Palaeogeography, Palaeoclimatology, Palaeoecology 449 (2016) 246–254

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Palaeobiology of *Schaubcylindrichnus heberti* comb. nov. from the Lower Jurassic of Northeast England

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ARTICLE INFO

Article history:
Received 17 November 2015
Received in revised form 20 January 2016
Accepted 9 February 2016
Available online 17 February 2016

Keywords:
Palaeophycus heberti
Schaubcylindrichnus
Trace fossil
Burrow wall
Palaeobiology
Three-dimensional reconstruction

ABSTRACT

The distinctive species of *Palaeophycus* known as *Palaeophycus heberti* is characterised by its thick burrow wall and passive burrow fill. This species is typically associated with intensely bioturbated, heterolithic sandstones and mudstones deposited in shoreface to offshore marine palaeoenvironments. Three-dimensional analysis of specimens attributed to *P. heberti* based on closely-spaced serially ground surfaces has revealed a number of hitherto unknown morphological elements more comparable to the ichnogenus *Schaubcylindrichnus*, thereby creating *Schaubcylindrichnus heberti* comb. nov. *Schaubcylindrichnus* burrows are typically passively filled, and have a thick burrow wall composed of sand-rich annular rings. The three-dimensional reconstructions importantly demonstrate that the gross morphology is a broad-open U-shape, which is inconsistent with the ichnogeneric diagnosis of *Palaeophycus. S. heberti* differs from all other species of *Schaubcylindrichnus* in that the burrow wall is mineralogically heterogeneous rather than purely quartzose; the ichnogeneric diagnosis is thus emended to accommodate *S. heberti.*

1. Introduction

The ichnogenus *Palaeophycus*, Hall, 1847 is considered to be a sand- or mud-lined, cylindrical – broadly bedding parallel – burrow with a passive fill. This morphologically simple ichnogenus has been the source of some confusion since its original description due to: 1) its similarity to other simple tubular burrows; 2) confusion surrounding its gross morphology; and 3) disagreement concerning which morphological characteristics should have greatest taxonomic importance (Fillion and Pickerill, 1990a; Keighley and Pickerill, 1995). *Palaeophycus*, like many ichnogenera, was originally described as a plant genus, but has since been shown – by study of syntype material – to be a trace fossil (Osgood, 1970; Keighley and Pickerill, 1995). The primary ichnotaxobase used by most modern workers to diagnose *Palaeophycus* is the presence of a burrow wall (Pemberton and Frey, 1982). Variations in the thickness and composition of the burrow wall, as well as differences in ornamentation, have led to the creation of several ichnospecies of *Palaeophycus*. Of the currently described ichnospecies *Palaeophycus heberti*, Saporta, 1872 is distinguished from all other ichnospecies by its much thicker sand-rich wall. The type material of *P. heberti* was originally described as *Siphonites heberti*, but was subsequently synonymised with *Palaeophycus* (Saporta and Marion, 1883; see review in Knaust, 2015). The mode of life of the *P. heberti* trace-maker is similarly in dispute, but most recently it has been considered to be the dwelling structure of a predaceous or suspension feeding worm (Pemberton and Frey, 1982; MacEachern et al., 2005; Gani et al., 2005). The reported palaeoenvironmental range of *P. heberti* is from shallow marine to continental settings, but this ichnotaxon is most typically associated with intensely bioturbated, heterolithic sands and muds of low to high-energy shoreface to offshore environments (Frey and Howard, 1990; Buatois and Mángano, 2011; Rajkonwar et al., 2013). Non-marine examples (Melchor et al., 2006; Tanner et al., 2006; Retallack, 2009) are in need of careful assessment and comparison with *Beaconites capronus* (cf. Boyd and McIlroy, 2016).

This study aims to morphologically characterise well-preserved specimens of *P. heberti* from hand-samples that originated in strata rich in *Phoebichnus trochoides* (cf. Evans and McIlroy, 2015). *P. trochoides* is a much larger trace fossil than *P. heberti* with similarly thick sand-lined burrow walls but, unlike *P. heberti*, has a central boss from which numerous branches radiate. The similar wall architecture of the two associated burrows leads us to consider the possibility that *P. heberti* might be burrows of the juvenile form of the *P. trochoides* trace-maker. This is important since assemblages of *P. trochoides* always have radial burrows of the same diameter (approx. 1–2 cm), and no ontogenetic series has been documented (Evans and McIlroy, 2015).

The specimens selected for this study were collected in order to investigate the full three-dimensional morphology and palaeobiology of *P. heberti* in *P. trochoides*-bearing strata. Three-dimensional reconstructions were undertaken through the creation of closely spaced serial surfaces that were precisely ground using a CNC milling machine, and the creation of digitally reconstructed whole-rock models (Bednarz et al., 2015). Previous morphological descriptions of *P. heberti* have been based on the study of hand specimens without the benefit of a full

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http://dx.doi.org/10.1016/j.palaeo.2016.02.020
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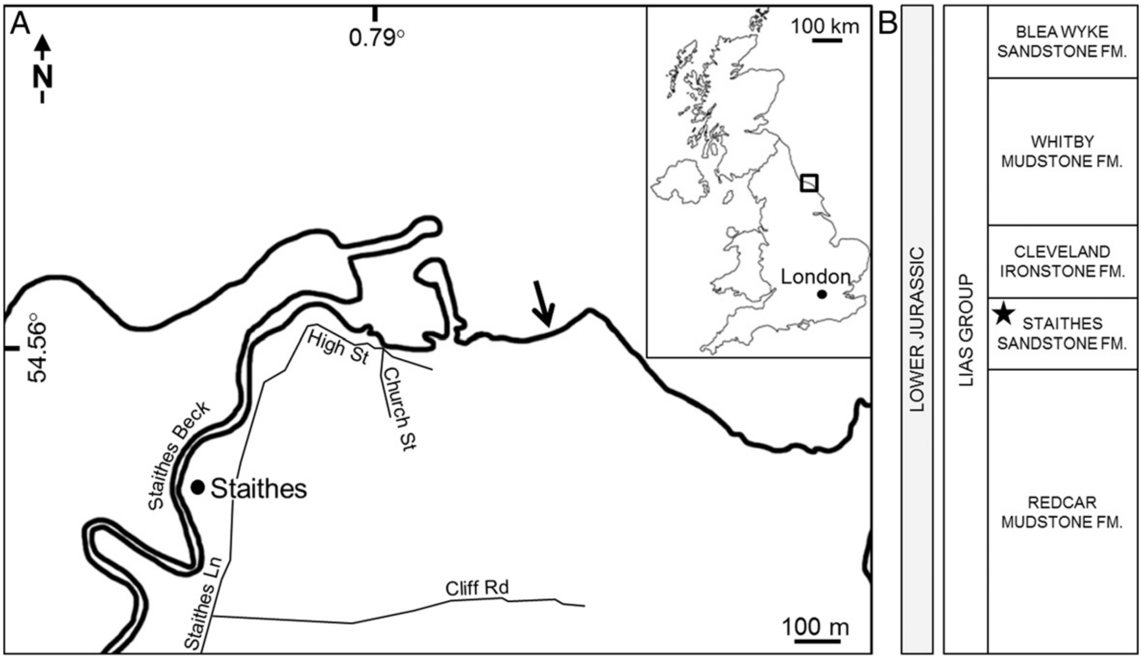

Fig. 1. Sample collection site and generalised stratigraphic column. A: Map of field location at Staithes, UK. Arrow shows approximate collection location of the samples. B: Stratigraphic column of the Lias Group showing the stratigraphic level studied. Double column.

three-dimensional dataset. The advantage of the methodology employed herein is that the burrow can be studied in the context of the reconstructed host sediment, and subtle morphological details – that can be used to infer organism-sediment interactions – can be examined in three dimensions. The serial grinding method, while destructive, also allows a detailed and direct study of the composition and structure of burrow walls and burrow fill at a resolution that is not easily attained by non-destructive methods such as computed axial tomographic (CT) scanning (e.g. Dufour et al., 2005; Herringshaw et al., 2010), or magnetic resonance imaging (MRI) (e.g. Gingras et al., 2002).

2. Geological and palaeoenvironmental settings

The samples for this study were collected from the Lower Jurassic Staithes Sandstone Formation of the Lias Group of the Cleveland Basin in northeastern England (Fig. 1). The Staithes Sandstone Formation is a net-upward fining succession rich in bioturbated silty sandstones, planar laminated to low-angle or hummocky cross-stratified fine-grained sandstones, and silty mudstones (Howard, 1985; Powell, 2010). Unbioturbated beds also occur throughout the sequence (Howard, 1985). The latter are most likely fluid mud deposits and suggest that the depositional setting may have been a storm-dominated delta, rather than a conventional shoreface (cf. Harazim and McIlroy, 2015). The presence of this sand-dominated succession between the Redcar Mudstone and the Cleveland Ironstone has been considered to be the result of relative sea-level fall, and concomitant increase in sand-supply (Hesslebo and Jenkyns, 1995; Powell, 2010).

3. Materials and methods

The collected samples were subjected to precision serial grinding and high-resolution digital photography. The hand-samples were encased in plaster and serially ground using a computer guided CNC milling machine. The two samples presented herein were ground at 0.1 mm increments. Each ground surface was consecutively labelled, wetted with oil to enhance contrast, and photographed under identical lighting conditions. The collection of precisely spaced, high-resolution, photographic images allows closer examination of the composition and structure of the wall and infilling sediment and, thus, more detailed interpretation of organism-sediment interactions. The successions of images were imported into VG Studio MAX producing whole rock models of the samples (see Bednarz et al., 2015 for full methodology). The modelling software enables the whole-rock models to be viewed at any angle and cut in any direction to create any number of cross-sections through the trace fossil to aid in understanding relationships between the burrows and their host sediment.

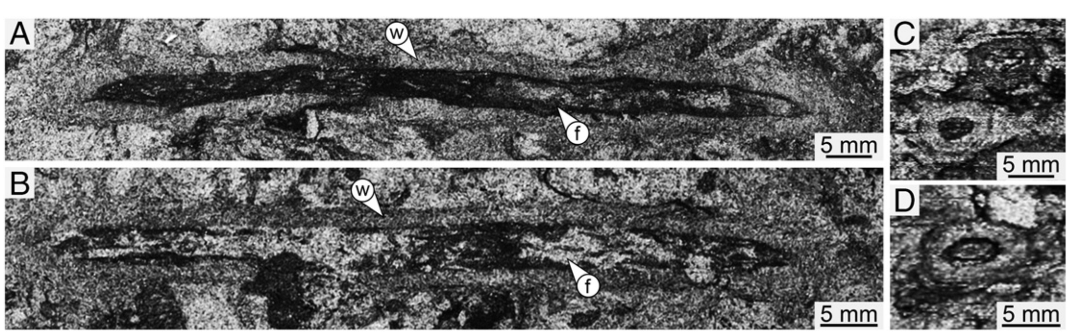

Fig. 2. Cross-sections through sand-walled burrows showing the thick wall (w) and passive fill (f). A and B: Horizontal longitudinal cross-sections with lithologically variable passive burrow fills (f). C and D: Transverse cross-sections of the same burrows showing the variability in cross-section shape from largely uncompressed circular in C, to elliptical and compacted in D. Double column.