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Reinvestigation of the type specimen of *Ginkgophyllum grassetii* Saporta 1875 using Reflectance Transforming Imaging

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Abstract: Reflectance Transforming Imaging (RTI) produces photographs in which the angle of the light can be changed at will, allowing to investigate remotely minute details of the 3D structure of sub-planar objects. Here we apply this technique to the type specimen of *Gingkophyllum grassetii*, a vegetative shoot with putative ginkgophyte affinities from the early Permian of Lodève (France). *Gingkophyllum grassetii*, the type species of the genus, was originally described by Saporta in 1875 and has never been illustrated other than by drawings representing only portions of the shoot. Using RTI, we describe and illustrate the specimen and discuss some key features, such as the arrangement of the leaves on the shoot or the presence of abundant secretory structures. Through an historical account, we show how the lack of illustration led to confusion about the morphology of *Ginkgophyllum* and we discuss the importance of reinvestigating type specimens of Paleozoic ginkgophyte taxa in order to clarify their taxonomy and better understand their evolutionary history. The sharing of RTI files is one example of approaches that can be further developed to improve remote access to specimens.

Key-words: Paleozoic; Permian; France; foliage; ginkgophytes; specimen remote access.

1. Introduction

Using technology available at the time, it was common during the 19th century that item documentation in the fields of cultural heritage and natural history, including paleobotany, was based on more or less precise descriptions and ink drawings. However, these drawings often lack accuracy, rendering it sometimes even difficult to identify the right specimen within an historical collection based on published illustrations alone. G. Saporta, who first described the specimen that is the focus of the current account, used to provide fairly good drawings accompanying taxa descriptions. However, in many cases only the gross morphology was represented, details being omitted. Many of these anciently described specimens, commonly having a status of type material, are still awaiting a proper revision. Moreover, specimens may have been left unattended for decades, leaving opportunities for a range of degradations. Concurrently, some specimens were never returned from loan and went lost. This situation makes it difficult to assess the occurrence, in a number of historical specimens, of diagnostic characters outlined later on based on additional material.

Progress in film photography accomplished during the 19th century made it possible to deliver a more informative documentation, and allowed useful revisions of anciently described material (e.g. Galtier and Scott, 1979). However, obtaining an optimal outcome by this technique required a good deal of experience. Indeed, whether settings used during primary data acquisition (i.e. film exposure) were adequate, or not, would be revealed only after a highly technical and time-consuming process of conversion onto photographic paper. Correcting for inadequate primary acquisition settings was possible during this second step, but with limitations.

The advent of commercially available digital cameras during the very end of the 20th century largely contributed alleviating this issue. Fundamentally, it hastened the access to the desired outcome, while retaining the two-steps process: the operator could immediately ensure that satisfactory primary data was obtained, and could quickly engage into data processing using dedicated software. It solicited skills largely similar to those involved in film photography (with some ‘refunctioning’ as some may see it). The acquisition of a digital camera body that could be coupled to a preferred lens or microscope (viz. a DSLR) has been an event to many, including the colleague honored in this special issue and the last author of this account.

Continuous increase in image resolution, computing capacities and data transfer fluxes led to more recent breakthroughs. The sharing of digital images is nowadays ordinary, with numerous institutions and online repositories providing online image datasets. However, how experienced an operator is with the items of interest, and with photographic equipment and image processing, remains essential in the production of informative images. A variety of computing-intensive processes are reducing this aspect to its *portion congrue* though. These include focus stacking, ensuring optimal sharpness without having to resort to high depth of field (resulting in sharpness loss, itself due to lens diffraction). It requires a set of photographs taken with a low depth of field and under a range of camera-to-item distances (while the angle of observation and illumination remain unchanged). Photogrammetry, providing 3D models, is particularly adequate for items which main dimensions are of the same order of magnitude. It requires a set of photographs taken at various angles of observation (while illumination remains unchanged, and the distance between camera and item remains more or less constant).

Sub-planar items in which subtle elevations and depressions are informative, such as fossil compressions/impressions, remain a difficult case to handle, as image informativity is highly dependent upon illumination orientation. Surface laser scanning is a performing but comparatively expensive option. The more accessible Reflectance Transforming Imaging (RTI) processing, also known has Polynomial Texture Mapping, was developed in the field of archaeology (see Earl et al. 2010; and references therein) to cope with such items. Basically, an

RTI file is a photograph which illumination can be modified at will. It is computed from a set of photographs taken with different orientations of the illumination sources (one per photograph), the distance between illumination sources and the item remaining constant (as well as the angle of observation and the distance between camera and item).

This technique has been applied recently to fossil material mainly of animal origin (Béthoux et al. 2016; Jäger et al. 2018; Klug et al. 2019; but see Hammer et al. 2002) but has an important potential for fossil plants preserved as compressions/impressions, as it allows the observer to appreciate slight differences in elevation that are important to reveal the original 3D organization of the plant, for example the venation pattern of a leaf or the organotaxis. In that respect, the leafy shoot of *Ginkgophyllum grassetii* described by Saporta in 1875 and kept in the collections of the Museum National d'Histoire Naturelle (MNHN) in Paris is of particular interest. This specimen, which is the holotype of the species, itself the type-species of the genus *Ginkgophyllum*, has indeed never been illustrated as a photograph in previous publications, all comparisons and assignment of specimens to this species and genus being based on drawings (e.g., Saporta, 1879; Renault, 1885; Seward, 1919). New documentation of this material was therefore necessary, which we endeavored by resorting to RTI.

Ginkgophyllum Saporta, like many morphogenera of late Paleozoic seed plants, is poorly circumscribed (e.g., Meyen, 1987; Archangelsky and Cúneo, 1990; Naugolnykh, 2007 and references therein). Indeed, many seed plant lineages from that time period show a mosaic of morphological features that, in many cases, are poorly understood in terms of homology (e.g., Taylor et al., 2009). Considering the relatively small number of significant characters preserved in many organs or plant reconstructions from that time, their minute analysis and description is crucial. This implies the revision of the type specimens of the most relevant morphogenera in the light of current knowledge and with the help of new technologies. Foliage assigned to the ginkgophytes are typically a case where this type of revision is strongly needed in order to re-evaluate the affinities of the different taxa and untangle the early evolutionary history of the group (e.g., Naugolnykh, 2007; Zhou, 2009; Bauer et al., 2013, 2014).

In this context, this paper aims (1) to illustrate and discuss important characters of the type specimen of *Ginkgophyllum* observed using RTI, (2) to highlight the importance of collection specimens, and (3) to provide a worldwide remote access to this type specimen in order to facilitate further comparison with other morphogenera and advance our understanding of late Paleozoic seed plant diversity.

2. Material and methods

2. 1. Specimen information

The specimen was first described by Gaston de Saporta in 1875. It is part of the Saporta collection at the Musem National d'Histoire Naturelle, Paris, France. It consists of one slab about 30 x 12 cm with collection number MNHN.F.11222.2M. The slab contains the leafy shoot described by Saporta and a few small fragments of conifer foliage (Plate I, 1-2). There is no known counterpart. The specimen was photographed in 2018 by Peter Massicart and included in the MNHN online database for the project RECOLNAT (ANR-11-INBS-0004).

Remark: in accordance with articles 60.8b and 60.8d of the International Code of Nomenclature for algae, fungi, and plants, we have replaced Saporta's original spelling "*grasseti*" by "*grassetii*" through the text.

2. 2. Geological and floristic context

The specimen was given to Saporta by Charles de Grasset who collected it in "the Permian schists of Lodève" (Saporta, 1875). The Lodève basin is located in Southern France, about 50 km NW of the city of Montpellier, and covers about 150 km². It overlaps the Stephanian (= Gzhelian, Late Pennsylvanian) deposits of Graissessac that crop out to the West. Its Permian continental infilling consists of fluvial and lacustrine grey sediments and red beds (e.g., Lopez et al., 2005; Schneider et al., 2006). Based on its preservation, the characteristics of the rock matrix, and the associated small conifer remains, the *Ginkgophyllum* specimen comes from the Usclas-St Privat Fm, likely from the historical locality of les Tuilères. While the age of some younger deposits in the Lodève Basin is disputed, the Usclas-St Privat Fm has been consistently dated from the late Asselian to earliest Sakmarian (Schneider et al., 2006; Michel et al., 2015).

The flora from les Tuilières has been the subject of several studies since the 19th century and although there is no published synthesis, over 40 different plant species have been reported from the locality (e.g., Grand'Eury, 1877; Zeiller, 1898; Carpentier, 1931, 1937; Florin, 1938-1945; Doubinger, 1956; Broutin et al., 1992; Galtier & Broutin, 1995; Galtier et al., 2017). The assemblage is dominated, in terms of abundance and diversity, by conifers, which represent >80% of the specimens and include 14 different morphospecies (Bertholon, 1996). Peltaspermales are also diversified, with at least 12 morphospecies, but represent <10% of the fossils. Other taxa are rarer. The most up to date list, compiled from the literature and personal observations by Galtier et al. (2017), includes lycopsids (*Sigillaria (Subsigillaria)*), sphenopsids (*Sphenophyllum*, *Annularia*, *Calamites*), filicopsids (*Pecopteris*), Medullosales (*Callipteridium*, *Odontopteris*, *Potoniea*), cycadopsids (*Taeniopteris*), and possible ginkgophytes. The latter include the fertile structure *Trichopitys heterophylla* described by Saporta at the same time than *Ginkgophyllum grassetii* (Saporta, 1875). J. Doubinger (1956) also described and illustrated several types of putative ginkgophyte foliage from that locality that she assigned to *Ginkgophyllum grassetii* but also to *Sphenobaiera* sp., *Baiera* sp., and *Ginkgoites lodevensis*.

2.3. Imaging

We used the so-called ‘stationary dome technique’ to produce nine RTI files (RTI a-i). Specifically, a horizontal 28-cm diameter light dome equipped with 54 LEDs (distributed over three rings) was placed above the specimen and used as illumination source. Automation of camera triggering and of changes in illumination were performed using the dedicated control box. Illumination reference was given by a black reflecting sphere placed aside the area of interest and cropped out during RTI processing (light dome, control box and reflecting sphere, FlyDome, Paris, France). All LEDs were used for RTI a-h (i.e. each set is composed of 54 photographs) but only a subset was used for RTI i (specifically, half of the LEDs of the two lower LED rings, i.e. 21 LEDs). As for photographic equipment, a Canon EOS 5D Mark III digital camera equipped with a Canon 100 mm macro lens (RTI a, b, e-h), a Canon 50 mm macro lens (RTI c, d) or a Canon MP-E 65 mm macro lens (RTI i) (all Tokyo, Japan), was used.

Photographs of a given set were then batch-processed using Adobe Photoshop (Adobe Systems, San Jose, CA, USA) to optimize focus and for adding legend and scale bar. RTI files were then computed using the RTIbuilder software using the third fitting order (Cultural Heritage Imaging, San Francisco, CA, USA). Snapshots were extracted from these RTI files and further optimized (levels, contrast, and sharpness) to compose illustrations. More specifically, photographs on plates II, III, IV (1, 2, 4, 5) and V were extracted using two rendering modes. For the default rendering mode (true colors images), the small hemisphere on each snapshot indicates the position of the illumination source. As for “normals visualization” mode (false colors images), the normal direction at each pixel is represented using a color code indicated by the associated hemispheres. The color of the frame around each hemisphere corresponds to the color assigned on Plate I, 3 to the RTI file from which the snapshot was extracted. These nine RTI files are available in an online Dryad Digital Repository (Decombeix et al., 2021) and can be viewed using a software such as RTIviewer, freely accessible (Cultural Heritage Imaging, San Francisco, CA, USA).

Locating veins and their dichotomies using the RTI files is relatively straightforward in the best-preserved zones, and near the center of the view. However, it is difficult to have a good image of veins that have slightly different orientations on a single snapshot, i.e., with only one direction of the light source, in particular if the observed area is large with respect to the dome diameter, in which case illumination is too uneven across the image (e.g., Plate IV, 1, 2). One option is to resort to normals vizualisation (e.g., Plate II, 4; Plate III, 3), but this implies a loss of the specimen color information. To address this issue, we processed composites based on multiple snapshots for the images on Plate IV, 3, 4. In essence, this approach is a digital way of combining multiple light sources, a common way of using gooseneck optic fibers. As for Plate IV, 3, four snapshots were used (light source coordinates: X:0.00, Y:0.00; X:-0.20, Y:0.50; X:0.00, Y:0.65; X:0.50, Y:0.60) and were combined using the ‘overlay’ blending mode (with further adjustments; see Adobe Photoshop working document available from Decombeix et al., 2021). As for Plate IV, 4, three snapshots were used (light source coordinates: X:-0.50, Y:0.75; X:-0.15, Y:0.65; X:0.50, Y:0.50) and were combined using the ‘multiply’ blending mode (with further adjustments; see Adobe Photoshop working document available from Decombeix et al., 2021). This highlights the value of RTI to investigate fine details and shows how RTI images can be further processed.

3. Results

The specimen is a compressed fragmentary leafy shoot approximately 30 cm long and 12 cm wide, considering stem and leaves together (Plate I, 1). The stem is up to 6 mm wide (Plate I, Plate II). It is straight for the first 10 cm, and then the visible part of the stem bends at an angle of 37º (Plate I, 1; Plate III, 1). The axis is covered with longitudinal striations and densely arranged secretory structures (Plate II; Plate III, 1-3) (see description below).

The leaves are in organic connection to the stem. At first sight, they seem to be attached on the two sides of the axis, i.e., in a distichous arrangement. However, like the stem, the leaf lamina shows fine longitudinal striations and secretory structures, which disposition and orientation are useful to understand their attachment. Towards the base of the stem, it is clear that the leaves are not in two rows, but are attached at different levels, all around the stem, describing a helicoidal phyllotaxy (Plate II, 1-4). The leaf bases are entirely connected to the axis, without evidence of basal constrictions (Plate II, 1-4; Plate III, 2, 3).

The leaves are dorsoventrally flattened with a distal region that is wedge-shaped and a basal region that is also laminar and adpressed on the stem, not forming a distinct petiole (Plate II; Plate IV). The leaves are 4.96-10.97 cm long (mean: 7.46, s.d.: 2.07, n: 7) and from 1-2 to 2.14 cm wide (mean: 1.65 cm, s.d.: 0.27 cm, n: 7), with a length/width ratio ranging 2.5 -7.2.

The basal leaf part has entire parallel margins, it varies from 0.22 to 0.29 cm in width (mean: 0.24) and its length represents approximately 40% of the leaf's total length. The leaf bases are adpressed to the stem for 6-8 mm, describing an angle between 11º and 15º with respect to the axis (Plate II, Plate III, 2, 3). They then rapidly curve basiscopically to form angles of 35º-45º, slightly decreasing towards the stem apical region probably indicating proximity to the shoot apex.

The distal part is expanded in angles that vary between 20º and 35º and is usually longer than the basal part ($\simeq$ 60% of leaf length). The leaves are dissected, with a least three orders of dissection (Plate I; Plate IV). The first dissection shows angles between 7º and 16º, the depth of the incision is variable, representing between ½ and ⅔ of the cuneiform region of the leaves. The second order of incisions shows similar angles to the first, and its occurrence is not symmetrical on the two sides of the leaf. In some cases a third, much shorter order of dissection is present. The distal segments are often linear, with entire parallel margins and a width similar to the basal part of the leaves (Plate IV, 3). Each lobe has an apical emargination, up to 0.5 mm deep, which is placed between veins.

The veins are fine and visible in a few parts of the specimen (Plate IV), but in some leaves they can be located by following a dark band that ranges from 0.55 to 0.70 mm in width. We interpret these bands as corresponding to the veins and possible accompanying tissues. Two veins/bands are observable in the basal part of the leaves, but it is unclear whether they are basally fused. These veins show at least three orders of dichotomies before the first incision, leading to leaf segments with four parallel veins (Plate IV, 3). The dichotomies do not always occur at the same level in the different segments of a same leaf. Distal segments show either two veins, each one located close to the leaf margin, or three/four bands in the cases where the third order of dissection is not present. No anastomoses are observable.

Abundant secretory structures are arranged on the leaf and stem surfaces (Plate II-IV). Their density is higher on the stem and the base of the leaves and decreases progressively towards the apex of the leaves (e.g., Plate IV, 1, 2). The secretory structures are variable in shape, from round to oval with a maximum length/width ratio of 2, and their size range between 0.09 and 0.52 mm in diameter, when rounded, and a similar maximum length in oval examples (Plate IV, 3). On the stem, the secretory structures are randomly distributed and are preferably oriented with their longer axis parallel or slightly oblique with respect to the stem of leaf axis (Plate II). On the leaves, they are almost entirely arranged on the dark bands that follow the veins, and their orientations also follow the main axis (Plate IV, 3). In most cases, the secretory structures are seen as a single bump, although in some examples the bump is surrounded by a circular ring with radiated appearance, probably corresponding to the cell arrangement in the mesophyll.

4. Discussion

4. 1. Historical descriptions of Ginkgophyllum *vs. features of the type specimen*

Our review of the various historical mentions of *Ginkgophyllum* and *G. grassetii* reveals that some important information present on the type specimen was lost through time. This is especially true of the shoot morphology, leaf attachment, and minute morphological details. This loss can be explained to a great extent by the lack of circulation of photos of the type specimen and the use of drawings that represented only parts of it (Fig. 1). The issue was accentuated by the propensity of several authors to focus on leaf morphology only, overlooking the complexity of the shoot's organization. The following (non-exhaustive) historical account summarizes this process and its taxonomic consequences.

In a note to the French Academy of Sciences, Saporta (1875) described two specimens from the early Permian of the Lodève Basin that he interpreted as representing two new genera related to ginkgophytes: a fertile shoot, *Trichopitys heteromorpha*, and a leafy vegetative shoot, *Ginkgophyllum grassetii*. In this note, Saporta did not provide illustrations or diagnoses for these new taxa. The specimen of *Ginkgophyllum* is described as a branch *"covered with numerous alternate leaves, which are confusedly scattered on the sides and thus affect a somewhat vague distichious arrangement."* Saporta also describes the leaves in detail, as decurrent, with a long petiole, wedge-shaped and divided twice, with dichotomous veins (See supplementary file 1 for the full original description in French and its translation).

This specimen of *Ginkgophyllum grassetii* was mentioned again by Saporta (1878) in a communication on *Nœggerathia*, and partially illustrated in his 1879 book (p.186) in the form of a drawing that corresponds to the two distal thirds of the shoot (Plate I, 2), where leaves are crowded and their insertion is not very clear. In his book with A. F. Marion (Saporta & Marion

1885, [pp. 145-146]) he provided a very short description that does not include information on leaf attachment: “*a complete branch, [that] shows leaves longly attenuated at the base in a sort of decurrent petiole and split at the top into dichotomous segments”.*

B. Renault showed Saporta’s illustration but with only the right side of the original drawing figured, the left side only showing the leaf bases (Renault, 1885, plate 3 fig. 1) (Fig. 1). He provided a short description for *Ginkgophyllum* and *G. grassetii* that focusses on the leaves and does not mention the leaf arrangement on the shoot. R. Zeiller in his textbook (1900) illustrated the same part of the specimen as Renault.

A. C. Seward (1919) included *Ginkgophyllum grassetii* in the genus *Psygmophyllum* - which in this context had taxonomic priority. He did not provide a specific diagnosis and included a drawing (Seward, 1919, p.87) that is only focused on a very small portion of the shoot and three leaves, none of them showing clearly the attachment to the shoot or the phyllotaxis (Fig. 1). As a result, the complexity of information present on the actual specimen was almost entirely lost to the readers.

In 1948, M. F. Neuburg provided a diagnosis for *Ginkgophyllum* in which she mentioned an alternate leaf arrangement, leaves that have a “petiole-like”, more or less long basal constriction, and a narrow triangular shape with several divisions into lobed and cuneate segments. Veins are described as dividing repeatedly. (See supplementary file 2 for the original description in Russian and its translation). This is the most recent and only diagnosis of the genus, following authors having only made informal taxonomic recommendations (e.g., Archangelsky and Cúneo, 1990).

Doubinger (1956) assigned to *Ginkgophyllum grassetii* some isolated leaves from the same early Permian locality of the Lodève Basin as Saporta’s specimen. She provided photographs of three of them and noted that such leaves are often fragmentary and can be confused with *Baiera,* but that the more complete ones can be distinguished from that genus by the existence of a clearly differentiated petiole, a wide and semicircular leaf outline, and truncated and angular leaf tips.

O. A. Høeg (1967) also focused on the leaves and used the partial drawing from Seward 1919. He also noted a "striking similarity" between *Ginkgophyllum grassetii* and *Baiera,* but said they could be distinguished based on the long sheathing base of the former leaf type. In a comparison of Indian taxa with the Palaeophyllales of Høeg (1967), P. K. Maithy (1972) described *Ginkgophyllum* as having "*pinnate leaves with large cuneate dissected leaflets*", apparently interpreting the stem as the rachis of a compound leaf.

S. Archangelsky and O. G. Arrondo (1974) described two new species of *Ginkgophyllum* from Upper Paleozoic formations of Argentina and proposed to keep the genus separate from *Psygmophyllum*, which has flabelliform leaves that are almost entire, multiveined, and sometimes shows vein anastomoses. They did address the question of leaf attachment and their discussion of the genus includes the diagnose of Neuburg that mentions "*leaves alternately inserted on the branches*". However, Archangelsky and Arrondo (1974) noted that this is based on Saporta's drawing and description, which both leave doubts about the actual phyllotaxis. They mention that it could be bilateral /distichious, irregular, or helicoidal.

In 1984, S. V. Meyen observed the type specimen during a visit to Paris and summarized his observations in a short note published in the 1985 International Organisation of Paleobotany newsletter (Meyen, 1985a,b). Meyen noted that Saporta had not figured the whole specimen and that his drawing was "*not quite accurate*". Meyen described an "*helical arrangement of palmately dissected leaves, dichotomous veination with several veins entering distal lobes and numerous resin bodies embedded in the compression.*" He concluded that *Ginkgophyllum* was similar to *Sphenobaiera* as defined by Harris et al. (1974). In his 1987 textbook Meyen mentioned the helical arrangement of leaves and the similarity with *Sphenobaiera*. The resin bodies were mentioned again in Meyen (1988), as present in "*both in the axis and leave*s" of the type specimen. Meyen (1985a, 1987, 1988) did not provide any illustration of *Ginkgophyllum.* He passed away in 1987 and it is not clear from the more recent literature whether his re-observation of Saporta's specimen was known to all the paleobotanists who later worked on *Ginkgophyllum* and other putative ginkgophyte foliage.

Archangelsky and N. R. Cúneo (1990) introduced a new interpretation of leaf attachment, stating that the genus *Ginkgophyllum* should be kept for "*sterile leaves bilaterally inserted on a rachis, dichotomized several times, deeply incised, and with one vein"*. More recently, I. H. Escapa and Cúneo (2003) mentioned the presence of several veins in each of the leaf segments of *G. grassetii.*

This short historical account shows that the representation of *Gingkophyllum* has changed through time. An important information provided by the type specimen, the leaf attachment to the shoot, has been overlooked in some descriptions and variously interpreted in others. Interestingly, most of the characters that have been used by authors to keep *Ginkgophyllum* separate from other leaf morphotypes are actually linked to the leaf attachment on the shoot. For example, the difference with *Baiera* for Høeg (1967) is that the leaf base appears to sheath the shoot without showing a conspicuous point of attachment. Archangelsky and Arrondo (1974) and Archangelsky and Cúneo (1990) also include the phyllotaxis as an important character for *Ginkgophyllum* - although the arrangement they describe departs from that of the type specimen. On the other hand, authors that have proposed to include *Ginkgophyllum* in other leaf morphogenera focused on leaf characters without discussing leaf attachment to the shoot (e.g., Seward, 1919). To the extent of our knowledge, the presence of conspicuous secretory structures on the shoot and leaves has only been mentioned by Meyen (1985a, 1988; “resin bodies”). None of these features have been illustrated by photographs.

In addition to the description by Doubinger (1956) of new material from the Lodève Basin assigned to *G. grassetii*, several new species of *Ginkgophyllum* have been erected for Late Paleozoic foliage from around the world. They include for example specimens of *Ginkgophyllum vsevolodii* found in Russia (Zalessky, 1934), *Ginkgophyllum diazii*, *Ginkgophyllum criciumensis,* and *Ginkgophyllum incisa* in Argentina (Archangelsky and Arrondo, 1974; Archangelsky and Leguizamón, 1980; Escapa and Cúneo 2003), *Ginkgophyllum spatulifolia* in South Africa (Anderson and Anderson, 1985), *Ginkgophyllum sahnii* in India (Maithy, 1972), *Ginkgophyllum zhongguoense* in China (Yao, 1989), or *Ginkgophyllum boureaui* in Spain (Broutin, 1985). Some morphotaxa of Devonian foliage have also been assigned to *Ginkgophyllum* but most have later been reassigned to other genera (e.g., *G. kiltorkense* Johnson, 1914, from the Late Devonian of Ireland to *Kiltorkensia* Johnson, 1917). These additional species of *Ginkgophyllum* erected since Saporta’s description are often based on fragmentary specimens and/or different interpretations of the genus as previously discussed. They need further revisions based on a detailed comparison with the type here redescribed and with other morphogenera. This is especially important considering that ginkgophyte leaves show a high degree of intraspecific variability, which is seen both in extant *Ginkgo biloba* L. (e.g., Sun et al 2003; Naugolnykh, 2018) and well-studied fossil species such as *Baiera digitata* Heer (e.g., Bauer et al., 2013). Although the type of *Ginkgophyllum grassetii* includes several leaves, they are part of a single shoot and in small number. This most likely implies that the description here included accounts for only a part of the possible leaf disparity in this species.

4.2. Comments on the morphology and implications for comparison with isolated leaves

4.2.1. Phyllotaxis and shoot morphology

Vegetative shoots of possible ginkgophytes with organically attached leaves described for the Paleozoic are extremely rare. Bauer et al. (2013) illustrated a shoot from the Permian of Germany with at least ten leaves of the *Baiera digitata* type attached, but the phyllotaxis and leaf insertion are unclear and the specimen is too small to determine whether it is a long or a short shoot. Archangelsky and Leguizamón (1980) illustrated a specimen from the Carboniferous of Argentina that corresponds to a branched stem bearing helically arranged *Ginkgophyllum diazii* leaves.

Observation of the specimen with RTI, especially the base of the shoot where leaves are more spaced and each one is individually visible, clearly shows that leaf attachment is indeed helical and not distichous/alternate, or "bilateral". While the general aspect suggests that there is a row of leaves attached on each side of the shoot, detailed observation reveals without doubt that the leaf bases join the shoot at different levels, some being clearly below and others above (Plate II). This is concordant with the phyllotaxy of *Ginkgophyllum diazii* that, unlike the fossil described here, shows a clear pattern of leaf bases and scars on the stem (Archangelsky and Leguizamón, 1980). Another character of the *G. grassetii* type specimen of importance when conducting comparison with other Late Paleozoic-early Mesozoic seed plants is the lack of evidence for short shoots. Leaf bases do not show a distinct petiole and, if they were deciduous, the leaf scars on the shoot could be expected to be small, slit-like, and inconspicuous.

The upper portion of the specimen (the one that has been illustrated in drawings) is more complicated to interpret, as there are suggestions of branching in addition to the presence of more crowded leaves (Plate III). It is possible that this portion represents an apical part of a branch. Although we could not identify a proper apex (Plate III, 2, 3), this is suggested by the more crowded leaf bases and leaf orientation. The curvature of the specimen's stem (Plate III, 1) can be interpreted in three ways. First, it could correspond to a natural orthotropic orientation of the distal part of the shoot (Barthelemy and Caraglio, 2007). This is however not very likely since it is not possible to see a clear continuity of the shoot in terms of orientation of the fine lines and secretory structures as one would expect if it was simply bent (Plate III, 1). Second, it is possible that the shoot was partly broken about 7 cm from the distal end. Finally, it is also possible that this was a zone where branching occurred and that we are only seeing one of the resulting branches. The lack of a counterpart makes it difficult to address this question.

4.2.2. Secretory structures

The secretory structures that cover the shoot and leaves are a very conspicuous character of the specimen when seen with the right light angle (e.g., Plate II-V). There is little doubt that they correspond to the “resin bodies” observed by Meyen (1985a).

These structures are clearly not a preservation artifact. This is evidenced by the fact that they are absent in the surrounding matrix, have a consistent, decreasing density along the shoot and leaves, and can have a different aspect depending on the preservation of the specimen (with or without cuticule for example). Their gradient of density and their arrangement also suggest that they are a feature of the plant itself and not related to animal or fungal activity -such as some of the structures reported on some younger fossil ginkgophyte leaves (e.g., Sun et al., 2015; Shi et al. 2018).

Based on their aspect and size, they are comparable to other structures described in Paleozoic and Mesozoic seed plant organs, especially foliage, under various names: resin bodies, schizogenic cavities, glands, etc. They are for example mentioned in *Lepidopteris* Schimper, *Callistophyton* Delevoryas and Morgan (Rothwell, 1975), and other pteridosperms (e.g., Krings, 2000; Zodrow et al., 2016). Resin bodies have been mentioned for fossil ginkgophytes varying in morphology and age, including in species of *Ginkgo*, *Czekanowskia,* or *Sphenobaiera* (e.g., Florin, 1936b, Lydon et al., 2003; Table 1). The presence of such structures on Paleozoic and Mesozoic ginkgophytes has been considered to have a taxonomic significance (e.g., Meyen, 1987). They seem to be characteristic of young parts of the plant (i.e., leaves and young shoots). Florin (1936b) discussed the secretory structures found in *Ginkgo* and fossil ginkgophyte-like foliage. In extant *Ginkgo biloba* “secretory canals” are found in the primary bark of the branches and in the petiole and lamina of the leaves (see also Dörken, 2013).

The resin bodies appear to differentiate early during organ formation in *Ginkgophyllum grassetii* as the shape follows the main direction of growth of the organ. For the purpose of comparison with other specimens, it is important to note that the leaves of the type of *G. grassetii*, especially their apical part, is the region with the less abundant and conspicuous secretory structures (e.g., Plate IV, 1). This means that isolated leaves would have to be examined very closely to reveal this feature.

4.2.3. Veins

Characters related to leaf venation, which are important from a taxonomic point of view, were poorly illustrated in previous accounts. On Saporta’s (1879) drawing, several veins are represented in each leaf segment, but not in great detail and their divisions are not figured (Plate I, 2). In Seward’s (1919) drawing (Fig. 1), one of the three leaves seems to have veins represented but a closer look shows that there is no information on how they branch or their exact course. It is possible that these lines are a way of indicating the presence of several veins rather than an accurate drawing. The venation of leaf segments in *Ginkgophyllum* has been interpreted as consisting of several veins (e.g. Meyen, 1985a) or a single vein (e.g., Archangelsky and Cúneo, 1990). Considering the diversity of species assigned to the genus, the pattern of venation on the leaf segments can be thought as a suite of different minor characters: the number of veins before the first incision, the correspondence of vein dichotomies and lamina incisions, and the number and symmetry of dichotomies. Our observations confirm that the type specimen has two veins at the leaf base, that the veins dichotomize repeatedly, independently from lamina incisions, and in an asymmetrical manner. There are several veins in each segment and no evidence of anastomosis between them.

4.3. *Ginkgophyllum* and the problem of vegetative morphogenera of early ginkgophytes

While there is a consensus that ginkgophytes originated in the late Paleozoic, the exact timing of this apparition remains uncertain. Reproductive structures tentatively assigned to the group are extremely rare in the Paleozoic. They include *Trichopitys*, first described by Saporta (1875) at the same time and from the same deposit as *Ginkgophyllum grassetii*, and two other early Permian genera, namely *Polyspermophyllum* from Argentina (Archangelsky and Cúneo 1990) and Russian specimens of *Karkenia* (Naugolnykh, 2007), a genus otherwise known in the Mesozoic (e.g., Del Fueyo and Archangelsky, 2001; Zhou et al., 2002). As a result, most putative Paleozoic ginkgophytes are only represented by compression/impressions of leaves. They have been assigned to *Gingkoites* Seward, *Baiera* (Braun) Florin, *Sphenobaiera* Florin, *Psygmophyllum* Schimper, *Kerpia* Naugolnykh, *Biarmobaiera* Zalessky, *Ginkgophytopsis* Høeg, and *Ginkgophyllum* Saporta, among others (see Naugolnykh, 2007, 2016, 2018; Zhou, 2009 for detailed reviews; Table 1), but the definition of these morphogenera is highly problematic.

Indeed, numerous morphogenera and taxonomic schemes have been proposed, for over a century, to describe Paleozoic and Mesozoic leaves varying within a range of features considered as related to the ginkgoalean lineage such as leaf shape, dichotomous venation producing segments with variable veins number and with an also variable number and depth of distal incisions. Alternative formal and informal taxonomic schemes used the same names but with different character combinations, further clouding the taxonomy of the group. For example, Harris (1935) suggested the use of *Baiera* for wedge-shaped leaves that lacked a petiole, suggesting that the genus *Ginkgoites* should be used for leaves characterized by a distinct petiole. Florin (1936a), on the other hand, emended the diagnosis so that *Baiera* would include leaves *with* a petiole and assigned wedge-shaped dissected leaves without a distinct petiole to the genus *Sphenobaiera* (Bauer et al., 2013).

In addition to being reduced in number, morphological characteristics used to distinguish among Upper Paleozoic ginkgophyte morphogenera are usually defined with discrete states, such as the presence/absence of a “distinct” petiole, the number and depth of distal incisions, the number of veins per segment, etc. However, when the whole diversity of fossil forms is considered, it is clear that such characters actually vary along a continuous range.

Also increasing the complexity of late Paleozoic and Mesozoic ginkgoalean taxonomy, some of the fossil genera represent isolated vegetative remains, while others were defined on the basis of associated vegetative and reproductive organs. For example, the original diagnosis of *Baiera* proposed by Braun (1843) included a few reproductive features (i.e., *sporocarpia capsulaeformia, ovalia pedunculata, ternata vel biternata*) together with the general morphology of the leaves, a diagnosis that was later emended by Florin (1936a) to circumscribe the genus to leaves.

Analyses of early ginkgophytes are further complicated since many of the mentioned foliar features intergrade with other Paleozoic seed plant groups (see Rothwell and Mapes, 2001 and citations therein). In the absence of reproductive organs, there is a number of taxa with simple forked leaves that have been related to ginkgophytes, but also to Dicranophyllales (*sensu* Meyen, 1987) and coniferophytes (e.g., Meyen, 1987; Archangelsky and Cúneo, 1990; Rothwell and Mapes, 2001), among other related groups. These compose a mosaic of features from vegetative organs lacking evident synapomorphies, resulting in a weakly-grounded taxonomic framework. The development of more complete plant concepts, combining reproductive and vegetative organs, seems to be the unique way to satisfactorily solve the relationships within this broad range of Paleozoic seed plants.

A deep analysis of the circumscription of genera and higher ginkgophyte taxa exceeds the objectives of this publication. Considering the highly homoplastic distribution of vegetative morphological features, both in fossil ginkgophytes and other Paleozoic gymnosperms (e.g., coniferophytes) it is logical to hypothesize that these weakly defined taxonomic groups within basal ginkgophytes do not represent natural groups. In this context, illustrating and extracting new information from type specimens may represent a first solid step to untangle this tricky situation.

5. Conclusion and perspectives

Our reinvestigation of the type of *Gingkophyllum grassetii* using RTI provides new information on the morpho-anatomy of this specimen and clarifies some issues linked to the lack of previous photographic illustrations. The specimen consists of a shoot bearing leaves in a spiral. The leaves are about 5-11 cm long and 1-2 cm wide, wedge-shaped, and divided at least three times in their upper half. They do not form a distinct petiole and their base is adpressed on the shoot for 6-8 mm. Each leaf segment has entire parallel margins and 2-4 veins, resulting from dichotomies of the 2 veins present in the base of the leaf. Vein dichotomies are slightly asymmetrical and independent from divisions of the lamina. There is no anastomoses. Secretory structures 0.1 to 0.5 mm in diameter are present on both the stem and leaves, with a higher density on the stem. A summary of macro-morphological features of *Ginkgophyllum grassetii* compared with other morphogenera of Permian ginkgophytes is provided in Table 1 but an emended generic diagnosis, while necessary, seems premature at this stage. It would indeed require both a review of all the species that have been included in *Ginkgophyllum* through the years and a review of other ginkgophyte genera, especially of *Sphenobaiera* with which *Ginkgophyllum* shows a significant overlap. We also consider inadvisable to provide an emended diagnosis for the type species until the genus is fully understood.

The digitization of natural history collections and the increased availability of online databases that include photographs are facilitating comparisons between specimens across the world. While this does not entirely replace an actual observation, it allows researchers to find out where specimens essential for their research are housed and to make preliminary comparisons in a more accessible way, without travelling or resorting to loans. In France, this process started with herbaria scans added to online databases and was then extended to zoology and paleontology collections. The RECOLNAT project for example has provided means to inventory, digitize and compare all specimens with particular nomenclatural interest in paleontology. This initiative will be extended via the European project DiSSCo (Distribution System of Scientific Collections) in the coming years. This is especially important in the case of historical specimens such as the one described in this paper, for which very few original illustrations were circulated through books and papers. About 140 years after its initial description by Saporta, a photo of the type specimen of *Ginkgophyllum grassetii* was made available online in 2018, thanks to the RECOLNAT project. The RTI technique presented in this paper now provides an option to go further: it allows researchers across the world to remotely investigate details of the specimen under all possible illumination angles, which is especially important to understand its 3D organization and to reveal informative but inconspicuous characters. Additional details could be expected with complementary methods, such as digital microscopy or forthcoming technics, and potentially added to the specimen information in the collection database. Clearly, improved data sharing will facilitate future studies of complex groups of morphotaxa -such as ginkgophyte foliage- and help to solve major evolutionary questions in paleobotany.

Data Availability

Specimen MNHN.F.11222.2M is housed at the Museum National d'Histoire Naturelle, Paris, France (https://science.mnhn.fr/institution/mnhn/collection/f/item/11222.2m?listIndex=1&listCount=2). All RTI files and the composite images (Plate IV, 3, 4) are available at https://doi.org/10.5061/dryad.np5hqbzsx, hosted at Dryad Digital Repository (Decombeix et al., 2021).

Declaration of competing interests

OB declares possessing shares in FlyDome.

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[dataset] Decombeix A-L, Escapa I.H, De Franceschi D, Béthoux O. Reinvestigation of the type specimen of *Ginkgophyllum grassetii* Saporta 1875 using Reflectance Transforming Imaging, Dryad, Dataset, http://dx.doi.org/10.5061/dryad.np5hqbzsx).[Note to editor &

reviewers: the link to the dataset (4.89 Gb) until it is made public is https://datadryad.org/stash/share/wDIQV4S58eygUopl4o5QopQkfF-RIXJTG5BYajhsb8k]

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FIGURE LEGENDS

Plate I - *Ginkgophyllum grassetii* Saporta, 1875, MNHN.F.11222.2m.

1. General view of the specimen (original photograph by Peter Massicard for Recolnat Project, MNHN).

2. Drawing of the specimen by Saporta (1879)

3. Map of the 9 different areas documented using Reflectance Transforming Imaging (RTI a-i)

Plate II. *Ginkgophyllum grassetii* Saporta, 1875, MNHN.F.11222.2m. Basal portion of the shoot.

1-3. Basal portion of the shoot seen with different directions of the light source using the default rendering mode. This area shows leaf insertion at different levels, their decurrent bases lacking a distinct petiole, and lines and secretory structures on the shoot and leaf bases (RTI a)

4. Same area as 1-3 seen using normals visualization rendering mode (RTI a)

Plate III. *Ginkgophyllum grassetii* Saporta, 1875, specimen MNHN.F.11222.2m. Middle and proximal portions of the shoot.

1. Median region of the shoot showing a change in direction. See text for interpretations (RTI b)

2-3. Shoot and leaf base insertion in the proximal part of the specimen with default (2) and normals vizualization (3) rendering modes (RTI e)

Plate IV. *Ginkgophyllum grassetii* Saporta, 1875, specimen MNHN.F.11222.2m. Leaf morphology.

1-3. Morphology a leaf located on the median right part of the specimen, showing the general wedge shape, incisions, and veins. (1, 2) are single snapshots and (3) a composite view built from 4 snapshots (RTI c)

4. Possible branch on the median left part of the specimen; composite view built from 3 snapshots (RTI d)

5. Morphology of large apical leaves (RTI h)

Plate V. *Ginkgophyllum grassetii* Saporta, 1875, specimen MNHN.F.11222.2m. Details of the secretory structures.

1. Close up of the apex of one leaf showing a few secretory structures (RTI h, detail see plate IV, 5)

2. Close up of the shoot showing abundant secretory structures (RTI i)

FIG 1. Drawings of the type specimen in Renault (1885) and in Seward (1919) at the same scale and with the same orientation. Compare also to Plate I, 1 (specimen) and 2 (Saporta’s 1879 drawing).

TABLE 1. Selected macro-morphological characters of *Ginkgophyllum grassetii* and other genera of Permian foliage assigned to the ginkgophytes. Note the morphological overlap between *Ginkgophyllum grassetii* and *Sphenobaiera*. Characters compiled from diagnoses and discussions in Seward (1919), Florin (1936a), Høeg (1967), Naugolnykh (1995, 2016),

SUPPLEMENTARY FILES

S1: Original description of *Ginkgophyllum grassetii* by Saporta (1875) in French, and its English translation.

S2: Diagnose of *Ginkgophyllum* by Neuburg (1948) in Russian, and its English translation.

PLATE I

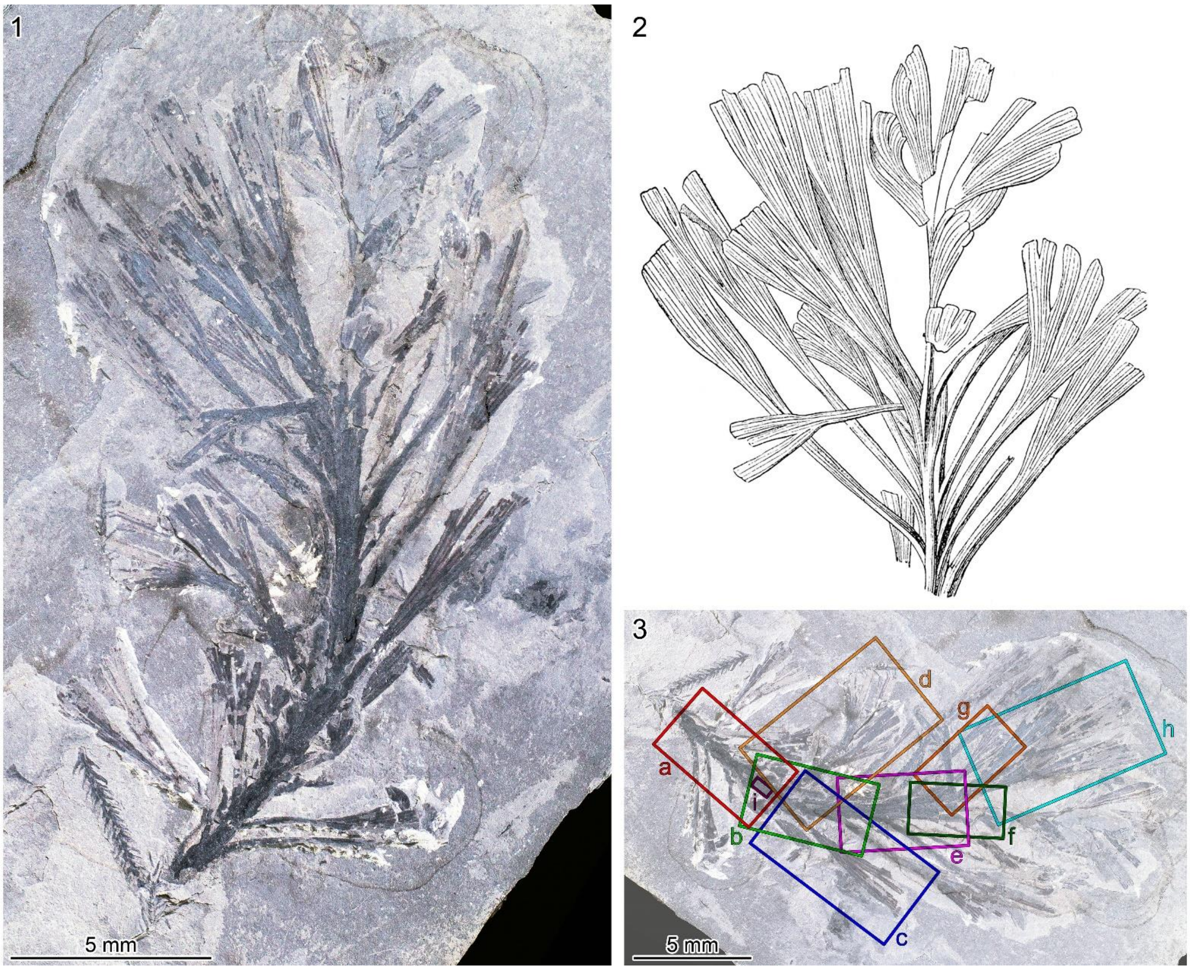

PLATE II

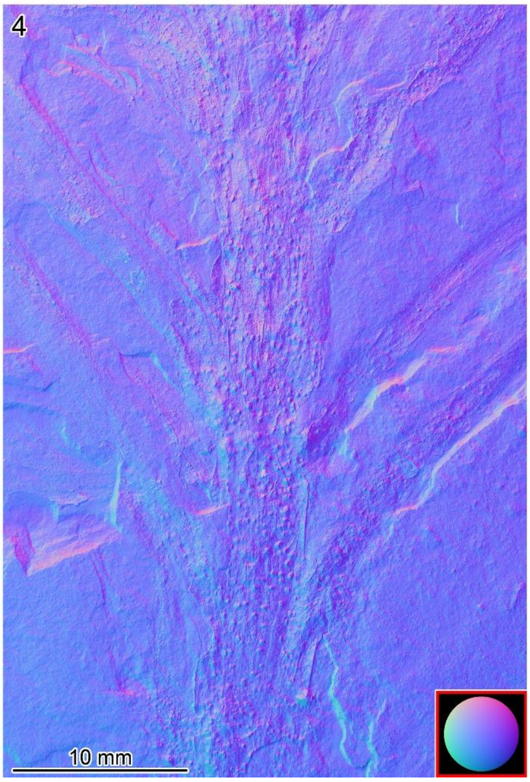

PLATE III

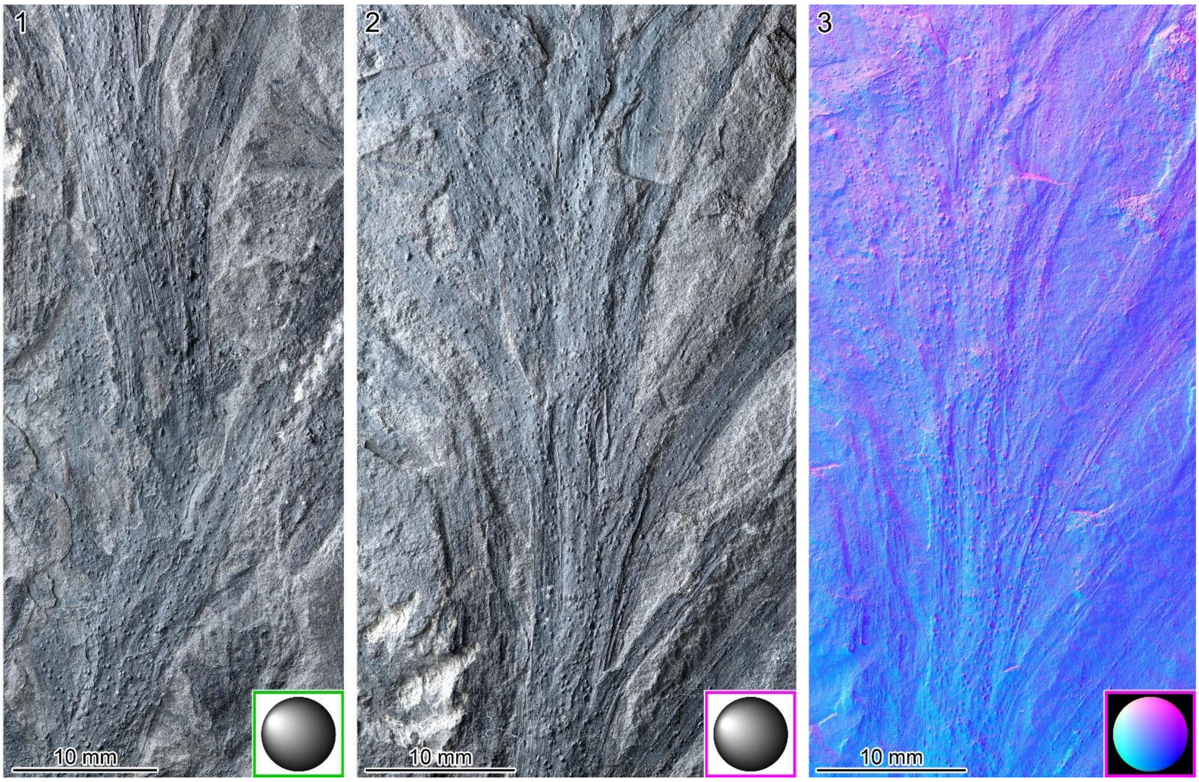

PLATE IV

PLATE V

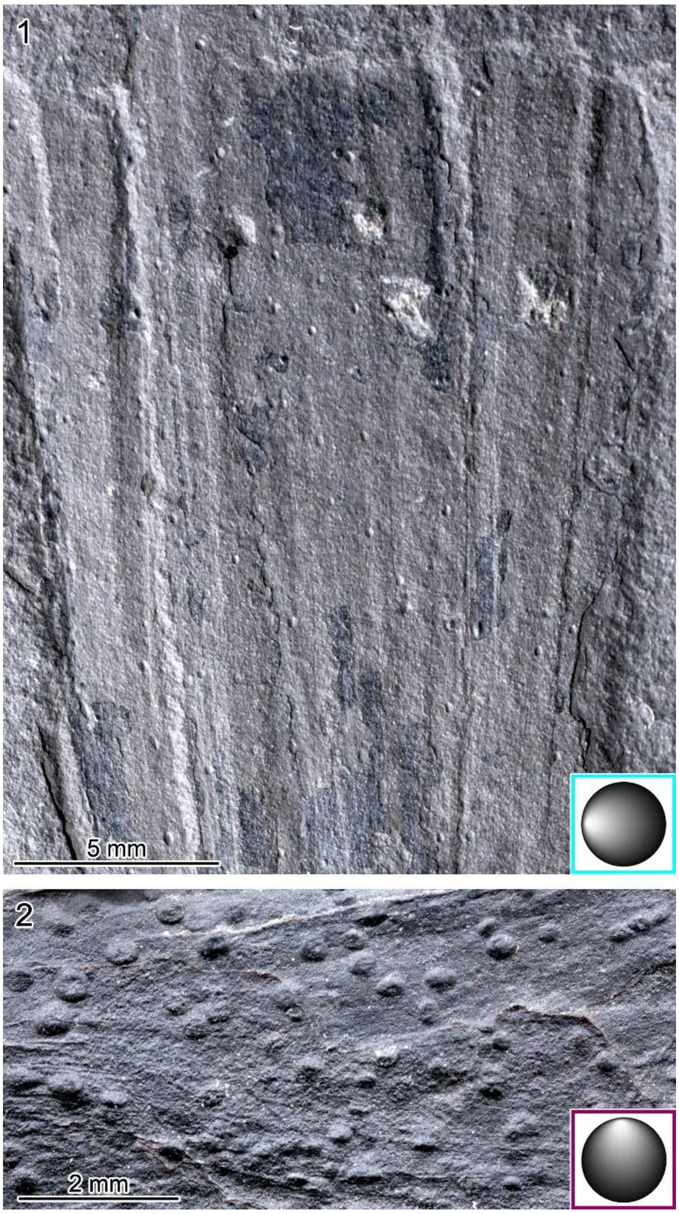

FIG 1