



UNICA

UNIVERSITÀ
DEGLI STUDI
DI CAGLIARI



Università di Cagliari

UNICA IRIS Institutional Research Information System

This is the Author's [*accepted*] manuscript version of the following contribution:

Gougeon R, Néraudeau D, Loi A, and Poujol M., 2021. New insights into the early evolution of horizontal spiral trace fossils and the age of the Brioverian series (Ediacaran–Cambrian) in Brittany, NW France. *Geological Magazine*, 1-11

The publisher's version is available at:

<https://doi.org/10.1017/S0016756820001430>

When citing, please refer to the published version.

1 **Title:** New insights into the early evolution of horizontal spiral trace fossils and the age of the
2 Brioverian series (Ediacaran–Cambrian) in Brittany, NW France

3 **Category of submission:** Original Article (Special Issue on the Ediacaran-Cambrian
4 transition)

5 **Authors:** Gougeon, R.^{1,2}, Néraudeau, D.², Loi, A.³ & Poujol, M.²

6 **Affiliations:**

7 ¹Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK, S7N 5E2,
8 Canada

9 ²Univ Rennes, CNRS, Géosciences Rennes - UMR 6118, F-35000 Rennes, France

10 ³Dipartimento di Scienze Chimiche e Geologiche, Università di Cagliari, Cittadella
11 Universitaria, 09042 Monserrato, Italy

12 **Short title:** Early evolution of horizontal spiral trace fossils

13 **Corresponding author:** gougeon.romain@gmail.com

14

15 **Abstract:** In northwestern France, the Brioverian is a thick siliciclastic succession
16 deposited during the Cadomian cycle (*ca.* 750-540 Ma). In the uppermost Brioverian beds,
17 previous studies unraveled an assemblage dominated by simple horizontal trace fossils
18 associated with microbially-stabilized surfaces. Here, we report additional one-way
19 planispiral trace fossils from Crozon (Finistère, Brittany), Montfort-sur-Meu and St-Gonlay
20 (Ille-et-Vilaine, Brittany). Planispiral trace fossils are unusual in the Ediacaran and the
21 Cambrian worldwide and were previously suspected to first appear in the deep-sea by the
22 Ordovician. After reviewing the literature on horizontal spiral trace fossils from the Ediacaran
23 to the Recent, a Cambrian pool is identified on marginal- to shallow-marine settings, while an
24 Ordovician-Recent trend formed in the deep-marine realm. These results indicate that an
25 onshore-offshore migration of horizontal spiral trace fossils took place from the Cambrian to
26 the Ordovician similarly to what happened in other graphoglyptids. In addition, the age of the
27 uppermost Brioverian beds (Ediacaran or Cambrian) is still a pending question, despite the
28 presence of fossils. Here, we report two new U-Pb detrital zircon dating from sandstone
29 samples in St-Gonlay, giving maximum deposition ages of 551 ± 7 Ma and 540 ± 5 Ma.
30 Although these results do not discard an Ediacaran age for the uppermost Brioverian beds, we
31 believe an early Cambrian age (Fortunian and/or Cambrian Age 2) is more appropriate
32 because they corroborate previous radiometric dating in Brittany, Mayenne and Normandy as
33 well as novel observations on trace fossils (*i.e.* presence of treptichnids, *Cochlichnus* and
34 planispiral trace fossils).

35 **Keywords (4-7):** Brioverian, Ediacaran-Cambrian, trace fossils, planispirals, U-Pb dating

36 1. Introduction

37 The potential of ichnology to decipher macro-evolutionary trends in animal behavior
38 has a long-undergone history. Compilation of ichnological data was a major part of the work
39 of A. Seilacher and P. Crimes. Seilacher focussed on the variety of graphoglyptid trace fossils
40 from the deep-sea (*i.e.* patterned trace fossils forming nets, regular meanders and spirals),
41 aiming to understand their environmental adaptation through time (*e.g.* size changes,
42 functional optimization; Seilacher, 1974, 1977, 1986). Seilacher (1956) was the first to
43 recognize the potential of trace fossils to delineate the Precambrian-Cambrian boundary;
44 Crimes (1987, 1992*a*, 1994) extended this idea by reviewing worldwide literature and
45 developed an ichnostratigraphic scheme that helped defining the Cambrian GSSP (Narbonne
46 *et al.*, 1987; Brasier *et al.*, 1994). In Crimes' comprehensive work, regular horizontal spiral
47 trace fossils are consistently absent from the Ediacaran and the Cambrian (Crimes, 1987,
48 1992*a*, 1992*b*, 1994), only appearing by the Ordovician in the deep-marine realm (Crimes *et*
49 *al.*, 1974, 1992; see also Pickerill, 1980; Xia *et al.*, 1987). Crimes suspected that most deep-
50 marine graphoglyptids originated in shallow-marine environments during the Cambrian
51 (Crimes, 1987; Crimes & Anderson, 1985; Crimes & Fedonkin, 1994; see also Orr, 2001), but
52 the absence of regular planispiral trace fossils in the Cambrian was then problematic (Crimes
53 *et al.*, 1992).

54 The Ediacaran-Cambrian transition (*ca.* 540 Ma) was the time of striking changes in
55 Earth ecosystems. Ediacaran seafloors were dominated by microbially-stabilized surfaces on
56 which epifaunal and very-shallow infaunal grazers thrived (Seilacher & Pflüger, 1994;
57 Gehling, 1999). Macroscopic animals of the earliest Cambrian started to disrupt the sediment
58 at depth, affecting the substrate ventilation (*e.g.* Mángano & Buatois, 2014; Gougeon *et al.*,
59 2018*a*), trophic webs (*e.g.* Bottjer *et al.*, 2000; Meysman *et al.*, 2006) and geochemical cycles
60 (*e.g.* Logan *et al.*, 1995; Canfield & Farquhar, 2009; Boyle *et al.*, 2018). In northwestern

61 France, the Brioverian of central Brittany is a thick siliciclastic succession that was deposited
62 during the Cadomian cycle (*ca.* 750-540 Ma); despite the report of fossils since the 19th
63 century, the exact position of its uppermost beds within the Ediacaran or the Cambrian is a
64 long-standing conundrum. Recently, new investigations unraveled a unique assemblage of
65 trace and body fossils in the vicinity of Rennes (Néraudeau *et al.*, 2016, 2019; Gougeon *et al.*,
66 2018b, 2019). Trace fossils are dominantly simple, horizontal and associated with
67 microbially-stabilized surfaces; of these, planispirals stand as a surprising discovery.

68 The aim of this study is threefold: (1) to describe a new assemblage of planispiral trace
69 fossils from the Brioverian of northwestern France; (2) to place this assemblage within a
70 macro-evolutionary framework and to interpret its significance; and (3) to provide new
71 radiometric dating and discuss the age of the uppermost Brioverian deposits.

72 **2. General background**

73 2.a. Geological setting and previous work

74 The Brioverian (*ca.* 660-540 Ma; Le Corre *et al.*, 1991; Guerrot *et al.*, 1989, 1992) is
75 an informal name given to a thick sedimentary succession deposited during the Cadomian
76 cycle (*ca.* 750-540 Ma) in northwestern France (Figs. 1a, 1b; Chantraine *et al.*, 2001; Ballèvre
77 *et al.*, 2009, 2013). In Brittany, the Brioverian lies unconformably on an Icartian basement
78 (*ca.* 2200-1800 Ma) and is unconformably overlain either by the Ordovician Red Bed Series
79 ('Séries Rouges Initiales') or by the Ordovician Armorican Sandstone ('Grès Armoricain';
80 Cogné, 1959; Bonjour & Chauvel, 1988; D'Lemos *et al.*, 1990; Le Corre *et al.*, 1991). The
81 terrigenous siliciclastic sediments of the Brioverian resulted from the erosion of the Cadomian
82 belt in northern Brittany and accumulated in a marginal, within-plate basin in central Brittany
83 (Denis, 1988; Dissler *et al.*, 1988; Rabu *et al.*, 1990; Dabard *et al.*, 1996). Locally,
84 carbonaceous cherts, limestones and igneous intrusions have also been reported (Denis &

85 Dabard, 1988; Dabard, 1990, 2000; Chantraine *et al.*, 2001). On a regional scale, the
86 correlation of the Brioverian sedimentary deposits is hindered by the discontinuous
87 outcropping, the facies changes, the absence of biostratigraphic markers and the metamorphic
88 overprint from the Devonian-Carboniferous Variscan orogeny (Denis & Dabard, 1988;
89 D’Lemos *et al.*, 1990; Le Corre *et al.*, 1991; Ballèvre *et al.*, 2013). While traditionally
90 interpreted as deeper-marine turbiditic deposits (Dangeard *et al.*, 1961; Darboux, 1973; Denis,
91 1988; Louvel, 1988; Trautmann *et al.*, 1999), the Brioverian sedimentary beds also show
92 evidence of shallow-marine storm-influenced settings (Dabard & Loi, 1998; Dabard & Simon,
93 2011) and marginal-marine tidally-influenced conditions (Graindor 1957; Dabard, 1990,
94 2000; Néraudeau *et al.*, 2019).

95 [insert Figure 1]

96 Fossils recovered from the Brioverian are algal microfossils in cherts and limestones
97 (Cayeux, 1894; Deflandre, 1955; Chauvel & Schopf, 1978; Chauvel & Mansuy, 1981;
98 Mansuy & Vidal, 1983), macroscopic body fossils of unknown origin (Néraudeau *et al.*, 2019;
99 Néraudeau & Gougeon, in review) and trace fossils. Ichnofossils were first discovered in the
100 late 19th century (Lebesconte, 1886) but did not draw attention of the scientific community for
101 a long time. Recently, new investigations in the vicinity of Rennes (Fig. 1b) unraveled an
102 assemblage dominated by simple horizontal grazing trails (*Circulichnis*, *Cochlichnus*, *Gordia*,
103 *Helminthoidichnites*, *Helminthopsis*), passively-filled horizontal burrows (*Palaeophycus*),
104 horizontal spiral trace fossils (*Spirodesmos*) and possible probing burrows (treptichnids;
105 personal observations from R. G. and D. N.; Néraudeau *et al.*, 2016; Gougeon *et al.*, 2018b,
106 2019; Néraudeau & Gougeon, in review). In addition, microbially-textured surfaces (MISS of
107 Noffke *et al.*, 2001) are common both in fossiliferous and azoic intervals (Lebesconte, 1886;
108 Gougeon *et al.*, 2018b).

109 The age of the uppermost Brioverian sedimentary beds has been highly debated in
110 Brittany, Normandy and Mayenne (Fig. 1b). In Brittany, the overlying Red Bed Series gave
111 an age of 472 ± 5 Ma (Rb-Sr dating from volcanic rocks; Auvray *et al.*, 1980), 473 ± 15 Ma
112 (U-Pb dating on volcanic rocks; Bonjour *et al.*, 1987), 465 ± 1 Ma (U-Pb dating from volcanic
113 rocks; Bonjour *et al.*, 1988; Bonjour & Odin, 1989) and 486 ± 28 Ma (Pb-Pb dating from
114 volcanic rocks; Guerrot *et al.*, 1992), placing these beds within the Ordovician period (*contra*
115 McMahon *et al.*, 2017; Went, 2017). In the westernmost part of Brittany (Crozon area; Fig.
116 1b), Guerrot *et al.* (1992) obtained an age of 543 ± 18 Ma (Pb-Pb dating) for a tuff
117 interlayered within the Brioverian beds while a maximum deposition age of 546 ± 2 Ma (U-
118 Pb dating) has been obtained by Ballouard *et al.* (2018) from detrital zircon grains extracted
119 from a sandstone. Around Rennes (Fig. 1b), detrital zircon grains gave a maximum age of
120 deposition of *ca.* 550 Ma (U-Pb dating from sandstone and siltstone; Gougeon *et al.*, 2018b);
121 however, five zircon grains dated at 532.1 ± 3.9 Ma which were problematic to interpret
122 (Gougeon *et al.*, 2018b). In Normandy, the Brioverian sediments were deposited in a different
123 palaeogeographic domain than in central Brittany as they are separated by the North-
124 Armorican Shear Zone (Fig. 1b; Chantraine *et al.*, 1982; Guerrot *et al.*, 1992). In this domain,
125 granitoid intrusions within the Brioverian sediments have been dated at 540 ± 10 Ma (U-Pb
126 dating on monazite; Pasteels & Doré, 1982). In Mayenne, where the Brioverian is in
127 continuity with its equivalent in central Brittany (Fig. 1b), radiometric dating on zircon grains
128 yielded an age of 540 ± 17 Ma (tuff and detrital horizons; Guerrot *et al.*, 1992).

129 2.b. Outcrops under study and depositional environments

130 The best outcrop is certainly at ‘La Lammerais’ in St-Gonlay (Fig. 1b): slates with
131 fossils are stacked in a pile of about two metres high and fifty metres long. These slates were
132 extracted from a pit that was exploited by locals to build houses and pathways decades ago;
133 unfortunately, the pit is now covered with vegetation and therefore impossible to sample *in*

134 *situ*. Slates mostly represent siltstone and rare very-fine- to fine-grained sandstone. One loose
135 sandstone sample has been collected for U-Pb dating, coming from a nearby agricultural field.
136 Sedimentary structures are parallel-lamination organised in siltstone-sandstone bundles (*i.e.*
137 rhythmite-like; Néraudeau *et al.*, 2019, Fig. 3), current-ripples (Néraudeau *et al.*, 2019, Fig.
138 2), tool-marks/spindle-shaped flute-marks, possible load-casts and microbial mats preserved
139 on surfaces and in cross-sections (Gougeon *et al.*, 2018b, Figs. 4, 7).

140 In St-Gonlay, another outcrop has been investigated at ‘Le Lorinou’, located 1.4
141 kilometres to the east of ‘La Lammerais’. This outcrop is very poor in trace fossils (no spiral
142 trace fossils were found there) but beds are preserved *in situ* and a sandstone sample was
143 collected for U-Pb zircon dating.

144 In Montfort-sur-Meu (Fig. 1b), ‘Le Bois-du-Buisson’ is a small outcrop (about three
145 metres high and ten metres long) with extensive vegetation covering most of the exposure.
146 However, a few siltstone beds are accessible and reveal fresh surfaces with trace fossils.
147 Sedimentary structures are parallel-lamination organised in siltstone-sandstone bundles (*i.e.*
148 rhythmite-like similar to what is found at ‘La Lammerais’) and microbial mats preserved on
149 surfaces.

150 In addition, Montfort-sur-Meu is the host of the classic outcrop of ‘Les Grippeaux’,
151 where P. Lebesconte recovered fossils for the first time in the late 19th century (Lebesconte,
152 1886; Gougeon *et al.*, 2018b). Nowadays, the pit is secured by a fence preventing any access.
153 Multiple samples were collected in the late 19th and early 20th century by P. Lebesconte, F.
154 Kerforne and other geologists; they are housed at the Geological Institute of the University of
155 Rennes 1 and at the Museum of Natural History of Nantes and are available for study.
156 Sedimentary structures are microbial mats observed on surfaces.

157 The outcrop in Crozon (Fig. 1b) is located on the coastal cliff at ‘La Plage-du-
158 Goulien’. This outcrop has not been visited by the authors and the only trace fossil discovered
159 was reported by E. Hanson in 2014 (pers. comm.). The sedimentology of the Brioverian from
160 the Bay of Douarnenez and the Cove of Dinan (both in the vicinity of Crozon) has been
161 studied in two doctoral thesis (Darboux, 1973; Denis, 1988). The succession displays parallel-
162 laminated/bedded sandstone and siltstone with flute-casts, load-casts, tool-marks, rip-up
163 clasts, carbonate concretions, normal and reverse grading, convolution, flame structures and
164 current, wave and climbing ripples. Both authors interpreted the succession as deposited by
165 turbidites located either below the limit of the storm wave-base action, or deeper in an abyssal
166 plain. However, Denis (1988) noted some inconsistencies to that model, notably the presence
167 of oscillatory flow structures, lenticular bedding (Facies 3 of Denis, 1988) and mud-drapes
168 that are more typical of shallower environments.

169 In Montfort-sur-Meu and St-Gonlay, the dominance of siltstone intercalated with
170 laminated very-fine-grained sandstone and the record of rhythmite-like bundles, current
171 ripples and tool/flute-marks argue for a mud- to mixed-flat intertidal depositional environment
172 (*cf.* Nio & Yang, 1991; Tessier *et al.*, 1995; Dalrymple, 2010). This conclusion is
173 strengthened by observation in Chanteloup and Nouvoitou (both in the vicinity of Rennes),
174 where a sandstone facies displays mudstone drapes within fine-grained sandstone samples
175 (*i.e.* flaser lamination; personal observations from R. G, A. L. and D. N.); these areas could
176 represent the seaward sand-flat of the intertidal system. Sedimentary structures made by
177 oscillatory flows (*e.g.* wave-ripples, hummocky-cross stratification) have not been observed
178 in the area so far. These conclusions are preliminary and await further support, notably from
179 Brioverian outcrops revealing bedding architecture and from more sampling of sedimentary
180 structures.

181 **3. Material & methods**

182 3.a. Terminology on planispiral trace fossils

183 This contribution focusses only on spirals formed on a horizontal plan (*i.e.*
184 planispirals). Other types of spirals with a vertical component (*e.g. Gyrolithes, Helicolithus*)
185 are three-dimensional and are not comparable with the Brioverian material. In order to
186 describe the spiral morphologies, the following terms will be used: (1) a *regular* spiral
187 maintains a constant distance in between whorls; (2) an *irregular* spiral has a variable
188 distance in between whorls; (3) a *one-way* spiral is a simple spiral with no central turnaround
189 (Seilacher, 1977; Crimes & McCall, 1995); (4) a *two-way* spiral is a double spiral with a
190 central turnaround (Seilacher, 1977; Crimes & McCall, 1995); and (5) a *bounded* spiral is an
191 irregular one-way spiral that decreases the distance in between whorls outward.

192 *Spirodesmos*, *Spirophycus* and *Spirorhaphe* are the most common planispirals from
193 the trace fossil record: however, their morphological boundaries are unclear. *Spirodesmos* is a
194 regular to irregular one-way spiral trace fossil (Geinitz, 1867; Andrée, 1920; Huckriede, 1952;
195 Xia *et al.*, 1987). For Seilacher (1977), *Spirodesmos* has a wide space in between whorls;
196 although this is clear from the type ichnospecies *S. interruptus* Andrée, 1920, *S. archimedeus*
197 Huckriede, 1952 has a narrower space in between whorls. This issue becomes critical with
198 *Spirodesmos kaihuaensis* Xia, He & Hu, 1987 and *S. spiralis* (Geinitz, 1867), both having an
199 irregular course with a variable distance in between whorls. *Spirophycus* is a regular to
200 irregular one-way spiral trace fossil that commonly grades into meanders (Heer, 1876;
201 Häntzschel, 1975). Seilacher (1977) argued that *Spirophycus* has wide strings with a
202 tubercular surface and backfilled laminae (see also Książkiewicz, 1977; but see Uchman,
203 1998). The spiral portion of *Spirophycus* (*e.g.* Heer, 1876, Pl. 66, Fig. b; Sacco, 1888, Pl. 2,
204 Fig. 14), with regular whorls distinctly spaced from each other, can however be very similar
205 to *Spirodesmos archimedeus*. *Spirorhaphe* is a regular to irregular spiral trace fossil with
206 either a one-way (*S. azteca*, *S. graeca*, *S. zumayensis*) or two-way (*S. involuta*) course

207 (Seilacher, 1977; Crimes & McCall, 1995). The inclusion of one-way spirals in *Spirorhappe*
208 is overlapping with *Spirodesmos* and *Spirophycus* morphologies which is problematic.
209 Considering these taxonomical issues (see also Crimes & Crossley, 1991; Uchman, 1998;
210 Minter & Braddy, 2009), we prefer to use informal descriptive terms (*i.e.* regular, irregular,
211 one-way, two-way) for the following study that pinpoint the morphological peculiarities of
212 planispirals.

213 3.b. U-Pb dating method

214 A classic mineral separation procedure has been applied to concentrate the zircon
215 grains for U-Pb dating. Rocks were crushed and only the powder fraction with a diameter <
216 250 μm has been kept. Heavy minerals were successively concentrated by Wilfley table,
217 heavy liquids and with an isodynamic Frantz separator. Zircon grains were then handpicked
218 under a binocular microscope to produce the most representative sampling, with the aim to
219 avoid any intentional bias (see Malusà *et al.*, 2013 and references therein). The selected grains
220 were then embedded in epoxy mounts, grounded and polished. Zircon grains were imaged by
221 cathodoluminescence (CL) using a Reliotron CL system equipped with a digital color camera
222 available in the GeOHeLiS analytical platform (University of Rennes 1).

223 U-Pb geochronology was conducted by *in situ* laser ablation inductively coupled
224 plasma mass spectrometry (LA-ICP-MS) at the GeOHeLiS analytical platform using an ESI
225 NWR193UC Excimer laser coupled to a quadrupole Agilent 7700x ICP-MS. The instrumental
226 conditions are reported in the Supplementary Table S1 while the analytical protocol can be
227 found in Manzotti *et al.* (2015). Kernel density diagrams for the analyses that are $100 \pm 10\%$
228 concordant were generated using IsoplotR (Vermeesch, 2018). When dealing with detrital
229 zircon geochronology, a minimum of 3 different ages obtained on 3 different zircon grains
230 overlapping in age at 2σ has been demonstrated to produce a statistically robust maximum
231 deposition age (Dickinson & Gehrels, 2009). The second important criteria in order to

232 determine this maximum deposition age is the degree of concordance of the individual
233 analysis used to calculate this age. Most of the authors consider all the analyses that are 90%
234 concordant or more, while some others only the analyses that are at least 95% concordant. In
235 this study, because of the complexity of one of the data set ('La Lammerais'), we decided to
236 consider only the analyses that were at least 95% concordant to calculate the maximum
237 deposition age in order to avoid using apparent ages that could be younger than the true age
238 due to a non-negligible Pb loss.

239 3.c. Museum repository

240 From 'La Lammerais' and 'Le Bois-du-Buisson', samples were collected and
241 repositated at the Geological Institute of the University of Rennes 1 (collections Gougeon and
242 Néraudeau). Historical specimens from 'Les Grippeaux' are repositated at the Museum of
243 Natural History of Nantes (collections Barrois and Lebesconte) and the Geological Institute of
244 the University of Rennes 1 (collections Kerforne, Rolland and Rouault). The trace fossil from
245 'La Plage-du-Goulien' has not been collected and was only photographed in the field.

246 4. Results

247 4. a. Planispiral trace fossils from the Brioverian

248 The Brioverian of central Brittany contains a rich assemblage of simple horizontal
249 trails, with *Helminthoidichnites* and *Helminthopsis* being the most common forms. Originally,
250 Lebesconte (1886, Pl. 34, Fig. 7) figured a planispiral trace fossil from Montfort-sur-Meu
251 without further discussion (also figured in Louvel, 1988, Pl. 5, Fig. 15). Since then, spiral
252 trace fossils have not been reported in the Brioverian. Here, we describe three types of
253 planispiral trace fossils from the Brioverian: (1) irregular one-way spiral trails with
254 overcrossing; (2) irregular one-way spiral trails without overcrossing; and (3) regular one-way
255 spiral trails.

256 One irregular one-way spiral trail with overcrossing was recovered from 'Le Bois-du-
257 Buisson' (Fig. 2a). The trail is 1 mm wide, has 1½ whorls and is preserved in negative relief
258 (*n.b.* the preservation as epirelief or hyporelief is unknown because the slates with trace
259 fossils are not preserved *in situ*). The trail starts with a straight course, turns back and curves
260 to form a loop that clearly overcrosses its previous path; the trail ends with an irregular
261 course, following more-or-less the main loop. *Helminthoidichnites* and *Helminthopsis* are
262 found associated on the same surface. A pustular, microbially-stabilized surface is preserved
263 on a partially exposed laminae from a different vertical level. The overall morphology is
264 extremely similar to *Spirodesmos spiralis* as reported by Stepanek & Geyer (1989, Pl. 7, Fig.
265 56), where a faint self-overcrossing is observable. However, because of the self-overcrossing,
266 this form would be better referred to *Gordia*. *Gordia* ranges from the Ediacaran (Narbonne &
267 Hofmann, 1987; Vidal *et al.*, 1994) to the Holocene (Metz, 1987; Scott *et al.*, 2009).

268 [insert Figure 2]

269 Four irregular one-way spiral trails without overcrossing were recovered from 'La
270 Lammerais', 'Le Bois-du-Buisson' and 'Les Grippeaux' (Figs. 2b-d). Trails are 0.3-1 mm
271 wide, have 1¼-1¾ whorls and are preserved in positive and negative reliefs. The spiral is
272 usually stretched, and the resulting course is forming a '6' shape (Figs. 2b, c). One specimen
273 (Fig. 2d) has a different infill than the host rock and a lining; this is potentially a burrow.
274 Rarely, they are associated with *Helminthoidichnites*, small-scale branching trace fossils (cf.
275 *Pilichnus*) and small pits of uncertain affinity (Fig. 2b). They are commonly found on
276 roughened and pustular microbially-stabilized surfaces (Fig. 2b). Similar forms have been
277 referred to 'pseudo-spiral' (Carbone & Narbonne, 2014, Fig. 4.5) and *Spirodesmos spiralis*
278 (Geinitz, 1867, Pl. 6, Fig. 1; Stepanek & Geyer, 1989, Pl. 7, Figs. 55, 57). With the absence of
279 self-overcrossing and the poor extent of the whorls, this form can be referred to cf.
280 *Spirodesmos*.

281 Two regular one-way spiral trails are reported from ‘La Plage-du-Goulien’ and ‘Les
282 Grippeaux’ (Figs. 2e, f). Trails are 1-3 mm wide, have 2¼-2½ whorls and are preserved in
283 positive and negative reliefs. The distance between whorls remains constant until the last
284 whorl, where the trail detaches from the spiral system and progressively disappear. The trail
285 from ‘La Plage-du-Goulien’ has a different infill than the host rock (Fig. 2f). They are
286 associated with *Helminthopsis* and pits of uncertain affinity. The surfaces they are found on
287 are not textured. With their regular one-way spiral courses, these trails are similar to
288 *Spirodesmos*. *Spirodesmos* ranges from the Cambrian (Gougeon *et al.*, 2018b; this study) to
289 the Holocene (Kitchell *et al.*, 1978; Smith *et al.*, 2005).

290 4.b. U-Pb dating

291 For the sandstone sample from ‘La Lammerais’, 118 zircon grains were analysed
292 among which 107 analyses have a concordance of $100 \pm 10\%$. Their U (49 to 1195 ppm) and
293 Pb (6 to 493 ppm) contents as well as their Th/U ratios (0.02 to 1) are highly variable
294 (Supplementary Table S2). A first group of 12 analyses yields apparent ages between 2.8 and
295 1.06 Ga. The remaining analyses form two major peaks at 600 Ma and 550 Ma, with minor
296 peaks around 850 and 650 Ma (Fig. 1c). The 10 youngest analyses that are more than 95%
297 concordant yield a weighted average $^{206}\text{Pb}/^{238}\text{U}$ age of 540 ± 5 Ma (MSWD = 1.2) that we
298 consider as the maximum deposition age for this sandstone.

299 For the sandstone sample from ‘Le Lorinou’, 89 grains were analysed out of which 68
300 are $100 \pm 10\%$ concordant (Supplementary Table S2). They are characterized by variable U
301 and Pb contents (21 to 726 ppm and 2 and 242 ppm respectively) with Th/U ratios between
302 0.05 and 1.4. A first group of 22 zircon grains yields Neoproterozoic (2.9 Ga) to
303 Palaeoproterozoic ages (1.8 Ga) followed by a gap until the end of the Mesoproterozoic. The
304 remaining grains present apparent ages around 1000, 900, 800, 680 with a major peak around

305 600 Ma (Fig. 1c). The youngest three grains provide a weighted $^{206}\text{Pb}/^{238}\text{U}$ age of 551 ± 7 Ma
306 (MSWD = 0.009) that we consider as the maximum deposition age for this sandstone.

307 6. Discussion

308 6.a. Critical review on Ediacaran and Cambrian planispiral trace fossils

309 Several trace fossils inaccurately referred to planispirals have been reported from the
310 Ediacaran and the Cambrian. Fedonkin (1985, 1990) erected *Planispiralichnus* Fedonkin,
311 1985 and *Protospiralichnus* Fedonkin, 1985 from the Cambrian Kessyuse Formation (Fm) of
312 northern Russia. *Planispiralichnus* is made of dense, overlapping loops (Fedonkin, 1990;
313 Marusin & Kuper, 2020) while *Protospiralichnus* starts as a bounded spiral until it scribbles
314 abundantly (Fedonkin, 1990; Marusin, 2016); because of their scribbling patterns, neither of
315 them represent spirals (Buatois *et al.*, 2017). Jenkins (1995, Pl. 2, Fig. E) reported cf.
316 *Protospiralichnus* from the Ediacaran Rawnsley Quartzite of southern Australia; the
317 development of a full circle and/or a loop affiliates this form to *Circulichnis* or *Gordia* instead
318 (cf. Buatois & Mángano, 2016, Fig. 2.8e). *Multilaqueichnus* Yang & Yin, 1982 from the
319 Cambrian Jiulaodong Fm of central China has overlapping loops (Yang *et al.*, 1982, Pl. 2,
320 Fig. 1); these clearly demonstrate a scribbling with following course (*sensu* Kim, 1996) and
321 are not spirals either (*contra* Buatois *et al.*, 2017). Finally, a trace fossil from the Cambrian
322 Chapel Island Fm of eastern Canada was considered a spiral by Crimes & Fedonkin (1994,
323 Fig. 2i). This trace fossil has been observed in the field by one of the authors (R. G.) and
324 represents the scribbling burrow of a large infaunal deposit-feeder.

325 In addition, non-ichnologic structures from the Ediacaran and the Cambrian can mimic
326 planispiral trace fossils. An important debate arose with the report of Precambrian spiral
327 fossils from the Lower Vindhyan Limestone of northeastern India (Beer, 1919) and from the
328 Belt Series of northwestern USA (Walcott, 1899). Both authors mentioned a trace fossil

329 origin, an opinion followed by Seilacher (1956). However, Cloud (1968) suspected an algal
330 origin, and re-evaluation of both materials confirmed that view (Walter *et al.*, 1976;
331 Runnegar, 1991). *Arenicolites spiralis* Billings, 1872 and *Helminthoidichnites*
332 *sangshuanensis* (Du, 1986) in Yan & Liu, 1998 are certainly of similar algal affinity
333 (Hofmann, 1971; Walter *et al.*, 1990; Shaowu, 1998). Furthermore, Aceñolaza (2005)
334 reported circular structures from the Cambrian Mesón Group of northwestern Argentina and
335 erected the new ichnospecies *Spirodesmos milanai*; Minter *et al.* (2006) argued these
336 structures were formed by shrinkage cracks in matgrounds instead (*cf.* Pflüger, 1999; Eriksson
337 *et al.*, 2007; Buatois *et al.*, 2013; Sedorko *et al.*, 2019).

338 Finally, few horizontal spiral trace fossils have been reported from the Ediacaran and
339 the Cambrian. *Planispiralichnus rarus* Menasova, 2003 is a unique one-way spiral trace fossil
340 discovered in the Cambrian Khmelnytsky Fm of western Ukraine. The holotype is made of 3
341 whorls with angular segments along the course; moreover, the first two whorls are continuous
342 while the last one has discontinuous segments (Ivantsov *et al.*, 2015, Pl. 7, Figs. 4a, b). This
343 specimen possesses the key features of a spiral trace fossil and should not be affiliated to
344 *Planispiralichnus* as described by Fedonkin (1990). Jensen & Palacios (2016, Fig. 4b)
345 reported one-way spiral trace fossils from the Ediacaran-Cambrian Cijara Fm of central Spain.
346 The photographed specimen is a continuous to discontinuous trail with 2½ whorls and an
347 irregular course. Jensen & Palacios (2016) considered these spirals to be morphologically
348 comparable to *Planispiralichnus rarus*. Carbone & Narbonne (2014, Fig. 4.5) also figured an
349 irregular one-way spiral with 1¾ whorls and a continuous course from the Cambrian Ingta Fm
350 of northwestern Canada. This specimen ends with a straight course which is reminiscent of an
351 irregular spiral from the Brioverian (Fig. 2d). Finally, Runnegar (1992, Fig. 3.9) figured an
352 irregular two-way spiral transitional with a meandering trace fossil from the Ediacaran

353 Rawnsley Quartzite of southern Australia. Jensen (2003) considered this trace fossil to
354 represent *Helminthorhapse* grading into *Spirorhapse*.

355 6.b. Age of the uppermost Brioverian beds with trace fossils

356 In 'Le Lorinou' (St-Gonlay), zircon grains from a sandstone bed associated with trace
357 fossils yield a maximum deposition age of *ca.* 550 Ma, while zircon grains from a loose
358 sandstone sample in 'La Lammerais' (St-Gonlay) give a maximum deposition age of *ca.* 540
359 Ma. In Crozon, the youngest U-Pb dating on zircon grains from Brioverian tuff gave an age of
360 543 ± 18 Ma (Guerrot *et al.*, 1992), while another U-Pb dating on zircon grains from a
361 sandstone gave a maximum deposition age of 546 ± 2 Ma (Ballouard *et al.*, 2018). In
362 Montfort-sur-Meu, no radiometric dating has been done so far.

363 The current radiometric age for the base of the Cambrian is given by U-Pb dating on
364 zircon grains from tuff in southern Oman, dated at 541.0 ± 0.13 Ma (Bowring *et al.*, 2007);
365 however, recent U-Pb dating on zircon grains from tuff in southern Namibia constrained this
366 age within a 538.6-538.8 Ma interval instead (Linnemann *et al.*, 2019). If we consider a
367 radiometric age of *ca.* 540 Ma for the base of the Cambrian, the Brioverian of Crozon could
368 either be Ediacaran (*ca.* 635-540 Ma) or younger, while the Brioverian of St-Gonlay could be
369 Ediacaran but is more probably Fortunian (*ca.* 540-529 Ma) or younger. Indeed, these results
370 agree with other dating elsewhere (maximum deposition age of *ca.* 550 Ma in Néant-sur-Yvel,
371 Brittany, with 5 zircons grains dated at 532.1 ± 3.9 Ma; 540 ± 10 Ma in Normandy; 540 ± 17
372 Ma in Mayenne; Pasteels & Doré, 1982; Guerrot *et al.*, 1992; Gougeon *et al.*, 2018b) and
373 argue for an early Cambrian age for the uppermost Brioverian beds from a radiometric
374 standpoint (see also Guerrot *et al.*, 1989, 1992).

375 In 1992, the Cambrian GSSP was ratified in Fortune Head, Newfoundland, Canada at
376 the first appearance of *Treptichnus pedum*, an infaunal burrow produced by a metazoan-grade

377 animal (Brasier *et al.*, 1994; Wilson *et al.*, 2012; Buatois, 2018; Kesidis *et al.*, 2019). Later,
378 the report of treptichnids (*i.e.* burrows made of short elements repeated in rows; Jensen *et al.*,
379 2000) within the Ediacaran at the type locality (Gehling *et al.*, 2001; Laing *et al.*, 2019) and in
380 other sections worldwide (Jensen *et al.*, 2000; Högström *et al.*, 2013) weakened the position
381 of the GSSP. However, the Ediacaran-Cambrian boundary is also constrained by the last
382 appearance of Ediacaran body fossils (*e.g.* *Harlaniella*, *Palaeopascichnus*) and the onset of
383 penetrative burrows typical of the Cambrian *Treptichnus pedum* Ichno-Assemblage Zone
384 (IAZ; *e.g.* *Bergaueria*, *Gyrolithes*; Narbonne *et al.*, 1987; MacNaughton & Narbonne, 1999;
385 Jensen, 2003; Mángano *et al.*, 2012; Högström *et al.*, 2013; Landing *et al.*, 2013). The IAZ
386 concept was first developed by Crimes (1987) and Narbonne *et al.* (1987) to depict the
387 progressive changes in ichnodiversity and bioturbation behaviors through the Ediacaran-
388 Cambrian boundary; since then, its utility has been demonstrated in many sections worldwide
389 (*e.g.* Walter *et al.*, 1989; Goldring & Jensen, 1996; Zhu, 1997; MacNaughton & Narbonne,
390 1999; McIlroy & Brasier, 2017). However, while the applicability of the IAZ concept is
391 optimal in normal shallow-marine conditions, it is more limited in marginal-marine settings
392 and below the storm-weather wave base (MacNaughton & Narbonne, 1999; MacNaughton,
393 2007; Buatois *et al.*, 2013; Shahkarami *et al.*, 2017; Buatois, 2018).

394 In the Brioverian, trace fossils were deposited on upper- to middle-intertidal
395 environments; these conditions can hamper organisms' physiology and, therefore, impacted
396 on bioturbation and the trace fossil diversity. Despite these stressful settings, recent reports of
397 treptichnids in the Brioverian of St-Gonlay and elsewhere (sandstone facies of Nouvoitou and
398 Chanteloup; personal observations of R. G. and D. N.) demonstrate that penetrative bilaterian
399 organisms still colonized these environments. Matgrounds survived during the rest of the
400 Cambrian in tidal environments (Hagadorn & Belt, 2008; Mata & Bottjer, 2009; Buatois &
401 Mángano, 2012; MacNaughton *et al.*, 2019) and are still common nowadays (*e.g.* Cardoso *et*

402 *al.*, 2019; Maisano *et al.*, 2019). Therefore, we suggest that whereas the Brioverian matground
403 ecology is more typical of Ediacaran times, the presence of distinctive Cambrian trace fossils
404 (*i.e.* treptichnids, but also *Cochlichnus* and regular planispirals which have not been
405 convincingly reported in the Ediacaran; Buatois & Mángano, 2016; this study) and the
406 peculiarities of Cambrian marginal-marine settings (*i.e.* the persistence of a matground
407 ecology) more likely argue for an early Cambrian age of the uppermost Brioverian deposits
408 from an ichnological standpoint. In addition, both the absence of body fossils with a
409 stratigraphic importance (*e.g.* trilobites of the Cambrian Stage 3) and uncontroversial
410 intertidal mollusk trails and arthropod ichnofossils of a younger Cambrian age (*e.g.*
411 *Climactichnites*, *Diplichnites*, *Protichnites*, *Rusophycus*; Yochelson & Fedonkin, 1993;
412 Mángano & Buatois, 2004; Hagadorn & Belt, 2008; Colette *et al.*, 2010; MacNaughton *et al.*,
413 2019) arguably constrain the Brioverian ichnofauna to the earliest Cambrian (*i.e.* Fortunian
414 and/or Cambrian Age 2).

415 6.c. Macro-evolutionary profile and the triggers of the Cambrian planispiraling behavior

416 Our detailed literature review (Section 6.a above and Supplementary Material)
417 unravels the environmental and temporal distribution of planispiral trace fossils (Fig. 3).
418 During the Ediacaran, simple horizontal trails are the norm (Buatois & Mángano, 2016;
419 Gehling & Droser, 2018) and the sole report of a planispiral trace fossil is an irregular two-
420 way spiral from Australia. This specimen is also transitional with poorly monitored
421 *Helminthorhaphé*-like meanders resembling to a weak tentative of surface-optimization, and
422 its evolutionary relationship with the Cambrian spirals is unclear. The absence of abundant
423 regular planispirals in the Ediacaran can be explained by: (1) a poor competitiveness for
424 space/food resource; (2) the absence of predators; (3) the homogenous repartition of the food
425 resource; and (4) primitive sensory systems (Papentin, 1973; Kitchell, 1979; Koy & Plotnick,
426 2007, 2010; Sims *et al.*, 2014).

427 [insert Figure 3]

428 In contrast, the Cambrian is composed of irregular to regular one-way planispirals
429 colonizing marginal- to shallow-marine environments: they form a Cambrian pool of
430 horizontal spiral trace fossils (Fig. 3). During the Ediacaran and the Cambrian, deposit-
431 feeding was the dominant feeding strategy (MacNaughton & Narbonne, 1999; Carbone &
432 Narbonne, 2014) and early planispirals were arguably made by epifaunal detritus-feeders and
433 shallow-infaunal deposit-feeders (the ‘surplus stretches’ or ‘alien U-turns’ inferring a vertical
434 open-burrow system have not been observed; *cf.* Seilacher, 1967*a, b*; 1977). Moreover,
435 planispirals of the Cambrian are often preserved on microbially-stabilized surfaces which
436 could represent their nutritive resource (Carbone & Narbonne, 2014). Possible producers are
437 enteropneusts and nematodes, both suspected to first appear during the Cambrian or before
438 (Knoll & Carroll, 1999; Budd & Jensen, 2000; Maletz, 2014; Cunningham *et al.*, 2017).
439 Enteropneusts produce regular horizontal spirals on the modern deep-sea floor on areas of
440 greater nutritional values, using tactile sensory systems of their head (Lemche *et al.*, 1976;
441 Smith *et al.*, 2005; Jones *et al.*, 2013). Nematodes can spiral by contracting all the muscles of
442 one side of their body (Wharton, 2004); however, spiraling in nematodes involves close
443 contact in between whorls and have been suggested for other purposes than feeding (*e.g.*
444 responses to increasing temperature, osmotic stress, desiccation and for reproduction; Huettel,
445 2004; Wharton, 2004).

446 Plotnick & Koy (2005; Koy & Plotnick, 2007, 2010; see also Kitchell, 1979)
447 demonstrated that a spiraling behavior primarily results from food heterogeneity. During the
448 early Cambrian, this heterogeneity may have formed from two phenomena: (1) the increasing
449 levels of bioturbation, and (2) the transformation of the planktic food web. The mat-
450 dominated ecology of the Ediacaran—with little competition and widespread, homogeneous
451 nutritive resource—progressively disappeared from shallow-marine settings by the Cambrian

452 Stage 2 as a result of increasing biogenic mixing (*i.e.* the Agronomic Revolution; Seilacher &
453 Pflüger, 1994; Dornbos *et al.*, 2004; Buatois & Mángano, 2012; Buatois *et al.*, 2014;
454 Mángano & Buatois, 2014; Gougeon *et al.*, 2018a). A transition between the Ediacaran and
455 the Cambrian Stage 2 can be observed in the Fortunian, represented by the coexistence of
456 matgrounds and mixgrounds generating a heterogeneous distribution of the food resource on
457 the shallow-marine shelf (Buatois & Mángano, 2012).

458 Moreover, in the early Cambrian, trophic webs of the water column experienced a
459 crucial change: the mesozooplankton, previously unknown in the Ediacaran, played a major
460 role in the Cambrian by linking the unicellular phytoplankton with larger animals of the
461 trophic chain (Butterfield, 1997, 2001). Large faecal pellets produced by the
462 macrozooplankton can sink massively and rapidly, accumulating on the ocean bottom (Fowler
463 & Knauer, 1986; Turner, 2002; Rex & Etter, 2010, pp. 1-49) and can generate a
464 heterogeneous distribution of food resources for the benthos (Butterfield, 1997; Koy &
465 Plotnick, 2007). In addition to these two phenomena, Budd & Jensen (2017) suggested that a
466 heterogeneous food distribution may have started even earlier, during the Ediacaran, with the
467 decay of large organisms representing food hotspots ('the Savannah hypothesis').

468 Although deep-marine deposits with trace fossils have been reported both from the
469 Ediacaran (*e.g.* Narbonne & Hofmann, 1987; Gibson, 1989; Liu *et al.*, 2010) and the
470 Cambrian (*e.g.* Aceñolaza & Durand, 1973; Hofmann *et al.*, 1994; Seilacher *et al.*, 2005),
471 spirals are consistently absent. Deep-marine bottoms are characterized by an absence of light,
472 high hydrostatic pressure, oxygen and temperature fluctuations, and low nutrient content
473 (Sanders & Hessler, 1969; Gage & Tyler, 1991, pp. 9-29; Rex & Etter, 2010, pp. 1-49). These
474 conditions can hamper animal fitness and their physiology (*e.g.* on animal body size; van der
475 Grient & Rogers, 2015) and can explain the delayed colonization of the deep-sea during the
476 Cambrian. However, deep-marine regular, one-way and two-way spirals are abundant through

477 the rest of the Phanerozoic and form an important Ordovician-Recent trend (Fig. 3). With the
478 increased competitiveness for space and/or food resource on early Cambrian shelves (Orr, 2001)
479 and the persistence of microbial mats in the deep-sea until the end of the Cambrian (Buatois
480 & Mángano, 2012), spiral trace-makers could have migrated to the deep-marine realm during
481 the Ordovician similarly to the producers of other graphoglyptids (Crimes & Anderson, 1985;
482 Crimes *et al.*, 1992; Crimes & Fedonkin, 1994; Orr, 2001; Uchman, 2003).

483 There are reports of continental, marginal-marine and shallow-marine planispiral trace
484 fossils in the Phanerozoic (Fig. 3), but their evolutionary patterns are difficult to decipher due
485 to the lack of data. Notably, there is a *ca.* 220 Ma gap between the Cambrian pool and the
486 next Phanerozoic reports in marginal- to shallow-marine environments. This gap reinforces
487 the evolutionary relationship existing between the marginal- to shallow-marine Cambrian
488 pool and the deep-marine Ordovician-Recent trend. Potentially, two additional trends could be
489 identified in the Phanerozoic: (1) in marginal-marine with spirals made by *Paraonis* worms
490 (from the Permian to the Recent); and (2) on the shoreface/foreshore with *Macaronichnus*
491 spirals (from the Cretaceous to the Recent). Both trends have very different spirals from the
492 Cambrian pool, and their clarification awaits further discoveries from the trace fossil record.

493 The Brioverian assemblage represents a key component of the macro-evolutionary
494 profile (Fig. 3). Indeed, this early Cambrian assemblage yields the oldest regular planispirals
495 (*i.e.* *Spirodesmos*) and the oldest planispirals from marginal-marine settings. Their association
496 with microbial mats underscores a detritus- or deposit-feeding strategy from their producer;
497 nematodes are a convincing candidate as sinusoidal trace fossils of *Cochlichnus* are also
498 reported in the succession (Néraudeau & Gougeon, in review). The reason for the spiraling
499 behavior, although arguably related to the heterogeneity of the food resource, cannot be linked
500 to the increasing biomixing of the shallow-marine Agronomic Revolution and is more likely
501 related to the restructuration of the planktic trophic chain.

502 **7. Conclusion**

503 Despite the presence of fossils, the age of the uppermost Brioverian deposits of central
504 Brittany, northwestern France, is a long-standing question. Two U-Pb zircon grain dating on
505 sandstone samples recovered from St-Gonlay give a maximum depositional age of 551 ± 7
506 Ma and 540 ± 5 Ma: although an Ediacaran age cannot be discarded, we believe these beds
507 are of earliest Cambrian in age (Fortunian and/or Cambrian Age 2), following previous
508 radiometric dating in Brittany, Normandy and Mayenne and strengthened by the trace fossil
509 record (*i.e.* presence of treptichnids, *Cochlichmus* and planispiral trace fossils).

510 A unique assemblage of irregular to regular, one-way planispiral trace fossils has been
511 recovered from the uppermost Brioverian beds of Crozon, Montfort-sur-Meu and St-Gonlay.
512 Planispiral trace fossils are unusual in the Ediacaran and the Cambrian, and an in-depth
513 literature review revealed that the Brioverian assemblage belongs to a Cambrian marginal- to
514 shallow-marine pool. Cambrian spiral trace fossils were made by deposit- and/or detritus-
515 feeders (possibly related to enteropneusts and nematodes), grazing on the seafloor where the
516 increasing food heterogeneity aided in triggering the spiraling behavior. However, by the
517 Ordovician, planispiral trace fossils retreated toward the deep-marine realm, underscoring an
518 onshore-offshore migration similar to what is observed in other graphoglyptids.

519 **Acknowledgements**

520 This manuscript is a follow-up of a poster presented at the International Meeting on
521 the Ediacaran System and the Ediacaran-Cambrian Transition (IMECT) that took place in
522 Guadalupe, Spain, in October 2019. Discussions and feedbacks from L. Buatois, P. Crimes, S.
523 Jensen, G. Mángano, V. Marusin and M. Paz are kindly acknowledged. We also thank: D.
524 Gendry and S. Regnault who granted access to the museum material of the Geological
525 Institute of the University of Rennes 1 and the Museum of Natural History of Nantes,

526 respectively; N. Hallot for the rock crushing; E. Hanson for sharing her photographs of the
527 spiral trace fossil from Crozon; X. Le Coz for the rock sawing and the preparation of thin
528 sections; Y. Lepagnot for the mineral separations; F. Polette and L. Guillois for their
529 assistance during the U-Pb dating; and the outcrops' owners for granting a continuous access
530 to their private properties. The work of A. L. has been partially supported by the 'Fondazione
531 Banco di Sardegna' and by the 'Regione Autonoma della Sardegna' (grant numbers
532 F74I19000960007, J81G17000110002). This publication is a contribution to the VIBRIO
533 project of the INSU InterrVie program and benefitted from a financial support from the
534 'Observatoire des Sciences de l'Univers de Rennes' (OSUR). We have a special thought for
535 our colleague M.-P. Dabard who passed away too soon.

536 **Declaration of Interest**

537 None.

538 **References**

- 539 ACEÑOLAZA, F. G. & DURAND, F. R. 1973. Trazas fósiles del basamento cristalino del
540 noroeste argentino. *Boletín de la Asociación Geológica de Córdoba* **2**, 45-55.
- 541 ACEÑOLAZA, G. F. 2005. *Spirodesmos milanai* n. isp.: A shallow-water spiral trace fossil
542 from the Cambrian of the eastern Cordillera, northwest Argentina. *Ichnos* **12**, 59-63.
- 543 ANDRÉE, K. 1920. Über einige fossile Problematika. I. Ein Problematikum aus dem
544 Paläozoikum von Battenberg an der Eder und des dasselbe beherbergende Gestein. *Neues*
545 *Jahrbuch für Mineralogie, Geologie und Paläontologie* **1**, 55-88.
- 546 AUVRAY, B., MACE, J., VIDAL, P. & VAN DER VOO, R. 1980. Rb-Sr dating of the
547 Plouézec volcanics, N Brittany: implications for the age of red beds ('Series rouges') in the
548 northern Armorican Massif. *Journal of the Geological Society* **137**, 207-210.

549 BALLÈVRE, M., BOSSE, V., DABARD, M.-P., DUCASSOU, C., FOURCADE, S.,
550 PAQUETTE, J.-L., PEUCAT, J.-J. & PITRA, P. 2013. Histoire géologique du Massif
551 Armoricaïn: Actualité de la recherche. *Bulletin de la Société Géologique et Minéralogique de*
552 *Bretagne* **10-11**, 5-96.

553 BALLÈVRE, M., BOSSE, V., DUCASSOU, C. & PITRA, P. 2009. Palaeozoic history of the
554 Armorican Massif: Models for the tectonic evolution of the suture zones. *Comptes Rendus*
555 *Geoscience* **341**, 174-201.

556 BALLOUARD, C., POUJOL, M. & ZEH, A. 2018. Multiple crust reworking in the French
557 Armorican Variscan belt: implication for the genesis of uranium-fertile leucogranites.
558 *International Journal of Earth Sciences* **107**, 2317-2336.

559 BEER, E. J. 1919. Note on a spiral impression on Lower Vindhyan Limestone. *Records of the*
560 *Geological Survey of India* **50**, 139.

561 BILLINGS, E. 1872. On some fossils from the primordial rocks of Newfoundland. *Canadian*
562 *Naturalist and Quarterly Journal of Science* **6**, 465-479.

563 BONJOUR, J. L. & CHAUVEL, J. J. 1988. Un exemple de sédimentation initiale dans un
564 bassin paléozoïque : étude pétrographique et géochimique de l'Ordovicien inférieur de la
565 presqu'île de Crozon (Finistère). *Bulletin de la Société géologique de France* **4**, 81-91.

566 BONJOUR, J. L. & ODIN, G. S. 1989. Recherche sur les volcanoclastites des Séries Rouges
567 Initiales en presqu'île de Crozon: Premier âge radiométrique de l'Arénig. *Géologie de la*
568 *France* **4**, 3-7.

569 BONJOUR, J. L., PEUCAT, J. J., CHAUVEL, J. J., PARIS, F. & CORNICHE, J. 1987. A
570 middle Arenigian radiometric age for the Paleozoic transgression in West Brittany (France).
571 *Fourth meeting of the European Union of Geosciences, Abstracts*, 250.

572 BONJOUR, J. L., PEUCAT, J. J., CHAUVEL, J. J., PARIS, F. & CORNICHE, J. 1988. U-
573 Pb zircon dating of the early Paleozoic (Arenigian) transgression in Western Brittany
574 (France): A new constraint for the lower Paleozoic time-scale. *Chemical Geology (Isotope
575 Geoscience section)* **72**, 329-336.

576 BOTTJER, D. J., HAGADORN, J. W. & DORNBOS, S. Q. 2000. The Cambrian substrate
577 revolution. *GSA today* **10**, 1-7.

578 BOWRING, S. A., GROTZINGER, J. P., CONDON, D. J., RAMEZANI, J., NEWALL, M. J.
579 & ALLEN, P. A. 2007. Geochronologic constraints on the chronostratigraphic framework of
580 the Neoproterozoic Huqf Supergroup, Sultanate of Oman. *American Journal of Science* **307**,
581 1097-1145.

582 BOYLE, R. A., DAHL, T. W., BJERRUM, C. J. & CANFIELD, D. E. 2018. Bioturbation and
583 directionality in Earth's carbon isotope record across the Neoproterozoic–Cambrian transition.
584 *Geobiology* **16**, 252-278.

585 BRASIER, M., COWIE, J. & TAYLOR, M. 1994. Decision on the Precambrian-Cambrian
586 boundary stratotype. *Episodes* **17**, 3-8.

587 BUATOIS, L. A. 2018. *Treptichnus pedum* and the Ediacaran–Cambrian boundary:
588 significance and caveats. *Geological Magazine* **155**, 174-180.

589 BUATOIS, L. A., ALMOND, J. & GERMS, G. J. 2013. Environmental tolerance and range
590 offset of *Treptichnus pedum*: Implications for the recognition of the Ediacaran-Cambrian
591 boundary. *Geology* **41**, 519-522.

592 BUATOIS, L. A. & MÁNGANO, M. G. 2012. The trace-fossil record of organism-matground
593 interactions in space and time. In *Microbial Mats in Siliciclastic Depositional Systems*

594 *Through Time* (eds N. Noffke & H. Chafetz), pp. 15-28. SEPM Special Publication, Vol.
595 101.

596 BUATOIS, L. A. & MÁNGANO, M. G. 2016. Ediacaran ecosystems and the dawn of
597 animals. In *The trace-fossil record of major evolutionary events, Volume 1: Precambrian and*
598 *Paleozoic* (eds M. G. Mángano & L. A. Buatois), pp. 27-72. Springer, Dordrecht.

599 BUATOIS, L. A., NARBONNE, G. M., MÁNGANO, M. G., CARMONA, N. B. &
600 MYROW, P. 2014. Ediacaran matground ecology persisted into the earliest Cambrian. *Nature*
601 *Communications* **5**, 3544.

602 BUATOIS, L. A., NETTO, R. G., MÁNGANO, M. G. & CARMONA, N. B. 2013. Global
603 deglaciation and the re-appearance of microbial matground-dominated ecosystems in the late
604 Paleozoic of Gondwana. *Geobiology* **11**, 307-317.

605 BUATOIS, L. A., WISSHAK, M., WILSON, M. A. & MÁNGANO, M. G. 2017. Categories
606 of architectural designs in trace fossils: a measure of ichnodisparity. *Earth-Science Reviews*
607 **164**, 102-181.

608 BUDD, G. E. & JENSEN, S. 2000. A critical reappraisal of the fossil record of the bilaterian
609 phyla. *Biological Reviews* **75**, 253-295.

610 BUDD, G. E. & JENSEN, S. 2017. The origin of the animals and a ‘Savannah’ hypothesis for
611 early bilaterian evolution. *Biological Reviews* **92**, 446-473.

612 BUTTERFIELD, N. J. 1997. Plankton ecology and the Proterozoic-Phanerozoic transition.
613 *Paleobiology* **23**, 247-262.

614 BUTTERFIELD, N. J. 2001. Ecology and evolution of Cambrian plankton. In *Ecology of the*
615 *Cambrian Radiation* (eds A. Y. Zhuravlev & R. Riding), pp. 200-216. Columbia University
616 Press, New York.

617 CANFIELD, D. E. & FARQUHAR, J. 2009. Animal evolution, bioturbation, and the sulfate
618 concentration of the oceans. *Proceedings of the National Academy of Sciences* **106**, 8123-
619 8127.

620 CARBONE, C. & NARBONNE, G. M. 2014. When life got smart: the evolution of
621 behavioral complexity through the Ediacaran and Early Cambrian of NW Canada. *Journal of*
622 *Paleontology* **88**, 309-330.

623 CARDOSO, D. C., CRETOIU, M. S., STAL, L. J. & BOLHUIS, H. 2019. Seasonal
624 development of a coastal microbial mat. *Scientific reports* **9**, 1-14.

625 CAYEUX, L. 1894. Sur la présence de restes de Foraminifères dans les terrains précambriens
626 de Bretagne. *Annales de la Société Géologique du Nord* **22**, 116-119.

627 CHANTRAINE, J., CHAUVEL, J.-J., DUPRET, L., GATINOT, F., ICART, J.-C., LE
628 CORRE, C., RABU, D., SAUVAN, P. & VILLEY, M. 1982. Inventaire lithologique et
629 structural du Briovérien (Protérozoïque supérieur) de la Bretagne centrale et du Bocage
630 normand. *Bulletin du BRGM* **1**, 3-17.

631 CHANTRAINE, J., EGAL, E., THIÉBLEMONT, D., LE GOFF, E., GUERROT, C.,
632 BALLÈVRE, M. & GUENNOG, P. 2001. The Cadomian active margin (North Armorican
633 Massif, France): a segment of the North Atlantic Panafrican belt. *Tectonophysics* **331**, 1-18.

634 CHAUVEL, J. J. & MANSUY, C. 1981. Micropaleontologie du Proterozoïque du Massif
635 Armoricaïn (France). *Precambrian Research* **15**, 25-42.

636 CHAUVEL, J. J. & SCHOPF, J. W. 1978. Late Precambrian microfossils from Brioverian
637 cherts and limestones of Brittany and Normandy, France. *Nature* **275**, 640-642.

638 CLOUD, P. E. 1968. Pre-metazoan evolution and the origins of the Metazoa. In *Evolution and*
639 *environment* (ed E. T. Drake), pp. 1-72. Yale University.

- 640 COGNÉ, J. 1959. Données nouvelles sur l'Antécambrien dans l'Ouest de la France :
641 Pentévrien et Briovérien en baie de Saint-Brieuc (Côtes-du-Nord). *Bulletin de la Société*
642 *géologique de France* **7**, 112-118.
- 643 COLLETTE, J. H., HAGADORN, J. W. & LACELLE, M. A. 2010. Dead in their tracks -
644 Cambrian arthropods and their traces from intertidal sandstones of Quebec and Wisconsin.
645 *Palaios* **25**, 475-486.
- 646 CRIMES, T. P. 1987. Trace fossils and correlation of late Precambrian and early Cambrian
647 strata. *Geological Magazine* **124**, 97-119.
- 648 CRIMES, T. P. 1992a. Changes in the trace fossil biota across the Proterozoic-Phanerozoic
649 boundary. *Journal of the Geological Society, London* **149**, 637-646.
- 650 CRIMES, T. P. 1992b. The record of trace fossils across the Proterozoic-Cambrian boundary.
651 In *Origin and early evolution of the Metazoa* (eds J. H. Lipps & P. W. Signor), pp. 177-199.
652 Plenum Press, New York.
- 653 CRIMES, T. P. 1994. The period of early evolutionary failure and the dawn of evolutionary
654 success: the record of biotic changes across the Precambrian-Cambrian boundary. In *The*
655 *palaeobiology of trace fossils* (ed S. K. Donovan), pp. 105-133. John Wiley & Sons,
656 Chichester, UK.
- 657 CRIMES, T. P. & ANDERSON, M. M. 1985. Trace fossils from Late Precambrian-Early
658 Cambrian strata of southeastern Newfoundland (Canada): temporal and environmental
659 implications. *Journal of Paleontology* **59**, 310-343.
- 660 CRIMES, T. P. & CROSSLEY, J. D. 1991. A diverse ichnofauna from Silurian flysch of the
661 Aberystwyth Grits Formation, Wales. *Geological Journal* **26**, 27-64.

662 CRIMES, T. P. & FEDONKIN, M. A. 1994. Evolution and dispersal of deepsea traces.
663 *Palaios* **9**, 74-83.

664 CRIMES, T. P., GARCIA HIDALGO, J. G. & POIRE, D. G. 1992. Trace fossils from Arenig
665 flysch sediments of Eire and their bearing on the early colonisation of the deep seas. *Ichnos* **2**,
666 61-77.

667 CRIMES, T. P., MARCOS, A. & PEREZ-ESTAUN, A. 1974. Upper Ordovician turbidites in
668 western Asturias: a facies analysis with particular reference to vertical and lateral variations.
669 *Palaeogeography, Palaeoclimatology, Palaeoecology* **15**, 169-184.

670 CRIMES, T. P. & MCCALL, G. J. H. 1995. A diverse ichnofauna from Eocene-Miocene
671 rocks of the Makran Range (SE Iran). *Ichnos* **3**, 231-258.

672 CUNNINGHAM, J. A., LIU, A. G., BENGTSON, S. & DONOGHUE, P. C. 2017. The origin
673 of animals: can molecular clocks and the fossil record be reconciled?. *BioEssays* **39**, 1-12.

674 D'LEMOS, R. S., STRACHAN, R. A. & TOPLEY, C. G. 1990. The Cadomian orogeny in
675 the North Armorican Massif: a brief review. *Geological Society Special Publication* **51**, 3-12.

676 DABARD, M. P. 1990. Lower Brioverian formations (Upper Proterozoic) of the Armorican
677 Massif (France) : geodynamic evolution of source areas revealed by sandstone petrography
678 and geochemistry. *Sedimentary Geology* **69**, 45-58.

679 DABARD, M. P. 2000. Petrogenesis of graphitic cherts in the Armorican segment of the
680 Cadomian orogenic belt (NW France). *Sedimentology* **47**, 787-800.

681 DABARD, M. P. & LOI, A. 1998. Environnement de dépôt des formations à phtanites
682 interstratifiés du Protérozoïque supérieur armoricain (France) : conséquences sur la genèse
683 des phtanites. *Comptes Rendus de l'Académie des Sciences de Paris* **326**, 763-769.

- 684 DABARD, M. P., LOI, A. & PEUCAT, J. J. 1996. Zircon typology combined with Sm-Nd
685 whole-rock isotope analysis to study Brioverian sediments from the Armorican Massif.
686 *Sedimentary Geology* **101**, 243-260.
- 687 DABARD, M. P. & SIMON, B. 2011. Discordance des Séries Rouges Initiales sur le socle
688 briovérien : exemple de la carrière des Landes. *Bulletin de la Société Géologique et*
689 *Minéralogique de Bretagne* **8**, 33-44.
- 690 DALRYMPLE, R. W. 2010. Tidal depositional systems. In *Facies Models 4* (eds N. P. James
691 & R. W. Dalrymple), pp. 201-231. The Geological Association of Canada.
- 692 DANGEARD, L., DORÉ, F. & JUIGNET, P. 1961. Le Briovérien supérieur de Basse
693 Normandie (étage de la Laize), série à turbidites, a tous les caractères d'un flysch. *Revue de*
694 *Géographie Physique et de Géologie Dynamique* **4**, 251-259.
- 695 DARBOUX, J. R. 1973. Le Briovérien de la baie de Douarnenez (Massif Armoricain) : étude
696 pétrographique et structurale. University of Brest, unpublished Ph.D. thesis.
- 697 DEFLANDRE, G. 1955. *Paleocryptidium* n. g. *cayeuxi* n. sp., microorganismes incertae sedis
698 des phtanites briovériens bretons. *Comptes Rendus Sommaires de la Société Géologique de*
699 *France* **9-10**, 182-185.
- 700 DENIS, E. 1988. Les sédiments briovériens (Protérozoïque supérieur) de Bretagne
701 septentrionale et occidentale : Nature, mise en place et évolution. *Mémoires et Documents du*
702 *Centre Armoricain d'Etude Structurale des Socles* **18**, pp. 263.
- 703 DENIS, E. & DABARD, M. P. 1988. Sandstone petrography and geochemistry of late
704 Proterozoic sediments of the Armorican Massif (France) - a key to basin development during
705 the Cadomian Orogeny. *Precambrian Research* **42**, 189-206.

706 DICKINSON, W. R. & GEHRELS, G. E. 2009. Use of U-Pb ages of detrital zircons to infer
707 maximum depositional ages of strata: a test against a Colorado Plateau Mesozoic database.
708 *Earth Planetary Science Letters* **288**, 115–125.

709 DISSLER, E., DORÉ, F., DUPRET, L., GRESSELIN, F. & LE GALL, J. 1988. L'évolution
710 géodynamique cadomienne du Nord-Est du Massif armoricain. *Bulletin de la Société*
711 *géologique de France* **4**, 801-814.

712 DORNBOS, S. Q., BOTTJER, D. J. & CHEN, J. Y. 2004. Evidence for seafloor microbial
713 mats and associated metazoan lifestyles in Lower Cambrian phosphorites of Southwest China.
714 *Lethaia* **37**, 127-138.

715 ERIKSSON, P. G., PORADA, H., BANERJEE, S., BOUOUGRI, E., SARKAR, S. &
716 BUMBY, A. J. 2007. Mat-destruction features. In *Atlas of microbial mats features preserved*
717 *within the siliciclastic rock record* (eds J. Schieber, P. K. Bose, P. G. Eriksson, S. Banerjee, S.
718 Sarkar, W. Altermann & O. Catuneanu), pp. 76-105. *Atlases in Geosciences 2*, Elsevier.

719 FEDONKIN, M. A. 1985. Paleoichnology of Vendian metazoa. In *The Vendian System 1:*
720 *Historic-Geological and Palaeontological Basis* (eds B. S. Sokolov & A. B. Ivanovskiy), pp.
721 112-116. Nauka, Moscow.

722 FEDONKIN, M. A. 1990. Paleoichnology of Vendian metazoa. In *The Vendian System 1:*
723 *Paleontology* (eds B. S. Sokolov & A. B. Iwanoski), pp. 132-341. Springer, Berlin.

724 FOWLER, S. W. & KNAUER, G. A. 1986. Role of large particles in the transport of elements
725 and organic compounds through the oceanic water column. *Progress in Oceanography* **16**,
726 147-194.

727 GAGE, J. D. & TYLER, P. A. 1991. *Deep-sea biology: a natural history of organisms at the*
728 *deep-sea floor*. Cambridge University Press, 504 pp.

729 GEINITZ, H. B. 1867. Die organischen Ueberreste im Dachschiefer von Wurzbach bei
730 Lobenstein. In *Ueber ein Aequivalent der takonischen Schiefer Nordamerika's in Deutschland*
731 *und dessen geologische Stellung* (eds H. B. Geinitz & K. T. Liebe), pp. 1-24. Druck von E.
732 Blochmann & Sohn, Dresden.

733 GEHLING, J. G. 1999. Microbial mats in terminal Proterozoic siliciclastics; Ediacaran death
734 masks. *Palaios* **14**, 40-57.

735 GEHLING, J. G. & DROSER, M. L. 2018. Ediacaran scavenging as a prelude to predation.
736 *Emerging Topics in Life Sciences* **2**, 213-222.

737 GEHLING, J. G., JENSEN, S., DROSER, M. L., MYROW, P. M. & NARBONNE, G. M.
738 2001. Burrowing below the basal Cambrian GSSP, fortune head, Newfoundland. *Geological*
739 *Magazine* **138**, 213-218.

740 GIBSON, G. G. 1989. Trace fossils from late Precambrian Carolina slate belt, south-central
741 North Carolina. *Journal of Paleontology* **63**, 1-10.

742 GOLDRING, R. & JENSEN, S. 1996. Trace fossils and biofabrics at the Precambrian-
743 Cambrian boundary interval in western Mongolia. *Geological Magazine* **133**, 403-415.

744 GOUGEON, R. C., MÁNGANO, M. G., BUATOIS, L. A., NARBONNE, G. M. & LAING,
745 B. A. 2018a. Early Cambrian origin of the shelf sediment mixed layer. *Nature*
746 *Communications* **9**, 1909.

747 GOUGEON, R., NÉRAUDEAU, D., DABARD, M. P., PIERSON-WICKMANN, A. C.,
748 POLETTE, F., POUJOL, M. & SAINT-MARTIN, J. P. 2018b. Trace Fossils from the
749 Brioverian (Ediacaran–Fortunian) in Brittany (NW France). *Ichnos* **25**, 11-24.

- 750 GOUGEON, R., NÉRAUDEAU, D., POUJOL, M. & LOI, A. 2019. Loops, circles, spirals
751 and the appearance of guided behaviors from the Ediacaran-Cambrian of Brittany, NW
752 France. *Estudios Geológicos* **75**, 11-13.
- 753 GRAINDOR, M.-J. 1957. Le Briovérien dans le Nord-Est du Massif Armoricaïn. *Mémoires*
754 *pour servir à l'explication de la Carte Géologique détaillée de la France*, 211 pp.
- 755 GUERROT, C., CALVEZ, J. Y., BONJOUR, J. L., CHANTAINE, J., CHAUVEL, J. J.,
756 DUPRET, L. & RABU, D. 1992. Le Briovérien de Bretagne centrale et occidentale :
757 nouvelles données radiométriques. *Comptes Rendus de l'Académie des Sciences de Paris* **315**,
758 1741–1746.
- 759 GUERROT, C., PEUCAT, J. J. & DUPRET, L. 1989. Données nouvelles sur l'âge du système
760 briovérien (Protérozoïque supérieur) dans le Nord du Massif armoricaïn. *Comptes Rendus de*
761 *l'Académie des Sciences de Paris* **308**, 89-92.
- 762 HAGADORN, J. W. & BELT, E. S. 2008. Stranded in upstate New York: Cambrian
763 scyphomedusae from the Potsdam Sandstone. *Palaios* **23**, 424-441.
- 764 HÄNTZSCHEL, W. 1975. *Treatise on invertebrate paleontology. Part W, Miscellanea,*
765 *supplement 1: Trace Fossils and Problematica.* Geological Society of America, University of
766 Kansas.
- 767 HEER, O. 1876. *Flora Fossilis Helvetiae. Die Vorweltliche Flora der Schweiz.* Verlag von J.
768 Wurster & Comp., Zürich.
- 769 HOFMANN, H. J. 1971. Precambrian fossils, pseudofossils and problematica in Canada.
770 *Geological Survey of Canada, Bulletin* **189**, 1-146.

771 HOFMANN, H. J., CECILE, M. P. & LANE, L. S. 1994. New occurrences of *Oldhamia* and
772 other trace fossils in the Cambrian of the Yukon and Ellesmere Island, arctic Canada.
773 *Canadian Journal of Earth Sciences* **31**, 767-782.

774 HÖGSTRÖM, A. E., JENSEN, S., PALACIOS, T. & EBBESTAD, J. O. R. 2013. New
775 information on the Ediacaran-Cambrian transition in the Vestertana Group, Finnmark,
776 northern Norway, from trace fossils and organic-walled microfossils. *Norwegian Journal of*
777 *Geology* **93**, 95-106.

778 HUCKRIEDE, R. 1952. Eine spiralförmige Lebensspur aus dem Kulmkieselschiefer von
779 Biedenkopf an der Lahn (*Spirodesmos archimedeus* n. sp.). *Paläontologische Zeitschrift* **26**,
780 175-180.

781 HUETTEL, R. N. 2004. Reproductive behavior. In *Nematode Behaviour* (eds R. Gaugler &
782 A. L. Bilgrami), pp. 127-149. CABI Publishing, Wallingford, UK.

783 IVANTSOV, A. Y., GRITSENKO, V. P., PALIY, V. M., VELIKANOV, V. A.,
784 KONSTANTINENKO, L. I., MENASOVA, A. S., FEDONKIN, M. A., ZAKREVSKAYA,
785 M. A. & SEREZHNIKOVA, E. A. 2015. *Upper Vendian macrofossils of Eastern Europe.*
786 *Middle Dniester area and Volhynia*. Moscow, PIN RAS, 144 pp.

787 JENKINS, R. J. 1995. The problems and potential of using animal fossils and trace fossils in
788 terminal Proterozoic biostratigraphy. *Precambrian Research* **73**, 51-69.

789 JENSEN, S. 2003. The Proterozoic and earliest Cambrian trace fossil record; patterns,
790 problems and perspectives. *Integrative and Comparative Biology* **43**, 219-228.

791 JENSEN, S. & PALACIOS, T. 2016. The Ediacaran-Cambrian trace fossil record in the
792 Central Iberian Zone, Iberian Peninsula. *Comunicações Geológicas* **103**, 83-92.

793 JENSEN, S., SAYLOR, B. Z., GEHLING, J. G. & GERMS, G. J. 2000. Complex trace fossils
794 from the terminal Proterozoic of Namibia. *Geology* **28**, 143-146.

795 JONES, D. O. B., ALT, C. H. S., PRIEDE, I. G., REID, W. D. K., WIGHAM, B. D.,
796 BILLET, D. S. M., GEBRUK, A. V., ROGACHEVA, A. & GOODAY, A. J. 2013. Deep-
797 sea surface-dwelling enteropneusts from the Mid-Atlantic Ridge: their ecology, distribution
798 and mode of life. *Deep Sea Research II* **98**, 374-387.

799 KESIDIS, G., SLATER, B. J., JENSEN, S. & BUDD, G. E. 2019. Caught in the act: priapulid
800 burrowers in early Cambrian substrates. *Proceedings of the Royal Society B* **286**, 20182505.

801 KIM, J. Y. 1996. Behavioral patterns expressed in scribbling trace fossils from Ordovician
802 strata of Yeongweol, Korea. *Ichnos* **4**, 219-224.

803 KITCHELL, J. A. 1979. Deep-sea foraging pathways: an analysis of randomness and resource
804 exploitation. *Paleobiology* **5**, 107-125.

805 KITCHELL, J. A., KITCHELL, J. F., JOHNSON, G. L. & HUNKINS, K. L. 1978. Abyssal
806 traces and megafauna: comparison of productivity, diversity and density in the Arctic and
807 Antarctic. *Paleobiology* **4**, 171-180.

808 KNOLL, A. H. & CARROLL, S. B. 1999. Early animal evolution: emerging views from
809 comparative biology and geology. *Science* **284**, 2129-2137.

810 KOY, K. & PLOTNICK, R. E. 2007. Theoretical and experimental ichnology of mobile
811 foraging. In *Trace fossils: concepts, problems, prospects* (ed W. Miller III), pp. 428-441.
812 Elsevier.

813 KOY, K. A. & PLOTNICK, R. E. 2010. Ichnofossil morphology as a response to resource
814 distribution: insights from modern invertebrate foraging. *Palaeogeography,*
815 *Palaeoclimatology, Palaeoecology* **292**, 272-281.

816 KSIAŹKIEWICZ, M. 1977. Trace fossils in the flysch of the Polish Carpathians.
817 *Palaeontologia Polonica* **36**, 1-208.

818 LAING, B. A., MÁNGANO, M. G., BUATOIS, L. A., NARBONNE, G. M. & GOUGEON,
819 R. C. 2019. A protracted Ediacaran–Cambrian transition: an ichnologic ecospace analysis of
820 the Fortunian in Newfoundland, Canada. *Geological Magazine* **156**, 1623-1630.

821 LANDING, E., GEYER, G., BRASIER, M. D. & BOWRING, S. A. 2013. Cambrian
822 evolutionary radiation: context, correlation, and chronostratigraphy - overcoming deficiencies
823 of the first appearance datum (FAD) concept. *Earth-Science Reviews* **123**, 133-172.

824 LE CORRE, C., AUVRAY, B., BALLÈVRE, M. & ROBARDET, M. 1991. Le Massif
825 Armoricaín. *Sciences Géologiques, Bulletin* **44**, 31-103.

826 LEBESCONTE, P. 1886. Constitution générale du Massif Breton. *Bulletin de la Société*
827 *Géologique de France, 3ème série* **17**, 776-791.

828 LEMCHE, H., HANSEN, B., MADSEN, F. J., TENDAL, O. S. & WOLFF, T. 1976. Hadal
829 life as analyzed from photographs. *Videnskabelige Meddelelser dansk naturhistorisk*
830 *Forening* **139**, 263-336.

831 LINNEMANN, U., OVTCHAROVA, M., SCHALTEGGER, U., GÄRTNER, A.,
832 HAUTMANN, M., GEYER, G., VICKERS-RICH, P., RICH, T., PLESSSEN, B., HOFMANN,
833 M., ZIEGER, J., KRAUSE, R. KRIESFELD, L. & SMITH, J. 2019. New high-resolution age
834 data from the Ediacaran–Cambrian boundary indicate rapid, ecologically driven onset of the
835 Cambrian explosion. *Terra Nova* **31**, 49-58.

836 LIU, A. G., MCILROY, D. & BRASIER, M. D. 2010. First evidence for locomotion in the
837 Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology* **38**, 123-
838 126.

839 LOGAN, G. A., HAYES, J. M., HIESHIMA, G. B. & SUMMONS, R. E. 1995. Terminal
840 Proterozoic reorganization of biogeochemical cycles. *Nature* **376**, 53-56.

841 LOUVEL, R. 1988. Sédimentologie et stratigraphie du Briovérien de Bretagne centrale.
842 University of Rennes 1, unpublished Master thesis.

843 MACNAUGHTON, R. B. 2007. The application of trace fossils to biostratigraphy. In *Trace*
844 *fossils: concepts, problems, prospects* (ed W. Miller III), pp. 135-148. Elsevier.

845 MACNAUGHTON, R. B., HAGADORN, J. W. & DOTT JR, R. H. 2019. Cambrian
846 wave-dominated tidal-flat deposits, central Wisconsin, USA. *Sedimentology* **66**, 1643-1672.

847 MACNAUGHTON, R. B. & NARBONNE, G. M. 1999. Evolution and ecology of
848 Neoproterozoic-Lower Cambrian trace fossils, NW Canada. *Palaios* **14**, 97-115.

849 MAISANO, L., CUADRADO, D. G. & GÓMEZ, E. A. 2019. Processes of MISS-formation
850 in a modern siliciclastic tidal flat, Patagonia (Argentina). *Sedimentary Geology* **381**, 1-12.

851 MALETZ, J. 2014. Hemichordata (Pterobranchia, Enteropneusta) and the fossil record.
852 *Palaeogeography, Palaeoclimatology, Palaeoecology* **398**, 16-27.

853 MALUSÀ, M. G., CARTER, A., LIMONCELLI, M., VILLA, I. M. & GARZANTI, E. 2013.
854 Bias in detrital zircon geochronology and thermochronometry. *Chemical Geology* **359**, 90–
855 107.

856 MÁNGANO, M. G. & BUATOIS, L. A. 2004. Reconstructing early Phanerozoic intertidal
857 ecosystems: ichnology of the Cambrian Campanario Formation in northwest Argentina.
858 *Fossils and Strata* **51**, 17-38.

859 MÁNGANO, M. G. & BUATOIS, L. A. 2014. Decoupling of body-plan diversification and
860 ecological structuring during the Ediacaran–Cambrian transition: evolutionary and

861 geobiological feedbacks. *Proceedings of the Royal Society B: Biological Sciences* **281**,
862 20140038.

863 MÁNGANO, M. G., BUATOIS, L. A. & MACNAUGHTON, R. B. 2012. Ichnostratigraphy.
864 In *Trace Fossils as Indicators of Sedimentary Environments* (eds D. Knaust & R. G.
865 Bromley), pp. 195-212. Elsevier, Developments in Sedimentology, Vol. 64.

866 MANZOTTI, P., POUJOL, M. & BALLÈVRE, M. 2015. Detrital zircon geochronology in
867 blueschist-facies meta-conglomerates from the Western Alps: implications for the late
868 Carboniferous to early Permian palaeogeography. *International Journal of Earth Sciences*
869 **104**, 703-731.

870 MANSUY, C. & VIDAL, G. 1983. Late Proterozoic Brioverian microfossils from France:
871 taxonomic affinity and implications of plankton productivity. *Nature* **302**, 606-607.

872 MARUSIN, V. V. 2016. Trace fossils from the Vendian-Cambrian transitional strata of the
873 Olenek Uplift of Siberian Platform. Unpublished Ph.D. thesis, IPGG, Novosibirsk, 275 pp.

874 MARUSIN, V. V. & KUPER, K. E. 2020. Complex tunnel systems of early Fortunian
875 macroscopic endobenthos in the Ediacaran-Cambrian transitional strata of the Olenek Uplift
876 (NE Siberian Platform). *Precambrian Research* **340**, 105627.

877 MATA, S. A. & BOTTJER, D. J. 2009. The paleoenvironmental distribution of Phanerozoic
878 wrinkle structures. *Earth-Science Reviews* **96**, 181-195.

879 MCILROY, D. & BRASIER, M. D. 2017. Ichnological evidence for the Cambrian explosion
880 in the Ediacaran to Cambrian succession of Tanafjord, Finnmark, northern Norway.
881 *Geological Society, London, Special Publications* **448**, 351-368.

- 882 MENASOVA, A. S. 2003. New representatives of the Vendian biota from localities of
883 Podolia. *Zbirnik naukovikh prats' IGN: Teoretichni ta prikladni aspekti suchasnoi*
884 *biostratigrafii fan erozoyu Ukraine*, 139-142.
- 885 METZ, R. 1987. Insect traces from nonmarine ephemeral puddles. *Boreas* **16**, 189-195.
- 886 MEYSMAN, F. J., MIDDELBURG, J. J. & HEIP, C. H. 2006. Bioturbation: a fresh look at
887 Darwin's last idea. *Trends in Ecology & Evolution* **21**, 688-695.
- 888 MINTER, N. J. & BRADDY, S. J. 2009. Ichnology of an Early Permian intertidal flat: The
889 Robledo Mountains Formation of southern New Mexico, USA. *Special Papers in*
890 *Paleontology* **82**, 1-107.
- 891 MINTER, N. J., BUATOIS, L. A., LUCAS, S. G., BRADDY, S. J. & SMITH, J. A. 2006.
892 Spiral-shaped graphoglyptids from an Early Permian intertidal flat. *Geology* **34**, 1057-1060.
- 893 NARBONNE, G. M. & HOFMANN, H. J. 1987. Ediacaran biota of the Wernecke Mountains,
894 Yukon, Canada. *Palaeontology* **30**, 647-676.
- 895 NARBONNE, G. M., MYROW, P. M., LANDING, E. & ANDERSON, M. M. 1987. A
896 candidate stratotype for the Precambrian–Cambrian boundary, Fortune head, Burin Peninsula,
897 southeastern Newfoundland. *Canadian Journal of Earth Sciences* **24**, 1277-1293.
- 898 NÉRAUDEAU, D., DABARD, M.-P., EL ALBANI, A., GOUGEON, R., MAZURIER, A.,
899 PIERSON-WICKMANN, A.-C., POUJOL, M., SAINT MARTIN, J.-P. & SAINT MARTIN,
900 S. 2019. First evidence of Ediacaran–Fortunian elliptical body fossils in the Brioverian series
901 of Brittany, NW France. *Lethaia* **51**, 513-522.
- 902 NÉRAUDEAU, D. & GOUGEON, R. In review. Les macrofossiles du Briovérien. In
903 *Stratotype Briovérien* (coords M. P. Dabard & D. Néraudeau). Muséum national d'Histoire
904 naturelle, Paris, Collection Patrimoine géologique, Biotope édition, Mèze.

905 NÉRAUDEAU, D., GOUGEON, R., DABARD, M.-P. & POUJOL, M. 2016. Les traces de
906 vie de la limite Ediacarien-Cambrien dans le Massif armoricain. *Géochroniques* **140**, 26-28.

907 NIO, S. D. & YANG, C. S. 1991. Diagnostic attributes of clastic tidal deposits: a review. In
908 *Clastic Tidal Sedimentology* (eds D. G. Smith, G. E. Reinson, B. A. Zaitlin & R. A.
909 Rahmani), pp. 3-28. Canadian Society of Petroleum Geologists, Memoir 16.

910 NOFFKE, N., GERDES, G., KLENKE, T. & KRUMBEIN, W. E. 2001. Microbially induced
911 sedimentary structures: a new category within the classification of primary sedimentary
912 structures. *Journal of Sedimentary Research* **71**, 649-656.

913 ORR, P. J. 2001. Colonization of the deep-marine environment during the early Phanerozoic:
914 the ichnofaunal record. *Geological Journal* **36**, 265-278.

915 PAPENTIN, F. 1973. A Darwinian evolutionary system: III. Experiments on the evolution of
916 feeding patterns. *Journal of Theoretical Biology* **39**, 431-445.

917 PASTEELS, P. & DORÉ, F. 1982. Age of the Vire-Carolles granite. In *Numerical Dating in*
918 *Stratigraphy* (ed G. S. Odin), pp. 784-791. Wiley New York, NY.

919 PFLÜGER, F. 1999. Matground structures and redox facies. *Palaios* **14**, 25-39.

920 PICKERILL, R. K. 1980. Phanerozoic flysch trace fossil diversity - observations based on an
921 Ordovician flysch ichnofauna from the Aroostook–Matapedia Carbonate Belt of northern
922 New Brunswick. *Canadian Journal of Earth Sciences* **17**, 1259-1270.

923 PLOTNICK, R. E. & KOY, K. 2005. Let us prey: simulations of grazing traces in the fossil
924 record. *Conference Proceedings, GeoComputation 2005: 8th International Conference on*
925 *GeoComputation*, 1-13.

- 926 RABU, D., CHANTRAINE, J., CHAUVEL, J. J., DENIS, E., BALÉ, P. & BARDY, P. 1990.
927 The Brioverian (Upper Proterozoic) and the Cadomian orogeny in the Armorican Massif.
928 *Geological Society Special Publication* **51**, 81-94.
- 929 REX, M. A. & ETTER, R. J. 2010. *Deep-sea biodiversity: pattern and scale*. Harvard
930 University Press, 368 pp.
- 931 RUNNEGAR, B. 1991. Precambrian oxygen levels estimated from the biochemistry and
932 physiology of early eukaryotes. *Global and Planetary Change* **5**, 97-111.
- 933 RUNNEGAR, B. N. 1992. Evolution of the earliest animals. In *Major events in the history of*
934 *life* (ed J. W. Schopf), pp. 65-93. Jones and Bartlett Publishers, Boston.
- 935 SACCO, F. 1888. Note di paleoicnologia Italiana. *Atti della Società Italiana di Scienze*
936 *Naturali* **31**, 151-192.
- 937 SANDERS, H. L. & HESSLER, R. R. 1969. Ecology of the deep-sea benthos. *Science* **163**,
938 1419-1424.
- 939 SCOTT, J. J., RENAUT, R. W., BUATOIS, L. A. & OWEN, R. B. 2009. Biogenic structures
940 in exhumed surfaces around saline lakes: an example from Lake Bogoria, Kenya Rift Valley.
941 *Palaeogeography, Palaeoclimatology, Palaeoecology* **272**, 176-198.
- 942 SEDORKO, D., NETTO, R. G. & HORODYSKI, R. S. 2019. Tracking Silurian-Devonian
943 events and paleobathymetric curves by ichnologic and taphonomic analyzes in the
944 southwestern Gondwana. *Global and Planetary Change* **179**, 43-56.
- 945 SEILACHER, A. 1956. Der Beginn des Kambriums als biologische Wende. *Neues Jahrbuch*
946 *für Geologie und Paläontologie, Abhandlungen* **103**, 155-180.
- 947 SEILACHER, A. 1967a. Vorzeitliche Mäanderspuren. In *Die Strassen der Tiere* (ed H.
948 Hediger), pp. 294-306. Vieweg+Teubner Verlag, Wiesbaden.

- 949 SEILACHER, A. 1967*b*. Fossil behavior. *Scientific American* **217**, 72-83.
- 950 SEILACHER, A. 1974. Flysch trace fossils: evolution of behavioural diversity in the deep-
951 sea. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 233-245.
- 952 SEILACHER, A. 1977. Pattern analysis of *Paleodictyon* and related trace fossils. In *Trace*
953 *fossils 2* (eds T. P. Crime & J. C. Harper), pp. 289-334. Geological Journal, Special Issue no.
954 9.
- 955 SEILACHER, A. 1986. Evolution of behavior as expressed in marine trace fossils. In
956 *Evolution of animal behavior: paleontological and field approaches* (eds J. A. Kitchell & M.
957 H. Nitecki), pp. 62-87. Oxford University Press, New York.
- 958 SEILACHER, A., BUATOIS, L. A. & MÁNGANO, M. G. 2005. Trace fossils in the
959 Ediacaran-Cambrian transition: behavioral diversification, ecological turnover and
960 environmental shift. *Palaeogeography, Palaeoclimatology, Palaeoecology* **227**, 323-356.
- 961 SEILACHER, A. & PFLÜGER, F. 1994. From biomats to benthic agriculture: a biohistoric
962 revolution. In *Biostabilization of sediments* (eds W. E. Krumbein, D. M. Paterson & L. J.
963 Stal), pp. 97-105. Bibliotheks und Informationssystem der Universität Oldenburg.
- 964 SHAHKARAMI, S., MÁNGANO, M. G. & BUATOIS, L. A. 2017. Ichnostratigraphy of the
965 Ediacaran-Cambrian boundary: new insights on lower Cambrian biozonations from the
966 Soltanieh Formation of northern Iran. *Journal of Paleontology* **91**, 1178-1198.
- 967 SHAOWU, N. 1998. Confirmation of the genus *Grypania* (megascopic alga) in Gaoyuzhuang
968 Formation (1434Ma) in Jixian (Tianjin) and its significance. *Progress in Precambrian*
969 *Research* **21**, 36-46.
- 970 SIMS, D. W., REYNOLDS, A. M., HUMPHRIES, N. E., SOUTHALL, E. J.,
971 WEARMOUTH, V. J., METCALFE, B. & TWITCHETT, R. J. 2014. Hierarchical random

972 walks in trace fossils and the origin of optimal search behavior. *Proceedings of the National*
973 *Academy of Sciences* **111**, 11073-11078.

974 SMITH, K. L., HOLLAND, N. D. & RUHL, H. A. 2005. Enteropneust production of spiral
975 fecal trails on the deep-sea floor observed with time-lapse photography. *Deep Sea Research*
976 *Part I: Oceanographic Research Papers* **52**, 1228-1240.

977 STEPANEK, J. & GEYER, G. 1989. Spurenfossilien aus dem Kulm (Unterkarbon) des
978 Frankenwaldes. *Beringeria* **1**, 1-55.

979 TESSIER, B., ARCHER, A. W., LANIER, W. P. & FELDMAN, H. R. 1995. Comparison of
980 ancient tidal rhythmites (Carboniferous of Kansas and Indiana, USA) with modern analogues
981 (the Bay of Mont-Saint-Michel, France). *Special Publication of the International Association*
982 *of Sedimentologists* **24**, 259-271.

983 TRAUTMANN, F., PARIS, F. & CARN, A. 1999. Notice explicative, Carte géol. France
984 (1/50 000), feuille Rennes (317). BRGM, Orléans, 85 pp.

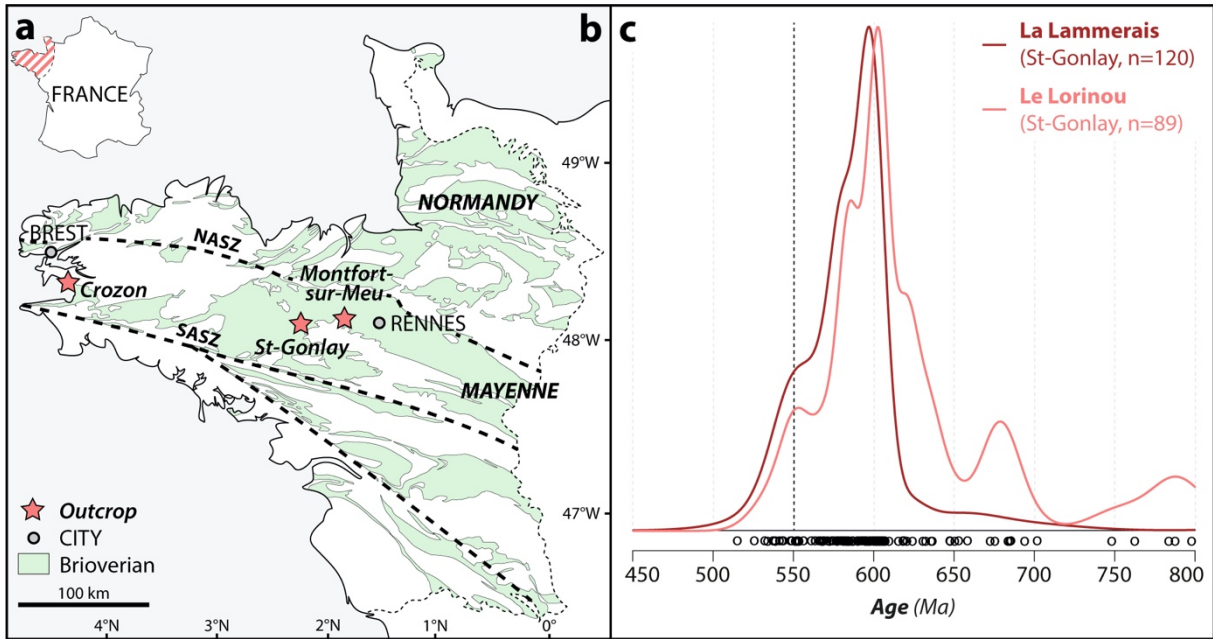
985 TURNER, J. T. 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton
986 blooms. *Aquatic microbial ecology* **27**, 57-102.

987 UCHMAN, A. 1998. Taxonomy and ethology of flysch trace fossils: revision of the Marian
988 Książkiewicz collection and studies of complementary material. *Annales Societatis*
989 *Geologorum Poloniae* **68**, 105-218.

990 UCHMAN, A. 2003. Trends in diversity, frequency and complexity of graphoglyptid trace
991 fossils: evolutionary and palaeoenvironmental aspects. *Palaeogeography, Palaeoclimatology,*
992 *Palaeoecology* **192**, 123-142.

- 993 VAN DER GRIENT, J. M. & ROGERS, A. D. 2015. Body size versus depth: regional and
994 taxonomical variation in deep-sea meio-and macrofaunal organisms. In *Advances in marine*
995 *biology* (ed B. E. Curry), pp. 71-108. Academic Press, Vol. 71.
- 996 VERMEESCH, P. 2018. IsoplotR: A free and open toolbox for geochronology. *Geoscience*
997 *Frontiers* **9**, 1479-1493.
- 998 VIDAL, G., JENSEN, S. & PALACIOS, T. 1994. Neoproterozoic (Vendian) ichnofossils
999 from Lower Alcludian strata in central Spain. *Geological Magazine* **131**, 169-179.
- 1000 WALCOTT, C. D. 1899. Pre-Cambrian fossiliferous formations. *Bulletin of the Geological*
1001 *Society of America* **10**, 199-244.
- 1002 WALTER, M. R., DU, R. & HORODYSKI, R. J. 1990. Coiled carbonaceous megafossils
1003 from the Middle Proterozoic of Jixian (Tianjin) and Montana. *American Journal of Science*
1004 **290**, 133-148.
- 1005 WALTER, M. R., ELPHINSTONE, R. & HEYS, G. R. 1989. Proterozoic and Early
1006 Cambrian trace fossils from the Amadeus and Georgina Basins, central Australia. *Alcheringa*
1007 **13**, 209-256.
- 1008 WALTER, M. R., OEHLER, J. H. & OEHLER, D. Z. 1976. Megascopic algae 1300 million
1009 years old from the Belt Supergroup, Montana: a reinterpretation of Walcott's
1010 *Helminthoidichnites*. *Journal of Paleontology* **50**, 872-881.
- 1011 WENT, D. J. 2017. Alluvial fan, braided river and shallow-marine turbidity current deposits
1012 in the Port Lazo and Roche Jagu formations, Northern Brittany: relationships to andesite
1013 emplacements and implications for age of the Plourivo-Plouézec Group. *Geological Magazine*
1014 **154**, 1037-1060.

- 1015 WHARTON, D. A. 2004. Survival strategies. In *Nematode Behaviour* (eds R. Gaugler & A.
1016 L. Bilgrami), pp. 371-399. CABI Publishing, Wallingford, UK.
- 1017 WILSON, J. P., GROTZINGER, J. P., FISCHER, W. W., HAND, K. P., JENSEN, S.,
1018 KNOLL, A. H., ABELSON, J., METZ, J. M., MCLOUGHLIN, N., COHEN, P. A. & TICE,
1019 M. M. 2012. Deep-water incised valley deposits at the Ediacaran-Cambrian boundary in
1020 southern Namibia contain abundant *Treptichnus pedum*. *Palaios* **27**, 252-273.
- 1021 XIA, B., LU, H., XIONG, B., HE, Y. & HU, B. 1987. *Spirodesmos kaihuensis* in the upper
1022 Ordovician flysch in the Kaihua County, west part of Zhejiang province. *Acta*
1023 *sedimentologica sinica* **5**, 73-79.
- 1024 YAN, Y. & LIU, Z. 1998. Does *Sangshuania* represent eukaryotic algae or trace fossils? *Acta*
1025 *Micropalaeontologica Sinica* **15**, 101-110.
- 1026 YANG, Z., YIN, J. & HE, T. 1982. Early Cambrian trace fossils from the Emei-Ganluo
1027 region, Sichuan, and other localities. *Geological Review* **28**, 291-298.
- 1028 YOCHELSON, E. L. & FEDONKIN, M. A. 1993. Paleobiology of *Climactichnites*, an
1029 enigmatic Late Cambrian fossil. *Smithsonian Contributions to Paleobiology* **74**, 1-74.
- 1030 ZHU, M. 1997. Precambrian-Cambrian trace fossils from eastern Yunnan, China:
1031 implications for Cambrian explosion. *Bulletin of National Museum of Natural Science* **10**,
1032 275-312.
- 1033



1034

1035

Figure 1. Geological map of northwestern France and new U-Pb dating. (a) Location of the

1036

Brioverian deposits in northwestern France. (b) Close-up showing the Brioverian deposits and

1037

the three localities with planispiral trace fossils. NASZ = North-Armorican Shear Zone;

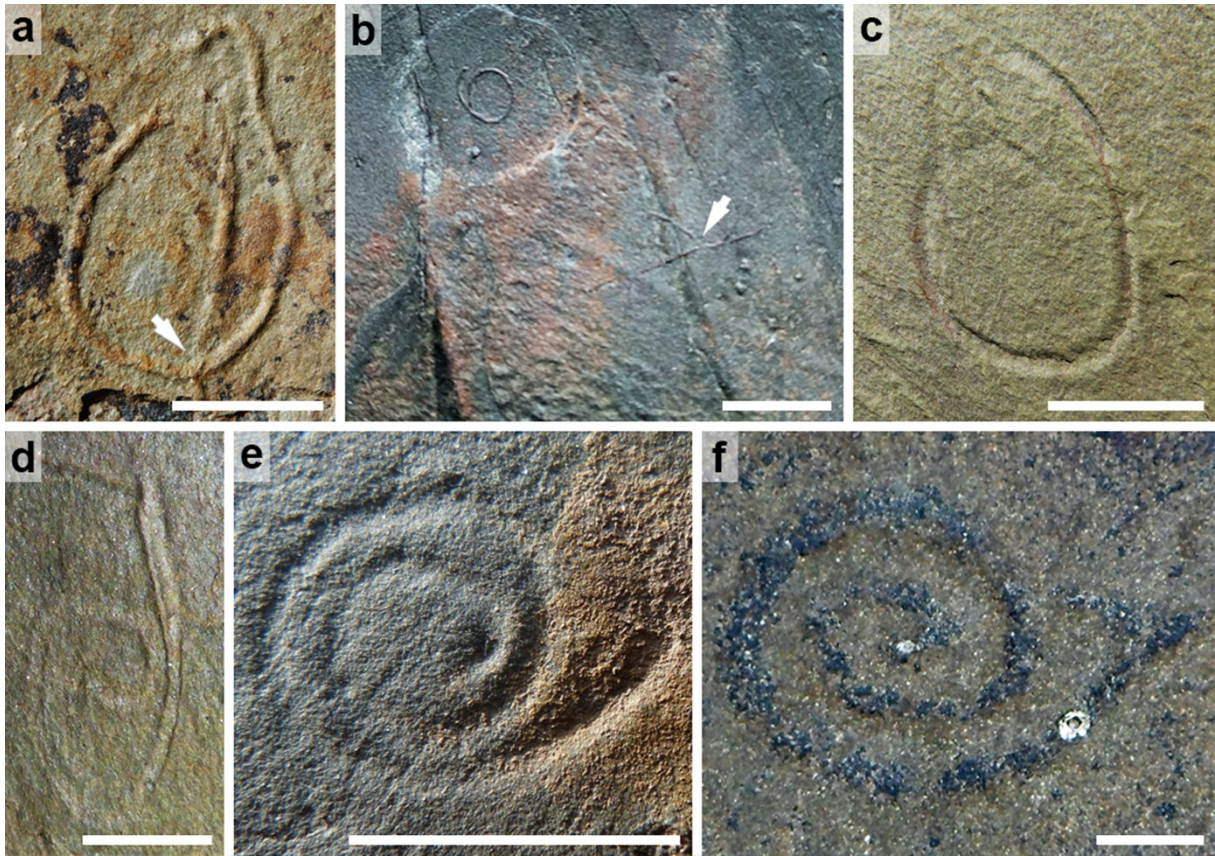
1038

SASZ = South-Armorican Shear Zone. (c) Kernel Density Estimation diagrams for ‘La

1039

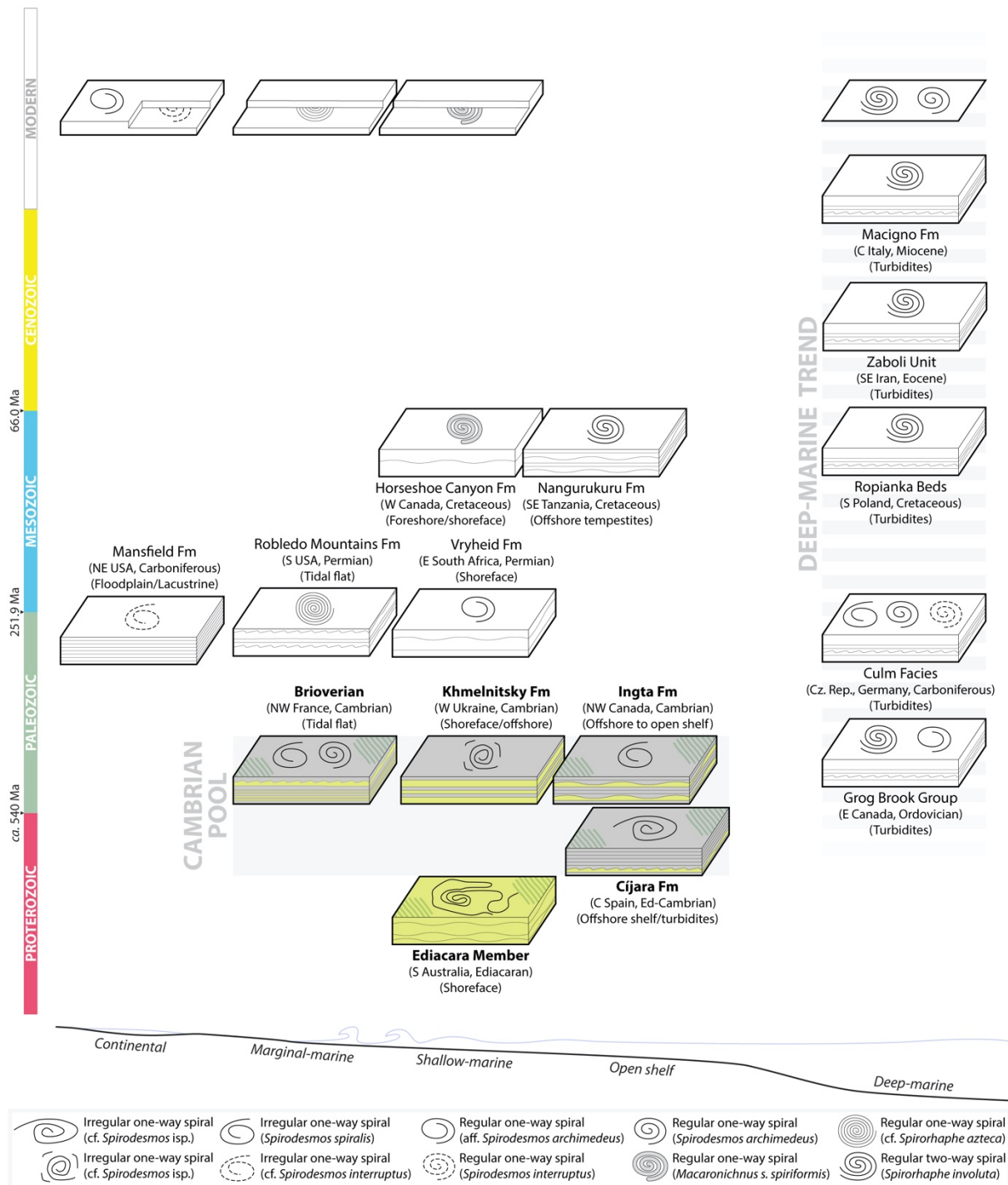
Lammerais’ and ‘Le Lorinou’ samples.

1040



1041
 1042 **Figure 2.** Planispiral trace fossils from the uppermost Brioverian beds of Brittany. (a)
 1043 Irregular one-way spiral trail with self-overcrossing (arrow) from ‘Le Bois-du-Buisson’. Note
 1044 that after the self-overcross, the course is following more-or-less closely the former loop (on
 1045 the right side). (b) Irregular one-way spiral trail without self-overcrossing from ‘Les
 1046 Grippeaux’ (upper left). Note the microbially-stabilized surface (bottom), the small-scale
 1047 branching trace fossils (arrow; cf. *Pilichnus*) and pits of uncertain affinity. (c, d) Irregular
 1048 one-way spiral trails without self-overcrossing from ‘Le Bois-du-Buisson’. (e, f) Regular one-
 1049 way spiral trails from ‘Les Grippeaux’ (e) and ‘La Plage-du-Goulien’ (f). Scale bars are 1 cm.

1050



1051
1052

Figure 3. Macro-evolutionary profile of planispirals in space and time, with emphasis on the

1053

Ediacaran and the Cambrian (colored diagrams). The Brioverian assemblage belongs to a

1054

marginal- to shallow-marine Cambrian pool. With the development of a deep-marine

1055

Ordovician-Recent trend and the gap (ca. 220 Ma) between the Cambrian pool and the next

1056

marginal- to shallow-marine planispirals of the Permian, an onshore-offshore migration is

1057 suggested from the Cambrian to the Ordovician. (Reports from the deep-marine are not
1058 exhaustive in this diagram.)