Ichnotology, sedimentology, and orbital cycles in the hemipelagic Early Jurassic Laurasian Seaway (Pliensbachian, Cardigan Bay Basin, UK)

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**ABSTRACT**

An uncommonly continuous Lower Jurassic (uppermost Sinemurian and Pliensbachian) section (Llanbedr (Mochras Farm) Borehole, Cardigan Bay Basin, UK) comprises hemipelagic calcareous mudstone, wackestone/siltstone and subordinate packstone/sandstone. Some beds show bigradational grading, and their sedimentary structures are typical of contourite drift facies. On the basis of the long-term persistence and stability of the currents that formed these deposits, sedimentation was likely controlled by thermohaline-driven geostrophic contour currents circulating between the Boreal ocean and Peri-Tethys through the narrow and relatively deep Cardigan Bay Strait (Cardigan Bay Strait). Trace fossils are strongly dominated by Phycosiphon incertum, which was produced by opportunistic colonizers. Thalassinoides, Schaubaehindrichnus and Teichichnus are common, accompanied by less common Zoophycos, Planolites, Palaichnus, Trichichnus and dwelling structures such as cf. Polykladichnus, Siphonichnus and Skolithos. The ichnofabrics are usually simple, which results from generally high rates of deposition, unstable, water-saturated soft-ground substrate, and the domination of well-adapted Skolithos. A new detailed analysis of the core has allowed cycles to be distinguished based on combination of ichnological and sedimentological features, pointing to distinct cyclicity of oceanographic mechanisms influenced by orbital forcing and driving the inferred fluctuations in benthic life conditions, controlled mainly by variation in contour current intensity and oxygenation of bottom water reflected by trace fossils. The ichnological cycles show four-order hierarchy, which can be attributed to the orbital cycles: precession and obliquity (4th order), short eccentricity (3rd order), and long eccentricity (2nd order). The longest (~2.5 Myr) 1st order cyclicity is attributable to the longer “grand orbital cycles” (period related to the Earth–Mars secular resonance), with long-term impacts on palaeoclimatic and oceanic circulation dynamics, and is recorded in large-scale changes in ichnodiversity, correlating with long-term changes of clay minerals and carbonate content. Possibly, there is also ~9 Myr cyclicity, expressed in observed modulation of frequency of precession cycles by eccentricity. Harmonic analysis of the cyclicity gives high confidence of orbital signals and allows refined estimation of duration of the Pliensbachian (~8.4 Myr) and the jamaeoni (~2.8 Myr), ibex (~2.0 Myr), davoe (~0.47 Myr), margaritatus (~2.33 Myr) and spinatum zones (~0.8 Myr) with an overall stable sedimentation rate of 4.5–5.1 cm/kyr. Obtained durations show improved fit between 2nd–3rd and 1st order cycle and removes the problem of an anomalously long duration and resulting much lower sedimentation rate for the spinatum Zone, previously obtained by other methods. A higher diversity of trace fossils is noticed in intervals enriched in smectite; most likely, this clay mineral occluded pore spaces and limited the competition from the opportunistic Phycosiphon makers, allowing development of other, more specialized forms. The continuous, expanded ichnologic record of deep-water hemipelagic/contour drift sediments is sensitive to climatic and oceanographic changes controlled by orbital cycles. The Cardigan Bay Strait played an important role in the Early Jurassic (at least Pliensbachian) oceanic circulation, providing a major link between the northern and southern part of the Laurasian Seaway (and in general between the Boreal and Peri-Tethys domains), funneling currents flowing from the north to the south.

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1. Introduction

The Llanbedr (Mochras Farm) borehole (hereafter referred to as Mochras) cored the Lower Jurassic of the Cardigan Bay Basin (Wales, UK), an extensional structure related to the break-up of Pangaea. During the Early Jurassic, the basin was located at a mid-palaeolatitude, on the NW fringe of the European shelf, in the Laurasian Seaway (Figs. 1, 2). The core has been studied in many respects, including biostratigraphy (the core was calibrated to a zonal or even subzonal level using ammonites), lithology (Woodland, 1971; Dobson and Whittington, 1987; Hesselbo et al., 2013; Copestake and Johnson, 2014), marine plankton (Van de Schootbrugge et al., 2005), clay minerals (Deconinck et al., 2019; Munier et al., 2021), and astrochronology (Ruhl et al., 2016; Storm et al., 2020).

The uppermost Sinemurian-Pliensbachian (Lower Jurassic) section of the Mochras core represents the most expanded and highest resolution cyclostratigraphic dataset for the Pliensbachian to date, and provides the most reliable basis for an astrochronological time scale, reflecting Milankovitch forcing, predominantly at precession/obliquity and the short- and long-eccentricity periodicities (Figs. 3, 4). The dominant expression of the medium-amplitude Carbon Isotope Excursions (CIEs) in Mochras testifies to the expanded stratigraphic resolution and relative completeness of sedimentary record therein, allowing distinction between intrinsic Earth processes and extrinsic solar system dynamics such as the driving mechanism for the Early Jurassic $^{13}$C fluctuations (Storm et al., 2020).

Astronomical duration of the Pliensbachian, based both on dominant spectral peaks in elemental Ca and Ti in lithology and geochemical palaeoenvironmental proxies (Ruhl et al., 2016) or carbon isotope fluctuations (Storm et al., 2020), was estimated at about 8.7–8.8 Myr, although durations of successive ammonite zones were slightly different in the two studies. Generally, fossils and lithology point to a consistently fully marine hemipelagic setting (Ruhl et al., 2016). In addition, climate changes have been interpreted on the basis of clay minerals (Deconinck et al., 2019) and organic geochemistry (Storm et al., 2020). However, a more focussed characterization of sedimentary environment, ichnology and benthic life conditions has not yet been carried out.

Herein, we present detailed sedimentological and ichnological analyses, which allow recognition of ecological parameters on the basis that trace fossils are sensitive in situ indicators of even very subtle environmental changes such as current strengths, oxygen content, food supply, and stability of the environment (Savrda, 1995; Savrda and Bottjer, 1994). Benthic invertebrates respond to various environmental changes driven by orbital forcing (e.g. Wetzel, 1991; Erba and Premoli Silva, 1994; Hünke and Stow, 2008; Perverzler et al., 2008; Rodríguez-Tovar et al., 2011; Rebesco et al., 2014; Rodríguez-Tovar, 2014; de Castro et al., 2020b), but the mechanisms of control (Valdes and Glover, 1999; Paillard, 2010) are still poorly understood. In this paper, we present an analysis of lithological and ichnological cycles related to the orbital cycles and a refined estimation of the astronomical duration of the Pliensbachian and the ammonite zones within this stage.

2. Material and methods

A nearly continuous 420 m-thick section of core (< 4 m missing), was investigated using standard sedimentological logging at a centimetre-scale accuracy (Figs. 3–10) with special attention paid to the integration of sedimentological and ichnological observations. Dunham’s (1962) classification of carbonate rock lithotypes was adopted as it focuses on depositional texture and is well suited for macroscopic observations (employing a hand lens or binocular microscope). Additionally, 93 thin sections (approximately one thin section for every 4–5 m of core) were examined for recognition of microfacies and lithology.

For the needs of the numerical cyclicity analysis, occurrences of trace fossils Phycosiphon, Thalassinoides and Schaubaeylindrichnus (Figs. 5, 6, 8–10), as well as intervals with preserved lamination within the sedimentary log were treated as discrete binary time series. Ranges of trace fossils and lamination were manually digitized with an even step of 10 cm, resulting in the time series consisting of approximately 4200 binary digits each (Supplementary 1).

To statistically verify whether particular trace fossils and lamination occur non-randomly, the runs test has been applied (Supplementary 2). The non-parametric runs test evaluates the null hypothesis that two states are distributed randomly in a binary time series. Ranges of trace fossils and lamination were manually digitized with an even step of 10 cm, resulting in the time series consisting of approximately 4200 binary digits each (Supplementary 1).

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- $H_0$: distribution of occurrences is random;
- $H_1$: distribution of occurrences is non-random.

Runs are defined as uninterrupted sequences of either occurrence ($N_1$) or non-occurrence ($N_0$) of particular trace fossil or lamination. Statistically significant discrepancy between the observed number of runs (R) and the number of runs expected in case the time series were random (R) allows rejection of the null hypothesis. The test statistic Z has been computed using the runs test module of PAST 3.2 software (Hammer et al., 2001) separately for each studied ichnotaxa and lamination. Absolute values of resultant Z-scores have been compared to the critical value of 1.96 corresponding to 5% significance level in a standard normal table.

Binary time series can be considered to represent a sum of component constant-frequency waves. The transform operation can be applied to extract the frequency spectrum of the component waves. Various numerical methods derivative of the Fourier transform, while commonly applied in the analysis of continuous time series, are inappropriate to analyze binary time series (Weedon, 2003). Power-spectral analysis based on the Walsh transform is considered to be the most correct method of finding periodicities within such time series. The Walsh transform outputs the spectral data as a function of sequency, defined as half of the average number of zero transitions per unit of time or space. In terms of the interpretation of results, the sequency of the Walsh domain coincides with the commonly recognized concept of frequency. Theoretical background behind the Walsh technique and its applicability in time series analysis have been provided by Negi and Tiwari (1984), Weedon (1989), Weedon and Read (1995), van Echelpoel (1994) and Maiti and Tiwari (2012). The studies of Tiwari (1987) and Negi et al. (1993) demonstrate that besides the main orbital cycles, the Walsh power-spectrum displays component periodicities, beat
periodicities, and combined effects of other periodicities, theoretically predicted by Berger (1977).

Occurrences of selected trace fossils and intervals with preserved lamination have been subjected to spectral analysis using the Walsh transform module of PAST 3.2 software (Hammer et al., 2001) (Tables 1, 2; Figs. 11, 12). The terminations of the time series were experimentally adjusted to obtain the optimal balance between the signal-to-noise ratio and spectral resolution. The spectral analysis outputs the power-spectra as a function of stratigraphic thickness – i.e. number of cycles per one metre (Fig. 11). The obtained spectrograms were converted from the thickness domain into the time values based on the average sedimentation rate adopted as 4.7 cm per 1000 years. This sedimentation rate was tuned for Jamesoni Zone to the 405 kyr cycles (Ruhl et al., 2016). Independently, similar long-term sedimentation rate estimates (4.9 cm/kyr) can be obtained by dividing the combined thickness of Margaritatus and Spinatum zones in Mochras (147 m) by approximate duration of these zones (~3 Myr), based on radiometric dates from Oregon, USA (De Lena et al., 2019). Thereby, the deposition of one-metre-thick sediment interval took 20,770 years on average. For a comparison, the conversion was also tested with 4.4 and 4.5 cm/kyr sedimentation rates (obtained herein for Jamesoni and Ibex zones), which resulted in very similar values and did not influence the interpretation of the cycle duration.

3. Results

3.1. Lithology and sedimentary structures

The succession primarily comprises calcareous mudstone/micrite, wackestone and grainstone with varying calcareous grains of silt to fine-sand size. Siliciclastic contribution in coarser silty-sandy lithofacies is weaker, usually between 10 and 30%, while the mudstone contains a greater siliciclastic component and locally (1232 m, 988 m and 865 m) is carbonate-free (Figs. 3, 4; Ruhl et al., 2016). Macrofossils are represented mainly by pelagic cephalopods. Widespread crinoid ossicles are most likely redeposited from shallower settings due to their buoyancy (Savarese et al., 1997). Benthic shelly organisms are rare on the slabbed core surfaces, and are represented by in situ burrowing bivalves found in a few horizons (Fig. 10E). Fossil collections made from the “working half” broadly confirm this distribution (Woodland, 1971; Ullmann et al., 2021). Benthic foraminifers are present as well (Copestake and Johnson, 2014). Drifted flora occurs locally, mostly in the Ibex and Davoei zones. Lamination and low-angle cross lamination are common, particularly upwards from the Ibex Zone. Carbonate-rich parts (uppermost Jamesoni Zone, and in particular the upper Margaritatus and the lowermost part of Spinatum zones) suggest early diagenetic processes, such as calcite cementation and formation of calcite nodules (Figs. 5D, 6A), which may result from the degradation of organic matter and the associated reduction of sulphates (Ruhl et al., 2016). Nodules are surrounded by...
more ductile, un cemented mudstone, which is deformed around them. However, conspicuous condensation/cementation levels with a hard crust are absent. Dewatering/compactional cracks are observed only in a few horizons (Fig. 10M).

Six main lithofacies types (Fig. 7) are identified in the Mochras section: (1) Dark grey, planar-laminated siliceous-calcareous micritic mudstone and siliceous claystone; bioturbation structures are typically not observed, but in silty parts small horizontal burrows are present; therefore, two sub-lithofacies were distinguished: with continuous (Figs. 3B2, 9A) and broken lamination (Fig. 9B); (2) ‘massive’, poorly bedded mudstone/carbonate micritic mudstone, in some cases showing centimetre- to decimetre-scale banding with faint, slightly undulated or cuboid parting, which is connected to homogenization by meiofaunal bioturbation of sub-millimetre size; in places, peloidal structure occurs; discrete trace fossils are relatively rare (Fig. 9E); (3) ‘pinstripe’ carbonaceous mudstone that is laminated with wackestone-siltstone, in which planar laminae are often discontinuous and lenticular to wavy, planar parallel, or low angle cross-lamination, starved ripples are present and, bioturbation structures can obliterate these in mottled mudstone-wackestone (Figs. 3B1, 9C, D); (4) interlaminated, heterolithic siltstone or wackestone with mudstone, usually bioturbated, with only local sedimentary structures; this lithofacies shows irregular arrangement of mudstone, wackestone-siltstone or grainstone-sandy siltstone in pockets, lenses and streaks, and less commonly, a rapid alternation of thin irregular layers of these three lithologies (Figs. 5A, B; 6A); (5) packstone/siltstone to very fine sandstone, with primary sedimentary structures - usually obliterated by bioturbation - including parallel bedding and small-scale cross-bedding (Fig. 9H); (6) sandstone-grainstone, usually bioturbated, with primary structures (parallel bedding and small-scale, low-angle cross-bedding) observed in some horizons (Figs. 4C, 9D).

Contacts between these different lithofacies may be either gradational, yielding indistinct bedding (Figs. 3B, 5B, 6B, 9H), or sharper due to the erosive action of relatively stronger bottom currents (Gross and Williams, 1991), thereby yielding more distinct bedding (Figs. 5C, 6A, 10N). However, sharp bed boundaries in the Mochras Pliensbachian section are rare and evidently not associated with significant hiatuses or erosion, which might be expected to be marked by induration of the sediment surface, or occur as semi-consolidated/firm muddy substrates with sharp-walled, unlined, uncompacted passively filled burrows exhibiting scratch traces along the walls underneath these boundaries.

Lithofacies types 1–6 (Fig. 7) and related ichnofabric in Mochras are not arranged randomly, but appear in a cyclical order (Figs. 3–7). Fully developed, usually 0.5–3 m thick bidirectional grading sequences (referred to as ‘couplets’ by previous authors) commonly begin from mudstone lithofacies type 2 (representing mixed layer, mottled by burrowing activity of meiofauna, or mudstone lithofacies type 1 (laminated), passing gradually into lithofacies type 3 – pinstripe mudstone with ripple-drift cross laminated siltstone, or lithofacies 4 – bioturbated mudstone-wackestone, followed by usually bioturbated wackestone-siltstone and packstone-grainstone with traces of stronger currents (Fig. 9D, H). Above this coarsening-upward part is a fining-upward suite, developed in reversed order, although less complete; usually only lithofacies types 6–5–4 are present. This fining-upward phase of the sequence is usually thinner compared to the coarsening-upward phase (Figs. 3B, 7). In many cases the whole sequence is incomplete; either top or bottom parts can be missing (bottom cut-out cycles or top cut-out cycles – Figs. 7, 5C, D, 6A). Additionally, internal erosion surfaces in some of the coarser parts occur (Figs. 5C, 10N), although they are generally rare in the Pliensbachian profile, with relatively more frequent occurrences only in few intervals – in the mid-bex, upper part of margaritatus and the lowermost part of spinatum zones (Figs. 3, 4). Of note is the ~5 m thick interval in the uppermost spinatum Zone with homogeneous carbonate-free mudstone, traces of iron compounds (Figs. 4, 6B), and distinct clay mineral assemblage of mixed-layer clay minerals with berthierine and detrital kaolinite (Deconinck et al., 2019).

3.2. Trace fossils, ichnofabrics

Trace fossils exhibit sharp outlines and possess a characteristic recurrent geometry that allows their classification in terms of ichnotaxonomy, while bioturbation structures have less distinct outlines and do not display a recurrent geometry (Wetzel and Uchman, 2012). Below, they are briefly described in the alphabetic order.

Arenicolites (Fig. 10A) is a U-shaped, tilted tube, 1.5–4 mm in diameter. The width increases towards top of the limbs. The trace fossil is 22 mm wide and up to 13 mm deep. Arenicolites Salters, 1857 is a dwelling and feeding burrow of suspension-feeding annelids (e.g., Hakes, 1976) or small crustaceans (Goldring, 1962). It occurs in facies of different environments, but is typical of shallow-marine settings (Crimes, 1977), especially in storm beds (Frey and Goldring, 1992).

Asterosoma (Fig. 10J) is visible in vertical section as oval spots, which are 14–18 mm thick. The spots are filled with slightly coarser material than in the surrounding rock. They may be in contact. The spots are interpreted as cross-sections of vertical to inclined elongated bulb-like structures tapering at both ends. They do not show concentric internal lamination typical of Asterosoma von Otto, 1854, but this is probably a matter of preservation. Clusters of such “bulbs” in Asterosoma form tree-
like structures spreading out from a common vertical or inclined shaft (e.g. Bromley and Uchman, 2003; Pervesler and Uchman, 2004). *Asterosoma* is interpreted as a selective-feeding burrow of a worm (Pemberton et al., 2001). It occurs in soft (mostly siliciclastic, rarely carbonate) substrates, typically in various shallow-marine settings, especially in the upper lower shoreface (Pemberton et al., 2001).

Fig. 4. Continuation of the Pliensbachian section in Mochras, depths are 1010.5–1123.8 m and 863.8–1010.5 m. Red squares in the depth columns – intervals presented in details in Figs. 5 and 6. For explanation see Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Monocraterion is manifested on the vertical plane as a triangular structure, c. 10 mm wide and 10 mm high, with vertex oriented downward. This structure is interpreted as a cross section of a funnel at the top of a shaft. Monocraterion Torell, 1870 is a domicnial structure produced by suspension feeders (e.g. Westergård, 1931; Hallam and Swett, 1966; Paczeńska, 1996; Jensen, 1997; Stachacz, 2016). For discussion of this ichnogenus see Jensen (1997) and Schlirf and Uchman (2005).

Phycosiphon incertum Fischer-Ooster, 1858 is the most abundant trace fossil, a small structure, 1–15 mm wide, which comprises repeated narrow, U-shaped, irregularly branching lobes containing dark centres and light mantles. Dark tubes (centres) are composed of darker, finer sediment and are surrounded by a lighter mantle, composed of coarser sediment – see Figs. 8A–D, 9F, G, I, 10A, B, D, G, I, N). In places, dark centres show fish-hook shapes and pairs of black spots. The lobes are oriented randomly, although generally more or less parallel to bedding (however, parallel orientation may be also caused by compaction). Most commonly, Phycosiphon shows a diffused appearance due to soft-soupy host sediment and spreite structures and marginal tubes are very rarely observed – although their poor preservation seems to be generally typical for Phycosiphon (Wetzel and Bromley, 1994). The mantle and spreite indicate manipulation of grains, pointing to deposit-feeding activity. Four morphotypes of P. incertum can be distinguished: (1) the large Ph1 is 8–15 mm long, and 2–3 mm wide, (2) the medium, most common Ph2 is 3–8 mm long and 0.3–2 mm wide, (3) the small Ph3 is up of 2–3 mm long and 0.1–0.3 mm wide, usually horizontally oriented, and (4) Ph4 is distinguished by its occurrence in isolated patches; in this case, burrows similar to the morphotype Ph2 occur preferentially in fillings of Thalassinoides or occasionally in Teichichnus. The four morphotypes largely resemble these distinguished by Rodríguez-Tovar et al. (2014), although size of the morphotypes from the Mochras core are more diversified. Ph2 and Ph3 dominate. Phycosiphon is interpreted as the deposit-feeding trace of a small, unknown vermiform organisms that exploited the sediment for organic-rich matter (Wetzel and Bromley, 1994; Wetzel, 2010; Izumi, 2014); its morphological problems were studied by Naruse and Nifuku (2008) and Bednarz and McIlroy (2009).

Phycosiphon is reported from a wide range of facies, but mostly from fine-grained lower shoreface and deeper, mainly siliciclastic deposits (Goldring et al., 1991; Savrda et al., 2001; Pemberton et al., 2012; Callow et al., 2013). Its tracemaker colonized freshly deposited turbidites in the sequential colonization model, when the sediment contained a lot of food and well oxygenated pore waters (Wetzel and Uchman, 2001). The Phycosiphon lobes can be inclined to varying degrees in the
Fig. 5. Sections of the Mochras core showing common types of lithology, ichnology and cyclicity of sedimentation. A – 1177.98-1178.97 m: bidirectional (symmetrical – cu – coarsening upward, fu – fining upward) cycle, m-md (micrite-calcareous mudstone) with Phycosiphon incertum type 3 is followed by muddy wackestone (w-st/m-md), wackestone (w-st) and subsequently again by mudstone – wackestone (w-st/m-md), all thoroughly bioturbated by Phycosiphon incertum type 2 (Ph2) makers, with appearances of the Phycosiphon incertum type 4 (Ph4) and sporadic Schaubcylindrichnus. This section is interpreted as a regular, C1-C2-C4-C5 contourite cycle with missing coarse division C3 (Stow and Faugères, 2008). The next cycle starts with mudstone (md) with Phycosiphon incertum type 3 (Ph3). Phycosiphon incertum obliterated primary sedimentary structures throughout the whole cycle, which points to well-oxygenated sea bottom. B – interval 1106.45–1107.39 m: bidirectional cycle (cu – coarsening upward, fu – fining upward), starting and ending with mudstone/micrite and wackestone/siltstone facies with common Phycosiphon incertum type 2 (Ph2), in places with current structures; in the middle packstone-very fine grained sandstone (p-fs) with Phycosiphon incertum type 2 (Ph2) and cf. Polykladichnus (Pol) dwelling structures. Next bidirectional cycle (above cycle boundary – continuous red line) is built of fine-grained micrite/mudstone (m-md) parts separated by 5 cm-thick grainstone/sandstone intercalation with gradational boundaries and current structures (see Fig. 6.12); the upper “pinstripes” m-md interval contain thin, broken silty lamina and incipient ripples pointing to weak currents. The section 1106.45–1107.39 m is interpreted as two C1-5 contourite cycles (Stow et al., 2002). C – 1098.55–1099.59 m: bidirectional cu-fu cycle showing subtle fluctuations in grain size (m-md – calcarceous mudstone with Phycosiphon incertum type 3 – Ph3; w-st/m-md – wackestone/mudstone bioturbated by Phycosiphon incertum type 2 – Ph2 makers, with rare occurrences of Thalassinoides – Th), topped by sharp erosional boundary with cross-bedded grainstone-sandstone (g-s) above, passing upwards into packstone - fine-grained sandstone (p-f) with Phycosiphon incertum type 2 (Ph2), Palaeophycus (Pa) and Planolites (Pl). The upper cycle (g-s and p-f) is interpreted as a base cut-out contourite C4-C5 – Stow and Faugères (2008). D – interval 914.50–915.49 m dominated by packstone and grainstone with subordinate micrite/mudstone, showing stacked coarsening-upward cycles (red lines = cycle boundaries). Carbonaceous cementations (d) and carbonate nodules (dn) are common. This section is interpreted as stacked topcut-out contourite cycles C1-C2 (Stow and Faugères, 2008). For other abbreviations see Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sediment or horizontal orientation in laminated deposits; this pattern probably reflects the homogeneous distribution of food material or the concentration of food material in certain layers, respectively (Bromley, 1996).

*Palaeophycus* (Fig. 10C) is a sub-horizontal cylindrical, lined, passively filled burrow, 2–4 mm wide. It may show trace of collapsing. *Palaeophycus Hall, 1847* is produced by variable filter or deposit-feeding, carnivorous or omnivorous invertebrates, mostly polychaetes in a wide range of facies (Pemberton and Frey, 1982; Jensen, 1997; Knaust, 2017).

*Phymatoderma* (Fig. 9J,K) is a horizontal to subhorizontal structure composed of partly overlapping and diverging lobes, which are up to 6 m thick, 10–14 mm wide, and show crude spreiten. Pellets arranged perpendicularly to the lobes, which are typical of *Phymatoderma* Brongniart, 1849 are not obvious (not preserved?). *Phymatoderma* is produced by deposit feeders which formed probes from a fixed position, which resulted in a fan-like structure (Fu, 1991; Uchman, 1999; Seilacher, 2007; Izumi, 2012).

*Planolites* (Fig. 8I) is a horizontal, unlined, cylindrical tunnel, actively filled with sediment usually differing from the surrounding. It is elliptical, sub-circular in cross sections, 2–3 mm in diameter. *Planolites* Nicholson, 1873 is an eurybathic, extremely facies-crossing ichnogenus referred to polyphyletic vermiciform deposit-feeders producing active filling (e.g. Pemberton and Frey, 1982; Fillion and Pickrell, 1990), and references therein). Locklair and Savrda (1998) interpreted *Planolites* as an open burrow that was filled with overlying sediment. It can be abundant in deposits of well-oxygenated as well as in dysaerobic environments (Wignall, 1991, p. 268; Bromley, 1996).

cf. *Polykladichnus* (Fig. 10H) occurs in clusters, which are up to 20 mm wide and up to 20 mm high. It is composed of crowded, vertical to subvertical, branched, unlined cylinders, which are ~1 mm wide. The branches diverge in the middle-upper part under acute angle. *Polykladichnus* Fürsich, 1981 is a domichnion, which occurs mostly in marginal marine and continental deposits (Schlirf and Uchman, 2005). Burrows of such pattern are produced by some nereidid polychaetes (Wang et al., 2019).

*Rhizocorallium* (Fig. 10L) is visible in vertical section as 1) a dumbbell structure, about 60 mm wide, with lens-like, swelled terminations, which are 15 mm wide, and the interconnecting thin bar, which is 1.4–2 mm thick, or as 2) spreite horizontal structures, 5 cm thick with a swelling at the end. The lens-like terminations are interpreted as cross-section of marginal rills. *Rhizocorallium* is interpreted as a structure produced by suspension feeding (only short oblique, retrusive forms) or by deposit feeding organisms, mostly crustaceans (Fürsich, 1974; Schlirf, 2000) or “worms” (Knaust, 2013). Occurrences of *Rhizocorallium* are usually associated with occurrences of dwelling structures (*Skolithos, Arenicollites, Monocraterion* or *Polykladichnus*), sharp lithological boundaries and rare appearances of grainstone/sandstone (e.g. 1092.5 m – ibex Zone and 884.0–898 m interval in the spinatum Zone), which may indicate periods of slower sedimentation, stiffer ground and more vigorous currents. *Rhizocorallium* occurs mostly in shallow marine and marginal marine deposits (e.g. Farrow, 1966; Hakes, 1976) and rarely in deep-sea (Uchman, 1992) or even in non-marine deposits (Fürsich and Mayr, 1981).

*Schaubcylindrichnus* (Figs. 8 F, 9I) is usually represented by horizontal to oblique, single, simple tubes – 2–5 mm in diameter, rarely by a bunch of subparallel tubes, that display a white, calcareous/silty wall. No cross cuts by other trace fossils occur, which can be attributed to both deeper tier and reinforced walls. In most cases, this trace fossil occurs in fine-grained deposits (mudstone and wackestone). It is common in the lower marginatum and the middle spinatum zones. *Schaubcylindrichnus* Frey and Howard, 1981 is interpreted as solitary funnel feeder and dwelling structure produced by enteropneusts, maldanid polychaetes or synaptid holothurians (Nara, 2006; Löwemark and Nara, 2013).

*Siphonichnus* (Fig. 9L) is a steeply inclined, simple tube, c. 1.5 mm thick, which shows a darker core and thick lighter mantle. In the upper part, it may show a swelling. *Siphonichnus* Stanistreet et al., 1980 is a
Representatives of Ph2 and Ph3, but is cut by Ph4, which is particularly abundant in the subnodosus Subzone (Fig. 4). Teichichnus and Schaubcylindrichnus usually do not occur together. Teichichnus Seilacher, 1955 is a typical feeding structure. For discussion of this ichnogenus see Knaust (2017).

Thalassinoides (Figs. 8J, 9G, I, M, 10B) is visible in vertical section mostly as elliptical spots up to 5–20 mm wide, or short bars of comparable size, whose colour differs from the surrounding rock. Their sectioning reveals that they represent mostly horizontal, branched, cylindrical burrow networks. The vertical shafts connecting the system to the sediment surface are rarely preserved. The burrows are filled actively or passively. They are usually associated with coarser (packstone-grainstone), somewhat stiffer sediments. The filling is preferentially burrowed with Phycosiphon. In poorly cohesive sediments the burrow margins are diffuse. Other deformations may result from compaction or diagenetic dissolution of carbonate (cf. Archer et al., 1989). Thalassinoides cross cuts Phycosiphon of the morphotypes Ph1, Ph2 and Ph3, but is cut by Ph4, Schaubcylindrichnus and Teichichnus. Representatives of Thalassinoides Ehrenberg, 1944 occur in deposits of variable, presumably shallow marine environments (Frey et al., 1984; Mángano and Buatois, 1991; Pemberton et al., 2001), but also in the deep-sea facies (Uchman, 1995, 1998; de Graciansky et al., 1998; Uchman and Tchoumatchenko, 2003; Wetzel et al., 2007). They are produced mostly by scavenging and deposit-feeding crustaceans and interpreted as domicinia and fodinichnia (Frey et al., 1978; Frey et al., 1984; Bromley, 1996; Schlirf, 2000). For further discussion of this ichnogenus and its ichnotaxonomic problems see Fürsich (1973), Ekdale (1992) and Schlirf (2000).

Teichichnus (Figs. 8G, H, 10F) is a vertical burrow, occasionally horizontal, straight or slightly winding, thread-like, unbranched or
Fig. 7. Six main lithofacies (1–6) and ichnofabrics in the Mochras profile; to the right – main types of bigradational contourite drift sedimentary cycles built of main lithofacies – full cycle, top cut-out cycle, bottom cut-out cycle (referred to Stow et al., 2002; Stow and Faugères, 2008). Contourite cycle divisions reflect variations in current velocity. C1–C5 – “full” contourite cycle. For lithology and trace fossil abbreviation see Fig. 3.
branched cylindrical structure, up to 1 mm in diameter. It is an exceptional trace fossil due to its very small diameter (mostly less than 1 mm) and common pyritic filling. *Trichichnus* is particularly common in the uppermost *spinatum Zone*, which is associated with declining abundance in *Phycosiphon*, low ichnodiversity and specific clay mineral composition (Deconinck et al., 2019) pointing to a stressed environment. Modern analogues link *Trichichnus* Frey, 1970 to large, filamentous mat-forming, sulfide-oxidizing bacteria, belonging mostly to *Thiobloca*-related taxa, which are able to house a complex bacterial consortium providing an electron exchange between oxic and suboxic/anoxic layers in the sediment (Kędzierski et al., 2015; Kjeldsen et al., 2019). *Trichichnus* occurs mostly in fine-grained sediments, in shallow water (e.g. Frey, 1970) as well as in deep-sea deposits (e.g. Kennedy, 1975; Wetzel, 1981, 1983). It is a deep-tier trace fossil having higher tolerance for dysoxia than *Chondrites* (Kotlarczyk and Uchman, 2012).

*Zoophycos* (Figs. 8J, 10I) is represented by a few mm thick, planar to oblique structures. The characteristic of *Zoophycos* spreiten structure is not observed, but this is common in some fine-grained deposits (Voigt and Hántzschel, 1956). *Zoophycos* is distributed rather evenly through the whole section, but rare in the lower *jamesoni* Zone and more frequent in the upper *margaritatus* to lower *spinatum* zones. Usually, only one, rarely two whorls appear (Figs. 8J, 10I). *Zoophycos* is not cut by other trace fossils. This indicates that it occupies the lowermost tier. *Zoophycos* Massalongo, 1855 is generally considered as a structure produced by some yet undiscovered deposit feeders, which are referred to as sipunculids (Wetzel and Werner, 1981), polychaete annelids, arthropods (Ekdale and Lewis, 1991), or echiuran worms (Kotake, 1992). The feeding strategy is, however, controversial (e.g. Bromley, 1991; Locklair and Savrda, 1988; MacEachern and Burton, 2000). Bromley and Uchman (2003) suggested that the upper helical part of a large Pliocene feeding strategy is, however, controversial (e.g. Bromley, 1991; Ekdale and Lewis, 1991), or echiuran worms (Kotake, 1992). The culids (Wetzel and Werner, 1981), polychaete annelids, arthropods mostly in fine-grained sediments, in shallow water (e.g. Frey, 1970) as sediment surface (Lefevre et al., 2006). Since the Mesozoic, *Zoophycos* has shown a tendency to occur in deeper environments than in the Palaeozoic, from below the shelf to abyssal depths (Zhang et al., 2015).

Trace fossil assemblages from the Mochras cores are strongly dominated by *Phycosiphon incertum*, which is the principal deposit-feeding trace. Other deposit-feeding traces, e.g. *Rhizocorallium* (Fig. 10J, 8F, 10H) and *Asterosoma* (Fig. 10J) are rare. Among other trace fossils, of note are occurrences of dwelling structures of filter-feeding organisms, building vertical structures stabilized by a mucus lining (*Skolithos, ?Monocraterion, Arenicolites, Siphonichnus, cf. Polykladichnus*).

All the described trace fossils are important components of ichnofabrics (ichnofabric is understood as an overall texture and structure formed by bioturbation or bioerosion; see Bromley and Ekdale, 1986). Constituents of ichnofabrics may be attributed to a number of controls and attributes, in particular to the tiering patterns and the manner of colonization (Ausch and Bottjer, 1982; Taylor et al., 2003). The complete (“ideal”) tiering pattern in the Mochras section can be summarized as follows. The shallowest tier consists first of an indistinct mottling that is produced in the mixed layer by bioturbation in water-saturated soupy sediment near the sea floor, followed next by shallow tier of *Phycosiphon* (Ph1, Ph2, Ph3) showing a patchy distribution. In the middle tier, is *Thalassinoidea* and bit deeper *Schaubcylindrichnus, Planolites, rare *Teichichnus* and yet deeper another generation of *Phycosiphon* (Ph4), reworking *Thalassinoidea* (and rarely *Teichichnus*) are present. The deepest tier is occupied by *Teichichnus* and *Zoophycos*. Rare traces (cf. *Polykladichnus, Skolithos, Arenicolites, Siphonichnus, Rhizocorallium, ?Phymatoderma*) usually occupy a middle tier, below *Phycosiphon* (Ph1, Ph2, Ph3). However, such a complete (“ideal”) tiering pattern occurs rarely, and the most common tiering pattern is limited to shallow tiers: *Phycosiphon* (Ph1, Ph2, Ph3), *Thalassinoidea* (middle tier) and (less frequently) a bit deeper a *Schaubcylindrichnus* tier.

Thus, in most common ichnological cycles/colonization successions, *Phycosiphon* (Ph3, Ph2, Ph1) is followed by *Thalassinoidea* (mostly in coarser sediments) and *Schaubcylindrichnus* (mostly in finer sediments). *Thalassinoidea* is often buried with secondary, “patchy” Ph4, whose maker exploited more porous sediment of the burrow infill. Presence of more nutritious material within the *Thalassinoidea* filling could be also considered. *Teichichnus* and *Zoophycos*, representing deeper tiers, are generally less common, except for in the mid-*margaritatus* Zone, where *Teichichnus* is very common, while *Zoophycos* is relatively more common in the *subnodosus-gibbosus* subzones to lower *spinatum* Zone. *Planolites, Palaeoepichnus* and other trace fossils occur sporadically.

In rare cases (e.g. lower *jamesoni* Zone, bottom of the *stokesi* Subzone, top of the *spinatum* Zone – the latter with domination of *Trichichnus* and scarcity or disappearance of other forms, including *Phycosiphon*), the impoverished tiering comprises from the bottom to the top: mottling or lamination-Ph3-Ph2-Ph1-Ph2-mottling; and in top cut-out cycles: mottling or lamination-Ph3-Ph2 (Fig. 7).

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**Fig. 8.** Photographs showing most common trace fossils: A – *Phycosiphon incertum* morphotype 1 (Ph1), 1148.30 m; B – *Phycosiphon incertum* morphotype 2 (Ph2), 1145.0 m; C – *Phycosiphon incertum* morphotype 3 (Ph3), 1160.3 m; D – *Phycosiphon incertum* morphotype 4 (Ph4), 1158.90 m; E – *Teichichnus*, 934.85 m; F – *Schaubcylindrichnus*, 1011.20 m; G, H – *Trichichnus*, 947.10 m; I – *Planolites*, 988 m; J – *Thalassinoidea* (Th), *Planolites* (P), *Phycosiphon* type 4 (Ph4) and *Zoophycos* (Z), 937.50 m. For more trace fossils examples see Figs. 9 and 10.
4. Discussion

4.1. Sedimentary environment, ichnodiversity, cyclicity of sedimentation

4.1.1. Sedimentary environment

On the basis of sediment transport processes, two different types of deep-water currents and their depositional products have been recognized and extensively documented in the literature, namely contourite drift facies produced by along-slope contour currents (Gong et al., 2017) and turbidite facies created predominantly by downslope sediment density flows. Turbidites are primarily bioturbated from the top (e.g. Uchman and Wetzel, 2011). The uppermost layers of the turbidite exhibit total bioturbation, which decreases with depth as lamination appears. In contrast, contourites typically exhibit a more continuous and uniform bioturbation, which appears throughout the entire contourite bed (Wetzel et al., 2008). It should be noted, that turbidites can be reworked by contourite currents. Recently, de Castro et al. (2020a) described a Quaternary case of mixed deposits, called “bottom current reworked sands” (BCRS). The sequence is defined as a partial bi-gradational contourite sequence including BCRS reworked from underlying turbiditic deposits due to the interaction of down- and along-slope processes within the contouritic drift and its adjacent contouritic channel. As a result, the contourite drift and the adjacent contourite channel are influenced by the interrelation of hemipelagic, gravitational, and bottom current induced depositional processes (de Castro et al., 2020b). Rodríguez-Tovar et al. (2019) showed an Oligocene-Miocene example with a more complex internal pattern of contourites, characterized by a more discontinuous, multiphase sedimentation, resulting also in ichnological differences between non-compacted and compacted interlayers. However, in Mochras such differentiation in compaction of trace fossils is not observed. Also, sandstone and grainstone or erosional features are very rare, while even distal turbidite deposits, hyperpycnites and BCRS or other mixed contourite-turbidite deposits contain appreciable sand and are dominated by numerous erosional features and variable scale cross-bedding which result from more or less instantaneous deposition (Etienne et al., 2014; Rodríguez-Tovar et al., 2019; de Castro et al., 2020a, 2020b). Moreover, rare sandy beds and laminae in Mochras show no systematic vertical grading and

Fig. 9. Some sedimentary and ichnological features. A – continuous planar lamination in mudstone, 1233.5 m; B – continuous planar lamination passing upwards into broken lamination with incipient ripples indicating weak currents, 1077.2–1077.3 m; C – “pinstripe” broken lamination, in places continuous, showing silty/calcareous lamina and ripples produced by currents, 1005.5–1005.6 m; D – succession showing “massive” mudstone with Phycosiphon morphotype 2 (Ph2) passing upwards into “pinstripe” mudstone laminated with calcareous siltstone with Phycosiphon morphotype 2 and 3 (Ph2 + Ph3) and subsequently into cross-bedded wackestone at the top, indicating increasing current activity, 1071.65 m; E – “massive” mudstone, result of meiofauna bioturbation, 1123.1 m; F – crinoid rotated by burrowing activity of Phycosiphon incertum makers, which points to soft-soupy ground conditions, 1098.35 m; G – Thalassinoides (Th), in the bottom filled with Phycosiphon incertum type 4 (Ph4), earlier Phycosiphon incertum morphotype 2 (Ph2) in the background, 888.25 m; H – grainstone/sandstone intercalation with gradational lower and upper contacts (cu – coarsening upward, fu – fining upward) and low-angle cross bedding; fragment of the Fig. 5.2, depth 1106.8 m; I – ichnofabric showing succession of the earliest/shallowest tier Phycosiphon incertum morphotype 2 (Ph2), followed by Thalassinoides (Th), Schauchylindrichnus (S) and Teichichnus (Te). Note Phycosiphon incertum morphotype 4 (Ph4) reworking (postdating) Thalassinoides, 973.25–973.45 m; J – feeding burrow ?Phymatoderma, cross-section, 978.2 m; K – plane view of the ?Phymatoderma shown above, 978.2 m; L – Siphonichnus, 913.1 m; M – Thalassinoides and Phycosiphon (Ph3 and Ph2 predating, Ph4 postdating Thalassinoides), 1069.8 m.
stacking of structures such as those recognized in the Bouma (1962) turbidite intervals or those occurring in some sandy contourites (Rodriguez-Tovar et al., 2019). Instead, the Pliensbachian section in Mochras records continuous sedimentation controlled by fluctuation of stable and generally weak bottom currents; thus intermittent deposition by distal turbidite/hydropynite or BCRS was unlikely and the traditional contourite drift model (dominated by muddy sediments) fits the Mochras case - perhaps, with a few exceptions mentioned above (occurrences of Rhizocorallium and more frequent dwelling structures, more common sharp lithological boundaries and appearances of grainstone/ sandstone, which may indicate periods of slower sedimentation, stiffer ground and more vigorous currents at 1092.5 m (ibex Zone) and between 884.0 and 898 m (spinatum Zone).

The lithofacies in the Pliensbachian at Mochras also contrast with those of other hemipelagic settings of the UK Jurassic. For example, the Pliensbachian in the Cleveland Basin, some 300 km to the NE of Cardigan Bay, is clearly dominated by structures attributable to storm processes in offshore shelf to shoreface environments (e.g. van Buchem and McCave, 1989; Van Buchem et al., 1994; Hesselbo and Jenkyns, 1995; Van Buchem and Knox, 1998; de Graciansky et al., 1998; Powell, 2010). Evidence of storm-influenced deposition in the Cleveland Basin includes winnowed shell beds and scours, symmetrical ripple structures, and ultimately in the sandy facies hummocky cross stratification. None of these diagnostically storm generated features has been observed in the Mochras Pliensbachian.

The contourites in Mochras can be classified as mixed calcareous
Table 1
Comparison of the Walsh power-spectrum periodicities recognized from the occurrences of trace fossils with the orbitally-forced periodicities calculated by Berger (1977).

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
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<tr>
<td>Phycosiphon</td>
<td>115.4</td>
<td>94.4</td>
<td>114</td>
<td>94.4</td>
<td>112</td>
<td>Eccentricity</td>
</tr>
<tr>
<td>morphotype 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>95 bands</td>
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<tr>
<td>Phycosiphon</td>
<td>64.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Combined effect</td>
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<tr>
<td>morphotype 3</td>
<td>54.6</td>
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<td>59-64</td>
</tr>
<tr>
<td>Phycosiphon</td>
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<td></td>
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<td></td>
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<td>Obliquity</td>
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<td>morphotype 4</td>
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<td></td>
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<td>40-42</td>
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<td>Schaubcylindrichnus</td>
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<td></td>
<td></td>
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<td>29-30</td>
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<tr>
<td>Thalassinoides</td>
<td>19</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>22-24 Precessional</td>
</tr>
<tr>
<td>Lamination</td>
<td>18.5</td>
<td>17</td>
<td>14.4; 15.5; 16.4</td>
<td>16-17</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orbital cycles [kyr]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2
Relative sedimentation rate (based on ichnology), number and average duration of 4th order (precession) cycles, number of 3rd and 2nd order cycles in the Pliensbachian stage of the Mochras core. Note fluctuation of average duration of 4th order cycles.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Ammonite Zone</th>
<th>Thickness [m]</th>
<th>Relative duration – based on ichnology (Myr)</th>
<th>Sedimentation rate -cm/1000 years</th>
<th>Number of 4th order cycles (precession-dominated)</th>
<th>Average duration of 4th order cycle</th>
<th>Number of 3rd order cycles (short eccentricity – 100 kya)</th>
<th>Number of 2nd order cycles (long eccentricity – 400 kya)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pliensbachian</td>
<td>spinatum</td>
<td>37</td>
<td>0.8</td>
<td>4.6 cm/1kyr</td>
<td>31</td>
<td>25.8 kyr</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>margaritatus</td>
<td>110</td>
<td>2.33</td>
<td>4.7 cm/1kyr</td>
<td>103</td>
<td>22.3 kyr</td>
<td>23.3</td>
<td>5.5</td>
</tr>
<tr>
<td></td>
<td>davoei</td>
<td>24</td>
<td>0.47</td>
<td>5.1 cm/1kyr</td>
<td>23</td>
<td>21.7 kyr</td>
<td>4.7</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>ibex</td>
<td>90</td>
<td>2.0</td>
<td>4.5 cm/1kyr</td>
<td>85</td>
<td>23.5 kyr</td>
<td>20</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td>jamesoni</td>
<td>126</td>
<td>2.8</td>
<td>4.5 cm/1kyr</td>
<td>113</td>
<td>24.8 kyr</td>
<td>28</td>
<td>6.7</td>
</tr>
</tbody>
</table>

Fig. 11. Walsh power-spectra of the time series based on occurrences of respective trace fossils: A – Phycosiphon morphotype Ph1; B – Phycosiphon morphotype Ph3; C – Phycosiphon morphotype Ph4; D – Thalassinoides.
Fig. 12. Overlapping Walsh power-spectra of the time series based on occurrences of respective trace fossils and lamination: A – *Phycosiphon* morphotype Ph1 and Ph3; B – *Phycosiphon* type Ph4 and Thalassinoides; C – *Schaub cylindrichnus* and lamination.
biogenic-clastic contourites, the most frequent contourite facies in the modern oceans (Faguere and Mulder, 2011). Hemipelagic mudstone, wackestone/siltstone and coarser packstone and grainstone of the Mochras section are usually poorly sorted or impure and appear to be structureless or mottled. The mottling results from intense bioturbation driven by the organic-matter supply from bottom currents (see Miguez-Salas et al., 2020 for a Miocene example). However, in less strongly bioturbated sections primary sedimentary structures are visible and they are mostly represented by current structures such as planar parallel lamination, low angle cross-lamination, starved ripples, in places subtle erosive bases, and gradational (rarely sharp) normal- and inverse-grading bed transitions, similar to cases studied by Shanmugam (2000) and Knapp et al. (2017). Stagnant conditions or very slow currents are interpreted to have allowed vertical settling of the suspended particles from the nepheloid layer (Ewing and Thorkildsen, 1965; Mulder et al., 2003), producing mottled mudstone (Figs. 3B, 9E) or laminated mudstone-claystone (Figs. 3B1, 9A, B), where the grain-supported laminae are interpreted to be the result of very weak contour currents that winnowed out clay-sized sediment (e.g. Shanmugam, 2000). Periodically higher bottom-current velocities led to deposition of silt or sand layers with planar or low-angle cross-bedding, produced by bedload transport (Figs. 5B, C, 9C, D, H). The concentrations of plant remains – a feature particularly of the Pliensbachian in Mochras (Ullmann et al., 2021) – indicates pyrothermal pulses in connection with fluvial discharges in the vegetated hinterland. Relatively weaker bioturbation can be attributed to oxygen depletion or high sedimentation rate (Stow and Faugères, 2008). Stronger bottom currents also do not favour preservation of biogenic structures (Tucholke et al., 1985).

Fully developed bidirectional intervals in the Mochras section (Figs. 3B, 5A, B, 7) correspond to a standard contour sequence (Faguere et al., 1984; Stow and Holbrook, 1984; Stow et al., 2002; Faugères and Stow, 2008; Hünke and Stow, 2008; Mulder, 2011; Rodriguez-Tovar and Hernández-Molina, 2018). The standard model was enhanced by introduction of interval divisions (C1 to C5; Stow et al., 2002; Stow and Faugères, 2008, their Fig. 13.9) and recognition of variations within partial contourite sequences (Rebesco et al., 2014; Shanmugam, 2017), corresponding to observations in the Mochras profile (Figs. 3B, 5–7) where most frequent vertical sequences consists of lithofacies types 1–2–3–4–5–6 (in coarsening-upward order) and subsequent fining-upwards couplet composed of 5–4 lithofacies types. The fining-upward phase of the fully developed cycle is usually thinner and incomplete (Figs. 3B, 5A–C, 7).

Additionally, observed types of more or less complete cycles were controlled by fluctuating sedimentation rate and, to a lesser extent, by carbonate dissolution, calcite replacement and cementation processes (Figs. 5D, 6A) at early diagenetic stage, possibly resulting from the degradation of organic matter and the associated reduction of sulphate, as evidenced by the occurrence of pyrite framboids (Rühl et al., 2016). Periods of stronger currents marked by sharp surfaces (Fig. 10N) and coarser material such as shell debris are rare, occurring mostly between 900 and 940 m (gibbous Subzone). In such cases the bidirectional grading cycles are often incomplete, lacking upper parts (top-cut-out cycles; see Figs. 5D, 7) or lower parts (base-cut-out cycles; see Figs. 5C, 7, 10N).

4.1.2. Ichnodiversity

Appearances of trace fossils show cyclic character, more or less continuous with frequent lithological changes and sedimentary cycles. Diffused shape of trace fossils indices of soft-bottom condition (Fig. 9F), and domination of opportunistic, r-selected Phycosiphon, mostly simple tiering, scarcity of highly-specialized, K-selected forms, all indicate generally high sedimentation rate associated with instability of substrate and benthic food availability (delivered either by currents or suspension fallout), interrupted by interim oxygen-depleted, more stagnant conditions – usually associated with darker sediments and lamination. The other end of the spectrum is characterized by higher substrate stability (stiffer conditions), diminishing sedimentation rate, continuous delivery of suspended nutrients by currents, and better bottom oxygenation leading to a more complex tiering under equilibria (Taylor et al., 2003). A high degree of bioturbation (Figs. 3B, 5A, D, 6A, 9F, I, L, M) is characteristic for contourites due to additional food supply and faunal abundance (Wetzel et al., 2008). In agreement with Caswell and Frid (2017), changes in community composition are usually linked to local redox conditions, whereas changes in populations of r-selected opportunists are driven by primary productivity. Because suspended organic matter is often adsorbed onto suspended clay minerals (Mayer, 1994), contour currents supply food to deep-marine benthic organisms (Thistle et al., 1985). If the vertical particle flux is supplemented by lateral current-carried supply, the benthos exhibits a higher biomass, population density, and resulting degree of bioturbation than on adjacent tranquil sea-floor fuelled only by a vertical flux of organic matter that decreases exponentially with water depth (Gess, 1986; Wetzel et al., 2008). As the whole Pliensbachian section is strongly dominated by Phycosiphon (Ph2), any lack of this morphotype is noteworthy as it indicates relatively rare, exceptionally unfavourable conditions, most likely associated with intermittent more stagnant conditions and oxygen depletion (occuring more frequently only in a few intervals: Sinemurian–Pliensbachian transition (lowermost jamesoni Zone), the mid-ibex Zone, the lower stokesi Subzone and the Pliensbachian–Toarcian transitional interval (uppermost spinatum Zone). Commonly, in such sections Phycosiphon (Ph3) appears (colonization after meiofauna motting) as the first recognizable trace fossil, before Ph2 and Ph1 return.

4.1.3. Cyclicity of sedimentation

Distinction of cycles identified in this paper is based mainly on grain size and ichnological features and their lower boundaries are placed in the fine-grained, mottled or laminated micritic mudstone (lithofacies 1 and 2; see Fig. 7). Primary sedimentary structures are commonly obliterated by bioturbation, so these play a subordinate role in determining sedimentary cycles. Both the fully-developed (bidirectional), and the incomplete lithological couplets with their ichnological content, constitute the 4th order cycles, basic “building blocks” of the hierarchical order of cycles in Mochras. These 4th order cycles are arranged in higher hierarchical successions, usually containing four 4th order cycles. The higher, 3rd order, cycles have different appearance depending on their position in the profile: in the Jamesoni to lower ibex Zone and lower margaritatus (lower stokesi Subzone) they usually start with laminating and end with denser Schaubcylindrichnus, while in the upper ibex and daveoi zones, the upper margaritatus Zone (subnodosus-gibbosus sub-zones) and spinatum Zone, they often start with Phycosiphon (Ph3) and end with denser Thalassinoides (in the uppermost spinatum Zone also Trichichnus). In some cases, larger deposit feeder structures (Phymatoderma, Rhizocorallium) or dwelling/suspension feeders’ structures (Siphonichnus, Arenicolites, Skolithos) appear in the upper parts of these cycles, interestingly in a few cases also in intervals indicating features of oxygen depletion in sediment (e.g. laminations at the depth 1245 m). This observation probably points to an episodic delivery of oxygen to the bottom waters (likely by currents) that allowed temporary development of bottom-dwelling fauna. With respect to behavioural groups, suspension feeders are not abundant, probably as their filter apparatus can easily be plugged when the mineral suspension concentration is high (Pierikowski, 1985; Thistle et al., 1991).

The next in hierarchy are 2nd order cycles, composed of 4 3rd order cycles – in most cases upper boundaries of these cycles are marked by the dwelling structures cf. Polykladichnus (in 9 cases) or by Skolithos, Arenicolites, Siphonichnus (11 cases), which characterise 20 of 21, 2nd order Pliensbachian cycles. Tops of the 2nd order cycles are marked also by increased (in relation to neighbouring beds) CaCO3 content (Figs. 1, 2). In the Mesozoic, periods of maximal eccentricity are often associated with annually dry climates, disturbed by short periods of intensive summer rainfalls and storms, alternately in the Northern Hemisphere.

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and the Southern Hemisphere (Bouilla et al., 2011; Martínez and Dera, 2015), which translated into oceanographic circulation and observed ichnological changes and appearances of dwelling structures. The 2nd order (long eccentricity) cycles of 405 kyr duration are considered as stable over hundreds of million years (Kent et al., 2018).

The longest, 1st order cycles are characterized by more general changes – the most visible is ichnodiversity and abundance of trace fossils, which increase in two longer sections, in the higher Jameson to lowermost ibex Zone, and then particularly in the middle margaritatus to lower spinatum zones. Recurrent higher ichnodiversity (excluding Trichinichus) is not associated with frequency of current structures (and bottom oxygenation), grain size or TOC content (Figs. 1, 2), but with higher content of CaCO3 in relation to siliciclastic clay mineral component (Figs. 1, 2; Ruhl et al., 2016). Interestingly, higher ichnodiversity is also associated with clay mineral composition (Deconinck et al., 2019), namely with higher content of smectite and mixed layer (smectite/illite) clay minerals, while sections enriched in kaolinite generally show beside lower abundance of trace fossils and more common lamination) a lower ichnodiversity. The relationship may be explained by the influence of expandable clay minerals (smectite and smectite/illite) on reduction of pore space and in consequence limitation (although not elimination) of the Phycosiphon trace makers, which are dependent on oxygen acquired from pore water. Only with limited competition from the Phycosiphon trace makers could other trace makers develop in a higher diversity and quantity. The 1st order cycles are divided by intervals showing oxygen depletion in bottom sediment (registered also by HI index; see Storr et al., 2020), more frequent appearances of lamination, carbonate depletions, oxygen deficiency resulting in Phycosiphon crises, and numerous occurrences of Trichichus representing filamentous mat-forming, sulphide-oxidizing bacteria. Such intervals appeared four times: in the Sinemurian–Pliensbachian transition zone, the mid-ibex Zone, the upper stokesi Subzone (c. 985 m), and at the Pliensbachian–Toarcian transition, although the latter level is distinctive with a dominance of Trichichus and poor diversity in benthic foraminiferal morphgroups, dominated by opportunista epifaunal forms of the genus Reinholdella (Rodríguez-Tovar et al., 2020). The topmost Pliensbachian section is characterized by abundance of mixed layer clay minerals and presence of berthierine, which has been attributed by Deconinck et al. (2019) to sea-level fall, climate cooling and enhanced physical weathering on the land, although according to Ruubsam et al. (2020), the Pliensbachian-Toarcian transition was characterized rather by elevated temperatures. Although bottom-life crises at the 1st order cycle boundaries occurred four times in Pliensbachian as described in the present study, the Pliensbachian-Toarcian crisis was exceptional in its severity and continued to the earliest Toarcian (Dera et al., 2011; Xu et al., 2018). Most likely, the benthic crisis was connected with general, exceptional stagnation of circulation through the Laurasian Seaway (and the Cardigan Bay Strait) at that time (Van de Schootbrugge et al., 2019).

The major clayey, carbonate-free or carbonate-depleted intervals with marked Phycosiphon crises (oxygen depletion) record major sedimentary changes, which seem to occur in a long-term, but approximately regular manner. Oxygen deficiency can be attributed to diminishing current intensity, but also to number of other related or independent causes, including sea-level, acidification of oceans and dissolution of CaCO3 related to carbon cycle (e.g. Lord et al., 2016). According to Ayrcani et al. (2018), highstand and transgressive systems tracts in contourites are both represented by dominantly massive mudstone, sparse bioclastic and high bioclastic features (or at least two of them) occur in the Sinemurian–Pliensbachian transitional section, the mid-ibex Zone, the lower stokesi Subzone and the Pliensbachian–Toarcian transitional section (Figs. 1, 2). However, the mid-ibex Zone retains significant CaCO3 content and the lower stokesi Subzone and the upper spinatum Zone are associated with regressions and relative sea-level fall in UK (de Graciansky et al., 1998; Hesselbo, 2008; Deconinck et al., 2019). Thus, changes in oceanic circulation, connected with major climate and carbon cycle changes, would be a more likely scenario than sea-level rise. Sea-level rise could possibly be a significant additional factor in the beginning of Pliensbachian, as the marked sea-level rise is widespread and documented not only in UK, but also in Germany, Poland and Scandinavia (Sellwood, 1972; de Graciansky et al., 1998; Hesselbo, 2008; Pienkowski, 2004; Barth et al., 2018).

The results obtained allow interpretation of palaeoceanographic circulation in Pliensbachian times. According to Shanmugam (2017), the facies term “contourite” is appropriate only for deposits of thermohaline-driven geostrophic contour currents in deep-water environments. However, according to other authors, a wide spectrum can be expected, as such currents are not confined to a deep sea and have been associated with either deep (e.g. Borisov et al., 2013; Martos et al., 2013), intermediate (e.g. Bein and Weiler, 1976; Van Rooij et al., 2010; Rebesco et al., 2013) or shallow (epicontinental) water masses (e.g. Vandorpe et al., 2011). Calcareous deposits (loosely clasts) from the North Sea region (for the Late Cretaceous case) suggest that deposition was influenced by geostrophic currents in an epeiric sea with water depths of 500–800 m, where the sea floor had a considerable relief, commonly of more than a hundred metres amplitude, comprising mounds, drifts, mounds and channels (Surlyk and Lykke-Andersen, 2007; Esmerode et al., 2008). The margins of the basin feature broad moat/trough-like channels that are juxtaposed next to accretionary forms of detrital carbonate and marl.

Thermohaline circulation in the deep ocean basins is driven by density differences between water masses due to variations in water temperature and salinity (see McCave et al., 1995 for a Quaternary example). Recently, the thermohaline circulation forms a large network of slowly moving currents flowing at a few centimetres per second, only periodically interrupted by higher current velocities and dominant erosion processes (Faugères and Mulder, 2011). Contour currents may carry in suspension muddy-silty fines and particulate organic matter, forming significant nepheloid (turbid) bottom water bodies (McCave, 1985, 2008; Rebesco et al., 2014). The Pliensbachian profile in Mochras is interpreted to represent such calcareous muddy and silty contourites, commonly interbedded with calcareous sandy contourites containing reworked shallow-water carbonate debris from off-shelf or off-ramp supply with variable admixture of siliciclastic material. The depositional rate at Mochras was stable and relatively high, probably due to biogenic input from shallower zones (carbonate platform), moderate or slow current velocity and weak erosion. Terrigenous (clays and fine silts) or carbonate (biogenic fragments) particles supplied by bottom currents may carry in suspension a considerable amount particulate organic matter, supplying food to deep-marine benthic organisms (Thistle et al., 1985). Likely, the deep-water circulation in the elongated, NE-SW trending Cardigan Basin (Fig. 2) was forced by enhanced geostrophic bottom-water circulation – i.e. cooler and denser waters flowing from the Boreal Sea, around the Shetland Platform-Scottish Landmass island, towards the south, to the Peri-Tethys/proto-Atlantic, approximately parallel to the bathymetric contours of the margin of the Welsh Platform (Figs. 1, 2).

Reconstructions of circulation that rely on numerical models (Bjerrum et al., 2001; Dera and Donnadieu, 2012; Ruvalcaba Baroni et al., 2018) have reached remarkably consistent conclusions about the predominant southwards flow from the Arctic into the Tethys through the Laurasian Seaway during Early Jurassic. The Cardigan Bay Strait, linking cooler and shallower waters of Boreal Sea and Scottish-English-Welsh archipelago with warmer and deeper waters of Peri-Tethys (Figs. 1, 2), was then situated to sustain a continuous thermohaline-driven geostrophic contour current circulation between these two marine realms. Thermohaline-driven geostrophic contour currents usually involve significant water mass over large areas and persist for very long time intervals of up to millions of years and over large areas (Shanmugam, 2008, 2017), which corresponds to the observed continuity of Early Jurassic sedimentation in Mochras. These stable flow conditions were punctuated by more sluggish currents or stagnant conditions.
Ruvalcaba Baroni et al. (2018) indicate that, under high atmospheric pCO₂, palaeoceanographic conditions in the Laurasian Seaway were dominated by strong clockwise circulation in the Tethys bringing warm saline waters onto European shelves. This strong circulation may have diminished the effects of flow through the Laurasian Seaway. Dera and Donnadieu (2012) concluded, that warming events, demise of polar sea ice, and stronger high-latitude continental runoff rates could result in a thermohaline circulation collapse and bottom oxygen depletion, also in ice, and stronger high-latitude continental runoff rates could result in a diminished the effects of flow through the Laurasian Seaway. Dera and

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would be of duration c. 2.5 Myr, corresponding to the period of around 2.4 Myr eccentricity modulation related with Mesozoic greenhouse sequences, caused by Earth-Mars secular resonance (Hinnov, 2000; Laskar, 2015). These ~2.5 Myr cycles are characterized by long-term shifts in CaCO$_3$ content and ichnodiversity, correlated with the variations in the opposing proportions of smectite and kaolinite. The kaolinite-rich intervals reflect an intensification of hydrolysis and an acceleration of the hydrological cycle, while the smectite-rich intervals indicate a more seasonally arid climate (Deconinck et al., 2019). In turn, kaolinite-rich intervals were connected with high atmospheric pCO$_2$ higher temperatures and influx of Tethyan warm saline waters onto European shelves (Ruvalcaba Baroni et al., 2018), diminishing flow through the Cardigan Bay Strait, which caused oxygen deficiency and reduced ichnodiversity at the "grand cycle" boundaries. On the other hand, lower pCO$_2$ and cooler conditions favoured intensification of currents, higher oxygenation and higher ichnodiversity, additionally enhanced by limited domination of Physcosphon, mainly caused by presence of smectite. It would indicate that changes of ichnodiversity was mainly controlled by orbitally-forced current intensity, where most general changes were associated with "grand eccentricity cycles" of ~2.5 Myr duration.

Diminished current flow/oxygen depletion in the Cardigan Bay Strait appears particularly severe at the very end of Pliensbachian (continuing to the beginning of Toarcian tenuicostatum Zone), but also the beginning of Pliensbachian is characterized by relatively more marked oxygen depletion and Physcosphon crisis, compared to the other (c. 2.5 Myr) "grand eccentricity cycles" boundaries in Pliensbachian. The mentioned above "wandering frequency" fluctuation would span ~9 Myr. As we have only one such sequence, it is not clear, if this represents a real cycle. However, existence of c. 9 Myr eccentricity cycle was postulated by Martinez and Dera (2015), based on analysis of orbital pacing of carbon cycle during the Mesozoic (spanning c. 70 Myr of Jurassic and Cretaceous periods). According to those authors, this orbital forcing affected carbon transfers by modulating the hydrological processes and sea-level changes, being an important metronome of the greenhouse climate dynamics. However, this question remains open until a longer time interval in Mochras and Prees is studied, particularly as Martinez and Dera (2015) did not see such a cycle specifically in Pliensbachian, attributed to major palaeoenvironmental disturbances or a chaotic transition affecting this cycle.

### 4.3. Duration of the Pliensbachian and the ammonite biozones based on ichnological astrochronology

The new results (Table 2) allow a re-estimation of the duration of Pliensbachian stage at about 8.4 Myr, which is shorter by ~0.3–0.4 Myr compared to the results obtained from elemental Ca content (8.7 Myr - Ruhl et al., 2016) and $\delta^{13}$COC (8.77 Myr - Storm et al., 2020). Results obtained from ichnological and sedimentological signals by counting successive 4th, 3rd and 2nd order cycles (interpreted respectively as precession/obliquity, short eccentricity, long eccentricity) (Figs. 3, 4, 11, 12; Tables 1–3) also show much more stable sedimentation rate in successive ammonite zones than the results based on elemental Ca or $\delta^{13}$COC. Astronomical durations for the ammonite biozones are: $jamesoni$ Zone = 2.8 Myr, $ibex$ Zone = 2.0 Myr, $davoei$ Zone = 0.47 Myr, $margaritatus$ Zone = 2.33 Myr and $spinatum$ Zone = 0.8 Myr. The $jamesoni$ Zone is slightly longer (by ~100 kyr) than determined by Ruhl et al. (2016) and more significantly longer than the value of ~2.43 Myr obtained by Storm et al. (2020). The $ibex$ Zone (2.0 Myr) and $davoei$ Zone (0.47 Myr) would be slightly longer than 1.8 Myr and 0.45 Myr, respectively (by Ruhl et al., 2016) or 1.76 Myr and 0.4 Myr (by Storm et al., 2020). On the other hand, duration of the $margaritatus$ Zone based on ichnological cycles (2.33 Myr) is shorter in comparison to 2.4 Myr (Ruhl et al., 2016) or 2.69 Myr (Storm et al., 2020). The most significant difference regards the $spinatum$ Zone, which is much shorter than the values provided by Ruhl et al. (2016) and Storm et al. (2020), i.e. 1.4 and 1.45 Myr, respectively. Consequently, results obtained by Ruhl et al. (2016) and Storm et al. (2020) imply radically slower sedimentation rate (~2.6 cm/kyr) for the $spinatum$ Zone in comparison to the older biozones (4.1–6.0 cm/kyr). This difference cannot be explained by conspicuous changes in the sedimentary environment; only the uppermost few metres of the $spinatum$ Zone section shows marked changes in lithology and ichnology, associated with carbonate crisis and oxygen depletion and possible changes in sedimentary rate. As shown by Storm et al. (2020), the $\delta^{13}$COC signals in this zone are not unequivocal when we adopt an option of two long-eccentricity cycles in the $spinatum$ Zone (Storm et al., 2020; Fig. 4, Table 1), calculation of the $spinatum$ Zone duration and total duration of Pliensbachian would be approximately consistent with results obtained from ichnological signal. Radiosotopic dates from the upper Pliensbachian in Oregon, United States (De Lena et al., 2019), are correlated to the $margaritatus$ and $spinatum$ zones using good ammonite-based constraints, albeit primarily for the North American zonal scheme. These dates range from 186.96 ± 0.07 Ma in the kunae Zone (i.e. lower $margaritatus$ Zone) to 184.02 ± 0.05 Ma, which lies above the highest ammonites of the carlottense Zone (i.e., approximately upper $spinatum$ Zone or lower Toarcian tenuicostatum Zone). About 3 Myr duration of $margaritatus$ and $spinatum$ zones combined (with approximately a 2 Myr long $margaritatus$ Zone and a 1 Myr long $spinatum$ Zone) corresponds to our estimates of duration of these two zones (Table 2). The ichnological cycles are quite consistent with those interpreted by Ruhl et al. (2016) and Storm et al. (2020) for the $jamesoni$, $ibex$ and $davoei$ zones, with offsets usually less than 100 kyr (one short-eccentricity cycle). More discrepancies with cycles based on Ca appear in $margaritatus$ Zone and we suggest this results from common CaCO$_3$ cementation producing numerous diffuse concretions observed in this zone. Rapid decrease of CaCO$_3$ content in the $spinatum$ Zone also negatively affects the reliability of the Ca elemental signal for cycle analysis. The ichnological signal (supported by high-resolution lithological, sedimentological and clay mineral data) may thus be the most reliable source of the orbital forcing signal, providing also a better fit to the ~2.5 Myr 1st order "grand" cycles.

### 5. Conclusions

1. An integrated ichnological-sedimentological study of the Pliensbachian calcareous-siliciclastic hemipelagic/contourite deposits in
Mochras helps facilitate understanding of contourite deposition processes in a long period of geological time and its ichnodiversity. The current study adds the most expanded ichnological and sedimentary record of contourite deposits, giving new information on the sedimentary dynamics, variability of oceanographic history, and basin interconnectivity.

2. **Phycosiphon** is by far the most common ichnotaxon and this is a new observation, because in the literature to date this taxon was considered sporadic in contourite deposits. Ichnological signals point to a common and strongly repetitive mechanism driving the observed fluctuations in benthi conditions, which is indicated by harmonic analysis and distinction of four hierarchical orders of cycles attributed to orbital forcing.

3. Long-term climate changes had consequences for deep-sea sediments at Mochras as increased content of expandable clay minerals (smectite and mixed-layer clay minerals) reduced pore space, thus limiting development of *Phycosiphon* trace makers and allowing other organisms which were less dependent on pore-space oxygen, to compete with otherwise dominating *Phycosiphon* trace makers.

4. The ichnological record shows a relatively stable sedimentation rate of 4.5–5.1 cm/kyr through the entire Pliensbachian stage.

5. Ichnological results (both macroscopic observations and harmonic analysis) support that the cycles that appear in the Mochras logs, previously indicated by Ruhl et al. (2016) and Storm et al. (2020) are astronomically forced, although their frequency through individual zones are refined and a new calibration of duration of Pliensbachian (c. 8.4 Myr) and successive ammonite zones is proposed.

6. Orbital forcing has set the timing for cyclic ichnological records, with the amplifying feedback of climate-related palaeoceanographic variations of thermohaline-driven geostrophic contour currents circulating between Boreal ocean and Peri-Tethys, through the Cardigan Bay Strait.

7. Contourites of the Cardigan Bay Basin provide essential information on ocean circulation, bottom life conditions and climate changes, which can be extracted using sedimentological and ichnological methods. The Cardigan Bay Strait played an important role in the Early Jurassic (at least Pliensbachian) oceanic circulation as a major link between the northern and southern parts of the Laurasian Seaway, and in general between the Boreal and Peri-Tethys domains.

8. Ichnological records in continuous hemipelagic successions seem to compete with otherwise dominating *Phycosiphon* trace makers.

9. Orbital forcing has set the timing for cyclic ichnological records, with the amplifying feedback of climate-related palaeoceanographic variations of thermohaline-driven geostrophic contour currents circulating between Boreal ocean and Peri-Tethys, through the Cardigan Bay Strait.

10. Orbital forcing has set the timing for cyclic ichnological records, with the amplifying feedback of climate-related palaeoceanographic variations of thermohaline-driven geostrophic contour currents circulating between Boreal ocean and Peri-Tethys, through the Cardigan Bay Strait.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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