

**Ichnology and Palaeobiology of *Phoebichnus trochoides*
and *Schaubcylindrichnus heberti* comb. nov.**

by

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Abstract

The three-dimensional reconstructions of *Phoebichnus trochoides* and *Schaubcylindrichnus (Palaeophycus) heberti* created as part of this thesis allow us to fully understand and characterize the three-dimensional morphology and palaeobiology of these common taxa. Three-dimensional reconstructions demonstrate that *P. trochoides* is a large stellate burrow composed of numerous long galleries produced by a deposit feeding organism. This study reports for the first time that the central zone is composed of stacked disk-shaped layers of highly bioturbated sediment, the radial burrows are composed of a sand-rich lining of pelleted annuli surrounding an active sand-rich fill, and the presence of subtle conical features above the radial galleries that are inferred to result from collapse cone feeding. Reconstructions of *heberti* demonstrate that the thick walled burrows are composed of sand-rich annular rings, are a broad U-shape, and may be either clustered or isolated. Our observations show that the morphology of *heberti* is inconsistent with the generic diagnosis of *Palaeophycus*, but is morphologically comparable to *Schaubcylindrichnus*, and is herein synonymised with *Schaubcylindrichnus* to create *S. heberti* comb. nov. The three-dimensional reconstructions have revealed a number of hitherto unknown morphological elements to both taxa which has facilitated new interpretations of the trace-makers behaviour. The data improves the taxonomic understanding of both *P. trochoides* and *S. heberti* which require significant taxonomic change and emendation of diagnoses at the species and genus level.

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Co-authorship Statement

This master's thesis is composed of four chapters. Chapter one is an introductory chapter that provides a review of the literature and sets out the objectives of the thesis. It is written by me, receiving editorial assistance from Dr. Duncan McIlroy. Chapters two and three are prepared in manuscript format and have been submitted to scientific journals. These chapters were a collaborative effort between myself, as a primary author, and Dr. McIlroy, as co-author. Chapter four provides a summary of the manuscript and unites the material in a cohesive way. I am the author of this chapter, having written its contents, receiving editorial assistance from Dr. McIlroy.

Chapter two entitled "Ichnology and Palaeobiology of *Phoebichnus trochoides* from the Middle Jurassic of north-east England" was published in *Papers in Palaeontology* in October 2015. The field location and samples were specified by Dr. McIlroy. Sample collection was completed by myself with the assistance of Dr. McIlroy, and though they are not authors, Chris Body and Mary Leaman with the assistance of Dr. Michael Garton also assisted in sample collection. I completed the sample preparation and processing with the assistance of Edgars Rudzitis. I was primarily responsible for data analysis and interpretation. Dr. McIlroy provided expert knowledge, editorial comments, and supervisory assistance during preparation of the manuscript.

Chapter three entitled "Palaeobiology of *Schaubcylindrichnus heberti* comb. nov. from the Lower Jurassic of North-Eastern England" was submitted to *Palaeogeography, Palaeoclimatology, Palaeoecology* in November 2015. The field location and samples

were specified by Dr. McIlroy. Sample collection was completed by myself and Dr. McIlroy. I completed the sample preparation and processing with the assistance of Edgars Rudzitis. I was primarily responsible for analysing and interpreting the data. I prepared the manuscript with editorial comments and supervisory assistance provided by Dr. McIlroy.

Chapter 1

Introduction and Overview

1.1 Introduction

Understanding the morphology and ethology of trace fossils is at the root of reliable integration of ichnology into sedimentological and palaeoenvironmental analyses (McIlroy 2004a; McIlroy 2008). Determining the complete morphology and palaeobiology of trace fossils, and their interactions with host sediment provides us with knowledge of palaeoenvironmental conditions and nutrient distributions that can be incorporated into facies analysis, and will help in reservoir characterisation studies.

This M.Sc. thesis aims to fully document the complete morphology, and organism-sediment interactions associated with two common Jurassic trace fossils, *Phoebichnus trochoides* Bromley and Asgaard 1972 and *Palaeophycus heberti* Saporta 1872 (Figs. 1.1, 1.2). This work will build on the palaeobiological interpretations of these taxa and affect how they can be integrated into palaeoenvironmental analyses. This is achieved through the creation of three-dimensional reconstructions of elements of the trace fossils along with whole-rock models of the trace fossils based upon precise serially ground surfaces through the trace fossil bearing samples. The morphological elements of the burrows and their relationships to the host sediment are analysed to provide insights into the palaeobiological and ethological mode of burrow construction. Recent studies have shown that, without complete three-dimensional characterisation, the full morphology and palaeobiology of ichnofabric-forming trace fossils is seldom fully understood (e.g. Bednarz and McIlroy 2009; Boyd *et al.* 2012; Bednarz *et al.* 2015; Leaman *et al.* 2015).

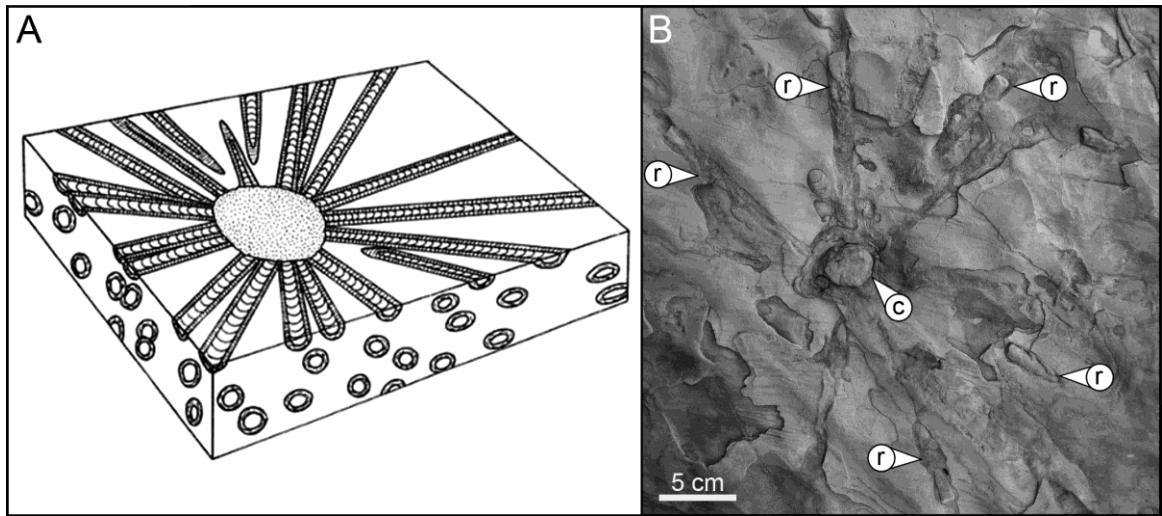


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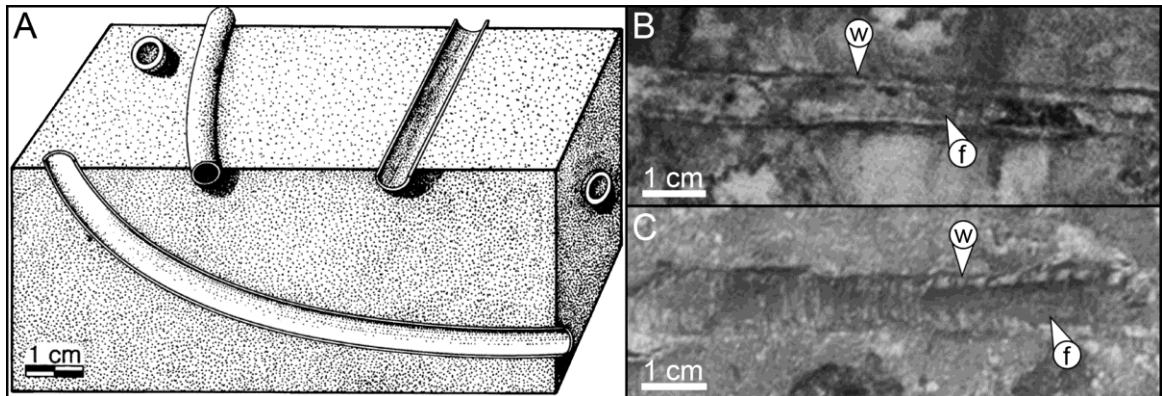


Fig. 1.2. Sketch and field photographs of *Palaeophycus heberti*. A: Sketch by Frey and Howard (1990) illustrating the form of *P. heberti* comprising thickly lined burrows orientated horizontal and oblique to bedding. B and C: Field photographs of bedding plane view of sandstone with *P. heberti* burrows exhibiting a thick wall (w) and fill (f).

The highly similar burrow wall structure and common association of *Phoebichnus trochoides* and *Palaeophycus heberti* burrows lead us to consider that *P. heberti* may be the burrows of the juvenile form of the *P. trochoides* trace-maker. The three-dimensional reconstructions of *P. trochoides* and *P. heberti* will help us to fully understand burrow morphology, assess the mode of feeding of these taxa, and will provide an aid in their identification in cross-section since synthetic cross-sections can be created at any orientation through the model. The outcomes of this research will serve as part of the growing library of ichnological characterisation that is integral to both the ichnological and sedimentological communities.

1.2 Methods

The project involved creating three-dimensional models and whole rock models of the trace fossils *Phoebichnus trochoides* and *Palaeophycus heberti*. From the reconstructed models and detailed serially ground surfaces we were able to define the full morphology of the trace fossils and interpret the palaeobiology of the trace maker. Outcrop samples of *P. trochoides* and were collected from Cloughton Wyke, UK and *P. heberti* samples were collected from Staithes, UK (Figs. 1.3, 1.4). The collected samples were subjected to precision serial grinding, high-resolution digital photography, and tomographic reconstruction (see Bednarz *et al.* 2015 for full methodology). The hand-samples were encased in plaster and serially ground, at precisely programmed increments, using a computer guided CNC milling machine. Each ground surface was consecutively labelled, wetted with oil to enhance contrast, and photographed under identical lighting conditions. This process enabled the collection of precisely spaced, high-resolution

images of consecutive ground surfaces through the trace fossils. Each surface was examined in detail to aid in understanding the subtle details of organism-sediment interactions and allowed a closer examination of the composition and structure of burrow linings and infilling sediment.

In modelling *Phoebichnus*, the burrows and related features were digitally selected from the serially ground surfaces using image processing software. The selected features were extracted from each surface and the stack of images imported into VG Studio MAX for three-dimensional modelling. In modelling *Palaeophycus* a different approach was used because of the simplicity of the burrows. Stacks of images of serially ground surfaces were imported directly into VG Studio MAX without isolation of the burrow component to produce whole rock models of the samples. The modelling software enables both the reconstructed trace fossils and 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 burrow elements and host sediment.

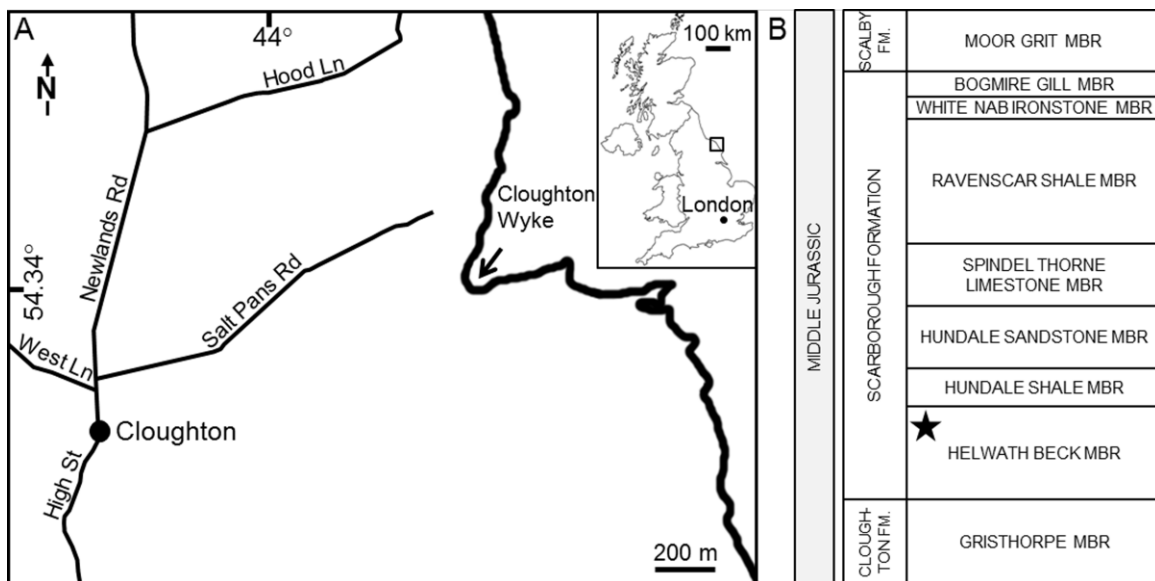


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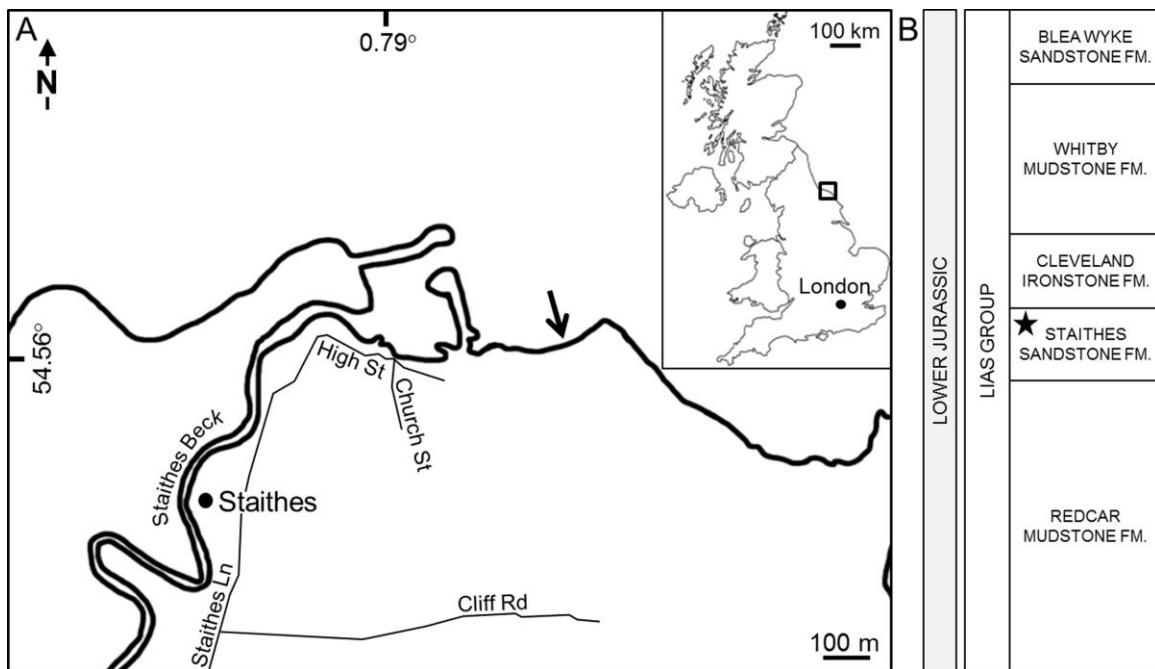


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1.3 Literature review

This study comprises two linked components which will form the basis for two published papers. The study investigates the full morphology and palaeobiology of the similarly thickly-lined trace fossils *Phoebichnus trochoides* and *Palaeophycus heberti*. The study is motivated by the need to better understand the palaeobiology and palaeoecological/palaeoenvironmental context of these common shallow marine trace fossils that are present in many shallow marine hydrocarbon reservoirs, particularly those of Mesozoic age (Bromley and Asgaard 1972; Frey and Howard 1990; Bromley and Mørk 2000; McIlroy 2004b; Rajkonwar *et al.* 2013).

1.3.1 *Phoebichnus*

The ichnogenus *Phoebichnus* is recognized as a large, radiating trace fossil characterised by a complex burrow system which consists of a cylindrical, bioturbated central zone of unknown depth from which extends numerous, long, radiating burrows (Bromley and Asgaard 1972; Bromley and Mørk 2000; Fig. 1.1). *Phoebichnus* galleries originate at, and radiate out from, the central cylindrical zone at a range of depths and angles. Although the radials are predominantly straight, they have been observed as being curved or making sudden bends (Bromley and Mørk 2000). *Phoebichnus* is generally considered to be a deposit feeding trace produced by the bulk-sediment deposit feeding activity of an endobenthic organism that sought buried organic detritus in otherwise clean sandy sediments (Dam 1990). Although *Phoebichnus* has been described in some detail the complete three-dimensional morphology and palaeobiology remain unknown.

Three valid ichnospecies of *Phoebichnus* have been described: *Phoebichnus trochoides* Bromley and Asgaard 1972, *P. minor* Li *et al.* 1999, and *P. bosoensis* Kotake 2003 (Figs. 1.1, 1.5, 1.6). *Phoebichnus trochoides* is defined as having a cylindrical, bioturbated central zone from which extend numerous radial burrows. The central zone has been described as having an irregular boundary with internal sediment grains showing no preferred orientation (Bromley and Asgaard 1972). Sediment grains at the boundary show a strong vertical orientation, tangential to boundary, sloping downwards and inwards (Bromley and Asgaard 1972). The radial burrows have a distinctive, thick sand-lined outer wall structure composed of annuli surrounding an active sand-rich burrow fill of similar grain size to the host sediment (Bromley and Asgaard 1972; Bromley and Mørk 2000). Previous descriptions of *Phoebichnus* have suggested that the trace-maker lived within the wide central zone and that the radial burrows, composed of a double meniscate structure, were produced by the trace-maker during two successive, opposed directions of movement into the surrounding sediment for deposit feeding purposes (Bromley and Asgaard 1972; Pemberton and Frey 1984; Dam 1989; Dam 1990; Bromley and Mørk 2000).

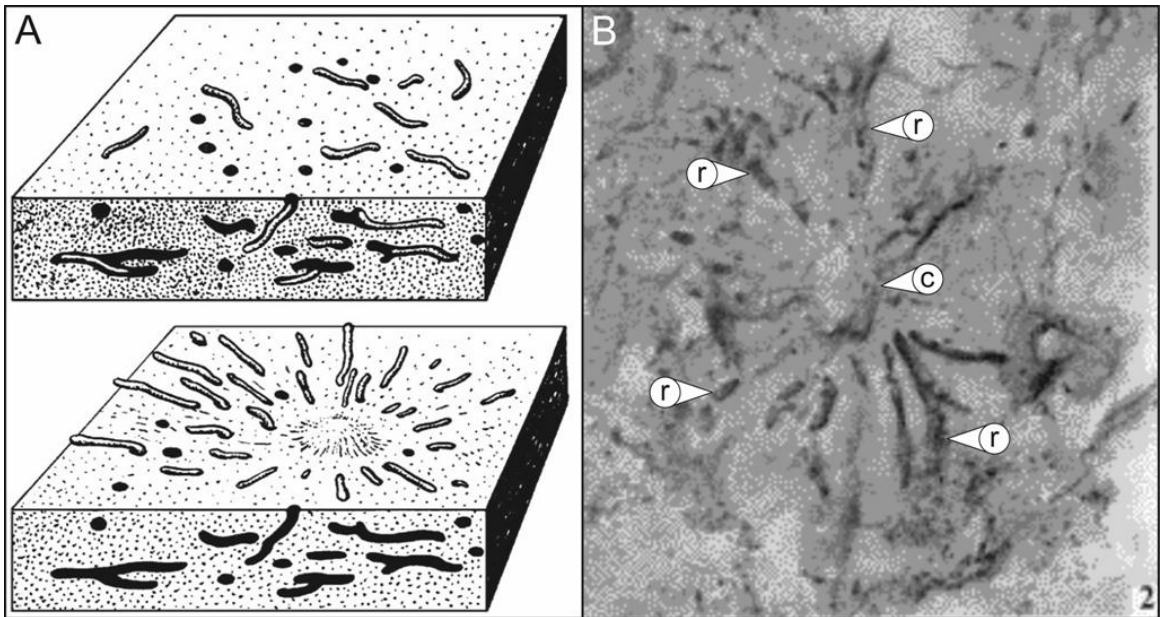


Fig. 1.5. Sketch and field photograph of *Phoebichnus minor*. A: Sketch by Li *et al.* (1999) illustrating how *P. minor* formed, organisms within the sediment become startled by a lime-mud pellet that has fallen onto the seafloor and attempt to escape (Modified from Li *et al.* 1999). B: Field photograph of bedding plane view of *P. minor* with central zone (c) and radiating burrows (r) (Modified from Li *et al.* 1999).

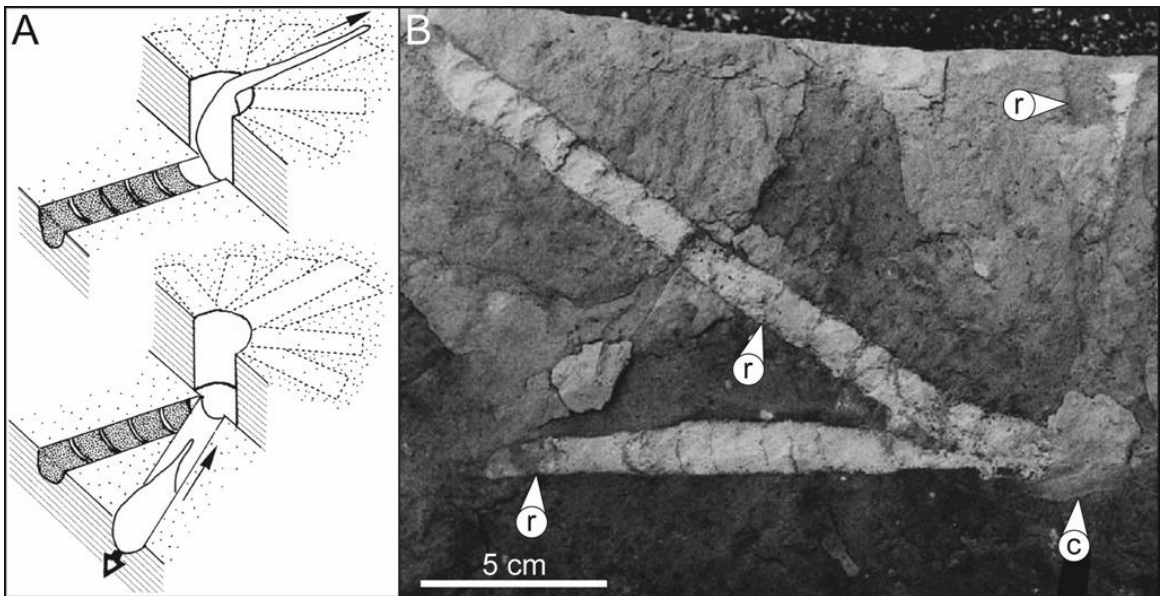


Fig. 1.6. Sketch and field photograph of *Phoebichnus bosoensis*. A: Sketch by Kotake (2003) illustrating how *P. bosoensis* formed, organism feeds on seafloor detritus and excretes faecal pellets into radials produced deep in the sediment (Modified from Kotake

2003). B: Field photograph of bedding plane view of *P. bosoensis* with central zone (c) and radiating burrows (r) (Modified from Kotake 2003).

The Cambrian taxon *Phoebichnus minor* has been defined as having a yellow central zone from which numerous, calcite-filled, narrow, straight burrows radiate (Li *et al.* 1999). This description deviates significantly from the ichnogenic diagnosis of *P. trochoides* with no description of an outer sand lining to the radials and significant differences in the fill of the central zone and radials. The current palaeobiological model for *P. minor* describes the trace as an escape structure, wherein the radials resulted from the producing organisms becoming startled and attempting to escape from a lime-mud pellet that had fallen onto the seafloor (Li *et al.* 1999). The poor quality of the photographic image makes it difficult to assess the validity of the taxon. The taxon has not been used since its original creation and may be considered a *nomen nudum*.

Phoebichnus bosoensis is characterised as a large stellate structure, with a central vertical shaft from which long, horizontal structures radiate (Kotake 2003). *P. bosoensis* differs from *P. trochoides* in that the radials of *P. bosoensis* have no outer sand lining and are filled with elliptical pellets consistent with surface deposit feeding (Kotake 2003). Clay-rich menisci in the radial elements have regular 1 cm spacings, and are slightly concave towards the central shaft (Kotake 2003), and are considered to result from active fill produced by the trace-making organism (Kotake 2003). Existing palaeobiological models suggest the ingestion of seafloor detritus by the extension of an anterior feeding apparatus followed by excretion of faecal pellets at the distal end of radials deep in the sediment (Kotake 2003). After each period of faecal deposition the animal returned to the

central shaft—which is considered to be a dwelling structure—before repeating the feeding-defecation cycle (Kotake 2003). Repetition of such behaviour would lead to the radials eventually being packed with faecal pellets at which stage it is inferred that the producer would initiate a new radial (Kotake 2003).

The ichnospecies *Phoebichnus bosoensis* Kotake and *P. minor* Li require careful reinvestigation of the type material as current descriptions do not include many morphological characteristics required by the current ichnogenic diagnosis. Both ichnospecies lack the characteristic sand-linings of the radial burrows of *Phoebichnus* and the sand-rich burrow fill, instead being calcite-filled (*P. minor*) or filled with elliptical faecal pellets (*P. bosoensis*). These ichnospecies are also lacking thorough descriptions of the central zone making reliable comparisons to the ichnogenus difficult. The significant differences are cause to consider that these ichnospecies may not belong in the *Phoebichnus* ichnogenus.

Phoebichnus is most commonly described from fine- to medium-grained sandstones deposited in low energy, mid to lower shoreface to offshore settings (Heinberg and Birkelund 1984; Pemberton and Frey 1984; Dam 1990; Goldring *et al.* 1991; Bromley and Mørk 2000; Wetzel and Uchman 2001; MacEachern and Gingras 2007; Pemberton *et al.* 2012). Long periods of slow sedimentation are inferred to be required for the construction of such large, complicated, structures as *Phoebichnus* (Bromley and Mørk 2000). Slight differences between *Phoebichnus* material, such as number of radials and diameter of the central zone, are possibly and likely due to palaeoenvironment and preservational factors (Bromley and Mørk 2000).

1.3.2 *Palaeophycus* versus *Schaubcylindrichnus*

The ichnogenus *Palaeophycus* Saporta 1872 is currently used for sand- or mud-lined, cylindrical, typically unbranched, predominantly horizontal burrows of variable diameter with a typically structureless passive fill that is of the same lithology as the host rock (Pemberton and Frey 1982). The primary ichnotaxobase used by most modern workers to diagnose *Palaeophycus* is the presence of a burrow lining (Pemberton and Frey 1982). Variations in the thickness and composition of the burrow lining, and differences in ornamentation are used to distinguish several ichnospecies of *Palaeophycus*. Of the currently described ichnospecies, *Palaeophycus heberti* is distinguished from all other ichnospecies by its characteristically thick sand-rich burrow lining (Pemberton and Frey 1982; Fig. 1.2). It is considered herein that the burrow lining is anomalous within the ichnogenus and requires careful consideration of the taxonomic status of *P. heberti*.

In addition to *Palaeophycus heberti* there are six other valid ichnospecies of *Palaeophycus* currently recognized based upon the thickness of the burrow lining and burrow ornamentation: *Palaeophycus tubularis* Hall 1847 is has a thin clay-rich burrow lining without ornamentation; *Palaeophycus striatus* Hall 1852 is thinly lined with continuous, parallel striae; *Palaeophycus sulcatus* Miller and Dyer 1878 is a thinly lined burrow with irregularly anastomosing striae; *Palaeophycus alternatus* Pemberton and Frey 1982 is a thinly lined form with alternately striate and annulate ornament; *Palaeophycus ferrovittatus* Hofmann 1983 is a thickly lined species with a core composed of iron oxide and parallel striae on the interior surface of the burrow lining; and

Palaeophycus crenulatus Buckman 1995 has a distinctive thin-walled burrows that is continuously annulate (Fig. 1.7).

Ichnospecies	Characteristics					
	Thinly lined	Thickly lined	No ornamentation	Striae	Annulate	Other
<i>P. tubularis</i>	X		X			
<i>P. striatus</i>	X			X (continuous, parallel)		
<i>P. heberti</i>		X	X			
<i>P. sulcatus</i>	X			X (irregularly anastomosing)		
<i>P. alternatus</i>	X			X (alternately)	X (alternately)	
<i>P. ferrovittatus</i>		X		X (internal)		Fe core
<i>P. crenulatus</i>	X				X (continuous)	

Fig. 1.7. *Palaeophycus* ichnospecies and their defining characteristics.

Palaeophycus burrows are conventionally interpreted to be the dwelling structures of predaceous or suspension feeding organisms (Pemberton and Frey 1982; MacEachern *et al.* 2005; Gani *et al.* 2005). *Palaeophycus* has been reported from palaeoenvironments ranging from shallow marine to continental settings, but it is most typically associated with intensely bioturbated, heterolithic sand and mud rich facies deposited in shallow marine settings (Frey and Howard 1990; Buatois and Mángano 2011; Rajkonwar *et al.* 2013).

The ichnogenus *Schaubcylindrichnus* Frey and Howard 1981 is similar to *Palaeophycus* in being composed of thickly lined burrows that may be isolated or bundled, are gently curved in the vertical to oblique plane, and do not normally branch or

interconnect (Frey and Howard 1981; Nara 2006; Löwemark and Nara 2010; Fig. 1.8).

The sandy burrow linings of *Schaubcylindrichnus* are lighter in color than the host sediment, and lack clays and other fine detritus (Miller 1995; Fig. 1.8). Various interpretations have been proposed for the complete morphology of *Schaubcylindrichnus*, the most current of which has the trace fossil consisting of three distinct parts: 1) a bundle of thickly lined tubes that were constructed in sequence by a solitary growing organism, 2) a funnel at one end of the burrow system, and 3) a faecal mound at the other end of the burrow system (Nara 2006; Löwemark and Nara 2010). The funnel and mound at the opposite ends of the burrows led to the interpretation of funnel feeding as the most plausible feeding behaviour of the organism (Nara 2006; Löwemark and Nara 2010).

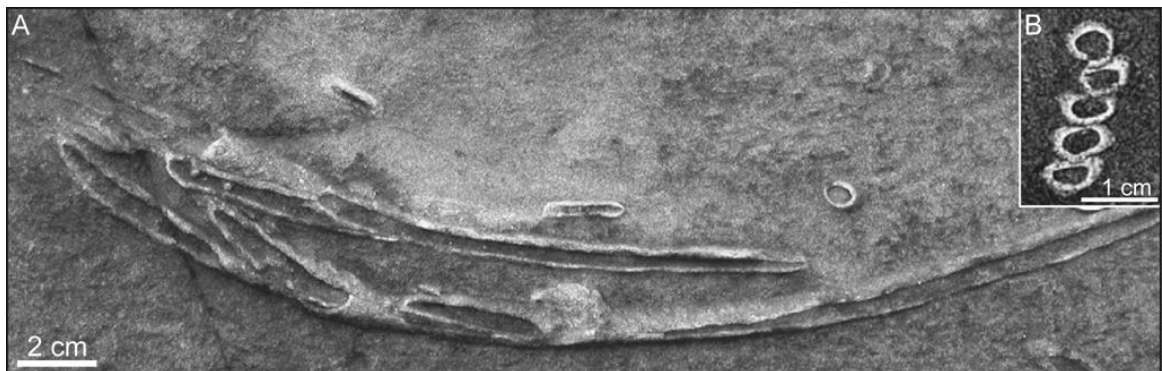


Fig. 1.8. Field photographs of *Schaubcylindrichnus*. A: Vertical view of *Schaubcylindrichnus* tubes (Modified from Löwemark and Hong 2006). B: Vertical transverse view of tightly packed tubes (Modified from Nara 2006).

The three ichnospecies of *Schaubcylindrichnus* are: *Schaubcylindrichnus coronus* Frey and Howard 1981, *S. freyi* Miller 1995, and *S. formosus* Löwemark and Hong 2006 (Fig. 1.9). *Schaubcylindrichnus coronus* is defined by distinct, isolated groups or bundles of congruent, lined tubes (Frey and Howard 1981; Fig. 1.9A). *S. freyi* is differentiated

from *S. coronus* based on loose bundles of burrows as opposed to congruent, closely bunched burrows (Fig. 1.9B) and *S. formosus* has converging sheaves of burrows of a considerably larger diameter than *S. coronus* (Miller 1995; Löwemark and Hong 2006; Fig. 1.9C). Review of the type material of *Schaubcylindrichnus* suggests that all existing *Schaubcylindrichnus* species can be accommodated within *Schaubcylindrichnus coronus* (Nara 2006). The topotype material includes the morphological characteristics that were subsequently used as the basis for the creation of *freyi* and *formosus* (Löwemark and Nara 2010) and as such are junior synonyms. *Schaubcylindrichnus* has been reported from most continents in a large variety of marine depositional settings, but is most commonly associated with shoreface strata (Löwemark and Hong 2006; Löwemark and Nara 2010).

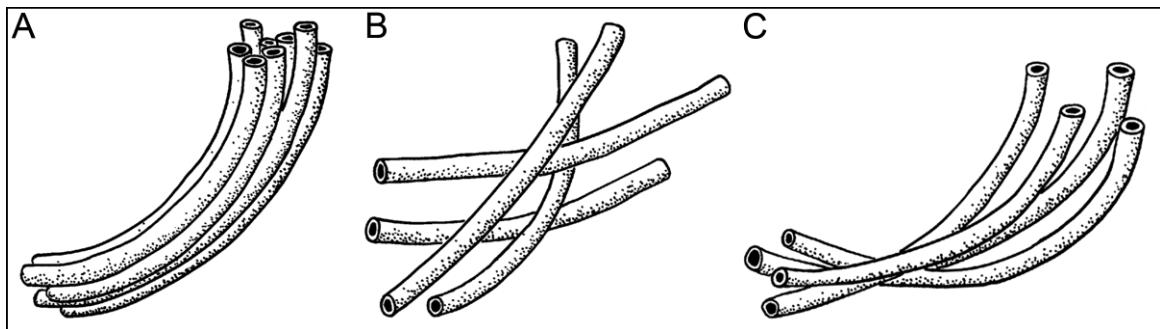


Fig. 1.9. Sketches illustrating the various ichnospecies of *Schaubcylindrichnus* which are considered synonymous with *S. coronus* (See Fig. 3.12). A: *S. coronus*. B: *S. freyi*. C: *S. formosus*. (Modified from Löwemark and Nara 2010).

1.3.3 Gleaning behavioural information from trace fossils

The classification of trace fossils is necessary to communicate ideas about them and maximizes their information potential (Goldring *et al.* 1997; Rindsberg 2012).

Morphological features possessed by trace fossils, such as the general form,

constructional features of burrow walls, and the grain size and structure of the filling material, all serve as ichnotaxobases which are used to distinguish between trace fossils (Bromley 1996). Ichnologists rely on the careful observation and description of these ichnotaxobases to classify trace fossils. One such classification scheme involves the ethological classification of trace fossils. The ethological classification scheme is restricted to a small number of well-founded categories and includes only those concepts that have proven to be consistently most useful in the functional study of trace fossils (Frey 1973). The ethological classification of trace fossils was first proposed by Seilacher (1953a). Seilacher (1953a) recognized that trace fossils could be classified according to their ethological function because similar functions can result in similar morphologies. Aspects of the behaviour of the trace maker can be inferred from: 1) the overall shape of the trace fossil; 2) the orientation and position of the trace fossil within the substrate; 3) the burrow boundary or lack thereof and whether the boundary is a wall, lining, or mantle, is ornamented, and is produced actively or passively by the organism; and 4) the fill or internal structure and whether it is passively or actively formed (Bromley 1996; Bertling *et al.* 2006).

In this study I have been concerned exclusively with the traces of burrowing organisms. Burrows can be simple structures or complex systems composed of several components. Most trace fossils are initially recognized based on their distinct morphology and overall shape which is most readily recognized (Bertling *et al.* 2006). Much can be revealed about the trace from its overall form however, it is not necessarily the most relevant ichnotaxobase (Bertling *et al.* 2006). In addition to the overall form, burrows can be further characterised according to their wall and fill.

Constructed burrow walls imply certain constructional traits and can reveal significant information on the ethology, burrowing technique, and biological affinity of the trace-making organism (Bromley 1996; Buatois and Mángano 2011). A constructed wall has typically been considered to be built by the burrowing organism for structural reinforcement (Frey 1973). However, the purpose of a constructed burrow wall is potentially diverse (e.g. Gingras *et al.* 2011). Thick burrow walls can provide protection from predation as many modern organisms secrete toxins into burrow walls to deter predators (Woodin *et al.* 1987), they also provide temporary or permanent protection from the external pore water environment (Keighley and Pickerill 1994) and allow for more effective bioirrigation (Herringshaw and McIlroy 2013). While burrow walls can have diverse functions, substantial wall structures (e.g. walls composed of mucus-bound sediment or agglutinated pellets) are generally equated with more or less permanent, maintained structures and imply that burrows may have been inhabited for longer periods of time as open structures (Frey and Pemberton 1985; Bromley 1996). Therefore, burrows with substantial walls built for stability purposes are suggestive dwelling structures of suspension feeders or deposit feeding organisms (Frey 1973; Bromley 1996; Gingras *et al.* 2011). Burrows that lack a substantial wall structure are commonly produced by vagile bulk-sediment deposit feeding organisms (Gingras *et al.* 2011).

The mineralogy and organization of burrow filling material can also provide information on the behaviour of the trace-making organism. Burrow fill can reveal information on burrow function and feeding strategies of the causative organism (Bromley 1996), and can be classified as being either passive or active. Passive burrow fill results from sediment entering a burrow gravitationally, for example during storm

events, the fill of the burrow may be lithologically similar to or different to the host sediment and may be structureless or display physical lamination; such fills generally betray an abandoned or open burrow system such as those of a dwelling or suspension feeder (Frey 1973; Pemberton and Frey 1985; Bromley 1996; Buatois and Mángano 2011). Active burrow fill results from active manipulation and emplacement of material by the trace-maker; such fills typically contrast with the host sediment, may be structureless, or composed of faecal pellets, or display internal structures such as meniscate laminae (Frey and Pemberton 1985; Bromley 1996; Buatois and Mángano 2011). Meniscate backfill structures are caused by the organism re-depositing sediment behind itself while burrowing (Keighley and Pickerill 1994). This may occur by material being transported externally around the organism or internally through the digestive tract (Keighley and Pickerill 1994). This type of fill is generally suggestive of a feeding trace of a vagile, infaunal, deposit feeding organism (Frey and Pemberton 1985; Bromley 1996; Buatois and Mángano 2011). Active burrow fill can also be produced by organisms that are capable of shovelling sediment within the burrow, filling burrows from a dwelling position, which can result in inclined or angle of repose laminae orientated in the direction of fill, towards the body position of the trace-maker. This type of fill suggests that the burrow was produced as the dwelling structure of a deposit feeding organism.

Phoebichnus trochoides has been characterised as a complex feeding trace.

Feeding traces are defined as more or less temporary burrows constructed by deposit feeding organisms (Osgood 1970; Frey 1973). The burrows may also provide shelter for the organism and may serve as permanent or semi-permanent dwelling structures (Osgood 1970; Frey and Seilacher 1980; Frey and Pemberton 1985). However, emphasis

of this ethological category is upon feeding and coverage of space is important (Frey and Pemberton 1985). Feeding traces can be characterised as single, branched or unbranched, cylindrical to sinuous shafts or U-shaped burrows, or spreiten structures, and may be oriented at various angles (Frey 1973; Frey and Seilacher 1980). Feeding traces that solely record the feeding activity of mobile organisms generally are not lined, unless by mucus, which may have been employed by the trace-maker to ease its passage (Gingras *et al.* 2011). Feeding traces that are also used for dwelling may be more complex structures with substantial walls built for structural reinforcement. Deposit feeding traces may be actively backfilled by the organism or left open and subsequently passively filled (Frey and Seilacher 1980).

Palaeophycus heberti, unlike other species of the genus, has been characterised as a dwelling trace (Pemberton and Frey 1982; MacEachern *et al.* 2005; Gani *et al.* 2005). Dwelling traces are defined as burrows or dwelling tubes that serve as more or less permanent domiciles for hemisessile suspension feeding organisms or carnivores (Frey 1973; Frey and Seilacher 1980; Frey and Pemberton 1985). Emphasis of this ethological category is upon habitation (Frey and Seilacher 1980). These traces may be simple or bifurcated burrows, vertical or curved shafts, sinuous or U-shaped structures orientated perpendicular or inclined to bedding, or complex burrow systems consisting of shafts, tunnels, and inclined burrows (Osgood 1970; Frey 1973). Most dwelling burrows are lined or walled which helps distinguish them from feeding traces (Frey 1973). The structures are maintained more or less permanently, and hence the burrow walls may be strengthened with mucus or agglutinated mud and sand pellets pressed into the margins to prevent collapse (Osgood 1970; Frey and Pemberton 1985). Most dwelling traces remain

open during occupation and are later passively filled with sediment (Frey and Pemberton 1985).

Trace fossils reflect the behaviour of the trace-making organism. These behaviours can be classified according to diagnostic morphologies because similar behaviours results in similar structures. Determining the full morphology associated with trace fossils can thus provide us with important information to help determine their ethological classification. The new information we will gain from the three-dimensional models of *Phoebichnus trochoides* and *Palaeophycus heberti* burrows will help lead to better interpretations of behaviour.

1.4 Relevance of the study

The outcomes of this research are relevant to the recognition and palaeobiological interpretation of the two taxa considered (*Phoebichnus trochoides* and *Palaeophycus heberti*). Both taxa are very common shallow marine trace fossils, but their morphology and palaeobiology are incompletely understood. The three-dimensional reconstructions of *P. trochoides* and *P. heberti* created as part of this thesis comprise the first full morphological understanding of both taxa, allowing us to fully understand the organism-sediment interactions and their full three-dimensional morphology. Understanding the complete morphology of these two taxa will improve their identification in the field and in core-based cross sections. The palaeobiological interpretation of these trace fossils can additionally be used to inform their use as palaeoenvironmental indicators. Importantly, the three-dimensional models improve the taxonomic understanding of both *P. trochoides* and *P. heberti* which require significant taxonomic change and emendation of diagnoses

at the species and genus level. This approach has been gaining momentum of late (Bednarz and McIlroy 2009; Boyd *et al.* 2012; Bednarz *et al.* 2015; Leaman *et al.* 2015; Leaman and McIlroy 2015; Boyd and McIlroy 2016 (in review)), and is overturning our understanding of what trace-making organisms were actually doing, which is the underlying basis for applying ichnology to real-world problems (McIlroy 2004a, 2008).

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Chapter 2

Ichnology and Palaeobiology of *Phoebichnus trochoides*

from the Middle Jurassic of north-east England

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Abstract

Phoebichnus trochoides is a large, radiating trace fossil most commonly found in shallow marine siliciclastic deposits. The structure consists of a central boss from which extend numerous, lined, radiating burrows which have an active fill. Serial grinding and modelling techniques employed allow the full three-dimensional morphology of *Phoebichnus trochoides* to be constructed for the first time. Three-dimensional models of the trace fossil demonstrate that the central zone is composed of stacked disk-shaped layers. The structure is inferred to result from collapse of sediment below a surficial cone created by the trace-maker from excavated sediment produced during burrowing. The fill of the radial burrows is herein determined to be composed of angle of repose laminae that are inclined towards the central zone rather than the meniscate backfill documented in the ichnogenic diagnosis and all subsequent descriptions. The structure of the fill resulted from the trace-making organism filling its burrows from a dwelling position close to the central boss, probably with material excavated from other parts of the burrow system. This study also reports for the first time subtle conical structures above the radial galleries that are inferred to result from collapse cone feeding. The new fully three-dimensional dataset created of the burrow and the near-burrow environment allows for a new palaeobiological understanding of the burrow, which suggests that a crustacean trace-maker is most likely.

Key words: *Phoebichnus*, trace fossil, serial grinding, three-dimensional, Helwath Beck Member.

2.1 Introduction

The trace fossil *Phoebichnus trochoides* Bromley and Asgaard 1972 has received little palaeobiological attention since its discovery from the Jurassic Neill Klinte and Vardekløft Formations of Jameson Land, East Greenland (Bromley and Asgaard 1972; Bromley and Mørk 2000). *P. trochoides* is a large radiating trace fossil characterised by a complex burrow fill that has been difficult to interpret in terms of mode of life of the trace-maker (Bromley and Asgaard 1972; Bromley and Mørk 2000; Dam 1990). The burrow was originally considered to have a wide central zone from which numerous radial burrows extended for the purpose of bulk-sediment deposit feeding (Bromley and Asgaard 1972; Fig. 2.1). The trace fossil is known mostly from Mesozoic marine deposits including many un-published accounts in petroleum reservoirs of the North Sea (Bromley and Asgaard 1972; Bromley and Mørk 2000; McIlroy 2004, unpublished observations). *P. trochoides* is most commonly described from fine- to medium-grained sandstones deposited in low energy, mid to lower shoreface to offshore settings (Heinberg and Birkelund 1984; Pemberton and Frey 1984; Dam 1990; Goldring *et al.* 1991; Bromley and Mørk 2000; Wetzel and Uchman 2001; MacEachern and Gingras 2007; Pemberton *et al.* 2012). However, *P. trochoides* has also been described from: deltaic deposits (MacEachern *et al.* 2005; Sadeque *et al.* 2007; Gani *et al.* 2007); shelf and slope deposits (Parrish *et al.* 2001; Hubbard *et al.* 2012); lagoonal deposits (Harding 1988); and in mixed siliciclastic-carbonate successions (Joseph *et al.* 2012).

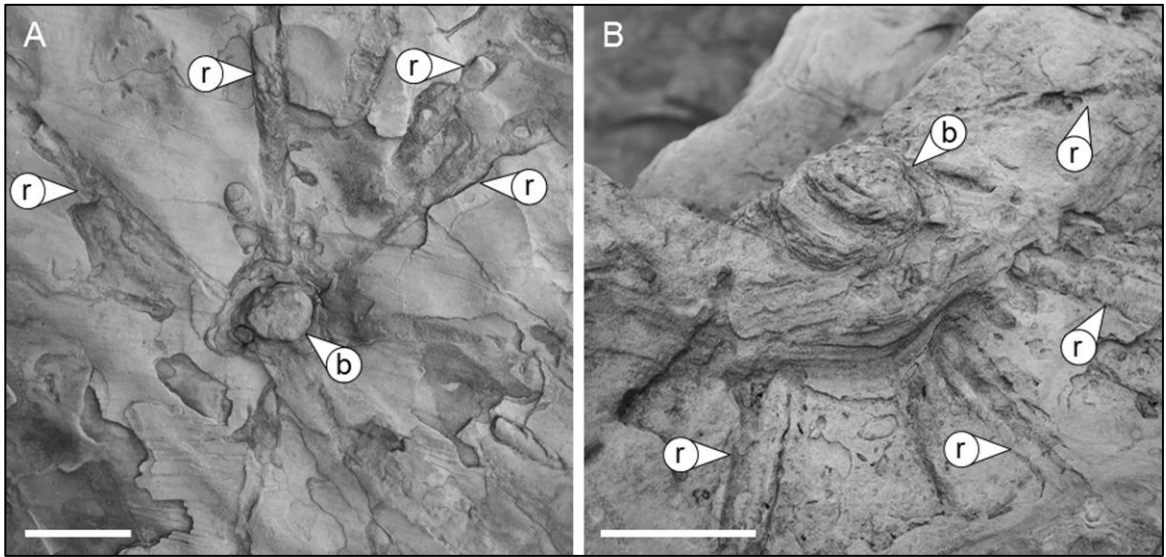


Fig. 2.1. Field photographs of *Phoebichnus trochoides*. A: Bedding plane of wave-rippled sandstone with *P. trochoides* B: Oblique view of *Phoebichnus trochoides* in which the central boss (b) protrudes above the top of the bed. Radial burrows (r) extend out from the central boss at a range of angles relative to the horizontal. Scale bars 5 cm.

In addition to the type ichnospecies *Phoebichnus trochoides*, two other ichnospecies of *Phoebichnus* have been described, *P. bosoensis* and *P. minor*. The type ichnospecies *P. trochoides* is characterised as having a cylindrical, bioturbated central zone from which extend numerous radial burrows that have distinctly thick, sand-lined outer walls composed of annuli which surround an active sand-rich burrow fill of similar grain size to the host sediment (Bromley and Asgaard 1972; Bromley and Mørk 2000). *P. bosoensis* is described as a large stellate structure that consists of a single central shaft with straight, long, unbranched elements radiating from the basal portion of the shaft (Kotake 2003). *P. bosoensis* differs from *P. trochoides* in a number of ways. *P. bosoensis* radials have no lining or mantle, are filled with elliptical pellets which are of lighter-coloured and finer-grained sediment relative to the host rock and appear to be composed of surface detritus (Kotake 2003). The Cambrian taxon *Phoebichnus minor* has been

defined as having a central zone from which numerous, calcite-filled, narrow, straight burrows radiate (Li *et al.* 1999).

This study focuses on samples of *Phoebichnus trochoides* that were collected from the Middle Jurassic, Helwath Beck Member of the Scarborough Formation at Cloughton Wyke, UK to allow us to investigate the full three-dimensional morphology of the trace fossil (Fig. 2.2). Pre-established precision serial grinding methods and three-dimensional modelling techniques have been used to produce the first high-resolution, three-dimensional models of *P. trochoides* (see Bednarz *et al.* 2015 for detailed methodology). The current morphological understanding of *P. trochoides* is based on bedding plane and cross sectional views in core or natural cross-sections in the field. The advantage of the methodology employed herein is that the burrow is studied in the context of the host sediment, such that subtle details of organism-sediment interactions can be revealed from the ground surfaces. This is particularly true of highly laminated sediments such as those studied herein.

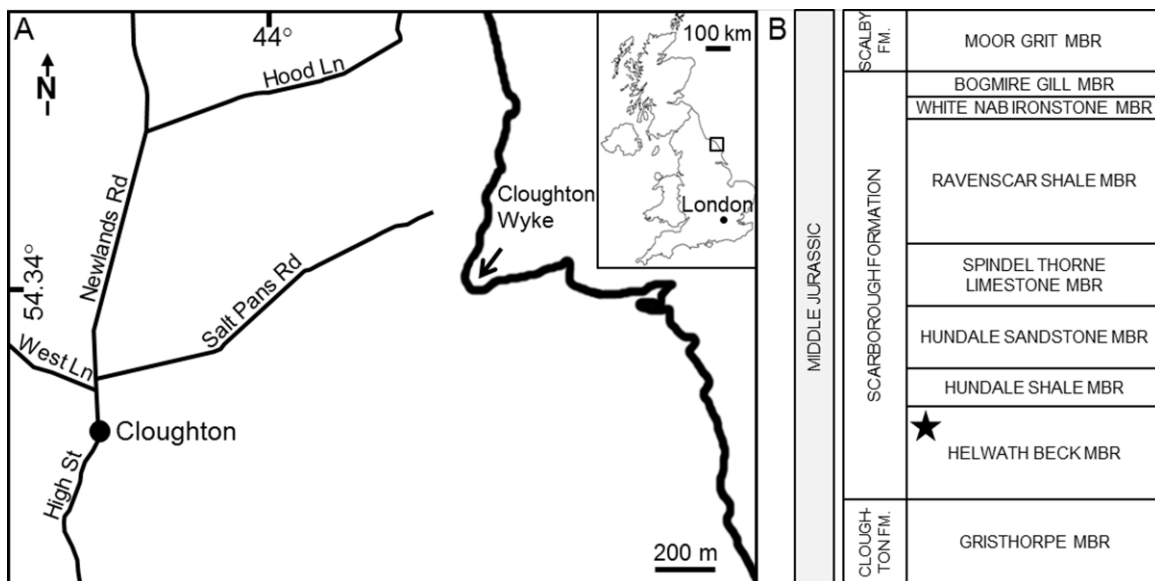


Fig. 2.2. Sample location of *Phoebichnus trochoides* and generalized stratigraphic column. A: Map of field location at Cloughton Wyke, UK. Arrow shows approximate collection location of the samples from the coastline of Cloughton. B: Stratigraphic column of the Scarborough Formation showing the stratigraphic level studied.

2.2 Geological and palaeoenvironmental settings

The Middle Jurassic, Helwath Beck Member at the base of the Scarborough Formation records a marine transgression located within the Ravenscar Group of the Cleveland Basin in Yorkshire, England (Gowland and Riding 1991; Powell 2010). The Helwath Beck Member consists of brackish to fully marine siliciclastic sediments deposited in subtidal settings above storm wave base, and unconformably overlies palaeosols of the topmost Gristhorpe Member of the Cloughton Formation (Gowland and Riding 1991). The ichnological assemblage of the Helwath Beck Member is fully marine in character, and includes the trace fossils: *Phoebichnus trochoides*; *Diplocraterion parallelum* (aff. *D. yoyo*); *Asterosoma* isp.; and *Palaeophycus heberti* (Gowland and Riding 1991; Leaman and McIlroy 2015). The Helwath Beck Member is comprised of: 1)

a lower succession of variably bioturbated heterolithic silty sandstones that coarsen upward and are capped by convolute-bedded micaceous sandstones with sauropod footprints; and 2) an upper, upward coarsening succession of fine-grained bioturbated sandstones with hummocky cross-stratification and *Phoebichnus trochoides*, which passes upwards into trough cross-bedding, and low angle planar cross-stratification towards the top (Gowland and Riding 1991; Rawson and Wright 1992). The upper part of the succession has been interpreted as a sheet-sand body deposited in a siliciclastic embayment during transgression and upward-shoaling under strong wave influence (Gowland and Riding 1991).

2.3 Methods

The collected samples were subjected to precision serial grinding, high-resolution digital photography, and tomographic reconstruction (see Bednarz *et al.* 2015 for full methodology). The hand-samples were encased in plaster and serially ground using a computer guided milling machine. The two samples presented herein were ground at different intervals (0.1 and 0.3 mm). Each ground surface was consecutively labelled, wetted with oil to enhance contrast, and photographed under identical conditions. The *Phoebichnus* burrows and related features were selected using image processing software, extracted from each surface and the stack of images imported into VG Studio MAX for three-dimensional modelling. The modelling software enables the reconstructed trace fossils 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 burrow elements and host sediment. The three-dimensional reconstructions were also augmented

with conventional thin sections cut from specific burrow portions in order to study subtle sedimentary fabrics.

2.4 Descriptive ichnology

The serial grinding and modelling techniques employed during this study have enabled the full three-dimensional morphology of *Phoebichnus trochoides* to be constructed (Fig. 2.3). This work builds on previous descriptions of *P. trochoides*, its ichnogeneric and ichnospecific diagnoses, and provides new data for emending those diagnoses. The various components of *Phoebichnus* are discussed separately for convenience; however they may all occur in a single well preserved specimen.

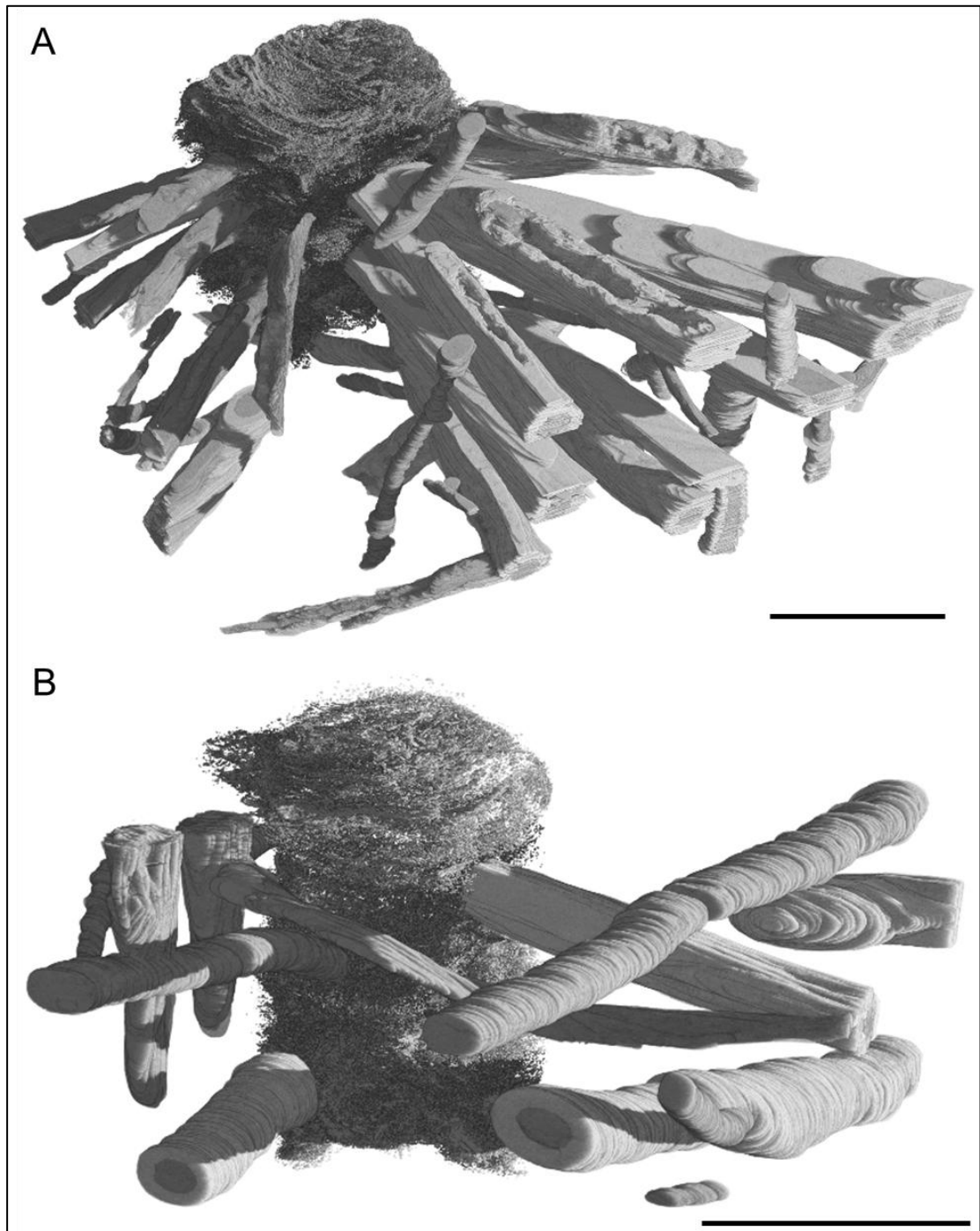


Fig. 2.3. Three-dimensional reconstructions of *Phoebichnus trochoides* from the Middle Jurassic, Helwath Beck Member of the Scarborough Formation at Cloughton Wyke, UK. A: *Phoebichnus trochoides* Sample 1. B: *Phoebichnus trochoides* Sample 2. Radial burrows are approximately 1 cm in diameter.

2.4.1 Central boss component

The central, broadly cylindrical, zone of *Phoebichnus trochoides*, termed the boss in outcrop expression, ranged from 4 to 8 cm in diameter, and 8 to 9 cm in depth, in the two specimens studied (Figs 2.3, 2.4). The central cylindrical portion of *P. trochoides* has been observed to be up to around 15 cm deep (Bromley and Asgaard 1972) though the internal morphology of this central zone has not hitherto been described in detail. Through serial grinding and three-dimensional reconstruction we demonstrate that the cylindrical burrow component is composed of a stack of disk-shaped layers of highly bioturbated sediment (Fig. 2.4B, C) that may be mistaken for *Piscichnus* spp. (Pearson *et al.* 2007). The serial cross-sectional images reveal little systematic structure within much of the central zone, but when the distribution of dark laminae is mapped in three-dimensions, the conical nature of the central zone is evident. Cross-sections through the lower portion of the central zone were, in both cases, found to consist of randomly oriented organic detritus (Fig. 2.4B-C, E-F). Close to the top of the bed, the organic detritus is concentrated in conical layers that slope downwards and inwards towards the centre of the central zone, which constitutes the central boss when seen in bedding plane expression in the field (Fig. 2.4B-D, F). Much of the organic detritus in the central boss was found to be coalified plant matter along with abundant black oval grains that are interpreted to be faecal pellets of the *Phoebichnus* trace-maker (Fig. 2.4E). The central boss is cut by a sub-vertical burrow shaft that is also attributed to the *Phoebichnus* trace-maker (Fig. 2.4F). There is evidence that the central zone extended or protruded above

the sediment-water interface from direct observation of specimens in the field in which the boss protrudes above the top of the bed (Figs. 2.1, 2.4F).

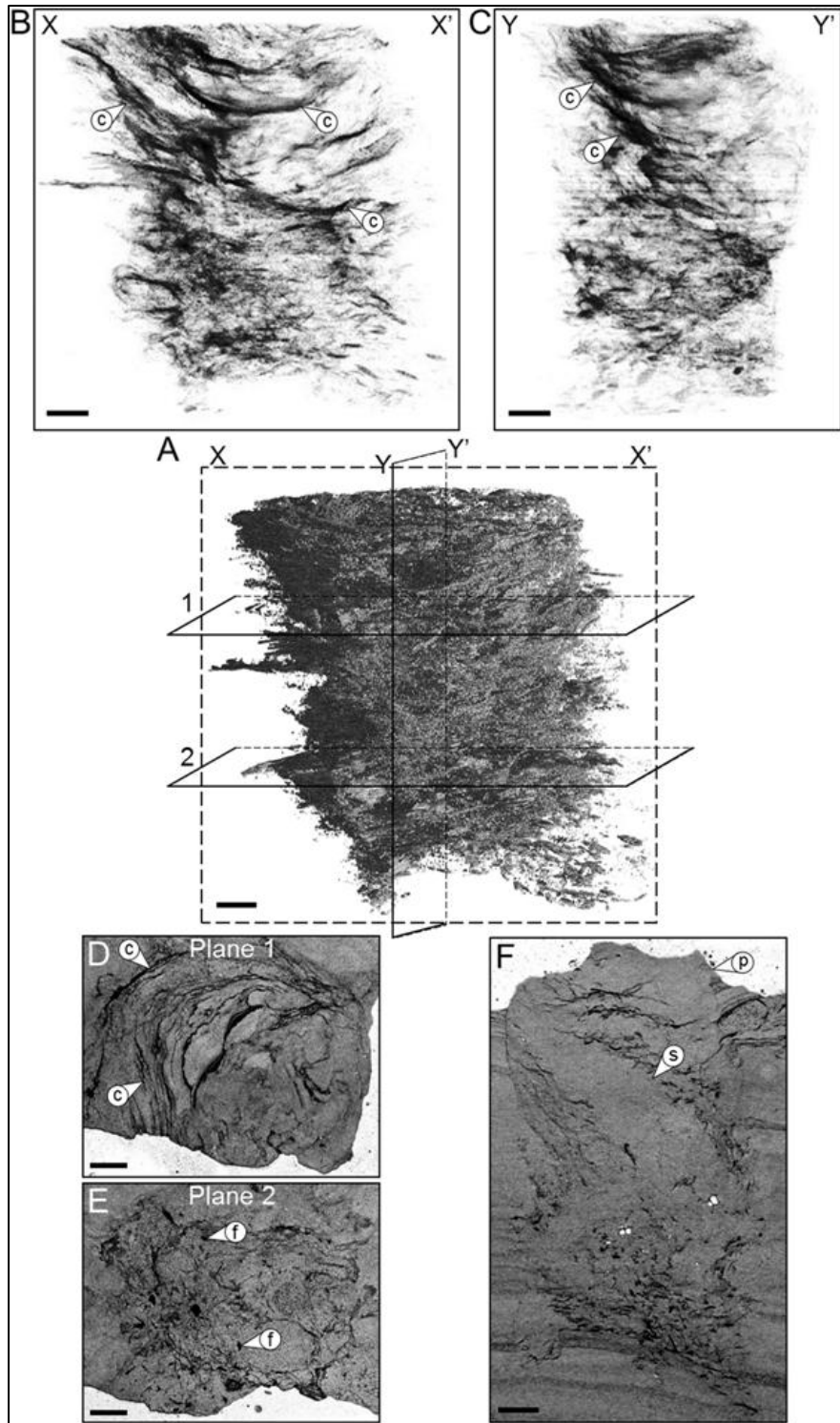


Fig. 2.4. Three-dimensional models and serial grind surfaces of the central boss structure of *Phoebichnus trochoides*. A: Three-dimensional reconstruction of the exterior of the central boss. B and C: Three-dimensional reconstruction, in which the darker areas have higher densities of organic detritus. This model rendering reveals the convex-down conical to discoidal nature of the central boss (c). D and E: Horizontal cross sections through the central boss. Plane 1 shows conical layers of organic detritus (c), whereas Plane 2 displays randomly oriented organic detritus and oval grains are interpreted to be faecal pellets (f). F: Vertical cross section through the central boss with the sub-vertical burrow shaft (s) preserved and the protrusion (p) of the central boss above the top of the bed. Scale bars represent 1 cm.

2.4.2 Radial gallery component

The radial burrows of *Phoebichnus trochoides* form cylindrical, straight to curved galleries that have a thick lining and a complex fill that is diagnostic of the ichnogenus (Bromley and Mørk 2000). Each radial burrow is approximately 1-2 cm in diameter and was observed in the field to be up to a metre in length (Bromley and Mørk 2000). The burrow morphology of the radial gallery component of *P. trochoides* broadly resembles the ichnogenus *Beaconites*, a taxon that currently encapsulates all thickly lined, non-stellate, meniscate trace fossils (Keighley and Pickerill 1994). Within a single sample of *P. trochoides* galleries can originate at, and radiate out from, the central cylindrical zone at a range of depths and angles. The radial galleries have hitherto been described as being straight, and have been considered to be oriented parallel to bedding (Bromley and Asgaard 1972; Bromley and Mørk 2000). Due to restrictions on the size of field specimens that can be serially ground, the natural end of a gallery could not be traced from a central boss to its natural termination. Therefore our understanding of the end of the radial galleries of *P. trochoides* galleries is mainly reliant upon reconstruction of

isolated burrow terminations that can be confidently attributed to *P. trochoides* based on burrow fill and architecture. The three dimensional reconstructions demonstrate that the terminations of the radial galleries were characterised by a steep upward curve from the horizontal to sub-vertical close to the sediment-water interface (Fig. 2.5).

One of the most distinctive features of the radial galleries of *Phoebichnus* is that they consist of a thick sand-lined outer wall surrounding a sand-rich burrow fill of similar grain size to the host sediment (Bromley and Asgaard 1972). The outer wall in our reconstructed material is uniformly around 0.5 cm thick, and the burrow fill is about 1 cm in diameter giving each radial gallery an average diameter of approximately 2 cm. In field specimens the annular structure of the outer burrow wall is clearly seen where the burrow fill has been removed (Bromley and Asgaard 1972). In our serial reconstruction, some heterolithic portions of the burrow wall allow the confirmation of this annular structure which is found to include sandy pellets with an arcuate outer edge that is comparable to that of the outer meniscus lining described previously (Bromley and Asgaard 1972; Fig.2.6). The structure of the outer wall is, however, not always easily discernible due to a lack of lithological contrast between the burrow wall and the host sediment. Along some portions of the radial galleries the roof is absent (Fig. 2.7). Some galleries have a thin patina of clay minerals at the boundary between the outer wall and burrow fill. The fill of the central part of the galleries does not have the meniscate backfill as previously described (Bromley and Asgaard 1972), but instead the galleries are filled with angle of repose laminae that are inclined toward the central zone (Fig. 2.8). The curved cross section of angle of repose laminae cut parallel to bedding can have the superficial appearance of meniscate backfill (Fig. 2.8A, C).

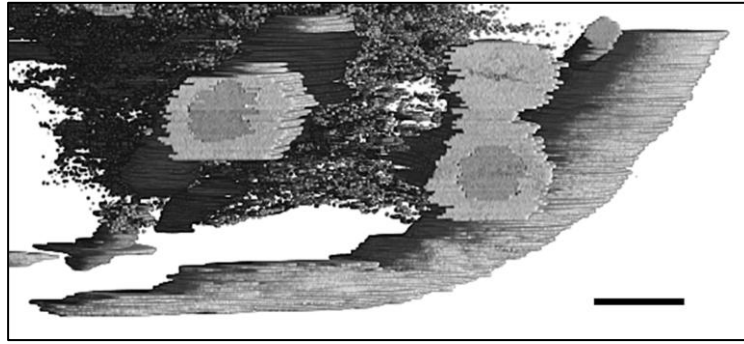


Fig. 2.5. Three-dimensional reconstruction of *Phoebichnus trochoides* showing a radial burrow rising sharply to become sub-vertical. Scale bar represents 1 cm.

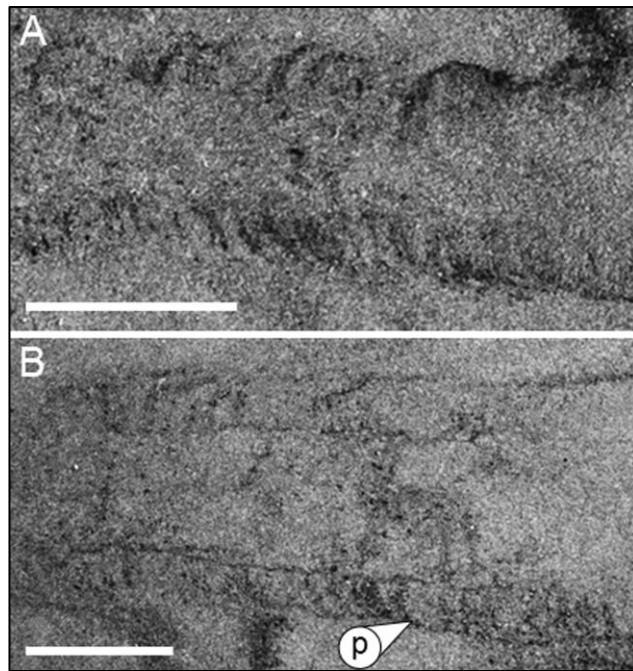


Fig. 2.6. Horizontal longitudinal cross sections through radial burrows of *Phoebichnus trochoides*. A and B: Horizontal longitudinal cross section through radiating limbs of *P. trochoides* showing the annular structure of the sandy burrow wall, that consists of curved clay-rich laminae, but also pellet-like structures (p). Scale bars represent 1 cm.

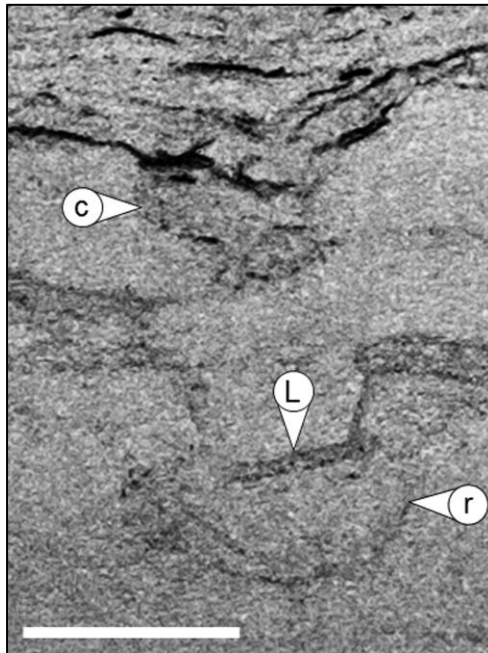


Fig. 2.7. Vertical transverse cross section through a radiating burrow of *Phoebichnus trochoides* showing collapse of the burrow roof, associated displacement of laminae (L) into the radial burrow (r), and the presence of a ‘collapse cone’ (c) above the burrow with down-warped sedimentary laminae. Scale bar represents 1 cm.

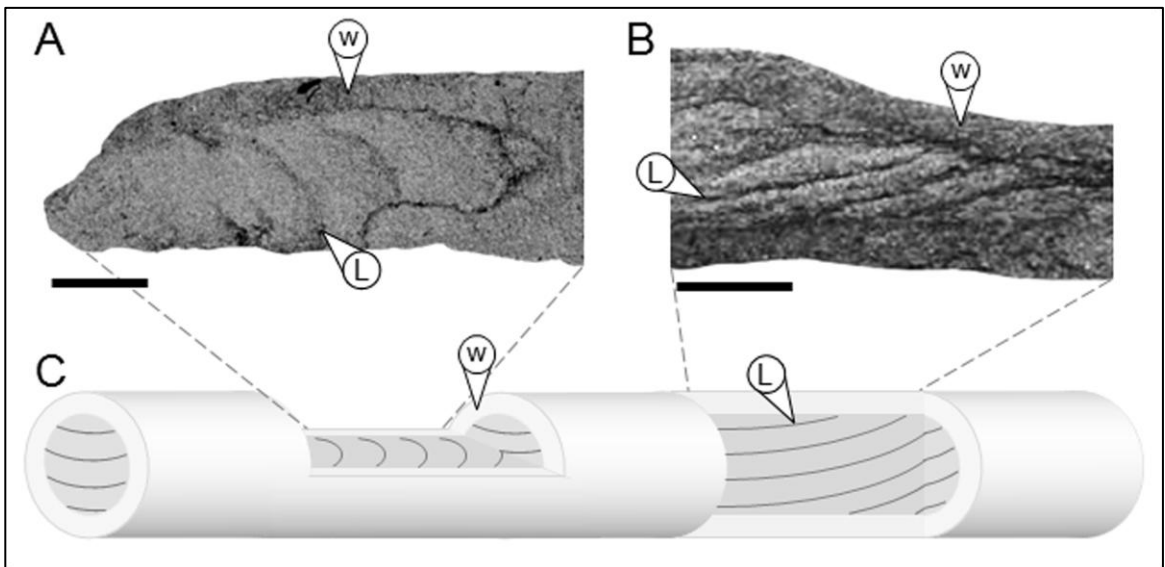


Fig. 2.8. Cross sections through radial burrows of *Phoebichnus trochoides* showing internal structure of the fill and idealized sketch. A: Horizontal longitudinal cross section through a radiating burrow showing outer wall (w) and laminae (L) of the fill curved concave towards the central boss. B: Vertical longitudinal cross section through a radiating burrow showing outer wall (w) and inclined laminae (L). C: Idealized sketch of

internal structure of a radial burrow depicting the angle of repose laminae of the burrow fill through various cross-sectional views. Scale bars represent 1 cm.

2.4.3 Collapse cone component

Above several of the galleries there is evidence of small-scale conical sediment collapse that can be inferred by the presence of downwardly deflected sedimentary laminae that overlie unlined portions of the *Phoebichnus* radial galleries (Fig. 2.9). The collapse cones observed in the studied samples range from 0.5 to 2 cm in maximum diameter, are around 2 cm in depth, and taper to a minimum diameter of 2 mm immediately above the *Phoebichnus* galleries. Several collapse cones may be present along a single radial gallery and at the termination of the vertically oriented burrows (Fig. 2.9).

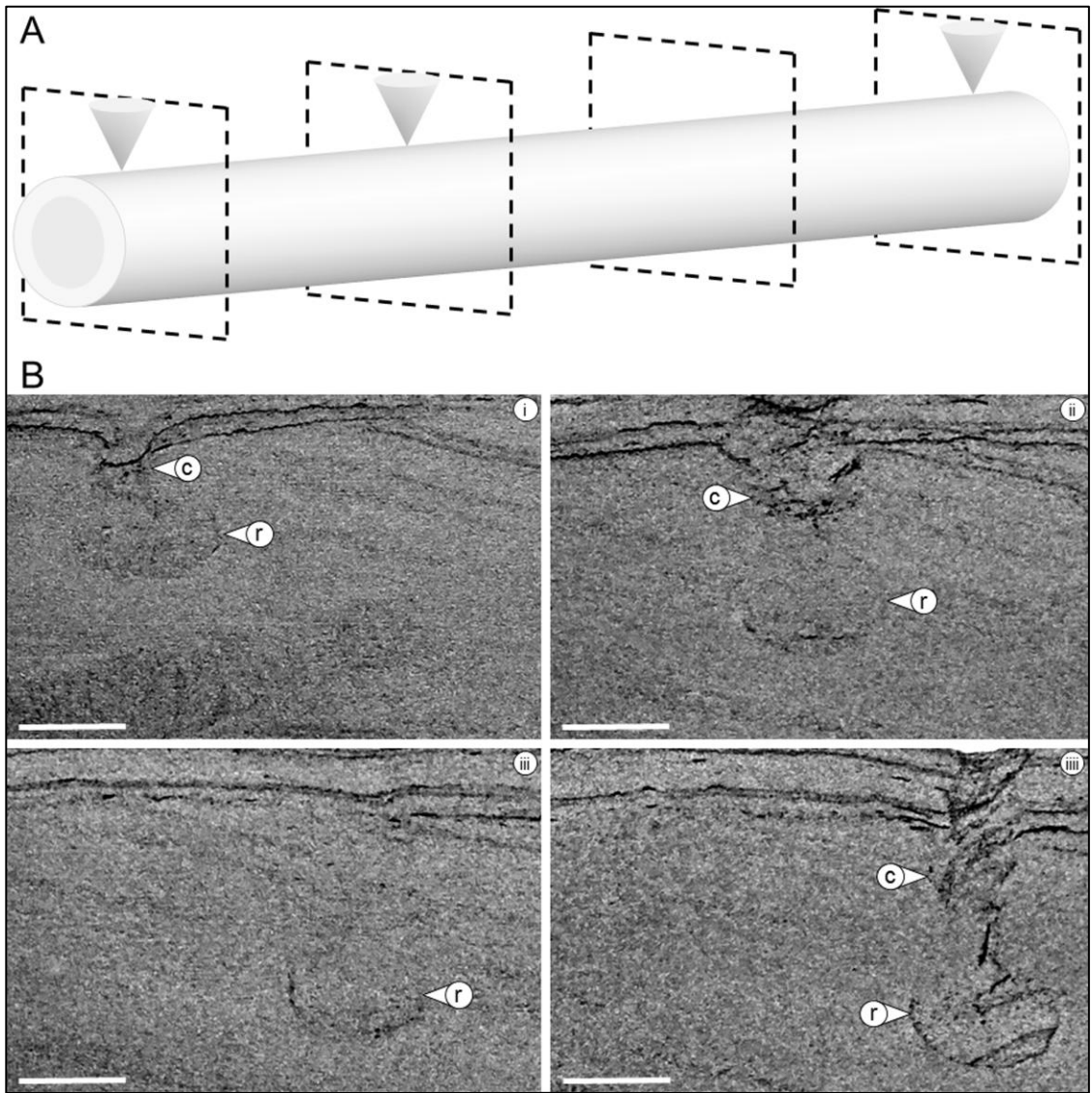


Fig. 2.9. Idealized sketch and serial photographs of a radial burrow of *Phoebichnus trochoides* with collapse cones at various locals along its length. A: Idealized sketch of radiating burrow with multiple collapse cones along its length. B: Series of vertical transverse cross sections following a single radial burrow (r) shows the presence of collapse cones (c) above the radial burrow (positions i, ii, iii), including a portion with no collapse cone (iii). This radial burrow highlights the presence of zones with poor lithological contrast between the burrow wall and host sediment, making the outer wall hard to discern. Scale bars represent 1 cm.

2.5 Palaeobiological interpretations

2.5.1 Central zone component

The original, highly detailed, descriptions of *Phoebichnus trochoides* (Bromley and Asgaard 1972) were based on surface expressions and cross-sectional views but were undertaken without the benefit of serial grinding. The complex nature of the burrow has previously been explained as being the product of bulk-sediment deposit feeding by an organism that lived in the central region of the structure that made excursions into the surrounding sediment for food, thereby producing the radial component of the burrow (Bromley and Asgaard 1972; Kotake 2003).

2.5.2 Discussion of the central zone component

The central zone of *Phoebichnus trochoides* is several times the diameter of the radiating burrows, suggesting that it was much larger than the trace-maker (Bromley and Asgaard 1972; Bromley and Mørk 2000). There is, however, no clear modern analogue in which a large, open, cylindrical burrow is used by a bulk-sediment deposit-feeding organism. Shallow pit dwelling shrimp such as *Alpheus bellulus* make transient surficial pits, but commonly either have a central shell to hide beneath, or have a single dwelling burrow at the centre made by a commensal fish, and is not produced as a product of bulk-sediment deposit feeding (e.g. McIlroy 2010). It is considered that the existing models of *Phoebichnus* palaeobiology that have the trace-maker living in an open cylindrical pit would leave the trace-maker open to predation and as such require careful re-assessment. Our modelling of *Phoebichnus* central shafts in three-dimensions demonstrates that the

central zone was not an open structure (contra Bromley and Asgaard 1972; Kotake 2003), but was much more comparable to the surface detritus cones of many crustaceans (cf. Leaman *et al.* 2015; Fig. 2.11B).

2.5.3 Radial burrow component

The structure of the radial burrows led Bromley and Asgaard (1972) to infer that the trace-making organism made the burrows during two separate phases of burrowing. On the outward journey the organism produced a burrow with a ringed wall structure surrounding a central meniscate backfill as a result of outwardly directed deposit feeding (i.e. with the interface between successive rings and menisci oriented such that they were convex toward the central cylinder) (Fig. 2.10A). The final central burrow fill—that was considered by Bromley and Asgaard (1972) to be meniscate—was inferred to be produced by the returning organism re-burrowing the outgoing burrow, producing new menisci oriented with the convex surface directed away from the centre of the trace (i.e. opposite to the orientation of the first formed menisci) (Bromley and Asgaard 1972; Bromley and Mørk 2000; Fig. 2.10B).

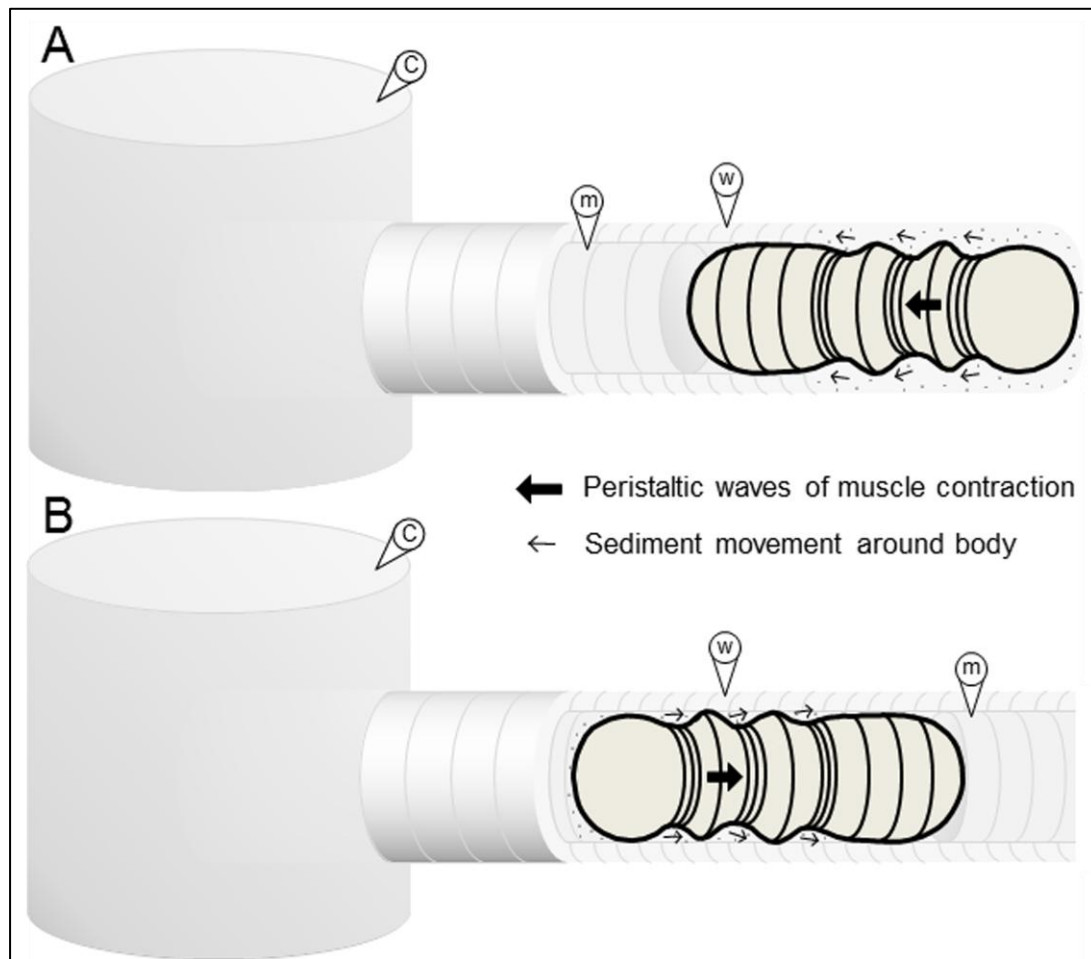


Fig. 2.10. Idealized sketch of Bromley and Asgaard's (1972) interpretation of how the structure of the radial galleries was formed. A: On the outward journey the organism produced a ringed wall structure (w) and meniscate backfill (m) convex toward the central zone (c). B: On the inward journey the organism re-burrowed the initial meniscate backfill with new meniscate (m) oriented convex away from the central zone. The model fails to explain several of the burrow features which were unknown at the time of interpretation including why there is no incidental lining produced by the returning organism, or whether the meniscate backfill is faecal or transported by peristaltic waves around the organism.

2.5.4 Discussion of radial burrow components

The burrowing hypothesis for the creation of the radial burrows, while architecturally and behaviourally possible, is considered to have a number of flaws. The final burrow fill in *Phoebichnus* is always perfectly centrally positioned within the horizontal burrow, which we find to be unlikely by way of the existing hypothesis. We have examined many specimens of *Phoebichnus* and have never found any exception to this rule. In addition, the authors fail to produce a hypothesis to explain why the trace-maker would re-burrow all of its radial burrows. The complex interpretation used to try to explain the structure of the radial burrows of *Phoebichnus* was driven by the assumption that the trace-making organism was producing meniscate backfill. Since meniscate backfill is by definition always convex in the direction from which the organism moved (d'Alessandro and Bromley 1987), it was logical to infer that—since the meniscae indicated the trace-maker returning to the centre of the structure—the trace-maker must also have first burrowed away from the central shaft. Our observations and careful cross sectioning show that the inference of meniscate backfill was erroneous, or at least does not apply to our material. We also note that convincing photographs of meniscate backfill have not been published from the type material. The angle of repose laminae that fill the central portion of the radial burrows is inconsistent with the re-burrowing model proposed (Bromley and Asgaard 1972), and therefore requires re-assessment.

The term mantle has been used by some authors to describe the outer structure of the radial burrows of *Phoebichnus trochoides* (e.g. Bromley 1996; Bromley and Mørk 2000), though the term wall is used in the original diagnosis (Bromley and Asgaard

1972). A lining and a mantle differ in that linings are actively produced by trace-making organisms, whereas mantles are passively formed during movement through sediment (Bromley 1996; Knaust 2015). Our interpretation agrees with the original diagnosis and considers that the outer structure of the radials is a wall, which was actively produced by the trace-maker.

2.6 Revised palaeobiological interpretation

The existing models for the formation of *Phoebichnus* (Bromley and Asgaard 1972; Kotake 2003) are based on flawed appreciation of the full three-dimensional nature of the burrow architecture. Such limitations in understanding the full three-dimensional morphology are common to many hand-specimen or field-based descriptions of trace fossils, especially where the organism-sediment interactions in the near-burrow environment have not been considered. This revised palaeobiological model is based upon our new observations and morphological characterisation of *Phoebichnus trochoides*. The ichnospecies *P. bosoensis* Kotake and *P. minor* Li also require careful reinvestigation of the type material as they appear to lack many of the key diagnostic features of the ichnogenus.

2.6.1 Central zone

The central zone of *Phoebichnus trochoides* is composed of irregularly stacked disk-shaped layers of sediment that are cut by a shaft-like burrow that is typically filled with sandstone (Fig. 2.11A). The layers of the central zone are clearly not the fill of an open shaft, and instead bear close resemblance to structures produced by the progressive

sinking of the sediment-water interface when covered by the surface cones of the modern crustacean *Neotrypea californiensis* in aquaria (Fig. 2.11B). The weight of the surficial mound of material excavated from the subsurface, and the active removal of sediment from below the surficial cone by *Neotrypea*, has been observed to cause the progressive sinking of the surface cone (Leaman *et al.* 2015). This collapse of the surface cone to deeper levels of the sediment is inferred to bring nutrient-rich sediment containing previously ejected faecal matter down into the subsurface portion of the burrow system (Leaman *et al.* 2015). Evidence for the presence of a surficial cone in *Phoebichnus*, above the central zone, comes from direct observation of specimens in the field that have a central boss protruding above the top of the bed (Figs. 2.4A-B, 2.11A).

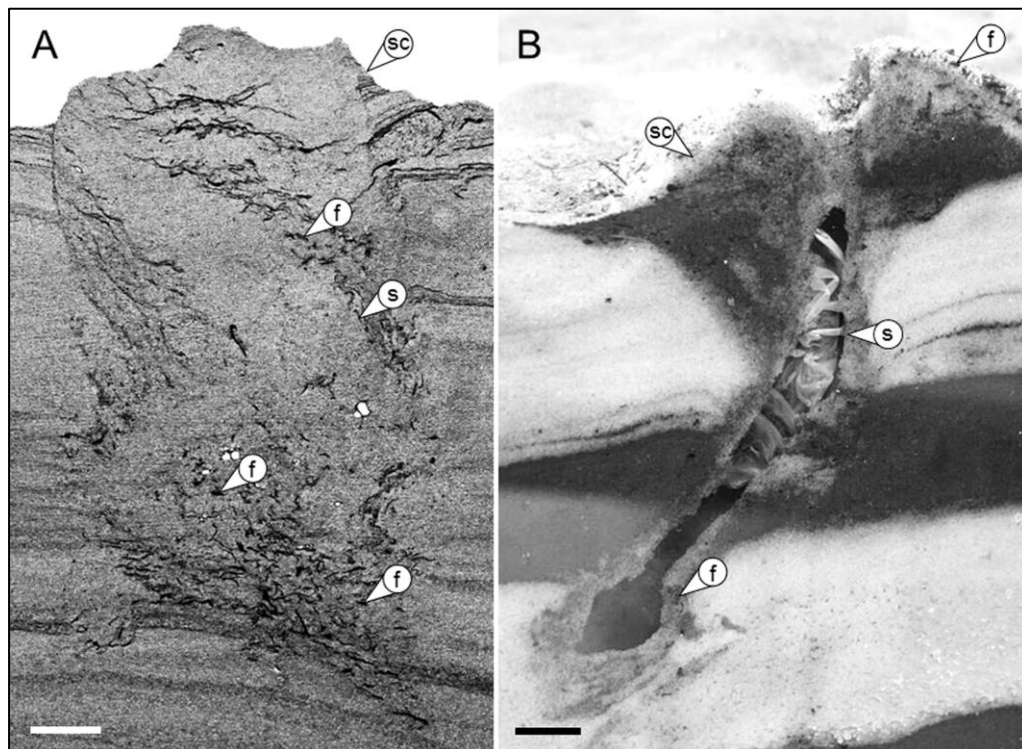


Fig. 2.11. Serial grind surface of *Phoebichnus trochoides* central boss and a central shaft built by *Neotrypea californiensis* in aquarium. A: Vertical transverse cross section through *Phoebichnus trochoides* central boss collapse cone structure with sub-vertical

central shaft (s), surface cone (sc), and faecal pellets (f). B: Sediment cone with sub-vertical central shaft (s), surface cone (sc), and faecal pellets (f) produced by *Neotrypea californiensis* in aquarium. Scale bars represent 1 cm.

2.6.2 Radial burrows

The sand-lined outer portion of the *Phoebichnus* galleries is inferred to be a sandy burrow lining comparable to that of *Palaeophycus heberti* and *Siphonichnus* (Stanistreet *et al.* 1980). Our direct observations of the ghost shrimp *Neotrypea* in sand-filled glass aquaria without clay demonstrate that crustaceans do create sandy linings to burrows (Fig. 2.12). Sand pellets about 2 mm in diameter have been observed to be produced by the mandibles of *Neotrypea*. In aquarium conditions without clay a burrow lining was created by *Neotrypea* by excavating a cavity which was then filled with sand grains, probably bound with mucus secreted by the shrimp (Fig. 2.12). Similar sandy pellets and sand rich linings have recently been documented in association with the inferred crustacean burrows *Thalassinoides* and *Ophiomorpha* (Tonkin *et al.* 2010; Boyd *et al.* 2012; Leaman *et al.* 2015). In the case of *Phoebichnus*, the pellets appear to have been organised as annuli around the open burrow, maintaining its circular form (compare to the muddy annuli of pellets characteristic of *Ophiomorpha annulata*). The curvature annuli described by several authors (Bromley and Asgaard 1972, Bromley and Mørk 2000) may be due to the progressive excavation of the distal portion of the previous pellet ring during the excavation that precedes the production of the subsequent—more distal—ring. The evidence for this mode of formation of annuli comes from the relatively common instances where the first formed—more proximal—pellets have not been cut during

excavation of the cavity into which the subsequent—more distal—ring of pellets was emplaced (Fig. 2.6B). We consider therefore that the outer sand-pellet lining of the radial burrows of *Phoebichnus* was probably structural in nature, and allowed the radiating galleries to be maintained as open burrows.

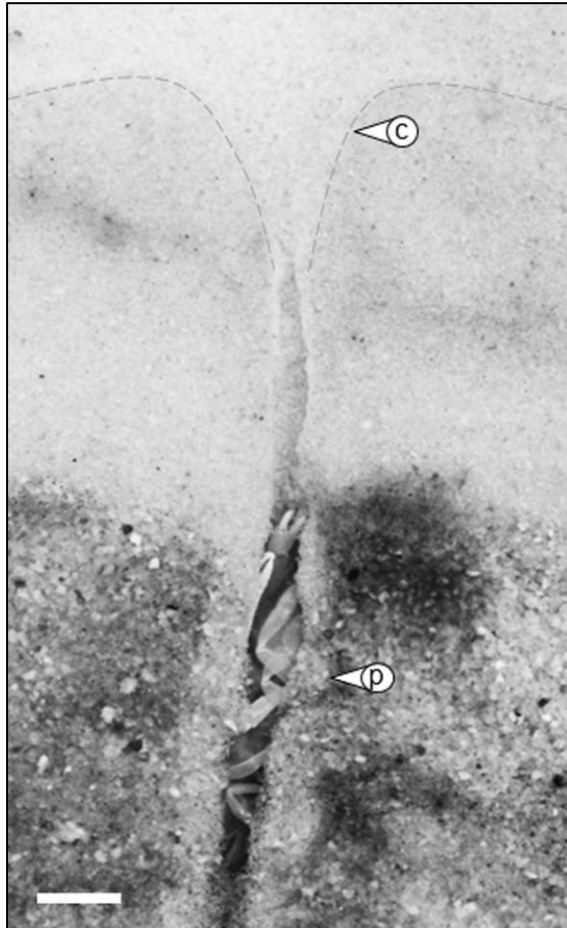


Fig. 2.12. *Neotrypea californiensis* creating a pelleted sand-lining to a burrow in a sand-dominated aquarium. Sand pellets (p) line the burrow walls; a collapse cone (c) is also visible. Scale bar represents 1 cm.

The creation of open galleries does however mean that the trace-maker requires somewhere to put the sediment excavated from the burrow. Burrowers that produce extensive open galleries—such as the makers of *Thalassinoides* and *Ophiomorpha*—must

dispose of sediment above the sediment-water interface in surface mounds. An alternative solution to sediment disposal exploited by the trace-makers of several common taxa involves sequestration of excess sediment in burrow galleries (*Ophiomorpha rudis*- Callow *et al.* 2013; *Ophiomorpha irregulaire*- Leaman *et al.* 2015; Fig. 2.13). The presence of angle of repose fill requires the burrow to have taken the form of an open gallery prior to filling by sediment grains. The fill of subsurface galleries is probably more energetically efficient than expelling sediment grains to the overlying sediment-water interface, but has the effect of rendering the filled portions of the burrow inoperative with regard to their original function. In this model the sediment grains filling the galleries are likely to have come from excavation of galleries in the same sediment horizon and explains the similarity of burrow fill to that of the host medium. This is unlike the case of *Phoebichnus bosoensis* that mainly fills its galleries with faecal pellets lithologically similar to the sediment at the contemporaneous seafloor, and requires reconsideration of the inclusion of that taxon within *Phoebichnus*.

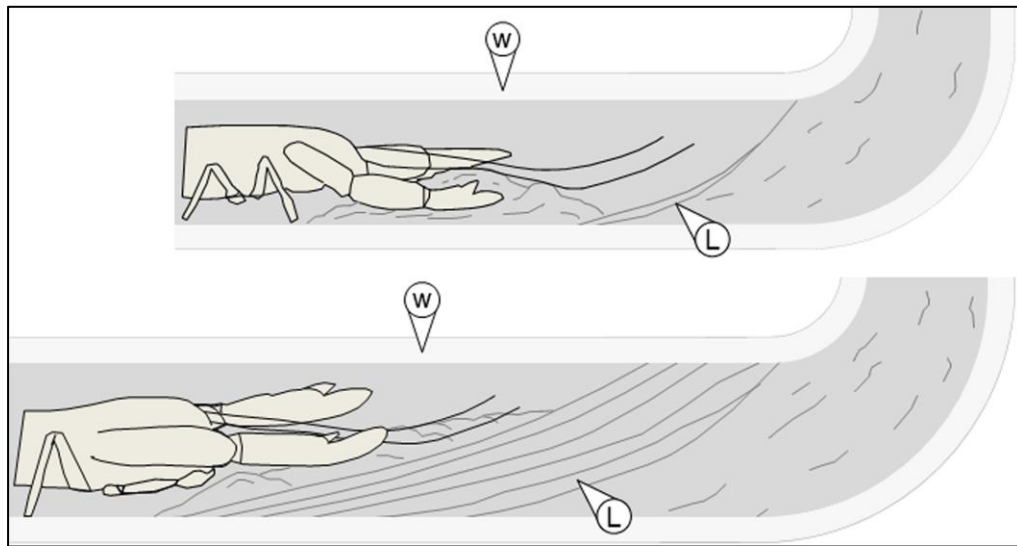


Fig. 2.13. Idealized sketches of a shrimp filling a sand-lined radial burrow (w) with inclined fill and angle of repose laminae (L).

2.6.3 Collapse cones

The presence of collapse cones above the radial galleries of *Phoebichnus trochoides* is taken to infer that the trace-maker engaged in collapse cone feeding in a manner similar to that observed in aquarium studies of the crustacean *Neotrypea* (Fig. 2.14). Periodically *Neotrypea* and other callianassid shrimp will destroy the pellets that line the gallery roof to allow sediment to collapse into gallery, thereby producing a funnel shaped disturbance (collapse cone) in the overlying sediment (cf. Thompson and Pritchard 1969; Leaman *et al.* 2015; Fig. 2.14). The sediment that falls into the galleries is typically moved, using the chelae, to other parts of the burrow, filling galleries with angle of repose laminae. This type of feeding has the advantage to an infaunal organism that it need not leave the burrow and search the seafloor in order to collect food, instead—following the creation of a collapse feature—the trace-maker can sift through the collapsed material in the safety of its burrow. The absence of a clear burrow lining in regions of the

Phoebichnus galleries with collapse cones is strongly suggestive of destruction of the burrow roof by the *Phoebichnus* trace-maker in order to feed using the collapse cone mechanism of modern *Neotrypea*. By comparison to the deliberate actions of *Neotrypea* in aquaria we are confident that as least most collapse cone of *Phoebichnus* are deliberately created in this way. Evidence from this study also suggests the end of the radial burrows may be distinguished by a steep curve up towards the bedding surface where the organism exhibited collapse cone feeding, perhaps comparable to the mechanism employed by various marine polychaetes which bioirrigate sediment cones to culture microbes before ingesting the same sediment (Rijken 1979; Bromley 1996; Herringshaw and McIlroy, 2013). In callianassid shrimp burrows, the creation of the collapse cones is inferred to be purely for deposit feeding without bioirrigation (e.g. Thompson and Pritchard 1969; Leaman and McIlroy 2015; Leaman *et al.* 2015).



Fig. 2.14. *Neotrypea californiensis* burrow gallery showing destruction of the pellet-lined roof (r) and sediment collapse (c) into the gallery. The right side of the photograph shows a previous collapse cone (c) under which the pellet-lined roof has been re-built. Scale bar represents 1 cm.

2.7 Palaeobiology

2.7.1 Full palaeobiological model for the formation of *Phoebichnus trochoides*

The new interpretation for the morphology of *Phoebichnus trochoides* arising from this work describes a central zone, which is defined by the progressive sinking of a surficial sediment cone. From this central zone many radial galleries radiate in an irregular manner (Fig. 2.15). The radial galleries have a sand-lined outer wall composed of concentric annuli of sand pellets that allowed the galleries to be maintained as open structures. After extending horizontally for a distance of 10-50 cm the burrows are found to curve sharply towards the bedding surface (Fig. 2.15). From this vertical shaft the organism is inferred to have exhibited collapse cone feeding behaviour (Fig. 2.15). Deliberate destruction of the burrow roof at intervals along the length of the gallery

allowed overlying sediment to collapse into the open burrow, creating conical “collapse cone” structures in the sediment overlying the radii of *P. trochoides* (Fig. 2.15). This sediment-collapse activity explains the localised lack of a sand-lining/wall to some of the radial galleries, which can be attributed to destruction of the roof in order to collapse cone feed. The organism employed two mechanisms of dealing with sediment from its galleries: 1) material was ejected onto the sediment via the shaft onto the surface sediment cone (often including faecal material and undigested organic detritus); and 2) transferred into other abandoned galleries as angle of repose fill.

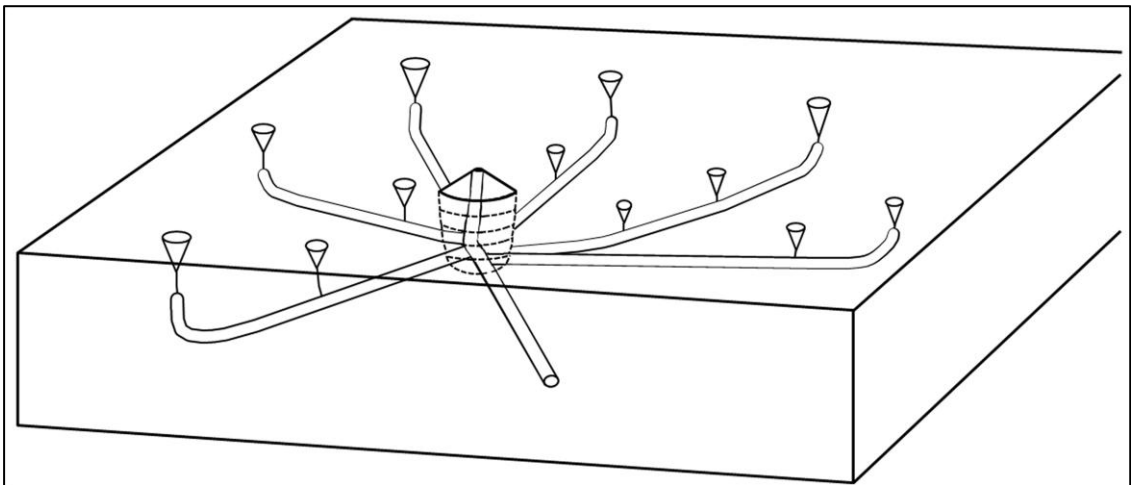


Fig. 2.15. Idealized sketch representing the full three-dimensional burrow reconstruction of *Phoebichnus trochoides* showing cylindrical central zone with multiple radiating burrows with collapse cones above the radial burrows along the burrow length and at terminations.

2.7.2 Possible communication between adjacent burrow systems

The bosses that represent the surface expression of the central cones of *Phoebichnus trochoides*, and are inferred to be the remnants of sediment cones, are typically spaced 50 cm to 1 m apart on bedding planes. Radial galleries documented in

the field do not generally cross-cut the galleries of other *Phoebichnus*, and the inclined fill of most radial galleries is directed towards the central zone. In one radial gallery observed in the field however, neither of these observations hold true. The gallery in question connects two adjacent central zones and has inclined laminae in the burrow fill directed towards the adjacent central zone. This may be evidence of the trace-maker abandoning one burrow system and establishing a new *Phoebichnus* in fresh sediment adjacent to its previous location. This observation is based on field observation only, and further observation of well-exposed outcrop examples should be sought before this hypothesis can be established as normal behaviour for the *Phoebichnus* trace-maker.

2.7.3 Possible biological affinity of the trace-maker

Previous studies of *Phoebichnus trochoides* have not speculated with respect to the taxonomic affinity of the trace-maker. We propose herein that, owing to significant similarities in the construction and behaviour—as inferred from interpretation of the morphological elements—that the trace-maker is likely to be an axiid shrimp crustacean similar to the producers of Mesozoic *Thalassinoides* and *Ophiomorpha*. To date, no modern axiid shrimp are known to produce such systematic radial structures as documented in *Phoebichnus*.

2.8 Ichnotaxonomy

Ichnogenus PHOEBICHNUS Bromley and Asgaard, 1972

Type ichnospecies: Phoebichnus trochoides Bromley and Asgaard 1972

Emended diagnosis: Large stellate structures up to 1.5m in diameter with a central zone of diffuse stacked dish-shaped structures 3-10cm wide that may be cut by both radial galleries and sub-vertical shafts. Radii are straight to slightly curved in vertical and lateral planes, have sand-rich linings of pelleted annuli, and a central tubular portion filled with angle of repose laminae typically inclined towards the central zone.

Remarks: *Phoebichnus* is interpreted as being the product of a deposit-feeding organism that excavated the sediment for its contained nutrients. Previous descriptions have suggested that the trace-maker lived within the wide central zone and that the radial burrows were produced during deposit feeding (Pemberton and Frey 1984; Dam 1989). The thorough three-dimensional investigation presented herein suggests that the central zone resulted from collapse of a surficial mound, up to 15cm wide, surrounding a central vertical shaft approximately 2cm wide. The organism did not live within the central cavity, but repeatedly returned to the central zone to deposit sediment and faecal matter on the sediment surface and to create the numerous radii at various depths in the sediment.

Global Distribution: *Phoebichnus trochoides* was first described from the Jurassic beds of the Neill Klintner and Vardekløft Formations of Jameson Land, East Greenland (Bromley and Asgaard 1972). From the Jameson Land, East Greenland locality it has since been described by Heinberg and Birkelund (1984), Dam (1990), and Bromley (1996). The Triassic Shublik Formation of Alaska (Parrish *et al.* 2001), the Triassic-Jurassic Wilhelmsøy subgroup of Festningen, Svalbard (Bromley and Mørk 2000), the Lower Jurassic Tilje Formation of the Mid Norwegian Continental Shelf (Taylor and

Goldring 1993), the Lower Jurassic Rør Formation of the Norwegian Continental Shelf (Goldring *et al.* 1991; Taylor and Goldring 1993), the Middle Jurassic Beryl Formation of the UK North Sea (Maxwell *et al.* 1999), the Middle Jurassic Lajas Formation of Argentina (McIlroy *et al.* 2005), the Middle Jurassic Kaladongar Formation of Western India (Joseph *et al.* 2012), the Upper Jurassic Nitron Member of west-central Alberta (Williams *et al.* 2013), the Lower Cretaceous Ben Nevis Formation of northeastern Newfoundland (Harding 1988), the Lower Cretaceous Viking Formation of Alberta (Coates and MacEachern 2007), the Upper Cretaceous Cardium Formation of Alberta (Pemberton and Frey 1984), the Upper Cretaceous Blackhawk Formation of Utah (Frey and Howard 1990), the Upper Cretaceous Wall Creek Member and Upper Ferron Sandstone Member of Wyoming and Utah (Gani *et al.* 2007), and the Upper Cretaceous Nise Formation of offshore Norway (Hubbard *et al.* 2012).

A second species of *Phoebichnus* (*P. bosoensis*) has recently been described from the Lower Pleistocene Otadai Formation of Japan, which differs from *P. trochoides* in a number of ways: 1) the radial burrows have no lining or mantle; 2) the radii are packed with elliptical pellets; 3) the pellets are composed of surface detritus; 4) the central zone is much narrower than it is deep; 5) the central zone was open throughout burrow construction; 6) the radii are composed of meniscate backfill; 7) there are no associated collapse cone features (see Kotake 2003). These morphological differences we consider to be sufficiently different to the type material of *Phoebichnus* that *P. bosoensis* would be better placed in its own genus (pending reconsideration of the type material).

Phoebichnus trochoides Bromley and Asgaard 1972

Emended diagnosis: Central vertical zone composed of stacked disk-shaped layers of organic detritus and sediment, sometimes cut by a sub-vertical shaft, from which long, narrow, radial galleries emerge. Radial galleries are typically straight but may curve in the vertical and lateral planes. Radial galleries have a sand-rich lining composed of annuli of sand pellets and are sand-filled with angle of repose laminae.

Studied Material: 3 specimens, 4 thin sections, and numerous field observations.

Description: Vertically oriented central zone, 4-8 cm in diameter but of unknown maximum depth, upper portion comprised of stacked dish-shaped layers defined by concentrations of organic detritus. Extending from the central zone at various depths and angles are numerous radial galleries 1-2 cm in diameter and observed up to 1 m in length. The radial galleries are circular in cross-section, and possess a distinct sand-rich burrow lining comprised of annuli 0.5 cm thick, the upper portion of which is locally absent where the gallery underlies collapse cones. The fill of the radial galleries is composed of angle of repose laminae that are generally directed towards the central zone. The radial galleries may be straight and parallel in the horizontal plane, may bend laterally, curve oblique to bedding, or curve sharply towards sediment surface to become vertically oriented. Funnel shaped zones of disturbed or collapsed sediment may be present above both horizontal and vertically oriented radial galleries, at any point along the length of the galleries.

2.9 Conclusion

The serial grinding and three-dimensional reconstruction techniques employed during this study have enabled the re-examination and revision of the morphology and palaeobiology of *Phoebichnus trochoides*. Several new discoveries have been presented herein:

- The cylindrical central boss is composed of irregularly stacked disk-shaped layers of highly bioturbated sediment and is compared to the sinking of a surficial cone of sediment ejected from the burrow as seen in modern trace-makers of *Ophiomorpha* (e.g. Leaman *et al.* 2015).
- The radial galleries have a thick outer wall of sandy pellets organised into concentric annuli that has previously been considered to be produced by meniscate backfill.
- The fill of the radial galleries is demonstrated to be angle of repose laminae inclined towards the central zone, rather than meniscate backfill as suggested in the ichnogenic diagnosis, implying that the trace-making organism filled its burrows from a dwelling position close to the central boss with material excavated from elsewhere in the burrow.
- The presence of subtle small-scale conical sedimentary collapse structures above radial galleries demonstrate that the trace-maker engaged in collapse cone feeding through destruction of portions of the burrow roof.
- The presence of a pelleted wall, the association of collapse cones above the burrow galleries, and the inclined fill of the radial galleries supports the inference

that the burrow was maintained as an open structure and subsequently passively filled.

- Axiid crustaceans are possible trace-makers, based on ethological comparisons with the burrows of modern axiids (e.g. Leaman *et al.* 2015).

2.10 Acknowledgements

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Chapter 3

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

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(Submitted to Palaeogeography, Palaeoclimatology, Palaeoecology)

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 have revealed a number of hitherto unknown morphological elements more comparable to the ichnogenus *Schaubcylindrichnus*, thereby creating *S. 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 ichnogenic diagnosis of *Palaeophycus*. *Schaubcylindrichnus heberti* differs from all other species of *Schaubcylindrichnus* in that the burrow wall is mineralogically heterogeneous rather than purely quartzose, the ichnogenic diagnosis is thus emended to accommodate *S. heberti*.

Key words: *Palaeophycus heberti*, *Schaubcylindrichnus*, trace fossil, burrow wall, palaeobiology, three-dimensional reconstruction.

3.1 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 1990; 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 & McIlroy 2016).

This study aims to morphologically characterise well-preserved specimens of *Palaeophycus heberti* from hand-samples that originated in strata rich in *Phoebichnus trochoides* (cf. Evans and McIlroy 2016). *Phoebichnus trochoides* is a much larger trace fossil than *Palaeophycus 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 *Palaeophycus heberti* might be burrows of the juvenile form of the *Phoebichnus 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 2016).

The specimens selected for this study were collected in order to investigate the full three-dimensional morphology and palaeobiology of *Palaeophycus 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 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).

3.2 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. 3.1). 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).

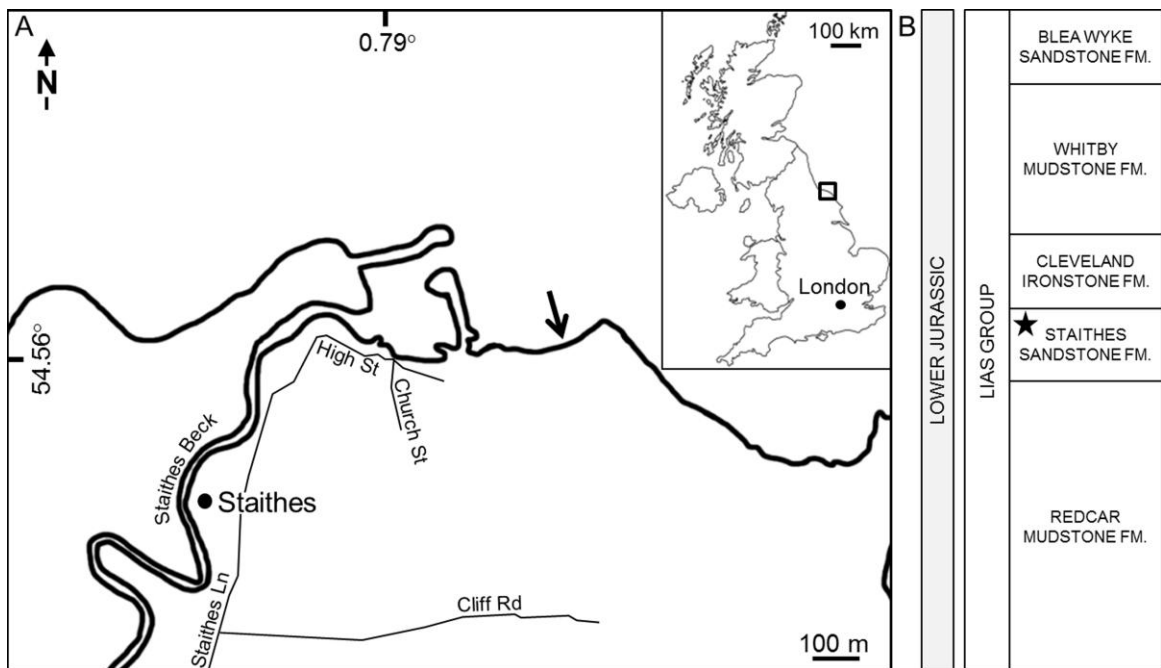


Fig. 3.1. Sample collection site and generalized stratigraphic column. A: Map of field location at Staithes, UK. Arrow shows approximate collection location of the samples. B: Stratigraphic column of the Lias Group showing the stratigraphic level studied.

3.3 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.

3.4 Descriptive ichnology

The cylindrical, sub-horizontal burrows characterised herein are typified by their thick sand-rich burrow wall, and would by convention be considered to be *Palaeophycus heberti* (Fig. 3.2; cf. Saporta 1872; Pemberton and Frey 1982, Fillion and Pickerill 1990). Burrow diameters range from 5 to 10 mm, of which the outer wall takes up a large portion of the total diameter of the burrows, being between 1 and 2.5 mm in thickness (Fig. 3.2). The thickness of the wall and the diameter of the central fill may vary along the length of any given burrow. Digital cross-sectioning shows that bedding-parallel portions of burrows can be compacted to produce an elliptical cross-section from the originally circular form (Fig. 3.2C–D). The sand-lined burrows in the studied samples show no preferential orientation. Perfect longitudinal cross-sections of long segments of burrows, created by digital cross-sectioning of the reconstructed rock volume, show that the gross morphology of the longest preserved burrow lengths is a very broad U-shape that curves downwards in a bedding perpendicular or oblique plane (Fig. 3.3). The longest, but still incomplete, burrow sampled was about 16 cm in length and up to 3.6 cm deep.

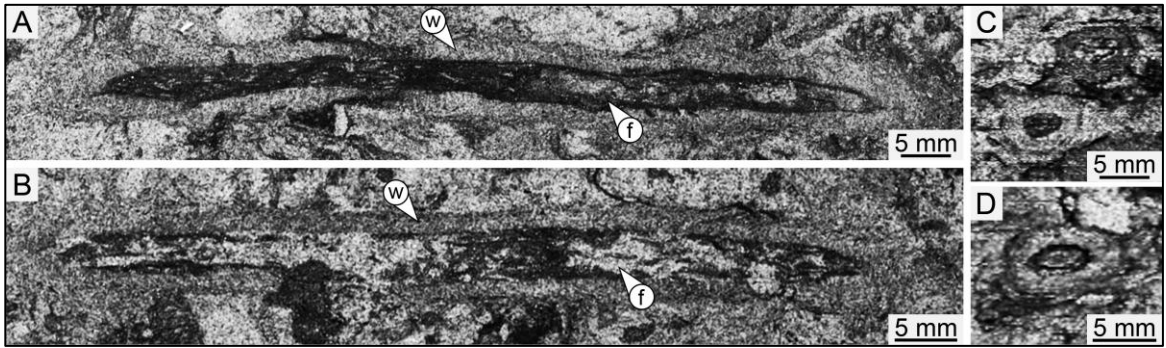


Fig. 3.2. Cross-sections through sand-walled burrows showing the thick wall (w) and passive fill (f). A and B: Horizontal longitudinal cross-sections with lithologically variable passive burrow fills (f). C and D: Transverse cross-sections of the same burrows showing the variability in cross-section shape from largely uncompressed circular in C, to elliptical and compacted in D.

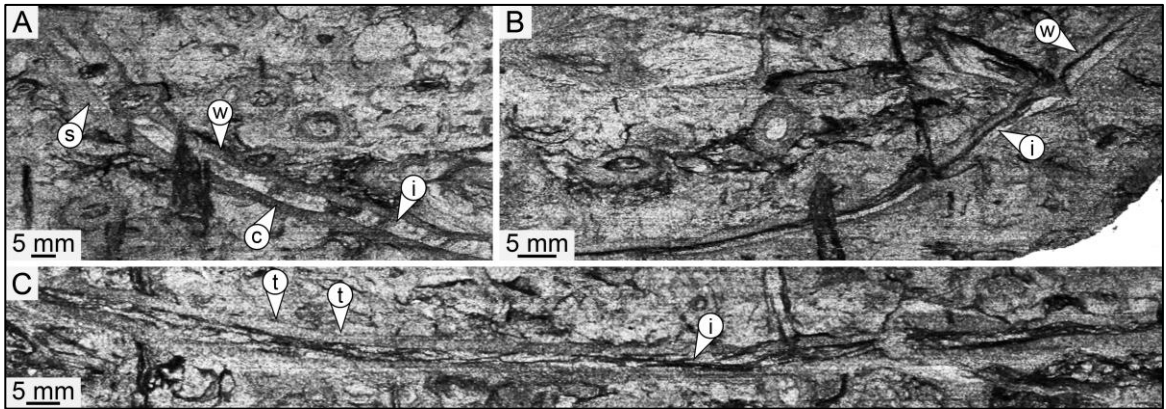


Fig. 3.3. Bedding perpendicular, longitudinal cross-sections showing the typical broad U-shaped morphology of the burrows. A and B: Longitudinal (digitally sliced) cross-sections of burrows curving from sub-horizontal in the centre of the U to nearly to sub-vertical close to the inferred sediment-water interface. A and B show laminated (passive) fill of inclined laminae (i), and demonstrate the variable proportions of sand to clay in the burrow wall along its length from sand-rich (s) to clay-rich (c) portions. C: Longitudinal (digitally sliced) cross-section showing physically laminated burrow fill with irregularly inclined laminae (i) and a burrow wall that is irregular in thickness (t).

The distinctively thick sand-rich wall in the studied material is directly comparable to *Palaeophycus heberti*. The wall makes up approximately half of the total burrow diameter and is lithologically similar to, but better sorted than the surrounding

sediment, containing a mixture of quartz, feldspar, clay minerals and micas (Fig. 3.2). Along the length of some burrows the darkness of the wall is variable, becoming darker where the proportion of clay and mica to quartzose sand increases (Fig. 3.3A). The thickness of the wall may change along the length of a burrow. This is demonstrable through direct observation of wall thickness variability along the length of burrows with unchanging diameter of the central burrow fill (Fig. 3.3). The wall has a finely laminated annular structure that is most prominent in the darker, clay-rich, portions of the wall (Fig. 3.4). In sections of burrows rich in clays and micas, the boundary between successive annular rings is curved in a consistent direction along the full length of the burrow (Fig. 3.4). Some burrows also have a thin patina of clay minerals at the boundary between the wall and fill (Fig. 3.4). Burrow walls may contain radial, clay-filled, cracks that extend 1–3 mm from the inner margin of the wall (Fig. 3.5).

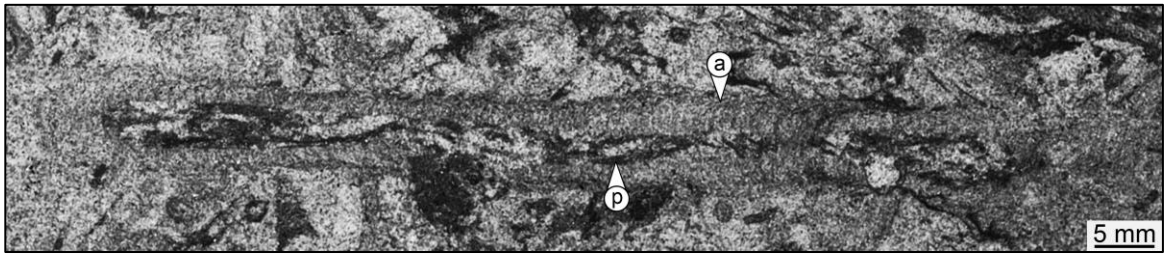


Fig. 3.4. Bedding-parallel longitudinal cross-section showing the annular structure of the sandy burrow wall with curved laminae (a) implying construction from left to right. Thin patina (p) of clay minerals is present between the burrow wall and fill.

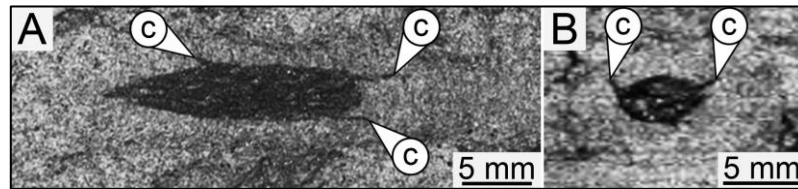


Fig. 3.5. Cross-sections showing clay-filled cracks extending from the inner surface of the burrow wall. A: Oblique cross-section and B: Vertical transverse (digitally sliced) cross-section showing cracks (c) in the burrow wall due to collapse or compaction of the burrow.

None of the reconstructed burrows show true branching, and most are isolated though some burrows are closely adjacent to one another (Fig. 3.6A), and may either re-burrow adjacent burrows, or share part of the wall (Fig. 3.6B–C) in a manner reminiscent of *Schaubcylindrichnus coronus* (Howard 1966; Chamberlain 1976; Nara 2006). This morphology is comparable to secondary successive branching wherein an organism followed an earlier burrow for some distance before deviating its course at an angle from the original burrow to produce a side branch that superficially resembles true branching (D’Alessandro and Bromley 1987).

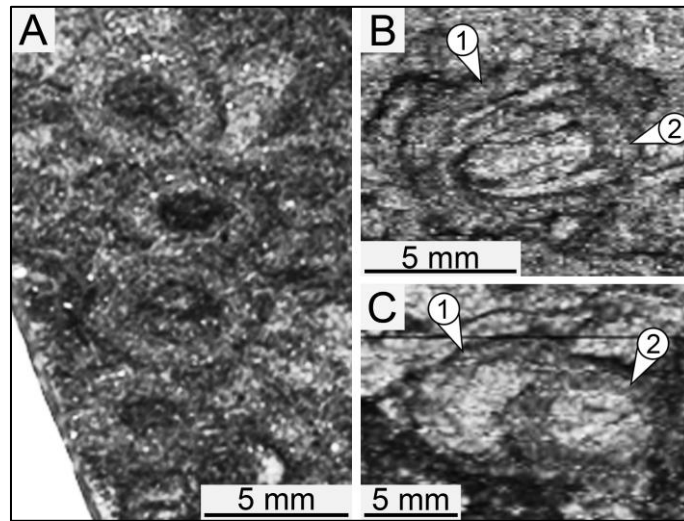


Fig. 3.6. Bedding perpendicular and transverse (digitally sliced) cross-sections of sand-lined burrows. A: Close vertical stacking of burrows. B: Re-burrowing. C: Burrow wall sharing which may be due to re-burrowing. The burrows in B and C are labelled in the order of successive creation.

The burrow fill may be massive or laminated and can contain variable proportions of clay and sand-grade material, which can vary along the length of a single burrow, and is not necessarily lithologically comparable to the host sediment (Fig. 3.7). Where the burrow fill is laminated, the laminae are typically either regularly spaced and gutter shaped, or irregular in morphology and discontinuous in distribution (Figs. 3.3C, and 3.8). This is dissimilar to the consistently high “angle of repose” laminae seen in the burrow fill of the burrow *Phoebichnus trochoides* (Evans and McIlroy 2016). A single burrow from the dozens of otherwise identical sand-lined burrows studied shows a well-developed meniscate backfill, in which the meniscas of the burrow fill are curved in the same direction as the curvature of the annular burrow wall (Fig. 3.9). This meniscate burrow does not have a stellate morphology or a central boss, which would have made it

more comparable with the associated (but much larger) *Phoebichnus trochoides* (Evans and McIlroy 2016).

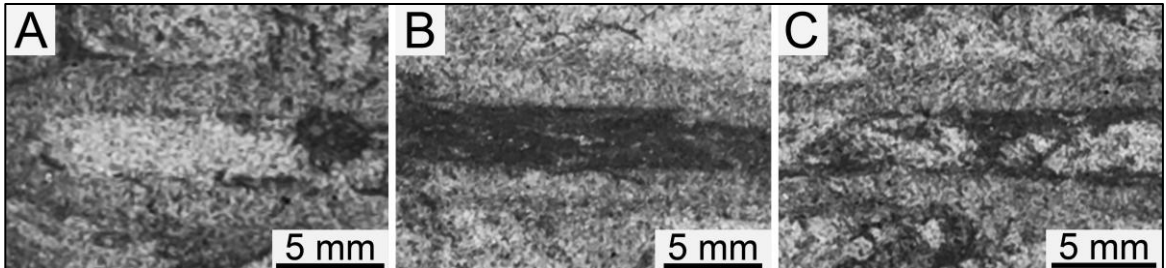


Fig. 3.7. Longitudinal cross-sections through burrows showing the variability of the burrow fill. A: Massive and lithologically similar to the host rock. B: Massive and more clay rich than the host rock. C: Irregularly, discontinuously laminated and laterally variable burrow fill broadly similar to the host rock in lithology.

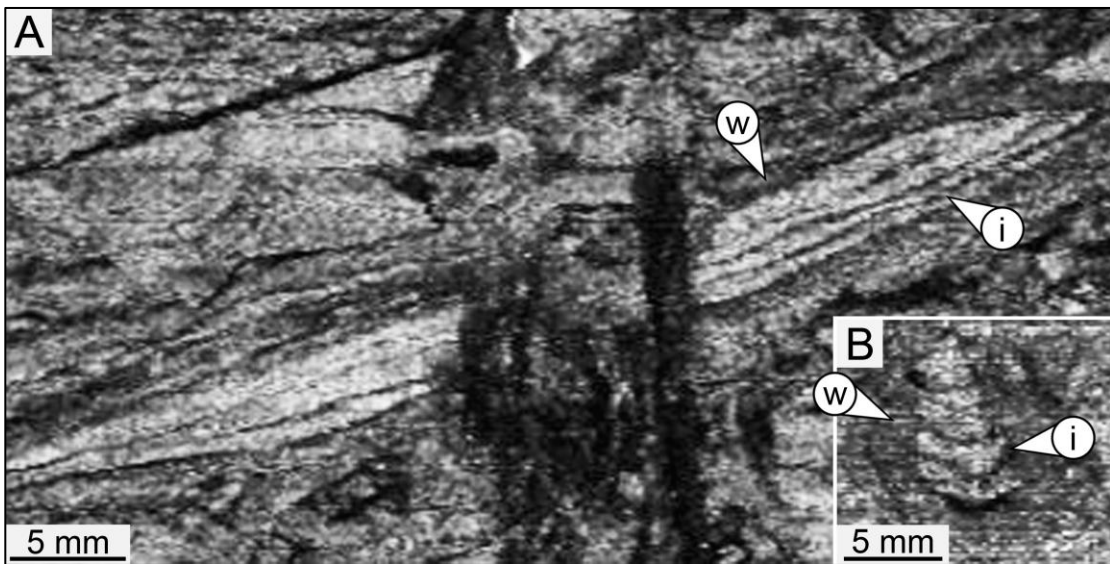


Fig. 3.8. Cross-sections of a burrow with inclined trough-like passive burrow fill. A: Bedding perpendicular longitudinal (digitally sliced) cross-section through a burrow with thick wall (w) with a fill composed of inclined laminae (i). B: Transverse (digitally sliced) cross-section of the same burrow showing the U-shaped cross section of the laminae (i) demonstrating that they are trough-like in three-dimensions.

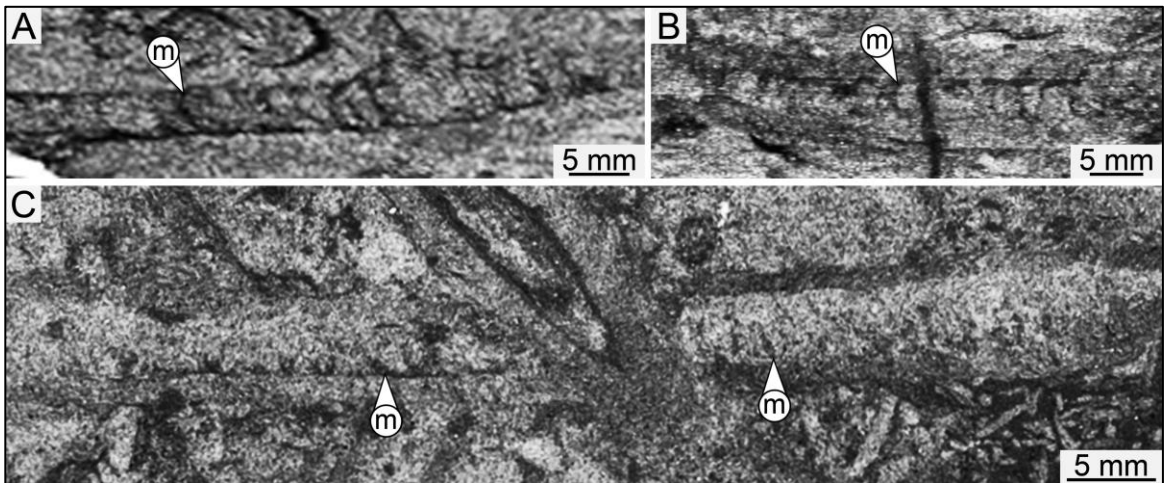


Fig. 3.9. Cross-sections through burrows with meniscate backfill. A and B: Vertical longitudinal (digitally sliced) cross-sections showing meniscate laminae (m) demonstrating backfilling behaviour of an organism moving from left to right. C: Bedding parallel cross-section in which the curved annular rings of the burrow wall are curved in the same direction as the meniscate backfill (m).

3.5 Taxonomic considerations

Palaeophycus has, in general, been considered to be simple passageways produced by bulk sediment, non-selective, vagile deposit feeders or the semi-permanent burrows of predacious endobenthic organisms (Osgood 1970; Pemberton and Frey 1982). The standard model for the production of all *Palaeophycus* is that as the trace-maker moved through the sediment it pushed the sediment around it such that the burrow would collapse behind it, except in cases where mucus was applied to the walls, which confers temporary rigidity prior to collapse (Osgood 1970). The material that fills *Palaeophycus* is typically the same as the host sediment, probably because vagile infaunal organisms, if they are not grain-selective deposit feeders (cf. Bednarz and McIlroy 2012), simply pass the majority of grains around their bodies, except those grains that are ingested and re-

deposited as faeces (Osgood 1970). The fact that the burrows studied herein do not have a consistent lithological fill suggests that they are unlike *Palaeophycus* in terms of mode of formation. Passively filled burrows are, by implication, those that are maintained as open burrows, and as such cannot be produced by the actions of vagile deposit-feeding organisms, since they largely live independently of the overlying water column and have no reason to maintain a connection to it. Organisms that live in open burrows can be predaceous, suspension feeding, surface deposit feeding, reverse conveyors, bioirrigators or microbial farmers (Pemberton and Frey 1982; Bromley 1996; Herringshaw *et al.* 2010). We note that most of these modes of feeding are at odds with the inferred mode of formation of most other species of *Palaeophycus*, and call into question the attribution of both the present material, and indeed all *Palaeophycus heberti*, to the ichnogenus *Palaeophycus*. If we accept that the material studied herein is typical of the species *heberti* then a number of key observations of taxonomic importance follow:

- 1) The annulate structure of the burrow wall and the broad U-shaped burrow morphology when seen in longitudinal cross section is inconsistent with the placement of *heberti* in *Palaeophycus*;

- 2) The bow-shaped morphology of the burrow (Fig. 3.3), along with the local vertical clustering of burrows (Fig. 3.6A) is highly comparable to the ichnogenus *Schaubcylindrichnus* Frey and Howard 1981;

- 3) *Schaubcylindrichnus*, as currently defined is reserved for burrows with thick, sandy walls composed of pure quartz, and thus have a distinctive white appearance in the field (Frey and Howard 1981; Miller 1995; Nara 2006; Löwemark and Hong 2006; Löwemark and Nara 2010). Otherwise, no component of the existing diagnosis is

incompatible with the newly revealed morphology of the Staithes Formation *heberti* described herein;

4) The recent description of *S. coronus* as a broad U-shaped burrow with associated collapse feeding cone at one end (Nara 2006; Löwemark and Nara 2010) is entirely consistent with our morphological reconstructions. Though we note that this observation has not hitherto been formally incorporated into the ichnogenic diagnosis of *Schaubcylindrichnus*.

We propose that the ichnogenic diagnosis of *Schaubcylindrichnus* could be usefully emended and broadened to include taxa with slightly thicker, less clean burrow walls, but that are otherwise morphologically identical, such as the ichnospecies *heberti*. Since *Schaubcylindrichnus coronus* and *heberti* commonly occur in the same successions, and even the same beds (e.g. Frey 1990; Frey and Howard 1990; Bann and Fielding 2004; McIlroy 2004; McIlroy 2007; Pervesler *et al.* 2011; Olivero and López Cabrera 2013), the difference in clay content of the wall would be better expressed at the level of ichnospecies rather than ichnogenus. We suggest therefore that *heberti* should be considered as a species of *Schaubcylindrichnus* that has a thick wall constructed of more diverse mineral grains than the other valid ichnospecies of *Schaubcylindrichnus* (i.e. *S. coronus*; see systematic treatment below).

We find no evidence in our material of *Schaubcylindrichnus (Palaeophycus) heberti* for the characteristic stellate structure and central boss associated with *Phoebichnus trochoides*. The passive burrow fill of *S. heberti* is dissimilar to the actively created angle of repose laminae characteristic of *P. trochoides* (Evans and McIlroy 2016). The only other remaining gross similarity is in that both taxa have thick, annulate, sand-

rich burrow walls that are composed of curved annuli. We consider that the annuli of the *S. heberti* walls were created as successive laminae (Fig. 3.10A-B) rather than by adjacent, slightly cross cutting, rings of pellets as is seen in *P. trochoides* (Evans and McIlroy 2016). The new data presented herein leads us to conclude that *Schaubcylindrichnus heberti* is not the burrow of the juvenile trace-makers of *Phoebichnus trochoides*, which leaves us with the ongoing issue of a lack of evidence for the activity of juvenile *Phoebichnus* trace-makers; a question that we cannot at present answer.

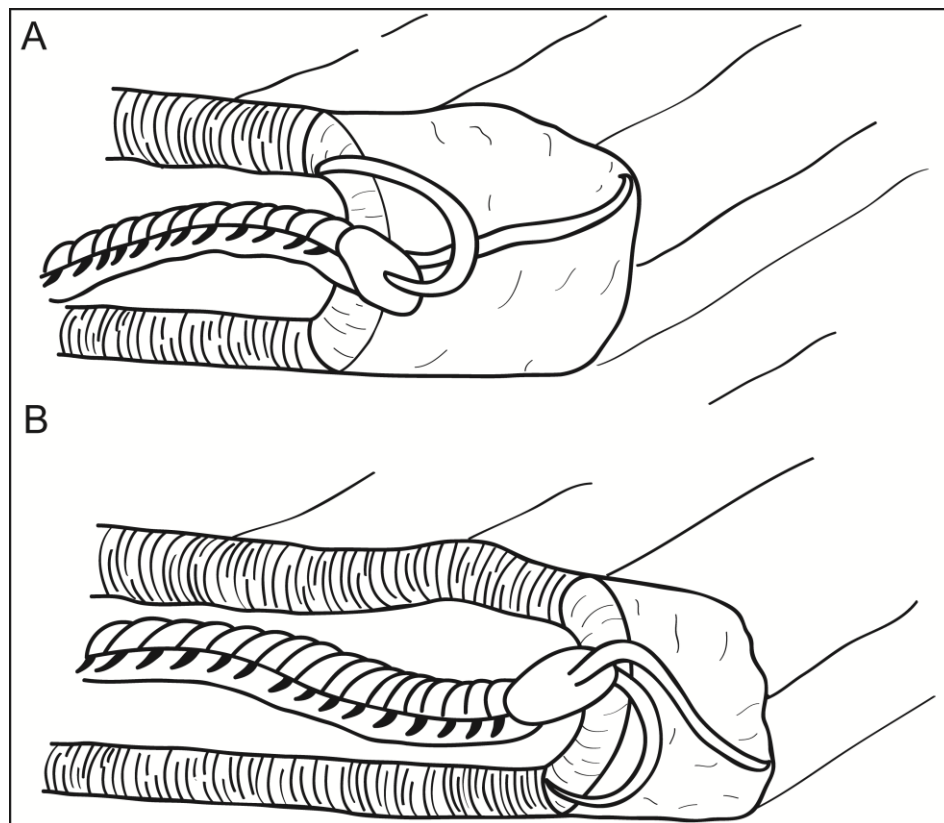


Fig. 3.10. Idealized sketch of how the structure of the burrow wall of *Schaubcylindrichnus (Palaeophycus) heberti* was formed. A: The trace-maker excavated sediment ahead of the burrow creating a cavity. B: Excavated sediment was packed into the burrow wall with mucus to produce a consecutive series of thin annuli. Variability in

the shape of the excavation in front of the burrow causes the local differences in burrow wall thickness (B).

3.6 Palaeobiology of *Schaubcylindrichnus heberti* comb. nov.

The burrow wall of *Schaubcylindrichnus heberti* was probably created by the active packing of sediment, excavated from ahead of the constructed burrow, into the wall to produce a series of thin annuli in the wall (Figs. 3.4, 3.10). We consider that the trace-maker excavated sediment ahead of the burrow to create a cavity (Fig 3.10A), possibly during the initial deposit-feeding phase, during which the open U-burrow was created (cf. Nara 2006). Since the laminae of the wall are convex towards one end of the burrow system (Fig. 3.11), and are typically slightly sandier than the host sediment it is likely that there was a component of grain-selective deposit feeding during initial burrow excavation. Any ingested material was likely excreted as faeces on the seafloor since no faecal pellets have been discovered in the burrow fill. During this deposit feeding/burrow excavation phase, at least some sediment must have been removed to create the open burrow. This was probably ejected onto the seafloor at one end of the burrow, probably as a sediment cone (Fig. 3.11; cf. Nara 2006). This is consistent with the conical subsidence feature documented around one end of some *Schaubcylindrichnus coronus* (Fig. 3.12A; Löwemark & Nara 2010).

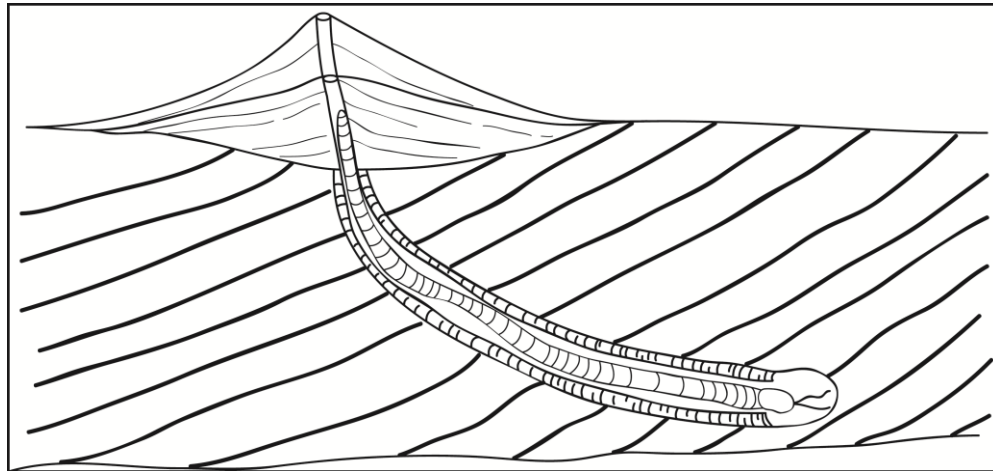


Fig. 3.11. Idealized sketch of the sediment cone and subsidence of the sediment cone into underlying strata at the tail end of a *Schaubcylindrichnus heberti* burrow.

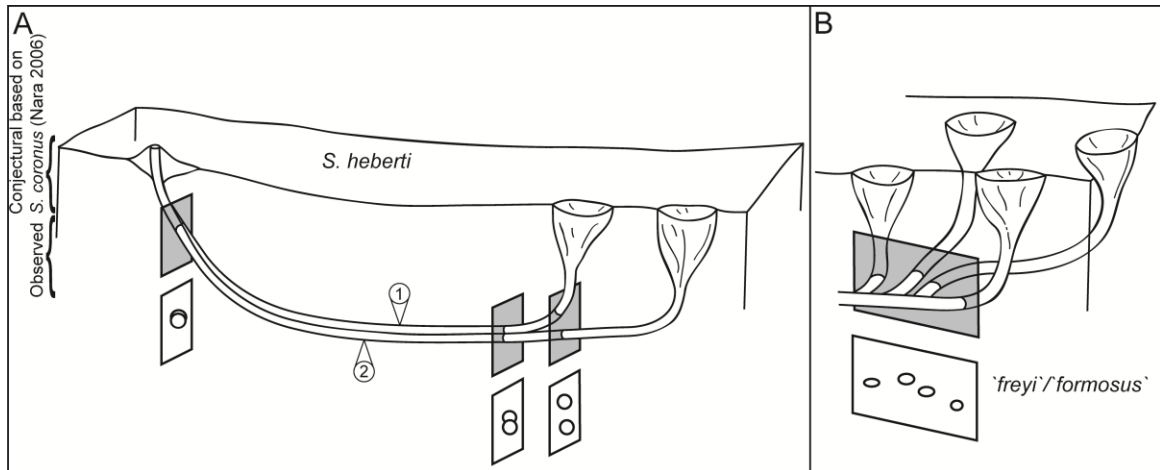


Fig. 3.12. Idealized sketch representing the full burrow reconstruction of *Schaubcylindrichnus heberti* based on our reconstruction of *Schaubcylindrichnus heberti* and inferred sediment surface and feeding cones following Nara (2006). A: Burrows contain a sediment cone at the tail end and collapse feeding cones at the head end. The burrows are labelled in the order of successive creation showing how the organism uses the previous burrows wall when constructing a new burrow. B: Lateral shifting of the position of the feeding cones.

The widespread paradigm that walls are constructed for structural reinforcement of burrows in loose sediments (e.g. Bromley 1996; Buatois and Mángano 2011), while true in some cases, is not universally applicable. Mucus applied to the burrow margin

alone is commonly enough to hold a burrow open, even in loosely consolidated sediments (Leaman *et al.* 2015). It may be that, in long-lived burrows, the thick walls provide protection from predation since many modern organisms secrete toxins into burrow walls to deter predators (e.g. Woodin *et al.* 1987). Building a thick wall of low clay and organic matter content may discourage accidental re-burrowing by deposit feeders seeking fine-grained sediment, thereby helping the *Schaubcylindrichnus* trace-maker avoid the metabolic cost of burrow-repair. Thick burrow walls can also provide temporary or permanent protection from the external pore-water environment (Keighley and Pickerill 1994) and allow for more effective bioirrigation (Herringshaw and McIlroy 2013).

The passive sediment fill typical of most *Schaubcylindrichnus heberti* burrows (Figs. 3.2, 3.3, 3.7, and 3.8) implies that the burrow was maintained as an open structure during the life of the trace-maker. This is consistent with the observation that *S. heberti* was an open U-shape structure. Clay patinas observed in some burrows also indicate that they were maintained as open structures (Fig. 3.4). Our material does not show the terminations of the U-burrow of *S. heberti*, though we would suggest that a collapse-cone typical of funnel feeding mode of life—as seen in *S. coronus* (Nara 2006; Löwemark and Nara 2010)—is likely (see Fig. 3.12A). The meniscate structure observed in the fill of a single burrow in this study is atypical of both *Palaeophycus* and *Schaubcylindrichnus*. We struggle to explain such a form during the normal inferred mode of life of the *Schaubcylindrichnus* trace-maker. Such meniscate backfill might, however, be created as part of an escape response to sediment inundation of the burrow in which the trace-maker abandoned the lined burrow by excavating a tunnel through one end to re-establish connection with the newly created—stratigraphically higher—seafloor. Instances where

burrows are observed to be adjacent to one another or have been re-burrowed may be the result of the *Schaubcylindrichnus*-producing organism utilizing the wall of an abandoned burrow when building a new burrow (Figs. 3.6, 3.12A). By using a pre-existing burrow wall the trace-maker would save on the metabolic energy needed to construct that part of the wall anew (Nara 2006).

The pattern of lateral shifting of the position of the feeding cones (Fig. 3.12B) is likely to account for the different burrow positions that have previously been used as a species defining characteristic (i.e. *Schaubcylindrichnus freyi* and *S. formosus*). This, however, has been rejected and the two species, *S. freyi* and *S. formosus*, informally considered to be junior synonyms of *S. coronus* (Nara 2006; Löwemark and Nara 2010). Our recognition of these same burrow distributions in association with the less clean walls of *S. heberti* supports the rejection of burrow distribution as a useful ichnotaxobase in *Schaubcylindrichnus*.

3.6.1. Full palaeobiological model for the formation of *Schaubcylindrichnus heberti* comb. nov.

We consider that the trace-maker created the U-burrow by excavating the sediment and then packing sediment around itself progressively as rings, creating a thick wall, with a curved heterolithic annular structure (Figs. 3.10, 3.11). The trace-maker lived within the open burrow and from one end exhibited funnel-feeding behaviour (Fig. 3.12). Faeces and excess sediment produced from burrowing was expelled onto the sediment surface at the opposite end of the burrow system (Fig. 3.12). Ultimately, the trace-maker would abandon the burrow and build a new one, sometimes using the abandoned burrows

wall when constructing the new burrow. This resulted in closely adjacent burrows that in some cases shared a burrow wall or re-burrowed the adjacent burrow (Fig. 3.13). The abandoned open burrow was passively filled with sediment.

3.7 Ichnotaxonomy

Ichnogenus SCHAUBCYLINDRICHNUS, Frey and Howard 1981

Type ichnospecies: Schaubcylindrichnus coronus, Frey and Howard 1981

Emended diagnosis: Wide U-burrows curved in the vertical plane, with thick sand-rich burrow lining that may contain some proportion of clay-grade material. May be either isolated or clustered, an inverted sediment cone may be associated with the upper terminations in some material.

Remarks: *Schaubcylindrichnus* is emended to accommodate taxa with similar wall architecture and gross-morphology as the type species, but containing variable amounts of dark clay or mica in the wall. *Schaubcylindrichnus* has hitherto been reserved for burrows with walls composed of pure quartz.

Schaubcylindrichnus (Palaeophycus) heberti comb. nov.

Emended diagnosis: *Schaubcylindrichnus* with sand-rich, finely laminated burrow lining containing dark clay minerals and micas. Burrow fill usually passive, rarely meniscate.

- 1872 *Siphonites heberti* Saporta, p. 110, pl. 22, fig. 1, 2.
- 1883 *Palaeophycus heberti* Saporta; Saporta and Marion, p. 97, text-fig. 23.
- 1925 *Palaeophycus heberti* Saporta; Fritel, p. 40.
- 1955 *Siphonites heberti* Saporta; Andrews, p. 238.
- 1955 ?worm tubes; Danner, p. 451, text-figs. 1-4.
- 1957 *Siphonites heberti* Saporta; Gardet *et al.*, p. 997, text-figs. 1, 2.
- 1962 *Siphonites heberti* Saporta; Häntzschel, p. W215, text-fig. 135-4.
- 1962 *Palaeophycus heberti* Saporta; Häntzschel, p. W215.
- 1963 *Siphonites* (?) Häntzschel, 1962; MacKenzie, pl. 2, figs. c-e, text-figs. 3, 4
[white-walled burrows] (see below).
- 1970 *Siphonites heberti* Saporta; Andrews, p. 197.
- 1971 white-walled burrows; MacKenzie, pl. 3, figs. c-e.
- p1973 *Siphonites heberti* Saporta; Heinberg, p. 232, text-figs. 3c-d, 8, 9.
- 1975 *Siphonites heberti* Saporta; Häntzschel, p. W106, text-fig. 65-2.
- 1975 *Palaeophycus heberti* (Saporta); Häntzschel, p. W106.
- 1975 *Palaeophycus heberti* Saporta; Alpert, p. 518.

- p1976 *Siphonites heberti* Saporta; Pollard and Lovell, p. 217, pl. 2, fig. A, text-figs. 4, 5.
- 1982 *Palaeophycus heberti* Saporta; Pemberton and Frey, p. 861, pl. 1, figs. 4, 9; pl. 4, fig. 4.
- 1984 *Palaeophycus heberti* Saporta; Howard and Frey, p. 206, fig. 12.
- p. 1985 *Palaeophycus* isp. Hall; Frey and Bromley, p. 811, fig. 13A, C.
- 1985a *Palaeophycus heberti* Saporta; Frey and Howard, p. 382, figs. 5.5, 5.9, 12, 16.10
- 1985b *Palaeophycus heberti* Saporta; Frey and Howard, p.133, fig. 11A.
- 1985 *Palaeophycus heberti* Saporta; Frey and Pemberton, fig. 3.
- 1987 *Palaeophycus heberti* Saporta; Badve, p. 117, pl. 4, fig. 1.
- 1988 *Palaeophycus heberti* Saporta; Vossler and Pemberton, p. 252.
- .1989 *Palaeophycus* isp. Hall; Dam, p. 137, fig. 11C.
- 1990 *Palaeophycus heberti* Saporta; Fillion and Pickerill, p. 43, pl. 10, figs. 14, 16.
- 1990 *Palaeophycus heberti* Saporta; Frey, fig. 4c.
- 1990 *Palaeophycus heberti* Saporta; Frey and Howard, p. 812, fig. 13.4, 16.5, 20.2.
- 1990 *Palaeophycus heberti* Saporta; Maples and Suttner, p. 872, fig. 12.8.
- 1996 *Palaeophycus heberti* Saporta; Bromley, p. 163, figs. 11.3, 11.16, 11.17.

- 1998 *Palaeophycus heberti* Saporta; Kundal and Sanganwar, p. 625, pl. 3, figs. 4, 5.
- 2000 *Palaeophycus heberti* Saporta; MacEachern and Burton, fig. 6, 7.
- 2001 *Palaeophycus heberti* Saporta; Tchoumatchenco and Uchman, p. 89, fig. 6b.
- 2004 *Palaeophycus heberti* Saporta; McIlroy, p. 243, figs. 4d, 5ai
- 2006 *Palaeophycus heberti* Saporta; Fernandes and Carvalho, p. 215, fig. 7.
- 2006 *Palaeophycus heberti* Saporta; Fürsich *et al.*, p. 603, fig. 4G, H.
- 2006 *Palaeophycus heberti* Saporta; Löwemark and Hong, fig. 8.
- 2006 *Palaeophycus heberti* Saporta; Melchor *et al.*, p. 262, fig. 6E.
- 2006 *Palaeophycus heberti* Saporta; Nara, p. 451.
- 2006 *Palaeophycus heberti* Saporta; Tanner *et al.*, p. 24, fig. 4A, B.
- 2007 *Palaeophycus heberti* Saporta; McIlroy, fig. 6d.
- 2008 *Palaeophycus heberti* Saporta; Uchman *et al.*, p. 64, fig. 4B, C.
- 2008 *Palaeophycus heberti* Saporta; Zhang *et al.*, p. 55, fig. 7b.
- 2009a *Palaeophycus heberti* Saporta; Rodríguez-Tovar *et al.*, p. 410, fig. 3C, D.
- 2009b *Palaeophycus heberti* Saporta; Rodríguez-Tovar *et al.*, p. 88, fig. 6.
- 2009 *Palaeophycus heberti* Saporta; Retallack, p. 373, fig. 9C, E.
- 2010 *Palaeophycus heberti* Saporta; Rodríguez-Tovar and Uchman, p. 580, fig. 6E.

- 2010 *Palaeophycus heberti* Saporta; Nagendra *et al.*, p. 527, fig. 3d.
- 2010 *Palaeophycus heberti* Saporta; Zonneveld *et al.*, fig. 10E
- 2011 *Palaeophycus* cf. *heberti* Saporta; Pervesler *et al.*, p. 584, fig. 2J.
- 2011 *Palaeophycus heberti* Saporta; Tiwari *et al.*, p. 1134, pl. 2b.
- 2012 *Palaeophycus heberti* Saporta; Desai and Saklani, fig. 3i
- 2012a *Palaeophycus heberti* Saporta; Mude *et al.*, p. 27, pl. 1, fig. 6.
- 2012b *Palaeophycus heberti* Saporta; Mude *et al.*, p. 160, pl. 1, fig. 5, pl. 2, fig. 4
- 2012 *Palaeophycus heberti* Saporta; Witts *et al.*, fig. 7b-E.
- 2013 *Palaeophycus heberti* Saporta; Šimo and Tomašovych, p. 266, figs. 6A, C, 11A, C.
- 2014 *Palaeophycus heberti* Saporta; Bayet-Goll *et al.*, p. 16.
- 2015 *Palaeophycus* cf. *heberti* Saporta; Song *et al.*, p. 5, fig. 4b.
- 2015 *Palaeophycus heberti* Saporta; Wang *et al.*, p. 7, fig. 3e.
- 2015 *Palaeophycus heberti* Saporta Zhang and Zhao, p. 334, fig. 5n
- 2015 *Palaeophycus heberti* Saporta; Zhao *et al.*, p. 110, fig. 7E

Studied material: 2 rock samples each containing numerous burrow specimens (available only as digital data) and numerous field observations.

Description: Burrow diameters range from 5–10 mm, the outer wall takes up a large portion of the total diameter of the burrows, ranging from 1–2.5 mm thick, and surrounds a fill 2.5–5 mm in diameter. Burrows are circular in cross-section except where they are compressed into an elliptical cross-section. The gross morphology is interpreted to be a broad U-shape in the vertical to oblique plane. Burrows may be isolated or occur as closely clustered adjacent burrows. Cross-sectional dimensions constant within individual burrows but vary between different burrows. The finely laminated wall has a curved annular structure defined by dark clay minerals and micas. The burrow fill is passive (either massive or laminated), or rarely meniscate.

Discussion: *Schaubcylindrichnus heberti* differs from other species of *Schaubcylindrichnus* in having clay and mica in the wall, which, in the only other currently valid ichnospecies, *S. coronus*, is composed of clean quartzose sand. *S. heberti* differs from other species of *Palaeophycus* in having a broad-open U-shaped burrow that in some cases may follow adjacent burrows or share portions of their burrow wall. Burrows of the similar, but much larger, *Phoebichnus* are radially arranged with an actively produced angle-of-repose burrow fill (Evans & McIlroy 2016) that is not seen in *S. heberti*. Short segments of *S. heberti* with meniscate backfill, considered herein to be an escape response, can look similar to *Beaconites capronus*, though the latter is much more continuous, commonly bedding parallel, vermiform, and never an open U-shape.

It is noted that *Schaubcylindrichnus* is most commonly found in highly bioturbated offshore facies, in which the collapse cones and sediment cones have low preservation potential. As such, these difficult-to-preserve features should not be used as a defining taxonomic feature of any species of this genus.

3.8 Conclusions

1. The studied thick-walled *Palaeophycus heberti* are determined herein to be a broadly U shaped, which requires their inclusion within the ichnogenus *Schaubcylindrichnus* to create *Schaubcylindrichnus heberti* comb. nov.
2. The burrows may be closely clustered or isolated in a manner comparable to *S. coronus* (sensu Löwemark & Nara 2010) from which it only differs in the mineralogical immaturity of the burrow wall in *S. heberti* (Fig. 3.6A).
3. The wall is composed of clay and sand-rich annular rings that are inferred to result from progressive accretion of a wall adjacent to the cavity excavated by the trace maker during initial creation of the open burrow (Fig. 3.10).
4. During initial burrow creation, grain-selective deposit feeding is likely to have affected the mineralogical composition of the wall due to ingestion of finer-grained material and the ejection of faeces at the seafloor.
5. The passive fill of the open burrows—either post-mortem, or following burrow abandonment—may be lithologically different to the host sediment, and may contain sedimentary laminae (Figs. 3.2, 3.3, 3.7, and 3.8).
6. Rare meniscate backfill of *S. heberti* is considered to record escape behaviour following the burrow being filled with sediment while occupied and escape through one end of the burrow (Fig. 3.9).
7. There is no behavioural/ichnological evidence to suggest that *S. heberti* was formed by juveniles of the commonly associated—but much larger—stellate burrow

Phoebichnus trochoides. The main morphological similarity—the thickly sand-lined wall—is considered to be behavioural convergence.

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Chapter 4

Summary

4.1 Introduction

This study explores the full three-dimensional morphology and palaeobiology of the similarly thickly lined trace fossils *Phoebichnus trochoides* and *Schaubcylindrichnus (Palaeophycus) heberti* through the tomographic creation of three-dimensional models of the trace fossils and whole rock models of trace fossil bearing samples. The study was motivated by the need to better understand the morphology, palaeobiology, and palaeoecological/palaeoenvironmental context of these common shallow marine trace fossils that are present in many shallow marine hydrocarbon reservoirs worldwide, particularly those of Mesozoic age (Bromley and Asgaard 1972; Frey and Howard 1990; Bromley and Mørk 2000; McIlroy 2004b; Rajkonwar *et al.* 2013). The three-dimensional reconstructions produced were essential to fully characterizing these structures and have significantly improved the understanding of these two taxa.

The outcomes of this research are relevant to the recognition and palaeobiological interpretation of the two taxa considered (*Phoebichnus trochoides* and *Schaubcylindrichnus (Palaeophycus) heberti*). The data collected has enabled us to determine the full three-dimensional morphology, fully understand the organism-sediment interactions, and assess the mode of life of the trace-making taxa. Understanding the complete morphology of these two taxa will additionally improve their identification in the field and in core-based cross sections since the models can be sliced in an infinite number of planes. The palaeobiological and ethological interpretations of these trace fossils can additionally be used to inform their use as palaeoenvironmental indicators. Importantly, the three-dimensional models improve the taxonomic

understanding of both *Phoebichnus trochoides* and *Schaubcylindrichnus (Palaeophycus) heberti*, which require significant taxonomic change and emendation of diagnoses at both the species and genus level.

4.2 *Phoebichnus trochoides*

The three-dimensional reconstructions of *Phoebichnus trochoides* created as part of this study have enabled the identification of the full morphology of the trace fossil which has facilitated new interpretations of the trace-makers behaviour. The broadly cylindrical, central zone of *P. trochoides* is revealed to be composed of irregularly stacked disk-shaped layers of highly bioturbated sediment surrounding a central vertical shaft rather than an open cylinder as has been previously implied (Evans and McIlroy 2016). The structure is comparable to structures produced by the modern crustacean *Neotrypea californiensis* in aquaria (Leaman *et al.* 2015). By analogy with the activities of the modern *N. californiensis*, the central zone is herein interpreted to be the product of the progressive sinking of a surficial sediment cone created by the trace-maker from excavated sediment produced during burrowing. The trace-making organism is inferred to have ejected displaced sediment and faecal matter onto the sediment surface surrounding the central shaft creating a mound (Evans and McIlroy 2016). The mound eventually sinks under its weight into the sediment below creating the conical structures around the central shaft (Evans and McIlroy 2016).

Radial galleries emanate from the central shaft, and are inferred to have been produced during the deposit feeding activity of the trace-maker (Evans and McIlroy 2016). The radial galleries have been found in this study to be composed of a thick outer

wall of sandy pellets organised into concentric annuli rather than the simple constructed wall inferred by previous work (Bromley and Asgaard 1972; Bromley and Mørk 2000). Observations of *Neotrypea californiensis* in sand-filled glass aquaria demonstrate that the crustacean creates sandy linings that result in similar burrow morphologies to *Phoebichnus trochoides* (Leaman *et al.* 2015). By analogy with the activities of *N. californiensis*, the *P. trochoides* trace-maker is inferred to have excavated a cavity which was then filled with sand grains probably bound with mucus (Evans and McIlroy 2016). In the case of *Phoebichnus*, the sand pellets appear to have been organised as annuli around the open burrow (Evans and McIlroy 2016). The curvature or arcuate outer edge of the annuli, that is comparable to that of the outer meniscus lining described previously (Bromley and Asgaard 1972), may be due to the progressive excavation of the distal portion of the previous pellet ring during the excavation that precedes the production of the subsequent—more distal—ring. The thick constructed wall allowed the galleries to be maintained as open structures. The outer wall surrounds a sand-rich burrow fill that is demonstrated, through study of digitally created cross-sections, to be composed of angle of repose laminae that are inclined toward the central zone rather than meniscate backfill which has been assumed to date, and forms an integral part of the original diagnosis of the ichnogenus (Evans and McIlroy 2016). The angle of repose laminae are inferred to have been actively produced by the trace-maker during the filling of open galleries (Evans and McIlroy 2016). It is considered likely that, when the trace-making organism had finished using a radial gallery, the open space in the centre of the radial element was

filled with sediment excavated during the creation of a new radial burrow associated with the same central shaft.

Whole rock models of *Phoebichnus trochoides* enabled the identification of organism-sediment interactions in the near burrow environment for the first time. Above several of the galleries there is evidence of small-scale conical sediment collapse that can be determined by the presence of downwardly deflected sedimentary laminae overlying unlined portions of the radial galleries (Evans and McIlroy 2016). These structures are comparable to collapse structures produced by *Neotrypea californiensis* in aquaria (Leaman *et al.* 2015). These structures are interpreted to be the result of the deliberate destruction and collapse of portions of the burrow roof at intervals along the length of the gallery. This caused overlying sediment to collapse into the open burrow, forming conical ‘collapse cone’ structures in the sediment overlying the radii (cf. Leaman *et al.* 2015). By analogy with the activities of *N. californiensis*, it is considered likely that after the trace-making organism had sifted through the collapsed sediment in the gallery for food the material was either ejected onto the sediment surface via the central shaft or transferred into other abandoned galleries as angle of repose fill (Evans and McIlroy 2016).

Several aspects of the morphology of *Phoebichnus trochoides* are comparable to features seen in studies of modern crustaceans (Leaman *et al.* 2015). While there is no known modern trace-maker that creates a stellate structure, this does not rule out the possibility of a similarly behaving organism.

4.3 *Schaubcylindrichnus heberti* comb. nov.

The three-dimensional analysis of specimens attributed to *Palaeophycus heberti* has revealed a number of hitherto unknown morphological elements that are more comparable to the ichnogenus *Schaubcylindrichnus*. Longitudinal cross-sections of long segments of burrows created by digital cross-sectioning of the reconstructed rock volume, demonstrate that the gross morphology of *heberti* is a broad open U-shape that curves downwards in a bedding perpendicular or oblique plane. This morphology is inconsistent with the ichnogenic diagnosis of *Palaeophycus* as sub-horizontal burrows, and more comparable to *Schaubcylindrichnus*. The burrows are typified by their thick sand-rich wall which makes up approximately half of the total diameter of the burrow and is lithologically similar to, but better sorted than the surrounding sediment. Through the examination of precisely ground serial surfaces the burrow wall was found to have a finely laminated annular structure, which is inconsistent with the placement of *heberti* in *Palaeophycus*. The walls of *heberti* are herein considered anomalous within the ichnogenus *Palaeophycus* and differ only in mineralogical immaturity from the walls of *Schaubcylindrichnus*. The walls of *Schaubcylindrichnus* are currently defined as being composed of pure quartz, and thus has a distinctive white appearance, while the walls of *heberti* are lithologically similar to the surrounding sediment, and may contain a mixture of quartz, feldspar, clay minerals, and micas (Frey and Howard 1981; Miller 1995; Nara 2006; Löwemark and Hong 2006; Löwemark and Nara 2010). The burrow fill was demonstrated to be passive and may contain variable proportions of clay and sand-grade material and sedimentary laminae also comparable to *Schaubcylindrichnus*. Some

burrows were observed to be closely adjacent to one another, and in some cases to either re-burrow adjacent burrows, or share their burrow wall in a manner analogous to *Schaubcylindrichnus* (cf. Löwemark & Nara 2010).

The newly identified morphological elements of *heberti* have led to a new interpretation of the trace-makers behaviour. The U-shaped morphology of the burrows and the passive sediment fill typical of most *heberti* burrows implies that the burrow was maintained as an open structure during the life of the trace-maker. The modes of feeding associated with passively filled, open burrows (e.g. suspension feeding, surface deposit feeding, reverse conveyor feeding, bioirrigation or microbial farming) are at odds with the inferred mode of formation of most other ichnospecies of *Palaeophycus* as being produced by vagile deposit feeders. However, recent descriptions of *Schaubcylindrichnus*, as a broad U-shaped burrow with a collapse feeding cone at one end (Nara 2006; Löwemark and Nara 2010), is consistent with our morphological reconstructions of *heberti*. Though our material does not show the distal termination of the U-burrow of *heberti*, we would suggest that a collapse-cone typical of funnel feeding mode of life is likely. The annular structure of the burrow walls is interpreted as being produced by the trace-maker excavating sediment ahead of the burrow to create a cavity. The trace-maker then progressively packed mucus-bound host sediment into the burrow wall in consecutive annular rings to produce a series of thin annuli. The fact that the walls are typically slightly sandier than the host sediment suggests that there was a component of grain-selective deposit feeding during initial burrow excavation. Some of the excavated sediment was likely ejected onto the seafloor at the tail end of the burrow, probably as a sediment cone as has been recently inferred for *Schaubcylindrichnus* by Nara (2006).

Instances of re-burrowing or clustering of burrows may be the result of the producing organism utilizing an abandoned burrows wall when building a new burrow as inferred for *Schaubcylindrichnus* (cf. Nara 2006). The different burrow positions that have previously been used as species defining characteristic (i.e. *Schaubcylindrichnus freyi* and *S. formosus*) are likely a result of lateral shifting of the position of the feeding cones. These same burrow distributions have been observed in association with *heberti*.

A review of the ichnospecies *Palaeophycus heberti* was undertaken and on the basis of its morphological characteristics the species is herein synonymised with *Schaubcylindrichnus* to create *S. heberti* comb. nov., which differs from all other species of *Schaubcylindrichnus* in that the constructed burrow wall is mineralogically heterogeneous rather than being purely quartzose. We herein propose the emendation and broadening of the ichnogenic diagnosis of *Schaubcylindrichnus* to include taxa with less clean burrow walls. Since *Schaubcylindrichnus* and *heberti* commonly occur in the same successions, and even the same beds (e.g. Frey 1990; Frey and Howard 1990; Bann and Fielding 2004; McIlroy 2004b; McIlroy 2007; Pervesler *et al* 2011; Olivero and López Cabrera 2013), the difference in clay content of the burrow wall would be better expressed at the level of species rather than genus. We suggest therefore that *heberti* should be considered as a species of *Schaubcylindrichnus* that has a thick burrow wall constructed of more diverse mineral grains than the other valid ichnospecies of *Schaubcylindrichnus*.

4.4 Concluding statement

The proper morphological description and palaeobiological understanding of trace fossils is at the root of reliable integration of ichnology into sedimentological and palaeoenvironmental analyses (McIlroy 2004a; McIlroy 2008). This thesis highlights how three-dimensional morphological reconstructions are essential to fully characterizing and understanding these structures (Bednarz and McIlroy 2009; Bednarz and McIlroy 2012; Boyd *et al.* 2012; Bednarz *et al.* 2015; Leaman *et al.* 2015; Leaman and McIlroy 2015; Boyd and McIlroy 2016 (in review)). As ichnology continues to develop, the need for a complete understanding of the three-dimensional morphology of a trace fossil is becoming more important. It is suggested that slowly all ichnotaxa should receive a similar treatment to that undertaken herein.

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