

1 **The early Cambrian deposits of the Le Rozel Formation (Normandy, NW France): Insight**
2 **into a new ichnofossil assemblage**

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9

10 **Abstract**

11 Cambrian trace fossils provide critical clues to track the evolution and diversification of early
12 animals. However, this unprecedented radiation and the full understanding of the environmental and
13 ecological drivers that led to their success are still shrouded by a dearth of fossil evidence and a
14 limited number of fossil sites. Here, we describe a unique trace fossils assemblage from the lower
15 Cambrian Le Rozel Formation in Normandy (Northwestern France) composed of the following
16 ichnogenera: *Archaeonassa*, *Bergaueria*, *Helminthoidichnites*, *Helminthopsis*, *Nereites*,
17 *Psammichnites*, and *Treptichnus*. Trace fossils are exquisitely preserved on top of strata (i.e.
18 epirelief), and are distributed along the entire thickness of the siliciclastic succession of about 200
19 meters. This thick sedimentary succession shows numerous sedimentary environments with ripples
20 generated by unidirectional current processes or by oscillatory processes, such as Hummocky cross-
21 stratification (HCS) storm facies, tidal facies with flaser stratification and unidirectional current
22 ripples. In addition, syneresis cracks (also called shrinkage cracks), and microbially induced
23 sedimentary structures (MISS), suggest that the Le Rozel Formation was deposited in a shallow
24 marine shelf environment. New U-Pb dating of detrital zircon grains suggests a late Ediacaran
25 maximum deposition age of 549 ± 3 Ma. This dating is compatible with the three-dimensional
26 burrow systems (i.e. *Treptichnus*) and the large sediment bulldozers (i.e. *Nereites*, *Psammichnites*)
27 found in the Le Rozel Formation, and together they suggest that the trace fossils assemblage was
28 deposited during the Cambrian period, likely during the Fortunian stage. The ichnofauna described
29 from the Le Rozel Formation complements the worldwide trace fossil record around this critical
30 time of life history.

31 **Keywords:** Armorican Massif; Fortunian; Invertebrate ichnofauna; Le Rozel Formation; Trace-
32 fossil record; U-Pb dating.

33 1. Introduction

34 The Cambrian Period is distinguished by the rise of many extant animal clades and the
35 establishment of metazoan-dominated ecosystem referred to as the ‘Cambrian Explosion’
36 (Marshall, 2006; Erwin et al., 2011; Briggs, 2015; Darroch et al., 2018). Besides the scarcity of
37 body fossils, the early Cambrian (ca. 539-521 Ma) is marked in many places by siliciclastic
38 successions locally rich in trace fossils (e.g., Crimes, 1987; Jensen, 1997; Carbone and Narbonne,
39 2014; Laing et al., 2019). The importance of ichnology to reconstruct early Cambrian ecosystems
40 has been exemplified with the definition of the Cambrian GSSP (Global Boundary Stratotype
41 Section and Point) in 1992 at Fortune Head, in Burin Peninsula (the Chapel Island Formation,
42 Newfoundland, Canada). This Formation records the appearance of complex and penetrative
43 burrows typical of the *Treptichnus pedum* Ichno-Assemblage Zone, above the uppermost Ediacaran
44 *Harlaniella podolica* Zone (Crimes 1987; Narbonne et al., 1987; Brasier et al., 1994).
45 Subsequently, the Ediacaran–Cambrian boundary has been the subject of many studies worldwide,
46 including, for instance, the Mackenzie Mountains succession in Canada (Narbonne and Aitken,
47 1990; MacNaughton and Narbonne, 1999; Carbone and Narbonne, 2014), the Meishucun sections
48 in China (Crimes and Jiang, 1986; Zhu, 1997), the Tanafjord sections in Norway (McIlroy and
49 Brasier, 2017) as well as the Death Valley succession in the United States (Waggoner and
50 Hagadorn, 2002; Jensen et al., 2002; Corsetti and Hagadorn, 2000) and the Nama group in southern
51 Namibia (Darroch et al., 2021; Turk et al., 2022).

52 Ediacaran–Cambrian trace fossils have also been mentioned in the Armorican Massif of
53 northwestern France, including the Brittany and Normandy regions (Doré, 1994; Gougeon et al.,
54 2018). However, the trace fossils were poorly described and, crucially, their depositional age was
55 uncertain. On the one hand, the Brittany region lacks uncontroversial strata of Cambrian age and
56 yields an assemblage of simple horizontal trace fossils and circular body fossils typical of the late
57 Ediacaran period in the Brioverian series covering the Precambrian-Paleozoic boundary (cf.
58 Gougeon et al. 2018; Néraudeau et al., 2018; Coutret and Néraudeau, 2022). On the other hand, the
59 Normandy region (in the Cotentin Peninsula) yields a skeletal fossil record (archeocyatha, hylothes,
60 trilobites) characteristic of the early Cambrian (Bigot, 1925, 1926; Doré and Reid, 1965; Doré,
61 1969, 1994; Doré et al., 1984; Pillola, 1993). The Le Rozel Formation in Normandy, presented in
62 this paper, has received little attention. Pioneer work by Hébert (1886) mentioned the evidence of
63 organic traces in shales from the Rozel Cape. Later, Lebesconte (1900:pl. XIV) described
64 *Montfortia rhedonensis* Lebesconte, 1886 in shale from the Le Rozel Formation, a common
65 ichnofossil from the Brioverian (Ediacaran–Fortunian) of the Armorican Massif, recently
66 reassigned to trace fossils such as *Helminthoidichnites* Fitch, 1850 and *Helminthopsis* Heer, 1877

67 (Gougeon et al., 2018). Doré et al. (1984), Doré (1994) and Went (2020) collectively noted the
68 presence of *Bergaueria* Prantl, 1945, *Cruziana* d’Orbigny, 1842, *Diplichnites* Dawson, 1873,
69 *Diplocraterion* Torell, 1870, *Monomorphichnus* Crimes, 1970, *Neonereites* Seilacher, 1960,
70 *Phycodes* Richter, 1850, *Planolites* Nicholson, 1873, *Rusophycus* Hall 1852, *Taphrhelminthopsis*
71 Sacco, 1888 and *Teichichnus* Seilacher, 1955 in the Le Rozel succession. However, no formal
72 taxonomic treatment of the trace fossil assemblage has been undertaken so far. Importantly, the age
73 of the Le Rozel Formation needs to be reconsidered to contextualize the ichnofossil assemblages.

74 The main objectives of the present work are : (1) to refine and revise the taxonomy of trace
75 fossils documented from the Le Rozel Formation; (2) to provide new U-Pb radiometric dating on
76 detrital zircon grains from sandstone sampled within the formation; (3) to discuss the age of the
77 trace fossil assemblage and to consider the ethological significance of the trace fossils in relation to
78 the worldwide ichnostratigraphic scheme of the late Ediacaran and early Cambrian; and (4) to
79 compare and contrast the trace fossil assemblage from the Le Rozel Formation with the assemblage
80 from the Brioverian (Ediacaran–Fortunian) series of Brittany.

81 **2. Geological Description**

82 *2.1. General background*

83 The Le Rozel Formation crops out along the northwestern coastline of the Cotentin
84 Peninsula, located in Normandy (NW France) (Fig. 1A), which provides large exposures of
85 marine strata from upper Proterozoic to early Paleozoic time related to the Cadomian orogenic
86 cycle (ca. 750–540 Ma). The Armorican Massif can be subdivided into the three following majors
87 North-Armorican, Central-Armorican, and South-Armorican domains (Ballèvre et al., 2009). The
88 Normandy region is in the North-Armorican domain where the Cadomian basement was slightly
89 deformed compared to the rest of the Armorican Massif (Dissler and Gresselin, 1988). The
90 Cadomian basement is composed of a volcano-sedimentary succession and plutonic rocks from
91 the Ediacaran to the early Cambrian (Dabard et al., 2021). During this period, the Armorican
92 Massif experienced several extensive and compressive episodes resulting from the development
93 of the Cadomian orogenic belt of peri-Gondwanan Europe (e.g., series of complex sedimentary,
94 magmatic, and tectono-metamorphic events) (D’Lemos et al. 1990; Linnemann et al., 2008,
95 2021). After the erosion of the Cadomian chain, a large Cambrian marine sedimentary succession
96 dominated by siliciclastic sediments of shallow environments was deposited. But, some other
97 sediments from fluvial or estuarine deposits (Bréhec and Erquy in Brittany) are also supposed to
98 be Cambrian in age (Went and Andrews, 1990; Went and McMahon, 2018; Went 2019). In fact,
99 some doubts still exist about these sections which are also interpreted as Ordovician deposits
100 based on fossil occurrence and igneous intrusions (Bonjour et al., 1988; Rolet and Plusquellec,

101 2016). Therefore, the interrogations between these two successive depositions of siliciclastic
102 sediments led to questioning the age of the marine transgression in North Brittany and its possible
103 diachronism feature among the Cambrian - Ordovician shallow marine deposit (see Doré, 1972,
104 1994). Then, Ordovician strata reflect a period of renewed subsidence and marine transgression
105 overlaying the Armorican Massif. These sedimentary events led to the widespread deposition of
106 shallow marine Armorican sandstones ('Grès Armoricain') that covered a part of the Cotentin
107 Peninsula (Doré, 1969,1972; Doré et al., 1977).

108

109 2. 2. *The lower Cambrian from the study area in Normandy*

110 The Cambrian outcrops from the Armorican Massif are mostly located in its northeastern
111 part, especially in Normandy (Fig. 1), but also in the Maine regions and small areas in the south
112 Vendée region (see Doré, 1994: fig. 3). The early Cambrian deposits from this study area (Fig.
113 1B) are composed of both siliciclastic and carbonate sediments containing trace fossils and the
114 oldest shelly fauna from the Armorican Massif (Doré and Reid 1965; Doré, 1969; Doré et al.,
115 1977, 1984). Cambrian strata (Fig. 1B) are mostly dominated by thick siliciclastic successions
116 (e.g., La Hague, Le Rozel, and Carteret formations). But some younger carbonates occur also in
117 Carteret (interbedded with sandstone and siltstone layers) as well as in Saint-Jean-de-la-Rivière
118 (dark blue-grey oolitic and bioclastic limestones). Stratigraphically, the sandstone and siltstone
119 beds of the Le Rozel Formation are a *ca.* 200 m thick succession. It is exposed in a broad area
120 between Le Rozel cliffs and the Channel (Fig. 2A-C). The Cambrian strata and the other
121 Paleozoic formations from the Le Rozel area are unconformably deposited on top of the Saint-
122 Germain-Le-Gaillard Complex which is composed of an ignimbrite crystalline basement, and on
123 the overlapping Couville Conglomerate and Arkose Formation (ca. 400 m) (Doré et al., 1984;
124 Dissler and Gresselin, 1988; Doré, 1994:fig.4; Guerrot et al., 1992). The ignimbrites of Saint-
125 Germain-le-Gaillard, inherited from the Cadomian orogenic cycle, have been previously dated
126 with a poorly constrained U-Pb age of 531 ± 20 Ma (Guerrot et al., 1992). However, recently a
127 sample of ignimbrites collected in the Grosville quarry (Fig. 1B) yielded a more precise U-Pb age
128 of 550.6 ± 5.0 Ma (Néraudeau et al., 2023). In addition, the Le Rozel Formation is located below
129 the Cambrian Carteret (ca. 650 m) and Saint-Jean-de-la-Rivière (ca. 170-?200 m) formations
130 (Fig. 1B) which contain skeletal (e.g. hyolithes) and microbial (stromatolites) fossil record (Doré,
131 1969; Doré et al., 1984; Pillola, 1993; Doré, 1994). The paleontological remains were found in
132 Carteret and Saint-Jean-de-la-Rivière, mostly from diagenetic calcareous nodules. The
133 fossiliferous calcareous nodules contain fossils of cancellorids, hyolithes, and sponges (*Allonia*
134 *tripodophora* Doré and Reid, 1965), which were dated Cambrian Stage 2 by biostratigraphy. Are

135 also present younger deposits from Cambrian Stage 3, dated by biostratigraphy, containing
136 trilobites (*Bigotina bivallata* Cobbold, 1935), archaeocyatha, and the lower Cambrian trace fossil
137 *Astropolichnus hispanicus* Crimes et al., 1977 as well as planar to columnar stromatolites (Bigot,
138 1925, 1926; Doré and Reid, 1965; Doré, 1969; Doré et al., 1984; Pillola, 1993; Pillola et al.,
139 1994).

140 Therefore, the Cambrian deposits from the Le Rozel Formation are older than the
141 Cambrian series containing shelly organisms (e.g. trilobites, chancellorids, and archaeocyatha)
142 but younger than their ignimbrite basement dating from ca. 550 Ma (Néraudeau et al., 2023).
143 Moreover, the complex and penetrative burrows like *Treptichnus pedum* Seilacher, 1955, typical
144 of the base of the Cambrian (Narbonne et al., 1987) are abundant in the Le Rozel Formation.
145 These biostratigraphic data support a post-Ediacaran to Fortunian age for the Le Rozel
146 Formation. The Le Rozel Formation has been described as fine-grained sandstone beds where the
147 bedding planes locally show primary sedimentary structures produced by unidirectional current
148 flow or oscillatory flow, such as linguoidal ripples and hummocky cross-stratification (Doré et
149 al., 1984; Went 2019, 2020). In addition, patchy MISS (Microbially Induced Sedimentary
150 Structures *sensu* Davies et al., 2016) have been mentioned by Went (2020) and published by
151 Davies et al. (2016:fig. 1.v) in form of “Kinneyia”-like wrinkle structures associated with trace
152 fossils. Finally, the Le Rozel Formation was interpreted by Went (2019, 2020) as an offshore
153 shallow marine environment that was periodically reworked by storms. Although these outcrops
154 were mentioned in large-scale studies, such as facies sequence stratigraphy in northwestern
155 France (e.g., Went, 2019, 2020), the Le Rozel Formation remains understudied although it has
156 important ichnological and sedimentological potential for the understanding of early Cambrian
157 life and benthic ecosystems.

158

159 **3. Material and methods**

160 All the material used for this study has been observed and sampled in the outcrops along the
161 coastline of the Rozel Cape (Fig. 3). The Cambrian series of the Rozel Cape are affected by faults
162 that dislocate deposits into compartments whose stratigraphic succession is not perfectly
163 continuous. Nevertheless, all the different compartments possess similar sedimentary and
164 paleontological characters, which allow us to exclude major tectonic dislocations. For this reason,
165 several logs have been carried out (Figs. 3 and 4), but for the time being it is not possible to
166 propose a vertical arrangement of these logs. Research has been conducted between the two
167 following GPS coordinates (49°28'33.27"N 1°50'41.00"W; 49°28'16.12"N 1°50'41.92"W; see the
168 black stars on Fig. 3).

170 *3. 1. Ichnotaxonomy*

171 The trace fossils have been identified based on the description of ichnotaxobases and
 172 morphological features corresponding to major behavioral aspects and are used to differentiate the
 173 ichnotaxa (see Buatois and Mángano, 2011). In keeping with the general consensus, five
 174 ichnotaxobases are applied: (1) general form, (2) wall, (3) branching, (4) fill, and (5) spreite
 175 (Buatois and Mángano, 2011). In the present study, we follow the preservation nomenclature of
 176 Seilacher (1964) as recommended by Buatois and Mángano (2011).

177 *3. 2. Bioturbation*

178 The study of bioturbation from both horizontal bedding planes and vertical sections is
 179 strongly influenced by the outcrop style. Following Shillito and Davies (2020), the exposed outcrop
 180 morphology (e.g., stepped, cliff, or coastal) determines, more or less, the sedimentary structures and
 181 trace fossils that can be observed. For example, the horizontal bedding plane from a cliff section is
 182 more difficult to observe than the vertical section (Shillito and Davies 2020). Thus, the presentation
 183 of the trace fossils could be a direct result of the different outcrop exposure. In Normandy, the Le
 184 Rozel Formation provides large exposures of horizontal coastal outcrops. The study of vertical
 185 sections is limited or cannot be realized with regularity.

Bioturbation Index (BPBI)	BPBI 1	BPBI 2	BPBI 3	BPBI 4	BPBI 5
Bioturbation intensity	No bioturbation (0% disruption)	sparse bioturbation (0-10% disruption)	low bioturbation (10-40% disruption)	moderate bioturbation (40-60% disruption)	intense bioturbation (60-100% disruption)
Additional remarks		discrete and isolated trace fossils	discrete trace fossils and partial zones of generalized disruption	discrete traces and zones of generalized disruption	bedding plane surface disrupted by the activity of animals

186

187

188

189 Table 1. Bioturbation index from Miller and Smail (1997)

190 Bedding-plane bioturbation indices plotted on stratigraphic logs (Figs. 3, 4) were obtained
191 by using the semi-quantitative field method of Miller and Smail (1997: fig. 2). Each index
192 corresponds to a relative bioturbation rate (Table 1). To facilitate the reading of the sedimentary
193 log, the index 1 has been removed (Table 1).

194

195 3.3. LA-ICP-MS geochronology on detrital zircon grains

196 U-Pb geochronology of detrital zircon grains was conducted by *in situ* laser ablation
197 inductively coupled mass spectrometry (LA-ICP-MS) in the GeOHeLiS analytical platform
198 (University of Rennes) using an ESI NWR193UC Excimer laser coupled to a quadrupole Agilent
199 7700x ICP-MS. The analytical protocol can be found in Supplementary material Table S1 and
200 Manzotti et al. (2015). In this study, we kept only the analyses that were 90–110% concordant with
201 the age calculations. To ensure a statistically robust estimate of the maximum depositional ages,
202 they were calculated only when the youngest cluster of values is made of at least 3 concordant
203 values obtained on three different grains returning the same apparent age within error, as proposed
204 by Dickinson and Gehrels (2009).

205 4. Result

206 4.1. Sedimentology

207 The deposits of the Le Rozel Formation are dominated by greenish and grey terrigenous
208 sediments (Figs. 3, 4), while reddish-purple and greenish alternations are observed only at the base
209 of the section south of the Rozel Cape (Log Roz-04). The most frequent grain sizes in these deposits
210 are siltstones and fine sandstones, while clays are present and associated with flaser-bedding
211 structures. The stratigraphic organisation of the sedimentary deposits is mainly decimetric and
212 pluridecimetric in the northern section of the Rozel Cape (Log Roz-01 and Log Roz-02, Figs. 3 and
213 4A-B), while in the outcrops of the section south of the Rozel Cape (Log Roz-03 and Log Roz-04,
214 Figs. 3, 4C-D) the strata are mainly centimetric and infracentimetric.

215 Throughout the succession of the Le Rozel Formation, microbially induced sedimentary structures
216 (MISS) were observed on top of sedimentary beds and attested to the presence of ancient microbial
217 mats activity (Noffke, 2010; Davies et al., 2016). We report patterned assemblages of fine, mosaic-
218 like regular reticulate ridges texture (Fig. 5A). Other patchy wrinkles structures (Fig. 5B), with sub-
219 linear and aligned patterns, have also been documented.

220 In the section north of Cape Rozel (Log Roz-01 and Log Roz-02, Figs. 3 and 4), the most
221 representative sedimentary structures are the Hummocky Cross-Stratification (HCS) of multimetre
222 wavelength and decimetric to pluridecimetric in thickness. The HCS are separated by layers of
223 clayey siltstones or are amalgamated together to form metric thicknesses of fine sandstone with
224 HCS lamination. These storm deposits are organised into pluri-metrically thick
225 prograding/retrograding depositional sequences that represent the Genetic Sequences (Very High
226 Frequency Depositional Sequences). Immediately below the Maximum Flooding Surfaces (MFS) of
227 the Genetic Sequences, there is often a horizon of nodular diagenetic concretions (Fig. 5C-D),
228 which are either carbonate (4 cm to more than 20 cm in diameter; (Fig. 5C) or phosphatic (multi-
229 millimetre thick; (Fig. 5D)) in composition. These levels are diagenetic concretions that highlight
230 the condensation levels of high-frequency depositional sequences and are placed at the inflection
231 point of the of rising of the eustatic curve (Dabard and Loi, 2012; Dabard et al., 2007). These
232 deposits and their stratigraphic organisation are consistent with shallow terrigenous platform
233 environments dominated by storm action. In the section south of the Rozel Cape (Log Roz-03 and
234 Log Roz-04, Figs. 3, 4C-D) HCS become rare, and the dominant sedimentary structures consist of
235 unidirectional current ripples with straight to sinuous crest lines (Fig. 5E-F). These 2D ripples have
236 a wavelength ranging from 10 to 20 cm and an amplitude ranging from 1 to 2.5 cm. Flaser
237 stratification is widespread and is the dominant and most represented facies. The most abundant
238 concentrations of bioturbations, with horizontal development, are observed in these depositional
239 facies (e.g., Fig. 5G). For this reason, in the Log Roz-03 section (Figs. 3, 4C), detailed observations
240 of the depositional facies were made (Fig. 6) and the stratigraphic organisation was represented in
241 two logs (Fig. 7, LOG 1, 2). In this portion of the Le Rozel Formation, flaser facies deposits are
242 abundant and are organised in metric-thick strata interbedded with centimetric levels of fine
243 sandstone with unidirectional current ripples or plane lamination. The flaser facies consists of
244 millimetric laminations (ca. 1 to 8 mm) of very well sorted fine sandstone interbedded with
245 millimetric laminations of silty mudstone, rich in organic matter (Fig. 8). Horizontal bioturbations
246 are present in almost all the laminae of this flaser facies. The metric flaser strata exhibit a cyclic,
247 decimetre-thick internal organisation determined by increasing/decreasing variations in the
248 thicknesses of the sandy and clayey laminae (Fig. 7). The unidirectional current ripples (Fig. 8A-C)
249 are characterised by Lee Side laminae consisting of alternating beddings of sand and silty clay grain
250 size (flaser ripple bedding). The small amplitude of these ripples (maximum 2.5cm) and the overall
251 depositional characteristics of this Flaser facies allow the assessment of a very shallow deposit
252 bathymetry consistent with a tidal flat environment.

253 The totality of facies of the Le Rozel Fm. clearly show shallow-water deposits compatible
254 with a terrigenous marine platform evolving between tidal plain and upper offshore sedimentary
255 environments.

256

257 4. 2. *Bioturbation intensity*

258 The Le Rozel Formation displays numerous well-preserved bioturbated bedding planes (Fig.
259 5I). These surfaces bearing trace fossils are widespread throughout the section and were analyzed
260 by conducting a bioturbation index (BPBI *sensu* Miller and Smail 1997). BPBI has been reported
261 throughout the Le Rozel Formation (4 sections, see Fig. 4) for a total number of 34 slabs where the
262 bioturbation occurred (number of total slabs $n=34$; see Fig. 4). Trace fossil slabs yield BPBI values
263 ranging from BPBI = 2 to 5. The majority ($n=28$) of traces fossils slabs in the Le Rozel Formation
264 yield primary BPBI = 2 (>10% of bioturbation), and additional five slabs yield BPBI = 3 (10-40%
265 of bioturbation), as well as one remaining slab with high bioturbation rate yield BPBI = 5 (60-100%
266 of bioturbation).

267

268 4. 3. *Thin section analyses*

269 To complete the sedimentological data and explore sediment-bioturbation features, vertical
270 polished sections and thin sections were also created and examined (Fig. 9). A thin section was
271 selected because it can be considered as representative of the Le Rozel Formation: its lithology is
272 composed of alternating millimetric laminae of fine sandstone and silty mudstone, both of which
273 are very well sorted and show a classic flaser-type stratification (Fig. 9A). The presence of abundant
274 organic matter (linked to the MISS) in the silty clay laminas is evident by their brown color (Fig. 9
275 B,C). They clearly show bioturbated sediment with distinctive burrows from the sub-surface
276 sedimentary layer (Fig. 9A). The infaunal bioturbation corresponds to a horizontal burrow with
277 circular to oval-shaped filled by coarse-grained (mostly silicate) (Fig. 9B-C). The bioturbated layer
278 (level n°2 - Fig. 9B-C) is bounded by two coarser layers of grained siltstone deposits (level n°1, 3 -
279 Fig. 9B-C) similar to the burrow infill (yellow arrow - Fig. 9B).

280

281 4. 4. *Detrital zircon geochronology*

282 In the absence of biostratigraphic or magmatic constraints, detrital zircon U–Pb
283 geochronology can be a powerful tool to provide a maximum age of deposition for sedimentary
284 rocks (Dickinson and Gehrels, 2009; Manzotti et al., 2015; Witt et al., 2017). Precise temporal

285 constraints can be provided because zircon grains are chemically stable during weathering and
286 mechanically durable during transport toward the depositional environments. They derive from the
287 erosion of basement rocks as well as syn-depositional or closely contemporaneous volcanic rocks,
288 located either within or outside of the basin.

289 Three sandstone samples (Roz-01, Roz 21-2, and Roz 21-4 housed in the IGR collection)
290 were selected for detrital zircon geochronology (see Fig. 4). They are located at different
291 stratigraphic levels within the sedimentary succession of the Le Rozel Formation. The first striking
292 feature is that, except for 6 grains, the 270 zircon grains that were analyzed for these three samples
293 yield very consistent crystallization ages bracketed between 600 and 550 Ma (see Table S2 in
294 supplementary material and Figure 10). This indicates a common and limited source of supply for
295 these three fine-grained sandstones. In more detail, 98 grains were analyzed in sample ROZ-01, out
296 of which 82 are more than 90% concordant (Fig.10). The youngest cluster consists of 10 grains that
297 yield a Concordia age of 549 ± 3 Ma (Fig. 10A, inset) considered as the maximum deposition age
298 for this sample. One hundred and eighteen grains were analyzed for sample ROZ 21-2. Ninety-nine
299 of them are more than 90% concordant (Table S2). The youngest cluster of 60 grains returns a
300 Concordia age of 549.7 ± 2.8 Ma (Fig. 10B, inset) which we consider again as the maximum age of
301 deposition for this sandstone. This age is identical to the maximum deposition age found for sample
302 Roz-01 and corresponds to the age of the underlying ignimbritic flow dated by Néraudeau et al.
303 (2023) which is, therefore, the most probable source for these zircon grains. For the last sample,
304 ROZ 21-4, only 60 grains were analyzed (Table S2 and Fig. 7C=new10C). The youngest cluster of
305 18 zircon grains yields a Concordia date of 565.5 ± 8.1 Ma (Fig. 10C, inset), which we interpret as
306 the maximum age of deposition for this sample. This sandstone is stratigraphically younger than
307 sample ROZ-01 (see Fig. 4) but the available zircon data yield an older maximum deposition age.
308 This could be the sign that the source of zircon grains changed between the deposition of these two
309 sandstones, with the presence of different (older) zircon crystals in the new source that did not
310 encompass the underlying ignimbritic flow anymore as no 550 Ma old zircon have been found in
311 ROZ 21-4. In conclusion, this detrital zircon dating study demonstrates that the fossiliferous
312 sediments of the Le Rozel Formation were deposited after 549 ± 3 Ma, therefore probably during
313 the early Fortunian.

314

315 4. 5. *Systematic ichnology*

316 Most of the trace fossils described herein were studied and photographed in the field,
317 particularly those that were difficult to collect without damage, while additional specimens are

318 housed in the IGR under the collection numbers IGR-PAL-23262 to 23266. Ichnotaxa are listed
319 alphabetically.

320 Ichnogenus *Archaeonassa* Fenton and Fenton, 1937

321 *Archaeonassa fossulata* Fenton and Fenton, 1937

322 (Fig. 11A-B)

323 **Material:** Two specimens were observed and photographed in the field.

324 **Description:** Horizontal, unbranched, straight to sinuous trail with a median groove flanked
325 by two distinct convex parallel lateral levees. Trail slightly curving, but exhibits no loops or self-
326 crossings. Trace width is 6-11 mm. Trace maximal length is 200 mm. Preserved as epirelief on fine-
327 grained siltstone and sandstone layers.

328 **Discussion:** The lateral levees are well-developed, continuous, and preserved throughout the
329 trail. The trace fossils are attributed to *Archaeonassa fossulata*, as defined by the type specimens
330 erected by Fenton and Fenton (1937) and also revised later by Yochelson and Fedonkin (1997). *A.*
331 *fossulata* is interpreted as a grazing trace, and potential trace-makers include a wide variety of
332 invertebrates, such as gastropods (Buckman, 1994; Yochelson and Fedonkin, 1997). *Archaeonassa*
333 is a simple horizontal trail (Buatois et al., 2017) that first appeared during the Ediacaran period and
334 is typically associated with shallow marine environments, such as intertidal flats or lagoons (Jensen
335 et al., 2006; Uchman & Martyshyn, 2020).

336 *Archaeonassa* isp.

337 (Fig. 11C)

338 **Material:** Three specimens were observed and photographed in the field. One slate with one
339 specimen is housed at the Geological Institute of Rennes 1 under the number IGR-PAL-23262.

340 **Description:** Horizontal, unbranched, straight to slightly meandering, occasionally
341 preserved with loops forming self-crossings. Slightly concave median groove flanked by two
342 convex lateral levees, not preserved continuously on the trail. Central groove typically wider than
343 levees. Trace width is 3-11 mm. Maximum trace length is 70 mm. Preserved as negative epirelief
344 on siltstone to fine-grained sandstone layers.

345 **Discussion:** The distinctive lateral levees present in this horizontal trail distinguish it from
346 *Gordia* Emmons 1844, *Helminthoidichnites*, and *Helminthopsis* (Jensen et al., 2006: fig. 2;
347 Buatois and Mángano, 2012b). The specimen (Fig. 11C) shares similarities with *Gordia* due to
348 the presence of a loop forming a characteristic self-crossing. However, the two lateral levees are
349 well-developed and flank the median groove. Consequently, the preferred attribution of

350 *Archaeonassa* isp. is selected rather than *Gordia* isp. following Buckman (1994: fig. 2E) and
351 Jensen (2003: fig. 3A). In fact, both authors reported *Archaeonassa* with a loop and self-crossing
352 pattern (*Archaeonassa fossulata*; *Archaeonassa* isp., respectively). At this stage of research, open
353 nomenclature as *Archaeonassa* isp. is preferred, because the "self-crossing pattern" is not a
354 diagnostic character of *Archaeonassa fossulata* erected by Fenton and Fenton (1937). Further
355 studies on the genus *Archaeonassa* are in progress to critically review various specimens
356 displaying the characteristics of *Archaeonassa* isp. presented here. The simple and horizontal
357 morphology of the trace, without resting evidence, suggests continuous movement left behind by
358 the trace-maker, providing strong evidence of confirmed locomotion.

359
360 Ichnogenus *Archaeonassa* cf. *fossulata* Fenton and Fenton, 1937

361 (Fig. 11D-F)

362 **Material:** Three specimens observed and photographed in the field. One slate with one
363 specimen is housed at the Geological Institute of Rennes 1 under the number IGR-PAL-23263.

364 **Description:** Horizontal, unbranched, curve to slightly meandering, with discontinuous and
365 isolated segments (or lobes with coffee bean shapes) preserved like a string. Discontinuous
366 segments are composed of a series of "dotted lines", slightly 'bilobed' on the flanks, and are usually
367 wider than the median furrow. A maximum of 7 segments are preserved in a chain (Fig. 11D-F).
368 The lobes can be asymmetric. The continuous trail is flanked by fine, irregular, non-homogeneous
369 lateral levees (Fig. 11D) that appear to be symmetric. Trace width is 3-5 mm. Maximum trace
370 length raises more than 330 mm. Discontinuous segments are spaced from 5 to 15 mm. Preserved as
371 positive epirelief on fine-grained siltstone layers.

372 **Discussion:** According to Yochelson and Fedonkin (1997), the trace fossil can be attributed
373 to the ichnogenus *Archaeonassa* Fenton and Fenton, 1937, which is exemplified by *A. fossulata*. It
374 is characterized by "a central furrow bordered by rounded ridges." However, our specimens *A. cf.*
375 *fossulata* display as well questioning discontinuous sections, also called lobes with coffee bean
376 shapes, that can't make the attribution *A. fossulata* surely correct. However, recently Uchman and
377 Martyshyn (2020) published disconnected lobes, with slightly undulating ridges (mostly 3–4 mm)
378 divided by the central furrow under the name *A. cf. fossulata*. To solve the taxonomic issues, the
379 most appropriate action is to assign the described trace fossil as *A. cf. fossulata* (Fig. 11D-G) using
380 an open nomenclature while being congruent with Uchman and Martyshyn (2020) in which
381 *Archaeonassa* can be treated under two types of preservation (Preservation I: type *A. fossulata*,
382 continuous trail with lateral levees divided by the central furrow; Preservation II: *A. cf. fossulata*,

383 discontinuous lobes divided by the central furrow; Fig. 11G). In fact, those two types of
384 preservation show a combination of both deep and shallow preservation, with the initial part
385 displaying well-preserved shallow tracks of *Archaeonassa* (Fig. 11G: Preservation I), while the
386 latter part appears as a scattered series of coffee bean-shaped impressions related to the deep
387 preservation of the trail (Fig. 11G: Preservation I). A summary of the distinction between *A.*
388 *fossulata* and *A. cf. fossulata* is proposed (Fig. 11). This dilemma is a clear example of compound
389 trace fossils that are frequently found in the ichnological record, showing in this case the deep
390 preservation of the trail, transitioning to shallower preservation represented by a sparse coffee bean-
391 like string. Compound trace fossils result from the changing behavior of a single producer, and can
392 represent two different situations: sequential or simultaneous formation (Buatois and Mángano,
393 2011:chap.2.4).

394 In addition, the continuous alignment of the disconnected and connected segments (Fig. 11D-E)
395 suggests that the entire trace fossil was made by a single animal, not by two different specimens
396 moving separately in different ways. As Xiao et al. (2019) interpreted the disconnected burrows of
397 *Yichnus levis* Xiao et al., 2019 the potential trace maker of *A. cf. fossulata* has also moved near the
398 substrate surface layer probably in contact with the seawater interface, navigating throughout the
399 sedimentary layers. Following the position in the sediments and in relation to the trace fossil record,
400 *A. cf. fossulata* was probably produced by a bilaterian animal that was able to move by using
401 directional movements and navigating from both surface and sub-surface sedimentary layers.

402 Ichnogenus *Bergaueria* Prantl, 1945

403 *Bergaueria* isp.

404 (Fig. 12A-B)

405 **Material:** A dozen specimens were identified on a single slab (bedding plane view) and
406 photographed in the field. One specimen, in cross-section, shows a vertical burrow exposure (Fig.
407 12B). Remark: Because the slab containing the trace fossils, observed on the western part of Log
408 Roz – 04, was not logged precisely, the stratigraphical position of *Bergaueria* isp. is not included
409 within the logs (Figs. 3, 4).

410 **Description:** Endichnial, smooth, rounded, distinctly vertical, and unornamented with sub-
411 cylindrical to sub-oval protuberances in cross-section. Infilling is visible and composed of 6 to 7
412 sections that include a series of overlapping compact sediment of grained sandstone. Occurs as
413 single, isolated burrows. The top of the burrow consists of a rounded, smooth, and globular to
414 circular shape without any distinctive ornamentation. The top is wider than the base of the burrow.

415 Trace width is 5 to 12 mm. Trace length (vertical measure) is 20 to 25 mm. Preserved as both
416 epirelief (Fig. 12A) and full relief (Fig. 12B) through the sandstone bed.

417 **Discussion:** The plug-shaped burrows *Bergaueria* have caused historically problematic
418 discussion concerning the distinction among some flat elliptical body fossils from Ediacaran-
419 Cambrian deposits. In some cases, *Bergaueria* may be difficult to differentiate from the body fossils
420 (“medusoids”) *Beltanelliformis*, and *Beltanelloides* (Seilacher et al., 2005). In our case, the vertical
421 infilling observed in cross-sections could not be compatible with the elliptical body fossils
422 preservation (e.g., Liu, 2011; Néraudeau et al., 2018, 2023). Other plug shaped burrows include
423 *Conichnus* Männil, 1966, *Conostichus* Lesquereux, 1876 and *Dolopichnus* Alpert and Moore, 1975.
424 However, *Bergaueria* can be distinguished from *Conichnus* and *Dolopichnus* based on its overall
425 geometry, which suggests a different shape or structure (Pemberton et al., 1988:fig.1). Additionally,
426 *Bergaueria* lacks a distinct apical disc and wall ornamentation, which distinguishes it from
427 *Conostichus* (Pemberton et al., 1988). Additionally, the orientation of the trace fossil can also help
428 differentiate between *Bergaueria* and *Conichnus*. *Bergaueria* is typically oriented perpendicular to
429 bedding planes, while *Conichnus* is usually oriented with an angle to bedding planes (Pemberton et
430 al., 1988). In addition, in our case the taxonomic position of *Bergaueria* isp. is preferred to
431 *Conichnus* isp. regarding the size range of the burrows (see Pemberton et al., 1988:table 2) and the
432 rounded basal morphology of the burrow distinguishing them from *Conichnus*. *Conichnus* appear to
433 have a wider range in diameter and height even though its conical shape is similar to the plug shape
434 of *Bergaueria* isp. The morphological variability of the plug-shaped burrows *Bergaueria* has led to
435 numerous ichnospecies (see the ichnotaxonomy revision of Pemberton et al., 1988). Nevertheless,
436 the lack of distinctive ornamentation (e.g., marginal ring, spiraling radial marking, and radial
437 ridges) and lateral displacement patterns around the central depression could exclude some
438 ichnospecies such as *Bergaueria sucta* Seilacher 1990, *Bergaueria radiata* Alpert, 1973,
439 *Bergaueria perata* Prantl, 1945 (Alpert, 1973; Pemberton et al., 1988; Pemberton and Magwood,
440 1990; Hofmann et al., 2012). By contrast, *Bergaueria* isp. from the Le Rozel Formation is slightly
441 similar to the lower Cambrian *Bergaueria hemispherica* Crimes et al., 1977 by lacking distinctive
442 ornament and a rounded, circular, and smooth general shape (Pemberton et al., 1988; Pemberton
443 and Magwood, 1990). But the taxonomic position *Bergaueria* isp. is preferred regarding the size
444 range of the burrow and the lack of additional specimens in vertical cross-section exposure. In fact,
445 the perceived difference in diameter from top to bottom is actually due to the exposure. *Bergaueria*
446 is a vertical plug-shaped burrow (Buatois et al., 2017) with a large geological time range and
447 worldwide occurrences (see Pemberton et al., 1988: Table 7). While most of the *Bergaueria* occur
448 in the late Ediacaran - lower Paleozoic deposits, a couple of specimens are described up to the
449 Cenozoic (Alpert, 1973; Seilacher, 1990; Crimes and Germs, 1982; Książkiewicz, 1977; Pemberton

450 and Magwood, 1990; Seilacher, 2007). *Bergaueria*, and ichnospecies associated, are commonly
451 interpreted as resting or dwelling trace fossils of sedentary organisms such as sea anemones
452 (anthozoans) (Alpert, 1973; Pemberton and Magwood, 1990; Pemberton et al., 1988).

453

454 Ichnogenus *Helminthoidichnites* Fitch, 1850

455 *Helminthoidichnites tenuis* Fitch, 1850

456 (Fig. 12C)

457 **Material:** A dozen specimens were identified on a single slab and photographed in the field.

458 **Description:** Horizontal, simple, unbranched, mostly straight to the slightly curved trail.
459 Trail width is 1-5 mm. Trail length is 10-85 mm. Preserved as positive and negative epirelief in
460 siltstone to fine sandstone layers.

461 **Discussion:** *Helminthoidichnites* differs from other simple horizontal trails (e.g.
462 *Helminthopsis*, *Gordia*) by the lack of meanders or loops (Jensen, 1997; Buatois et al., 1998).
463 *Helminthoidichnites* is regarded as a grazing trace, likely produced by vermiform animals, and is
464 one of the most common trace fossils from Ediacaran and Cambrian deposits (Hofmann and Patel,
465 1989; Jensen et al., 2006). *Helminthoidichnites* is a simple horizontal trail (Buatois et al., 2017) first
466 appearing during the Ediacaran period.

467

468 Ichnogenus *Helminthopsis* Heer, 1877

469 *Helminthopsis tenuis* Książkiewicz, 1968

470 (Fig. 12D)

471 **Material:** Four specimens were observed and photographed in the field.

472 **Description:** Horizontal, simple, unbranched, irregularly winding to meandering trails (non-
473 closed loop). Trace width is close to 1 mm. Trace maximal length is 90 mm. Preserved as negative
474 epirelief in siltstone to fine sandstone layers.

475 **Discussion:** *Helminthopsis* is commonly regarded as a grazing trace and is common in
476 Ediacaran and Cambrian deposits (Buatois and Mángano 2012a). *Helminthopsis tenuis* is
477 distinguished from *H. abeli* Książkiewicz, 1977 and *H. hieroglyphica* Wetzel and Bromley, 1996 by
478 the lack of horseshoe-like trail and its high-amplitude meandering and winding respectively (Wetzel
479 and Bromley, 1996). Moreover, it differs from *Helminthoidichnites* by the meandering course

480 (Hofmann and Patel, 1989). *Helminthopsis* is a simple horizontal trail (Buatois et al., 2017) first
481 appearing during the Ediacaran period.

482

483 Ichnogenus *Nereites* MacLeay in Murchison, 1839

484 *Nereites* isp.

485 (Fig. 13A-F)

486 **Material:** A dozen specimens were observed and photographed in the field isolated (Fig.
487 13A-C) or observed on the same large slate (Fig. 13D-F).

488 **Description:** Horizontal, unbranched, straight, sinuous to meandering trail, sometimes with
489 loops and windings. Median furrow flanked by two thin and smooth rows of lobes (pustules), ovoid,
490 spaced, or joined. Evidence of backfilling is induced by the rows of lobes that are remixed and not
491 related to the single passage of the animals. Pustules arranged in pairs forming lateral lobes around
492 the median furrow. Trace width is 3-6 mm and the maximum trace length is 214 mm. Preserved as
493 positive epirelief in very fine argillite to fine-grained sandstone layer.

494 **Discussion:** Doré (1994) mentioned the presence of *Neonereites* in the Le Rozel Formation.
495 However, a long ichnotaxonomic debate has existed concerning the position of *Nereites* in relation
496 to *Neonereites*. Today, *Neonereites* and *Scalarituba* Weller, 1899 are considered junior synonyms
497 of *Nereites* (D'Alessandro and Bromley, 1987; Mángano et al., 2000). Seilacher (2007 p. 99)
498 illustrates why some authors use three separate ichnogenera. These three ichnotaxa represent the
499 preservation variants of the same form (e.g. *Scalarituba* preservation). While *Nereites* is not a
500 common trace fossil referred to the Cambrian period, some are described from Precambrian-
501 Cambrian top of sandstone beds from Australia (Walter et al., 1989), Namibia (Crimes and Germs,
502 1982) as well as in Canada (Crimes and Anderson, 1985). *Nereites* trace fossils from the Le Rozel
503 Formation are like those specimens with a median furrow, flanked on both sides by spherical or
504 ovate lobes. But, even though '*Palaeobullia*' preservation and *Scolicia* de Quatrefages, 1849 were
505 defined by Seilacher (2007) as analogous to *Nereites*, the lower Cambrian material of
506 '*Palaeobullia*' from Greenland presented by Bryant and Pickerill (1990), which is composed of
507 large (1cm) irregularly meandering to looping trail with a rare and irregular lobate appearance, is
508 strongly different compared to *Nereites* from the Le Rozel Formation.

509 While some specimens are unambiguously *Nereites* (e.g. Fig. 13A-B, D-E), we can observe an
510 apparent overlap in morphology of some specimens with *A. cf. fossulata* (Discontinuous segments,
511 e.g. Fig. 13C, F). However, the disconnected segments do not look like 'coffee bean shapes'
512 described for *A. cf. fossulata*. In addition, the discontinuous segments are also automatically
513 continuous with the *Nereites* isp. trace fossils (Fig. 13F) into the same trace fossils (over 5 to 10

514 cm). Thus, we assume that these differences are preserving variants and do not necessarily need to
515 be included in a specific taxonomic placement. *Nereites* trace fossils are interpreted as feeding
516 traces of deposit feeders, and potential trace-makers include invertebrates like worm-like organisms
517 (Mángano et al., 2000; Pazos et al., 2015). *Nereites* is a complex actively filled horizontal structure
518 (Buatois et al., 2017) first appearing during the Fortunian stage.

519

520 Ichnogenus *Psammichnites* Torell, 1870

521 *Psammichnites gigas circularis* (Crimes, Legg, Marcos and Arboleya, 1977)

522 (Fig. 14A-D)

523 **Material:** Five specimens were observed and photographed in the field.

524 **Description:** Horizontal, large, massive, unbranched, slightly curved to meandering bilobate
525 trails with self-crossing patterns. Fine-grained burrows backfill similar to the host sediment.
526 Bilobate trails with smooth, convex lobes separated by a central, straight to sinuous groove. The
527 horizontal burrow can be collapsed (Fig. 14C). Trace width is 8-25 mm when the maximum trace
528 length is over 800 mm. Preserved as positive epirelief in fine-sandstone beds.

529 **Discussion:** *Psammichnites* is distinctive by an impressive, bilobed, sinuous to looped
530 horizontal trail with characteristic median furrow and back-filled traces (McIlroy & Heys, 1997;
531 Mángano et al., 2002, 2022). The characteristic ‘lassoing type’ shape (e.g. Zhu, 1997; Seilacher et
532 al., 2005) is identified in the Le Rozel Formation (Fig. 14B, D) and strongly supports the taxonomic
533 position. Doré (1994) mentions the presence of *Taphrhelminthopsis* at Le Rozel. Zhu (1997) and
534 Mángano and Buatois (2016) have written that *Taphrhelminthopsis* is a preservation variant of
535 *Psammichnites*. Thus, *Taphrhelminthopsis* is known as a junior synonym of *Psammichnites*
536 (Goldring & Jensen, 1996; McIlroy & Heys, 1997; Zhu, 1997). *P. gigas circularis* differs from
537 other *Psammichnites* such as *P. grumula* Romano and Melendez, 1979 and *P. implexus* Rindsberg,
538 1994 by the lack of transverse ridges and holes on the burrow (Mángano et al., 2002, 2022; for
539 discussions of nomenclatural issues regarding *Psammichnites*, see Hofmann and Patel (1989), Zhu
540 (1997), and especially Mángano et al. (2002)).

541 Except for the smaller specimens, the bilobate *Psammichnites gigas circularis* from the Le
542 Rozel Formation are strongly similar to the lower Cambrian *Psammichnites* from New Brunswick,
543 Canada (Hofmann and Patel, 1989), Greenland (Pickerill and Peel, 1990), China (Zhu, 1997),
544 France (Álvaro and Vizcaíno, 1999), and South Australia (Jago and Gatehouse, 2007).
545 *Psammichnites* is interpreted as a back-filled structure, representing the feeding strategies and
546 locomotion of a soft-bodied organism (like a vagile mollusks) through the subsurface layer

547 (Seilacher, 2007:pl. 28). *Psammichnites* is a complex actively filled horizontal structure (Buatois et
548 al., 2017) first appearing during the Fortunian stage.

549

550 Ichnogenus *Treptichnus* Miller, 1889

551 *Treptichnus coronatum* (Crimes and Anderson, 1985)

552 (Fig. 15A-C)

553 **Material:** Two specimens observed and photographed in the field. One extra specimen
554 collected under the number IGR-PAL-23265.

555 **Description:** Horizontal to vertical burrow, smooth, and parallel to the bedding plane.
556 Burrow trajectory forms distinctive circles (Fig. 15A, C) or half-circles (Fig. 15B) including
557 meandering trajectories. Burrow is composed of 25 to 35 distinctive rounds to oval shape knobs,
558 uniformly spaced with very discrete extended branches on the outer margin (Fig. 15B). Trace width
559 is 3.5 - 8 mm. Trace length is 125 mm. Spacing between circular burrows is 2-8 mm. Preserved as
560 positive epirelief in fine-sandstone beds.

561 **Discussion:** *T. coronatum* is distinguished from other ichnospecies of *Treptichnus* (i.e.
562 *Treptichnus bifurcus* Miller, 1889, *Treptichnus triplex* Palić, 1976, *Treptichnus lublinensis*
563 Paczesna, 1986 and *Treptichnus pollardi* Buatois and Mángano, 1993) by a characteristic circular
564 trajectory and multiple small successive knobs, as first erected by Crimes and Anderson (1985).
565 Specimen type described by Crimes and Anderson (1985) have the same general characteristic that
566 the *T. coronatum* from Le Rozel such as circular burrows with sand-filled knobs. However, the
567 preservation seems to be better in our specimens and the sand-filled knobs stand out with
568 pronounced relief. Because *T. coronatum* is a three-dimensional burrow with branching structure
569 (Buatois et al., 2017), multiple expressions can be observed regarding the level of erosion. This can
570 explain the difference between some specimens. In this regard, *T. coronatum* from Le Rozel has
571 also a semi-circular trajectory (Fig. 15B), strongly similar to the morphology of *T. coronatum* from
572 Cambrian GSSP in Newfoundland, which supports the identification made in this paper (Buatois et
573 al., 2014; Laing et al., 2019).

574 *Treptichnus pedum* (Seilacher, 1955)

575 (Fig. 16A-C)

576 **Material:** Three specimens were observed and photographed in the field.

577 **Description:** Horizontal to vertical burrows, branched, with a trajectory highly curving
578 ending frequently with a loop. Traces are mainly composed of uniserial rows of discontinuous,

579 smooth, unornamented, and subcircular to oval burrows. Burrows are preserved as massive,
580 continuous or discontinuous, horizontal pits or segments filled with sediments (Fig. 16A-C).
581 Occasionally, the burrows display lateral projections that are preserved in the margin (mainly on
582 Fig. 16A-B), much smaller on Fig. 16C). Trace width is 1.5-8 mm and maximal trace length is 80
583 mm. Spacing between circular burrows is 1-3 mm. Preserved as positive epirelief in fine-siltstone to
584 sandstone beds.

585 **Discussion:** The Ediacaran-Cambrian boundary is marked by the first appearance of
586 *Treptichnus pedum* (Narbonne et al., 1987; Brasier et al., 1994; Buatois, 2018). Seilacher (2007)
587 described *Treptichnus pedum*, which includes straight, sinusoidal, curved, or looping burrows
588 constructed from upward curving segments. Due to the three-dimensional burrows morphology,
589 multiple expressions of *T. pedum* can be found worldwide (e.g. Jensen, 1997; Wilson et al., 2012;
590 Buatois et al., 2013; Buatois, 2018; Laing et al., 2019). Interestingly, the Le Rozel Formation is
591 particularly rich in *Treptichnus* including *Treptichnus* isp. *T. coronatum*, and *T. pedum*, which the
592 latest has been first reported by Néraudeau et al. (2023).

593 While treptichnids occur before the appearance of *T. pedum* from the late Ediacaran (e.g. Cribb et
594 al., 2019), the horizontal burrows with horizontal to vertical branches of *Treptichnus* (Buatois et al.,
595 2017) appear in the Fortunian (Mángano and Buatois, 2020). Their typical three-dimensional
596 morphology with repeated arcuate probing burrows suggests that their function was related to a
597 specific feeding strategy of predator worms such as priapulids (Dzik, 2005). Those potential
598 Cambrian trace-makers were also supported by Vannier et al. (2010), following neo-ichnologic
599 experiments.

600 *?Treptichnus* isp.

601 (Fig. 16D-E)

602 **Material:** Dozens of specimens were observed and photographed in the field. Two slates
603 with highest specimen density are housed at the Geological Institute of Rennes 1 under the numbers
604 IGR-PAL-23264, IGR-PAL-23266.

605 **Description:** Horizontal to vertical burrows, branched, smooth, parallel to the bedding plane
606 with straight to meandering trajectories including loops and self-crossing (Fig. 16D-E). Burrows are
607 composed of uniserial rows of discontinuous, smooth, unornamented, and subcircular beads
608 (*Treptichnus* isp. like a string of beads; Fig. 16D-E). *?Treptichnus* isp. does not preserve lateral
609 projections. Trace width is 2-8 mm and the maximal trace length is 120 mm. Spacing between
610 circular burrows is < 2 mm. Preserved as positive epirelief in fine-siltstone to sandstone beds.

611 **Discussion:** *?Treptichnus* isp. does not preserve lateral projections and/or intense "zig-zag"
612 sections characteristic of the other *Treptichnus* (e.g. *Treptichnus bifurcus*, *Treptichnus triplex*,
613 *Treptichnus lublinensis* or *Treptichnus pedum*) (see Buatois & Mángano, 1993:fig.4; Singh et al.,
614 2017). However, we observe discrete angles changing the trajectory of the burrow characteristic of
615 a probing burrowing behavior. *?Treptichnus* isp. like a "string of beads" is also different from the
616 segmented *T. pollardi* presented here. In fact, some previous work have published numerous *T.*
617 *pedum* with string of beads pattern (e.g. Wilson et al., 2012; Cribb et al., 2019) and support the
618 identification of *?Treptichnus* isp. in the Le Rozel Formation rather than the unclear nomenclature
619 of '*Hormosiroidea* Schaffer, 1928' or expression of '*Saerichnities*' that are uncommonly used.
620 However, regarding the high variability of the genus *Treptichnus* in terms of environmental context,
621 and point of view in the three-dimensional burrow we believe that include the specimens of
622 *?Treptichnus* isp. like a string of beads in a separate taxonomic position is a reasonable idea. In
623 addition, *T. pedum* published by Wilson et al. (2012) and Cribb et al. (2019) present more
624 diagnostic patterns (e.g. lateral projections) for some specimens on the same stratigraphic position.
625 Carefully, at this stage of research, open nomenclature as *?Treptichnus* isp. is preferred considering
626 that the "string of beads pattern" is not a clearly diagnostic character of the other *Treptichnus* (e.g.
627 *T. bifurcus*, *T. triplex*, *T. lublinensis* or *T. pedum*). Further discussion might be interesting to
628 conduct to include or not the string of beads pattern in *T. pedum*.

629 *Treptichnus* indet.
630 (Fig. 16F)

631 **Material:** One specimen was observed and photographed in the field.

632 **Description:** Horizontal trace to discrete vertical burrows (pits), parallel to the bedding
633 plane with a trajectory highly winding, including a loop and a distinct self-crossing (Fig. 16F).
634 Trace shows discrete segmented parts with discrete angles changing constantly the trajectory. Trace
635 width is 1-3 mm and the maximal trace length is 40 mm. Preserved as positive epirelief in fine-
636 siltstone to sandstone beds.

637 **Discussion:** *Treptichnus* indet. is not preserved as uniserial rows of discontinuous beads and
638 does not preserve lateral projections and/or "zig-zag" pattern sections characteristic of other
639 *Treptichnus*. However, the discrete angles changing the trajectory represent shallow preservation of
640 a probing burrowing behavior. But, the lack of diagnostic characters does not allow any
641 ichnospecific assignment.

642

643 **5. Discussion**

644 *5. 1. Depositional environment*

645 The deposits of the Le Rozel Formation consist of siliciclastic sediments that have been deposited
646 in shallow platform environments. The set of sedimentary facies observed along the thick
647 sedimentary succession show the recurrence of storm-dominated open marine environments (upper
648 offshore) and protected marine environments where tidal processes dominate (tidal plain). These
649 deposits are organized in various orders of depositional sequences that vertically repeat a set of
650 shallow-water facies between the tidal environments and the upper offshore.

651 The numerous well-represented sedimentary structures such as the Hummocky cross-stratifications
652 are in agreement with previous interpretations, such as that of Went (2020), which indicates for the
653 Le Rozel Formation a storm-dominated depositional environment in an open marine platform. Our
654 observations show that in addition to storm facies a large part of the Le Rozel Formation was
655 deposited in restricted marine environments, where rhythmic low-energy selective processes and
656 unidirectional current flows are present. These deposits are characterized by flaser stratification
657 with characteristic alternations of sandy and silty clay laminae in which the different grain sizes are
658 well sorted. The flaser stratification is exclusively associated with 2D ripples of unidirectional
659 currents of small wavelength and very small amplitude. In addition, a decimetric-scale cyclicity is
660 evident in the flaser deposits, produced by increasing/decreasing variations in the thickness of the
661 laminae, which can be attributed to the cyclic nature of the semi-lunar tide (Figs. 6, 7, 8).

662 Consistently associated with these depositional facies of tidal flats of the Le Rozel Formation are
663 the MISS and trace fossil surfaces. In addition, horizontally developed traces are present in varying
664 quantities in all the laminae of the flaser stratification (Figs. 6, 8 and 9). This characteristic shows
665 that trace and MISS surfaces have a high potential of preservation in these low-energy sedimentary
666 environments. In contrary, trace and MISS surfaces are absent or very rare in deposits where HCS
667 storm facies are present. This shows clear evidence of deposition under tidal influence, favorable
668 for fossilization of microbial biomats and preservation of trace fossils (Schieber, 2007; Noffke,
669 2010; Johnson and Baarli, 2012; Hofmann et al., 2012; Buatois et al., 2013). In addition, these areas
670 of shallow, oxygenated waters, rich not only in light but also in nutrients transported from the
671 continent, are favorable for the colonization of benthic organisms (Buatois and Mángano, 2011;
672 Johnson and Baarli, 2012).

673

674 *5. 2. Ichnological age significance*

675 Previous studies have discussed the age of the Le Rozel Formation. Doré (1994), for
676 instance, has considered a “Vendian to Tommotian” age. Nowadays, according to the worldwide

677 ichnostratigraphic scheme of the late Ediacaran and early Paleozoic, the new ichnological data
678 suggest a Fortunian ichnostratigraphic age congruent with Doré's original interpretation. This age is
679 principally supported by the first report of crucial key ichnotaxas (i.e. *Nereites*, *Psammichnites*,
680 *Treptichnus*), which appear at the beginning of the Cambrian period (Narbonne et al., 1987;
681 Mángano et al., 2012; Mángano and Buatois, 2020). Especially in detail of the two important
682 ichnospecies *T. pedum* and *P. gigas circularis* which are typical to the lower Cambrian
683 biostratigraphy (Narbonne et al., 1987; MacNaughton and Narbonne, 1999; Mángano et al., 2012).
684 Specifically, *Psammichnites* have been recorded worldwide in Cambrian shallow water deposits
685 (Álvaro and Vizcaïno, 1999; Seilacher et al., 2005; Mángano et al., 2012; MacNaughton et al.,
686 2021; Mángano et al., 2022). For example, in France and Canada, where respectively Álvaro and
687 Vizcaïno (1999) and MacNaughton et al. (2021) discussed the evidence of *P. gigas* from
688 Tommotian sandstones (pre-trilobitic age), below the first occurrence of trilobites and
689 archaeocyatha (as analogous to well the Le Rozel Formation). In addition, the first appearance of
690 the trace fossil *T. pedum* is widely recognized for its role in marking the beginning of the Cambrian
691 period (Crimes and Anderson, 1985; Narbonne et al., 1987; Brasier et al., 1994; Buatois et al.,
692 2013). But some considerations need to be taken because, employing the first evidence of the trace
693 fossil *T. pedum* as the only proxy available to define the base of the Cambrian could sometimes
694 pose significant interpretation problems (see Topper et al., 2022). Nevertheless, combining *T.*
695 *pedum* from *Treptichnus pedum* Ichno-Assemblage Zone as well as *P. gigas circularis* (one of the
696 most diagnostic elements of the *Rusophycus avalonensis* Zone), the biostratigraphy offers an
697 ichnostratigraphic age which spans from the late Fortunian into Cambrian Age 2 (MacNaughton
698 and Narbonne, 1999; Mángano et al., 2012; Mángano et al., 2022). Following modern
699 ichnostratigraphic models (e.g. Carbone and Narbonne, 2014; Mángano and Buatois, 2014, 2020)
700 associated with the radiochronological results, a Fortunian ichnostratigraphic age is suggested for
701 the Le Rozel Formation deposition. The arguments are twofold: (1) the presence of strong
702 ichnostratigraphic markers *Treptichnus pedum* and *P. gigas circularis*; (2) the maximum deposition
703 age of 549.0 ± 2.8 Ma according to the U-Pb dating of detrital zircon grains (Fig. 10A); this age is
704 actually provided by sample ROZ-01 which is stratigraphically located below the other samples
705 ROZ-21-2 (549.7 ± 3 Ma) and ROZ-21-4 (565 ± 8.1 Ma) (Figs. 4; 10B-C). Consequently, this
706 stratigraphically oldest level yields the youngest maximum depositional age that should therefore be
707 considered the maximum depositional age for the Le Rozel Formation.

708 Therefore, even though *T. pedum* is locally found in the Le Rozel Formation (Figs. 3, 4, 14B-F), the
709 ichnostratigraphic age assignment to the Cambrian period for the Le Rozel Formation is also
710 supported by the association of the different Cambrian ichnospecies and ichnogenera together from
711 the same locality. In support of this, we present for the first time in the Armorican Massif the trace

712 fossils associations of *Bergaueria* isp., *Nereites* isp. and more importantly *P. gigas circularis* as
713 well as the three-dimensional treptichnid burrows of *Treptichnus* isp., *T. coronatum* and *T. pedum*.
714 Otherwise, the other trace fossils from the Le Rozel Formation (i.e. *Archaeonassa*, *Bergaueria*,
715 *Helminthoidichnites*, *Helminthopsis*) could not refute the Fortunian age, because these taxa are
716 found both before and after the Precambrian/Cambrian boundary (Jensen et al., 2006; Laing et al.,
717 2019; Mángano and Buatois, 2020).

718 5. 3. Early Cambrian sea floor colonization and behavioral diversification

719 Even though some late Ediacaran succession demonstrated unusual complex trace fossils (e.g. Oji et
720 al., 2018), the early Cambrian is mostly marked by the advent of complex burrows and the diversity
721 of bioturbation behaviors that radiated dominantly in shallow marine environments (Mangano and
722 Buatois, 2015; Herringshaw et al., 2017; Cribb et al., 2023). As a result of the increase in size and
723 diversity of animals as well as a diversification of motile strategies in sediments (Butterfield, 2007;
724 Gingras et al., 2011a,b; Mangano and Buatois, 2016). Those facts have been heavily supported by
725 critical reviews of the early Cambrian trace fossils record, showing undoubtedly a drastic increase
726 in global ichnodiversity that proves evidence of novel behaviors throughout the Cambrian (e.g.,
727 Buatois et al., 2020; Mangano and Buatois, 2017, 2020). The Le Rozel Formation incrementing the
728 early Cambrian trace fossil record illustrating the development of complex search patterns into
729 sediments, such as the three-dimensional burrow systems (i.e penetrative burrows of *Treptichnus*),
730 as well as the large sediment bulldozers *Nereites* and *Psammichnites* from possible predator or
731 deposit feeders. We observe that the bedding planes are widely colonized (for instance the *Nereites*
732 and *Psammichnites* illustrated in Fig. 13, 14 respectively) and congruent with a increase in mobile
733 strategies in sediments characteristics from the Fortunian age when diverse Cambrian revolutions
734 took place (see, Mángano and Buatois, 2017). However, except for *Bergaueria* isp., ichnofabrics
735 dominated by deep-dwelling bioturbation (vertical burrows) of suspension feeders typical to the
736 Cambrian stages 2 and 3 (Mángano and Buatois, 2020) have not been discovered. We further
737 observed that the trace fossils only penetrate the uppermost centimeters of the sediment and are
738 typically oriented parallel to the bedding plane, causing a limited to moderate disturbance in the
739 primary sedimentary ichnofabric with the bedding plane bioturbation index that tends from BPBI: 2
740 to BPBI: 3 (except for one level: BPBI: 5) (Fig. 4A-D) (Gougeon et al., 2018; Mángano et al.,
741 2022). Finally, the trace fossil assemblage from the Le Rozel Formation illustrate the explosion of
742 new styles of animal-substrate interactions, reflecting both the appearance of new body plans and
743 feeding strategies of the first complex metazoans in the basal Cambrian (Mángano and Buatois,
744 2014).

745

747 The stratigraphic record of MISS is known throughout the Precambrian/Cambrian transition
748 (e.g. Hagadorn and Bottjer, 1997 ;Gehling, 1999; Noffke, 2010; Gingras et al., 2011a) and have
749 been reinterpreted by Davies et al. (2016). The collective focus of many studies has suggested that
750 ancient MISS are predominantly shallow marine or tidal features (Davies et al., 2016). By the late
751 Ediacaran to earliest Cambrian (Fortunian), when the benthic colonization took place (e.g.
752 Cambrian revolutions), microbial mats turned indeed into a food resource for early metazoans
753 (Seilacher, 1999; Seilacher et al., 2005; Buatois and Mángano, 2011; Gingras et al., 2011a Carbone
754 and Narbonne, 2014; Mángano and Buatois, 2017). As a consequence, the distribution of microbial
755 mats was constantly reduced during the Phanerozoic (Seilacher, 1999; Davies et al., 2016).
756 Nowadays microbial mats are also mostly established in more extreme habitats such as hot spring,
757 saline environments where animal controls (e.g. grazing and undermat-mining organisms) are
758 minimal (e.g., Gingras et al., 2011a; Prieto-Barajas et al., 2018; Scott et al., 2019).

759 The widespread distribution of biomats during the Ediacaran and lower Paleozoic strata as played
760 an important ecological role on seafloor colonization and ecosystem structuration (Seilacher 1999;
761 Tarhan et al., 2017; Mángano & Buatois, 2016, 2020). This includes, for instance, the replacement
762 of Proterozoic-style biomats dominated by microorganisms exhibiting a Phanerozoic-style
763 bioturbated mixground. This ecological turnover in benthic sea floor structuration (e.g. sediment
764 mixing, vertical bioturbation) through the Proterozoic - Phanerozoic transition is accompanying
765 with progressive regression of the microbial mats (Seilacher 1999; Bottjer et al., 2000; Buatois et
766 al., 2014). This in turn made MISS an important proxy for understanding the ecological turnovers
767 across the late Ediacaran - Cambrian ages (Seilacher, 1999; Buatois et al., 2014; Mángano and
768 Buatois, 2017). In this regard, the presence of ancient MISS in the Le Rozel Formation, with only
769 rare associations with grazing trace fossils, is surprising because it has been demonstrated that the
770 Ediacaran mat-ground ecology persisted locally during the early Cambrian and present grazing trace
771 fossil with microbial mats (Buatois et al., 2014).

772 Interestingly and assuming that the trace fossils from the Le Rozel Formation are well preserved,
773 we also suppose that the microbial mats have played a key role concerning the preservation settings
774 of the trace fossils and some elliptical body fossils (Néraudeau et al., 2023). For example, tidal flats
775 settings are favorable for the development of microbial matgrounds (biofilms) and have a
776 significant role in the preservation of delicate morphologic details of trace fossils (Mangano and
777 Buatois, 2015). However, the limitans here is that even though some large bedding planes record
778 record both trace fossils and biomats and the same surface, but without clear association.

780 5. 5. *Ediacaran to Cambrian ichnofauna from Armorican Massif: resume and perspectives*

781 The Armorican Massif contains at the present day two distinctive early trace fossils
782 assemblages (summarized in Fig. 17) both associated with detrital zircons dating. On the one hand,
783 the Brioverian series in central Brittany, previously supposed to be Precambrian, yielded a trace
784 fossil assemblage mostly composed of simple horizontal ichnofossils (e.g., *Gordia*,
785 *Helminthoidichnites*, *Helminthopsis*, *Spirodesmos*, *Palaeophycus*) associated as well to microbial
786 mats (i.e. *Neantia*) which is interpreted to belong to the Ediacaran matground ecology (Gougeon et
787 al., 2018; Coutret and Neraudeau, 2022). Two U–Pb detrital zircon grain datings on sandstone
788 samples collected in St-Gonlay gave maximum depositional ages of 551 ± 7 Ma and 540 ± 5 Ma
789 and suggested being latest Ediacaran in age (ca. 538,8-530 Ma). According to Gougeon et
790 al. (2021), the age of these deposits remains uncertain because the proxies are not fully congruent.
791 On the other hand, in Normandy, the lower Cambrian from Le Rozel Formation yielded an
792 assemblage mostly composed of three-dimensional burrows (i.e. *Treptichnus*) and large sediment
793 bulldozers (i.e. *Nereites*, *Psammichnites*) which are unambiguously interpreted to belong to the
794 Cambrian according to the global ichnostratigraphy (Mángano et al., 2020). However detrital zircon
795 dating provides a maximum of deposition (ca. 549 ± 3 Ma). However, this result is congruent with
796 an early Cambrian age for these fossiliferous beds.

797 Recent studies have also discussed the depositional environment of the Brioverian deposit (e.g.,
798 Gougeon et al., 2018, 2021; Néraudeau et al., 2018) and broadly suggested a relatively shallow
799 shelf environment. Nevertheless, because the trace fossils localities in the Brioverian are
800 represented by small surface outcrops (Saint-Gonlay and Montfort-sur-Meu), it remains difficult to
801 critically interpret the environmental setting associated with the Brioverian trace fossils assemblage
802 (Gougeon et al., 2018).

803 Therefore, two hypotheses could be offered on the relationship between the two Armorican
804 ichnofauna: 1) the trace fossil assemblages are respectively located on either side of the
805 Precambrian/Cambrian boundary, with the Brioverian ichnofauna being of Ediacaran age and the
806 Le Rozel ichnofauna of Cambrian age; 2) the ichnofaunas are contemporaneous (Fortunian) but
807 were deposited in strongly different environments.

808

809 **6. Conclusion**

810 The early Cambrian from the Le Rozel Formation in Normandy contains an important
811 dataset of biogenic structures represented by a well-preserved trace fossil assemblage and MISS.
812 Paleontological remains are preserved in the siliciclastic deposits of a shallow marine environment.

813 This trace fossil assemblage is mentioned in some papers (e.g. Doré et al., 1994; Went, 2020) but
814 has remained relatively ignored by the scientific community during the last decades. From an
815 ichnostratigraphic standpoint, a Fortunian age is strongly suggested. Behaviors like sediment
816 bulldozers (*Psammichnites*), subsurface and complex sediment grazers (*Nereites*), and three-
817 dimensional burrow systems made by probing organisms (*Treptichnus*) are typical of the early
818 Cambrian. In addition, the Le Rozel Formation deposition is unambiguously younger than 551 ± 5
819 Ma as it rests unconformably on top of this ignimbrite basement. This is confirmed by the
820 maximum deposition age of 549 ± 3 Ma found for one of the stratigraphically oldest sandstone
821 layers. Also, preliminary observations on the trace fossils distribution recorded on the bedding
822 planes, following the lack of vertical burrows made by deep suspension feeders, suggest that the
823 ecological turnover of the Cambrian Stage 2 (i.e Agronomic Revolution) was not established in
824 Normandy. Finally, the Le Rozel Formation displays a complex trace fossil assemblage that
825 highlights sophisticated feeding and grazing strategies by early animals, mostly stimulated by the
826 exploitation of new ecological niches. The assemblage differs significantly from the Brioverian
827 trace fossils of Brittany, which are mostly composed of simple horizontal trails. By combining
828 several paleontological and sedimentological approaches, further works on the lower Cambrian
829 series from the Cotentin Peninsula (i.e. Le Rozel Formation; Carteret Formation; Saint-Jean-de-la-
830 Rivière Formation) could lead to establishing a gradual chronology of the different steps of
831 diversification concerning the first metazoans and ecosystems in the early Cambrian peri-
832 Gondwana terranes.

833

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853 **Declaration of interests**

854 The authors declare that they have no known competing financial interests or personal relationships
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856

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