



# New insights into the early evolution of horizontal spiral trace fossils and the age of the Brioherian series (Ediacaran–Cambrian) in Brittany, NW France

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## ► To cite this version:

Romain Gougeon, Didier Néraudeau, Alfredo Loi, Marc Poujol. New insights into the early evolution of horizontal spiral trace fossils and the age of the Brioherian series (Ediacaran–Cambrian) in Brittany, NW France. *Geological Magazine*, 2022, 159 (7), pp.1284-1294. 10.1017/S0016756820001430 . insu-03124898

HAL Id: insu-03124898

<https://insu.hal.science/insu-03124898>

Submitted on 31 Aug 2022

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**New insights on the early evolution of horizontal spiral trace fossils and the age of the Brioherian (Ediacaran-Cambrian) in Brittany, NW France**

Journal:	<i>Geological Magazine</i>
Manuscript ID	GEO-20-2562.R3
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Gougeon, Romain; University of Saskatchewan, Geological Sciences Neraudeau, Didier; Université de Rennes 1, Institut de Géologie Loi, Alfredo; Università di Cagliari, Dipartimento di Scienze Chimiche e Geologiche Poujol, Marc; Université de Rennes 1, Géosciences Rennes
Keywords:	U-Pb dating, Ichnology, Planispiral, Ediacaran-Fortunian, Spirodesmos
Abstract:	In northwestern France, the Brioherian is a thick siliciclastic succession deposited during the Cadomian cycle (c. 750–540 Ma). In the uppermost Brioherian beds, previous studies unraveled an assemblage dominated by simple horizontal trace fossils associated with microbially-stabilized surfaces. Here, we report <i>Spirodesmos</i> trace fossils—one-way, irregular and regular horizontal spirals—from Crozon (Finistère, Brittany), Montfort-sur-Meu and St-Gonlay (Ille-et-Vilaine, Brittany). After reviewing the literature on horizontal spiral trace fossils from the Ediacaran to the Recent, an Ediacaran-Fortunian <i>Spirodesmos</i> pool is identified from marginal-marine to shelf settings, while an Ordovician-Recent trend formed in the deep-marine realm. These results suggest that an onshore-offshore migration in <i>Spirodesmos</i> took place from the Ediacaran-Fortunian to the Ordovician, similarly to what happened in graphoglyptids. In addition, the age of the uppermost Brioherian beds (Ediacaran or early Cambrian) is still a pending question. Here, we report two new U-Pb detrital zircon dating from sandstone samples in St-Gonlay, giving maximum deposition ages of $551 \pm 7$ Ma and $540 \pm 5$ Ma. Although these results do not discard an Ediacaran age for the uppermost Brioherian beds, a Fortunian age is envisioned because the new dating corroborate previous dating from Brittany, Mayenne and Normandy. However, the intervals of error of the radiometric dating, and the dominance of non-penetrative trace fossils associated with matgrounds (an ecology more typical of the Ediacaran), do not allow definitive conclusions on the age of the uppermost Brioherian beds.

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3     2 Briovertian (Ediacaran-Cambrian) in Brittany, NW France  
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6     3 **Category of submission:** Original Article (Special Issue on the Ediacaran-Cambrian  
7     4 transition)  
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3     15 **Abstract:** In northwestern France, the Brioherian is a thick siliciclastic succession deposited  
4     16 during the Cadomian cycle (*c.* 750–540 Ma). In the uppermost Brioherian beds, previous  
5     17 studies unraveled an assemblage dominated by simple horizontal trace fossils associated with  
6     18 microbially-stabilized surfaces. Here, we report *Spirodesmos* trace fossils—one-way, irregular  
7     19 and regular horizontal spirals—from Crozon (Finistère, Brittany), Montfort-sur-Meu and St-  
8     20 Gonlay (Ille-et-Vilaine, Brittany). After reviewing the literature on horizontal spiral trace  
9     21 fossils from the Ediacaran to the Recent, an Ediacaran-Fortunian *Spirodesmos* pool is  
10     22 identified from marginal-marine to shelf settings, while an Ordovician-Recent trend formed in  
11     23 the deep-marine realm. These results suggest that an onshore-offshore migration in  
12     24 *Spirodesmos* took place from the Ediacaran-Fortunian to the Ordovician, similarly to what  
13     25 happened in graphoglyptids. In addition, the age of the uppermost Brioherian beds (Ediacaran  
14     26 or early Cambrian) is still a pending question. Here, we report two new U-Pb detrital zircon  
15     27 dating from sandstone samples in St-Gonlay, giving maximum deposition ages of  $551 \pm 7$  Ma  
16     28 and  $540 \pm 5$  Ma. Although these results do not discard an Ediacaran age for the uppermost  
17     29 Brioherian beds, a Fortunian age is envisioned because the new dating corroborate previous  
18     30 dating from Brittany, Mayenne and Normandy. However, the intervals of error of the  
19     31 radiometric dating, and the dominance of non-penetrative trace fossils associated with  
20     32 matgrounds (an ecology more typical of the Ediacaran), do not allow definitive conclusions  
21     33 on the age of the uppermost Brioherian beds.  
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24     34 **Keywords:** Ediacaran-Fortunian, ichnology, planispiral, *Spirodesmos*, U-Pb dating  
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## 1 2 3     36   **1. Introduction** 4 5

6         37         The potential of ichnology to decipher macro-evolutionary trends in animal behavior  
7  
8         38         has a long history. Compilation of ichnological data was a major part of the work of A.  
9  
10        39         Seilacher and P. Crimes. Seilacher (1974, 1977, 1986) focussed on the variety of  
11  
12        40         graphoglyptid trace fossils from the deep-sea (i.e. patterned trace fossils forming nets, regular  
13  
14        41         meanders and spirals), aiming to understand their environmental adaptation through time (e.g.  
15  
16        42         size changes, functional optimization). Seilacher (1956) was the first to recognize the  
17  
18        43         potential of trace fossils to delineate the Precambrian-Cambrian boundary; Crimes (1987,  
19  
20        44         1992a, 1994) extended this idea by reviewing worldwide literature, and developed an  
21  
22        45         ichnostratigraphic scheme that helped defining the Cambrian GSSP (Narbonne *et al.* 1987;  
23  
24        46         Brasier *et al.* 1994). In Crimes' comprehensive work, horizontal spiral trace fossils (as  
25  
26        47         defined in this contribution) were consistently absent from the Ediacaran and the Cambrian  
27  
28        48         (Crimes, 1987, 1992a, 1992b, 1994), only appearing by the Ordovician in the deep-marine  
29  
30        49         realm (Crimes *et al.* 1974, 1992). Crimes suspected that most deep-marine graphoglyptids  
31  
32        50         originated in shallow-marine environments during the Cambrian (Crimes, 1987; Crimes &  
33  
34        51         Anderson, 1985; Crimes & Fedonkin, 1994), but the absence of regular planispiral trace  
35  
36        52         fossils in the Cambrian was then problematic (Crimes *et al.* 1992).

43  
44         53         The Ediacaran-Cambrian transition (*c.* 539 Ma) was a time of striking changes in  
45  
46         54         Earth ecosystems. Ediacaran seafloors were dominated by microbially-stabilized surfaces on  
47  
48         55         which epifaunal and very shallow infaunal grazers thrived (Seilacher & Pflüger, 1994;  
49  
50         56         Gehling, 1999). Macroscopic animals of the earliest Cambrian started to disrupt the sediment  
51  
52         57         at depth, affecting the substrate ventilation (e.g. Mángano & Buatois, 2014; Gougeon *et al.*  
53  
54         58         2018a), trophic webs (e.g. Bottjer *et al.* 2000; Meysman *et al.* 2006), and geochemical cycles  
55  
56         59         (e.g. Logan *et al.* 1995; Canfield & Farquhar, 2009; Boyle *et al.* 2018). In northwestern  
57  
58         60         France, the Brioherian of central Brittany is a thick siliciclastic succession that was deposited

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2     61 during the Cadomian cycle (*c.* 750–540 Ma). Despite the report of fossils since the 19<sup>th</sup>  
3 century, the age of its uppermost beds (Ediacaran or early Cambrian) is a long-standing  
4 conundrum. Recently, new investigations unraveled a unique assemblage of trace and body  
5 fossils in the vicinity of Rennes (Néraudeau *et al.* 2016, 2019; Gougeon *et al.* 2018*b*, 2019).  
6  
7     62 Trace fossils are dominantly simple, horizontal, and associated with microbially-stabilized  
8 surfaces; of these, planispirals stand as a surprising discovery.  
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67         The aim of this study is threefold: (1) to describe a new assemblage of planispiral trace  
68 fossils from the Brioherian of northwestern France; (2) to place this assemblage within a  
69 macro-evolutionary framework, and to interpret its significance; and (3) to provide new  
70 radiometric dating, in order to discuss the age of the uppermost Brioherian deposits.

## 71     **2. General background**

### 72     **2.a. Geological setting and previous work**

73         The Brioherian (*c.* 660–540 Ma; Le Corre *et al.* 1991; Guerrot *et al.* 1989, 1992) is an  
74 informal name given to a thick sedimentary succession deposited during the Cadomian cycle  
75 (*c.* 750–540 Ma) in northwestern France (Fig. 1a, b; Chantraine *et al.* 2001; Ballèvre *et al.*  
76 2013). In the Rennes area (Fig. 1b), only the uppermost Brioherian beds are exposed, with a  
77 thickness evaluated at *c.* 1300 m (Trautmann *et al.* 1999). The Brioherian of Brittany lies  
78 unconformably on an Icartian basement (*c.* 2200–1800 Ma) and is unconformably overlain  
79 either by the Ordovician Red Bed Series ('Séries Rouges Initiales') or by the Ordovician  
80 Armoric Sandstone ('Grès Armoricain'; Cogné, 1959; D'Lemos *et al.* 1990; Le Corre *et al.*  
81 1991). The terrigenous siliciclastic sediments of the Brioherian resulted from the erosion of  
82 the Cadomian belt in northern Brittany and accumulated in a marginal, intra-plate basin in  
83 central Brittany (Denis, 1988; Dissler *et al.* 1988; Rabu *et al.* 1990; Dabard *et al.* 1996).  
84 Locally, carbonaceous cherts ('phtanites'), limestones, and igneous intrusions have also been

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3       85 reported (Denis & Dabard, 1988; Dabard, 1990, 2000; Chantraine *et al.* 2001). On a regional  
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5 scale, the correlation of the Brioherian sedimentary deposits is hindered by the discontinuous  
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7 outcropping, facies changes, the absence of biostratigraphic markers, and the metamorphic  
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9 overprint from the Devonian-Carboniferous Variscan orogeny (Denis & Dabard, 1988;  
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11 D'Lemos *et al.* 1990; Le Corre *et al.* 1991; Ballèvre *et al.* 2013). While traditionally  
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13 interpreted as deeper-marine turbiditic deposits (Dangeard *et al.* 1961; Denis, 1988;  
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15 Trautmann *et al.* 1999), the Brioherian sedimentary beds also show evidence of shallow-  
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17 marine storm-influenced (Dabard & Loi, 1998; Dabard & Simon, 2011) and marginal-marine  
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19 tidally-influenced conditions (Graindor, 1957; Dabard, 1990, 2000; Néraudeau *et al.* 2019).  
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23       94 [insert Figure 1]

27       95 Fossils recovered from the Brioherian are algal or bacterial organic-walled  
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29 microfossils in cherts and limestones (Cayeux, 1894; Deflandre, 1955; Chauvel & Schopf,  
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31 1978; Chauvel & Mansuy, 1981; Mansuy & Vidal, 1983), macroscopic body fossils of  
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33 unknown origin (Néraudeau *et al.* 2019), and trace fossils. Ichnofossils were first discovered  
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35 in the late 19<sup>th</sup> century (Lebesconte, 1886), but did not draw the attention of the scientific  
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37 community for a long time. Recently, new investigations in the vicinity of Rennes (Fig. 1b)  
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39 have unraveled an assemblage dominated by simple horizontal grazing trails (*Circulichnus*,  
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41 101 *Gordia*, *Helminthoidichnites*, *Helminthopsis*), passively-filled horizontal burrows  
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43 (102 *Palaeophycus*), and horizontal spiral trace fossils (*Spirodesmos*; Néraudeau *et al.* 2016;  
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45 103 Gougeon *et al.* 2018b, 2019). In addition, microbially-textured surfaces (MISS of Noffke *et*  
46  
47 104 *al.* 2001) are common both in fossiliferous and azoic intervals (Lebesconte, 1886; Gougeon *et*  
48  
49 105 *al.* 2018b).

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56       107 The age of the uppermost Brioherian sedimentary beds in Brittany, Normandy, and  
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58 Mayenne, has been highly debated (Fig. 1b). In Brittany, the overlying Red Bed Series gave  
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60 an age of  $472 \pm 5$  Ma (Rb-Sr dating from volcanic rocks; Auvray *et al.* 1980),  $465 \pm 1$  Ma (U-

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3 110 Pb dating from volcanic rocks; Bonjour *et al.* 1988; Bonjour & Odin, 1989), and  $486 \pm 28$  Ma  
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5 111 (Pb-Pb dating from volcanic rocks; Guerrot *et al.* 1992), placing these beds within the  
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7 112 Ordovician period (*contra* McMahon *et al.* 2017; Went, 2017). In the westernmost part of  
8  
9 113 Brittany (Crozon area; Fig. 1b), Guerrot *et al.* (1992) obtained an age of  $543 \pm 18$  Ma (Pb-Pb  
10  
11 114 dating) for a tuff intercalated within Brioverian beds, whereas a maximum deposition age of  
12  
13 115  $546 \pm 2$  Ma (U-Pb dating) has been obtained by Ballouard *et al.* (2018) from detrital zircon  
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15 116 grains extracted from a sandstone (see also Dabard *et al.* 2021). In the vicinity of Rennes (Fig.  
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17 117 1b), detrital zircon grains gave a maximum deposition age of *c.* 550 Ma (U-Pb dating from  
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19 118 sandstone and siltstone; Gougeon *et al.* 2018b); however, five zircon grains, dated at  $532.1 \pm$   
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21 119 3.9 Ma, were problematic to interpret (Gougeon *et al.* 2018b). In Normandy, Brioverian  
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23 120 sediments were deposited in a different palaeogeographic domain than in central Brittany, as  
24  
25 121 they are separated by the North-Armorian Shear Zone (Fig. 1b; Chantraine *et al.* 1982;  
26  
27 122 Guerrot *et al.* 1992). In this domain, granitoid intrusions within Brioverian sediments have  
28  
29 123 been dated at  $540 \pm 10$  Ma (U-Pb dating on monazite; Pasteels & Doré, 1982). In Mayenne,  
30  
31 124 where the Brioverian is in continuity with its equivalent of central Brittany (Fig. 1b),  
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33 125 radiometric dating on zircon grains yielded an age of  $540 \pm 17$  Ma (tuff and detrital horizons;  
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35 126 Guerrot *et al.* 1992).

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42 127 **2.b. Outcrops under study and depositional environments**

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45 128 The outcrop at ‘La Lammerais’ village nearby St-Gonlay (Fig. 1b) yields slates with  
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47 129 trace fossils, stacked in a pile about two metres high and fifty metres long (outcrops for this  
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49 130 contribution are located on private properties, which do not allow details on their exact  
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51 131 locations). These slates were extracted from a pit that was exploited by locals to build houses  
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53 132 and pathways decades ago; unfortunately, the pit is now covered with vegetation and  
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55 133 therefore impossible to sample *in situ*. Slates are made of siltstone and rare very fine- to fine-  
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57 134 grained sandstone. One loose sandstone sample was collected for U-Pb dating, coming from a

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3     135 nearby agricultural field. At ‘La Lammerais’ outcrop, sedimentary structures are parallel-  
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5     136 lamination organised in siltstone-sandstone bundles (i.e. rhythmite-like; Néraudeau *et al.*  
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7     137 2019, fig. 3), current-ripples (Néraudeau *et al.* 2019, fig. 2), tool-marks/spindle-shaped flute-  
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9     138 marks, possible load-casts, and pustular and wrinkled microbially-textured surfaces (Gougeon  
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11     139 *et al.* 2018b, figs 4, 7).

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15     140         Nearby St-Gonlay, another outcrop has been investigated at ‘Le Lorinou’ village,  
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17     141 located 1.4 kilometres to the east of ‘La Lammerais’. This outcrop is very poor in trace fossils  
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19     142 (no spiral trace fossils were found there), but beds are preserved *in situ* and a sandstone  
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21     143 sample was collected for U-Pb zircon dating.

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25     144         The outcrop of ‘Le Bois-du-Buisson’ is located at the entrance of a small forest in  
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27     145 Montfort-sur-Meu (Fig. 1b). It consists of a small quarry of about three metres high and ten  
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29     146 metres long, with vegetation extensively covering the sedimentary beds. However, a few  
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31     147 siltstone beds are accessible and reveal fresh surfaces with trace fossils. Sedimentary  
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33     148 structures are parallel-lamination organised in siltstone-sandstone bundles (i.e. rhythmite-like,  
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35     149 similarly to what is found at ‘La Lammerais’), and pustular and wrinkled microbially-  
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37     150 stabilized surfaces.

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42     151         In addition, Montfort-sur-Meu is the host of ‘Les Grippeaux’ quarry, where P.  
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44     152 Lebesconte recovered fossils for the first time in the late 19<sup>th</sup> century (Lebesconte, 1886;  
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46     153 Gougeon *et al.* 2018b). Nowadays, the quarry is secured by a fence preventing any access.  
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48     154 Many samples were collected in the late 19<sup>th</sup> and early 20<sup>th</sup> century by P. Lebesconte, F.  
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50     155 Kerforne, and other geologists; they are housed at the Geological Institute of the University of  
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52     156 Rennes 1 and at the Museum of Natural History of Nantes, and are available for study.  
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54     157 Sedimentary structures are pustular microbially-stabilized surfaces.

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3 158 The outcrop in Crozon (Fig. 1b) is located on the coastal cliff at 'La Plage-du-  
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5 159 Goulien'. This outcrop has not been visited by the authors, and the only trace fossil  
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7 160 discovered was reported by E. Hanson in 2014 (pers. comm.). The sedimentology of the  
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9 161 Brioherian from the Bay of Douarnenez and the Cove of Dinan (both in the vicinity of  
10  
11 162 Crozon) has been studied in two doctoral theses ([Darboux, unpubl. Ph.D. thesis, University of](#)  
12  
13 [Brest, 1973](#); Denis, 1988). The succession displays parallel-laminated/bedded sandstone and  
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15 siltstone with flute-casts, load-casts, tool-marks, rip-up clasts, carbonate concretions, normal  
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17 164 and reverse grading, convolute bedding, flame structures, and current, wave, and climbing  
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19 165 ripples. Both authors interpreted the succession as deposited by turbidites, located either  
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21 166 below the limit of the storm wave-base action, or deeper in an abyssal plain. However, Denis  
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23 167 (1988) noted the presence of oscillatory flow structures, lenticular bedding (Facies 3 of Denis,  
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25 168 1988) and mud-drapes, which are more typical of shallower environments.  
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32 170 In Montfort-sur-Meu and St-Gonlay, the dominance of siltstone intercalated with  
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34 laminated very fine-grained sandstone, and the record of rhythmite-like bundles and current  
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36 172 ripples, suggest a marginal-marine, tidally-influenced depositional environment (cf. Nio &  
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38 173 Yang, 1991; Tessier *et al.* 1995; Dalrymple, 2010). This conclusion is strengthened by  
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40 174 observations in Chanteloup and Nouvoitou (both in the vicinity of Rennes), where a sandstone  
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42 175 facies displays mudstone drapes within fine-grained sandstone samples (i.e. flaser lamination;  
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44 176 Supplementary Figure 1); these areas could represent the seaward, sandier part of the  
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46 177 intertidal system. Sedimentary structures made by oscillatory flows (e.g. wave ripples,  
47  
48 178 hummocky cross-stratification) have not been observed in the area so far. These conclusions  
49  
50 179 are preliminary and await further support, notably from Brioherian outcrops revealing  
51  
52 180 bedding architecture, and from more sampling of sedimentary structures.

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58 181 **3. Material and methods**

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60 182 **3.a. Terminology of planispiral trace fossils**

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3 183 This contribution focusses only on spirals formed on a horizontal plane (i.e.  
4 planispirals). Three-dimensional, vertically (e.g. *Gyrolithes*, *Lapispira*) or horizontally (e.g.  
5 184 *Avetoichnus*, *Helicodromites*, *Helicolithus*) oriented spirals, are not comparable with the  
6 185 Brioherian material. In order to describe spiral morphologies, the following terms will be  
7 186 used: a *regular* spiral maintains a constant distance between whorls (Fig. 2b, c); an *irregular*  
8 187 spiral has a variable distance between whorls (Fig. 2a, d); a *one-way* spiral is a simple spiral  
9 188 with no central turnaround (Fig. 2a, b, d; Seilacher, 1977; Crimes & McCall, 1995); a *two-*  
10 189 *way* spiral is a double spiral with a central turnaround (Fig. 2c; Seilacher, 1977; Crimes &  
11 190 McCall, 1995); and a *bounded* spiral is an irregular, one-way spiral that decreases the distance  
12 191 between whorls outward (Fig. 2d).

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27 193 [insert Figure 2]

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30 194 **3.b. U-Pb dating method**

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33 195 A classic mineral separation procedure has been applied to concentrate zircon grains  
34 for U-Pb dating. Rocks were crushed and only the powder fraction with a diameter < 250 µm  
35 196 was kept. Heavy minerals were successively concentrated by Wilfley table, heavy liquids, and  
36 197 with an isodynamic Frantz separator. Zircon grains were then handpicked under a binocular  
37 198 microscope to produce the most representative sampling, with the aim to avoid any intentional  
38 199 bias (see Malusà *et al.* 2013 and references therein). Selected grains were then embedded in  
40 200 epoxy mounts, grounded and polished. Zircon grains were imaged by cathodoluminescence  
41 201 (CL) using a Reliotron CL system equipped with a digital color camera available at the  
42 202 GeOHeLiS analytical platform (University of Rennes 1).

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54 204 U-Pb geochronology was conducted by *in situ* laser ablation inductively coupled  
55 plasma mass spectrometry (LA-ICP-MS) at the GeOHeLiS analytical platform using an ESI  
56 205 NWR193UC Excimer laser coupled to a quadipole Agilent 7700x ICP-MS. Instrumental  
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3 conditions are reported in Supplementary Table S1, while the analytical protocol can be found  
4  
5 in Manzotti *et al.* (2015). Kernel density diagrams for analyses that are  $100 \pm 10\%$  concordant  
6  
7 were generated using IsoplotR (Vermeesch, 2018). When dealing with detrital zircon  
8  
9 geochronology, a minimum of 3 different ages obtained on 3 different zircon grains  
10  
11 overlapping in age at  $2\sigma$  has been demonstrated to produce a statistically robust maximum  
12  
13 deposition age (Dickinson & Gehrels, 2009). The second important criteria in order to  
14  
15 determine this maximum deposition age is the degree of concordance of the individual  
16  
17 analysis used to calculate this age. Most authors consider all analyses that are 90% concordant  
18  
19 or more, while others only analyses that are at least 95% concordant. In this study, because of  
20  
21 the complexity of one of the data set ('La Lammerais'), only analyses that were at least 95%  
22  
23 concordant were considered to calculate the maximum deposition age, in order to avoid using  
24  
25 apparent ages that could be younger than the true age due to a non-negligible Pb loss.  
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### 3.c. Museum repository

33  
34 From 'La Lammerais' and 'Le Bois-du-Buisson', samples were collected and  
35  
36 reposed at the Geological Institute of the University of Rennes 1 (collections Gougeon and  
37  
38 Néraudeau). Historical specimens from 'Les Grippeaux' are reposed at the Museum of  
39  
40 Natural History of Nantes (collections Barrois and Lebesconte) and the Geological Institute of  
41  
42 the University of Rennes 1 (collections Kerforne, Rolland and Rouault). The trace fossil from  
43  
44 'La Plage-du-Goulien' has not been collected and was only photographed in the field by E.  
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46 Hanson.  
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## 50 51 4. Results 52 53

### 54 4. a. Planispiral trace fossils from the Brioverian 55 56

57 The Brioverian of central Brittany contains a rich assemblage of simple horizontal  
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59 trace fossils, with *Helminthoidichnites* and *Helminthopsis* being the most common forms.  
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3 231 Originally, Lebesconte (1886, pl. 34, fig. 7) figured a planispiral trace fossil from Montfort-  
4 sur-Meu, without further discussion. Since then, spiral trace fossils have not been reported in  
5  
6 232 the Brioverian. Here, we describe two types of planispiral trace fossils: (1) irregular, one-way  
7 spiral trace fossils; and (2) regular, one-way spiral trace fossils.  
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9 233  
10 234  
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12 235 [insert Figure 3]  
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16 236 Four irregular, one-way spiral trace fossils were recovered from 'La Lammerais', 'Le  
17  
18 237 Bois-du-Buisson', and 'Les Grippeaux' (Fig. 3a). Specimens are 0.3–1 mm wide, have 1½–  
19  
20 238 1¾ whorls, and are preserved in positive and negative reliefs (preservation as epirelief or  
21  
22 239 hyporelief is unknown because slates with trace fossils are not preserved *in situ*). One  
23  
24 240 specimen (Fig. 3a) has a different infill than the host rock and a lining; this is potentially a  
25  
26 241 burrow. Rarely, they are associated with *Helminthoidichnites*, small-scale branching trace  
27  
28 242 fossils (cf. *Pilichnus*), and pits of uncertain affinity. They are commonly found on pustular  
29  
30 243 microbially-textured surfaces.  
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35 244 Two regular, one-way spiral trace fossils were recovered from 'La Plage-du-Goulien'  
36  
37 245 and 'Les Grippeaux' (Fig. 3b, c). Specimens are 1–3 mm wide, have 2¼–2½ whorls, and are  
38  
39 246 preserved in positive and negative reliefs. The distance between whorls remains constant until  
40  
41 247 the last whorl, where the course detaches from the spiral system and progressively disappears.  
42  
43 248 They are associated with *Helminthopsis* and pits of uncertain affinity. The surfaces they are  
44  
45 249 found on are not textured.  
46  
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49 250 *Spirodesmos*, *Spirophycus* and *Spirorhaphe* are the most common planispirals from  
50  
51 251 the trace fossil record; however, their morphological boundaries are unclear. *Spirodesmos* is a  
52  
53 252 regular to irregular, one-way spiral trace fossil (Geinitz, 1867; Andrée, 1920; Huckriede,  
54  
55 253 1952; Xia *et al.* 1987). For Seilacher (1977), *Spirodesmos* has a wide spacing between whorls;  
56  
57 254 although this is clearly so in the type ichnospecies *S. interruptus* Andrée, 1920, *S.*  
58  
59  
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1  
2  
3 255 *archimedeus* Huckriede, 1952 has a narrower spacing between whorls. This issue becomes  
4 critical with *Spirodesmos kaihuaensis* Xia, He & Hu, 1987 and *S. spiralis* (Geinitz, 1867),  
5 both having irregular courses with variable distances between whorls. *Spirophycus* is a regular  
6 to irregular, one-way spiral trace fossil that commonly grades into meanders (Heer, 1876;  
7 Häntzschel, 1975). Seilacher (1977) argued that *Spirophycus* has wide strings with a  
8 tubercular surface and backfilled laminae (see also Książkiewicz, 1977; but see Uchman,  
9 1998). The spiral portion of *Spirophycus* (e.g. Heer, 1876, pl. 66, fig. b; Sacco, 1888, pl. 2,  
10 261 fig. 14), with regular whorls distinctly spaced from each other, can however be very similar to  
11 262 *Spirodesmos archimedeus*. *Spirorhaphe* is a regular to irregular spiral trace fossil with either a  
12 263 one-way (*S. azteca*, *S. graeca*) or two-way (*S. involuta*) course (Seilacher, 1977; Crimes &  
13 264 McCall, 1995). The inclusion of one-way spirals in *Spirorhaphe* is overlapping with  
14 265 *Spirodesmos* and *Spirophycus* morphologies, which is problematic.  
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267 Despite these taxonomical issues (see also Crimes & Crossley, 1991; Uchman, 1998;  
268 Minter & Braddy, 2009), planispirals from the Brioherian are comparable to *Spirodesmos*.  
269 Brioherian irregular, one-way spiral trace fossils are reminiscent of *Spirodesmos spiralis* (cf.  
270 Geinitz, 1867; Stepanek & Geyer, 1989). However, because of its irregular course and the  
271 poor extent of its whorls, *Spirodesmos spiralis* needs to be re-evaluated taxonomically; in this  
272 study, Brioherian forms are referred to *Spirodesmos* isp. Conversely, Brioherian regular, one-  
273 way spiral trace fossils belong to *Spirodesmos archimedeus* (cf. Huckriede, 1952; Zapletal &  
274 Pek, 1971; Horn, 1989). *Spirodesmos* ranges from the Ediacaran-Cambrian (this study) to the  
275 Holocene (e.g. Kitchell *et al.* 1978; Smith *et al.* 2005).

#### 276 **4.b. U-Pb dating**

277 For the sandstone sample from 'La Lammerais', 118 zircon grains were analysed,  
278 among which 107 analyses have a concordance of  $100 \pm 10\%$ . Their U (49 to 1195 ppm) and  
279 Pb (6 to 493 ppm) contents, as well as their Th/U ratios (0.02 to 1), are highly variable

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3 280 (Supplementary Table S2). A first group of 12 analyses yields apparent ages between 2.8 and  
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5 281 1.06 Ga. The remaining analyses form two major peaks at 600 Ma and 550 Ma, with minor  
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7 282 peaks around 850 and 650 Ma (Fig. 1c). The 10 youngest analyses that are more than 95%  
8  
9 283 concordant yield a weighted average  $^{206}\text{Pb}/^{238}\text{U}$  date of  $540 \pm 5$  Ma (MSWD = 1.2) that we  
10  
11 284 consider as the maximum deposition age for this sandstone.  
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15 285 For the sandstone sample from ‘Le Lorinou’, 89 grains were analysed, out of which 68  
16  
17 286 are  $100 \pm 10\%$  concordant (Supplementary Table S2). They are characterized by variable U  
18  
19 287 and Pb contents (21 to 726 ppm and 2 to 242 ppm, respectively), with Th/U ratios between  
20  
21 288 0.05 and 1.4. A first group of 22 zircon grains yields Neoarchean (2.9 Ga) to  
22  
23 289 Palaeoproterozoic ages (1.8 Ga), followed by a gap until the end of the Mesoproterozoic. The  
24  
25 290 remaining grains present apparent ages around 1000, 900, 800, and 680, with a major peak  
26  
27 291 around 600 Ma (Fig. 1c). The youngest three grains provide a weighted  $^{206}\text{Pb}/^{238}\text{U}$  date of  $551 \pm 7$  Ma  
28  
29 292 (MSWD = 0.009) that we consider as the maximum deposition age for this sandstone.  
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34 293 **6. Discussion**  
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37 294 **6.a. Radiometric age of the uppermost Brioverian beds with trace fossils**  
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40 295 At ‘Le Lorinou’ (St-Gonlay), zircon grains from a sandstone bed associated with trace  
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42 296 fossils yielded a maximum deposition age of  $551 \pm 7$  Ma, whereas zircon grains from a loose  
43  
44 297 sandstone sample at ‘La Lammerais’ (St-Gonlay) gave a maximum deposition age of  $540 \pm 5$  Ma  
45  
46 298 (this study). In Crozon, the youngest U-Pb dating on zircon grains from Brioverian tuff  
47  
48 299 gave an age of  $543 \pm 18$  Ma (Guerrot *et al.* 1992), whereas another U-Pb dating on zircon  
50  
51 300 grains from a sandstone gave a maximum deposition age of  $546 \pm 2$  Ma (Ballouard *et al.*  
52  
53 301 2018). In Montfort-sur-Meu, no radiometric dating has been done so far.  
54  
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56  
57 302 The radiometric age for the base of the Cambrian is given by U-Pb dating on zircon  
58  
59 303 grains from tuff in southern Oman, dated at  $541.0 \pm 0.13$  Ma (Bowring *et al.* 2007). However,  
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3 304 recent U-Pb dating on zircon grains from tuff in southern Namibia constrained the age of the  
4  
5 305 basal Cambrian within a 538.6–538.8 Ma interval (Linnemann *et al.* 2019). If we consider a  
6  
7 306 radiometric age of *c.* 539 Ma for the base of the Cambrian, the Brioherian of Crozon could  
8  
9 307 either be Ediacaran (*c.* 635–539 Ma) or younger, while the Brioherian of St-Gonlay could be  
10  
11 308 Ediacaran but is suspected to be Fortunian (*c.* 539–529 Ma) or younger. Indeed, the new  
12  
13 309 results of this study agree with earlier dating elsewhere (maximum deposition age of *c.* 550  
14  
15 310 Ma in Néant-sur-Yvel, Brittany, with 5 zircons grains dated at  $532.1 \pm 3.9$  Ma;  $540 \pm 10$  Ma  
16  
17 311 in Normandy; and  $540 \pm 17$  Ma in Mayenne; Pasteels & Doré, 1982; Guerrot *et al.* 1992;  
18  
19 312 Gougeon *et al.* 2018b) and suggest an early Cambrian age for the uppermost Brioherian beds,  
20  
21 313 from a radiometric standpoint (see also Guerrot *et al.* 1989, 1992; Dabard *et al.* 2021). In  
22  
23 314 terms of trace fossil biostratigraphy, the matground ecology of the Brioherian is more typical  
24  
25 315 of late Ediacaran assemblages (Gougeon *et al.* 2018b). Because of the differences provided by  
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27 316 these two proxies (radiometric dating and ichnostratigraphy), definitive conclusions on the  
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29 317 age of the uppermost Brioherian beds with trace fossils are not possible, at this point.  
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36 318 **6.b. Critical review on Ediacaran and Cambrian planispiral trace fossils**

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39 319 Several trace fossils inaccurately described or suggested to be planispirals, have been  
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41 320 reported from the Ediacaran and the Cambrian. Fedonkin (1985, 1990) erected  
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43 321 *Planispiralichnus* Fedonkin, 1985 and *Protospiralichnus* Fedonkin, 1985 from the Fortunian  
44  
45 322 Kessyuse Formation (Fm.) of northern Russia. *Planispiralichnus* is made of dense,  
46  
47 323 overlapping loops (Fedonkin, 1990; Marusin & Kuper, 2020), whereas *Protospiralichnus*  
48  
49 324 starts as a bounded spiral until it scribbles abundantly (Fedonkin, 1990); because of their  
50  
51 325 scribbling patterns, neither of them represent spirals (Buatois *et al.* 2017). Jenkins (1995, pl.  
52  
53 326 2, fig. E) reported cf. *Protospiralichnus* from the Ediacaran Rawnsley Quartzite of southern  
54  
55 327 Australia; the development of a full circle and/or a loop affiliates this trace fossil to  
56  
57 328 *Circulichnus* or *Gordia* instead (see also Buatois & Mángano, 2016, fig. 2.8e).

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3 329 *Multilaqueichnus* Yang & Yin, 1982 from the Cambrian Stage 3 Jiulaodong Fm. of central  
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5 330 China has overlapping loops (Yang *et al.* 1982, pl. 2, fig. 1); these trace fossils distinctly  
6  
7 331 scribble and are not spirals either (*contra* Mángano & Buatois, 2016, 2020). Finally, a trace  
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9 332 fossil from the Fortunian part of the Chapel Island Fm. of eastern Canada was considered a  
10  
11 333 spiral by Crimes & Fedonkin (1994, fig. 2i). This trace fossil has been observed in the field by  
12  
13 334 one of the authors (R. G.) and represents the scribbling burrow of a large infaunal deposit-  
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15 335 feeder.  
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20 336 In addition, non-ichnological structures from the Ediacaran and the Cambrian have  
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22 337 been mistaken for planispiral trace fossils. An important debate arose with the report of  
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24 338 Precambrian spiral fossils from the Lower Vindhyan Limestone of northeastern India (Beer,  
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26 339 1919) and from the Belt Series of northwestern USA (Walcott, 1899). Both authors suggested  
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28 340 a trace fossil origin, an opinion followed by Seilacher (1956). However, Cloud (1968)  
29  
30 341 suspected an algal origin, and re-evaluation of both materials confirmed that view (Walter *et*  
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32 342 *al.* 1976; Runnegar, 1991). *Arenicolites spiralis* Billings, 1872 and *Helminthoidichnites*  
33  
34 343 *sangshuanensis* (Du, 1986) in Yan & Liu, 1998 are certainly of similar algal affinity  
35  
36 344 (Hofmann, 1971; Walter *et al.* 1990; Shaowu, 1998). Furthermore, Aceñolaza (2005) reported  
37  
38 345 circular structures from the Cambrian Mesón Group of northwestern Argentina, and erected  
39  
40 346 the new ichnospecies *Spirodesmos milanai*; Minter *et al.* (2006) argued these structures were  
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42 347 formed by shrinkage cracks in matgrounds instead (cf. Pflüger, 1999; Buatois *et al.* 2013;  
43  
44 348 Sedorko *et al.* 2019).

45  
46 349 Finally, rare horizontal spiral trace fossils have been reported from the Ediacaran and  
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48 350 the Cambrian. *Planispiralichnus rarus* Menasova, 2003 is a one-way spiral trace fossil  
49  
50 351 discovered in the Fortunian Khmelnitsky Fm. of western Ukraine. The holotype is made of 3  
51  
52 352 whorls, with angular intervals along the course; the first two whorls are continuous, while the  
53  
54 353 last one is made of unconnected segments (Ivantsov *et al.* 2015, pl. 7, fig. 4a, b). This

specimen possesses the key features of a spiral trace fossil and should not be affiliated to *Planispiralichnus* as described by Fedonkin (1990). Jensen & Palacios (2016, fig. 4b) reported one-way spiral trace fossils from the Ediacaran-Fortunian Cíjara Fm. of central Spain. The photographed specimen is a continuous to discontinuous trail, with 2½ whorls and an irregular course. Carbone & Narbonne (2014, fig. 4.5) also figured an irregular one-way spiral with 1¾ whorls and a continuous course from the Fortunian part of the Ingta Fm. of northwestern Canada. Finally, Runnegar (1992, fig. 3.9) figured an irregular two-way spiral transitional with a meandering trace fossil from the Ediacaran Rawnsley Quartzite of southern Australia. Jensen (2003) considered this trace fossil to represent *Helminthorhaphe* grading into *Spirorhaphe*.

### 6.c. Macro-evolutionary profile and onshore-offshore migration

Our detailed literature review (Section 6.b above and Supplementary Material) unraveled the environmental and temporal distribution of *Spirodesmos* (Fig. 4). The Ediacaran-Fortunian is then marked by the appearance of a *Spirodesmos* pool, composed of irregular and regular forms colonizing marginal-marine to shelf environments. The Brierian assemblage represents a key component of that pool, holding the oldest regular one-way planispirals (*Spirodesmos archimedaeus*) both in marginal-marine and open shelf settings (in Montfort-sur-Meu and Crozon, respectively). During the Ediacaran and the Cambrian, deposit-feeding was the dominant feeding strategy (MacNaughton & Narbonne, 1999; Carbone & Narbonne, 2014), and early *Spirodesmos* were arguably made by epifaunal detritus-feeders and shallow-infaunal deposit-feeders. Indeed, ‘surplus stretches’ as observed in *Spirorhaphe* and inferring open-burrow systems (Seilacher, 1967a, b, 1977) have not been observed in Ediacaran-Fortunian material. Moreover, Ediacaran-Fortunian *Spirodesmos* are often preserved on microbially-stabilized surfaces, which could represent the nutritive resource of their tracemaker (Carbone & Narbonne, 2014). Possible producers are

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3 379 enteropneusts and nematodes, both suspected to first appear during the Cambrian or before  
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5 380 (Knoll & Carroll, 1999; Budd & Jensen, 2000; Maletz, 2014; Cunningham *et al.* 2017).  
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7 381 Enteropneusts produce regular horizontal spirals on the modern deep-sea floor on areas of  
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9 greater nutritional values, using tactile sensory systems in their head (Lemche *et al.* 1976;  
10  
11 382 Smith *et al.* 2005; Jones *et al.* 2013). Nematodes spiral by contracting all the muscles of one  
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13 383 side of their body (Wharton, 2004). However, spiraling in nematodes has been suggested for  
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15 384 other purposes than feeding (e.g. responses to increasing temperature, osmotic stress,  
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17 385 desiccation, and for reproduction; Huettel, 2004; Wharton, 2004).  
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22 387 [insert Figure 4]  
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25 388 Although deep-marine deposits with trace fossils have been reported both from the  
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27 389 Ediacaran (e.g. Narbonne & Hofmann, 1987; Liu *et al.* 2010) and the Cambrian (e.g.  
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29 390 Hofmann *et al.* 1994; Seilacher *et al.* 2005), planispirals are consistently absent. However,  
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31 391 planispirals are common through the rest of the Phanerozoic in the deep-sea, and *Spirodesmos*  
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33 392 forms a conspicuous Ordovician–Recent deep-marine trend (Fig. 4 and Supplementary  
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35 Material). Deep-marine seafloors are characterized by an absence of light, high hydrostatic  
36  
37 393 pressure, oxygen and temperature fluctuations, and low nutrient content (Sanders & Hessler,  
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39 394 1969; Gage & Tyler, 1991, pp. 9–29; Rex & Etter, 2010, pp. 1–49). These stressful conditions  
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41 395 play an important role on animal fitness and their physiology (e.g. Childress & Thuesen,  
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43 396 1992; Yancey *et al.* 2004; van der Grinten & Rogers, 2015). However, with the increased  
44  
45 397 competition for space and food on early Cambrian shelves (Orr, 2001), planispiral  
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47 398 tracemakers may have adapted their metabolisms to the deep-sea. An onshore-offshore  
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49 399 migration in *Spirodesmos* is then suggested from the Ediacaran-Fortunian to the Ordovician,  
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51 400 similarly to the migration observed in graphoglyptids (Crimes & Anderson, 1985; Crimes *et*  
52  
53 401 *al.* 1992; Crimes & Fedonkin, 1994; Orr, 2001; Uchman, 2003). The existence of an onshore-  
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55 402 offshore migration is also reinforced by the presence of an important gap (*c.* 230 Ma) between  
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3 404 the Ediacaran-Fortunian *Spirodesmos* pool, and the next shallow-marine *Spirodesmos* report  
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5 405 from the Permian Vryheid Fm. of eastern South Africa (Mason *et al.* 1983; Fig. 4).  
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8 406 **7. Conclusion**  
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11 407 The age of the uppermost Brioherian deposits of central Brittany, northwestern France,  
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13 408 is a long-standing question. Here, two U-Pb **detrital** zircon grain dating on sandstone samples  
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15 409 collected in St-Gonlay gave maximum depositional ages of  $551 \pm 7$  Ma and  $540 \pm 5$  Ma.  
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17  
18 410 Although **an Ediacaran** age for the uppermost Brioherian beds cannot be discarded, a  
19  
20 411 Fortunian age is suggested in this study, following previous dating in Brittany, Normandy,  
21  
22 412 and Mayenne. However, **the** intervals of error of **the** radiometric dating and trace fossil  
23  
24 413 biostratigraphy do not allow definitive conclusions.  
25  
26  
27  
28 414 A unique assemblage of irregular and regular, one-way planispiral trace fossils of  
29  
30 415 *Spirodesmos* affinity has been recovered from the uppermost Brioherian beds in Crozon,  
31  
32 416 Montfort-sur-Meu, and St-Gonlay. Planispiral trace fossils are unusual in the Ediacaran and  
33  
34 417 the Cambrian, and an in-depth literature review revealed that the Brioherian assemblage  
35  
36 418 belonged to an Ediacaran-Fortunian, marginal-marine to shelf *Spirodesmos* pool. Ediacaran-  
37  
38 419 Fortunian *Spirodesmos* were arguably made by **detritus- or deposit-feeders**, possibly related to  
40  
41 420 enteropneusts or nematodes. However, by the Ordovician, *Spirodesmos* became conspicuous  
42  
43 421 mostly in the deep-marine realm, underscoring an onshore-offshore migration similar to what  
44  
45 422 has been reported in graphoglyptids.  
46  
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48  
49 423 **Acknowledgements**  
50  
51  
52 424 This manuscript is a follow-up of a poster presented at the International Meeting on  
53  
54 425 the Ediacaran System and the Ediacaran-Cambrian Transition (IMECT) that took place in  
55  
56 426 Guadalupe, Spain, in October 2019. Discussions and feedbacks from L. Buatois, P. Crimes,  
57  
58 427 G. Mángano, V. Marusin, and M. Paz are kindly acknowledged. We also thank: M. Ferguson  
59  
60

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2  
3 428 for double-checking the English writing; D. Gendry and S. Regnault for granting access to the  
4  
5 429 museum of the Geological Institute of the University of Rennes 1 and the Museum of Natural  
6  
7 430 History of Nantes, respectively; N. Hallot for the rock crushing; E. Hanson for sharing her  
8  
9 431 photographs of the trace fossil from Crozon; X. Le Coz for the rock sawing and preparation of  
10  
11 432 thin sections; Y. Lepagnot for mineral separations; F. Polette and L. Guillois for their  
12  
13 433 assistance during U-Pb dating; and the outcrops' owners for granting access to their private  
14  
15 434 properties. The manuscript benefited from insightful reviews by A. Uchman and an  
16  
17 435 anonymous reviewer, as well as editor S. Jensen. The work of A. L. has been partially  
18  
19 436 supported by the 'Fondazione Banco di Sardegna' and by the 'Regione Autonoma della  
20  
21 437 Sardegna' (grant numbers F74I19000960007, J81G17000110002). This publication is a  
22  
23 438 contribution to the VIBRIO project of the INSU InterrVie program, and benefitted from a  
24  
25 439 financial support from the 'Observatoire des Sciences de l'Univers de Rennes' (OSUR). We  
26  
27 440 have a special thought for our colleague M.-P. Dabard who passed away too soon.

32  
33  
34 441 **Declaration of Interest**

35  
36  
37 442 None.

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3 810 **Figure 1.** Geological map of northwestern France, and new U-Pb dating. (a) Location of the  
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5 811 Brioherian deposits in northwestern France. (b) Close-up showing the Brioherian deposits,  
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7 812 and the three localities with planispiral trace fossils. NASZ = North-Armorican Shear Zone;  
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9 813 SASZ = South-Armorican Shear Zone. (c) Kernel Density Estimation diagrams for ‘La  
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11 814 Lammerais’ and ‘Le Lorinou’ samples.  
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15 815 **Figure 2.** Terminology of planispirals. (a) An irregular one-way spiral. (b) A regular one-way  
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17 816 spiral. (c) A regular two-way spiral. (d) A bounded spiral. See text for further explanations.  
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20 817 **Figure 3.** *Spirodesmos* isp. and *Spirodesmos archimedeus* from the uppermost Brioherian  
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22 818 beds of Brittany. (a) *Spirodesmos* isp. (irregular one-way spiral trace fossil) from ‘Le Bois-du-  
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24 819 Buisson’. (b, c) *Spirodesmos archimedeus* (regular one-way spiral trace fossils) from ‘Les  
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26 820 Grippeaux’ (b) and ‘La Plage-du-Goulien’ (c). Scale bars are 1 cm across.  
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30 821 **Figure 4.** Macro-evolutionary profile of *Spirodesmos* comparable to the Brioherian material,  
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32 822 with emphasis on the Ediacaran and the Cambrian (colored diagrams). Positions suggested for  
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34 823 the Brioherian material are emphasized by diagrams with dashed lines. Brioherian  
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36 824 *Spirodesmos* belonged to an Ediacaran-Fortunian, marginal-marine to shelf pool. A  
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38 825 *Spirodesmos* onshore-offshore migration is suggested, from the Ediacaran-Fortunian to the  
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40 826 Ordovician. See text for further explanations.  
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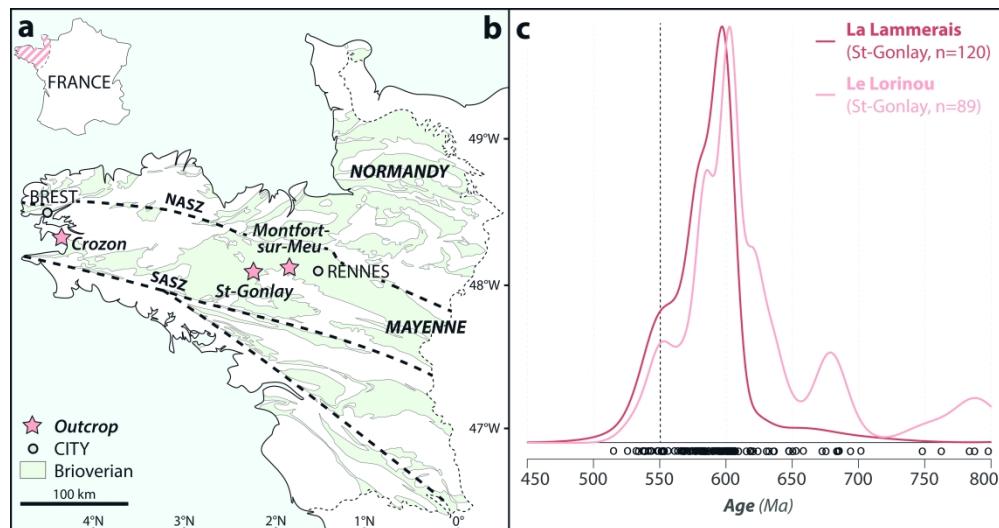


Figure 1. Geological map of northwestern France, and new U-Pb dating. (a) Location of the Brioverian deposits in northwestern France. (b) Close-up showing the Brioverian deposits, and the three localities with planispiral trace fossils. NASZ = North-Armorican Shear Zone; SASZ = South-Armorican Shear Zone. (c) Kernel Density Estimation diagrams for 'La Lammerais' and 'Le Lorinou' samples.

168x88mm (600 x 600 DPI)

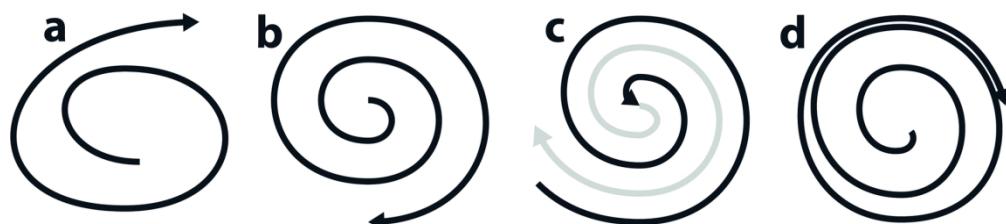
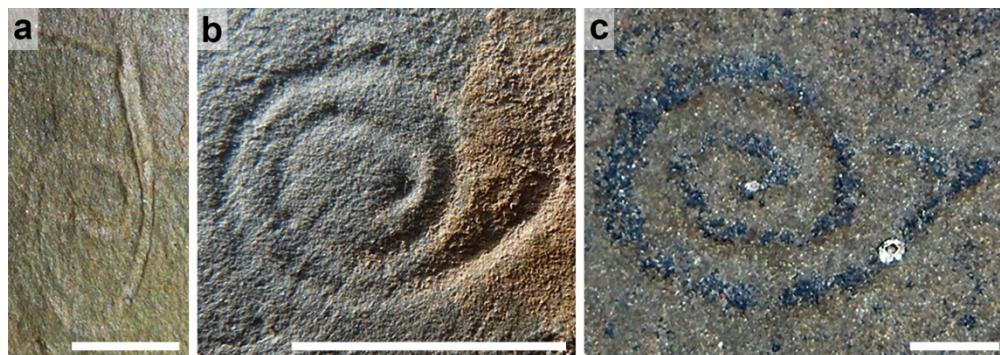


Figure 2. Terminology of planispirals. (a) An irregular one-way spiral. (b) A regular one-way spiral. (c) A regular two-way spiral. (d) A bounded spiral. See text for further explanations.

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Figure 3. *Spirodesmos* isp. and *Spirodesmos archimedeus* from the uppermost Brionian beds of Brittany.  
(a) *Spirodesmos* isp. (irregular one-way spiral trace fossil) from 'Le Bois-du-Buisson'. (b, c) *Spirodesmos archimedeus* (regular one-way spiral trace fossils) from 'Les Grippeaux' (b) and 'La Plage-du-Goulien' (c).  
Scale bars are 1 cm across.

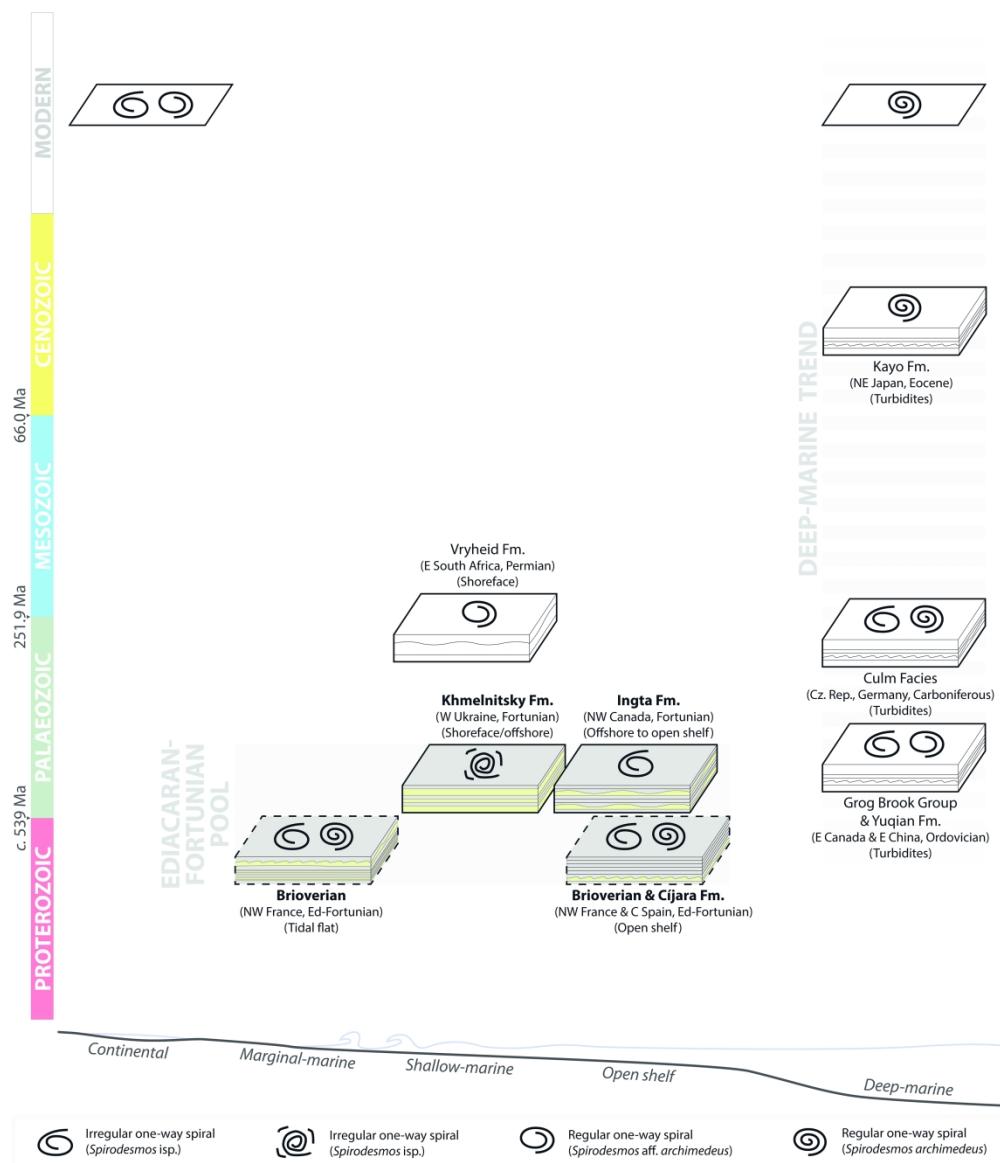


Figure 4. Macro-evolutionary profile of *Spirodesmos* comparable to the Brioverian material, with emphasis on the Ediacaran and the Cambrian (colored diagrams). Positions suggested for the Brioverian material are emphasized by diagrams with dashed lines. Brioverian *Spirodesmos* belonged to an Ediacaran-Fortunian, marginal-marine to shelf pool. A *Spirodesmos* onshore-offshore migration is suggested, from the Ediacaran-Fortunian to the Ordovician. See text for further explanations.

168x195mm (600 x 600 DPI)

*Geological Magazine*

New insights on the early evolution of horizontal spiral trace fossils and the age of the  
Brioverian (Ediacaran-Cambrian) in Brittany, NW France

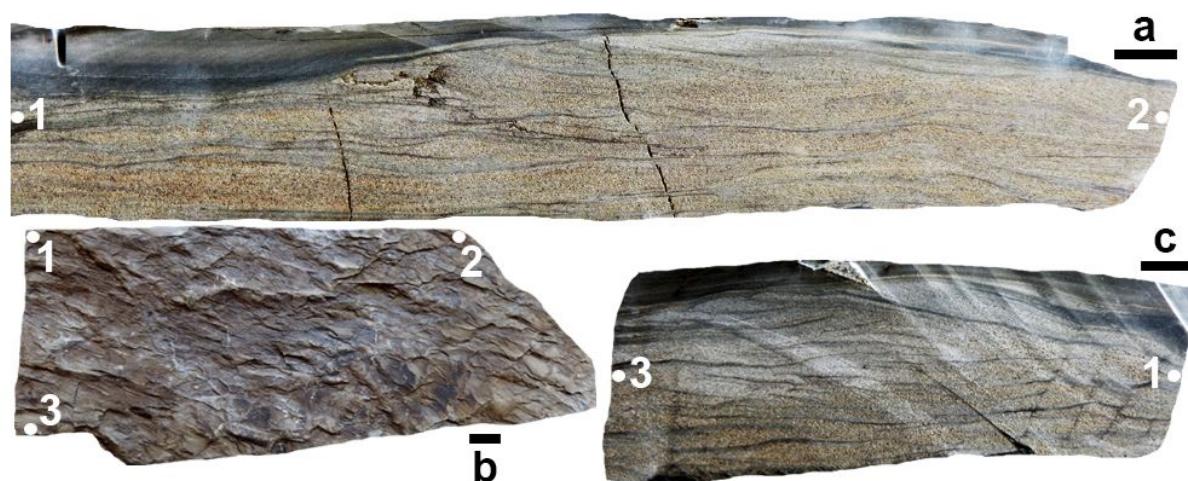
Romain Gougeon,, Didier Néraudeau, Alfredo Loi and Marc Poujol

Supplementary Material

For Peer Review

<b>Laboratory &amp; Sample Preparation</b>	
Laboratory name	GeOHeLiS Analytical Platform (OSUR, Univ. Rennes 1)
Sample type/mineral	Zircon
Sample preparation	Conventional mineral separation, 1 inch resin mount, 1micron polish to finish
Imaging	RELION CL instrument, Olympus Microscope BX51WI, Leica Color Camera DFC 420C
<b>Laser ablation system</b>	
Make, Model & type	ESI NWR193UC, Excimer
Ablation cell	ESI NWR TwoVol2
Laser wavelength	193 nm
Pulse width	< 5 ns
Fluence	7.4 J/cm <sup>2</sup>
Repetition rate	3Hz
Spot size	20 µm
Sampling mode / pattern	Single spot
Carrier gas	100% He, Ar make-up gas and N2 (3 ml/mn) combined using in-house smoothing device
Background collection	20 seconds
Ablation duration	60 seconds
Wash-out delay	15 seconds
Cell carrier gas flow (He)	0.75 l/min
<b>ICP-MS Instrument</b>	
Make, Model & type	Agilent 7700x, Q-ICP-MS
Sample introduction	Via conventional tubing
RF power	1350W
Sampler, skimmer cones	Ni
Extraction lenses	X type
Make-up gas flow (Ar)	0.80 l/min
Detection system	Single collector secondary electron multiplier
Data acquisition protocol	Time-resolved analysis
Scanning mode	Peak hopping, one point per peak
Detector mode	Pulse counting, dead time correction applied, and analog mode when signal intensity > ~ 10 <sup>6</sup> cps
Masses measured	<sup>204</sup> (Hg + Pb), <sup>206</sup> Pb, <sup>207</sup> Pb, <sup>208</sup> Pb, <sup>232</sup> Th, <sup>238</sup> U
Integration time / peak	10–30 ms ( <sup>207</sup> Pb)
Sensitivity / Efficiency	22000 cps/ppm Pb (50µm, 10Hz)
<b>Data Processing</b>	
Gas blank	20 seconds on-peak
Calibration strategy	GJ1 zircon standard used as primary reference material, Plešovice used as secondary reference material (quality control)
Common-Pb correction	No common-Pb correction.
Reference Material info	GJ1 (Jackson <i>et al.</i> 2004), Plešovice (Sláma <i>et al.</i> 2008)
Data processing package	Glitter (Van Achterbergh <i>et al.</i> 2001)
Uncertainty level and propagation	Ages are quoted at 2 sigma absolute, propagation is by quadratic addition according to Horstwood <i>et al.</i> (2016). Reproducibility and age uncertainty of reference material are propagated.
Quality control/ Validation	Plešovice: concordia age = 336.9± 2.0 Ma (N=36; MSWD=1.7)

**Supplementary Table S1.** Operating conditions for the LA-ICP-MS equipment.



**Supplementary Figure 1.** A fine-grained sandstone sample from Chanteloup under three different views (a, c: side views; b: surface view) showing abundant and discontinuous mud-drapes (i.e. flaser-lamination; cf. Nichols, 2009, fig. 4.37). The numbers are marker points for a three-dimensional understanding of the sample. Scale bars are 1 cm across.

### Supplementary Discussion

#### 1. Review on Phanerozoic planispirals

The Ordovician is marked by the first record of uncontroversial *Spirorhaphe* in turbidites from the Grog Brook Group in eastern Canada (Pickerill, 1980, fig. 2b). This specimen is a regular two-way spiral with 1½ whorls; also associated is a regular *Spirodesmos* with 1¼ whorls (Pickerill, 1980, fig. 2d). Fillion & Pickerill (1990, pl. 17, figs 17, 18) described ‘scribbling grazing traces’ from the Ordovician Redmans Fm. in eastern Canada; few of these specimens represent distinctive one-way spirals with 1–1½ whorls (i.e. *Spirodesmos* affinity; Fillion & Pickerill, 1990, pl. 17, fig. 18). In eastern China, the Ordovician Yuqian Fm. contains an assemblage of trace fossils with *Spirodesmos kaihuaensis* deposited in deep-water turbidites (Xia *et al.* 1987; Jin & Li, 1998); these are irregular one-way spirals made of 3–5 whorls (Xia *et al.* 1987, pl. 1, fig. 1). Crimes *et al.* (1974, fig. 2) mentioned *Spirophycus* in turbidites from the Ordovician Agüeira Fm. of northwestern Spain, but only a sketch representing an irregular one-way spiral with 1¼ whorls is provided. Interestingly, a spiral burrow was reported from the Ordovician Kermeur Fm. in northwestern France (Vidal *et al.* 2011, fig. 4b), close to the locality where a Brioverian spiral was also found (Fig. 2c). Deposited in proximal settings, the irregular one-way spiral burrow has a variable width, develops 1½ whorls and has a fill clearly different from the host rock. Its closest relatives are *Spirophycus* as described by Chamberlain & Clark (1973, pl. 2, fig. 1) from the Carboniferous of western USA, and by Mikuláš (1993, pl. 2, fig. 1) from the Ordovician of northern Czech Republic. Finally, *Spirodesmos spiralis* from the Ordovician Železný Brod Phyllites of northern Czech Republic (Chlupáč, 1997, pl. 6, fig. 2) is deformed (possibly due to metamorphism), and its ichnotaxonomic affiliation is problematic.

After the Ordovician, abundant *Spirophycus* (e.g. Sacco, 1888; Chamberlain & Clark, 1973; Crimes, 1977; Książkiewicz, 1977; Crimes & McCall, 1995; Buatois *et al.* 2001;

Uchman, 2007) and *Spirorhaphe* (e.g. Abel, 1935, pp. 291, 292; Macsotay, 1967; Książkiewicz, 1977; McCann & Pickerill, 1988; Crimes & McCall, 1995; Uchman, 2001; Monaco & Trecci, 2014) were reported from the deep-sea as part of the *Nereites* ichnofacies. Most of the record of post-Ordovician deep-marine *Spirodesmos* is coming from the Carboniferous Culm Facies of Germany and Czech Republic, represented by *S. archimedaeus* (Huckriede, 1952; Zapletal & Pek, 1971; Horn, 1989; Pek & Zapletal, 1990), *S. interruptus* (Andrée, 1920; Horn, 1989), and *S. spiralis* (Geinitz, 1867; Stepanek & Geyer, 1989; Pek & Zapletal, 1990). Other occurrences of *Spirodesmos* in the Phanerozoic are: (1) from the Triassic Al Ayn Fm. of Oman, with only  $\frac{1}{2}$  whorl preserved which is problematic (Wetzel *et al.* 2007); and (2) from the Eocene Kayo Fm. of northeastern Japan, with  $3\frac{1}{2}$  whorls preserved (Fukuda & Hayasaka, 1978).

Continental occurrences are scarce and only comprise a large *Spirodesmos interruptus* from the Carboniferous Mansfield Fm. of northeastern USA (Archer & Maples, 1984, fig. 5b). This irregular one-way spiral has  $1\frac{1}{2}$  whorls, and is made of segments of variable length; Rindsberg & Kopaska-Merkel (2005) argued for a *Treptichnus* affinity instead. Kim *et al.* (2002, fig. 5h) recorded a partially preserved *Spirodesmos* isp. from the Cretaceous Hasandong Fm. of southern Korea; with the absence of at least one fully developed whorl, this continental occurrence remains dubious.

In marginal-marine settings, Minter *et al.* (2006) and Minter & Braddy (2009) reported cf. *Spirorhaphe azteca* from the Permian Robledo Mountains Fm. of southern USA. These are regular one-way spirals with closely spaced, millimetric whorls (up to 19 whorls; Minter *et al.* 2006, fig. 1).

In shallow-marine environments, *Spirodesmos archimedaeus* is reported from the Permian Vryheid Fm. of eastern South-Africa (Mason *et al.* 1983). These regular one-way spirals, with  $1\frac{1}{4}$ – $1\frac{1}{2}$  whorls, are reminiscent of the Ordovician ‘scribbling grazing traces’ of

Fillion & Pickerill (1990, pl. 17, fig. 18). *Macaronichnus segregatis spiriformis* Bromley, Milà, Uchman & Hansen, 2009 has been reported from the Cretaceous Horseshoe Canyon Fm. of western Canada (Pemberton *et al.* 2001). Although these planispirals are regular with multiple whorls, they differ from other spiral trace fossils by their light-colored infill and their thin, dark mantle (Pemberton *et al.* 2001, fig. 104). Finally, Gierlowski-Kordesch & Ernst (1987) reported a unique assemblage of graphoglyptids with *Spirorhaphe* deposited under storm conditions in the Cretaceous Nangurukuru Fm. of southeastern Tanzania (see also Ernst & Zanders, 1993; Nicholas *et al.* 2006).

## 2. Review on modern planispirals

From continental settings, Schäfer (1965) reported one-way, tightly coiled spirals from mud banks of the Rhine river in Germany. Although Schäfer (1965) suspected grazing gastropod tracemakers, he failed in observing an animal in action. MacNaughton (2003) found one-way spirals with either irregular tight whorls or regular whorls increasing space outward (i.e. logarithmic spirals) from a lake beach in eastern Canada. MacNaughton (2003) suspected a small infaunal arthropod to be the originator. Muñiz Guinea *et al.* (2014) described regular one-way spirals from a wet orange grove in southwestern Spain. These traces were made by an infaunal fly larvae, and are continuous (incipient *Spirodesmos*) or displaying lateral projections (combination of incipient *Spirodesmos* and *Treptichnus*). Finally, a one-way spiral trace was reported by Metz (1987, fig. 4) from a puddle in eastern USA, made by an epifaunal ground beetle larva.

In tidal settings, *Paraonis* polychaete worms are well-known for constructing infaunal, tightly-coiled regular one-way spirals (Röder, 1971; Schäfer, 1972, p. 296; Risk & Tunnicliffe, 1978; Bromley, 1996, pp. 105-108; Minter *et al.* 2006; Lehane & Ekdale, 2013). The burrow system is made of multiple horizontal spirals occupying different vertical levels, and connected by vertical shafts (Gripp, 1927; Röder, 1971; Gingras *et al.* 1999). In addition,

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2  
3 incipient *Macaronichnus segregatis spiriformis* are made by *Ophelia* and *Thoracophelia*  
4 polychaete worms in beach sands (Pemberton *et al.* 2001; Bromley *et al.* 2009; Quiroz *et al.*  
5  
6 2019).  
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9  
10 Owing to the development of submarine photography in the middle of the 20<sup>th</sup> century  
11 (Ewing *et al.* 1946; Emery, 1952), the deep ocean exposed two categories of spiral traces: (1)  
12 one-way spirals (incipient *Spirodesmos*), and (2) two-way spirals (incipient *Spirorhaphes*).  
13 Reports of one-way spirals are prolific in the literature (e.g. Bourne & Heezen, 1965;  
14 Hülsemann, 1966; Jacobs *et al.* 1970, pp. 391, 445; Lemche *et al.* 1976; Foell & Pawson,  
15 1986; Holland *et al.* 2005; Durden *et al.* 2019); they are made by acorn worms, a type of giant  
16 enteropneust (Bourne & Heezen, 1965; Holland *et al.* 2005), and can be extremely abundant  
17 below 2500 m (Heezen & Hollister, 1971, pp. 176, 177; Kitchell *et al.* 1978*a, b*; Kitchell,  
18 1979; Bell *et al.* 2013). Two-way spiral traces are more rarely photographed on the deep-sea  
19 floor (Ewing & Davis, 1967; Ekdale & Berger, 1978; Berger *et al.* 1979; Ekdale, 1980;  
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						<i>Isoto</i>	
	Analysis_#	Pb ppm	Uppm	Th ppm	Th/U	Pb207/U235	PropErr2sigAbs.
<b><i>Carrière de Lammerais:</i></b>							
6	S-230517a-01	49	534	48	0.09	0.947	0.012
7	S-230517a-02	16	164	60	0.37	0.779	0.010
8	S-230517a-03	65	151	152	1.00	6.876	0.087
9	S-230517a-04	27	278	103	0.37	0.770	0.010
10	S-230517a-05	11	111	53	0.48	0.770	0.011
11	S-230517a-06	29	300	130	0.43	0.752	0.010
12	S-230517a-07	27	333	18	0.05	0.748	0.010
13	S-230517a-08	23	259	75	0.29	0.727	0.010
14	S-230517a-09	11	114	38	0.33	0.819	0.011
15	S-230517a-10	61	565	278	0.49	0.838	0.011
16	S-230517a-11	20	194	83	0.43	0.787	0.011
17	S-230517a-12	18	178	68	0.38	0.839	0.012
18	S-230517a-13	34	316	201	0.64	0.791	0.010
19	S-230517a-14	18	186	92	0.49	0.760	0.010
20	S-230517a-15	45	504	153	0.30	0.728	0.010
21	S-230517a-16	30	294	106	0.36	0.810	0.011
22	S-230517a-17	20	205	63	0.31	0.792	0.011
23	S-230517a-18	19	189	57	0.30	0.805	0.011
24	S-230517a-19	18	190	42	0.22	0.811	0.011
25	S-230517a-20	23	235	69	0.29	0.816	0.012
26	S-230517a-21	17	179	64	0.36	0.756	0.011
27	S-230517a-22	31	333	134	0.40	0.749	0.010
28	S-230517a-23	18	196	56	0.29	0.786	0.012
29	S-230517a-24	18	193	63	0.33	0.785	0.011
30	S-230517b-01	36	369	294	0.80	0.826	0.011
31	S-230517b-02	26	293	105	0.36	0.738	0.010
32	S-230517b-03	18	178	64	0.36	0.793	0.011
33	S-230517b-04	33	336	101	0.30	0.809	0.011
34	S-230517b-05	44	451	118	0.26	0.812	0.011
35	S-230517b-06	27	275	83	0.30	0.806	0.011
36	S-230517b-07	25	254	77	0.30	0.851	0.011
37	S-230517b-08	39	383	229	0.60	0.772	0.010
38	S-230517b-09	25	263	89	0.34	0.759	0.010
39	S-230517b-10	36	380	192	0.50	0.743	0.010
40	S-230517b-11	25	261	54	0.21	0.837	0.011
41	S-230517b-12	41	446	87	0.20	0.807	0.011
42	S-230517b-13	21	177	94	0.53	0.948	0.013
43	S-230517b-15	72	720	289	0.40	0.792	0.010
44	S-230517b-16	20	192	94	0.49	0.793	0.011
45	S-230517b-17	40	431	156	0.36	0.751	0.010
46	S-230517b-18	22	265	48	0.18	0.704	0.009
47	S-230517b-19	27	311	54	0.17	0.722	0.010
48	S-230517b-21	60	410	117	0.29	1.439	0.019

1	S-230517b-22	29	313	102	0.33	0.764	0.010
2	S-230517b-23	28	284	115	0.40	0.766	0.010
3	S-230517b-24	24	281	80	0.29	0.710	0.010
4	S-230517c-01	48	516	128	0.25	0.781	0.010
5	S-230517c-02	66	813	17	0.02	0.756	0.010
6	S-230517c-03	29	248	88	0.35	1.008	0.013
7	S-230517c-04	39	386	165	0.43	0.812	0.011
8	S-230517c-05	107	1195	186	0.16	1.278	0.016
9	S-230517c-06	38	379	129	0.34	0.813	0.011
10	S-230517c-07	35	355	125	0.35	0.810	0.011
11	S-230517c-08	18	187	42	0.23	0.800	0.011
12	S-230517c-09	28	308	85	0.27	0.772	0.010
13	S-230517c-10	24	264	35	0.13	0.771	0.010
14	S-230517c-11	29	331	94	0.29	0.712	0.009
15	S-230517c-12	33	357	147	0.41	0.730	0.010
16	S-230517c-13	70	813	167	0.21	0.770	0.010
17	S-230517c-14	33	344	70	0.20	0.808	0.011
18	S-230517c-15	26	257	59	0.23	0.863	0.011
19	S-230517c-16	27	253	56	0.22	0.936	0.013
20	S-230517c-17	10	65	34	0.53	1.333	0.019
21	S-230517c-18	39	348	90	0.26	0.959	0.013
22	S-230517c-19	23	110	91	0.83	1.792	0.024
23	S-230517c-20	31	315	108	0.34	0.804	0.011
24	S-230517c-21	30	302	114	0.38	0.846	0.011
25	S-230517c-22	27	281	88	0.31	0.787	0.010
26	S-230517c-23	28	299	74	0.25	0.780	0.010
27	S-230517c-24	43	451	45	0.10	0.860	0.011
28	S-230517d-01	86	897	262	0.29	0.784	0.010
29	S-230517d-02	493	1011	276	0.27	10.172	0.127
30	S-230517d-03	161	394	160	0.41	6.604	0.083
31	S-230517d-04	71	193	86	0.45	5.350	0.067
32	S-230517d-05	165	425	114	0.27	6.486	0.081
33	S-230517d-06	253	758	24	0.03	5.792	0.073
34	S-230517d-07	85	206	100	0.49	6.658	0.084
35	S-230517d-08	139	230	56	0.24	14.951	0.188
36	S-230517d-09	192	645	12	0.02	4.876	0.062
37	S-230517d-10	108	309	179	0.58	6.851	0.087
38	S-230517d-11	100	184	16	0.09	13.293	0.169
39	S-230517d-12	65	160	79	0.50	6.183	0.079
40	S-230517d-13	30	283	165	0.58	0.801	0.011
41	S-230517d-14	104	809	1084	1.34	0.871	0.011
42	S-230517d-15	8	86	25	0.29	0.908	0.013
43	S-230517d-16	24	183	153	0.84	1.174	0.016
44	S-230517d-17	12	49	51	1.04	2.352	0.037
45	S-230517d-18	24	249	96	0.39	0.949	0.013
46	S-230517d-19	21	212	97	0.46	0.807	0.011

1	S-230517d-20	31	313	111	0.36	0.799	0.011
2	S-230517d-21	15	148	128	0.86	0.704	0.010
3	S-230517d-22	39	419	136	0.32	0.770	0.010
4	S-230517d-23	26	261	114	0.44	0.791	0.011
5	S-230517d-24	30	238	231	0.97	0.915	0.013
6	S-230517e-01	6	59	26	0.45	0.785	0.012
7	S-230517e-02	52	521	319	0.61	0.745	0.010
8	S-230517e-03	17	186	42	0.23	0.894	0.012
9	S-230517e-04	16	172	78	0.45	0.724	0.010
10	S-230517e-05	17	181	59	0.32	0.775	0.010
11	S-230517e-06	24	257	89	0.35	0.759	0.010
12	S-230517e-07	41	405	178	0.44	0.794	0.010
13	S-230517e-08	17	167	71	0.43	1.018	0.013
14	S-230517e-09	14	140	55	0.39	0.807	0.011
15	S-230517e-10	21	214	54	0.25	0.803	0.011
16	S-230517e-11	27	292	31	0.11	0.808	0.011
17	S-230517e-12	34	359	77	0.21	0.809	0.011
18	S-230517e-13	34	351	52	0.15	0.949	0.012
19	S-230517e-14	69	687	235	0.34	0.852	0.011
20	S-230517e-15	11	104	57	0.54	0.766	0.011
21	S-230517e-16	28	308	114	0.37	0.730	0.010
22	S-230517e-17	15	125	45	0.36	1.146	0.016
23	S-230517e-18	43	476	139	0.29	0.736	0.010
24	S-230517e-19	21	224	40	0.18	0.792	0.011
25	S-230517e-20	31	321	81	0.25	0.783	0.010
26	S-230517e-21	22	233	120	0.52	0.720	0.010
27	S-230517e-22	26	255	99	0.39	0.805	0.011
28	S-230517e-23	26	254	175	0.69	0.810	0.011
29	S-230517e-24	48	481	311	0.65	0.731	0.010
30	<b>Carrière le Lorinou</b>						
31	S-140414a-1	25	280	94	0.33	0.741	0.009
32	S-140414a-2	9	96	35	0.37	0.760	0.010
33	S-140414a-3	242	631	189	0.30	6.313	0.076
34	S-140414a-4	12	103	39	0.38	0.977	0.013
35	S-140414a-5	45	476	79	0.17	0.817	0.010
36	S-140414a-6	3	27	13	0.50	0.885	0.017
37	S-140414a-7	36	360	159	0.44	0.772	0.010
38	S-140414a-8	15	169	54	0.32	0.715	0.009
39	S-140414a-9	94	144	84	0.59	13.867	0.168
40	S-140414a-10	30	255	194	0.76	0.909	0.012
41	S-140414a-11	15	143	67	0.47	0.822	0.011
42	S-140414a-12	41	101	68	0.67	5.736	0.071
43	S-140414a-13	22	207	78	0.38	0.840	0.011
44	S-140414a-14	67	117	124	1.06	10.163	0.125
45	S-140414a-15	45	356	130	0.37	1.090	0.014

1	S-140414a-16	214	362	165	0.46	14.056	0.172
2	S-140414a-17	35	80	54	0.68	6.804	0.085
3	S-140414a-18	52	113	55	0.49	8.106	0.100
4	S-140414a-19	133	218	26	0.12	16.275	0.200
5	S-140414a-20	19	164	56	0.34	0.949	0.012
6	S-140414a-21	148	545	73	0.13	4.200	0.052
7	S-140414a-22	20	132	91	0.69	1.268	0.017
8	S-140414a-23	56	470	213	0.45	1.005	0.014
9	S-140414a-24	9	90	28	0.31	0.811	0.011
10	S-140414a-25	16	45	26	0.56	5.017	0.065
11	S-140414a-26	3	34	15	0.46	0.834	0.014
12	S-140414a-27	23	176	73	0.41	1.104	0.014
13	S-140414a-28	195	566	42	0.07	5.907	0.074
14	S-140414a-29	28	235	134	0.57	0.950	0.012
15	S-140414a-30	57	124	56	0.45	8.017	0.102
16	S-140414a-31	14	119	87	0.73	0.935	0.013
17	S-140414a-32	26	179	106	0.59	1.168	0.015
18	S-140414a-33	204	726	270	0.37	3.801	0.046
19	S-140414a-34	191	570	64	0.11	5.336	0.065
20	S-140414a-35	27	232	120	0.52	0.941	0.012
21	S-140414a-36	24	241	46	0.19	0.841	0.011
22	S-140414a-37	18	159	121	0.76	0.797	0.011
23	S-140414a-38	5	40	42	1.05	0.979	0.015
24	S-140414a-39	24	129	146	1.13	1.421	0.018
25	S-140414a-40	30	281	164	0.59	0.807	0.010
26	S-140414a-41	22	57	73	1.29	4.682	0.059
27	S-140414a-42	41	414	196	0.47	0.802	0.010
28	S-140414a-43	13	131	49	0.37	0.845	0.011
29	S-140414a-44	20	185	127	0.69	0.823	0.011
30	S-140414a-45	72	127	48	0.37	14.286	0.175
31	S-140414a-46	32	195	70	0.36	1.617	0.021
32	S-140414a-47	144	357	122	0.34	6.854	0.084
33	S-140414a-48	34	367	152	0.41	0.760	0.010
34	S-140414a-49	12	125	38	0.30	0.783	0.011
35	S-140414a-50	22	222	61	0.27	0.802	0.010
36	S-140414a-51	58	343	131	0.38	1.703	0.021
37	S-140414a-52	9	65	88	1.35	0.882	0.013
38	S-140414a-53	4	42	13	0.31	0.794	0.013
39	S-140414a-54	15	160	39	0.25	0.804	0.011
40	S-140414a-55	27	212	240	1.13	0.838	0.011
41	S-140414a-56	24	232	102	0.44	0.855	0.012
42	S-140414a-57	24	246	52	0.21	0.806	0.011
43	S-140414a-58	2	21	7	0.34	0.912	0.016
44	S-140414a-59	55	138	58	0.42	6.251	0.079
45	S-140414a-60	27	264	120	0.46	0.801	0.011
46	S-140414a-61	124	273	97	0.36	8.212	0.104

1	S-140414a-62	13	138	44	0.32	0.787	0.011
2	S-140414a-63	8	78	37	0.48	0.804	0.012
3	S-140414a-64	20	199	74	0.37	0.814	0.011
4	S-140414a-65	10	64	53	0.82	1.153	0.016
5	S-140414a-66	11	101	39	0.39	0.887	0.012
6	S-140414a-67	69	161	68	0.42	6.961	0.089
7	S-140414a-68	9	85	44	0.52	0.859	0.013
8	S-140414a-69	22	147	100	0.68	1.231	0.016
9	S-140414a-70	6	52	49	0.93	0.874	0.015
10	S-140414a-71	24	239	131	0.55	0.765	0.010
11	S-140414a-72	62	622	112	0.18	0.883	0.011
12	S-140414a-73	44	394	415	1.05	0.776	0.010
13	S-140414a-74	48	552	126	0.23	0.726	0.009
14	S-140414a-75	143	245	153	0.63	12.112	0.144
15	S-140414a-76	19	213	85	0.40	0.727	0.010
16	S-140414a-77	18	162	102	0.63	0.854	0.014
17	S-140414a-78	37	57	32	0.56	13.935	0.172
18	S-140414a-79	60	116	30	0.26	11.560	0.141
19	S-140414a-80	19	191	53	0.28	0.834	0.012
20	S-140414a-81	25	267	14	0.05	0.863	0.012
21	S-140414a-82	58	649	243	0.37	0.711	0.009
22	S-140414a-83	41	186	206	1.11	1.800	0.023
23	S-140414a-84	17	39	35	0.88	6.278	0.083
24	S-140414a-85	43	434	144	0.33	0.824	0.011
25	S-140414a-86	8	68	71	1.05	0.818	0.014
26	S-140414a-87	49	284	164	0.58	1.580	0.021
27	S-140414a-88	12	127	37	0.30	0.769	0.012
28	S-140414a-89	28	56	80	1.42	6.209	0.083

		<i>Appar.</i>						
		Pb206/U238	PropErr2sigAbs.	Rho	Conc.	Pb207/Pb206	PropErr2sigAbs.	Pb206/U238
1								
2								
3								
4								
5								
6		0.0932	0.0012	0.97	85	1033	21	575
7		0.0948	0.0012	0.93	100	590	24	584
8		0.3341	0.0042	0.98	90	2338	18	1858
9		0.0938	0.0012	0.96	100	586	23	578
10		0.0945	0.0012	0.90	100	570	25	582
11		0.0933	0.0012	0.95	101	550	24	575
12		0.0847	0.0011	0.94	93	741	24	524
13		0.0901	0.0011	0.94	100	550	24	556
14		0.0938	0.0012	0.90	95	719	25	578
15		0.1007	0.0013	0.96	100	616	23	618
16		0.0965	0.0012	0.93	101	573	25	594
17		0.0950	0.0012	0.91	95	743	24	585
18		0.0964	0.0012	0.95	100	588	24	593
19		0.0936	0.0012	0.93	100	564	25	577
20		0.0888	0.0011	0.93	99	585	24	548
21		0.0985	0.0012	0.94	100	593	23	605
22		0.0974	0.0012	0.92	101	566	25	599
23		0.0985	0.0012	0.92	101	578	25	606
24		0.0980	0.0012	0.92	100	604	25	603
25		0.0978	0.0012	0.90	99	622	26	602
26		0.0919	0.0012	0.90	99	593	25	567
27		0.0909	0.0012	0.93	99	595	25	561
28		0.0936	0.0012	0.87	98	636	27	577
29		0.0953	0.0012	0.91	100	594	26	587
30		0.0817	0.0010	0.94	83	1025	23	506
31		0.0869	0.0011	0.95	96	661	23	537
32		0.0964	0.0012	0.94	100	592	24	593
33		0.0976	0.0012	0.95	100	608	24	600
34		0.0977	0.0012	0.97	100	615	23	601
35		0.0978	0.0012	0.95	100	595	24	602
36		0.0982	0.0012	0.94	97	704	23	604
37		0.0941	0.0012	0.95	100	585	24	580
38		0.0926	0.0012	0.94	100	582	24	571
39		0.0901	0.0011	0.96	99	598	23	556
40		0.0948	0.0012	0.92	95	743	25	584
41		0.0943	0.0012	0.96	97	676	23	581
42		0.1075	0.0014	0.93	97	739	24	658
43		0.0966	0.0012	0.97	100	584	23	595
44		0.0962	0.0012	0.93	100	595	25	592
45		0.0913	0.0011	0.95	99	590	24	564
46		0.0860	0.0011	0.93	98	579	25	532
47		0.0880	0.0011	0.93	98	587	24	544
48		0.1438	0.0018	0.95	96	1003	22	866

1							
2	0.0923	0.0012	0.93	99	607	25	569
3	0.0937	0.0012	0.93	100	578	25	577
4	0.0850	0.0011	0.90	97	625	25	526
5	0.0944	0.0012	0.97	99	605	23	581
6	0.0889	0.0011	0.95	96	664	23	549
7	0.1150	0.0014	0.95	99	727	23	702
8	0.0983	0.0012	0.96	100	601	23	605
9	0.0787	0.0010	0.97	58	1922	19	489
10	0.0980	0.0012	0.95	100	612	23	603
11	0.0975	0.0012	0.96	100	612	23	600
12	0.0976	0.0012	0.93	101	584	24	601
13	0.0922	0.0012	0.93	98	630	24	568
14	0.0938	0.0012	0.95	100	588	24	578
15	0.0871	0.0011	0.94	99	576	24	539
16	0.0880	0.0011	0.93	98	611	24	544
17	0.0858	0.0011	0.94	92	776	23	531
18	0.0971	0.0012	0.94	99	617	24	597
19	0.1008	0.0013	0.94	98	678	24	619
20	0.1066	0.0013	0.93	97	733	24	653
21	0.1428	0.0018	0.88	100	860	25	861
22	0.1122	0.0014	0.94	100	675	24	685
23	0.1743	0.0022	0.92	99	1056	23	1036
24	0.0944	0.0012	0.93	97	666	24	581
25	0.0964	0.0012	0.92	95	731	24	593
26	0.0958	0.0012	0.92	100	588	25	590
27	0.0948	0.0012	0.93	100	591	25	584
28	0.1006	0.0012	0.93	98	675	24	618
29	0.0949	0.0012	0.98	99	602	22	584
30	0.4497	0.0056	0.99	98	2498	17	2394
31	0.3763	0.0047	0.99	100	2061	18	2059
32	0.3384	0.0042	0.98	100	1875	19	1879
33	0.3709	0.0046	0.99	99	2055	18	2034
34	0.3395	0.0042	0.99	97	2011	18	1884
35	0.3753	0.0047	0.98	99	2080	18	2054
36	0.5480	0.0068	0.98	100	2809	17	2817
37	0.3069	0.0038	0.97	95	1884	19	1725
38	0.3031	0.0038	0.98	84	2497	18	1707
39	0.5178	0.0064	0.98	100	2709	17	2690
40	0.3660	0.0045	0.97	100	1994	19	2010
41	0.0961	0.0012	0.94	99	620	24	592
42	0.0987	0.0012	0.95	95	742	23	607
43	0.0910	0.0011	0.85	86	997	26	561
44	0.1109	0.0014	0.91	86	1117	23	678
45	0.2064	0.0026	0.82	97	1261	27	1210
46	0.0908	0.0011	0.92	83	1089	23	560
47	0.0966	0.0012	0.92	99	625	25	595

1	0.0968	0.0012	0.93	100	601	25	595
2	0.0876	0.0011	0.88	100	539	27	541
3	0.0918	0.0011	0.92	98	634	24	566
4	0.0966	0.0012	0.91	100	582	25	594
5	0.1056	0.0013	0.91	98	703	25	647
6	0.0945	0.0012	0.83	99	613	29	582
7	0.0914	0.0011	0.97	100	573	23	564
8	0.0882	0.0011	0.94	84	1029	22	545
9	0.0895	0.0011	0.93	100	555	25	553
10	0.0931	0.0012	0.92	98	619	25	574
11	0.0937	0.0012	0.95	101	557	24	578
12	0.0972	0.0012	0.96	101	575	23	598
13	0.0946	0.0012	0.94	82	1148	22	583
14	0.0964	0.0012	0.91	99	630	25	593
15	0.0975	0.0012	0.94	100	595	24	600
16	0.0980	0.0012	0.95	100	595	24	603
17	0.0979	0.0012	0.96	100	600	24	602
18	0.0981	0.0012	0.96	89	934	22	603
19	0.0977	0.0012	0.96	96	717	23	601
20	0.0940	0.0012	0.88	100	569	26	579
21	0.0879	0.0011	0.94	98	613	24	543
22	0.1184	0.0015	0.89	93	935	25	721
23	0.0896	0.0011	0.95	99	589	24	553
24	0.0964	0.0012	0.93	100	589	25	594
25	0.0959	0.0012	0.94	101	576	24	590
26	0.0895	0.0011	0.91	100	544	26	552
27	0.0975	0.0012	0.91	100	600	25	600
28	0.0897	0.0011	0.92	92	790	24	554
29	0.0894	0.0011	0.93	99	579	24	552
30							
31							
32							
33							
34							
35							
36							
37							
38							
39							
40							
41							
42	0.0894	0.0011	0.94	91	609	24	552
43	0.0920	0.0011	0.88	94	602	26	567
44	0.3623	0.0043	1.00	97	2048	18	1993
45	0.1104	0.0013	0.91	90	747	25	675
46	0.0981	0.0012	0.98	98	618	23	603
47	0.1037	0.0013	0.65	95	671	39	636
48	0.0952	0.0011	0.96	104	562	23	586
49	0.0892	0.0011	0.92	103	536	26	551
50	0.5555	0.0067	0.99	107	2663	17	2848
51	0.1030	0.0012	0.94	85	741	23	632
52	0.0987	0.0012	0.90	98	619	25	607
53	0.3582	0.0043	0.97	104	1898	19	1974
54	0.1006	0.0012	0.94	99	626	24	618
55	0.4482	0.0054	0.98	95	2502	18	2387
56	0.1230	0.0015	0.96	100	750	23	748

1							
2	0.5105	0.0061	0.98	94	2824	17	2659
3	0.3770	0.0046	0.97	98	2110	19	2062
4	0.4146	0.0050	0.97	99	2249	18	2236
5	0.5637	0.0068	0.98	99	2901	17	2882
6	0.1118	0.0014	0.92	104	660	24	683
7	0.2718	0.0033	0.97	85	1834	19	1550
8	0.1349	0.0016	0.92	93	874	24	816
9	0.1120	0.0014	0.89	88	779	25	684
10	0.0943	0.0012	0.88	85	686	26	581
11	0.3251	0.0039	0.93	99	1832	20	1814
12	0.0953	0.0012	0.73	81	725	33	587
13	0.1255	0.0015	0.93	104	734	24	762
14	0.3486	0.0042	0.96	96	1999	19	1928
15	0.1099	0.0013	0.92	96	698	24	672
16	0.4147	0.0050	0.95	100	2230	19	2236
17	0.1038	0.0013	0.90	81	784	25	637
18	0.1299	0.0016	0.95	101	781	23	788
19	0.2606	0.0031	0.99	86	1728	19	1493
20	0.3359	0.0041	0.99	99	1884	18	1867
21	0.1104	0.0013	0.95	101	669	23	675
22	0.1010	0.0012	0.95	101	616	23	620
23	0.0980	0.0012	0.92	106	566	25	603
24	0.1136	0.0014	0.81	100	691	29	694
25	0.1502	0.0018	0.95	101	889	23	902
26	0.0968	0.0012	0.95	96	621	24	595
27	0.2947	0.0036	0.96	88	1884	20	1665
28	0.0946	0.0011	0.96	89	658	23	582
29	0.0960	0.0012	0.90	80	736	25	591
30	0.0948	0.0012	0.90	82	708	25	584
31	0.4958	0.0060	0.98	90	2898	17	2596
32	0.1590	0.0019	0.94	92	1036	22	951
33	0.3765	0.0045	0.98	97	2126	18	2060
34	0.0896	0.0011	0.95	84	659	23	553
35	0.0947	0.0012	0.88	97	603	27	583
36	0.0971	0.0012	0.92	100	600	25	597
37	0.1593	0.0019	0.96	84	1135	21	953
38	0.1036	0.0013	0.85	95	667	28	635
39	0.0975	0.0012	0.75	105	569	33	600
40	0.0949	0.0012	0.91	89	657	25	584
41	0.1010	0.0012	0.92	102	610	25	620
42	0.0991	0.0012	0.89	88	695	25	609
43	0.0985	0.0012	0.93	104	580	25	606
44	0.1061	0.0013	0.69	95	685	36	650
45	0.3673	0.0044	0.95	100	2007	19	2017
46	0.0977	0.0012	0.92	103	585	25	601
47	0.4180	0.0050	0.95	100	2258	19	2251

1		0.0958	0.0012	0.89	100	589	26	590
2		0.0983	0.0012	0.85	104	580	28	604
3		0.0966	0.0012	0.90	92	644	25	594
4		0.1292	0.0016	0.86	102	766	27	783
5		0.1056	0.0013	0.87	101	638	27	647
6		0.3884	0.0047	0.94	101	2098	20	2115
7		0.1016	0.0012	0.75	96	649	32	624
8		0.1317	0.0015	0.87	92	863	25	797
9		0.1010	0.0012	0.70	88	701	34	620
10		0.0936	0.0011	0.86	100	577	27	577
11		0.1027	0.0012	0.91	92	687	24	630
12		0.0921	0.0011	0.89	88	644	25	568
13		0.0893	0.0010	0.92	97	566	25	551
14		0.4940	0.0056	0.96	98	2633	18	2588
15		0.0871	0.0010	0.84	86	625	27	538
16		0.0978	0.0012	0.71	83	721	34	601
17		0.5518	0.0063	0.93	106	2682	19	2833
18		0.4700	0.0054	0.93	94	2638	18	2483
19		0.0983	0.0011	0.83	92	658	28	605
20		0.1001	0.0011	0.84	89	693	27	615
21		0.0863	0.0010	0.89	89	597	25	533
22		0.1758	0.0020	0.88	100	1049	24	1044
23		0.3550	0.0041	0.87	94	2074	22	1959
24		0.0970	0.0011	0.88	90	662	26	597
25		0.0986	0.0012	0.68	99	610	36	606
26		0.1515	0.0017	0.86	84	1086	25	909
27		0.0928	0.0011	0.76	94	607	31	572
28		0.3647	0.0042	0.85	100	2007	22	2004
29								
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2	<b>Event Ages</b>		
3	PropErr2sigAbs.	Pb207/U235	PropErr2sigAbs.
4			
5			
6		7	677
7		7	585
8		20	2096
9		7	580
10		7	580
11		7	570
12		7	567
13		7	555
14		7	607
15		7	618
16		7	589
17		7	618
18		7	592
19		7	574
20		7	555
21		7	603
22		7	592
23		7	600
24		7	603
25		7	606
26		7	572
27		7	568
28		7	589
29		7	588
30		6	612
31		6	561
32		7	593
33		7	602
34		7	604
35		7	600
36		7	625
37		7	581
38		7	573
39		7	564
40		7	618
41		7	601
42		8	677
43		7	592
44		7	593
45		7	569
46		6	541
47		7	552
48		10	905
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1		7	577	6
2		7	577	6
3		6	545	6
4		7	586	6
5		7	572	6
6		8	708	7
7		7	604	6
8		6	836	7
9		7	604	6
10		7	602	6
11		7	597	6
12		7	581	6
13		7	580	6
14		6	546	6
15		6	557	6
16		6	580	6
17		7	601	6
18		7	632	6
19		8	671	7
20		10	860	8
21		8	683	7
22		12	1042	9
23		7	599	6
24		7	622	6
25		7	589	6
26		7	585	6
27		7	630	6
28		7	588	6
29		25	2451	12
30		22	2060	11
31		20	1877	11
32		22	2044	11
33		20	1945	11
34		22	2067	11
35		28	2812	12
36		19	1798	11
37		19	2092	11
38		27	2701	12
39		21	2002	11
40		7	598	6
41		7	636	6
42		7	656	7
43		8	789	7
44		14	1228	11
45		7	677	7
46		7	601	6

1			
2	7	597	6
3	7	541	6
4	7	580	6
5	7	592	6
6	8	660	7
7	7	588	7
8	7	565	6
9	7	648	6
10	7	553	6
11	7	583	6
12	7	573	6
13	7	593	6
14	7	713	7
15	7	601	6
16	7	599	6
17	7	601	6
18	7	602	6
19	7	678	6
20	7	626	6
21	7	577	6
22	6	557	6
23	9	775	8
24	7	560	6
25	7	593	6
26	7	587	6
27	7	551	6
28	7	600	6
29	7	602	6
30	7	557	6
31			
32	6	563	5
33	7	574	6
34	21	2020	11
35	8	692	7
36	7	606	6
37	8	644	9
38	7	581	6
39	6	548	6
40	28	2741	11
41			
42	7	656	6
43	7	609	6
44	20	1937	11
45	7	619	6
46	24	2450	11
47	9	748	7
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1		26	2754	12
2		21	2086	11
3		23	2243	11
4		28	2893	12
5		8	678	7
6		17	1674	10
7		9	831	7
8		8	707	7
9		7	603	6
10		19	1822	11
11		7	616	8
12		9	755	7
13		20	1962	11
14		8	678	6
15		23	2233	11
16		7	670	7
17		9	786	7
18		16	1593	10
19		20	1875	10
20		8	674	6
21		7	620	6
22		7	595	6
23		8	693	8
24		10	898	8
25		7	601	6
26		18	1764	11
27		7	598	6
28		7	622	6
29		7	610	6
30		26	2769	12
31		11	977	8
32		21	2093	11
33		6	574	6
34		7	587	6
35		7	598	6
36		11	1010	8
37		7	642	7
38		7	593	7
39		7	599	6
40		7	618	6
41		7	627	6
42		7	600	6
43		8	658	9
44		21	2012	11
45		7	597	6
46		23	2255	11

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2	7	590	6
3	7	599	6
4	7	605	6
5	9	779	8
6	7	645	7
7	22	2106	11
8	7	629	7
9	9	815	7
10	7	638	8
11	6	577	6
12	7	642	6
13	6	583	6
14	6	554	5
15	24	2613	11
16	6	555	6
17	7	627	8
18	26	2745	12
19	23	2569	11
20	7	616	6
21	7	632	6
22	6	546	5
23	11	1045	8
24	19	2015	12
25	6	610	6
26	7	607	8
27	10	963	8
28	6	579	7
29	20	2006	12
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	Pb207/U235	ErrAbs	Pb206/U238	ErrAbs	rho
1					
2	Pleso 1	0.3947	0.0054	0.05345	0.00067
3	Pleso 2	0.3996	0.0064	0.05317	0.00068
4	Pleso 3	0.3966	0.0053	0.05375	0.00067
5	Pleso 4	0.3956	0.0053	0.05384	0.00067
6	Pleso 5	0.3981	0.0053	0.05342	0.00067
7	Pleso 6	0.3966	0.0053	0.05321	0.00066
8	Pleso 7	0.3938	0.0053	0.05377	0.00066
9	Pleso 8	0.3892	0.0052	0.05379	0.00067
10	Pleso 9	0.3924	0.0053	0.05329	0.00066
11	Pleso 10	0.3920	0.0054	0.05336	0.00067
12	Pleso 11	0.3943	0.0052	0.05371	0.00067
13	Pleso 12	0.3889	0.0051	0.05374	0.00067
14	Pleso 13	0.3895	0.0053	0.05364	0.00067
15	Pleso 14	0.3918	0.0051	0.05378	0.00065
16	Pleso 15	0.3905	0.0050	0.05375	0.00065
17	Pleso 16	0.3908	0.0052	0.05377	0.00065
18	Pleso 17	0.3895	0.0051	0.05379	0.00065
19	Pleso 18	0.3924	0.0054	0.05388	0.00065
20	Pleso 19	0.3949	0.0049	0.05364	0.00064
21	Pleso 20	0.3949	0.0050	0.05370	0.00064
22	Pleso 21	0.3916	0.0049	0.05369	0.00064
23	Pleso 22	0.3944	0.0050	0.05349	0.00064
24	Pleso 23	0.3939	0.0051	0.05383	0.00064
25	Pleso 24	0.3962	0.0049	0.05392	0.00065
26	Pleso 25	0.3945	0.0049	0.05384	0.00064
27	Pleso 26	0.3998	0.0050	0.05351	0.00064
28	Pleso 27	0.3941	0.0050	0.05369	0.00064
29	Pleso 28	0.3928	0.0050	0.05377	0.00064
30	Pleso 29	0.3872	0.0050	0.05365	0.00065
31	Pleso 30	0.3927	0.0053	0.05344	0.00065
32	Pleso 31	0.3939	0.0051	0.05379	0.00065
33	Pleso 32	0.3909	0.0052	0.05369	0.00065
34	Pleso 33	0.3932	0.0053	0.05376	0.00065
35	Pleso 34	0.3955	0.0050	0.05379	0.00062
36	Pleso 35	0.3947	0.0053	0.05377	0.00061
37	Pleso 36	0.3945	0.0053	0.05342	0.00061
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