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5 **The core of *Sporocarpon asteroides*, an enigmatic fungal fossil from the**
6 **Carboniferous**

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9 **Michael Krings, Carla J. Harper, Anne-Laure Decombeix and Jean Galtier**

10 With 3 figures

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17

18 **Abstract:** The various types of spherical microfossils collectively termed fossil fungal
19 “sporocarps” exhibit basic congruities in morphology that have been used to suggest they all
20 may belong to the same higher taxonomic category. Both the Ascomycota and zygomycete
21 fungi have been discussed in this respect, but features that precisely delimit the nature and
22 taxonomic position of these fossils have not been documented. Here, we present two new
23 specimens of the Pennsylvanian “sporocarp” *Sporocarpon asteroides* from the Lower Coal
24 Measures of Great Britain. Both provide evidence that a spore with a multi-layered wall was
25 formed in this structure by blastic inflation of a hyphal tip. The outer spore walls appear to be
26 continuous with the wall of the subtending hypha, while the inner wall (the spore wall proper)
27 more likely developed de novo. *Sporocarpon asteroides* is interpreted as a unisporic
28 sporocarp with a pseudoparenchymatous peridium, likely with affinities to the
29 Glomeromycota. This discovery supports the notion that the fossil fungal “sporocarps”
30 include several biologically different structures.

31

32 **Key words:** fossil fungal “sporocarp”, Glomeromycota, Lower Coal Measures,
33 Pennsylvanian, pseudoparenchymatous investment, spore wall

34

35

36 **1 Introduction**

37 Various types of small spherical structures often collectively termed fossil fungal
38 “sporocarps”¹ are commonly found in Pennsylvanian coal balls and certain chert deposits
39 (surveyed by STUBBLEFIELD et al. 1983; TAYLOR et al. 2015). All consist of a central cavity
40 bounded by a contiguous perimeter wall and additionally surrounded by a prominent
41 investment composed of loosely entwined or tightly interwoven hyphae. “Sporocarps” occur
42 singly or in small clusters; hardly any of them provide information on the systems on or in
43 which they were borne. Several different genera, including *Dubiocarpon* S.A. HUTCH.,
44 *Mycocarpon* S.A. HUTCH., *Sporocarpon* WILL., and *Traquairia* CARRUTH., have been erected
45 to accommodate these fossils, which are distinguished from one another based primarily on
46 the construction of the investment. While fossil fungal “sporocarps” are mostly known from
47 the Pennsylvanian, there are also several forms described from the Mississippian (SCOTT
48 1911; TAYLOR et al. 1994; KRINGS et al. 2010b) and Triassic (WHITE & TAYLOR 1988, 1989a,
49 1991; TAYLOR & WHITE 1989), and one from the Lower Devonian Rhynie cherts (KRINGS et
50 al. 2014). What relationship, if any, exists between the “sporocarps” and a number of other,
51 structurally similar but generally much smaller Rhynie chert fossils referred to as mantled
52 fungal reproductive units (e.g., KRINGS & TAYLOR 2014, 2015a, 2015b; KRINGS et al. 2016;
53 KRINGS & HARPER 2017, 2020) remains uncertain.

54 Fossil fungal “sporocarps” in general have been attributed to the Ascomycota based on
55 specimens containing one or more spheres believed to represent asci that in turn contain small
56 spherules interpreted as ascospores (HUTCHINSON & WALTON 1953; HUTCHINSON 1955;
57 STUBBLEFIELD et al. 1983). According to this idea, the “sporocarp” would be a
58 cleistothecium. Another hypothesis, however, uses specimens that contain a single, large
59 sphere to suggest affinities to the zygomycete fungi (PIROZYNSKI 1976; TAYLOR & WHITE
60 1989). The sphere is interpreted as a zygospore, while the “sporocarp” would be the
61 zygosporangium enveloped in a hyphal investment equivalent to that seen in certain extant
62 Endogonales (Mucoromycotina). Smaller spheres in some cases present in the large sphere
63 are regarded as intrusive parasites. There is circumstantial evidence to corroborate the latter
64 hypothesis (e.g., KRINGS et al. 2010b, 2011a, 2011d; KRINGS & TAYLOR 2012), but structural

¹The term sporocarp, used in mycology to refer to a multicellular structure in which spores or spore-producing entities are formed, is put in quotation marks because it may not be applicable to all of these fossils (for details, see KRINGS et al. 2011d).

65 features that precisely delimit the nature and taxonomic position of the fungal “sporocarps”
66 have not been documented to date.

67 Every new specimen that displays features not hitherto seen can provide critical new
68 information on these enigmatic fossils, and thus deserves thoughtful consideration. Here, we
69 present two specimens of *Sporocarpon asteroides* WILL. from the Lower Coal Measures of
70 Great Britain that both contain a structure suggestive of the formation of a spore with a multi-
71 layered wall in this “sporocarp” species. The outer walls appear to be continuous with the
72 wall of a subtending hypha, while the inner wall more likely developed de novo.

73

74 **2 Material and Methods**

75 The specimens of *Sporocarpon asteroides* described in this study are present in a single thin
76 section (c. 60 µm thick) that was prepared from a coal ball from the Lower Coal Measures of
77 Great Britain. The coal ball was collected sometime in the 1970s by John HOLMES, and comes
78 from the Union Seam at Rowley Tip, Burnley (Lancashire), which is Westphalian A or
79 Langsettian (Bashkirian/Lower Pennsylvanian) in age. The Union Seam and its stratigraphic
80 equivalent in Great Britain, the Halifax Hard Seam, together with the contemporaneous
81 Bouxharmont Seam in Belgium and the Finefrau-Nebenbank Seam in the Netherlands and
82 Germany, represent the source strata of the richest European coal ball floras (for details, refer
83 to GALTIER 1997).

84 The thin section was prepared according to a standard procedure in which a piece of
85 the coal ball was cemented to a glass slide and then ground with abrasive until it was
86 sufficiently thin to be examined with transmitted light (HASS & ROWE 1999). John HOLMES
87 had already marked the *Sporocarpon* specimens on a drawing of the cut faces and labelled
88 them as “curious spores 400 µm”. The coal ball, offcuts, and slide are deposited in the
89 Collections de Paléobotanique, Université de Montpellier, France, under accession numbers
90 B07 and B07A1aT 01. Fossils were analysed using normal transmitted light microscopy
91 equipment. Digital images were captured with a Leica DFC-480 camera and gently processed
92 in Adobe Photoshop CS4 for brightness and contrast.

93

94 **3 Results**

95 Coal ball B07 contains an accumulation of permineralized stigmarian rootlets, fragments of
96 arborescent lycophyte axes, microphylls, megaspores, and *Lepidocarpon* sp., calamite
97 remains, and several fern rachides, including *Botryopteris hirsuta* (WILL.) SCOTT and *B.*
98 *ramosa* (WILL.) SCOTT, all embedded in a clear matrix interspersed with abundant organic

99 debris, scattered fungal hyphae, and small propagules. Six three-dimensionally preserved
100 specimens of *Sporocarpon asteroides* in different sectional planes occur in thin section
101 B07A1aT 01. All, except two are, as far as we can see, typical examples of *S. asteroides* (for
102 details on the morphology of this “sporocarp” species, refer to STUBBLEFIELD et al. 1983).
103 The two atypical specimens (denoted I and II in Fig. 1A), which are detailed in the paragraphs
104 below, are ideally cut and provide excellent median longitudinal section views of the fossils.
105 They occur in close proximity to a third specimen (denoted III in Fig. 1A) sectioned slightly
106 off center, and a fourth one (denoted IV in Fig. 1A) of which only a part of the outer surface
107 can be seen because it is located in a different plane.

108 Specimens I and II correspond in size and overall appearance to typical *Sporocarpon*
109 *asteroides*, but differ from all previously described individuals in regard to the outer boundary
110 of the cavity and the cavity contents (Figs. 1B, C, E, 2A–D). Both specimens exhibit the
111 characteristic, irregularly lobed pseudoparenchymatous investment enveloping a (near-
112)spherical cavity approximately 300 μm in diameter. A contiguous wall that extends along,
113 and is closely appressed to, the inner surface of the investment, as it occurs in typical *S.*
114 *asteroides*, is present in neither specimen (Figs. 1E, 2C, D). Instead, each of the two cavities
115 contains a single large sac-like vesicle (sv in Figs. 1B, C₁, E, 2A₁, B₁, C, D) with a thin,
116 wrinkled, and finely granulose wall (e.g., Fig. 2C); the position of the vesicle within the
117 cavity is eccentric. The vesicle is c. 230 μm high and 215 μm wide in specimen I and c. 260
118 μm high and 230 μm wide in specimen II. A similar, but distinctly smaller and bulb-shaped
119 vesicle is present in specimen III (arrow in Fig. 1D). What appear to be short fragments of
120 narrow filament- or fiber-like structures of some kind are recognizable here and there in the
121 space between the investment and the vesicle wall, particularly where the two structures are in
122 close proximity to each other (fs in Fig. 1E).

123 Located within the confines of the vesicle in specimens I and II is a compound
124 structure that comprises a basal, squat-columnar component (less than 40 μm high and 20 μm
125 wide), which is hollow in specimen II (sce in Figs. 1C₁, E, 2A₁) but apparently massive in
126 specimen I (sce in Figs. 1B, 2B₁). Attached laterally to the columnar component are the
127 remains of at least two walls (w1 and w2 in Figs. 1B, C₁, 2A₂, B₂) of which, unfortunately,
128 only fragments are preserved. Moreover, at the tip of the columnar component is a walled
129 sphere, which is more or less intact and c. 155 μm in diameter in specimen I (cs in Figs. 1B,
130 2B₁), but collapsed and mostly disintegrated (but still recognizable) in specimen II (cs in Figs.
131 1C₁, 2B₁). The wall of this sphere appears to be layered (csw in Fig. 2D). As to whether the
132 sphere was physically connected to the tip of the columnar component or developed freely (de

133 novo) within the confines of the innermost surrounding wall (w2) cannot be determined. The
134 latter seems to be more likely, however, based on the position of the collapsed sphere in
135 specimen II (Fig. 1C₁). Specimen II also suggests that the columnar component was
136 connected to, or continued into, some structure on the outside of the “sporocarp” (arrows in
137 Fig. 1C₂). Unfortunately, this structure is either not preserved, or not located in the portion
138 (slice) of the “sporocarp” present in the thin section. The vesicle in the cavity of specimen III
139 is empty (Fig. 1D). Tiny, dot-shaped inclusions, which occur in large numbers in the spaces
140 between the individual wall layers (Fig. 2D), are probably remains of the decayed parts of the
141 compound structure (but see below).

142

143 **4 Discussion**

144 Fossil fungal “sporocarps” range among the most extensively studied pre-Cretaceous fungal
145 fossils, and their morphology is well understood today (KRINGS et al. 2014). Nevertheless, the
146 biological nature and affinities of these structures have remained a matter of controversy since
147 they were first brought to the attention of the scientific community by CARRUTHERS (1873)
148 and WILLIAMSON (1878, 1880, 1883). The fact that virtually all “sporocarp” specimens
149 documented to date appear to be fully developed (mature) structures, in tandem with the lack
150 of information on other life cycle stages of the organisms that produced them, and the
151 inconsistency that exists with regard to the cavity contents are the main obstacles to a more
152 complete understanding of these fossils (TAYLOR et al. 2015).

153

154 **4.1 The sac-like vesicle**

155 The most recent taxonomic revision of the “sporocarp” genus *Sporocarpon* by STUBBLEFIELD
156 et al. (1983) recognizes three species, *S. asteroides*, *S. cellulorum* WILL., and *S. leismanii*
157 STUBBLEFIELD et al., all of them characterized by a prominent, cohesive investment that is
158 pseudoparenchymatous. The species differ primarily in the organization of the investment,
159 which is irregularly lobed in *S. asteroides*, constructed of radiating files of cells in *S.*
160 *cellulosum*, and prolonged into narrow, conical rays in *S. leismanii*. The cavities of the
161 *Sporocarpon* specimens figured in literature are either empty or contain small spheres, or they
162 contain a single large sphere, which is either empty or contains one or more smaller spheres
163 (WILLIAMSON 1880; MCLEAN 1922; HUTCHINSON 1955; BAXTER 1960, 1975; DAVIS &
164 LEISMAN 1962; STUBBLEFIELD et al. 1983). However, structures corresponding to the ones
165 present in the fossils described in this study have not been documented previously in
166 *Sporocarpon*, with the exception of the sac-like vesicle. STUBBLEFIELD et al. (1983) found

167 that the wall lining the inner surface of the investment (i.e. the cavity perimeter wall) in *S.*
168 *asteroides* is multi-layered and granulose on the outer surface of the innermost layer. The sac-
169 like vesicles in the specimens described here (sv in Fig. 1B, C, arrow in Fig. 1D) all possess a
170 finely granulose wall (sv in Figs. 1E, 2C), suggesting that the vesicle actually is the innermost
171 layer of the perimeter wall that has separated from the outer layers. The outer layers, in turn,
172 no longer exist. They appear to have disintegrated, except for remnants occurring in the form
173 of short filament- or fiber-like fragments in the space between the inner surface of the
174 investment and the vesicle (fs in Fig. 1E). If this is accurate, then the question arises why the
175 vesicle is so much smaller than the cavity? One possible explanation could be that the
176 perimeter wall in vivo was of considerable thickness. However, a thick perimeter wall has not
177 been recorded for any fossil fungal “sporocarp” to date, which renders this hypothesis
178 improbable. More likely, based on the wrinkled wall, is that the vesicle has shrunk during
179 fossilization (see below). An alternative, albeit highly speculative, interpretation of the
180 filament- or fiber-like structures in *S. asteroides*, and likewise of the dot-shaped inclusions
181 visible in the spaces between the individual wall layers (Fig. 2D), is that they are
182 endosymbionts, perhaps bacteria comparable to the endobacteria found in fungi today
183 (BONFANTE & DESIRÒ 2017), including Endogonales (DESIRÒ et al. 2015) and many species
184 of Glomeromycota (e.g., DESIRÒ et al. 2014; TOOMER et al. 2015; VENICE et al. 2021).

185

186 **4.2 The compound structure**

187 The compound structure that occurs in the vesicle in specimens I and II is evidence that a
188 spore of some kind (i.e. the central sphere) was formed inside these “sporocarps,” and that
189 this spore had a complex wall comprised of a wall proper (i.e. the layered wall of the central
190 sphere; csw in Fig. 2D) and the two outer walls labelled w1 and w2 in Figs. 1B, C₁, 2A₂, and
191 B₂. A spore-like body bounded by a multi-layered wall has previously been documented
192 solely in the Mississippian “sporocarp” *Roannaisia bivitalis* T.N. TAYLOR et al. from France
193 (TAYLOR et al. 1994: pl. II, 1). What appear to be concentrically arranged walls or wall layers
194 are also visible in several Pennsylvanian *Traquairia* specimens from Great Britain and the
195 United States (SCOTT 1911: textfig. 4; STUBBLEFIELD & TAYLOR 1983; KRINGS et al. 2011d:
196 pl. I, 1). It has been suggested, however, that these layers have formed from the splitting of
197 the cavity perimeter wall during fossilization (STUBBLEFIELD & TAYLOR 1983). By contrast,
198 KRINGS et al. (2011d) believe that they represent an artefact which came into being during the
199 permineralization process as a result of several successive phases of shrinking of the spore-
200 like body in the cavity. Walls w1 and w2 in *Sporocarpon asteroides* originate from the base

201 of the compound structure, where they arise from the squat-columnar component, which we
202 interpret as the tip of a subtending hypha. Accordingly, the physical connection between w1
203 and w2 and the columnar component would imply that these walls were continuous with the
204 wall of the subtending hypha. The wall bounding the central sphere probably formed de novo.
205

206 **4.3 Affinities to Glomeromycota**

207 Based on the preceding considerations, we entertain the possibility that *Sporocarpon*
208 *asteroides* was a unispore sporocarp with a pseudoparenchymatous peridium that enclosed a
209 spore with a multi-layered wall (Fig. 3). The cavity perimeter wall is viewed as a product of
210 the innermost layer of the peridium, rather than as a part of the spore. The origin of the
211 peridium remains elusive. No evidence of paired or single gametangia (and suspensors) has
212 been found, suggesting that the spore developed asexually and by blastic expansion of a
213 hyphal tip, and thus that *S. asteroides* may have been a member of the Glomeromycota. This
214 concurs with a major counterargument to the interpretation of fossil fungal “sporocarps” in
215 general as zygosporangia containing zygospores, namely the total lack of evidence of
216 gametangia in these structures (KRINGS & TAYLOR 2012; KRINGS et al. 2013a). Even if the
217 gametangia, as argued elsewhere (KRINGS & HARPER 2020; KRINGS 2022), were small and
218 embedded in the investment, if they have existed, then at least some would have been
219 detected, given the large number of “sporocarp” specimens examined to date. Several bona
220 fide zygomycete fungi that also have been described from the Carboniferous and Triassic
221 show zygosporangia with attached gametangia, and investments similar to the ones seen in
222 fossil fungal “sporocarps” (WHITE & TAYLOR 1989b; KRINGS et al. 2012, 2013b).

223 Glomeromycota are soil-borne fungi that enter into mycorrhizal associations with
224 plants. They produce large (up to more than 800 µm in diameter) spores with multi-layered
225 walls on non-septate hyphae (REDECKER & RAAB 2006; WALKER et al. 2018). The oldest
226 bona fide fossil glomeromycotan spores are Early Devonian in age (e.g., STUBBLEFIELD &
227 BANKS 1983; HARPER et al. 2020; WALKER et al. 2021; LALICA & TOMESCU 2022), and there
228 is also documented evidence of Glomeromycota from several of those Carboniferous deposits
229 that have yielded “sporocarp” fossils (e.g., WAGNER & TAYLOR 1981, 1982; STUBBLEFIELD et
230 al. 1985; KRINGS et al. 2011c). In addition, there are various types of mantled fungal
231 reproductive units from the Lower Devonian Rhynie chert that are morphologically similar to
232 Carboniferous fungal “sporocarps” and demonstrably borne on a simple tubular subtending
233 hypha. These fossils have also been considered to belong to the Glomeromycota (KRINGS &
234 TAYLOR 2014; KRINGS & HARPER 2017, 2020). Unfortunately, the continuation of the

235 subtending hypha on the outside of *Sporocarpon asteroides* remains unknown. There is, in
236 fact, very little documented evidence of the structures that gave rise to any of the fossil fungal
237 “sporocarps.” One putative subtending structure occurs in a specimen of *Mycocarpon cinctum*
238 M. KRINGS et al. from the Mississippian of France in the form of an inflated appendage
239 extending from the outer surface of the investment (KRINGS et al. 2010b: pl. 1, fig. 1a, pl. 2,
240 fig. 4). This structure appears to interface the “sporocarp” with its source organism, and is
241 perhaps congruent with the bulbous bases seen in present-day species of the glomeromycotan
242 order Gigasporales (KHADE 2011; WALKER et al. 2018).

243

244 **4.4 Possible objections**

245 The interpretation of *Sporocarpon asteroides* as a member of the Glomeromycota could be
246 countered by pointing out that the putative spore is considerably smaller than the cavity
247 bounded by the investment. The question therefore is what gave shape to the spherical cavity
248 in this fossil? A peridium typically precedes spore formation or develops concomitantly with
249 the spores, encloses the spores, and expands as the spores grow larger (GIOVANNETTI et al.
250 1991; MEIER & CHARVAT 1992, and references therein). We believe that the size difference
251 between the cavity and spore in *S. asteroides* is a preservation artefact resulting from
252 shrinkage of the spore due to plasmolysis caused by the physico-chemical properties of the
253 depositional environment and the permineralization process (see SCOTT & REX 1985). A
254 similar effect can be seen in present-day glomeromycotan spores after they have been
255 exposed to certain acidic mounting media. It is known, for instance, that spores embedded in
256 PVLG (polyvinyl-lacto-glycerol) may shrink considerably or collapse with plasmolysis of the
257 spore contents (GAMPER et al. 2009). An ensuing question is, why is there not a spore in every
258 specimen of *S. asteroides*? We speculate that the pseudoparenchymatous investment may
259 have been durable and remained (largely) intact for an extended period of time after the spore
260 had germinated or become non-viable for some other reason and its walls decayed. If so, then
261 the majority of *S. asteroides* fossils would be empty investments.

262 It might also be argued that cohesive, pseudoparenchymatous investments like that of
263 *Sporocarpon asteroides* do not occur in present-day Glomeromycota (e.g., FURRAZOLA et al.
264 2016; GUPTA 2017; JOBIM et al. 2019; YAMAMOTO et al. 2019). It is basically correct that the
265 fossil differs from all present-day members of the Glomeromycota producing spores enclosed
266 in an evidently differentiated hyphal peridium. However, there are certain unisporic
267 sporocarps that, in section view, display a relatively high level of organization in the hyphal
268 coverings (e.g., MEIER & CHARVAT 1992: fig. 8). Moreover, we have to consider the

269 possibility that fossil lineages of glomeromycotan fungi, as well as fossil representatives of
270 present-day lineages, have existed that were characterized by structural features unknown in
271 any present-day representative.

272 Finally, an interesting specimen of *Sporocarpon asteroides* has been figured by
273 MCLEAN (1922: pl. VIII, fig. 9) and described as “containing a spherical structure apparently
274 dehiscing and extruding a mass of what appear to be small spores united by filaments.” It is
275 more likely, however, that the spherical structure and the alleged spores do not belong
276 together. The former appears to correspond to the sac-like vesicle seen in the specimens
277 described here, whereas the latter probably represent an intrusive organism that had entered *S.*
278 *asteroides* and produced its own thallus and reproductive units. Support for this view comes
279 from abundant occurrences of spore-like bodies interconnected by filaments in Carboniferous
280 plant parts preserved in coal balls and chert (DOTZLER et al. 2011; KRINGS et al. 2010a,
281 2011b; STRULLU-DERRIEN et al. 2021). Moreover, there is evidence of mycoparasitism in
282 *Dubiocarpon* which demonstrates that Carboniferous fungal “sporocarps” were invaded by
283 other organisms and used as a habitat (KRINGS et al. 2011a).

284

285 **5 Conclusions**

286 Fossil fungal “sporocarps” continue to invite speculation as to their biological nature and
287 systematic affinities. Although there are morphological differences that have been used to
288 classify the “sporocarps” into a number of fossil genera and species, there are also basic
289 similarities, which could mean that they all belong to the same higher taxonomic category.
290 Both the Ascomycota and zygomycete fungi have been discussed in this respect, but neither
291 of these attributions has received undivided approval. The specimens presented in this study
292 strongly suggest that the “sporocarp” species *Sporocarpon asteroides* was a unisporic
293 glomeromycotan sporocarp. This does not necessarily mean, however, that the other
294 *Sporocarpon* species, let alone the other “sporocarp” genera, were also Glomeromycota.
295 Rather, we consider it likely that the assemblage of fossils subsumed under fossil fungal
296 “sporocarps” is heterogeneous and includes a range of biologically different structures. Our
297 knowledge of these structures in general continues to be incomplete, and there is need for
298 additional specimens to be discovered, thoroughly investigated, and documented. The present
299 study demonstrates that new features of fossil fungal “sporocarps” can still be found, and can
300 be used to refine current interpretations of these common but as yet enigmatic fossils, and
301 eventually take us to the core of their biological nature and affinities.

302

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309

310

311 **6 References**

312 BAXTER, R.W. (1960): *Sporocarpon* and allied genera from the American Pennsylvanian. –
313 *Phytomorphology*, **10**: 19–25.

314 BAXTER, R.W. (1975): Fossil fungi from American Pennsylvanian coal balls. – University of
315 Kansas Paleontological Contributions, **77**: 1–6.

316 BONFANTE, P. & DESIRÒ, A. (2017): Who lives in a fungus? The diversity, origins and
317 functions of fungal endobacteria living in Mucoromycota. – *ISME Journal*, **11**: 1727–
318 1735.

319 CARRUTHERS, W. (1873): On *Traquairia*, a radiolarian rhizopod from the coal-measures. –
320 Report of the 42nd Meeting of the British Association for the Advancement of Science;
321 held at Brighton in August 1872, p. 126; London, UK (John Murray).

322 DAVIS, B. & LEISMAN, G.A. (1962): Further observations on *Sporocarpon* and allied genera.
323 – *Bulletin of the Torrey Botanical Club*, **89**: 97–109.

324 DESIRÒ, A., SALVIOLI, A., NGONKEU, E., MONDO, S., EPIS, S., FACCIO, A., KAECH, A.,
325 PAWLOWSKA, T. & BONFANTE, P. (2014): Detection of a novel intracellular microbiome
326 hosted in arbuscular mycorrhizal fungi. – *ISME Journal*, **8**: 257– 270.

327 DESIRÒ, A., FACCIO, A., KAECH, A., BIDARTONDO, M.I. & BONFANTE, P. (2015): *Endogone*,
328 one of the oldest plant-associated fungi, host unique Mollicutes-related endobacteria. –
329 *New Phytologist*, **205**: 1464–1472.

330 DOTZLER, N., TAYLOR, T.N., GALTIER, J. & KRINGS, M. (2011): *Sphenophyllum*
331 (Sphenophyllales) leaves colonized by fungi from the Upper Pennsylvanian Grand-Croix
332 cherts of central France. – *Zitteliana A*, **51**: 3–8.

333 FURRAZOLA, E., TORRES-ARIAS, Y., THOEN, D., BERBARA, R.L.L., JOBIM, K. & GOTO, B.T.
334 (2016): *Glomus segmentatum*, rediscovery of a rare epigeous sporocarpic fungus to Cuba.
335 – *Current Research in Environmental & Applied Mycology*, **6**: 143–149.

- 336 GALTIER, J. (1997): Coal-ball floras of the Namurian-Westphalian of Europe. – Review of
337 Palaeobotany and Palynology, **95**: 51–72.
- 338 GAMPER, H.A., WALKER, C. & SCHÜBLER, A. (2009): *Diversispora celata* sp. nov.: molecular
339 ecology and phylotaxonomy of an inconspicuous arbuscular mycorrhizal fungus. – New
340 Phytologist, **182**: 495–506.
- 341 GIOVANNETTI, M., AVIO, L. & SALUTINI, L. (1991): Morphological, cytochemical, and
342 ontogenetic characteristics of a new species of vesicular-arbuscular mycorrhizal fungus. –
343 Canadian Journal of Botany, **68**: 161–167.
- 344 GUPTA, M.M. (2017): Differential response of arbuscular mycorrhizal sporocarps in long-
345 term trap culturing. – Phytomorphology, **67**: 1–11.
- 346 HARPER, C.J., WALKER, C., SCHWENDEMANN, A.B., KERP, H. & KRINGS, M. (2020):
347 *Archaeosporites rhyniensis* gen. et sp. nov. (Glomeromycota, Archaeosporaceae), from
348 the Lower Devonian Rhynie chert – a fungal lineage morphologically unchanged from
349 more than 400 million years. – Annals of Botany, **126**: 915–928.
- 350 HASS, H. & ROWE, N.P. (1999): Thin sections and wafering. – In: T.P. JONES & N.P. ROWE
351 (Eds.): Fossil Plants and Spores: Modern Techniques, p. 76–81; London, UK (The
352 Geological Society).
- 353 HUTCHINSON, S.A. (1955): A review of the genus *Sporocarpion* Williamson. – Annals of
354 Botany, **19**: 425–435.
- 355 HUTCHINSON, S.A. & WALTON, J. (1953): A presumed ascomycete from the Upper
356 Carboniferous. – Nature, **172**: 36–37.
- 357 JOBIM, K., BŁASZKOWSKI, J., NIEZGODA, P., KOZŁOWSKA, A., ZUBEK, S., MLECZKO, P.,
358 CHACHUŁA, P., ISHIKAWA, N.K. & GOTO, B.T. (2019): New sporocarpic traxa in the
359 phylum Glomeromycota: *Sclerocarpum amazonicum* gen. et sp. nov. in the family
360 Glomeraceae (Glomerales) and *Diversispora sporocarpica* sp. nov. in the
361 Diversisporaceae (Diversisporales). – Mycological Progress, **18**: 369–384.
- 362 KHADE, S.W. (2011): New characteristics for morphotaxonomy of *Gigaspora* species
363 belonging to arbuscular mycorrhizal fungi. – Journal of Plant Development, **18**: 71–80.
- 364 KRINGS, M. (2022): An unusual specimen of the enigmatic fungal reproductive unit *Windipila*
365 *spinifera* from the Lower Devonian Rhynie cherts of Scotland. – Zitteliana, **96**: 145–152.
- 366 KRINGS, M. & HARPER, C.J. (2017): A mantled fungal reproductive unit from the Lower
367 Devonian Windyfield chert, Scotland, with prominent spines and otherwise shaped
368 projections extending out from the mantle. – Neues Jahrbuch für Geologie und
369 Paläontologie, Abhandlungen, **285**: 201–211.

- 370 KRINGS, M. & HARPER, C.J. (2020): Morphological diversity of fungal reproductive units in
371 the Lower Devonian Rhynie and Windyfield cherts, Scotland: A new species of the genus
372 *Windipila*. – *PalZ*, **94**: 619–632.
- 373 KRINGS, M. & TAYLOR, T.N. (2012): Fungal reproductive units enveloped in a hyphal mantle
374 from the Lower Pennsylvanian of Great Britain, and their relevance to our understanding
375 of Carboniferous fungal “sporocarps”. – *Review of Palaeobotany and Palynology*, **175**:
376 1–9.
- 377 KRINGS, M. & TAYLOR, T.N. (2014): A mantled fungal reproductive unit from the Lower
378 Devonian Rhynie chert that demonstrates Carboniferous “sporocarp” morphology and
379 development. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **273**:
380 197–205.
- 381 KRINGS, M. & TAYLOR, T.N. (2015a): A fungal reproductive unit from the Lower Devonian
382 Rhynie chert (Aberdeenshire, Scotland) that demonstrates an unusual hyphal investment
383 pattern. – *Scottish Journal of Geology*, **51**: 131–139.
- 384 KRINGS, M. & TAYLOR, T.N. (2015b): Mantled fungal reproductive units in land plant tissue
385 from the Lower Devonian Rhynie chert. – *Bulletin of Geosciences*, **90**: 1–6.
- 386 KRINGS, M., DOTZLER, N., TAYLOR, T.N. & GALTIER, J. (2010a): A fungal community in plant
387 tissue from the Lower Coal Measures (Langsettian, Lower Pennsylvanian) of Great
388 Britain. – *Bulletin of Geosciences*, **85**: 679–690.
- 389 KRINGS, M., DOTZLER, N., TAYLOR, T.N. & GALTIER, J. (2010b): Microfungi from the upper
390 Visean (Mississippian) of central France: Structure and development of the sporocarp
391 *Mycocarpon cinctum* nov. sp. – *Zitteliana A*, **50**: 127–135.
- 392 KRINGS, M., DOTZLER, N. & TAYLOR, T.N. (2011a): Mycoparasitism in *Dubiocarpon*, a fungal
393 sporocarp from the Carboniferous. – *Neues Jahrbuch für Geologie und Paläontologie*,
394 *Abhandlungen*, **262**: 241–245.
- 395 KRINGS, M., TAYLOR, T.N., DOTZLER, N. & GALTIER, J. (2011b): Fungal remains in cordaite
396 (Cordaitales) leaves from the Upper Pennsylvanian of central France. – *Bulletin of*
397 *Geosciences*, **86**: 777–784.
- 398 KRINGS, M., TAYLOR, T.N., TAYLOR, E.L., DOTZLER, N. & WALKER, C. (2011c): Arbuscular
399 mycorrhizal-like fungi in Carboniferous arborescent lycopsids. – *New Phytologist*, **191**:
400 311–314.
- 401 KRINGS, M., TAYLOR, T.N. & WHITE, J.F. (2011d): Fungal sporocarps from the Carboniferous:
402 An unusual specimen of *Traquairia*. – *Review of Palaeobotany and Palynology*, **168**: 1–
403 6.

404 KRINGS, M., TAYLOR, T.N., DOTZLER, N. & PERSICHINI, G. (2012): Fossil fungi with
405 suggested affinities to the Endogonaceae from the Middle Triassic of Antarctica. –
406 Mycologia, **104**: 835–844.

407 KRINGS, M., TAYLOR, T.N. & DOTZLER, N. (2013a): Fossil evidence of the zygomycetous
408 fungi. – Persoonia, **30**: 1–10.

409 KRINGS, M., WHITE, J.F., DOTZLER, N. & HARPER, C.J. (2013b): A putative zygomycetous
410 fungus with mantled zygosporangia and apposed gametangia from the Lower Coal
411 Measures (Carboniferous) of Great Britain. – International Journal of Plant Sciences,
412 **174**: 269–277.

413 KRINGS, M., TAYLOR, T.N., TAYLOR, E.L., KERP, H. & DOTZLER, N. (2014): First record of a
414 fungal “sporocarp” from the Lower Devonian Rhynie chert. – Palaeobiodiversity and
415 Palaeoenvironments, **94**: 221–227.

416 KRINGS, M., TAYLOR, T.N., DOTZLER, N. & HARPER, C.J. (2016): Morphology and
417 ontogenetic development of *Zwergimyces vestitus*, a fungal reproductive unit enveloped
418 in a hyphal mantle from the Lower Devonian Rhynie chert. – Review of Palaeobotany
419 and Palynology, **228**: 47–56.

420 LALICA, M.A.K. & TOMESCU, A.M.F. (2022): The early fossil record of glomeromycete fungi:
421 New data on spores associated with early tracheophytes in the Lower Devonian (Emsian;
422 c. 400 Ma) of Gaspé (Quebec, Canada). – Review of Palaeobotany and Palynology, **298**:
423 ID104590.

424 MCLEAN, R.C. (1922): On the fossil genus *Sporocarpon*. – Annals of Botany, **36**: 71–90.

425 MEIER, R. & CHARVAT, I. (1992): Peridial development in *Glomus mosseae* (Glomaceae). –
426 American Journal of Botany, **79**: 928–936.

427 PIROZYNSKI, K.A. (1976): Fossil fungi. – Annual Review of Phytopathology, **14**: 237–246.

428 REDECKER, D. & RAAB, P. (2006): Phylogeny of the Glomeromycota (arbuscular mycorrhizal
429 fungi): recent developments and new gene markers. – Mycologia, **98**: 885–895.

430 SCOTT, A.C. & REX, G. (1985): The formation and significance of Carboniferous coal balls. –
431 Philosophical Transactions of the Royal Society of London B: Biological Sciences, **311**:
432 123–137.

433 SCOTT, R. (1911): On *Traquairia*. – Annals of Botany, **25**: 459–467.

434 STRULLU-DERRIEN, C., GÈZE, M., SPENCER, A.R.T., DE FRANCESCHI, D., KENRICK, P.,
435 SELOSSE, M.A. & KNOLL, A.H. (2021): An expanded diversity of oomycetes in
436 Carboniferous forests: Reinterpretation of *Oochytrium lepidodendri* (Renault 1894) from
437 the Esnost chert, Massif Central, France. – PLoS ONE, **16**: e0247849.

438 STUBBLEFIELD, S.P. & BANKS, H.P. (1983): Fungal remains in the Devonian trimerophyte
439 *Psilophyton dawsonii*. – American Journal of Botany, **70**: 1258–1261.

440 STUBBLEFIELD, S.P. & TAYLOR, T.N. (1983): Studies of Paleozoic fungi. I. The structure and
441 organization of *Traquairia* (Ascomycota). – American Journal of Botany, **70**: 387–399.

442 STUBBLEFIELD, S.P., TAYLOR, T.N., MILLER, C.E. & COLE, G.T. (1983): Studies in
443 Carboniferous fungi. II. The structure and organization of *Mycocarpon*, *Sporocarpon*,
444 *Dubiocarpon*, and *Coleocarpon* (Ascomycotina). – American Journal of Botany, **70**:
445 1482–1498.

446 STUBBLEFIELD, S.P., TAYLOR, T.N. & MILLER, C.E. (1985): Studies of Paleozoic fungi. IV.
447 Wall ultrastructure of fossil endogonaceous chlamydospores. – Mycologia, **77**: 83–96.

448 TAYLOR, T.N. & WHITE, J.F. Jr. (1989): Fossil fungi (Endogonaceae) from the Triassic of
449 Antarctica. – American Journal of Botany, **76**: 389–396.

450 TAYLOR, T.N., GALTIER, J. & AXSMITH, B.J. (1994): Fungi from the Lower Carboniferous of
451 central France. – Review of Palaeobotany and Palynology, **83**: 253–260.

452 TAYLOR, T.N., KRINGS, M. & TAYLOR, E.L. (2015): Fossil Fungi. 1st Edition – xv + 382 pp.;
453 Amsterdam, Boston, Heidelberg, London (Elsevier/Academic Press Inc.).

454 TOOMER, K.H., CHEN, X., NAITO, M., MONDO, S.J., DEN BAKKER, H.C., VANKUREN, N.W.,
455 LEKBERG, Y., MORTON, J.B. & PAWLOWSKA, T.E. (2015): Molecular evolution patterns
456 reveal life history features of mycoplasma-related endobacteria associated with
457 arbuscular mycorrhizal fungi. – Molecular Ecology, **24**: 3485–3500.

458 VENICE, F., CHIALVA, M., DOMINGO, G., NOVERO, M., CARPENTIERI, A., SALVIOLI DI
459 FOSSALUNGA, A., GHIGNONE, S., AMORESANO, A., VANNINI, C., LANFRANCO, L. &
460 BONFANTE, P. (2021): Symbiotic responses of *Lotus japonicus* to two isogenic lines of a
461 mycorrhizal fungus differing in the presence/absence of an endobacterium. – The Plant
462 Journal, **108**: 1547–1564.

463 WAGNER, C.A. & TAYLOR, T.N. (1981): Evidence for endomycorrhizae in Pennsylvanian age
464 plant fossils. – Science, **212**: 562–563.

465 WAGNER, C.A. & TAYLOR, T.N. (1982): Fungal chlamydospores from the Pennsylvanian of
466 North America. – Review of Palaeobotany and Palynology, **37**: 317–328.

467 WALKER, C., HARPER, C.J., BRUNDRETT, M.C. & KRINGS, M. (2018): Looking for arbuscular
468 mycorrhizal fungi (AMF) in the fossil record – an illustrated guide. – In: M. KRINGS, C.J.
469 HARPER, N.R. CÚNEO & G.W. ROTHWELL (Eds.): Transformative Paleobotany:
470 Commemorating the Life and Legacy of Thomas N. Taylor, pp. 481–518; London
471 (Elsevier/Academic Press Inc.).

- 472 WALKER, C., HARPER, C.J., BRUNDRETT, M. & KRINGS, M. (2021): The Early Devonian
473 fungus *Mycokidstonia sphaerialoides* from the Rhynie chert is a member of the
474 Ambisporaceae (Glomeromycota, Archaeosporales), not an ascomycete. – Review of
475 Palaeobotany and Palynology, **287**: ID104384.
- 476 WHITE, J.F. Jr. & TAYLOR, T.N. (1988): Triassic fungus from Antarctica with possible
477 ascomycetous affinities. – American Journal of Botany, **75**: 1495–1500.
- 478 WHITE, J.F. Jr., TAYLOR, T.N. (1989a): An evaluation of sporocarp structure in the Triassic
479 fungus *Endochaetophora*. – Review of Palaeobotany and Palynology, **61**: 341–345.
- 480 WHITE, J.F. Jr. & TAYLOR, T.N. (1989b): Triassic fungi with suggested affinities to the
481 Endogonales (Zygomycotina). – Review of Palaeobotany and Palynology, **61**: 53–61.
- 482 WHITE, J.F. Jr. & TAYLOR, T.N. (1991): Fungal sporocarps from the Triassic peat deposits in
483 Antarctica. – Review of Palaeobotany and Palynology, **67**: 229–236.
- 484 WILLIAMSON, W.C. (1878): On the organization of the fossil plants of the coal-measures. Part
485 IX. – Philosophical Transactions of the Royal Society of London, **169**: 319–364.
- 486 WILLIAMSON, W.C. (1880): On the organization of the fossil plants of the coal-measures. Part
487 10 – including an examination of the supposed radiolarians of the Carboniferous rocks. –
488 Philosophical Transactions of the Royal Society, London, **B171**: 493–539.
- 489 WILLIAMSON, W.C. (1883): On the organization of the fossil plants of the coal-measures: –
490 Part XII. – Philosophical Transactions of the Royal Society of London, **174**: 459–475.
- 491 YAMAMOTO, K., TAKASHIMA, Y., SUYAMA, M., MASAKI, T. & DEGAWA, Y. (2019): A
492 sporocarpic species of Glomeromycotina, *Glomus radiatum* new to Japan. – Truffology,
493 **2**: 6–9.

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519 **Figure captions**

520

521 **Fig. 1.** New specimens of the Carboniferous fungal “sporocarp” *Sporocarpon asteroides* from
522 the Lower Coal Measures of Great Britain. **A.** Cluster of four specimens (labelled I–IV) in
523 coal ball matrix rich in organic debris; bar = 300 µm. **B, C₁.** Cavities of specimens I and II in
524 higher magnification (in the median longitudinal section view), showing contents; sv = sac-
525 like vesicle, sce = squat-columnar component, w1 and w2 = outer walls, cs = central sphere
526 bounded by a layered wall proper; bars = 100 µm. **C₂.** Lower part of specimen II, same
527 magnification as Fig. 1C₁ but slightly different focal plane, showing squat-columnar
528 component apparently continuing into some structure on the “sporocarp” outside (arrows); bar
529 = 100 µm. **D.** Cavity of specimen III, containing an empty sac-like vesicle (arrow); bar = 100
530 µm. **E.** Detail of Fig. 1C₁, focusing on proximal portion of investment and compound
531 structure; fs = layer of filament- or fiber-like structures between investment and vesicle wall
532 (sv); sce = squat-columnar component; bar = 20 µm.

533

534 **Fig. 2.** New specimens of the Carboniferous fungal “sporocarp” *Sporocarpon asteroides* from
535 the Lower Coal Measures of Great Britain. **A, B.** Proximal portions of cavities of specimens I
536 and II (in longitudinal section views) in normal (A₁, B₁) and, in a slightly different focal
537 plane, inverted (A₂, B₂) light, showing sac-like vesicle (sv) and compound structure, the latter
538 comprised of squat-columnar component (sce), two outer walls (w1, w2), and central sphere
539 (cs) bounded by layered wall proper; bars = 50 µm. **C.** Detail of Fig. 1B, showing finely

540 granular wall of sac-like vesicle (sv) and portion of investment (in); bar = 20 μ m. **D.** Detail of
541 Fig. 1B, focusing on layered wall of central sphere (csw), sac-like vesicle (sv), and investment
542 (in); bar = 30 μ m.

543

544 **Fig. 3.** *Sporocarpon asteroides* in vivo, reconstruction. Median longitudinal section, showing
545 the characteristic pseudoparenchymatous investment (in), the cavity perimeter wall with its
546 finely granular innermost layer (cpw), two spore walls w1 and w2 that are continuous with
547 the wall of the subtending hypha, and a spore wall proper (csw) that formed de novo.

548