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Original article

Three-dimensional morphology and palaeobiology of the trace fossil *Dactyloidites jordii* nov. isp. from the Carboniferous of England☆

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ABSTRACT

The diverse ichnological assemblage from the outcrops near Howick (Northumberland, United Kingdom) is exceptionally well-preserved. Among these Carboniferous ichnotaxa is a new ichnospecies of *Dactyloidites*. Specimens were collected and processed using high-resolution serial grinding and photography to produce an accurate and precise three-dimensional model of these new burrows in full colour. The model produced in association with petrographic thin sections and field observations is used as the basis for comparison between *Dactyloidites jordii* nov. isp. and other ichnospecies of *Dactyloidites*. The current taxonomic status of the ichnogenus is examined and reviewed. *D. jordii* nov. isp. is a broadly bisymmetrical, stellate to palmate burrow composed of numerous long, narrow rays that exhibit three orders of branching arranged into tiered galleries radiating from a central shaft. The trace maker is suggested to be a vermiform organism with an adaptive burrowing strategy that facilitates alteration of its burrow construction to accommodate suboptimal sediment conditions. The adaptive nature of trace-making organisms and the inherent anisotropy of many burrowed media highlight the need for ichnologists to provide a type series rather than a single holotype, in order to capture the inherent range of common burrow morphologies.

1. Introduction

Exceptionally well-preserved stellate trace fossils of the ichnogenus *Dactyloidites* from the interbedded sandstones and siltstones of the Carboniferous Stainmore Formation of the Yoredale Group in Northumberland, United Kingdom (Fig. 1) were investigated using serial grinding and three-dimensional reconstruction (Bednarz and McIlroy, 2009; Boyd et al., 2012; Bednarz et al., 2015). The detailed reconstructions allow consideration of the bauplan for the construction of the ichnogenus *Dactyloidites* Hall, 1886. The modelling approach employed herein, when integrated with field observations and petrographic analysis, allows the trace fossil to be considered within the context of the surrounding sediment.

The ichnogenus *Dactyloidites*, like many radiating trace fossil taxa, has a complex taxonomic history and is in need of thorough revision. This paper aims to summarize the current ichnotaxonomic status of *Dactyloidites* and to consider the present material within that framework. Outside the material presented herein are four valid ichnospecies: *D. asteroides* Fitch, 1850, *D. cabanasi* (Meléndez in Cabanás, 1966), *D. ottoi* (Geinitz, 1849), and *D. peniculus* (D'Alessandro and Bromley, 1986). As both *D. asteroides* and *D. cabanasi* differ significantly from *D. ottoi* and *D. peniculus*, our material is compared only with the more similar *D. ottoi* and *D. peniculus*.

Dactyloidites is found in interbedded siltstones and sandstones that range from centimeter to decimeter in thickness. The Stainmore Formation shows net upward-coarsening, and is composed of several upward-coarsening parasequences. The *Dactyloidites*-bearing part of the succession consists of clean sandstones with hummocky cross stratification interbedded with micaceous siltstones in which bioturbation generally ranges from 5 to 20%, except for rare, highly bioturbated mudstones that are upwards of 90% bioturbated. The depositional setting is inferred to have been that of a storm-dominated marine shoreface, with the *Dactyloidites* being found in strata deposited below the fair-weather wave base, but above the storm wave base (Fig. 2).

2. Methodology

Eight field samples were collected and analysed for this study using the serial grinding and photographic methods developed by

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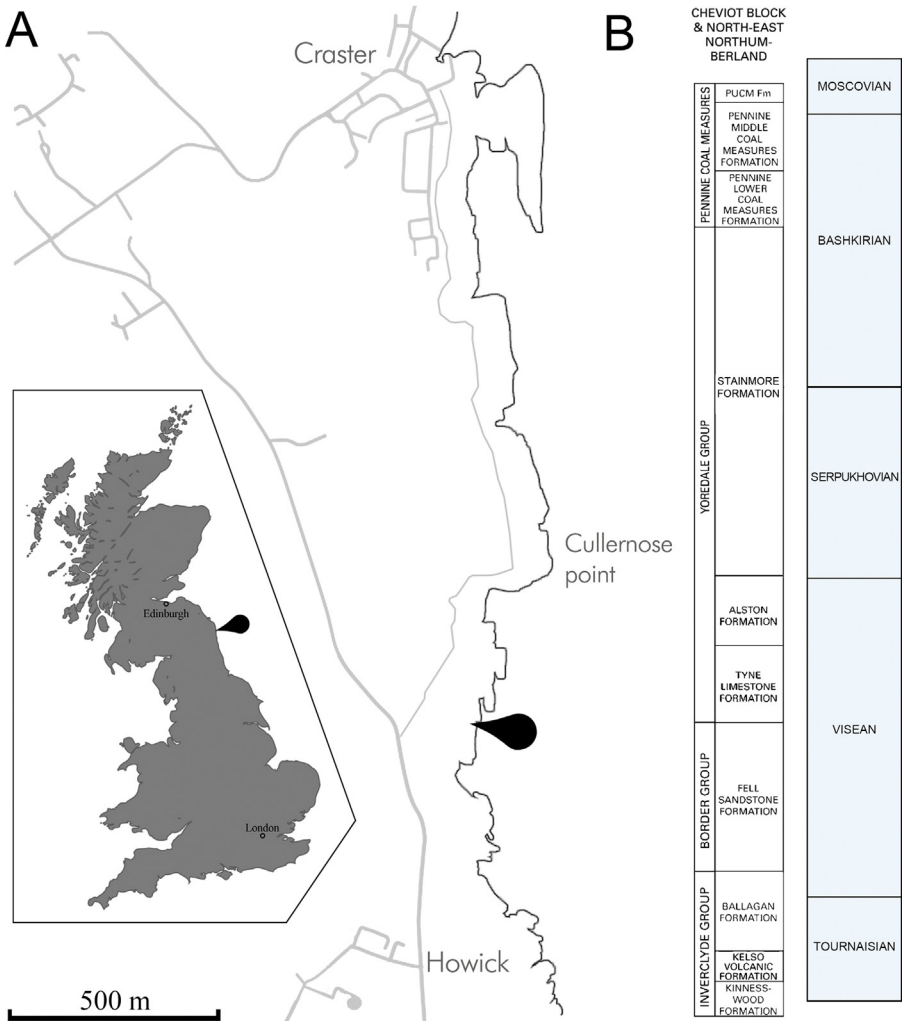

Fig. 1. A. Map of field and sample location (55°27′30.38″N, 1°35′34.32″W) on the coast between Howick and Craster. The inset identifies the field location within the United Kingdom. **B**. Generalised stratigraphic column showing the Stainmore Formation in relation to the Yoredale Group and others from Northeast Northumberland. Modified from Dean et al. (2011).

Bednarz et al. (2015). This method involves encasing the samples in plaster and then sequentially removing minute increments using a computer-guided milling machine with an abrading tool. The grind increment used in this study was 0.3 mm. After each increment was ground, the sample surface was coated with oil, to enhance colour contrast, and photographed under controlled conditions. The stack of photographs was then image-processed and aligned using Adobe Photoshop. The features of interest were then extracted from the images and modelled using the volume graphic software VG Studio Max (Fig. 3). All images were left in full colour so as to facilitate visualization of any feature within the volume in its natural lithological expression. The resultant high-resolution interactive models can be digitally cross-sectioned in any plane as well as rendered partially transparent to facilitate morphological and morphometric analysis (see Appendices A, C for an example of such interactive model). The three-dimensional model allows examination of burrow morphology (e.g., branching characteristics) that is difficult to achieve in a hand-sample. Modelling the fossil burrows and the host sediment importantly allows consideration of the interaction between the trace fossils and adjacent strata, which can be invaluable to improve palaeobiological understanding of organism-sediment interactions in three dimensions.

3. Systematic ichnology

Ichnogenus ***Dactyloidites*** Hall, 1886

Type ichnospecies: *Buthotrephis asteroides* (Fitch, 1850); lower Cambrian, New York State, USA.

Emended diagnosis: Mid-to-deep burrow system forming stellate to palmate rosettes composed of branched or unbranched actively filled spreite-bearing branches radiating horizontally to sub-horizontally from a single vertical to sub-vertical central shaft.

Remarks: The ichnogenus *Dactyloidites* Hall, 1886 has a complicated ichnotaxonomic history and has undergone numerous significant revisions (Walcott, 1898; Häntzschel, 1970, 1975; Fürsich and Bromley, 1985; D'Alessandro and Bromley, 1986; Vyalov, 1989; Schweigert, 1998; Ciampaglio et al., 2006; Uchman and Pervesler, 2007; Wilmsen and Niebuhr, 2013). The type ichnospecies, *Dactyloidites asteroides*, was originally introduced as the fossil alga *B. asteroides* Fitch, 1850. The type material of *B. asteroides* is considered as junior synonyms of preexisting ichnospecies of *Chondrites*, and as such *B. asteroides* needed to be reassigned to another ichnogenus (Fillion and Pickerill, 1990). The ichnogenus *Dactyloidites* was introduced as an unknown body fossil, and was originally considered to be a fucoid algae or a sponge (Hall, 1886). The type species, *Dactyloidites bulbosus*, was