



Priapulid neoichnology, ecosystem engineering, and the Ediacaran–Cambrian transition

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Abstract: The evolutionary rise of powerful new ecosystem engineering impacts is thought to have played an important role in driving waves of biospheric change across the Ediacaran–Cambrian transition (ECT; *c.* 574–538 Ma). Among the most heavily cited of these is bioturbation (organism-driven sediment disturbance) as these activities have been shown to have critical downstream geobiological impacts. In this regard priapulid worms are crucial; trace fossils thought to have been left by priapulid-grade animals are now recognized as appearing shortly before the base of the Cambrian and represent some of the earliest examples of bed-penetrative bioturbation. Understanding the ecosystem engineering impacts of priapulids may thus be key to reconstructing drivers of the ECT. However, priapulids are rare in modern benthic ecosystems, and thus comparatively little is known about the behaviours and impacts associated with

their burrowing. Here, we present the early results of neoichnological experiments focused on understanding the ecosystem engineering impacts of priapulid worms. We observe for the first time a variety of new burrowing behaviours (including the formation of linked burrow networks and long in-burrow residence times) hinting at larger ecosystem engineering impacts in this group than previously thought. Finally, we identify means by which these results may contribute to our understanding of tracemakers across the ECT, and the role they may have had in shaping the latest Ediacaran and earliest Cambrian biosphere.

Key words: ecosystem engineering, *Treptichmus pedum*, Ediacaran–Cambrian transition, bioturbation, neoichnology, Priapulida.

THE Ediacaran–Cambrian transition (ECT; *c.* 574–538 Ma) records one of the most dramatic transformations in Earth Systems history, witnessing major disruptions to planetary geochemical cycles, a permanent change in the character of the sedimentary record, and the advent of modern-style, animal-dominated ecosystems with successive waves of evolutionary radiation (Wood *et al.* 2019) and one or more pulses of extinction (Knoll & Carroll 1999; Amthor *et al.* 2003; Butterfield 2015; Darroch *et al.* 2018, 2023; Mussini & Dunn 2023). One hypothesized driver of these ECT bioevents is the rise in intensity and diversity of metazoan ecosystem engineering (defined as behaviours through which an organism creates, modifies, or maintains its environment; Jones *et al.* 1994) and in particular the advent of organism-driven mechanical sediment disturbance ('bioturbation') (Seilacher & Pflüger 1994; Seilacher 1999; Mángano & Buatois 2014, 2017; Herringshaw *et al.* 2017; Darroch *et al.* 2020). In

the modern oceans, bioturbation plays a critical role in influencing seafloor sediment structuring, as well as controlling habitable ecospace distribution via the downwards transport of surficial materials, changes to porewater chemistries, and potential shifts in subsurface oxygenation (Aller 1982; McIlroy & Logan 1999; Mermillod-Blondin & Rosenberg 2006; Mermillod-Blondin 2011; Herringshaw *et al.* 2017; Laing *et al.* 2022; Cribb *et al.* 2023). The ecosystem engineering impacts of many metazoan groups thought to have diversified over the ECT are, however, broadly unknown, and thus the extent to which a rise in ecosystem engineering led to changes in the structure of the biosphere is untested.

One group potentially thought to have had an outsized impact on the ECT development of bioturbation are priapulid worms. Priapulids (family Priapulidae; 'priapulans' refers to members of phylum Priapulida) are members of Scalidophora, defined by their scolid-bearing, evaginable

introverts that shift into annulated trunks and 1–2 caudal appendages (Hammond 1970a; Calloway 1975; Wills 1998; Schmidt-Rhaesa 2013; Schmidt-Rhaesa & Raeker 2023). While priapulids are relatively rare in modern benthic ecosystems (largely limited to high-latitude and poorly oxygenated muddy sediments, and comprising just 22 living species; Oeschger & Vetter 1992; Vaquer-Sunyer & Duarte 2008; Vannier *et al.* 2010; Schmidt-Rhaesa 2013; Schmidt-Rhaesa *et al.* 2017; Vannier & Martin 2017) they are common constituents of Cambrian fossil assemblages (Conway Morris 1977; Conway Morris & Robinson 1986; Zhao *et al.* 2013; Smith *et al.* 2015). Moreover, recent exploration of the Nama Group of southern Namibia has uncovered likely priapulid burrows from the latest Ediacaran (Turk *et al.* 2022), as well as agglutinated burrow linings built by priapulids from the earliest Cambrian (Turk *et al.* 2024), suggesting that this group was already ecologically diverse by the time of the Ediacaran–Cambrian transition.

Perhaps most importantly, priapulid-grade animals are thought to be responsible for producing *Treptichnus pedum*, a complex trace fossil that currently defines the base of the Cambrian (Brasier *et al.* 1994; Gehling *et al.* 2001; Vannier *et al.* 2010; Buatois 2018; Kesidis *et al.* 2019). *Treptichnus pedum* consists of a horizontal master burrow with regularly-spaced short branches ('probes') inclined oblique to the bedding plane, that reach up towards the sediment–water interface (Seilacher 2007; Vannier *et al.* 2010; Wilson *et al.* 2012; Buatois 2018). *Treptichnus pedum* is thus one of the earliest forays into infaunalization, and represents a complex animal–substrate interaction characteristic of the Phanerozoic, distinguishing it from earlier, 'simple' (e.g. surficial grazing trails) traces typical of the Ediacaran (Jensen 1997; MacNaughton & Narbonne 1999; Seilacher 1999; Jensen *et al.* 2006; Buatois & Mángano 2016; Darroch *et al.* 2020; Evans *et al.* 2020). Recent work has also shown that *T. pedum* belongs to a broader group of trace fossils, 'treptichnids', which appeared in the late Ediacaran and rapidly increased in both size and architectural complexity in the lead-up to the Cambrian, thus indicating a much longer 'fuse' for these behaviours and ecosystem engineering impacts (Gehling *et al.* 2001; Jensen 2003; Darroch *et al.* 2020; Turk *et al.* 2022). There is therefore a large (and growing) body of evidence to indicate that scalidophorans (or a closely-related group) were important members of benthic communities in the late Ediacaran and early Cambrian, and may have played a role in structuring ecosystems. Understanding the ecosystem engineering impacts of priapulid worms may thus shed valuable light on the drivers of biospheric change over the ECT (see e.g. Laing *et al.* 2019).

This paper serves two purposes. First, we provide a brief overview of previous neoichnological experimentation with

priapulid worms, and the extent to which experiments have been used to understand both the surface and subsurface behaviours and impacts of this group. We discuss the morphology of burrows produced under laboratory conditions, similarities to the ichnofossil *T. pedum*, the potential ecosystem engineering impacts of these bioturbators, and the broader roles they may have played in structuring the agronomic revolution and Cambrian explosion. Second, we present early results stemming from a suite of neoichnological experiments performed using the priapulid species *Priapululus caudatus*, illustrating a new experimental set-up and the documentation of several new behaviours which may require us to re-evaluate the ecosystem engineering impacts of these organisms in deep time.

NEOICHOLOGICAL EXPERIMENTS

One powerful tool for understanding fossil record patterns is via the study of modern animal traces; an actualistic approach termed 'neoichnology'. Traces left by known producers in modern sedimentary environments have historically been crucial to understanding their fossil counterparts (Abel 1935; Häntzschel 1939; Schäfer 1962; Frey 1968, 1970; Ekdale & Berger 1978; Zonneveld 2016; Seike 2023). Experiments undertaken in controlled laboratory settings are particularly useful for isolating or standardizing specific variables (e.g. conducting experiments under a set of parameters which would be difficult to control in field studies, such as sediment composition, water flow velocity, temperature, or availability of resources), observing behaviours under particular environmental conditions, and working with taxa from inaccessible environments (Zonneveld 2016; Zonneveld & Gingras 2023).

The downstream effects of burrowing are numerous, including the subsurface redistribution of nutrients (Aller 1982; McIlroy & Logan 1999), changes to sediment fabric and stability (Young 1970), water column oxygenation (Aller 1982), and the creation of habitable ecospace (McIlroy & Logan 1999; Laing *et al.* 2022). The appearance and rapid diversification of these behaviours over the ECT as seen in the fossil record (Mángano & Buatois 2014; Turk *et al.* 2024) thus warrants further investigation via neoichnological experimentation, particularly in the context of potential modern analogues for ECT bioturbators.

PRIAPULID BURROWING & BEHAVIOUR

Modern priapulids are a relatively sparse group comprising 22 species (Schmidt-Rhaesa *et al.* 2017) and usually

restricted to cold water (in the case of *Priapulus caudatus*, *c.* 3–10°C, and not more than 12–13°C; Shirley 1990; Oeschger *et al.* 1992; Trott 2017) muddy sediments, with the exception of a few tropical meiobenthic species found in medium- to coarse-grained sands (van der Land 1968; Morse 1981; Schmidt-Rhaesa *et al.* 2013). *Priapulus caudatus* is among the largest species of priapulid, with adults often reaching lengths of 15 cm (Shirley 1990). The species is most often found in high latitude subtidal sediments (Shirley 1990; Trott 2017), although there have been occasional reports of their presence in intertidal zones fed by cold water (Trott 2017; Vannier & Martin 2017). The optimum water depth range for *P. caudatus* has been reported as 10–200 m (Wesenberg-Lund 1929), although its status as a eurybiontic species means it is able to live at depth ranges between intertidal and abyssal (van der Land 1970; Kolbasova *et al.* 2023).

The burrowing mechanics of modern priapulids are well studied, and in the case of *P. caudatus*, locomotion can be broadly described as a pattern of seven discrete phases during which the organism initially retracts (or evaginates) its frontal introvert followed by forcefully expelling it in the direction of motion (Video S1) to provide a terminal anchor that can then be used pull the rest of the body forward via contraction by direct peristaltic waves (see Elder & Hunter 1980, fig. 1, table 1; Vannier *et al.* 2010, fig. 1; Kesidis *et al.* 2019, fig. 5). Elder & Hunter (1980) reported that while actively burrowing, these cycles occur *c.* 5 times per minute over a duration of 10–15 s, although the authors note that these measurements may have been affected by a difference in temperature between the priapulids' natural environment and the experimental conditions under which they were studied. While probing on the surface, the rapid inflation of the now-everted proboscis results in relatively low body fluid pressure (0.2–0.3 kPa), but upon attempted oblique entry into muddy substrate pressure levels rise sharply to *c.* 1.3 kPa (roughly equivalent to 13.25 cm of water pressure) before dropping sharply once the animal is below the sediment surface, suggesting broaching of the sediment–water boundary may be the most intensive portion of the burrowing process (Elder & Hunter 1980).

Far less, however, is known about what Elder & Hunter (1980) term 'stationary activity', or periods during which the priapulid is not undertaking active locomotion. During these intervals, studies have recorded individuals often lying horizontally underneath the sediment surface, usually with introverts everted; this is thought to be when the organism is undertaking feeding or respiratory pumping via the back-and-forth transfer of bodily fluid from the trunk to the caudal appendage (Hammond 1970b; Elder & Hunter 1980; Vannier & Martin 2017). *Priapulus caudatus* has also been reported to orient itself vertically at or near the sediment–water interface for periods of

time when stationary, although there are conflicting reports as to which end of the organism is positioned where (see Leckenby 1855; Lang 1948; Kesidis *et al.* 2019); the caudal-appendage-up orientation is interpreted to serve a respiratory function.

In recent years there has been an increasing interest in the morphology of priapulid traces, in part due to their relevance to ECT palaeoecology and ichnology (Vannier 2009). Vannier *et al.* (2010) found that when restricted to a single horizontal plane (in sediments 10 mm thick), *P. caudatus* will use its introvert to probe in a regular horizontal fashion and at angles between 20° and 40° from the previous probe; the traces left behind by these probes are similar in morphology to that of *T. pedum*. However, this vertical constraint is artificial and does not allow for the organism's tendency to burrow vertically and at depths of greater than 1 cm, as seen when observing *P. caudatus* in its natural habitat (Vannier & Martin 2017; Kesidis *et al.* 2019; Turk *et al.* 2022). Kesidis *et al.* (2019) produced fine-scale casts of priapulid burrows generated under experimental conditions, demonstrating that lineations observed along the surface of these burrows are likely to have been produced by a worm bearing longitudinal rows of surface protrusions such as scalds.

The chemical and physical impacts of priapulid burrowing, however, remain understudied, and thus reveal a substantial gap in our understanding of how these animals affect their greater environments. While the vast majority of biomechanical and ichnological priapulid studies centre on *P. caudatus* (probably due to their comparatively larger size), the few existing studies quantifying the physical and ecological impacts of priapulid burrowing largely focus on the macrobenthic species *Halicryptus spinulosus*. The available data, however, suggest that this taxon is a powerful ecosystem engineer with substantial impacts on sediment mixing as well as downstream effects on other benthic fauna. Powilleit *et al.* (1994) found that the introduction of *H. spinulosus* into sediment cores resulted in a ten-fold increase in downwards tracer (sodium bromide) porewater diffusion as compared to controls; this, coupled with the relatively high experimentally-derived individual particle reworking rate (0.14–1.05 cm³ ind⁻¹ hour⁻¹, comparable to both holothurians and decapods during periods of feeding, as well as small amphipods; Lee & Swartz 1980; Powilleit *et al.* 1994) is suggestive of a potentially high impact on vertical sediment and chemical redistribution. Experimental work on contaminant remobilization in Baltic Sea invertebrates by Bradshaw *et al.* (2006) demonstrated that the average mixing depths and biotransport rates of *H. spinulosus* were noticeably greater than those of the amphipod *Monoporeia affinis* and Baltic clam *Macoma balthica*; also of note was that the 4 cm-deep burial of a ¹⁴C and ⁵¹Cr tracer layer resulted in higher overlying water

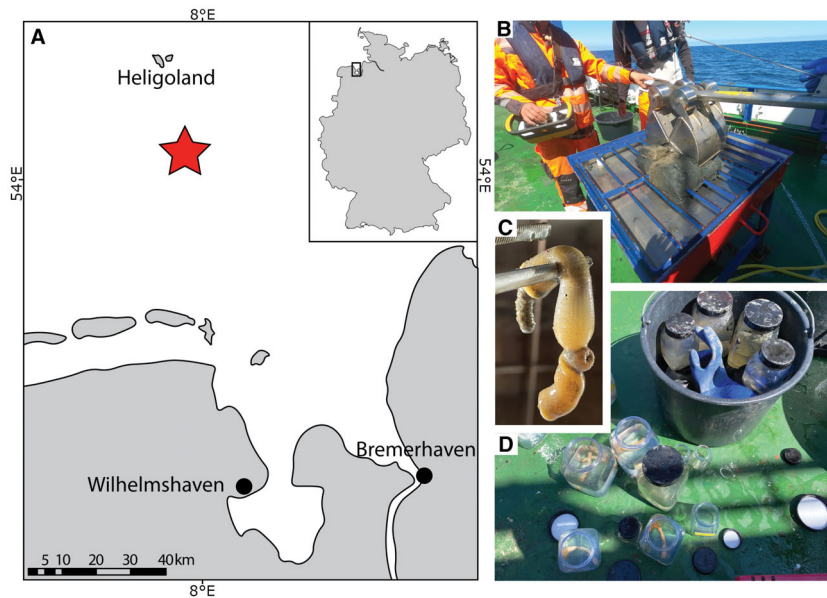


FIG. 1. A, map of *Priapulus caudatus* collection locality (marked by star) from the North Sea SSE of Heligoland. B, collection procedure using Van Veen grab aboard the *F.K. Senckenberg*. C, specimen of *P. caudatus* latched onto another worm, probably in a predatory capacity. D, on-ship storage of sampled organisms.

concentrations of those isotopes for *H. spinulosus* as compared to the other species, probably due to the direct conduits from deeper sediments to the sediment–water boundary and a corresponding increase in the surface area of said interface. Structurally, the authors noted that the burrowing of *H. spinulosus* produced heavy disruption to sediment laminations within the upper 10 cm of sediment, and upon examination found their burrows displayed aerated linings which visually contrasted with the anoxic sediments surrounding them. Findings by Aarnio *et al.* (1998) demonstrated that within field enclosures, *H. spinulosus* had a net negative effect on meio- and macrofaunal abundances, including nematodes, polychaete worms and oligochaete worms; both via predation (in the case of oligochaetes) and burrowing-related sediment disturbance (for nematodes and small polychaetes). Perhaps most notably, the authors found that the introduction of *H. spinulosus* into controlled aquarium environments greatly disrupted the settling of pelagic *Macoma balthica* larvae, with 100 ± 6 settled larvae (out of an original 200) in the control tanks vs 34 ± 14 for those tanks including *H. spinulosus*; as no *M. balthica* larvae were found in the digestive tracts of the priapulids, the authors determined that the deleterious impacts were likely to stem from the bioturbative activities of the worms.

METHOD

We performed a suite of neoichnological experiments using the priapulid species *Priapulus caudatus*, using the

research facilities at Senckenberg am Meer in Wilhelmshaven, Germany.

Specimen collection

Forty adult specimens of *P. caudatus* (Fig. 1C) were collected using a 0.1 m² Van Veen grab from muddy sediments (*c.* 35 m water depth) in the German EEZ portion of the North Sea in June 2022 (*c.* 20 km SSE of Heligoland; see Fig. 1A) and were transferred to aquaria inside a refrigerated shipping container (Fig. 2A) on the premises of Senckenberg am Meer. The shipping container was kept at a constant 8°C so as to mimic ambient water temperatures from the collection site.

Experimental protocol

Four 35 cm³ aquaria were filled with *c.* 12 cm sediment, broadly subdivided into four 3 cm-thick intervals of sieved (2–3 cm) mud collected from the same localities as the priapulids, and bounded by thin (3 mm) layers of coloured aquarium sands (grain size 0.5–1 mm) intermixed with mud so as to allow for passage through (Fig. 2B); although modern priapulid burrowing environments contain minimal sand, the coloured layers used in these experiments were intended to facilitate visualization of these worms' impacts on sediment reworking. The colours of these layers corresponded to depths within the sediment column, with blue placed at 9 cm depth, yellow

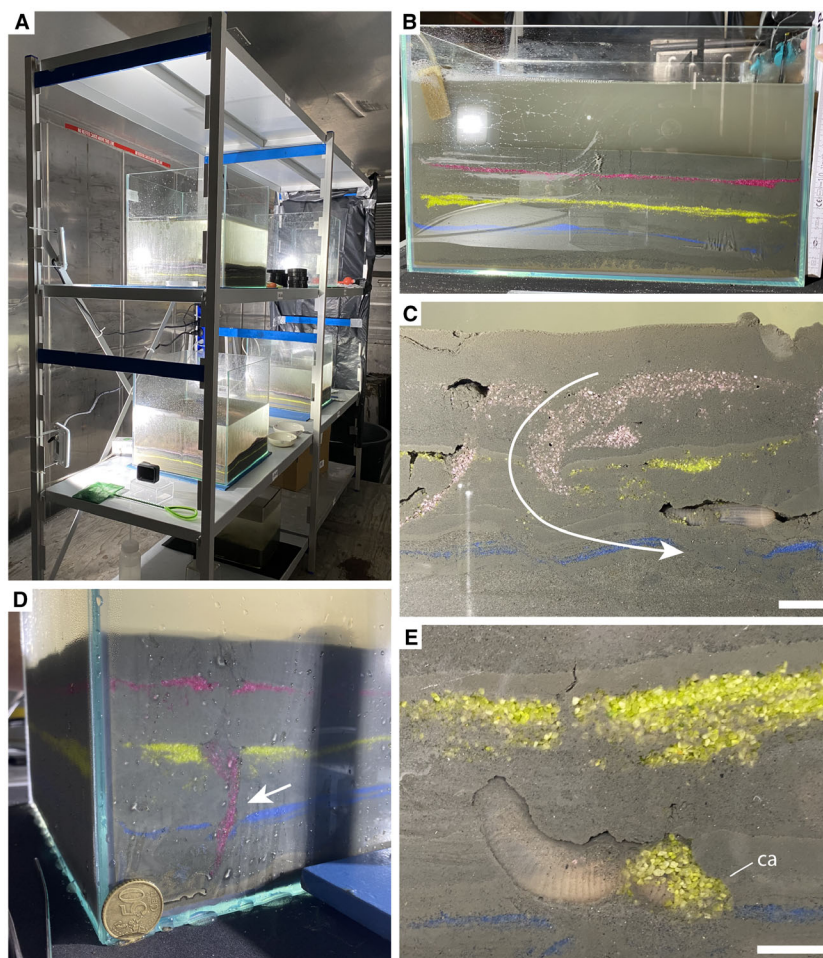


FIG. 2. A, experimental tank arrangement within the refrigerated shipping container. B, initial stratified tank setup. C, coloured sand layers indicating the movement of a priapulid through the sediment. D, rapid downwards movement (arrow) of uppermost sand layer *c.* 10 min after worms were released into the tank. E, coloured sand trapped in the caudal appendage (ca) of a worm. Scale bars in C, E represent 1 cm; diameter of coin in D is 2.4 cm.

at 6 cm depth, and pink at 3 cm depth. On top of the sediments were *c.* 18 cm of seawater (salinity *c.* 31 PSU), manually exchanged every 3–4 days to compensate for the lack of tank flow-through systems. Oxygen pumps were placed in each tank to maintain sufficient water oxygenation, and four 10 W LED floodlights were installed facing the same side of each tank exposed to light when opening the door of the shipping container. Groups of 8–12 priapulids (each *c.* 5 cm long, although a few individuals reached lengths of 7 cm) were introduced into two of the aquaria, while the other two were used as controls (e.g. set up in the same manner but without priapulids added); these tanks were observed daily over a period of between 3 and 4 weeks and reset two times at the end of each period to allow for repeated trials. Visual observations at a range of intervals were captured using a combination of time lapse video and photography on four GoPro HERO8 Black cameras. Remaining priapulids were

kept in the shipping container for the duration of experiments in a large aquarium filled with *c.* 20 cm mud and 18–20 cm seawater; as experiments progressed, worms were collected from this holding tank for introduction into the experimental tanks at the beginning of each reset.

RESULTS

Observations

Upon release into the tanks, priapulids began to rapidly burrow downwards, usually fully disappearing from view within 3 min (Video S2). Individuals typically did not re-emerge during the course of the experiments; however, as sediments compacted over time due to burrowing, worms would occasionally eject themselves from the

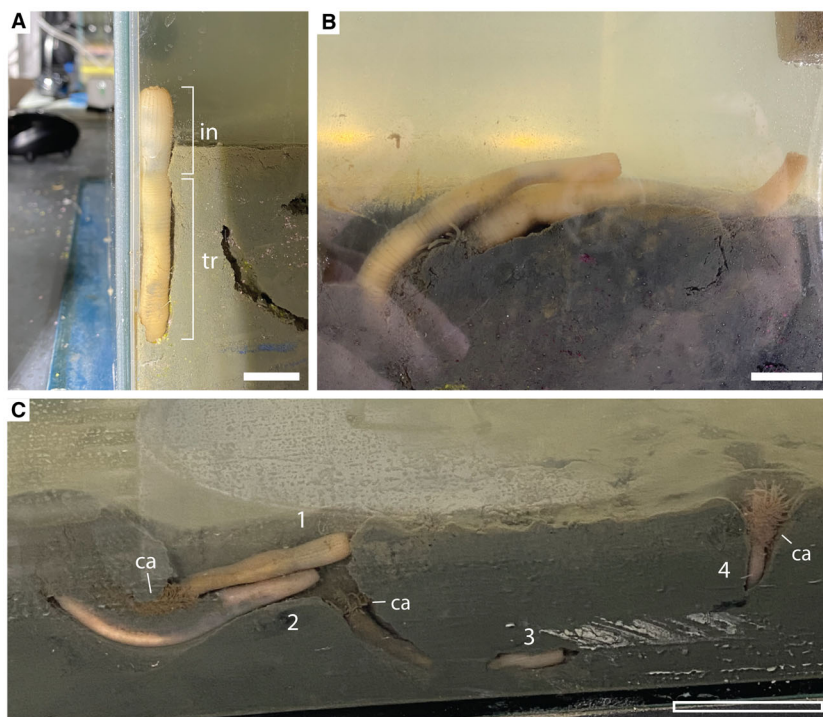


FIG. 3. A, priapulid oriented vertically with introvert largely above sediment surface; B, two adjacent priapulids on the sediment surface; C, four worms in the holding tank. *Abbreviations:* ca, caudal appendage; in, introvert; tr, trunk. Scale bars represent: 1 cm (A, B); 5 cm (C; hollow).

sediment and attempt to re-enter without success (Video S3), thus remaining on the sediment surface and often dying within 1 or 2 days.

The coloured sand grain particles frequently became lodged in caudal appendage crevices (Fig. 2C, E) and thus were transported along with the worm; at the experiment start (and prior to intense mixing) this would often indicate the layer the worm had most recently passed through. Downwards transport of the uppermost pink sand layer (*c.* 3 cm depth) was almost immediate and visible (see Fig. 2D). Individuals were regularly observed in direct association with each other, often appearing ‘stacked’ on top of one another (Fig. 3B, C), although we note that this may be the result of a higher population density within the tanks than is usually encountered in natural settings, and that the degree to which this influenced behaviour is an open question. The worms most often oriented themselves horizontally within the sediment; however, on at least three occasions they were seen positioned vertically with *c.* 50% of their introvert above the sediment surface and the remainder of their bodies in the subsurface (Fig. 3A). This behaviour was observed for several minutes at a time and would end either of the worm’s own volition or when gently prodded by a metal instrument such as aquarium tweezers; in these instances, the worm would retract and

reposition its introvert to facilitate movement away from the surface (Video S4).

Separate from the main experiments (sediment columns comprising mud with three interbedded sand layers) were two instances of specimens placed atop a sandy surficial layer. While not something typically encountered in the wild (see *Experimental protocol*, above) this exercise allowed us to document the range of behaviours and potential responses to a change in environment (added to which, a majority of ECT trace fossils attributed to priapulids are found in sandstones); thus the observations are valuable. When presented with a sandy surface, several specimens were observed rapidly probing and retracting their introverts (Video S5; also see Fig. 4B), followed by a slight rotation to a different orientation, after which the process would begin anew. Probe direction was almost never retraced, and individuals would often rotate their entire body in a circle around their centre of mass over the course of several probe repetitions. This behaviour was also observed once in an individual placed atop a muddy surface layer; however, another individual released simultaneously *c.* 8 cm away within the same tank immediately began to burrow downwards. Similar difficulties with sandy substrate were also observed when the upper few centimetres of sediment comprised mud underlain by a

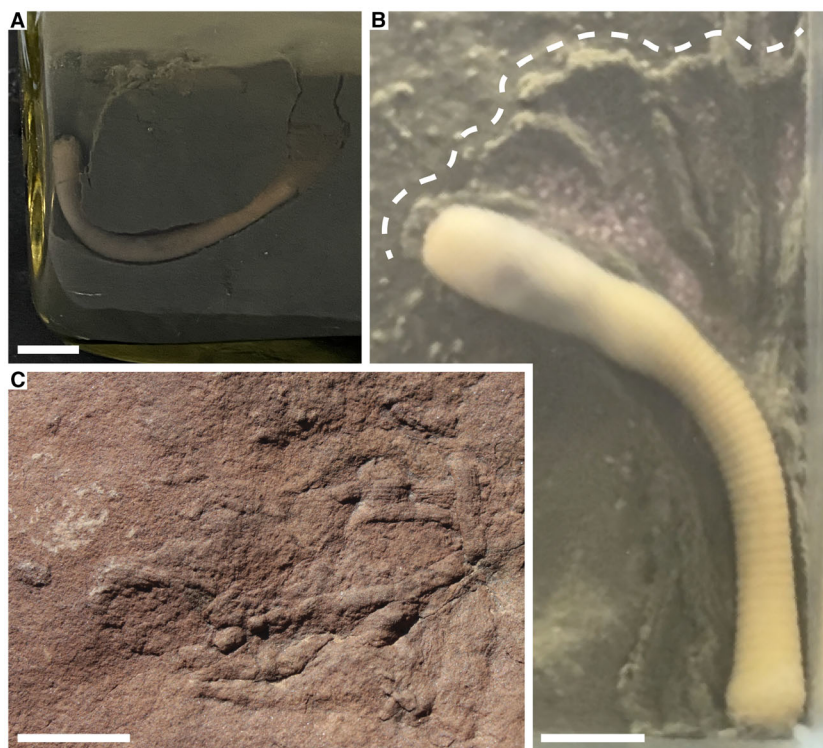


FIG. 4. A, priapulid pumping water through a U-shaped burrow. B, individual on top of sand layer exhibiting offset probe behaviour. C, putative priapulid probes from the late Ediacaran of Namibia (GSN F1643; The Geological Survey of Namibia). Scale bars represent 1 cm.

c. 2 mm-thick sand layer. In this instance, the priapulid penetrated the sediment surface but was prohibited from moving further downwards by the sand layer, and thus began to burrow upwards again until emerging at the sediment–water interface. Layers of intermixed mud and sand did not pose a barrier to downwards movement.

While priapulids tend to probe rapidly and with constant directional changes when vertically limited (Vannier *et al.* 2010; also see Video S5), their burrowing behaviours are markedly different when provided subsurface space and substrate akin to that of their natural environment (e.g. mud instead of sand). On several occasions, worms were observed remaining largely stationary (i.e. not changing position within the tank) in horizontal burrows (and in several instances, U-shaped burrows; see Fig. 4A; Video S6) on the order of several hours to a full day; however, individuals would generate consistent peristaltic waves which would travel down the length of their body (Video S7). Sediment particles were visibly and continuously displaced by this process (Video S8), first moving in a posterior-to-anterior fashion as the wave was generated in the introvert, then reversing direction as the wave began to travel down the length of the worm. In several instances the priapulids produced burrows that were horizontal in cross section with small vertical components (Fig. 5A, B); these

remained open post-passage until disturbed by the burrowing of another worm.

DISCUSSION

We discuss three novel observations of priapulid behaviour as seen over the course of the experiments; each description is then followed by an exploration of the potential ecosystem engineering implications of these behaviours in the context of the Ediacaran–Cambrian transition.

Surface probing behaviours

The surficial probing shown in our experiments (Video S5; Fig. 4B) match closely to those shown by Vannier *et al.* (2010) and suggest that subsurface burrowing in this group is controlled by both adequate vertical space as well as substrate composition. The natural burrowing environments of *P. caudatus* are sediments comprising >80% mud, as is found in their North Sea collection localities; any layer containing significant (*c.* >50%) amounts of sand precluded the worms from any further downwards movement.

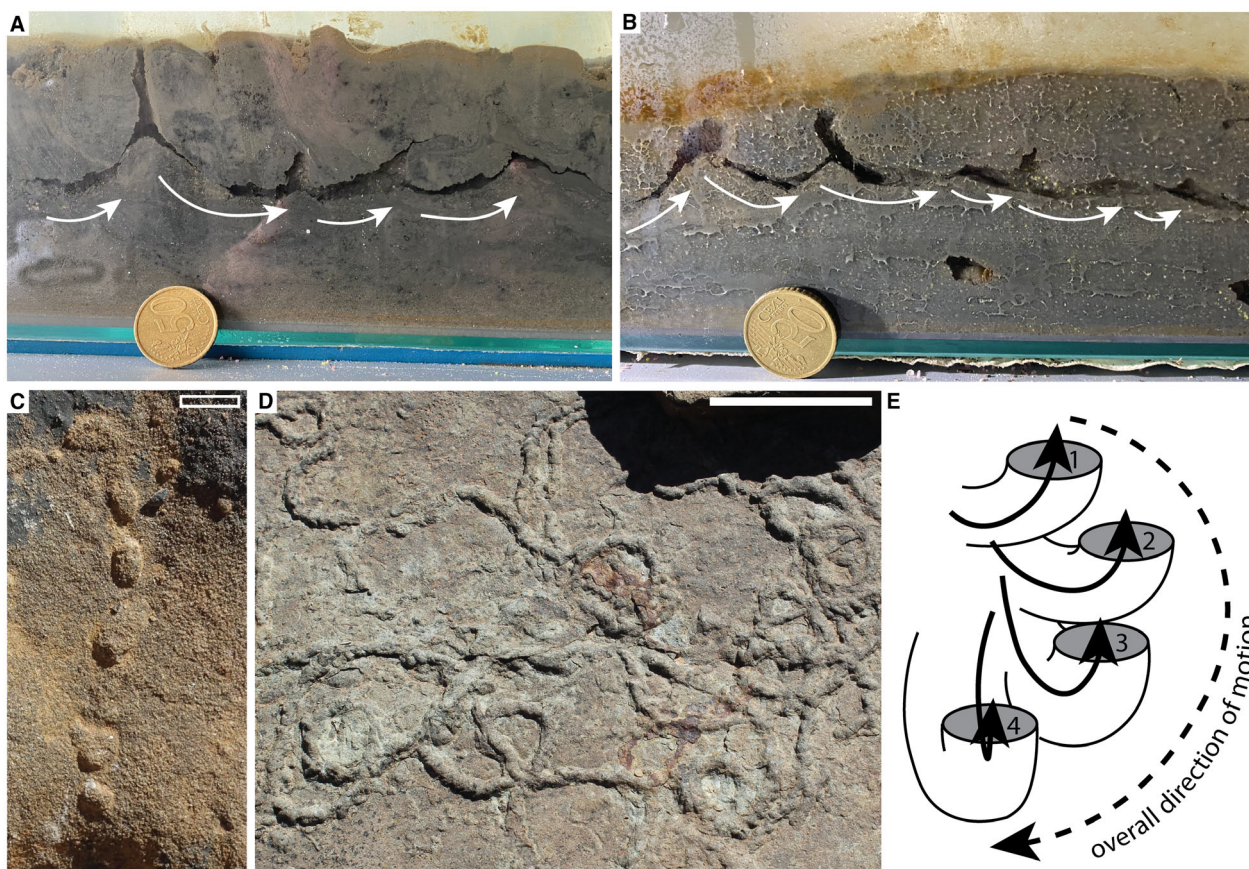


FIG. 5. A–B, cross-section of burrows produced by priapulids over experimental runs, with arrows denoting general inclined probe/chained-u movement. C, treptichnid from the terminal Ediacaran of Namibia (field specimen; Spitskop Mbr, Urusis Fm.; Koelkrans Camp, Fish River Canyon). D, *Treptichnus pedum* from the early Cambrian of Namibia (field specimen; unit 'VF2' of Farm Sontaagsbrunn, as described in Wilson *et al.* 2012). E, schematic of *T. pedum* 3D structure, with solid line numbered arrows denoting individual probe order offset by 20°–40° and dotted line showing general direction of movement. Diameter of coin is 2.4 cm (A, B). Scale bars represent: 0.5 cm (C; hollow); 5 cm (D).

The observations are potentially relevant to interpreting similar trace fossils from the ECT. Late Ediacaran scalidophoran traces constrained to between 542.62 ± 0.15 and 539.63 ± 0.15 Ma (Nelson *et al.* 2022) from Namibia (Fig. 4C; also see Turk *et al.* 2022, fig. 9) exhibit a similar surficial probing akin to those described by Vannier *et al.* (2010). In terms of what behaviour(s) these activities represent, two hypotheses offered by Kesidis *et al.* (2019) are that: (1) the largely horizontal nature of ECT scalidophoran traces may derive from either concentration of food and other resources (see e.g. Llobet-Brossa *et al.* 1998; Jensen & Atkinson 2001; Vannier *et al.* 2010); and/or (2) these traces reflect a preferential preservational window at the sediment surface. Our experimental results suggest instead a physical or chemical barrier to deeper movement, such as a redox discontinuity surface (RDS) close to the surface (also a possibility discussed by Buatois & Mángano 2011 and Kesidis *et al.* 2019). A shallow

RDS may have prohibited access to the subsurface due to insufficient oxygen levels (Rosenberg *et al.* 2001). In this scenario, these behaviours may represent the very earliest onset of the agronomic revolution; previous work (Seilacher 1999; Mángano & Buatois 2014) has suggested that increase in bioturbation frequency and intensity across the ECT could have generated a positive feedback loop, lowering the RDS and thus making further subsurface space available for exploitation by burrowing fauna (we note, however, that recent geochemical models suggest that bioturbation during this interval may not have oxygenated the sediment subsurface; see Cribb *et al.* 2023). Although the experiments presented here do not explicitly speak to this hypothesis, future geochemical characterization of our sediment columns will allow us to test to what extent priapulid burrowing was limited by levels of dissolved oxygen at depth and to what extent these gradients were changed following burrowing.

Burrow architecture & within-burrow residence times

While surficial probing is a relatively fast process occurring on the order of minutes (Video S5; also see Vannier *et al.* 2010), when given adequate vertical space, *P. caudatus* will spend much longer periods of time within subsurface burrows. Our experiments recorded individuals remaining within their burrows for timespans ranging from hours to days, all while pumping water through the burrow system at a mostly stable rate (revealed by the back-and-forth movement of sediment particles within the burrows; see Video S8). This long residence time, coupled with continuous pumping of water through the burrow structures, is likely to have a significant impact on sediment chemistry. Bioirrigation, the process by which an organism flushes water through its burrow for the purposes of both oxygenation and waste ejection, has a marked influence on the biogeochemistry of surrounding sediments (Davis 1974; Aller & Aller 1998; Wenzhöfer & Glud 2002; Jørgensen *et al.* 2005; Meysman *et al.* 2006) as well as exerting population and structural control on local micro-, meio- and macrofaunal benthos (Reise 1981; Aller & Yingst 1985; Marinelli *et al.* 2002; Engel *et al.* 2012; Volkenborn *et al.* 2012) and influencing sediment–water interface solute exchange (Christensen *et al.* 1984; Archer & Devol 1992; Meile & Cappellen 2003). We hypothesize that this lengthy residence time of priapulids in burrows, coupled with sustained pumping of water through the burrow system, serves to increase the diffusion of oxygen into surrounding sediments (Volkenborn *et al.* 2012; Murniati *et al.* 2017) as well as chemical alteration of the burrow walls (Furukawa *et al.* 2001), while also limiting the abundance of compounds toxic at high concentrations, such as sulphide and ammonium (Volkenborn *et al.* 2007). In turn, we suggest that this bioirrigation-driven increase in sediment oxygenation levels would lead to a greater diversity of other taxa in these parts of the seafloor, thus demonstrating a powerful ecosystem engineering impact of these behaviours. We acknowledge that the analogue explored here is not perfect; priapulids in the present day primarily inhabit poorly oxygenated sediments and as such the extent to which their burrowing activities support diverse communities of other benthic macrofauna are limited (although they demonstrably perform a variety of ecosystem engineering roles with effects on community diversity; see Aarnio *et al.* 1998). However, we argue that this was probably not the case over the ECT, when these behaviours and burrowing styles were appearing for the first time, in greater densities and in a wider variety of facies settings (Geyer & Uchman 1995; Wilson *et al.* 2012; Buatois *et al.* 2013, 2020; Buatois 2018). Although the key tenets of this model require more explicit testing, it is

possible that the proliferation of burrow architectures documented here would have had crucial impacts on the chemistry, quality and rheology of sediment at local to regional scales, and may have in turn expanded the distribution of habitable subsurface ecospace (Herringshaw *et al.* 2017; Buatois *et al.* 2020; Laing *et al.* 2022).

Lastly, the observation of priapulids within U-shaped burrows (Video S6; Fig. 4A) is (to our knowledge) new for this taxon. While this was observed on only a few occasions and under artificial conditions with limited space (and as such should be viewed cautiously) we note that the sampling depth of the Van Veen grab used for specimen collection (15 cm) is similar to the depth of our experimental sediment columns, and thus does not represent a significant departure from the worms' natural environments. Further behavioural observations (preferably in the field) should be undertaken to establish how prevalent this behaviour is in natural settings. Of additional note is that one ichnospecies of *Treptichnus* (*T. apsorum*, described from the early Pennsylvanian of Alabama, USA) comprises interconnected U-shaped burrows; however, this trace is attributed to the burrowing of insects and is thus indicative of some degree of behavioural convergence (Rindsberg & Kopaska-Merkel 2005).

Comparisons with T. pedum

Perhaps the most notable result of this study is that when provided adequate vertical space in which to burrow, *P. caudatus* will create linked burrow systems comprising a horizontal master burrow with multiple inclined vertical 'probes' that reach up towards the sediment–water interface (Fig. 5A, B); an organization similar to the structure of *Treptichnus pedum* (Fig. 5D, E) (Seilacher 1955; Buatois 2018) as well as several late Ediacaran treptichnids (Jensen & Runnegar 2005; Darroch *et al.* 2020; Turk *et al.* 2022). This lends support to the hypothesis that priapulids (or a closely related taxon) may have been the *T. pedum* tracemaker; however, further work (e.g. via CT scanning) is needed to make a full morphological comparison. While each aquarium was provided with a dedicated camera, we were only able to film one side (out of a possible four) per tank at a time. These *T. pedum*-like linked burrow systems were always found after the fact and on one of the three un-filmed sides; this meant that no worms were observed in the process of constructing these linked burrow systems and as such, additional observations are needed to determine what this behaviour actually represents. Some studies (see e.g. Vannier *et al.* 2010; Wilson *et al.* 2012) have suggested that the probing seen in *T. pedum* may represent feeding attempts; however, in our attempts to feed the priapulids we placed various food sources (e.g. dead polychaetes, fragments of

the mussel *Mytilus edulis*) on the surface and all remained untouched for at least several days before they were removed due to decay concerns. Wilson *et al.* (2012) also suggested the probing behaviour may have been a response to low O₂ levels in muddier sediments but modern priapulids display a high tolerance for such environments, making this explanation unlikely as well.

In addition, *T. pedum* is part of a broader group of ichnofossils ('treptichnids') that appear in the late Ediacaran (Jensen *et al.* 2000; Jensen & Runnegar 2005; Darroch *et al.* 2020; Turk *et al.* 2022). These traces (which possess the same general structure: repeated, regular intervals of probing, although without the characteristic arcuate behaviour of *T. pedum*) rapidly increase in size and complexity prior to the Cambrian boundary (Fig. 5C; also see Jensen *et al.* 2000; Darroch *et al.* 2020; Turk *et al.* 2022); this is followed by a rapid diversification of the *Treptichnus* ichnogenus in the earliest Cambrian (Zhang *et al.* 2022). If we assume that these traces were also made by priapulids or a closely related group, the increase in size and complexity of these burrows across the ECT would suggest that the ecosystem engineering impacts of these animals increased substantially during this critical interval in Earth history.

CONCLUSION

The early results of our neoichnological experiments reveal several novel observations surrounding their bioturbative activities: (1) burrowing patterns are influenced by both substrate composition and access to vertical space; (2) the residence time of priapulid worms in subsurface (including U-shaped) burrows is much longer than previously thought; and finally (3) when provided with muddy sediments and adequate subsurface space (i.e. conditions mimicking their natural environment), priapulids will create burrows very similar in form to both treptichnids and the Cambrian index fossil *Treptichnus pedum*. These new observations indicate that the ecosystem engineering impacts of this taxon are much greater than previously understood. When these inferences are extended to the fossil record, they suggest that these activities may have played major roles in influencing the habitability of Ediacaran–Cambrian sediments; especially in the context of a shallow redox discontinuity surface. Future work along these lines will focus on quantifying the impact of these behaviours, and tying specific burrow morphologies (i.e. surficial probing, U-shaped burrows, and linked burrow networks) with specific biological and/or ecological functions. Together, these data will help to shed invaluable new light on the ecosystem engineering impacts of priapulids and related groups over the ECT and help us to understand the

changing ecology of benthic ecosystems during the earliest stages of the Cambrian explosion.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12721>):

Video S1. Close view of *P. caudatus* movement cycle in a confined space.

Video S2. Time lapse of *P. caudatus* breaching the sediment surface over a period of c. 2–3 min.

Video S3. *Priapulid caudatus* attempting oblique re-entry into compacted sediment.

Video S4. *Priapulid caudatus* oriented vertically within the tank before introvert retraction and reposition away from surface.

Video S5. Time lapse of a priapulid exhibiting probe-retract-probe behaviour when placed on top of a surficial sand layer.

Video S6. Priapulid pumping water at a constant rate through a U-shaped burrow.

Video S7. Stationary priapulid generating peristaltic waves within a horizontal burrow.

Video S8. Back-and-forth particle movement as a result of stationary priapulid pumping water.

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