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

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

25

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

27 **1. Introduction**

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

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

48 The advent of commercially available digital cameras during the very end of the 20th
49 century largely contributed alleviating this issue. Fundamentally, it hastened the access to the
50 desired outcome, while retaining the two-steps process: the operator could immediately ensure

51 that satisfactory primary data was obtained, and could quickly engage into data processing using
52 dedicated software. It solicited skills largely similar to those involved in film photography (with
53 some ‘refunctioning’ as some may see it). The acquisition of a digital camera body that could be
54 coupled to a preferred lens or microscope (viz. a DSLR) has been an event to many, including the
55 colleague honored in this special issue and the last author of this account.

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

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

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

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

91 *Ginkgophyllum* Saporta, like many morphogenera of late Paleozoic seed plants, is poorly
92 circumscribed (e.g., Meyen, 1987; Archangelsky and Cúneo, 1990; Naugolnykh, 2007 and
93 references therein). Indeed, many seed plant lineages from that time period show a mosaic of
94 morphological features that, in many cases, are poorly understood in terms of homology (e.g.,
95 Taylor et al., 2009). Considering the relatively small number of significant characters preserved
96 in many organs or plant reconstructions from that time, their minute analysis and description is
97 crucial. This implies the revision of the type specimens of the most relevant morphogenera in the
98 light of current knowledge and with the help of new technologies. Foliage assigned to the

99 ginkgophytes are typically a case where this type of revision is strongly needed in order to re-
100 evaluate the affinities of the different taxa and untangle the early evolutionary history of the
101 group (e.g., Naugolnykh, 2007; Zhou, 2009; Bauer et al., 2013, 2014).

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

107

108 **2. Material and methods**

109 ***2.1. Specimen information***

110 The specimen was first described by Gaston de Saporta in 1875. It is part of the Saporta
111 collection at the Muséum National d'Histoire Naturelle, Paris, France. It consists of one slab about
112 30 x 12 cm with collection number MNHN.F.11222.2M. The slab contains the leafy shoot
113 described by Saporta and a few small fragments of conifer foliage (Plate I, 1-2). There is no
114 known counterpart. The specimen was photographed in 2018 by Peter Massicart and included in
115 the MNHN online database for the project RECOLNAT (ANR-11-INBS-0004).

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

119

120 ***2.2. Geological and floristic context***

121 The specimen was given to Saporta by Charles de Grasset who collected it in "the
122 Permian schists of Lodève" (Saporta, 1875). The Lodève basin is located in Southern France,

123 about 50 km NW of the city of Montpellier, and covers about 150 km². It overlaps the Stephanian
124 (= Gzhelian, Late Pennsylvanian) deposits of Graissessac that crop out to the West. Its Permian
125 continental infilling consists of fluvial and lacustrine grey sediments and red beds (e.g., Lopez et
126 al., 2005; Schneider et al., 2006). Based on its preservation, the characteristics of the rock matrix,
127 and the associated small conifer remains, the *Ginkgophyllum* specimen comes from the Usclas-St
128 Privat Fm, likely from the historical locality of les Tuilières. While the age of some younger
129 deposits in the Lodève Basin is disputed, the Usclas-St Privat Fm has been consistently dated
130 from the late Asselian to earliest Sakmarian (Schneider et al., 2006; Michel et al., 2015).

131 The flora from les Tuilières has been the subject of several studies since the 19th century
132 and although there is no published synthesis, over 40 different plant species have been reported
133 from the locality (e.g., Grand'Eury, 1877; Zeiller, 1898; Carpentier, 1931, 1937; Florin, 1938-
134 1945; Doubinger, 1956; Broutin et al., 1992; Galtier & Broutin, 1995; Galtier et al., 2017). The
135 assemblage is dominated, in terms of abundance and diversity, by conifers, which represent
136 >80% of the specimens and include 14 different morphospecies (Bertholon, 1996).

137 Peltaspermales are also diversified, with at least 12 morphospecies, but represent <10% of the
138 fossils. Other taxa are rarer. The most up to date list, compiled from the literature and personal
139 observations by Galtier et al. (2017), includes lycopsids (*Sigillaria* (*Subsigillaria*)), sphenopsids
140 (*Sphenophyllum*, *Annularia*, *Calamites*), filicopsids (*Pecopteris*), Medullosales (*Callipteridium*,
141 *Odontopteris*, *Potoniea*), cycadopsids (*Taeniopteris*), and possible ginkgophytes. The latter
142 include the fertile structure *Trichopitys heterophylla* described by Saporta at the same time than
143 *Ginkgophyllum grassetii* (Saporta, 1875). J. Doubinger (1956) also described and illustrated
144 several types of putative ginkgophyte foliage from that locality that she assigned to
145 *Ginkgophyllum grassetii* but also to *Sphenobaiera* sp., *Baiera* sp., and *Ginkgoites lodevensis*.

146

147 **2.3. Imaging**

148 We used the so-called ‘stationary dome technique’ to produce nine RTI files (RTI a-i).
149 Specifically, a horizontal 28-cm diameter light dome equipped with 54 LEDs (distributed over
150 three rings) was placed above the specimen and used as illumination source. Automation of
151 camera triggering and of changes in illumination were performed using the dedicated control box.
152 Illumination reference was given by a black reflecting sphere placed aside the area of interest and
153 cropped out during RTI processing (light dome, control box and reflecting sphere, FlyDome,
154 Paris, France). All LEDs were used for RTI a-h (i.e. each set is composed of 54 photographs) but
155 only a subset was used for RTI i (specifically, half of the LEDs of the two lower LED rings, i.e.
156 21 LEDs). As for photographic equipment, a Canon EOS 5D Mark III digital camera equipped
157 with a Canon 100 mm macro lens (RTI a, b, e-h), a Canon 50 mm macro lens (RTI c, d) or a
158 Canon MP-E 65 mm macro lens (RTI i) (all Tokyo, Japan), was used.

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

171 using a software such as RTIviewer, freely accessible (Cultural Heritage Imaging, San Francisco,
172 CA, USA).

173 Locating veins and their dichotomies using the RTI files is relatively straightforward in
174 the best-preserved zones, and near the center of the view. However, it is difficult to have a good
175 image of veins that have slightly different orientations on a single snapshot, i.e., with only one
176 direction of the light source, in particular if the observed area is large with respect to the dome
177 diameter, in which case illumination is too uneven across the image (e.g., Plate IV, 1, 2). One
178 option is to resort to normals visualization (e.g., Plate II, 4; Plate III, 3), but this implies a loss of
179 the specimen color information. To address this issue, we processed composites based on
180 multiple snapshots for the images on Plate IV, 3, 4. In essence, this approach is a digital way of
181 combining multiple light sources, a common way of using gooseneck optic fibers. As for Plate
182 IV, 3, four snapshots were used (light source coordinates: X:0.00, Y:0.00; X:-0.20, Y:0.50;
183 X:0.00, Y:0.65; X:0.50, Y:0.60) and were combined using the ‘overlay’ blending mode (with
184 further adjustments; see Adobe Photoshop working document available from Decombeix et al.,
185 2021). As for Plate IV, 4, three snapshots were used (light source coordinates: X:-0.50, Y:0.75;
186 X:-0.15, Y:0.65; X:0.50, Y:0.50) and were combined using the ‘multiply’ blending mode (with
187 further adjustments; see Adobe Photoshop working document available from Decombeix et al.,
188 2021). This highlights the value of RTI to investigate fine details and shows how RTI images
189 can be further processed.

190

191 **3. Results**

192 The specimen is a compressed fragmentary leafy shoot approximately 30 cm long and
193 12 cm wide, considering stem and leaves together (Plate I, 1). The stem is up to 6 mm wide (Plate
194 I, Plate II). It is straight for the first 10 cm, and then the visible part of the stem bends at an angle

195 of 37° (Plate I, 1; Plate III, 1). The axis is covered with longitudinal striations and densely
196 arranged secretory structures (Plate II; Plate III, 1-3) (see description below).

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

204 The leaves are dorsoventrally flattened with a distal region that is wedge-shaped and a
205 basal region that is also laminar and adpressed on the stem, not forming a distinct petiole (Plate
206 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
207 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.

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

214 The distal part is expanded in angles that vary between 20° and 35° and is usually longer
215 than the basal part (\approx 60% of leaf length). The leaves are dissected, with a least three orders of
216 dissection (Plate I; Plate IV). The first dissection shows angles between 7° and 16°, the depth of
217 the incision is variable, representing between $\frac{1}{2}$ and $\frac{2}{3}$ of the cuneiform region of the leaves. The
218 second order of incisions shows similar angles to the first, and its occurrence is not symmetrical

219 on the two sides of the leaf. In some cases a third, much shorter order of dissection is present.
220 The distal segments are often linear, with entire parallel margins and a width similar to the basal
221 part of the leaves (Plate IV, 3). Each lobe has an apical emargination, up to 0.5 mm deep, which
222 is placed between veins.

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

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

243

244 4. Discussion

245 4.1. *Historical descriptions of Ginkgophyllum vs. features of the type specimen*

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

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

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

267 1885, [pp. 145-146]) he provided a very short description that does not include information on
268 leaf attachment: “a complete branch, [that] shows leaves longly attenuated at the base in a sort
269 of decurrent petiole and split at the top into dichotomous segments”.

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

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

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

288 Doubinger (1956) assigned to *Ginkgophyllum grassetii* some isolated leaves from the
289 same early Permian locality of the Lodève Basin as Saporta’s specimen. She provided
290 photographs of three of them and noted that such leaves are often fragmentary and can be

291 confused with *Baiera*, but that the more complete ones can be distinguished from that genus by
292 the existence of a clearly differentiated petiole, a wide and semicircular leaf outline, and
293 truncated and angular leaf tips.

294 O. A. Høeg (1967) also focused on the leaves and used the partial drawing from Seward
295 1919. He also noted a “striking similarity” between *Ginkgophyllum grassetii* and *Baiera*, but said
296 they could be distinguished based on the long sheathing base of the former leaf type. In a
297 comparison of Indian taxa with the Palaeophyllales of Høeg (1967), P. K. Maithy (1972)
298 described *Ginkgophyllum* as having “*pinnate leaves with large cuneate dissected leaflets*”,
299 apparently interpreting the stem as the rachis of a compound leaf.

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

308 In 1984, S. V. Meyen observed the type specimen during a visit to Paris and summarized
309 his observations in a short note published in the 1985 International Organisation of Paleobotany
310 newsletter (Meyen, 1985a,b). Meyen noted that Saporta had not figured the whole specimen and
311 that his drawing was “*not quite accurate*”. Meyen described an “*helical arrangement of*
312 *palmately dissected leaves, dichotomous veination with several veins entering distal lobes and*
313 *numerous resin bodies embedded in the compression.*” He concluded that *Ginkgophyllum* was
314 similar to *Sphenobaiera* as defined by Harris et al. (1974). In his 1987 textbook Meyen

315 mentioned the helical arrangement of leaves and the similarity with *Sphenobaiera*. The resin
316 bodies were mentioned again in Meyen (1988), as present in “*both in the axis and leaves*” of the
317 type specimen. Meyen (1985a, 1987, 1988) did not provide any illustration of *Ginkgophyllum*. He
318 passed away in 1987 and it is not clear from the more recent literature whether his re-observation
319 of Saporta’s specimen was known to all the paleobotanists who later worked on *Ginkgophyllum*
320 and other putative ginkgophyte foliage.

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

326 This short historical account shows that the representation of *Ginkgophyllum* has changed
327 through time. An important information provided by the type specimen, the leaf attachment to the
328 shoot, has been overlooked in some descriptions and variously interpreted in others. Interestingly,
329 most of the characters that have been used by authors to keep *Ginkgophyllum* separate from other
330 leaf morphotypes are actually linked to the leaf attachment on the shoot. For example, the
331 difference with *Baiera* for Høeg (1967) is that the leaf base appears to sheath the shoot without
332 showing a conspicuous point of attachment. Archangelsky and Arrondo (1974) and Archangelsky
333 and Cúneo (1990) also include the phyllotaxis as an important character for *Ginkgophyllum* -
334 although the arrangement they describe departs from that of the type specimen. On the other
335 hand, authors that have proposed to include *Ginkgophyllum* in other leaf morphogenera focused
336 on leaf characters without discussing leaf attachment to the shoot (e.g., Seward, 1919). To the
337 extent of our knowledge, the presence of conspicuous secretory structures on the shoot and leaves

338 has only been mentioned by Meyen (1985a, 1988; “resin bodies”). None of these features have
339 been illustrated by photographs.

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

360

361 **4.2. Comments on the morphology and implications for comparison with isolated leaves**

362 **4.2.1. Phyllotaxis and shoot morphology**

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

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

381 The upper portion of the specimen (the one that has been illustrated in drawings) is more
382 complicated to interpret, as there are suggestions of branching in addition to the presence of more
383 crowded leaves (Plate III). It is possible that this portion represents an apical part of a branch.
384 Although we could not identify a proper apex (Plate III, 2, 3), this is suggested by the more
385 crowded leaf bases and leaf orientation. The curvature of the specimen’s stem (Plate III, 1) can be

386 interpreted in three ways. First, it could correspond to a natural orthotropic orientation of the
387 distal part of the shoot (Barthelemy and Caraglio, 2007). This is however not very likely since it
388 is not possible to see a clear continuity of the shoot in terms of orientation of the fine lines and
389 secretory structures as one would expect if it was simply bent (Plate III, 1). Second, it is possible
390 that the shoot was partly broken about 7 cm from the distal end. Finally, it is also possible that
391 this was a zone where branching occurred and that we are only seeing one of the resulting
392 branches. The lack of a counterpart makes it difficult to address this question.

393

394 **4.2.2. Secretory structures**

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

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

405 Based on their aspect and size, they are comparable to other structures described in
406 Paleozoic and Mesozoic seed plant organs, especially foliage, under various names: resin bodies,
407 schizogenic cavities, glands, etc. They are for example mentioned in *Lepidopteris* Schimper,
408 *Callistophyton* Delevoryas and Morgan (Rothwell, 1975), and other pteridosperms (e.g., Krings,
409 2000; Zodrow et al., 2016). Resin bodies have been mentioned for fossil ginkgophytes varying in

410 morphology and age, including in species of *Ginkgo*, *Czekanowskia*, or *Sphenobaiera* (e.g.,
411 Florin, 1936b, Lydon et al., 2003; Table 1). The presence of such structures on Paleozoic and
412 Mesozoic ginkgophytes has been considered to have a taxonomic significance (e.g., Meyen,
413 1987). They seem to be characteristic of young parts of the plant (i.e., leaves and young shoots).
414 Florin (1936b) discussed the secretory structures found in *Ginkgo* and fossil ginkgophyte-like
415 foliage. In extant *Ginkgo biloba* “secretory canals” are found in the primary bark of the branches
416 and in the petiole and lamina of the leaves (see also Dörken, 2013).

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

423

424 **4.2.3. Veins**

425 Characters related to leaf venation, which are important from a taxonomic point of view,
426 were poorly illustrated in previous accounts. On Saporita’s (1879) drawing, several veins are
427 represented in each leaf segment, but not in great detail and their divisions are not figured (Plate
428 I, 2). In Seward’s (1919) drawing (Fig. 1), one of the three leaves seems to have veins
429 represented but a closer look shows that there is no information on how they branch or their exact
430 course. It is possible that these lines are a way of indicating the presence of several veins rather
431 than an accurate drawing. The venation of leaf segments in *Ginkgophyllum* has been interpreted
432 as consisting of several veins (e.g. Meyen, 1985a) or a single vein (e.g., Archangelsky and
433 Cúneo, 1990). Considering the diversity of species assigned to the genus, the pattern of venation

434 on the leaf segments can be thought as a suite of different minor characters: the number of veins
435 before the first incision, the correspondence of vein dichotomies and lamina incisions, and the
436 number and symmetry of dichotomies. Our observations confirm that the type specimen has two
437 veins at the leaf base, that the veins dichotomize repeatedly, independently from lamina incisions,
438 and in an asymmetrical manner. There are several veins in each segment and no evidence of
439 anastomosis between them.

440

441 **4.3. *Ginkgophyllum* and the problem of vegetative morphogenera of early ginkgophytes**

442 While there is a consensus that ginkgophytes originated in the late Paleozoic, the exact
443 timing of this apparition remains uncertain. Reproductive structures tentatively assigned to the
444 group are extremely rare in the Paleozoic. They include *Trichopitys*, first described by Saporta
445 (1875) at the same time and from the same deposit as *Ginkgophyllum grassetii*, and two other
446 early Permian genera, namely *Polyspermophyllum* from Argentina (Archangelsky and Cúneo
447 1990) and Russian specimens of *Karkeniania* (Naugolnykh, 2007), a genus otherwise known in the
448 Mesozoic (e.g., Del Fueyo and Archangelsky, 2001; Zhou et al., 2002). As a result, most putative
449 Paleozoic ginkgophytes are only represented by compression/impressions of leaves. They have
450 been assigned to *Gingkoites* Seward, *Baiera* (Braun) Florin, *Sphenobaiera* Florin,
451 *Psygmophyllum* Schimper, *Kerpia* Naugolnykh, *Biarmobaiera* Zalessky, *Ginkgophytopsis* Høeg,
452 and *Ginkgophyllum* Saporta, among others (see Naugolnykh, 2007, 2016, 2018; Zhou, 2009 for
453 detailed reviews; Table 1), but the definition of these morphogenera is highly problematic.

454 Indeed, numerous morphogenera and taxonomic schemes have been proposed, for over a
455 century, to describe Paleozoic and Mesozoic leaves varying within a range of features considered
456 as related to the ginkgoalean lineage such as leaf shape, dichotomous venation producing
457 segments with variable veins number and with an also variable number and depth of distal

458 incisions. Alternative formal and informal taxonomic schemes used the same names but with
459 different character combinations, further clouding the taxonomy of the group. For example,
460 Harris (1935) suggested the use of *Baiera* for wedge-shaped leaves that lacked a petiole,
461 suggesting that the genus *Ginkgoites* should be used for leaves characterized by a distinct petiole.
462 Florin (1936a), on the other hand, emended the diagnosis so that *Baiera* would include leaves
463 *with* a petiole and assigned wedge-shaped dissected leaves without a distinct petiole to the genus
464 *Sphenobaiera* (Bauer et al., 2013).

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

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

477 Analyses of early ginkgophytes are further complicated since many of the mentioned
478 foliar features intergrade with other Paleozoic seed plant groups (see Rothwell and Mapes, 2001
479 and citations therein). In the absence of reproductive organs, there is a number of taxa with
480 simple forked leaves that have been related to ginkgophytes, but also to Dicranophyllales (*sensu*
481 Meyen, 1987) and coniferophytes (e.g., Meyen, 1987; Archangelsky and Cúneo, 1990; Rothwell

482 and Mapes, 2001), among other related groups. These compose a mosaic of features from
483 vegetative organs lacking evident synapomorphies, resulting in a weakly-grounded taxonomic
484 framework. The development of more complete plant concepts, combining reproductive and
485 vegetative organs, seems to be the unique way to satisfactorily solve the relationships within this
486 broad range of Paleozoic seed plants.

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

494

495 **5. Conclusion and perspectives**

496 Our reinvestigation of the type of *Gingkophyllum grassetii* using RTI provides new
497 information on the morpho-anatomy of this specimen and clarifies some issues linked to the lack
498 of previous photographic illustrations. The specimen consists of a shoot bearing leaves in a spiral.
499 The leaves are about 5-11 cm long and 1-2 cm wide, wedge-shaped, and divided at least three
500 times in their upper half. They do not form a distinct petiole and their base is adpressed on the
501 shoot for 6-8 mm. Each leaf segment has entire parallel margins and 2-4 veins, resulting from
502 dichotomies of the 2 veins present in the base of the leaf. Vein dichotomies are slightly
503 asymmetrical and independent from divisions of the lamina. There is no anastomoses. Secretory
504 structures 0.1 to 0.5 mm in diameter are present on both the stem and leaves, with a higher
505 density on the stem. A summary of macro-morphological features of *Gingkophyllum grassetii*

506 compared with other morphogenera of Permian ginkgophytes is provided in Table 1 but an
507 emended generic diagnosis, while necessary, seems premature at this stage. It would indeed
508 require both a review of all the species that have been included in *Ginkgophyllum* through the
509 years and a review of other ginkgophyte genera, especially of *Sphenobaiera* with which
510 *Ginkgophyllum* shows a significant overlap. We also consider inadvisable to provide an emended
511 diagnosis for the type species until the genus is fully understood.

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

530 potentially added to the specimen information in the collection database. Clearly, improved data
531 sharing will facilitate future studies of complex groups of morphotaxa -such as ginkgophyte
532 foliage- and help to solve major evolutionary questions in paleobotany.

533

534 **Data Availability**

535 Specimen MNHN.F.11222.2M is housed at the Museum National d'Histoire Naturelle, Paris,
536 France

537 (<https://science.mnhn.fr/institution/mnhn/collection/f/item/11222.2m?listIndex=1&listCount=2>).

538 All RTI files and the composite images (Plate IV, 3, 4) are available at

539 <https://doi.org/10.5061/dryad.np5hqbzxs>, hosted at Dryad Digital Repository (Decombeix et al.,
540 2021).

541

542 **Declaration of competing interests**

543 OB declares possessing shares in FlyDome.

544

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557

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746 **FIGURE LEGENDS**

747

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

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

751 2. Drawing of the specimen by Saporta (1879)

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

753

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

755 1-3. Basal portion of the shoot seen with different directions of the light source using the default
756 rendering mode. This area shows leaf insertion at different levels, their decurrent bases lacking a
757 distinct petiole, and lines and secretory structures on the shoot and leaf bases (RTI a)

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

759

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

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

763 2-3. Shoot and leaf base insertion in the proximal part of the specimen with default (2) and
764 normals visualization (3) rendering modes (RTI e)

765

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

768

769 1-3. Morphology a leaf located on the median right part of the specimen, showing the general
770 wedge shape, incisions, and veins. (1, 2) are single snapshots and (3) a composite view built from
771 4 snapshots (RTI c)

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

774 5. Morphology of large apical leaves (RTI h)

775

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

778 1. Close up of the apex of one leaf showing a few secretory structures (RTI h, detail see plate IV,
779 5)

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

781

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

785

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

790

791

792 **SUPPLEMENTARY FILES**

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

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

PLATE I

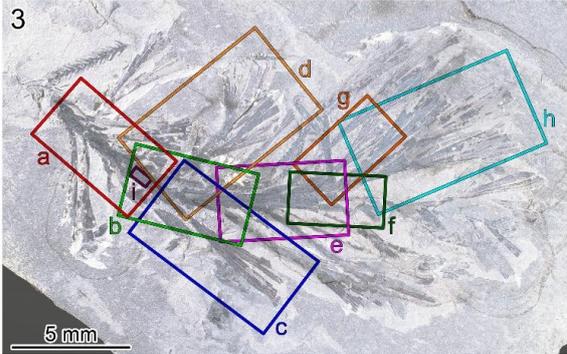
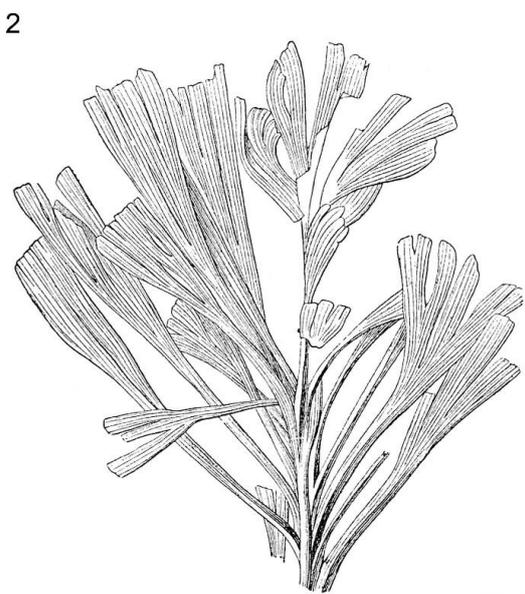


PLATE II

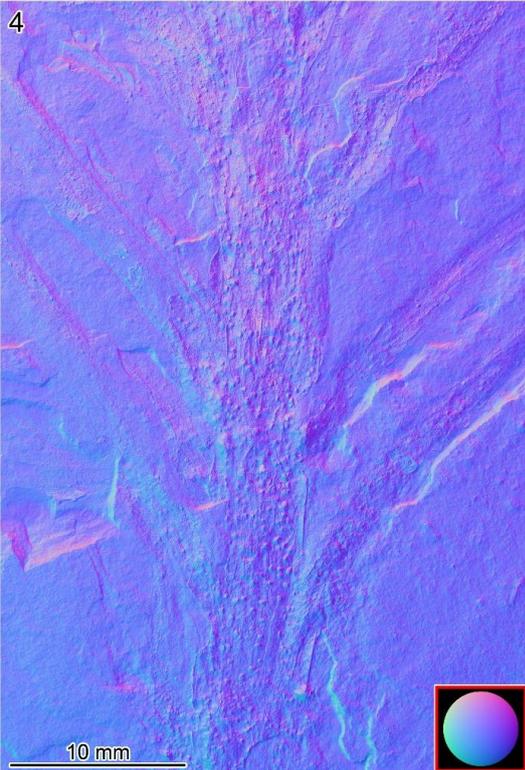


PLATE III



PLATE IV



PLATE V

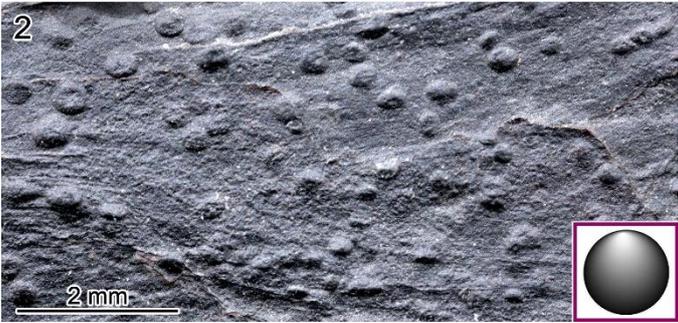
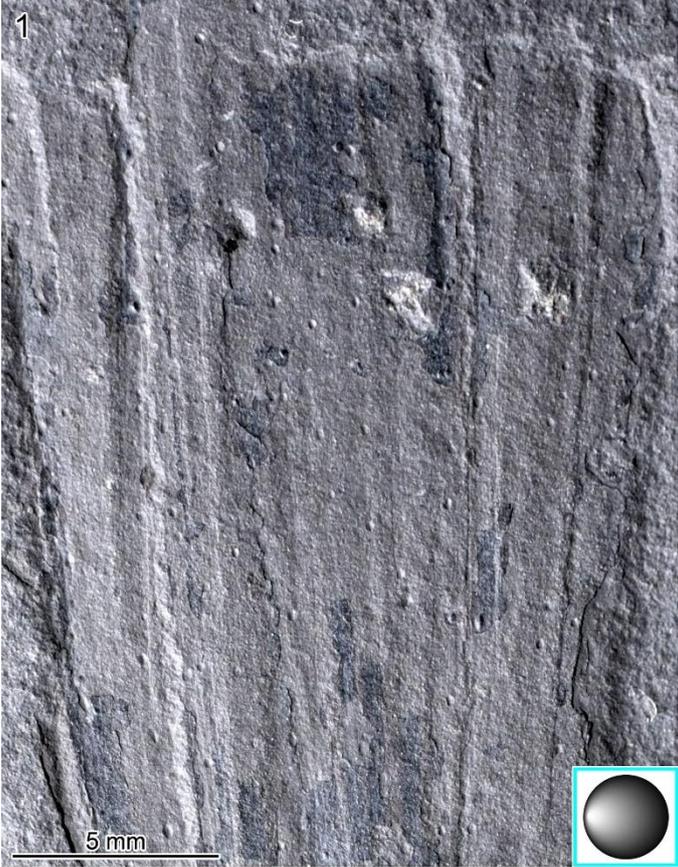


FIG 1

