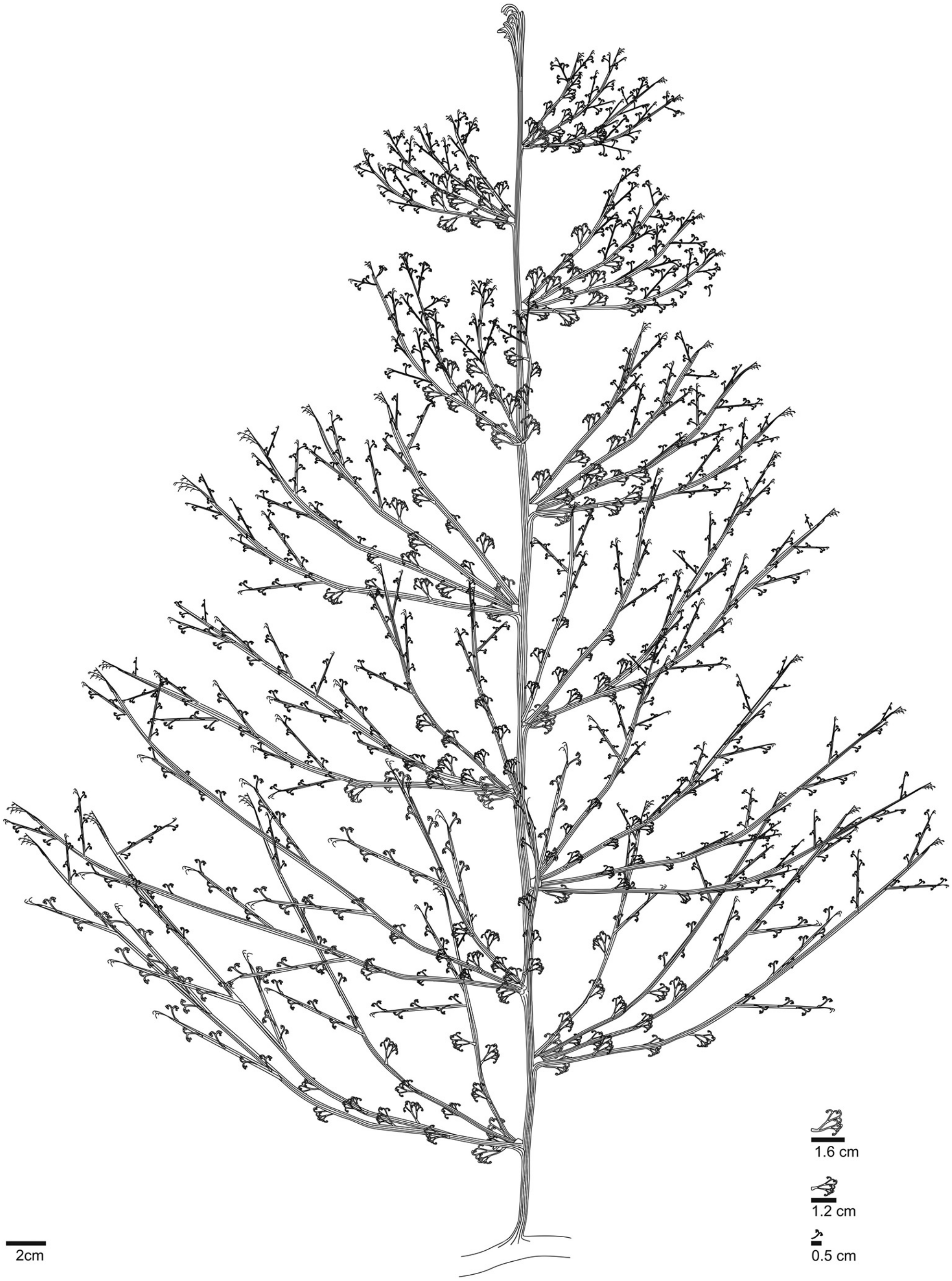

Fig. 3. Proposed whole plant reconstruction of *Flabellopteris lococannensis* with a hypothetical rhizome at the base.

organic connection ensures a good understanding of the plant branching architecture. The spacing and the regularly arranged orientation of the first order axes suggest that they probably branched from a lower order axis to which they were in attachment at the time of preservation, but which lay beyond the edge of the rock slab. This is further supported by a regular inflexion of all three axes (towards the left in the main slab), suggesting a slight upward curvature. The three-dimensional organisation of the first order axes however supports an erect life habit. We thus suggest that they were part of a single plant connected by a horizontal lower order axis that would correspond to a rhizome.

A reconstruction of the plant is proposed in Fig. 3. Several morphological features of *Flabellopteris lococannensis* gen. sp. nov. can be highlighted:

(1) The first order axis is interpreted as monopodial in habit with only occasional dichotomies.
(2) The lateral organs (both branches and appendages) are borne helically on all branching orders. Furthermore, a 1/3 organotaxy is suggested.
(3) The first order axes give the impression of bearing both second order axes and fertile appendages at the same nodes (though anatomical details would be necessary to clarify their exact position).
(4) Axes of the second and third branching orders bear appendages with several isotomous dichotomies.
(5) Recurved paired sporangia are present and borne on dichotomizing appendages similar to vegetative appendages.

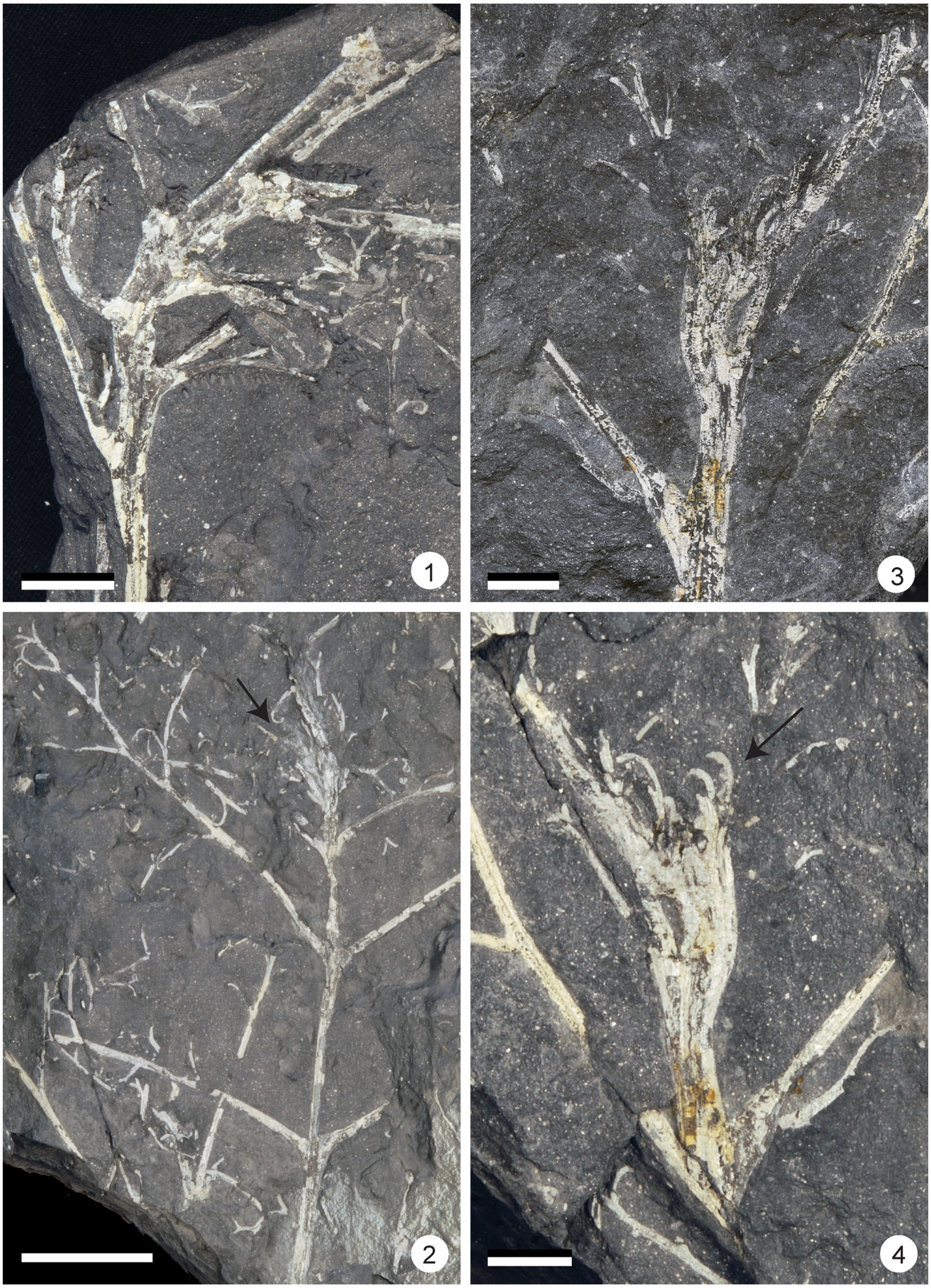

Plate VI. 1. Detail of condensed zone S2 (counterpart specimen of Plate I, 1). Scale bar = 1 cm.
2. Isolated specimen interpreted at the tip of a fist order axis (situated between a and b Plate I, 1). Note the presence of circination (see arrow). Scale bar = 2 cm
3. Isolated specimen showing circination (see arrow). Scale bar = 5 mm.
4. Counterpart of specimen Plate VI, 3. Scale bar = 5 mm.

6. Comparisons

The monopodial habit is shared by many Devonian plants such as the Trimerophytales, the Aneurophytales, the Stenokoleales, the cladoxylopsids, the iridopterids and even the Rhacophytales (Taylor et al., 2008). The occurrence of both branches and fertile parts at the same nodes excludes this taxon from both the Aneurophytales and the Stenokoleales (Momont et al., 2016; Scheckler, 1976).

6.1. Comparison with the Cladoxylopsida

The Cladoxylopsida (sensu Berry and Stein, 2000) are comprised of the pseudosporochnalean and nonpseudosporochnalean cladoxylopsids, and of the Iridopteridales (see Meyer-Berthaud et al., 2007). They are mainly grouped based on characteristics of their primary xylem architecture.

The pseudosporochnalean cladoxylopsids consist of the genera *Calamophyton* Kraüsel et Weyland, *Pseudosporochnus* Potonié and Bernard, *Lorophyton* Fairon-Demaret and Li, and *Wattieza* Stockmans (Berry and Stein, 2000). They all share a similar structural plan comprising an upright trunk bearing helically arranged branches that typically have digitate divisions and irregularly arranged LBS (Berry and Fairon-Demaret, 2002; Fairon-Demaret and Li, 1993; Giesen and Berry, 2013; Stein et al., 2007). The markedly distinct branching orders as well as the occurrence of digitate divisions strongly differ from the organisation of *Flabellopteris*.

Our knowledge of the informally grouped nonseudosporochnalean cladoxylopsids has recently been greatly expanded (Meyer-Berthaud et al., 2007), with taxa ranging from the Middle Devonian up to the Mississippian. The group is notably comprised of the genera *Cladoxylon* Unger, *Panxia* Wang and Berry, *Pietzschia* Gothan, *Polypetalophyton* Hilton, Geng & Kenrick and *Rhipidophyton* Berry and Wang. Except for *Panxia* and *Rhipidophyton*, they are based exclusively on anatomically preserved fossils. They all present a marked hierarchized architecture, in which axes in each order of branching differ from those of the subtending order, particularly in their symmetry. Furthermore, in all these plants a single type of lateral is produced at nodes. This differs from *Flabellopteris* in that the latter presents two types of laterals inserted at the same node on the primary axis and all branching orders are iterative as they all share the same organotaxy.

Flabellopteris bears closest morphological resemblance to members of the Iridopteridales, with which it shares a clearly iterative architecture and the production of two types of laterals at a single node. The order Iridopteridales was erected by Stein (1982) in order to group permineralized material sharing a deeply lobed protostelic mesarch primary xylem, comprised of a small number of centrally united xylem segments. The segments present simple protoxylem strands located near the tips of the lobes and two types of vascular traces have been identified (major and minor). Stein (1982) explicitly excluded morphologically preserved material from definition of the order as he considered that the morphological features described for *Ibyka amphikoma* were insufficiently distinct from those of other Devonian plants.

In 1996, Berry and Edwards, however tentatively included within the Iridopteridales compression material attributed to *Anapaulia moodyi*. This taxonomic placement was based on inferred morphological characteristics of anatomically preserved iridopteridalean material as well as on comparison with *Ibyka amphikoma* - that remained the only representative of the order exhibiting preservation of both anatomy and morphology. Subsequently the hypothesis of Berry and Edwards (1996) has been confirmed by study of a number of morphologically and/or anatomically preserved plants such as *Compsocradus* Berry and Stein, *Ramophyton* Wang and *Rotoxylon* Cordi and Stein (Berry and Edwards, 1996; Berry and Stein, 2000; Cordi and Stein, 2005; Fu et al., 2011). They allow for a better understanding of the morphological organisation of iridopteridalean plants. Meyer-Berthaud et al. (2007) further suggested that, among other features, members of the Iridopteridales could be characterised by (1) an iterative architecture, (2) the production of two types of laterals at one node, and (3) lateral organs each supplied by one trace originating from one stelar rib.

The Iridopteridales is currently comprised of seven genera, of which *Asteropteris* Dawson, *Arachnoxylon* Read, *Keraphyton* Champreux et al., *Rotoxylon* Cordi & Stein and *Iridopteris* Arnold are only anatomically preserved (Bertrand, 1913; Champreux et al., 2020; Cordi and Stein, 2005; Stein, 1982; Stein et al., 1983), *Ibyka* Skog & Banks and *Compsocradus* Berry & Stein preserve both anatomy and morphology (Berry and Stein, 2000; Skog and Banks, 1973) and *Anapaulia* Berry & Edwards is only known from compressed material (Berry and Edwards, 1996). The lack of anatomically preserved details in *Flabellopteris* precludes accurate comparison with exclusively anatomically preserved plants.

6.2. Comparison with Ibyka amphikoma and Ibyka vogtii

Unfortunately, *Ibyka amphikoma* was fossilised in a coarse-grained matrix that limited the quality of the preservation, and comparison is restricted by the sparse description of several features (Skog and Banks, 1973). These notably include the fertile structures and the organisation of the appendages on the different branching orders. Considering the importance of this plant in bridging anatomically and morphologically preserved plants, a redescription enriched by the knowledge recently accumulated on iridipterids would be very helpful.

Similarly, to *Flabellopteris* the description of *Ibyka amphikoma* is based on one single large slab of rock presenting several intricate three-dimensional specimens. However, the orientations of those specimens with respect to each other are not clearly stated in the literature. Both plants are comparable in size, the first order axis measuring up to 55 cm long in *Ibyka amphikoma* and 45 cm long (though incomplete) in *Flabellopteris*. They are known to present three branching orders. The first order axis, in both plants, bears helically arranged second order axes and appendages, though in *Ibyka amphikoma* they do not seem to occur at the same nodes. The organisation of the first order axis is not, however, given a detailed treatment in the original description of *Ibyka* and it is not clear from the photographs where appendages occur on the first order axis. The only available information is provided by the reconstruction, where appendages seem to occur on the first order axis replacing second order branches in the organotactic helix. It is also notable that in *Ibyka amphikoma* branches seem to occur singly on the first order axis while in *Flabellopteris* they are produced in groups of four. Berry et al. (1997) challenged the original description of *Ibyka amphikoma* suggesting that larger lower branching levels were in fact distinctly whorled. These observations are, however, yet to be formally detailed in the literature.

The organisation of the second order branches in both *Ibyka amphikoma* and *Flabellopteris* is similar. Second order axes bear both appendages and third order axes. Though not described in *Ibyka amphikoma*, evidence from the photographs (fig. 2 in Skog and Banks, 1973) indicates that second order axes present only appendages in the first few centimetres whereas third order axes only occur on them more distally. This also appears to be the case in *Flabellopteris*. Third order axes in *Ibyka amphikoma* are described as being helically arranged. However, the authors highlight the fact that they could well be arranged in whorls.

Both fertile and vegetative appendages are incompletely preserved in *Ibyka amphikoma*. They have the same organisation and are described as being three dimensional, strictly dichotomous, dividing up to five times and presenting small, recurved tips when vegetative and rounded sporangia when fertile. Appendages are therefore similar in terms of organisation, those of *Flabellopteris* being simpler with only up to four dichotomies. There is no evidence in *Ibyka amphikoma* of a simpler organisation of appendages in the axes of higher orders, as is seen in *Flabellopteris*.

Berry (2005) transferred *Hyena vogtii* Høeg (1942) to the genus *Ibyka*. This plant, despite its fragmentary state, provides interesting additional information allowing for better understanding of the branching pattern within the genus. Three orders of branching are known. They all are whorled in organisation. Up to five times dichotomizing appendages are present at all branching levels. Both species of the genus *Ibyka* are in many respects very different from what is observed in *Flabellopteris* and can be easily distinguished from it.

6.3. Comparison with other morphologically preserved Iridopterids

Anapaulia moodyi is only known morphologically (Berry and Edwards, 1996) and is similar to *Ibyka* in overall morphology. It is a relatively large plant with a marked monopodial habit. Four branching orders are known. Branches are produced in whorls or pseudowhorls separated by long internodes. First order axes bear two types of laterals that are produced at the same nodes. Appendages, both fertile and vegetative, consist of axes that dichotomize up to four times. When vegetative, they are terminated by small, recurved tips. When fertile, they bear recurved paired sporangia. Appendages are borne in whorls or compressed helices.

The genus *Compsocradus* is known from two Givetian species, *C. laevigatus* Berry and Stein discovered in Venezuela and *C. givetianus* Fu et al. from China (Berry and Stein, 2000; Fu et al., 2011). *Compsocradus laevigatus* is only known from its two highest branching orders. It was first described by Berry and Stein (2000) and the description was later slightly emended by Fu et al. (2011). In this plant, the first order of axes to be preserved are straight or slightly curved. They are relatively densely covered with appendages and bear second order axes at irregular intervals. Both appendages and second order axes are inserted at the same nodes and form whorls of three to four appendages, replaced when present by second order axes. They are organised in six to seven rows. Nodes and internodes are well separated. Appendages can be fertile or vegetative. They are mostly dichotomous and divide up to six times. They terminate either in sterile recurved tips or erect paired ovate sporangia. The insertion of the appendages on second order axes is unclear.

Compsocradus givetianus has a more complex branching pattern and preserves three branching orders (Fu et al., 2011). First order axes bear both appendages and second order axes arranged in loose whorls, forming 10 longitudinal rows. Second order axes bear both appendages and third order branches arranged in loose whorls and forming 6 longitudinal rows. Third order axes only bear appendages forming 4 rows with no clear pattern. Appendages can be either fertile or sterile and consist of dichotomizing axes that divide up to 5 times and bear small, recurved tips when vegetative and recurved pairs of fusiform sporangia when fertile.

The organisation of the appendages is similar in both species of *Compsocradus* and *Anapaulia* and strongly resembles that of *Flabellopteris*. In general, the iterative architecture of all branching orders, the occurrence at the same nodes of both appendages and higher order branches are characteristics shared by these three plants and by *Flabellopteris*. However, the latter can be easily distinguished by the complete lack of whorled organisation.

6.4. Comparison with Denglongia hubeiensis

Denglongia hubeiensis (Xue and Hao) Xue et al. has been described from the Frasnian of China (Xue et al., 2010; Xue and Hao, 2008). It has not been assigned to any specific order but affinities with the iridopterids have been investigated (Xue et al., 2010). *Denglongia* is known from three branching orders. The first order axes only bear second order axes in conspicuous whorls. Second order axes can be either fertile or vegetative. In both cases they bear both appendages and third order axes, however not at the same nodes. Appendages occupy the more basal portions of the axes and whorls of third order branches are found distally. Fertile appendages are arranged in a subopposite manner. They are anistomous and in some cases present evidence of webbing. Fertile appendages are complex and made of several anisotomous divisions terminated by densely packed masses of sporangia. *Denglongia hubeiensis* differs from *Flabellopteris lococannensis* in many ways, including the whorled organisation of the different branching orders and the architecture of both fertile and vegetative appendages.

6.5. Comparison with the Rhacophytales

The Rhacophytales (sensu Taylor et al., 2008) have recently been rediscussed by Xue and Basinger (2016) and are now comprised of six genera: *Rhacophyton* Crépin, *Cephalopteris* Nathorst, *Protocephalopteris* Ananiev, *Ellesmeris* Hill et al., *Protopteridophyton* Li and Hsü and *Melvillipteris* Xue and Basinger.

Protocephalopteris praecox (Hoeg) Ananiev was redescribed by Schweitzer (1968) and shows several features worth discussing. Only two branching orders are known. The first order axis bears both second order axes and appendages. The first-order branches are described as being borne in alternate pairs arranged on opposite sides of the main axes in a quadriseriate pattern, though this character is not convincingly illustrated in the original publications. At the base of the paired first-order branches (second order axes) two dichotomous appendages described as aphlebiae are present. They can be either fertile or vegetative and are made of up to five dichotomies. The second order axes bear alternately arranged sterile and fertile appendages described by Schweitzer (1968) as being borne in pairs, in a manner similar to the first-order branches. Vegetative appendages consist of dichotomous branching systems dividing twice and terminated by sharply recurved tips. Fertile appendages are similar to the vegetative ones, but recurved tips are replaced by a pair of elongate sporangia.

Several challenges exist regarding the description of *Protocephalopteris praecox*, in that the description is, in our opinion, strongly influenced by that of *Cephalopteris mirabilis* Nathorst. Furthermore, *P. praecox* is only known from a few fragmentary specimens that were never completely dégaged. Thus, the available description though interesting must be treated with caution. Reinvestigation of the specimens and more thorough illustrations of the described details would therefore be required to facilitate meaningful comparison. At this stage however, although superficially very different, *Protocephalopteris* and *Flabellopteris* have several characters in common. Notably:

(1) both second order axes and appendages are borne at the same nodes on the first order axis.
(2) Fertile and sterile appendage have a similar organisation.
(3) Appendages on the first order axis are notably more complex than appendages on higher branching orders.
(4) Appendages are comprised of several dichotomizing segments.
(5) Sporangia are borne in pairs.
(6) Vegetative appendages have recurved tips.

Rhacophyton Crépin is comprised of three species: *Rhacophyton condrusorum* Crépin, *Rhacophyton zygopteroides* Leclercq and *Rhacophyton ceratangium* Andrews and Phillips. *Rhacophyon condrusorum*, though historically the first to be described and relatively abundant in terms of number of specimens found, has, so far, not received a good, detailed description nor a whole plant reconstruction (Crépin, 1875; Gilkinet, 1922; Leclercq, 1951; Stockmans, 1948). Our comparison will therefore mainly focus on *Rhacophyton zygopteroides* and *Rhacophyton ceratangium.* These two are known both anatomically (very partially) and morphologically but have been interpreted relatively differently (Andrews and Phillips, 1968; Cornet et al., 1976; Dittrich et al., 1983; Leclercq, 1954, 1951). *Rhacophyton zygopteroides* is interpreted as having an erect main stem helically bearing two types of fronds (vegetative and fertile). Vegetative fronds are bipinnate. Fertile fronds are three-dimensional, bear second order pinnae, and are borne in alternate pairs. These are arranged on opposite sides of the first order pinna in a quadriseriate pattern. At the base of each pair of second order pinnae, two aphlebia-like appendages are present so that each node bears four structures (Leclercq, 1954, 1951). By contrast, the whole plant of *Rhacophyton ceratangium* corresponds morphologically to the described fertile fronds in *Rhacophyton zygopteroides*, with pairs of second order branches inserted alternately on two sides of an erect first order axis and presenting at their base two aphlebia-like appendages. In both species, the fertile parts are very complex, and hold elongated beaked sporangia. *Flabellopteris* is clearly distinct from *Rhacophyton*. They however share certain morphological features, most notably the occurrence of several second order axes and appendages inserted at the same node.

6.6. Comparison with *Chlidanophyton dublinensis* Gensel

Chlidanophyton dublinensis has been described from the Tournaisian of North America and of the United Kingdom (Gensel, 1973; Hilton, 1999). It consists of an erect first order axis bearing second order axes that in turn bear third order axes. Though not described, the first order axes seem to be characterised by deep longitudinal ridges similar to those observed in *Flabellopteris*. Second order axes are borne singly. A pair of non-laminate appendages are borne by first order axes at the same node as second order axes, flanking them. These appendages can be either fertile or vegetative. Second and third order axes present an alternate arrangement. Appendages can be fertile or vegetative and exhibit comparable morphology consisting of several isotomous divisions. When fertile, they bear at the tips recurved rounded sporangia with a distinct cellular pattern. *Flabellopteris* and *Chlidanophyton* are morphologically very distinct. However, they share several features including: (1) helically arranged first order axes; (2) the occurrence at the same node of second order axes and appendages; (3) similar organisation of vegetative and fertile appendages; (3) deep longitudinal ridges on the first order axis; and (4) rounded sporangia with a distinct cellular pattern.

7. Taxonomic considerations

Based on the comparisons above, it appears that *Flabellopteris lococannensis* presents a combination of characters that distinguishes it from all previously described Devonian plants. This justifies the erection of both a new genus and a new species.

Comparison of the fertile material of *Flabellopteris lococannensis* with previously published material from South Africa, collected from the Howison's Poort shale horizon near the base of the Witpoort Formation, highlights a strong similarity between it and a single isolated fertile appendage diagnosed as *Dutoitia maraisia* (Plumstead, 1967, pl. II, 3; reillustrated in Anderson and Anderson, 1985, pl. I). The latter was taxonomically erroneously identified as *Dutoitia* Hoeg - that is a genus erected for a rhyniophytoid species from the early Devonian strata of the uppermost Table Mountain Group (Gess and Prestianni, 2021). Unfortunately, the extremely fragmentary nature of the specimen precludes full comparison. We propose that the historic material be more properly referred to as cf. *Flabellopteris*. Notably, a branched axis from the same locality (Anderson and Anderson, 1985, pl. 14, 4) diagnosed as *Praeranunculus alternatiramus* (Anderson and Anderson, 1985) is similar to medial fragments of second order axes of *Flabellopteris*. There is however no organic connection to either fertile or vegetative fertile appendages. We thus suggest keeping *Praeranunculus* as a form genus.

8. Discussion

In many ways, *Flabellopteris* resembles members of the Iridopteridales, particularly if the occurrence of an iterative architecture and the presence of two types of laterals at one node are retained as characters of the order. Furthermore, the fertile and vegetative structures of *Flabellopteris* are identical, overall, to those described from members of the Iridopteridales. Nevertheless, the occurrence of a whorled organotaxy is an important feature shared by most, if not all, previously described Iridopteridales and is at the core of current morphological concepts of this order (Berry et al., 1997; Berry and Edwards, 1996; Berry and Stein, 2000; Champreux et al., 2020; Cordi and Stein, 2005; Meyer-Berthaud et al., 2007). This character is of sufficient importance to exclude *Flabellopteris* from a formal inclusion within the Iridopteridales, although a close relationship is possible.

On the other hand, the occurrence at the same nodes of appendages and second order axes is a character observed within members of the Rhacophytales. The best-known members of this group are however characterised by a quadriseriate arrangement absent in *Flabellopteris*. Interestingly, the Tournaisian monospecific genus *Chlidanophyton* also presents both second order axes and associated appendages on the same nodes of the first order axes that like *Flabellopteris* is helically arranged.

Based on all the above considerations, we believe that assignment of *Flabellopteris* to an existing order could only be tentative. *Flabellopteris* possesses a combination of characters that places it at a peculiar position somewhere between the Iridopteridales, the Rhacophytales and plants such as *Chlidanophyton dublinensis.* The lack of anatomy nevertheless hampers clear taxonomic placement.

Despite several cladistic analyses and an increasing fossil record, phylogenetic relationships among basal euphyllophytes remain highly problematic (Kenrick and Crane, 1997; Xue et al., 2010). Several challenges can be highlighted, such as the scarcity of the fossil record, the lack of reliable whole plant concepts and the relative morphological and anatomical simplicity of the taxa involved. One important problem when dealing with plants in general and especially in deep time evolution, is the identification of specific “organs” based on homology. As highlighted by several authors, the axis represents the ancestral state of most plant organs (Kenrick and Crane, 1997; Sanders et al., 2009). Recent discussions concerning the nature of a highly iterative organ such as the leaf gives a good example of the complexity of the question (Galtier, 2010; Sanders et al., 2009; Toledo et al., 2021, 2018). This is especially obvious when dealing with plants such as *Flabellopteris* but also other plants of similar complexity. In *Flabellopteris* three structures/organs have been referred to, by us, as appendages. These are the dichotomous branching systems associated, on the first order axis, with second order branches (1), the reduced branching systems along the proximal portion of second order axes (2) and the small branching systems inserted on third order axes. Although all three structures share obvious morphological characteristics, nothing in the fossil material permits inference that they arise from the same developmental pathways.

As mentioned above, the lack of reliable whole plant concepts is a major obstacle to understanding diversification patterns among the earliest euphyllophytes. Lack of information on the basal-most/proximal regions (including roots) has, in many cases, resulted in first observed order axes being interpreted as main stems (Berry and Stein, 2000; Farahimanesh et al., 2014). The zygopterid ferns are a good example of erect orthotropic branching systems with an apparent main stem, that are in fact leaf homologues (Galtier, 2010; Phillips and Galtier, 2005). In zygopterid ferns, radially symmetrical protostelic stems give rise to bilaterally symmetrical petioles. The two very contrasting reconstructions available for *Rhacophyton* exemplify this problem. The architectural model available for *Rhacophyton zygopteroides* is based on very small specimens in which basal portions were preserved (Leclercq, 1951). By contrast, *Rhacophyton ceratangium* is based on very large fossils that are never found attached to any higher order axes (Andrews and Phillips, 1968; Cornet et al., 1976). Whether the quadriseriate branching system of *Rhacophyton* is a stem or a leaf is of great importance to the understanding of early euphyllophyte evolution and to a clear understanding of the evolution of leaves. Similar questions exist regarding the nature of *Stauropteris* (Farahimanesh et al., 2014).

Based on what is observed in the zygopterid ferns, the radially symmetrical first order axes of *Flabellopteris* could be interpreted as cauline in nature. However, though no basal organs were found, we propose that the first order axes of *Flabellopteris* were originally connected to a horizontal higher order axis. Furthermore, as said earlier, the organisation of the branching system (symmetry of the axes aside) is similar to what is seen in *Rhacophyton*. It is, thus, possible that the structures of *Flabellopteris* described here could entirely comprise a leaf in terms of homology and, as such, like in *Chlidanophyton*, could represent an additional step documenting initial stages in the evolution of leaves.

9. Systematic palaeobotany

Subdivision: Euphyllophytina Kenrick and Crane (1997).

Class: uncertain.

Order: uncertain.

Genus: **Flabellopteris** Gess and Prestianni, gen. nov. (Plates I–VI; Figs. 1-3).

Type species: Flabellopteris lococannensis Gess and Prestianni, sp. nov.

Generic diagnosis: Plant monopodial. First order axes bearing both second order axes and appendages. Second order axes in helically arranged groups, each group consisting of two pairs of second order axes attached at each node, with fertile appendages attached at the same node. Second order axes bearing helically arranged appendages proximally and third order axes distally. Third order axes bearing helically arranged appendages. Appendages with multiple dichotomies; sporangia borne paired on recurved tips of terminal segments of appendages. Fertile appendages essentially identical to sterile appendages.

Etymology: Combination of the latin words *Flabellia* meaning fan and referring to the shape of the group of lateral second order axes and *Pteris* meaning fern.

Flabellopteris lococannensis Gess and Prestianni sp. nov.

Specific diagnosis: Plant with monopodial habit. Three known branching orders all helically arranged following 1/3 organotaxy. First order axes 7.5–9.0 mm wide, more than 40 cm long, with rare dichotomies. Four second order axes inserted at same node with fertile appendages. Second order axes 1.5–3.5 mm wide, more than 20 cm long, basal 7.0–9.0 cm bearing appendages, then third order axes distally. Third order axes 1.0 to 1.5 mm wide bearing only appendages. Appendages on first order axes 2.0–2.5 cm wide and 2.0–2.5 cm long dichotomous branching systems. Always fertile, up to three dichotomies bearing up to 16 recurved sporangia in pairs. Appendages inserted at angle of 75° on second order axes, up to three dichotomies, 1.5–2.0 cm wide and 1.5–2.0 cm long. Appendages inserted at angles of 45° – 90° on third order axes, with two dichotomies, 0.5–1.0 cm wide and 0.5–1.0 cm long. When sterile last dichotomy of appendages producing two recurved acute tips. When fertile, terminal segments bearing pair of sporangia. Sporangia, ovate, 0.9–1.5 mm long and 0.5–0.7 mm wide, epidermal pattern striated, dehiscence mechanism unknown.

Holotype: AM 5343 (Plates I–VI).

Repository: Albany Museum Devonian Lab, 87 Beaufort Street, Makhanda/Grahamstown, Eastern Cape, South Africa.

Type locality: Waterloo Farm, Eastern Cape, South Africa.

Stratigraphic horizon: Witpoort Formation, Witteberg Group, Cape Supergroup.

Age: Upper Famennian.

Etymology: *lococannensis* meaning "from the place of reads"; from lococannis "place of reeds" in latin; translation of eRini (or eRhini), the traditional Xhosa name for Grahamstown/Makhanda which probably derives from a hybrid word with a Khoi root (/=Axa-b) meaning reeds coupled with "e——-ini" meaning "place of" in isiXhosa, hence 'place of reeds'. Records show this usage going back to before the 1850s, though it is probably far older. This word was perhaps translated into 'de Rietfontein', the name of the Dutch farm that occupied the valley in the 1700s before development of Grahamstown.

10. Conclusions

Flabellopteris is a new genus of early euphyllophyte with putative affinities to fern-like taxa such as the Iridopteridales and the Rhacophytales. Though the lack of anatomical details prevents accurate taxonomic placement, *Flabellopteris* shows several characters interpreted as intermediate between these two groups. It is characterised by a generalised helical organotaxy expressed on first order axes by second order axes occurring in groups of four and inserted at apparently the same nodes as appendages. Though the cauline or leaf nature of the different parts of the plant is not entirely ascertained, *Flabellopteris* very likely documents early stages in the evolution of the frond. Nevertheless, *Flabellopteris lococannensis* documents yet another combination of characters illustrating the extraordinary explosion of diversity within euphyllophytes during the Devonian.

Declaration of Competing Interest

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

Acknowledgments

This paper is submitted in recognition of the numerous, outstanding, and precise contributions by Jean Galtier to the field of palaeobotany. CP would particularly like to thank him for the many rich and fruitful discussions as well as the guidance and friendship he received over the years. RG would like to acknowledge the support of the Millennium Trust; of GENUS (DSI-NRF Centre of Excellence in Palaeosciences) and of the National Research Foundation (NRF). The South African NSCF (Natural Science Collections Facility) is thanked for supporting Dr. Prestianni's visit to South Africa in 2019, and for provision of lab equipment. CP is hired under a Belspo FED-tWIN project from the Belgian Federal Government (Prf-2019(R)-017_PaleoGreen). This research was supported by a FNRS travel grant. RG thanks Dr. Norton Hiller for support, mentorship, and discussions on the here studied material during its initial preparation and study in the 1990s. Mr. Ryan Nel is thanked for digitising Fig. 2 and creating the digital reconstructions in Fig, 3. We would like to thank Pr. M. Tomescu and Dr. Jinzhuang Xue for the careful and very useful revision of the manuscript that helped greatly improving it.

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