

## Original Article

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

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**Abstract**

In northwestern France, the Brioverian series is a thick siliciclastic succession deposited during the Cadomian cycle (c. 750–540 Ma). In the uppermost Brioverian beds, previous studies unravelled an assemblage dominated by simple horizontal trace fossils associated with microbially stabilized surfaces. Here, we report *Spirodesmos* 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, an Ediacaran–Fortunian *Spirodesmos* 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 *Spirodesmos* took place during Ediacaran–Fortunian to Ordovician time, similar to what happened in graphoglyptids. In addition, the age of the uppermost Brioverian beds (Ediacaran or early Cambrian) is still a pending question. Here, we report two new U–Pb detrital zircon datings 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 Brioverian beds, a Fortunian age is envisioned because the new dating corroborates 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 Period), do not allow definitive conclusions on the age of the uppermost Brioverian beds.

**1. Introduction**

The potential of ichnology to decipher macro-evolutionary trends in animal behaviour has a long history. Compilation of ichnological data was a major part of the work of A. Seilacher and P. Crimes. Seilacher (1974, 1977, 1986) focused on the variety of graphoglyptid trace fossils from the deep sea (i.e. patterned trace fossils forming nets, regular meanders and spirals), aiming to understand their environmental adaptation through time (e.g. size changes, functional optimization). Seilacher (1956) was the first to recognize the potential of trace fossils to delineate the Precambrian–Cambrian boundary; Crimes (1987, 1992a, 1994) extended this idea by reviewing worldwide literature, and developed an ichnostratigraphic scheme that helped to define the Cambrian GSSP (Narbonne *et al.* 1987; Brasier *et al.* 1994). In Crimes' comprehensive work, horizontal spiral trace fossils (as defined in this contribution) were consistently absent from the Ediacaran and the Cambrian systems (Crimes, 1987, 1992a, b, 1994), only appearing in the Ordovician System in the deep-marine realm (Crimes *et al.* 1974, 1992). Crimes suspected that most deep-marine graphoglyptids originated in shallow-marine environments during the Cambrian Period (Crimes, 1987; Crimes & Anderson, 1985; Crimes & Fedonkin, 1994), but the absence of regular planispiral trace fossils in the Cambrian System was then problematic (Crimes *et al.* 1992).

The Ediacaran–Cambrian transition (c. 539 Ma) was a time of striking changes in Earth ecosystems. Ediacaran seafloors were dominated by microbially stabilized surfaces on which epifaunal and very shallow infaunal grazers thrived (Seilacher & Pflüger, 1994; Gehling, 1999). Macroscopic animals of the earliest Cambrian Period started to disrupt the sediment at depth, affecting the substrate ventilation (e.g. Mángano & Buatois, 2014; Gougeon *et al.* 2018a), trophic webs (e.g. Bottjer *et al.* 2000; Meysman *et al.* 2006) and geochemical cycles (e.g. Logan *et al.* 1995; Canfield & Farquhar, 2009; Boyle *et al.* 2018). In northwestern France, the Brioverian series of central Brittany is a thick siliciclastic succession that was deposited during the Cadomian cycle (c. 750–540 Ma). Despite the report of fossils since the 19th century, the age of its uppermost beds (Ediacaran or early Cambrian) is a long-standing conundrum. Recently, new investigations

unravelling a unique assemblage of trace and body fossils in the vicinity of Rennes (Néraudeau *et al.* 2016, 2019; Gougeon *et al.* 2018b, 2019). Trace fossils are dominantly simple, horizontal and associated with microbially stabilized surfaces; of these, planispirals represent a surprising discovery.

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

## 2. General background

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

The Brioverian series (*c.* 660–540 Ma; Le Corre *et al.* 1991; Guerrot *et al.* 1989, 1992) is the informally named thick sedimentary succession deposited during the Cadomian cycle (*c.* 750–540 Ma) in northwestern France (Fig. 1a, b; Chantraine *et al.* 2001; Ballèvre *et al.* 2013). In the Rennes area (Fig. 1b), only the uppermost Brioverian beds are exposed, with a thickness evaluated at *c.* 1300 m (Trautmann *et al.* 1999). The Brioverian series of Brittany lies unconformably on an Icartian basement (*c.* 2200–1800 Ma) and is unconformably overlain either by the Ordovician Red Bed Series ('Séries Rouges Initiales') or by the Ordovician Armorican Sandstone ('Grès Armoricain'; Cogné, 1959; D'Lemos *et al.* 1990; Le Corre *et al.* 1991). The terrigenous siliciclastic sediments of the Brioverian series resulted from the erosion of the Cadomian belt in northern Brittany and accumulated in a marginal, intra-plate basin in central Brittany (Denis, 1988; Dissler *et al.* 1988; Rabu *et al.* 1990; Dabard *et al.* 1996). Locally, carbonaceous cherts ('phtanites'), limestones and igneous intrusions have also been reported (Denis & Dabard, 1988; Dabard, 1990, 2000; Chantraine *et al.* 2001). On a regional scale, the correlation of the Brioverian sedimentary deposits is hindered by the discontinuous cropping out, facies changes, the absence of biostratigraphic markers and the metamorphic overprint from the Devonian–Carboniferous Variscan orogeny (Denis & Dabard, 1988; D'Lemos *et al.* 1990; Le Corre *et al.* 1991; Ballèvre *et al.* 2013). While traditionally interpreted as deeper-marine turbiditic deposits (Dangeard *et al.* 1961; Denis, 1988; Trautmann *et al.* 1999), the Brioverian sedimentary beds also show evidence of shallow-marine storm-influenced (Dabard & Loi, 1998; Dabard & Simon, 2011) and marginal-marine tidally influenced conditions (Graindor, 1957; Dabard, 1990, 2000; Néraudeau *et al.* 2019).

Fossils recovered from the Brioverian series are algal or bacterial organic-walled microfossils in cherts and limestones (Cayeux, 1894; Deflandre, 1955; Chauvel & Schopf, 1978; Chauvel & Mansuy, 1981; Mansuy & Vidal, 1983), macroscopic body fossils of unknown origin (Néraudeau *et al.* 2019) and trace fossils. Ichnofossils were first discovered in the late 19th century (Lebesconte, 1886), but did not draw the attention of the scientific community for a long time. Recently, new investigations in the vicinity of Rennes (Fig. 1b) have unravelled an assemblage dominated by simple horizontal grazing trails (*Circulichnis*, *Gordia*, *Helminthoidichnites*, *Helminthopsis*), passively filled horizontal burrows (*Palaeophycus*) and horizontal spiral trace fossils (*Spirodesmos*; Néraudeau *et al.* 2016; Gougeon *et al.* 2018b, 2019). In addition, microbially textured surfaces (MISS of Noffke *et al.* 2001) are common both in fossiliferous and azoic intervals (Lebesconte, 1886; Gougeon *et al.* 2018b).

The age of the uppermost Brioverian sedimentary beds in Brittany, Normandy and Mayenne has been highly debated (Fig. 1b). In Brittany, the overlying Red Bed Series gave an age of  $472 \pm 5$  Ma (Rb–Sr dating from volcanic rocks; Auvray *et al.* 1980),  $465 \pm 1$  Ma (U–Pb dating from volcanic rocks; Bonjour *et al.* 1988; Bonjour & Odin, 1989) and  $486 \pm 28$  Ma (Pb–Pb dating from volcanic rocks; Guerrot *et al.* 1992), placing these beds within the Ordovician Period (*contra* McMahon *et al.* 2017; Went, 2017). In the westernmost part of Brittany (Crozon area; Fig. 1b), Guerrot *et al.* (1992) obtained an age of  $543 \pm 18$  Ma (Pb–Pb dating) for a tuff intercalated within Brioverian beds, whereas a maximum deposition age of  $546 \pm 2$  Ma (U–Pb dating) has been obtained by Ballouard *et al.* (2018) from detrital zircon grains extracted from a sandstone (see also Dabard *et al.* 2021). In the vicinity of Rennes (Fig. 1b), detrital zircon grains gave a maximum deposition age of *c.* 550 Ma (U–Pb dating from sandstone and siltstone; Gougeon *et al.* 2018b); however, five zircon grains dated at  $532.1 \pm 3.9$  Ma were problematic to interpret (Gougeon *et al.* 2018b). In Normandy, Brioverian sediments were deposited in a different palaeogeographic domain than in central Brittany, as they are separated by the North Armorican Shear Zone (Fig. 1b; Chantraine *et al.* 1982; Guerrot *et al.* 1992). In this domain, granitoid intrusions within Brioverian sediments have been dated at  $540 \pm 10$  Ma (U–Pb dating on monazite; Pasteels & Doré, 1982). In Mayenne, where the Brioverian series is in continuity with its equivalent of central Brittany (Fig. 1b), radiometric dating on zircon grains yielded an age of  $540 \pm 17$  Ma (tuff and detrital horizons; Guerrot *et al.* 1992).

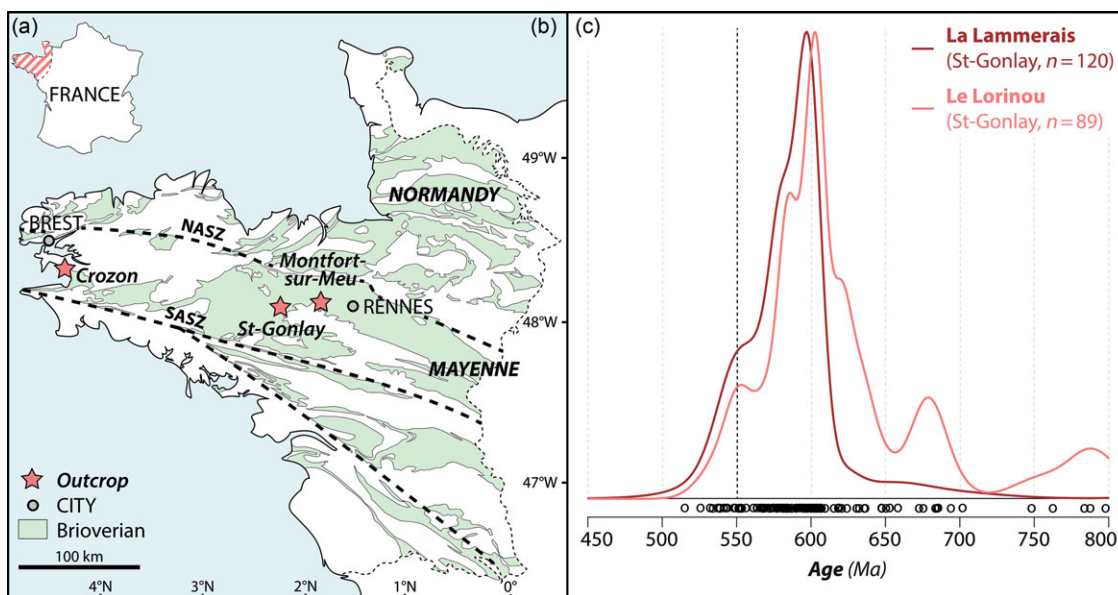
### 2.b. Outcrops under study and depositional environments

The outcrop at La Lammerais village nearby St-Gonlay (Fig. 1b) yields slates with trace fossils, stacked in a pile *c.* 2 m high and 50 m long (outcrops for this contribution are located on private properties, which do not allow details on their exact locations). These slates were extracted from a pit that was exploited by locals to build houses and pathways decades ago; unfortunately, the pit is now covered with vegetation and therefore impossible to sample *in situ*. Slates are made of siltstone and rare very-fine- to fine-grained sandstone. One loose sandstone sample was collected for U–Pb dating, coming from a nearby agricultural field. At La Lammerais outcrop, sedimentary structures are parallel-lamination organized in siltstone–sandstone bundles (i.e. rhythmite-like; Néraudeau *et al.* 2019, fig. 3), current-ripples (Néraudeau *et al.* 2019, fig. 2), tool-marks/spindle-shaped flute-marks, possible load-casts, and pustular and wrinkled microbially textured surfaces (Gougeon *et al.* 2018b, figs 4, 7).

Nearby St-Gonlay, another outcrop has been investigated at Le Lorinou locality, situated 1.4 km to the east of La Lammerais. This outcrop is very poor in trace fossils (no spiral trace fossils were found there), but beds are preserved *in situ* and a sandstone sample was collected for U–Pb zircon dating.

The outcrop of Le Bois-du-Buisson is located at the entrance of a small forest in Montfort-sur-Meu (Fig. 1b). It consists of a small quarry of *c.* 3 m high and 10 m long, with vegetation extensively covering the sedimentary beds. However, a few siltstone beds are accessible and reveal fresh surfaces with trace fossils. Sedimentary structures are parallel-lamination organized in siltstone–sandstone bundles (i.e. rhythmite-like, similar to what is found at La Lammerais), and pustular and wrinkled microbially stabilized surfaces.

In addition, Montfort-sur-Meu is the host of Les Grippeaux quarry, where P. Lebesconte recovered fossils for the first time



**Fig. 1.** Geological map of northwestern France, and new U–Pb dating. (a) Location of the Brioiverian deposits in northwestern France. (b) Close-up showing the Brioiverian 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 Lamerrais and Le Lorinou samples.

in the late 19th century (Lebesconte, 1886; Gougeon *et al.* 2018b). Nowadays, the quarry is secured by a fence preventing any access. Many samples were collected in the late 19th and early 20th century by P. Lebesconte, F. Kerforne and other geologists; they are housed at the Geological Institute of the University of Rennes 1 and at the Museum of Natural History of Nantes, and are available for study. Sedimentary structures are pustular microbially stabilized surfaces.

The outcrop in Crozon (Fig. 1b) is located on the coastal cliff at La Plage-du-Goulien. This outcrop has not been visited by the authors, and the only trace fossil discovered was reported by E. Hanson in 2014 (pers. comm.). The sedimentology of the Brioiverian series from the Bay of Douarnenez and the Cove of Dinan (both in the vicinity of Crozon) has been studied in two doctoral theses (J.R. Darboux, unpubl. Ph.D. thesis, University of Brest, 1973; Denis, 1988). The succession displays parallel-laminated/bedded sandstone and siltstone with flute-casts, load-casts, tool-marks, rip-up clasts, carbonate concretions, normal and reverse grading, convolute bedding, flame structures, and current, wave and climbing ripples. Both authors interpreted the succession as deposited by turbidites, located either below the limit of the storm wave-base action, or deeper in an abyssal plain. However, Denis (1988) noted the presence of oscillatory flow structures, lenticular bedding (Facies 3 of Denis, 1988) and mud-drapes, which are more typical of shallower environments.

In Montfort-sur-Meu and St-Gonlay, the dominance of siltstone intercalated with laminated very-fine-grained sandstone, and the record of rhythmite-like bundles and current ripples, suggest a marginal-marine, tidally influenced depositional environment (cf. Nio & Yang, 1991; Tessier *et al.* 1995; Dalrymple, 2010). This conclusion is strengthened by observations in Chanteloup and Nouvoitou (both in the vicinity of Rennes), where a sandstone facies displays mudstone drapes within fine-grained sandstone samples (i.e. flaser lamination; see online Supplementary Fig. S1); these areas could represent the seaward, sandier part of the intertidal system. Sedimentary structures made by oscillatory flows (e.g. wave ripples, hummocky cross-stratification) have

not been observed in the area so far. These conclusions are preliminary and await further support, notably from Brioiverian outcrops revealing bedding architecture, and from more sampling of sedimentary structures.

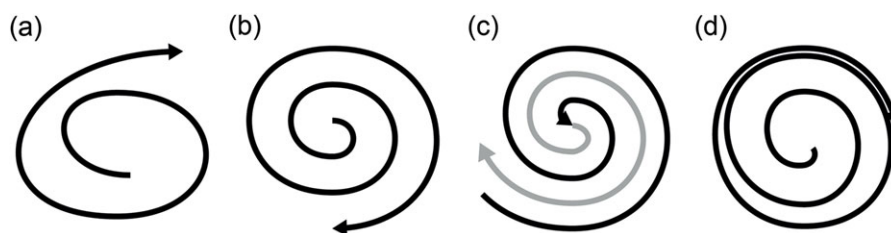
### 3. Materials and methods

#### 3.a. Terminology of planispiral trace fossils

This contribution focuses only on spirals formed on a horizontal plane (i.e. planispirals). Three-dimensional, vertically (e.g. *Gyrolithes*, *Lapispira*) or horizontally (e.g. *Avetoichnus*, *Helicodromites*, *Helicolithus*) oriented spirals are not comparable with the Brioiverian material. In order to describe spiral morphologies, the following terms will be used: a *regular* spiral maintains a constant distance between whorls (Fig. 2b, c); an *irregular* spiral has a variable distance between whorls (Fig. 2a, d); a *one-way* spiral is a simple spiral with no central turnaround (Fig. 2a, b, d; Seilacher, 1977; Crimes & McCall, 1995); a *two-way* spiral is a double spiral with a central turnaround (Fig. 2c; Seilacher, 1977; Crimes & McCall, 1995); and a *bounded* spiral is an irregular, one-way spiral that decreases the distance between whorls outward (Fig. 2d).

#### 3.b. U–Pb dating method

A classic mineral separation procedure has been applied to concentrate zircon grains for U–Pb dating. Rocks were crushed and only the powder fraction with a diameter < 250  $\mu\text{m}$  was kept. Heavy minerals were successively concentrated by Wilfley table, heavy liquids and an isodynamic Frantz separator. Zircon grains were then handpicked under a binocular microscope to produce the most representative sampling, with the aim of avoiding any intentional bias (see Malusà *et al.* 2013). Selected grains were then embedded in epoxy mounts, grounded and polished. Zircon grains were imaged by cathodoluminescence (CL) using a Reliotron CL system equipped with a digital colour camera available at the GeOHeLiS analytical platform (University of Rennes 1).



**Fig. 2.** Terminology of planispirals: (a) an irregular one-way spiral; (b) a regular one-way spiral; (c) a regular two-way spiral; and (d) a bounded spiral. See text for further explanations.

U–Pb geochronology was conducted by *in situ* laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the GeOHeLiS analytical platform using an ESI NWR193UC Excimer laser coupled to a quadrupole Agilent 7700× ICP-MS. Instrumental conditions are reported in online Supplementary Table S1, while the analytical protocol can be found in Manzotti *et al.* (2015). Kernel density diagrams for analyses that are  $100 \pm 10\%$  concordant were generated using IsoplotR (Vermeesch, 2018). When dealing with detrital zircon geochronology, a minimum of three different ages obtained on three different zircon grains overlapping in age at  $2\sigma$  has been demonstrated to produce a statistically robust maximum deposition age (Dickinson & Gehrels, 2009). The second important criteria in order to determine this maximum deposition age is the degree of concordance of the individual analysis used to calculate this age. Most authors consider all analyses that are 90% concordant or more, while others only consider analyses that are at least 95% concordant. In this study, because of the complexity of one of the datasets (La Lammerais), only analyses that were at least 95% concordant were considered to calculate the maximum deposition age, in order to avoid using apparent ages that could be younger than the true age due to a non-negligible Pb loss.

### 3.c. Museum repository

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

## 4. Results

### 4.a. Planispiral trace fossils from the Brioverian series

The Brioverian series of central Brittany contains a rich assemblage of simple horizontal trace fossils, with *Helminthoidichnites* and *Helminthopsis* being the most common forms. Originally, Lebesconte (1886, pl. 34, fig. 7) figured a planispiral trace fossil from Montfort-sur-Meu without further discussion. Since then, spiral trace fossils have not been reported in the Brioverian series. Here, we describe two types of planispiral trace fossils: (1) irregular, one-way spiral trace fossils; and (2) regular, one-way spiral trace fossils.

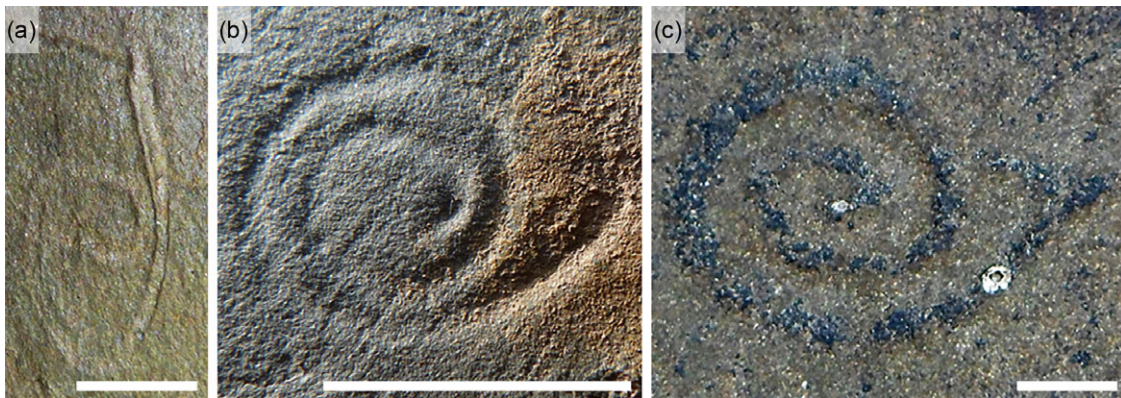
Four irregular, one-way spiral trace fossils were recovered from La Lammerais, Le Bois-du-Buisson and Les Grippeaux (Fig. 3a). Specimens are 0.3–1 mm wide, have  $1\frac{1}{4}$ – $1\frac{3}{4}$  whorls, and are preserved in positive and negative reliefs (preservation as epirelief or

hyporelief is unknown because slates with trace fossils are not preserved *in situ*). One specimen (Fig. 3a) has a different infill than the host rock and a lining; this is potentially a burrow. Rarely, they are associated with *Helminthoidichnites*, small-scale branching trace fossils (cf. *Pilichnus*), and pits of uncertain affinity. They are commonly found on pustular microbially textured surfaces.

Two regular, one-way spiral trace fossils were recovered from La Plage-du-Goulien and Les Grippeaux (Fig. 3b, c). Specimens are 1–3 mm wide, have  $2\frac{1}{4}$ – $2\frac{1}{2}$  whorls, and are preserved in positive and negative reliefs. The distance between whorls remains constant until the last whorl, where the course detaches from the spiral system and progressively disappears. They are associated with *Helminthopsis* and pits of uncertain affinity. The surfaces they are found on are not textured.

*Spirodesmos*, *Spirophycus* and *Spirorhaphe* are the most common planispirals from the trace fossil record: however, their morphological boundaries are unclear. *Spirodesmos* is a regular to irregular, one-way spiral trace fossil (Geinitz, 1867; Andrée, 1920; Huckriede, 1952; Xia *et al.* 1987). For Seilacher (1977), *Spirodesmos* has a wide spacing between whorls; although this is clearly so in the type ichnospecies *S. interruptus* Andrée, 1920, *S. archimedeus* Huckriede, 1952 has a narrower spacing between whorls. This issue becomes critical with *Spirodesmos kaihuaensis* Xia, He & Hu, 1987 and *S. spiralis* (Geinitz, 1867), both having irregular courses with variable distances between whorls. *Spirophycus* is a regular to irregular, one-way spiral trace fossil that commonly grades into meanders (Heer, 1876; Häntzschel, 1975). Seilacher (1977) argued that *Spirophycus* has wide strings with a tubercular surface and backfilled laminae (see also Książkiewicz, 1977; but see Uchman, 1998). The spiral portion of *Spirophycus* (e.g. Heer, 1876, pl. 66, fig. b; Sacco, 1888, pl. 2, fig. 14), with regular whorls distinctly spaced from each other, can however be very similar to *Spirodesmos archimedeus*. *Spirorhaphe* is a regular to irregular spiral trace fossil with either a one-way (*S. azteca*, *S. graeca*) or two-way (*S. involuta*) course (Seilacher, 1977; Crimes & McCall, 1995). The inclusion of one-way spirals in *Spirorhaphe* is overlapping with *Spirodesmos* and *Spirophycus* morphologies, which is problematic.

Despite these taxonomical issues (see also Crimes & Crossley, 1991; Uchman, 1998; Minter & Braddy, 2009), planispirals from the Brioverian series are comparable to *Spirodesmos*. Brioverian irregular, one-way spiral trace fossils are reminiscent of *Spirodesmos spiralis* (cf. Geinitz, 1867; Stepanek & Geyer, 1989). However, because of its irregular course and the poor extent of its whorls, *Spirodesmos spiralis* needs to be re-evaluated taxonomically; in this study, Brioverian forms are referred to *Spirodesmos* isp. Conversely, Brioverian regular, one-way spiral trace fossils belong to *Spirodesmos archimedeus* (cf. Huckriede, 1952; Zapletal & Pek, 1971; Horn, 1989). *Spirodesmos* ranges from the Ediacaran–Cambrian (this study) to the Holocene periods (e.g. Kitchell *et al.* 1978; Smith *et al.* 2005).



**Fig. 3.** *Spirodesmos isp.* and *Spirodesmos archimedeus* from the uppermost Brioverian beds of Brittany. (a) *Spirodesmos isp.* (irregular one-way spiral trace fossil) from Le Bois-du-Buisson (IGR 2852). (b, c) *Spirodesmos archimedeus* (regular one-way spiral trace fossils) from (b) Les Grippeaux (IGR 112628) and (c) La Plage-du-Goulien. Scale bars are 1 cm across.

#### 4.b. U–Pb dating

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

For the sandstone sample from Le Lorinou, 89 grains were analysed, out of which 68 are  $100 \pm 10\%$  concordant (online Supplementary Table S2). They are characterized by variable U and Pb contents (21–726 ppm and 2–242 ppm, respectively), with Th/U ratios between 0.05 and 1.4. A first group of 22 zircon grains yields Neoproterozoic (2.9 Ga) to Palaeoproterozoic (1.8 Ga) ages, followed by a gap until the end of the Mesoproterozoic. The remaining grains present apparent ages around 1000, 900, 800 and 680 Ma, with a major peak around 600 Ma (Fig. 1c). The youngest three grains provide a weighted  $^{206}\text{Pb}/^{238}\text{U}$  date of  $551 \pm 7$  Ma (MSWD, 0.009) that we consider as the maximum deposition age for this sandstone.

## 5. Discussion

### 5.a. Radiometric age of the uppermost Brioverian beds with trace fossils

At Le Lorinou (St-Gonlay), zircon grains from a sandstone bed associated with trace fossils yielded a maximum deposition age of  $551 \pm 7$  Ma, whereas zircon grains from a loose sandstone sample at La Lammerais (St-Gonlay) gave a maximum deposition age of  $540 \pm 5$  Ma (this study). In Crozon, the youngest U–Pb dating on zircon grains from Brioverian tuff gave an age of  $543 \pm 18$  Ma (Guerrot *et al.* 1992), whereas another U–Pb dating on zircon grains from a sandstone gave a maximum deposition age of  $546 \pm 2$  Ma (Ballouard *et al.* 2018). In Montfort-sur-Meu, no radiometric dating has been done so far.

The radiometric age for the base of the Cambrian is given by U–Pb dating on zircon grains from tuff in southern Oman, dated at  $541.0 \pm 0.13$  Ma (Bowring *et al.* 2007). However, recent U–Pb

dating on zircon grains from tuff in southern Namibia constrained the age of the basal Cambrian within a 538.6–538.8 Ma interval (Linnemann *et al.* 2019). If we consider a radiometric age of c. 539 Ma for the base of the Cambrian System, the Brioverian beds of Crozon could either be Ediacaran (c. 635–539 Ma) in age or younger, while the Brioverian of St-Gonlay could be Ediacaran but is suspected to be Fortunian (c. 539–529 Ma) in age or younger. Indeed, the new results of this study agree with earlier dating elsewhere (maximum deposition age of c. 550 Ma in Néant-sur-Yvel, Brittany, with five zircon grains dated at  $532.1 \pm 3.9$  Ma;  $540 \pm 10$  Ma in Normandy; and  $540 \pm 17$  Ma in Mayenne; Pasteels & Doré, 1982; Guerrot *et al.* 1992; Gougeon *et al.* 2018b) and suggest an early Cambrian age for the uppermost Brioverian beds, from a radiometric standpoint (see also Guerrot *et al.* 1989, 1992; Dabard *et al.* 2021). In terms of trace fossil biostratigraphy, the matground ecology of the Brioverian series is more typical of late Ediacaran assemblages (Gougeon *et al.* 2018b). Because of the differences provided by these two proxies (radiometric dating and ichnostratigraphy), definitive conclusions on the age of the uppermost Brioverian beds with trace fossils are not possible at this point.

### 5.b. Critical review on Ediacaran and Cambrian planispiral trace fossils

Several trace fossils inaccurately described or suggested to be planispirals, have been reported from the Ediacaran and the Cambrian systems. Fedonkin (1985, 1990) erected *Planispiralichnus* Fedonkin, 1985 and *Protospiralichnus* Fedonkin, 1985 from the Fortunian Kessyuse Formation of northern Russia. *Planispiralichnus* is made of dense, overlapping loops (Fedonkin, 1990; Marusin & Kuper, 2020), whereas *Protospiralichnus* starts as a bounded spiral until it scribbles abundantly (Fedonkin, 1990); because of their scribbling patterns, neither of them represent spirals (Buatois *et al.* 2017). Jenkins (1995, pl. 2, fig. E) reported cf. *Protospiralichnus* from the Ediacaran Rawnsley Quartzite of southern Australia; the development of a full circle and/or a loop affiliates this trace fossil to *Circulichnis* or *Gordia* instead (see also Buatois & Mángano, 2016, fig. 2.8e). *Multilaqueichnus* Yang & Yin (in Yang *et al.* 1982) from the Cambrian Stage 3 Jiulaodong Formation of central China has overlapping loops (Yang *et al.* 1982, pl. 2, fig. 1); these trace fossils distinctly scribble and are not spirals either (*contra* Mángano & Buatois, 2016, 2020). Finally, a trace fossil from the Fortunian part of the Chapel Island Formation of eastern

Canada was considered a spiral by Crimes & Fedonkin (1994, fig. 2i). This trace fossil has been observed in the field by one of the authors (R.G.) and represents the scribbling burrow of a large infaunal deposit-feeder.

In addition, non-ichnological structures from the Ediacaran and the Cambrian have been mistaken for planispiral trace fossils. An important debate arose with the report of Precambrian spiral fossils from the Lower Vindhyan Limestone of northeastern India (Beer, 1919) and from the Belt Series of northwestern USA (Walcott, 1899). Both authors suggested a trace fossil origin, an opinion followed by Seilacher (1956). However, Cloud (1968) suspected an algal origin, and re-evaluation of both materials confirmed that view (Walter *et al.* 1976; Runnegar, 1991). *Arenicolites spiralis* Billings, 1872 and *Helminthoidichnites sangshuanensis* Du (in Du *et al.* 1986; Yan & Liu, 1998) are certainly of similar algal affinity (Hofmann, 1971; Walter *et al.* 1990; Shaowu, 1998). Furthermore, Aceñolaza (2005) reported circular structures from the Cambrian Mesón Group of northwestern Argentina, and erected the new ichnospecies *Spirodesmos milanai*; Minter *et al.* (2006) argued these structures were formed by shrinkage cracks in matgrounds instead (cf. Pflüger, 1999; Buatois *et al.* 2013; Sedorko *et al.* 2019).

Finally, rare horizontal spiral trace fossils have been reported from the Ediacaran and the Cambrian systems. *Planispiralichnus rarus* Menasova, 2003 is a one-way spiral trace fossil discovered in the Fortunian Khmel'nitsky Formation of western Ukraine. The holotype is made of three whorls with angular intervals along the course; the first two whorls are continuous, while the 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 Cijara Formation 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 1¼ whorls and a continuous course from the Fortunian part of the Ingta Formation of northwestern Canada. Finally, Runnegar (1992, fig. 3.9) figured an irregular two-way spiral transitional with a meandering trace fossil from the Ediacaran Rawsley Quartzite of southern Australia. Jensen (2003) considered this trace fossil to represent *Helminthorhapse* grading into *Spirorhapse*.

### 5.c. Macro-evolutionary profile and onshore–offshore migration

Our detailed literature review (Section 5.b above and online Supplementary Material) unravelled the environmental and temporal distribution of *Spirodesmos* (Fig. 4). The Ediacaran System and the Fortunian Stage are then marked by the appearance of a *Spirodesmos* pool, composed of irregular and regular forms colonizing marginal-marine to shelf environments. The Brioverian assemblage represents a key component of that pool, holding the oldest regular one-way planispirals (*Spirodesmos archimedeus*) both in marginal-marine and open-shelf settings (in Montfort-sur-Meu and Crozon, respectively). During the Ediacaran and the Cambrian periods, 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 *Spirorhapse* and inferring

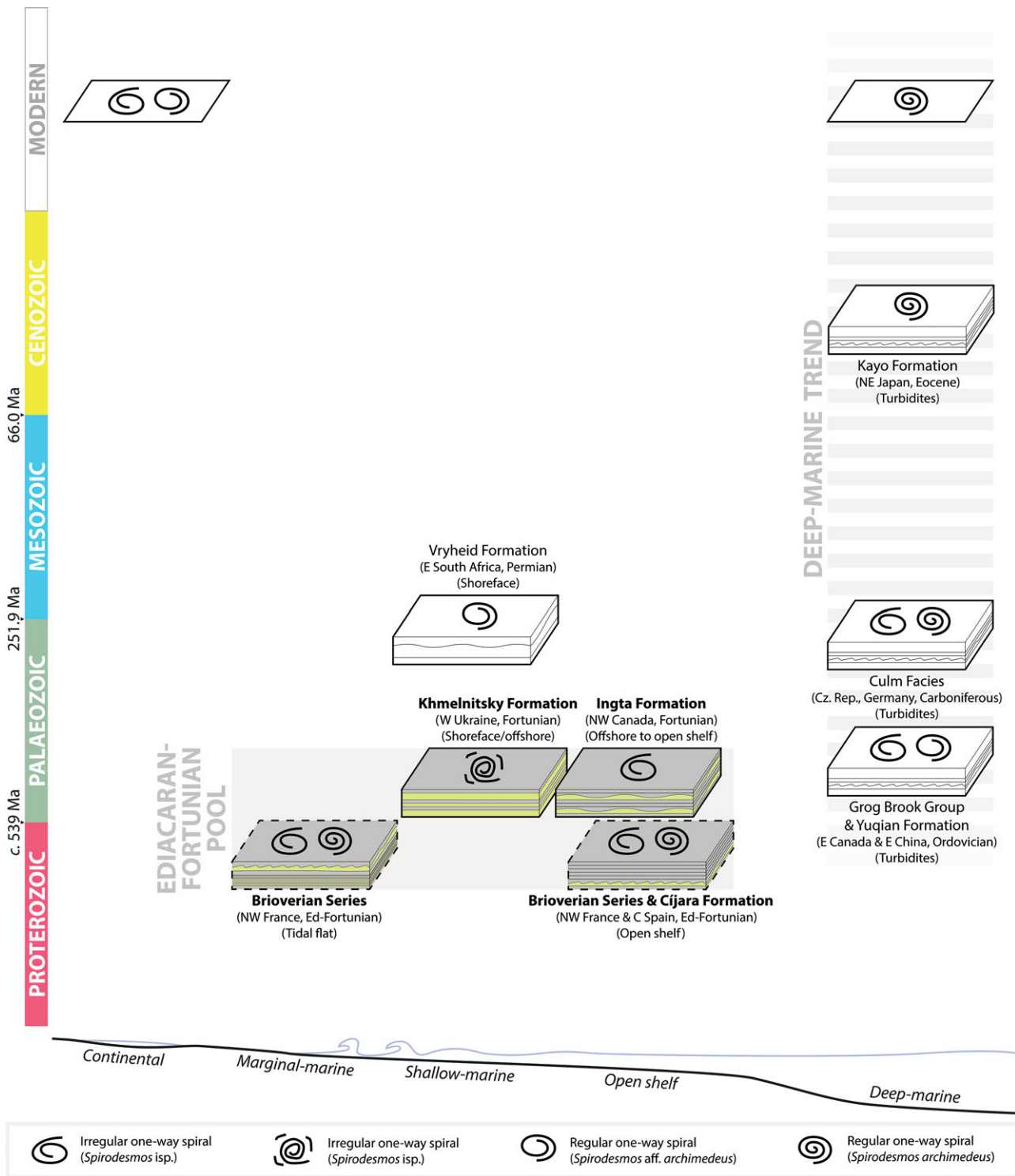
open-burrow systems (Seilacher, 1967a, b, 1977) have not been observed in Ediacaran–Fortunian material. Moreover, Ediacaran–Fortunian *Spirodesmos* are often preserved on microbially stabilized surfaces, which could represent the nutritive resource of their trace-maker (Carbone & Narbonne, 2014). Possible producers are enteropneusts and nematodes, both suspected to first appear during the Cambrian Period or before (Knoll & Carroll, 1999; Budd & Jensen, 2000; Maletz, 2014; Cunningham *et al.* 2017). Enteropneusts produce regular horizontal spirals on the modern deep-sea floor on areas of greater nutritional values, using tactile sensory systems in their head (Lemche *et al.* 1976; Smith *et al.* 2005; Jones *et al.* 2013). Nematodes spiral by contracting all the muscles of one side of their body (Wharton, 2004). However, spiralling in nematodes has been suggested for other purposes than feeding (e.g. responses to increasing temperature, osmotic stress, desiccation and for reproduction; Huettel, 2004; Wharton, 2004).

Although deep-marine deposits with trace fossils have been reported both from the Ediacaran (e.g. Narbonne & Hofmann, 1987; Liu *et al.* 2010) and the Cambrian (e.g. Hofmann *et al.* 1994; Seilacher *et al.* 2005) systems, planispirals are consistently absent. However, planispirals are common through the rest of the Phanerozoic Eonothem in the deep-sea, and *Spirodesmos* forms a conspicuous Ordovician–Recent deep-marine trend (Fig. 4; online Supplementary Material). Deep-marine seafloors are characterized by an absence of light, high hydrostatic pressure, oxygen and temperature fluctuations, and low nutrient content (Sanders & Hessler, 1969; Gage & Tyler, 1991, pp. 9–29; Rex & Etter, 2010, pp. 1–49). These stressful conditions play an important role on animal fitness and their physiology (e.g. Childress & Thuesen, 1992; Yancey *et al.* 2004; van der Grient & Rogers, 2015). However, with the increased competition for space and food on early Cambrian shelves (Orr, 2001), planispiral tracemakers may have adapted their metabolisms to the deep-sea. An onshore–offshore migration in *Spirodesmos* is then suggested during Ediacaran–Fortunian to Ordovician time, similarly to the migration observed in graphoglyptids (Crimes & Anderson, 1985; Crimes *et al.* 1992; Crimes & Fedonkin, 1994; Orr, 2001; Uchman, 2003). The existence of an onshore–offshore migration is also reinforced by the presence of an important gap (c. 230 Ma) between the Ediacaran–Fortunian *Spirodesmos* pool and the next shallow-marine *Spirodesmos* report from the Permian Vryheid Formation of eastern South Africa (Mason *et al.* 1983; Fig. 4).

## 6. Conclusion

The age of the uppermost Brioverian deposits of central Brittany, northwestern France, is a long-standing question. Here, two U–Pb detrital zircon grain datings on sandstone samples collected in St-Gonlay gave maximum depositional ages of  $551 \pm 7$  Ma and  $540 \pm 5$  Ma. Although an Ediacaran age for the uppermost Brioverian beds cannot be discarded, a Fortunian age is suggested in this study, following previous dating in Brittany, Normandy and Mayenne. However, the intervals of error of the radiometric dating and trace fossil biostratigraphy do not allow definitive conclusions.

A unique assemblage of irregular and regular, one-way planispiral trace fossils of *Spirodesmos* affinity has been recovered from the uppermost Brioverian beds in Crozon, Montfort-sur-Meu and St-Gonlay. Planispiral trace fossils are unusual in the Ediacaran and the Cambrian systems, and an in-depth literature review revealed that the Brioverian assemblage belonged to an Ediacaran–Fortunian, marginal-marine to shelf *Spirodesmos* pool. Ediacaran–Fortunian *Spirodesmos* were arguably made by



**Fig. 4.** Macro-evolutionary profile of *Spirodesmos* comparable to the Brioverian material, with emphasis on the Ediacaran and the Cambrian systems (coloured 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, during Ediacaran–Fortunian to Ordovician time. See text for further explanations.

detritus- or deposit-feeders, possibly related to enteropneusts or nematodes. However, by the Ordovician Period, *Spirodesmos* became conspicuous mostly in the deep-marine realm, underscoring an onshore–offshore migration similar to what has been reported in graphoglyptids.

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