

RAPID COMMUNICATION

Treptichnus pedum and the Ediacaran–Cambrian boundary: significance and caveats

LUIS A. BUATOIS*

Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2, Canada

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Abstract

The Ediacaran–Cambrian (E–C) boundary is based on the first appearance of the ichnofossil *Treptichnus pedum*. Investing an ichnotaxon with such biostratigraphic pre-eminence has been the focus of criticism. Points of contention have revolved around four main issues: (1) ichnotaxonomy, (2) behavioural significance, (3) facies controls and (4) stratigraphic occurrence. First, confusion results from the fact that *Treptichnus pedum* was originally referred to as *Phycodes pedum* and, more recently, some authors have placed it in *Trichophycus* or *Manykodes*. However, the overall geometry of these burrows indicates they belong in *Treptichnus*. Second, regardless of its precise mode of feeding, the behaviour involved is iconic of the Cambrian explosion. Third, objections are based on the idea that trace fossils show a closer link to facies than body fossils. Notably, in contrast to common assumptions, *T. pedum* is not only present in the low-energy offshore of wave-dominated marine settings, but it occurs at considerably shallower water in intertidal and shallow-subtidal zones of tide-dominated systems, as well as in mouth bars of deltaic systems and lower shoreface to offshore transition zones of wave-dominated marine settings. Its broad environmental tolerance supports evolutionary innovations rather than facies controls as the main mechanism underlying the observed vertical pattern of distribution of *T. pedum* in most E–C successions comprising shallow-marine deposits. Fourth, although treptichnids have been documented below the E–C boundary, *T. pedum* is not known from Ediacaran rocks. The delayed appearance of *T. pedum* in E–C successions should be analysed on a case-by-case basis.

Keywords: Ichnology, trace fossils, biostratigraphy, ichnostratigraphy, Global Stratotype, Fortunian

1. Introduction

The Ediacaran–Cambrian (E–C) boundary is arguably the most important transition in the geologic timescale. Interestingly, this is the only stratigraphic boundary based on the occurrence of a trace fossil, namely *Treptichnus pedum* (Brasier, Cowie & Taylor, 1994; Landing, 1994; Peng, Babcock & Cooper, 2012), an ichnospecies interpreted as produced by priapulids (Vannier *et al.* 2010). Unsurprisingly, investing a trace-fossil taxon with such biostratigraphic pre-eminence has been the focus of criticism (e.g. Babcock

et al. 2014; Smith *et al.* 2016a). The utility of *T. pedum* has been criticized based on its ichnotaxonomy, behavioural significance, facies controls and stratigraphic occurrence. The aim of this paper is to critically assess each of these issues in order to evaluate the potential and caveats of using *Treptichnus pedum* as an indicator of the E–C boundary.

2. A critical assessment of the utility of *Treptichnus pedum* as a biostratigraphic index

Overall, points of contention have revolved around four main issues (1) ichnotaxonomy, (2) behavioural significance, (3) facies controls and (4) stratigraphic occurrence.

2.a. Ichnotaxonomical aspects

First, from an ichnotaxonomical standpoint, confusion among non-specialists results from the fact that *Treptichnus pedum* was originally referred to as *Phycodes pedum* by Seilacher (1955) and, more recently, some authors have placed it in *Trichophycus* (Geyer & Uchman, 1995) or *Manykodes* (Dzik, 2005). *Trichophycus* consists of endichnial burrows displaying a flattish U-shaped geometry, typically retrusive spreiten, and striations on the ventral and lateral surface of the burrow (Osgood, 1970; Mángano & Buatois, 2011). Also, although *Trichophycus* may locally display rare vertical bifurcations, it never develops the systematic branching pattern that characterizes *Treptichnus pedum*. In short, the overall geometry of *Treptichnus pedum*, which consists of branching burrow systems comprising straight to slightly curved segments (Fig. 1), is clearly different from that shown by *Trichophycus* (Jensen, 1997; cf. plates 17 and 64 in Seilacher, 2007).

The name *Manykodes* has been suggested by Dzik (2005) as a genus to place some ichnospecies of *Treptichnus*, including *T. pedum*. Unfortunately, this practice is based on the assumption that trace fossils can be understood in the same way as body fossils and that a particular trace fossil can be directly and invariably linked to a producer. However, behavioural convergence rules out establishing a one-to-one relationship between a producer and an ichnotaxon. At least 40 years of ichnotaxonomical work has led to the consensus that nomenclatures of biotaxa and ichnotaxa needs to be kept separate (e.g. Bromley, 1990; Bertling *et al.* 2006; Buatois & Mángano, 2011). Accordingly, the approach by Dzik (2005) can be accepted neither on theoretical nor on practical bases. Regardless of ichnotaxonomical technicalities and different philosophical approaches to ichnotaxonomy, *Treptichnus*

* Author for correspondence: luis.buatois@usask.ca

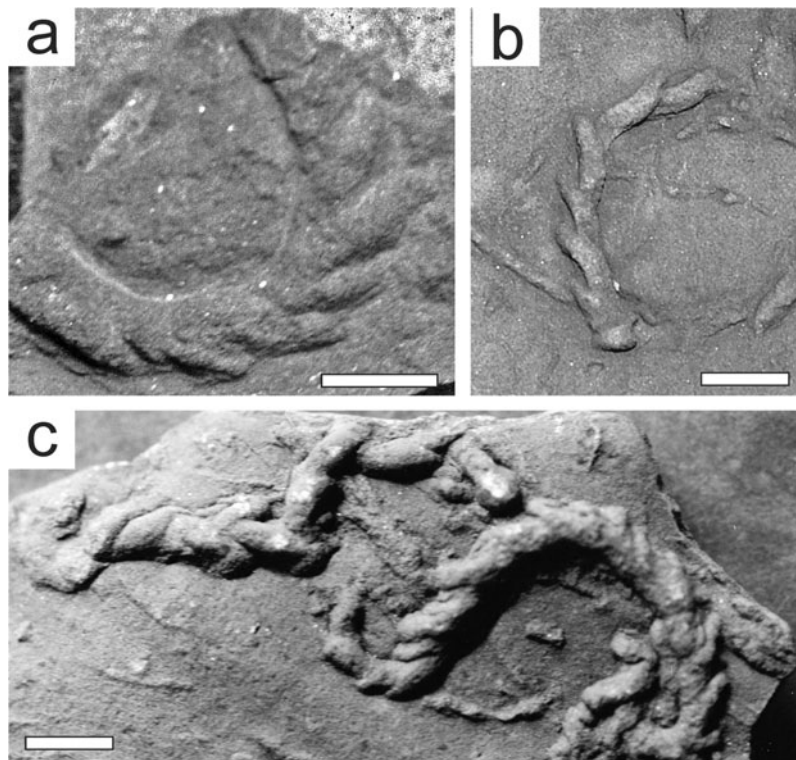


Figure 1. Morphology of *Treptichnus pedum*. (a) Specimen from the type locality. Nobulus Shale, lower Cambrian, Salt Range, Pakistan. Specimen housed at the Palaeontological Collection, Geologisches Institut, University of Tübingen, Germany. (b) Klipbak Formations, Brandkop Subgroup, lower Cambrian, near Brandkop, South Africa. Field photograph. (c) Lower Bright Angel Shale, middle Cambrian, Indian Gardens, AZ, USA. Specimen housed at the Palaeontological Collection, Geologisches Institut, University of Tübingen. Scale bars are 1 cm.

pedum is a distinct and easily identifiable ichnotaxon (see also Babcock *et al.* 2014).

2.b. Behavioural significance

There is overwhelming agreement in that *T. pedum* represents a feeding trace. However, there are four alternative interpretations regarding the trophic type involved: (1) a surface detritus feeder (Jensen, 1997), (2) a deposit feeder (Seilacher, 1955), (3) a predator (Vannier *et al.* 2010) and (4) an undermat miner (Seilacher, 2007). Regardless of the specific mode of feeding, the behaviour involved represents a sophisticated mechanism of exploiting new ecospace by a metazoan-grade animal. The issue of this style of animal–sediment interaction representing evidence of vertical bioturbation or not (Babcock *et al.* 2014) is merely a semantic problem. Strictly speaking, *T. pedum* is not a vertical burrow (such as *Skolithos* or *Arenicolites*), but a horizontal burrow with inclined branches oriented oblique to the bedding plane. What is really significant here is that *T. pedum* represents the onset of infaunalization by means of systematically probing within the substrate (Jensen, 1997), and this is a signature of the changes in animal–substrate interactions that is iconic of the Phanerozoic world (MacNaughton & Narbonne, 1999; Seilacher, 1999; Jensen, 2003; Mángano & Buatois, 2014, 2016). This level of complexity in burrowing style is unknown in Ediacaran strata (for reviews of Ediacaran ichnofaunas, see Jensen, Droser & Gehling, 2006; Buatois & Mángano, 2016).

The issue of behavioural convergence has also been regarded as problematic (Babcock *et al.* 2014). Although behavioural convergence is definitely a trait of trace fossils, its implications with respect to the position of the E-C boundary are virtually non-existent. Because it is the first appear-

ance of *Treptichnus pedum* that is relevant for this problem, subsequent occurrences in the stratigraphic record as a result of behavioural convergence, although of interest in other respects, do not seem to have any further implication for arguments on the location of the E-C boundary. For example, incipient *T. pedum* has been recorded in modern continental deposits, where they are produced by fly larvae of the genus *Symplecta* (Muñiz-Guinea *et al.* 2014), clearly underscoring the importance of behavioural convergence in ichnology, but obviously lacking any relevance for E-C biostratigraphy.

2.c. Facies controls

The third set of objections, those dealing with facies controls, is more significant (Babcock *et al.* 2014; Smith *et al.* 2016a). These objections are based on the idea that trace fossils show a closer link to sedimentary facies than body fossils. Although this may be regarded as generally correct, this view fails to appreciate that the vast majority of individual ichnotaxa occur in a wide variety of sedimentary facies and environments and it is a trace-fossil assemblage that shows a more direct link to a certain set of environmental conditions (Bromley, 1990; Pemberton, MacEachern & Frey, 1992; Buatois & Mángano, 2011; MacEachern *et al.* 2012). This is precisely the reason why individual ichnotaxa are hardly used as indicators of sedimentary environments and the checklist approach has been abandoned in applied ichnology. Although the issue of facies control in trace-fossil distribution in E-C successions has been raised many times (e.g. Mount & McDonald, 1992; Mount & Signer, 1992; Lindsay *et al.* 1996; Babcock *et al.* 2014; Smith *et al.* 2016a), only a handful of ichnological studies have empirically examined this problem in a systematic fashion (e.g. MacNaughton & Narbonne, 1999; Buatois, Almond

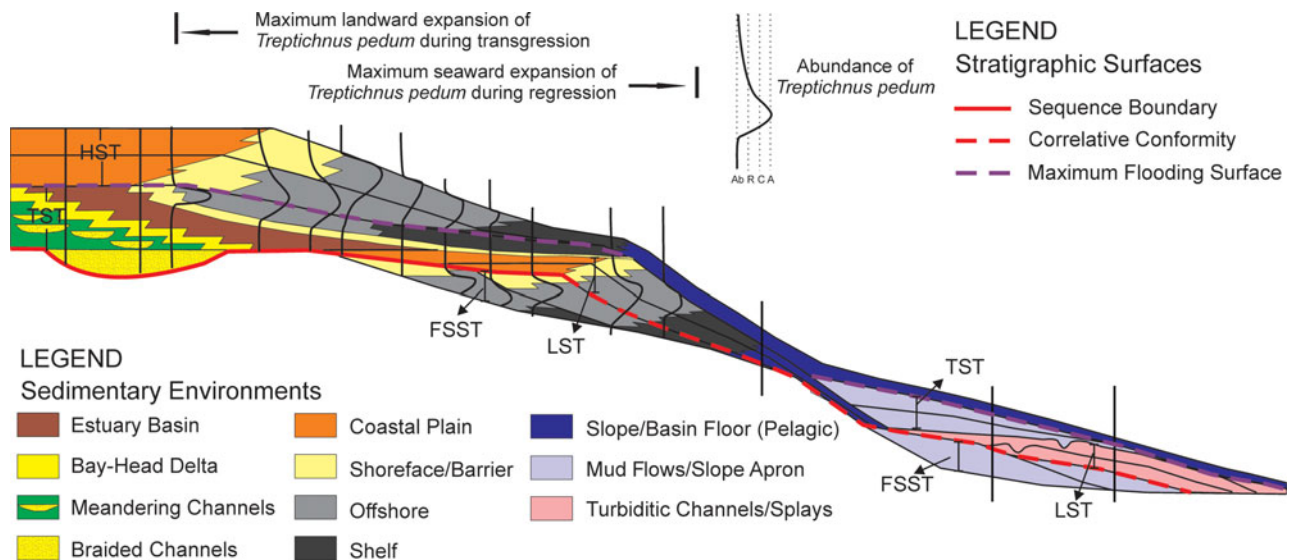


Figure 2. Sequence-stratigraphic architecture, and environmental tolerance and range offset of *Treptichnus pedum* (modified from Buatois, Almond & Germs, 2013). A single valley incision is illustrated for simplicity, although compound valleys may occur in some sections spanning the E-C boundary (e.g. Namibia, see Wilson *et al.* 2012). A wave-dominated regime is depicted for the fully marine segment, but a similar diagram can be produced for a tide-dominated regime by changing the facies belt of the shallow-marine segment. Ab = absent, R = rare, C = common, A = abundant.

& Germs, 2013; Shahkarami, Mángano & Buatois, 2017). The scarcity of studies has resulted in the notion of facies control unfortunately becoming an untested assumption in the E-C boundary literature. Interestingly, the available studies integrating ichnological and sedimentological information within a sequence-stratigraphic framework suggest a more nuanced scenario, where trace-fossil distribution reveals a complex interplay of evolutionary and environmental controls (e.g. Shahkarami, Mángano & Buatois, 2017).

The environmental tolerance and range offset of *Treptichnus pedum* are key issues that can be assessed using the principles and methods of stratigraphic palaeobiology (Patzkowsky & Holland, 2012), helping to illuminate this problem (Buatois, Almond & Germs, 2013) (Fig. 2). Studies in Namibia and South Africa show that, in contrast to common assumptions, *Treptichnus pedum* is not only present in the low-energy offshore of wave-dominated marine settings, but it occurs at considerably shallower water in intertidal and shallow-subtidal zones of tide-dominated systems (Geyer & Uchman, 1995; Buatois, Almond & Germs, 2013). Also, detailed work in the Mackenzie Mountains of western Canada demonstrated its occurrence in mouth bars of deltaic systems and lower shoreface to offshore transition zones of wave-dominated marine settings (MacNaughton & Narbonne, 1999). The maximum landward range of *T. pedum* in wave-dominated systems is probably controlled by the frequency and intensity of storms (Buatois, Almond & Germs, 2013). In the case of high intensity and frequency of storms, amalgamated hummocky cross-stratified sandstone is typical, precluding colonization by the *T. pedum* producer. Under moderate or low intensity and frequency of storms, the presence of *T. pedum* is promoted by longer colonization windows during fair weather. *Treptichnus pedum* seems to have high values of peak abundance in the upper-offshore and lower-intertidal sandflats.

The common absence of *T. pedum* in settings below storm wave base may reflect the seaward boundary of its habitat or a preservational bias resulting from the lack of lithological heterogeneities (Shahkarami, Mángano & Buatois, 2017). The latter is supported by the presence of *T. pedum* in thin siltstone layers intercalated in a shale suc-

cession formed right below storm wave base in the Soltanieh Formation of Iran (Shahkarami, Mángano & Buatois, 2017). These slightly coarser-grained beds were emplaced by storm-generated turbidity currents providing the adequate lithological contrast for preservation of *T. pedum*, suggesting that the common absence of this ichnospecies in settings below storm wave base may be a taphonomical artefact. A deep-marine occurrence has been documented in Devonian deposits (Neto de Carvalho, 2008). Although this may possibly reflect an onshore–offshore pattern, the absence of further recordings prevents the establishment of any trend. In any case, the broad environmental tolerance of this ichnospecies supports evolutionary innovations rather than facies controls as the main mechanism underlying the observed vertical pattern of distribution of *T. pedum* in E-C successions comprising shallow-marine deposits.

2.d. Stratigraphic distribution

Concerns have been raised with respect to the stratigraphic distribution of *T. pedum*, regarding both potential occurrences below the boundary and its delayed appearance or absence in others (Babcock *et al.* 2014). The so-called treptichnids have been documented below the E-C boundary in a number of sections, most notably Namibia (Jensen *et al.* 2000) and Norway (Högström *et al.* 2013). In both cases, the authors were cautious enough not to provide an ichnospecific assignment and even left the ichnogeneric assignment uncertain. In addition, recent work by Jensen *et al.* (2017) showed that the structures from Norway may belong in the horizontally corkscrew-shaped ichnogenus *Helicolithus*. Even assuming that the specimens from Namibia may record the basic morphological plan of *Treptichnus*, meriting assignment to *Treptichnus* *isp.*, clearly they do not display the diagnostic features of *T. pedum*. South African specimens of *T. pedum* figured by Seilacher (2007) as E-C in age occur in Fortunian but not in Ediacaran strata (Buatois *et al.* 2007; Almond *et al.* 2008). Babcock *et al.* (2014) speculated that some Ediacaran examples identified as *Treptichnus* may represent preservational variants of *T. pedum*, but this has not been demonstrated so far. In addition, the diagnostic style

of branching of *T. pedum* makes this suggestion unlikely. The occurrence of the ichnospecies *T. pedum* 4.41 m below the Global Boundary Stratotype Section and Point (GSSP) (Gehling *et al.*, 2001) simply represents a problem of confidence intervals (Landing *et al.* 2013).

More problematic is the issue of delayed appearance or absence of *T. pedum* in certain sections (Babcock *et al.* 2014), a topic which is directly connected with its environmental range. The delayed appearance of *T. pedum* may be understood by means of the concept of range offset, which is essentially dictated by the ecological characteristics of taxa and by the stratigraphic architecture, the latter controlling to a large extent the types of sedimentary environments preserved in a stratigraphic section (Patzkowsky & Holland, 2012). Range offset of *T. pedum* is typically greater above sequence boundaries (SB) within lowstand systems tracts (LST) and parts of transgressive systems tracts (TST), which explains its delayed appearance in some sections spanning the E-C boundary (Buatois, Almond & Germs, 2013). In particular, incision of fluvio-estuarine valleys is detrimental to colonization by the *T. pedum* producers. In this regard, the fact that the Fortune Head succession (Chapel Island Formation) lacks a valley incision coincident with the E-C boundary (Myrow & Hiscott, 1993) makes it particularly appropriate as the GSSP. A systematic review of the occurrences of *T. pedum* is beyond the scope of this paper, but a brief overview of the sections where this ichnotaxon occurs significantly above the E-C boundary is discussed in order to assess potential causes.

The sequence-stratigraphic context of the South Australia succession (Uratanna and Parachilna formations) consists of valley incision (SB) and subsequent transgression (Gehling, 2000). The Uratanna Formation (LST–TST) is incised into the underlying Rawnsley Quartzite (HST or highstand systems tract), and passes up into the shallow-marine Parachilna Formation (Daily, 1973; Gehling, 2000, fig. 9). The first appearance of *T. pedum* is more than 200 m above the base of the Uratanna Formation (Jensen *et al.* 1998). However, the E-C boundary is thought to be broadly coincident with the base of the Uratanna Formation (Gehling, 2000). The absence of this ichnotaxon in the marginal-marine deposits of the lower and middle intervals of the Uratanna Formation most likely reflects the stress associated with brackish-water conditions that may have precluded colonization. Further work on the integration of ichnological, sedimentological and sequence-stratigraphic datasets in this unit is essential to further evaluate the distribution of *T. pedum*.

Valley incision also occurs in the Nama Group of Namibia (Germs, 1972; Wilson *et al.* 2012). The Nomtsas Formation (LST to TST) is incised into the Spitskopf Member (HST) of the Urusis Formation. However, and in contrast to the Uratanna Formation, the lower interval of the Nomtsas Formation contains two subsequent episodes of valley incision (valley fills 1 and 2 of Wilson *et al.* 2012), representing a compound valley-fill. The LST deposits of both incised valleys consist of pebble, cobble and boulder conglomerate, which is clearly unsuitable for preservation of *T. pedum*. Unsurprisingly, this ichnotaxon first occurs within the transgressive fine-grained sandstone of VF2 (Wilson *et al.* 2012). Historically, the E-C boundary was regarded as roughly coincident with the SB at the base of the Nomtsas Formation (Grotzinger *et al.* 1995). However, recent recalibration of radiometric dating may indicate that the E-C boundary is placed within the upper part of the Spitskopf Member (Schmitz, 2012; for ongoing work on the geochronology of these strata, see Linnemann *et al.* 2017). Interestingly, the upper part of this unit is host to *Streptichnus narbonnei*, an ichnotaxon as complex in terms of mor-

phology and behavioural significance as *T. pedum* (Jensen & Runnegar, 2005).

A similar situation is represented by the Vanrhynsdorp Group of South Africa. The Besonderheid Formation is incised into the underlying Gannabos Formation (Buatois *et al.* 2007; Almond *et al.* 2008). Whereas the Gannabos Formation represents shallow-marine deposits, the lower interval of the Besonderheid Formation records deposition within a fluvio-estuarine valley (LST–TST), rapidly passing upward into distal deltaic deposits (HST) (Buatois, Almond & Germs, 2013). The first appearance of *T. pedum* is in the overlying tidal-flat deposits of the Kalk Gat Formation (Gresse, 1992; Buatois *et al.* 2007; Almond *et al.* 2008; Buatois, Almond & Germs, 2013). Although there is a lack of radiometric dates in this unit, current schemes place the E-C boundary at the SB represented by the base of the Besonderheid Formation. The delayed appearance of *T. pedum* in the Vanrhynsdorp Group most likely reflects unsuitable environments, initially freshwater to brackish-water conditions and subsequently sub-storm wave base settings that resulted from the rapid sea-level rise. Notably, the complex feeding trace *Oldhamia geniculata* occurs in the prodeltaic portion of the Besonderheid Formation, providing ichnological evidence of a Cambrian age for this unit (Buatois *et al.* 2007; Almond *et al.* 2008).

The Soltanieh Formation of Iran represents another example of delayed appearance of *T. pedum*. This unit consists of five members, from bottom to top: the Lower Dolomite, Lower Shale, Middle Dolomite, Upper Shale and Upper Dolomite members (Hamdi, Brasier & Jiang, 1989). The siliciclastic intervals are dominated by shale, with minor occurrences of thin sandstone beds (Hamdi, Brasier & Jiang, 1989; Shahkarami, Mángano & Buatois, 2017). The succession displays a large-scale progradational trend. Deposition took place in settings below storm wave base (shelf *sensu strictu*) for the Lower Shale, and settings ranging from below the storm wave base to below the fair-weather wave base (shelf to upper offshore) for the Upper Shale (Shahkarami, Mángano & Buatois, 2017). The presence of the *Anabarites trisulcatus*–*Protohertzina anabarica* zone in the upper interval of the Lower Dolomite Member (Hamdi, Brasier & Jiang, 1989) supports a location of the E-C boundary either at the base of the Soltanieh Formation or within the Lower Dolomite Member (Shahkarami, Mángano & Buatois, 2017, in press). However, the first appearance of *T. pedum* occurs 171 m above the base of the Lower Shale Member. Its appearance coincides with a subtle shallowing event from distal to proximal shelf deposits, characterized by thin siltstone interbeds representing the distal ends of storm-generated turbidites (Shahkarami, Mángano & Buatois, 2017). It has been indicated that the delayed appearance of *T. pedum* either reflects deep-water conditions unsuitable for colonization or lack of lithologic interfaces therefore preventing trace-fossil preservation (Shahkarami, Mángano & Buatois, 2017).

The Bayangol Formation of western Mongolia displays some similarities with the E-C succession in Iran, most notably the presence of a small shelly fauna below the first appearance of *T. pedum*. This unit is divided into five informal members, BG2–BG6 (Smith *et al.* 2016a). The Bayangol Formation shows a complex facies mosaic, involving both carbonate and siliciclastic rocks, encompassing deposition from slope, shelf (i.e. below storm wave base) to shoreface (i.e. above fair-weather wave base) environments (Smith *et al.* 2016a). A diverse ichnofauna, including *T. pedum*, occurs at the contact between BG3 and BG4 of the Bayangol Formation (Goldring & Jensen, 1996; Smith *et al.* 2016a). Because of this, the E-C boundary has historically

been placed at the contact between these two informal members. However, this is inconsistent with the first occurrence of small shelly fossils *c.* 250 m below the first appearance of *T. pedum* and the presence of arthropod trace fossils in BG3, suggesting that the E-C boundary should be lower in the section, probably at the base of the Bayangol Formation (Smith *et al.* 2016a). It has been indicated that this delayed appearance of *T. pedum* in Mongolia underscores its facies dependence (Smith *et al.* 2016a, 2017), but it is unclear which is the environmental tolerance of this ichnotaxon in this mixed carbonate–siliciclastic setting. In addition, it has been noted that *T. pedum* has only been documented in the Bayangol Formation from a single bed, precluding further discussion on potential controls (Landing & Kruse, 2017).

In the Meishucun section of eastern Yunnan Province, South China, the Xiaowaitoushan Member is separated from the overlying Meishucun Formation by a karst surface, representing a SB (Zhu, 1997). This formation is subdivided into Lower Phosphate, White Clay, Upper Phosphate and Dahai members (Zhu, 1997; Zhu *et al.* 2001). The Xiaowaitoushan Member is dominantly dolomite, whereas the Meishucun Formation consists mostly of phosphorite and tuff (Zhu *et al.* 2009). In this section the first appearance of *Treptichnus pedum* occurs in strata near the top of the Lower Phosphate Member (Zhu, 1997). However, as in the case of the Soltanieh and Bayangol formations, small shelly fossils occur below this interval and, therefore, the E-C boundary has been placed at the contact between the Xiaowaitoushan Member and the Meishucun Formation (Zhu, 1997; Qian, Li & Zhu, 2001). The phosphorites of the Meishucun Formation represents a condensed section, and high-energy conditions have been inferred (Zhu, 1997). Environmental conditions may have been detrimental for the producer of *T. pedum*. Also, the condensed nature of the Fortunian in the Meishucun section compromises the accuracy of compiling vertical distribution of trace fossils within a sound stratigraphic framework. In sharp contrast to the Fortunian succession in Burin Peninsula, the lack of recurrence in sedimentary facies prevents differentiation between environmental and evolutionary factors.

In addition to Burin Peninsula, the first appearance of *Treptichnus pedum* is roughly coincident with the base of the Cambrian in other regions of Laurentia, such as the western United States (e.g. Jensen, Droser & Heim, 2002; Smith *et al.* 2016b), as well as of Baltica, most notably in N Norway (Högström *et al.* 2013). Claims of diachronism in the appearance of *T. pedum* in Gondwana (Babcock *et al.* 2014) require a precise evaluation of associated facies and sequence-stratigraphic architecture in order to be substantiated.

3. Discussion

Of the four classes of concerns raised with respect to the utility of *T. pedum* as a biostratigraphic marker, the ichnotaxonomical and behavioural objections are the ones that can easily be regarded as less significant. The ones underscoring facies controls and stratigraphic occurrences are more relevant and directly linked to each other. Ichnological and sedimentological studies framing observations within sequence-stratigraphic architectures are particularly illustrative with respect to the interplay between evolutionary and environmental controls. For example, a detailed analysis of trace-fossil distribution in the E-C succession of the Mackenzie Mountains has shown that evolution was a first-order factor, whereas environmental factors played an important, but second-order control (MacNaughton & Narbonne, 1999). In the same vein, a recent study of the E-C succession in Iran outlined the necessity of placing ichnofaunas within

a palaeoenvironmental and sequence-stratigraphic framework in order to evaluate their evolutionary and biostratigraphic implications for trace fossils (Shahkarami, Mángano & Buatois, 2017). In other words, the nature of the controls of the first appearance of *T. pedum* should not be established *a priori* but as a result of integrated and systematic ichnological, sedimentological and sequence-stratigraphic studies.

Application of concepts and methods of stratigraphic palaeobiology underscored the broad environmental tolerance of *T. pedum*, supporting its biostratigraphic utility in E-C successions formed under shallow-marine conditions, specifically encompassing environments ranging between right above fair-weather wave base to above storm wave base (Buatois, Almond & Germs, 2013). The applicability of *T. pedum* to biostratigraphic studies in marginal-marine (brackish water) or deep-water successions is limited. However, these limitations are probably shared by most available biostratigraphic tools for the lower Cambrian, such as trilobites and small shelly fossils.

Finally, emphasis on the potential and caveats of *T. pedum* should not divert our attention from the basic fact that a single tool is never the most adequate strategy to solve geological problems. For example, defining the E-C boundary based not strictly on the occurrence of *Treptichnus pedum*, but on a *Treptichnus pedum* Ichnofossil Assemblage Zone (Narbonne, Myrow & Anderson, 1987; Landing *et al.* 2013; Laing *et al.* 2016), will be of help to overcome the problem of those areas where this ichnospecies has not been recognized or occurs significantly above the boundary. In addition, regardless of biostratigraphic conventions, the use of multiple sets of evidence would be conducive to more robust zonations and correlations of E-C successions worldwide. The fact that trace fossils tend to be more abundant in siliciclastics, whereas small shelly fossils are abundant in carbonates, clearly illustrates the complementary nature of these two biostratigraphic tools. In addition, non-biostratigraphic tools, such as carbon isotope chemostratigraphy, will play an increasingly important role (Smith *et al.* 2016a, 2017).

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