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Himatiichnus mangano igen. et isp. nov., a scalidophoran trace fossil from the late Ediacaran of Namibia

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Himatiichnus mangano igen. et isp. nov., a new trace fossil from the late Ediacaran Huns Member of the Urusis Formation, southern Namibia, comprises intertwining tubes exhibiting dual lineation patterns and reminiscent of both modern and early Cambrian examples of priapulid worm burrows. These similarities support the interpretation of a total-group scalidophoran tracemaker for *H. mangano*, thus providing direct evidence for the first appearance date of Scalidophora in the late Ediacaran *ca* 539 Ma. This new material is thus indicative of the presence of total-group scalidophorans below the Cambrian boundary and supports inference of a lengthy Precambrian fuse for the Cambrian explosion.

1. Introduction

The terminal Ediacaran ‘Nama’ assemblage approximately 550–538 Ma [1–3] is a key interval in the history of life, preserving both soft-bodied Ediacara biota (an enigmatic collection of soft-bodied organisms with uncertain relationships to extant animal phyla) and a burgeoning fauna of more recognizable animals reminiscent of the Cambrian [4–9]. This interval is thus increasingly thought to record a ‘long fuse’ for the Cambrian explosion and is key to understanding the origins of the modern animal-dominated marine biosphere [5,7,10–15].

While evidence from molecular clocks suggests Ediacaran divergence times for many animal taxa [16,17], there remains a lack of definitive fossil evidence for many of these groups from below the Ediacaran–Cambrian boundary (ECB). Of particular interest are the Ecdysozoa—a clade united by the common process of cuticular moulting—and comprises the Panarthropoda (Arthropoda, Onychophora and Tardigrada), Nematoida (Nematoda and Nematomorpha) and Scalidophora (Kinorhyncha, Loricifera and Priapulida) [18–20]. Ecdysozoa represents the vast majority of both extant and fossil animal diversity, with an estimated 5.5 million living species [21,22]. The recent discovery of putative ecdysozoans from the late Ediacaran of China [23] aside, the earliest indisputable ecdysozoan body fossils are known from the Fortunian [24], and the ichnofossil *Treptichmus pedum*—interpreted as the repeated arcuate probing of a priapulid-grade organism [25]—is used as a biostratigraphic marker for the base of the Cambrian [26,27]. However, divergence time estimation analyses [20] suggest crown-group ecdysozoans first appeared between 636 and 578 Ma, thus indicating a substantial missing Ediacaran fossil record for this group.

Within Ecdysozoa, priapulids and palaeoscolecid s represent two groups that are potentially crucial to understanding the character of benthic ecosystems over the Ediacaran–Cambrian transition. Priapulid worms (Cambrian–recent) are scalidophorans distinguishable by their evaginable frontal introvert possessing rings of equally spaced protruding scalids. This introvert transitions into an annulated trunk and often one or two caudal appendages thought to serve respiratory and/or defensive functions [28–32]. Priapulids are common components of Cambrian assemblages [33–36], although they are today represented by a comparatively sparse 19 species largely restricted to high-latitude, poorly oxygenated muddy sediments [25,37–39]. Traces attributed to priapulids are also notable, with the aforementioned *T. pedum* used to mark the ECB and well-preserved ichnofossils known from the Lower Cambrian of Sweden [40].

By contrast, palaeoscolecid s (Cambrian–Silurian) are worm-like animals bearing an annulated cuticle possessing phosphatic or phosphatized arrays of transverse sclerites and are often interpreted as scalidophorans, although their exact taxonomic placement within the Ecdysozoa remains a subject of debate [34,41–44]. Palaeoscolecid s represent the most diverse subset of fossil record scalidophorans, with more than 60 species (45 genera) described; one-third of palaeoscolecid genera have been described on the basis of microscopic cuticle and scleritome fragments alone [44]. Palaeoscolecid s have been posited as major sediment bioturbators [45], although their endobenthic life habits have largely been inferred based on morphological features such as aboral hooks, cylindrical bodies and radial sclerite distribution [34,46–48].

Here, we describe a new trace fossil attributable to vermiform scalidophorans such as priapulids or palaeoscolecid s from the late Ediacaran Huns Member (Urusis Formation) of the Nama Group, with broad implications for understanding late Ediacaran palaeoecology and the early history of a key extant animal phylum.

2. Geologic setting

The Ediacaran–Cambrian Nama Group of southern Namibia consists of more than 3000 m of mixed siliciclastic-carbonate sedimentary rocks deposited in a foreland basin formed due to orogenic activity associated with the assembly of Gondwana (figure 1) [49–55]. South of Windhoek, the Nama is subdivided into two sub-basins (the northern Zaris and southern Witputs) partitioned by the central high Osis Arch [49,55].

Within the Witputs Sub-basin, the Urusis Formation is subdivided into the Nasep, Huns, Feldschuhhorn and Spitskop members [55,56]. The Nasep–Huns transition is interpreted as representing a transgressive sequence, with the upper Nasep sandstone interpreted as a delta slope-to-coastal plain depositional environment [55–57]. The overlying Huns limestone, by contrast, represents a storm-dominated carbonate ramp succession with an inner ramp, ramp crest and ramp-to-basin transition facies recognized in various parts of the basin [53,55–57]. The Huns Member primarily comprises thin stromatolitic intervals, cross-stratified limestone grainstone and interspersed limestone intraclast conglomerate, with the lower Huns (0–40 m) characterized by shale–limestone interbeds that transition into metre-scale stromatolitic units and small patch reefs in the upper approximately 260 m [56,58].

The position of the ECB in the Nama Group is currently disputed. Traditionally, the boundary has been placed stratigraphically between the Urusis and Nomtsas Formations, which in many localities is marked by an erosive unconformity [49,53,55,58–60]. While some studies have argued that the ECB lies toward the top of the Spitskop Member [61], recent work on Nama-equivalent strata from the nearby

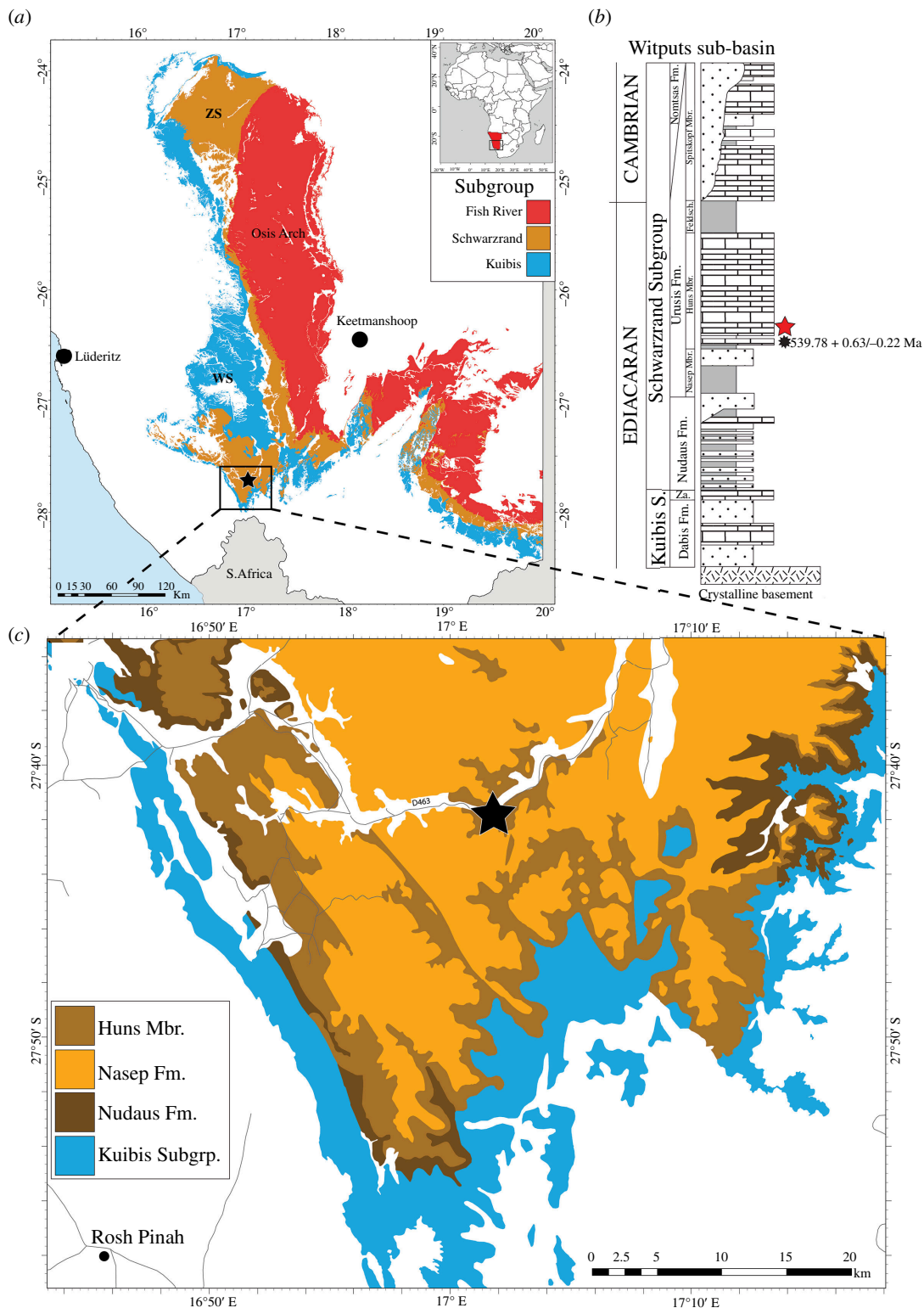


Figure 1. (a) Map of Nama Group sediments in Namibia south of Windhoek; Zaris (ZS) and Witputs (WS) sub-basins are indicated (modified from [6]); shapefiles are sourced from the Geological Survey of Namibia. (b) Generalized stratigraphy of the Witputs sub-basin, with star indicating position of Farm Arimas (adapted from [6]; dates follow from [3]). (c) Close view of the study area within the Witputs; star indicates the location of Farm Arimas.

Neint Nababep Plateau in South Africa suggests that much of the Nomtsas Formation may also be Ediacaran, and thus, the ECB is stratigraphically higher [3]. In all current models, however, the Huns Member is interpreted as Ediacaran, underlying dense accumulations of erniettomorph Ediacara biota in the Spitskop Member and below the last appearance dates of *Cloudina* and *Namacalathus* [59,61–

63]. Employing a Bayesian age-depth model, the Nasep–Huns contact and, thus, the approximate stratigraphic position of the trace fossil material described here can be precisely constrained to 539.78 ± 0.63/–0.22 Ma (see electronic supplementary material, table S3 in [3]).

3. Description of new trace material

Institutional abbreviations. Geological Survey of Namibia (GSN), Windhoek, Namibia.

Ichnogenus *Himatiichnus* igen. nov.

Type and only ichnospecies. *Himatiichnus mangano* isp. nov.

Diagnosis. Complex trace fossil comprising non-tapering, meandering, longitudinally striated tubes, with rare faint transverse annulations in the medial portion. In some instances, tubes appear to dip below and re-emerge from the sediment surface and terminate with rounded, bulbous structure(s).

Etymology. From the ancient Greek garment *himation*, the draped parallel folds of which are visually similar to the longitudinal striations present on this material.

Himatiichnus mangano isp. nov.

2022 Unnamed longitudinally striated traces; Turk *et al.* [57], fig. 9.

Holotype. Specimen A preserved on GSN F1643 (figure 2a).

Diagnosis. As for ichnogenus.

Etymology. In recognition of the significant contributions of Dr. M. Gabriela Mángano to ichnology and our understanding of the Ediacaran–Cambrian transition.

Material and stratigraphic setting. One slab (GSN F1643) with four prominent specimens; specimen A (figure 2a) is denoted as the holotype. These traces were recovered from the lower Huns Member of the Urusis Formation at Farm Arimas (27°41'36.1" S, 17°1'50.5" E), approximately 55 km west of the Fish River Canyon. The material is repositied at the GSN in Windhoek.

Traces are preserved in convex semi-relief (probably from bed sole) on reddish sandstone collected from an interval of subcrop (approx. 78 m above the lowermost exposures at Arimas) also preserving examples of *Corumbella*, bounded both below and above by thick- to very thick-bedded sandy limestone.

Description. Intertwining 1–3 cm long tubes (approx. 2–3 mm in width) preserved in convex semi-relief and exhibiting consistently spaced longitudinal striations approximately 0.4 mm apart; in some instances, this patternation shifts to a transverse annulation in the more proximal (i.e. closer to the point of radiation) portions of the material. Individual tubes are 2–3 cm in width and appear in several instances to disappear beneath and re-emerge on top of the sediment surface. Structures maintain constant width with no evidence of terminal tapering; distal ends (furthest from the point of radiation) terminate in a rounded, bulbous manner. Some distal portions preserve a series of nub-like protrusions (figure 2b,d) immediately adjacent to burrow terminations.

Remarks. *Himatiichnus mangano* is interpreted to have formed as an animal bearing convex frontal ornamentation, and anterior transverse lineation moved across—and penetrated slightly beneath—the sediment surface, while the series of nub-like structures found adjacent to the terminations suggest a repeated probing behaviour by the organism along the direction of motion. These factors are consistent with both the anatomy and burrowing behaviours of extant priapulid worms. Priapulid locomotion is a multi-step process, beginning with an evagination of the frontal introvert on which are present lines of equally spaced protrusions (scalids; figure 3b) that converge at the mouth [29,64]. These posteriorly oriented scalids serve to increase friction between the animal and substrate, anchoring the proboscis and thus allowing the worm to generate a peristaltic wave that shortens the annulated trunk, which then shifts into the space previously occupied by the frontal portions of the animal. Upon reaching the posterior praesoma, the muscular contractions cease, and the introvert is evaginated to begin the process anew [65]. A neoichnological study [40] demonstrated that experimentally produced casts of modern priapulid burrows bear notable resemblance to early Cambrian material described in the same paper; of particular note was the dual patternation of equally spaced longitudinal striations transitioning into transverse annulations. The multi-pronged, braided structure is indicative of repeated probe–retract–probe behaviour commonly exhibited by modern priapulids (i.e. *Priapululus caudatus*) when vertically restricted [25,66] (figure 3a).

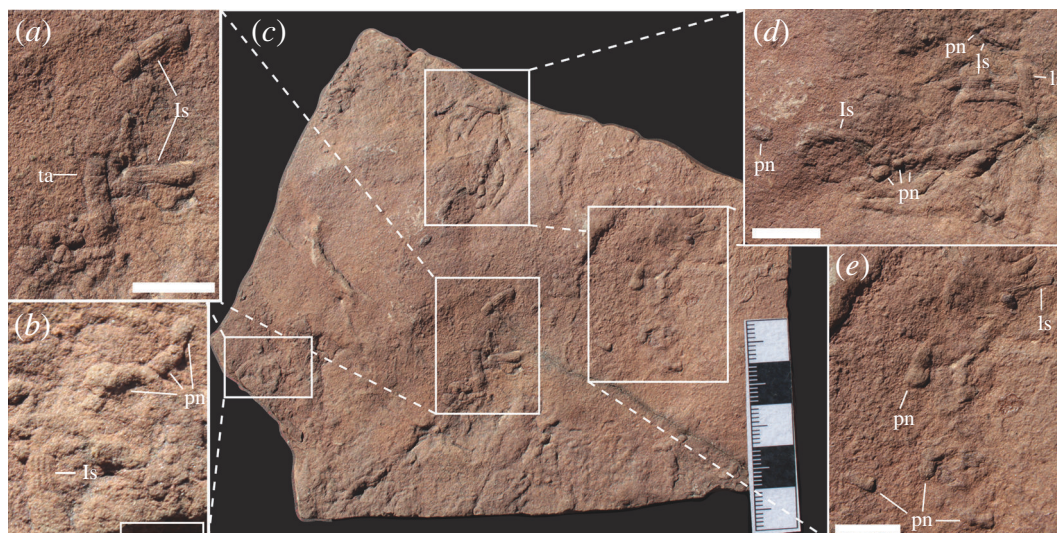


Figure 2. (a) Holotype specimen of *H. mangano*, probably representing bed sole. (b,d,e) Additional examples of *H. mangano*. (c) Full slab (GSN F1643). Abbreviations: ls, longitudinal striations; ta, transverse annulations; pn, probing nubs. Filled scale bars in (a), (d), (e) = 1 cm, hollow in (b) = 5 mm.

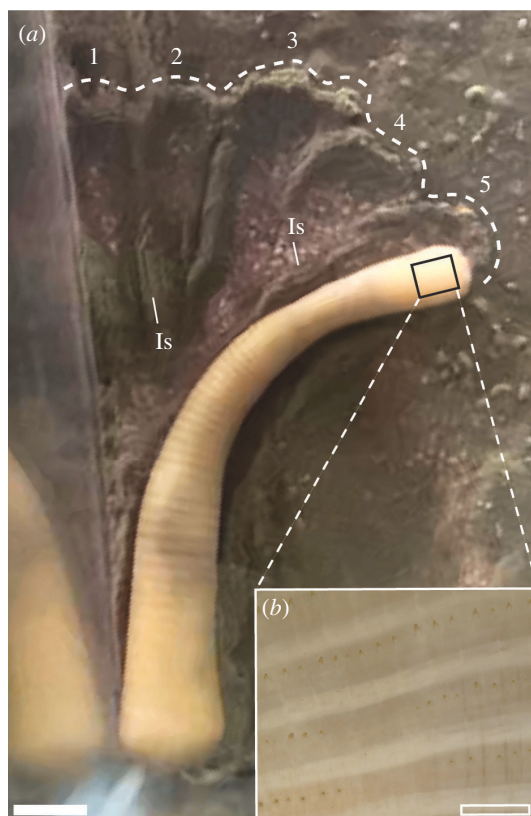


Figure 3. (a) Specimen of *P. caudatus* exhibiting surficial probe-retract-probe behaviour; individual probes marked with numbers, where 1 indicates the first probe and 5 indicates the most recent. The outline of greater probing structure is marked by a dotted line. Abbreviation: ls, longitudinal striations. (b) Close view of introvert displaying evenly spaced scalids. Filled scale bar in (a) = 1 cm, hollow in (b) = 1 mm.

4. Discussion

The attribution of *H. mangano* to probing traces left by vermiform scalidophorans aids our understanding of the timing and impacts of animal evolution in the late Ediacaran. We first discuss the anatomy of priapulids versus palaeoscoleccids in the context of these new traces, a potential match with divergence

times for these groups obtained from molecular clocks, and explore the roles these organisms and behaviours may have played in late Ediacaran communities. Lastly, we discuss the evolving picture of a transitional Nama interval comprising elements of both Ediacaran and Cambrian-type faunas, thus lending new support for a ‘long fuse’ model for the Cambrian explosion and emergence of Phanerozoic-type ecosystems.

4.1. Scalidophorans in the late Ediacaran

Several features seen in the *H. mangano* holotype material are suggestive of priapulid or palaeoscolecoid tracemakers. Both priapulids and palaeoscolecids exhibit an overall dual surface patternation, with their anterior portions characterized by cuticular ornaments (scalids and spines, respectively). In modern macroscopic priapulids, there is no transition between the introvert and the densely annulated trunk, the morphology of which is controlled by regular spacing of circular muscle bundles along its length [39]. Palaeoscolecids also possess annulated trunks, with individual annulations marked by regularly spaced button-like sclerites along the length of the body [42,67]. The material described here as *H. mangano* displays a double patterned surface, with the distal portions (furthest from the point of tube origination) characterized by equally spaced longitudinal striations. In some examples, these appear to transition into proximal sections (closer to the tube origination point) exhibiting equidistant transverse annulations. This surface patternation closely matches the priapulid and palaeoscolecoid anatomies described above, with neoichnological work [40,66] showing that the burrowing of modern priapulids produces visually similar striae as the friction-generating scalids (figure 3b) are dragged parallel to the overall direction of motion. The largely horizontal nature of the traces is also consistent with experimental results demonstrating that modern priapulids restricted to a single horizontal plane produce similar ‘probing’ traces to the material found here [25,66] (also see figure 3a).

The age constraints on these new fossils also provide a close match with divergence time estimates obtained via molecular clocks. A fossil-calibrated Bayesian analysis of protein-coding genes has obtained a divergence time estimate of 617–534 Ma for crown-group Scalidophora [20]. Using a Bayesian age-depth model, the Nasep–Huns contact and, thus, the approximate stratigraphic position of *H. mangano* can be precisely constrained to 539.78 +0.63/–0.22 Ma [3]. While trace fossils left by potential ecdysozoans are known between 551 and 555 Ma [23,68,69], *H. mangano* represents the earliest-known example of trace material with clear total-group scalidophoran affinity, especially in the context of comparison with both early Cambrian and modern priapulid traces [40,70]. Our trace fossil material thus represents an updated first appearance date (FAD) for scalidophorans and provides support for a deeper Ediacaran divergence of sister lineages of Priapulida and/or Scalidophora (i.e. total-groups Kinorhyncha, Loricifera and Cryptovermes [20]).

It is important to note, however, that the extent to which these lineages stretch into the Ediacaran is dependent on the placement of the ECB. While the current geologic time scale places the ECB at 538.8 Ma [61,71], recent high-precision geochronological work on the lower Wood Canyon Formation of Nevada has suggested that the boundary (as defined by the FAD of *T. pedum*) may be as young as 533 Ma [72]. As it currently stands, *H. mangano* precedes the ECB by approximately one million years; however, successive calibrations of the ECB over the last 40 years have indicated progressively younger dates [72]. Thus, with further refinement, it is quite possible this new material may instead represent a several million year-long antecedent to the Cambrian.

4.2. Late Ediacaran community palaeoecology

The new trace fossils described here form part of a diverse ichnofossil assemblage from the Nasep–Huns transition, alongside *Archaeonassa*, *Gordia*, *Helminthoidichnites*, *Helminthopsis*, *Torowangea*, small treptichnids and meiofaunal traces [57]. Other studies [73,74] targeting this transition have also described *Curvolithus*, *Didymaulichnus*, *Palaeophycus*, *Planolites* and *Skolithos*, although these ichnotaxa have not been found by our group (and occurrences of *Skolithos* in particular are now thought to instead represent plug-shaped burrows such as *Conichnus* and *Bergaueria* [6,75]). Alongside these trace fossils, the body fossil *Corumbella werneri*—interpreted as either an early scyphozoan cnidarian [76–78] or a calcareous sinotubulitid [79]—has been reported from nearby horizons [57]. The addition of *H. mangano*—a trace fossil more easily attributed to the responsible animal tracemaker(s) than many others from this interval—paints a clearer picture of late Ediacaran ecological diversity and reinforces the inference that benthic communities preserved in the upper Schwarzsand Subgroup of the Nama Group possess many ecological features typically associated with the Cambrian.

Based on preserved morphology, the *H. mangano* tracemaker probably bore affinities with scalidophorans such as priapulids or palaeoscolecids. As an entirely extinct group, the ecology of palaeoscolecids is little understood, although preserved gut remains [47,48,80–82] indicate that Cambrian examples were carnivorous [83] and deposit feeders that often consumed smaller invertebrates such as *Isoxys* [46,48]. Priapulids, by contrast, survive into the present day, and as such, more is known about their behaviour and ecology. Priapulids are thought to have been overwhelmingly predatory since at least the early Palaeozoic [84–86]; preserved gut contents from these animals have been found to contain a variety of small marine invertebrate material, including elements from hyolithids, brachiopods, bradoriids, trilobites, agnostids, polychaetes and wixwaxiids [87]. These new trace fossils thus reinforce the inference that predatory and/or deposit-feeding behaviours were well-established by the late Ediacaran [88,89] and, thus, probably played a part in structuring benthic communities and driving successive waves of evolutionary radiation over the Cambrian explosion [13,16,90].

Lastly, the attitude and orientation of *H. mangano* traces may also offer insight into the character of organism–substrate interactions over the ECB. Despite the dramatic increase in trace fossil diversity seen in the Nama interval (relative to the older White Sea and Avalon), recent work [6,91] indicates that ichnofossil assemblages continued to be dominated by biomixing, rather than bioirrigative behaviours, and moreover, that the impact of these traces would probably have been to shallow the depth of oxygen penetration [91]. Our specimens of *H. mangano* indicate an overall burrow architecture similar to those of treptichnids (i.e. gallery-type burrows characterized by repeated offset probes beneath the sediment–water interface) but which would have been extremely shallow, probably less than 1 cm deep. This contrasts starkly with modern priapulids, which will burrow along a horizontal path (often with offset probes deviating 20°–40° from the overall direction of motion) only when vertical motion is restricted [25,66] (figure 3a). The shallow depth of *H. mangano* burrows may potentially reflect a barrier to subsurface movement imposed, for example, by both lower shallow marine oxygen levels and a redox discontinuity surface close to the surface and largely unaffected by the predominant biomixers [40,92], with more modern-looking deep-tier scalidophoran burrows only appearing later in the Cambrian with the emergence of more intense bioirrigators facilitating increased subsurface oxygenation [91].

5. Summary

We describe *H. mangano*, a new, complex trace fossil from low in the Ediacaran Huns Member of the Nama Group in southern Namibia, characterized by repeated probes possessing both longitudinal and transverse lineations. We interpret these burrows as being formed by scalidophorans such as priapulids or palaeoscolecids, with longitudinal striations produced by a circular arrangement of frontal extrusions as they are pushed through the sediment, and transverse structures representing the preserved impressions of an annulated trunk. The late Ediacaran horizons preserving these traces are constrained to precisely 539.78 ± 0.63/–0.22 Ma, representing an updated first appearance date for total-group Scalidophora and providing support for a deeper Ediacaran divergence of Ecdysozoa. These burrows also contribute to an emerging picture of Nama-aged Ediacaran ecosystems that is far more similar to those of the lower Cambrian than previously appreciated, with a diversity of metazoan clades present and exhibiting a variety of predatory, deposit-feeding and suspension-feeding lifestyles. In turn, these late Ediacaran communities contribute to a burgeoning weight of support for the ‘long fuse’ model for the Cambrian explosion, illustrating that organisms, behaviours and ecological interactions once thought to be confined to the Palaeozoic now extend millions of years back into the late Ediacaran.

Ethics. Namibia fieldwork permits: National Heritage Council Permit no. 04/2017 and Research visa no. W5658/2019. Animal research: The manuscript presents research on animals that do not require ethical approval for their study.

Data accessibility. The specimens used as the basis for this study are accessioned at the Geological Survey of Namibia in Windhoek; accession number: GSN F1643.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. K.A.T.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, visualization, writing—original draft, writing—review and editing; M.A.P.: investigation, project administration, resources, writing—review and editing; H.M.: project administration, resources, writing—review and editing; M.L.: funding acquisition, investigation, writing—review and editing; S.A.F.D.: conceptualization, funding acquisition, investigation, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Waggoner B. 2003 The Ediacaran biotas in space and time. *Integr. Comp. Biol.* **43**, 104–113. (doi:10.1093/icb/43.1.104)
2. Boag TH, Darroch SAF, Laflamme M. 2016 Ediacaran distributions in space and time: testing assemblage concepts of earliest macroscopic body fossils. *Paleobiology* **42**, 574–594. (doi:10.1017/pab.2016.20)
3. Nelson LL, Ramezani J, Almond JE, Darroch SAF, Taylor WL, Brenner DC, Furey RP, Turner M, Smith EF. 2022 Pushing the boundary: a calibrated Ediacaran-Cambrian stratigraphic record from the Nama Group in northwestern Republic of South Africa. *Earth Planet. Sci. Lett.* **580**, 117396. (doi:10.1016/j.epsl.2022.117396)
4. Zhuravlev Ay, Wood RA, Penny AM. 2015 Ediacaran skeletal metazoan interpreted as a lophophorate. *Proc. R. Soc. B* **282**, 20151860. (doi:10.1098/rspb.2015.1860)
5. Darroch SAF, Smith EF, Laflamme M, Erwin DH. 2018 Ediacaran extinction and Cambrian explosion. *Trends Ecol. Evol.* **33**, 653–663. (doi:10.1016/j.tree.2018.06.003)
6. Darroch SAF *et al.* 2021 The trace fossil record of the Nama Group, Namibia: exploring the terminal Ediacaran roots of the Cambrian explosion. *Earth Sci. Rev.* **212**, 103435. (doi:10.1016/j.earscirev.2020.103435)
7. Wood R, Liu AG, Bowyer F, Wilby PR, Dunn FS, Kenchington CG, Cuthill JFH, Mitchell EG, Penny A. 2019 Integrated records of environmental change and evolution challenge the Cambrian explosion. *Nat. Ecol. Evol.* **3**, 528–538. (doi:10.1038/s41559-019-0821-6)
8. Shore AJ, Wood RA, Butler IB, Zhuravlev AY, McMahon S, Curtis A, Bowyer FT. 2021 Ediacaran metazoan reveals lophotrochozoan affinity and deepens root of Cambrian explosion. *Sci. Adv.* **7**, eabf2933. (doi:10.1126/sciadv.abf2933)
9. Leme JM, Van Iten H, Simões MG. A new conulariid (Cnidaria, Scyphozoa) from the terminal Ediacaran of Brazil. *Front. Earth Sci.* **10**, 777746. (doi:10.3389/feart.2022.777746)
10. Conway Morris S. 2000 The Cambrian 'explosion': slow-fuse or megatonnage? *Proc. Natl Acad. Sci. USA* **97**, 4426–4429. (doi:10.1073/pnas.97.9.4426)
11. Fortey R. 2001 The Cambrian explosion exploded? *Science* **293**, 438–439. (doi:10.1126/science.1062987)
12. Xiao S. 2014 Oxygen and early animal evolution. In *Treatise on geochemistry* (ed. J Farquhar), pp. 231–250. Dordrecht, The Netherlands: Elsevier. (doi:10.1016/B978-0-08-095975-7.01310-3)
13. Schiffbauer JD, Huntley JW, O'Neil GR, Darroch SAF, Laflamme M, Cai Y. 2016 The latest Ediacaran wormworld fauna: setting the ecological stage for the Cambrian explosion. *GSA Today* **26**, 4–11. (doi:10.1130/GSATG265A.1)
14. Schiffbauer JD, Selly T, Jacquet SM, Merz RA, Nelson LL, Strange MA, Cai Y, Smith EF. 2020 Discovery of bilaterian-type through-guts in clouidnomorphs from the terminal Ediacaran period. *Nat. Commun.* **11**, 205. (doi:10.1038/s41467-019-13882-z)
15. Mussini G, Dunn FS. 2024 Decline and fall of the Ediacarans: late-Neoproterozoic extinctions and the rise of the modern biosphere. *Biol. Rev.* **99**, 110–130. (doi:10.1111/brv.13014)
16. Erwin DH, Laflamme M, Tweedt SM, Sperling EA, Pisani D, Peterson KJ. 2011 The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* **334**, 1091–1097. (doi:10.1126/science.1206375)
17. dos Reis M, Thawornwattana Y, Angelis K, Telford MJ, Donoghue PCJ, Yang Z. 2015 Uncertainty in the timing of origin of animals and the limits of precision in molecular timescales. *Curr. Biol.* **25**, 2939–2950. (doi:10.1016/j.cub.2015.09.066)
18. Schmidt-Rhaesa A, Bartolomeaus T, Lemburg C, Ehlers U, Garey JR. 1998 The position of the Arthropoda in the phylogenetic system. *J. Morphol.* **238**, 263–285. (doi:10.1002/(SICI)1097-4687(199812)238:3<263::AID-JMOR1>3.0.CO;2-L)
19. Giribet G, Edgecombe GD. 2017 Current understanding of Ecdysozoa and its internal phylogenetic relationships. *Integr. Comp. Biol.* **57**, 455–466. (doi:10.1093/icb/ixc072)
20. Howard RJ *et al.* 2022 The Ediacaran origin of Ecdysozoa: integrating fossil and phylogenomic data. *J. Geol. Soc. London* **179**. (doi:10.1144/jgs2021-107)
21. Telford MJ, Boulrat SJ, Economou A, Papillon D, Rota-Stabelli O. 2008 The evolution of the Ecdysozoa. *Phil. Trans. R. Soc. B* **363**, 1529–1537. (doi:10.1098/rstb.2007.2243)

22. Chapman AD. 2009 *Number of living species in australia and the world*. Canberra, Australia: Department of the Environment, Heritage, Water, and the Arts.
23. Chen Z, Zhou C, Yuan X, Xiao S. 2019 Death march of a segmented and trilobate bilaterian elucidates early animal evolution. *Nature* **573**, 412–415. (doi:10.1038/s41586-019-1522-7)
24. Liu Y, Xiao S, Shao T, Broce J, Zhang H. 2014 The oldest known priapulid-like scalidophoran animal and its implications for the early evolution of cycloneuralians and ecdysozoans. *Evol. Dev.* **16**, 155–165. (doi:10.1111/ede.12076)
25. Vannier J, Calandra I, Gaillard C, Žylińska A. 2010 Priapulid worms: pioneer horizontal burrowers at the Precambrian-Cambrian boundary. *Geology* **38**, 711–714. (doi:10.1130/G30829.1)
26. Landing E. 1994 Precambrian-Cambrian boundary global stratotype ratified and a new perspective of Cambrian time. *Geology* **22**, 179. (doi:10.1130/0091-7613(1994)022<0179:PCBGSR>2.3.CO;2)
27. Buatois LA. 2018 *Treptichnus pedom* and the Ediacaran–Cambrian boundary: significance and caveats. *Geol. Mag.* **155**, 174–180. (doi:10.1017/S0016756817000656)
28. Hammond RA. 1970 The surface of *Priapulus caudatus* (Lamarck, 1816): Nematelminthes, Priapulida. *Z. Für Morphol. Tiere.* **68**, 255–268. (doi:10.1007/BF00277505)
29. Calloway CB. 1975 Morphology of the introvert and associated structures of the priapulid *Tubiluchus corallicola* from Bermuda. *Mar. Biol.* **31**, 161–174. (doi:10.1007/BF00391628)
30. Wills MA. 1998 Cambrian and recent disparity: the picture from priapulids. *Paleobiology* **24**, 177–199. (doi:10.1666/0094-8373(1998)024[0177:CARDTP]2.3.CO;2)
31. Schmidt-Rhaesa A, Cañete JJ, Mutschke E. 2022 New record and first description including SEM and μ CT of the rare priapulid *Acanthopriapulus horridus* (Priapulida, Scalidophora). *Zool. Anz.* **298**, 1–9. (doi:10.1016/j.jcz.2022.03.001)
32. Schmidt-Rhaesa A, Raeker J. 2023 Morphology of larval and postlarval stages of *Priapulopsis bicaudatus* (Danielssen, 1869) (Priapulida) from the North Atlantic ocean. *Zool. Anz.* **302**, 1–16. (doi:10.1016/j.jcz.2022.11.006)
33. Conway Morris S. 1977 Fossil priapulid worms. *Spec. Pap. Palaeontol.* **20**, 1–103.
34. Conway Morris S, Robinson RA. 1986 Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. *Univ. Kans. Paleontol. Contrib.* **117**, 1–22.
35. Zhao F, Caron JB, Bottjer DJ, Hu S, Yin Z, Zhu M. 2014 Diversity and species abundance patterns of the early Cambrian (series 2, stage 3) Chengjiang biota from China. *Paleobiology* **40**, 50–69. (doi:10.1666/12056)
36. Smith MR, Harvey THP, Butterfield NJ. 2015 The macro- and microfossil record of the Cambrian priapulid *Ottoia*. *Palaeontology* **58**, 705–721. (doi:10.1111/pala.12168)
37. Oeschger R, Vetter RD. 1992 Sulfide detoxification and tolerance in *Halicryptus spinulosus* (Priapulida): a multiple strategy. *Mar. Ecol. Prog. Ser.* **86**, 167–179. (doi:10.3354/meps086167)
38. Vaquer-Sunyer R, Duarte CM. 2008 Thresholds of hypoxia for marine biodiversity. *Proc. Natl Acad. Sci. USA* **105**, 15 452–15 457. (doi:10.1073/pnas.0803833105)
39. Schmidt-Rhaesa A. 2012 Nematomorpha, Priapulida, Kinorhyncha, Loricifera. In *Handbook of zoology*, p. 381, vol. 1. Berlin, Germany: De Gruyter. (doi:10.1515/9783110272536)
40. Kesidis G, Slater BJ, Jensen S, Budd GE. 2019 Caught in the act: priapulid burrowers in early Cambrian substrates. *Proc. R. Soc. B* **286**, 20182505. (doi:10.1098/rspb.2018.2505)
41. Ivantsov AY, Wrona R. 2004 Articulated palaeoscolecoid sclerite arrays from the lower Cambrian of eastern Siberia. *Acta Palaeontol. Pol.* **54**, 1–22.
42. Harvey THP, Dong X, Donoghue PCJ. 2010 Are palaeoscolecids ancestral ecdysozoans? *Evol. Dev.* **12**, 177–200. (doi:10.1111/j.1525-142X.2010.00403.x)
43. Smith MR. 2015 A palaeoscolecoid worm from the Burgess Shale. *Palaeontology* **58**, 973–979. (doi:10.1111/pala.12210)
44. Leibach W, Lerosey-Aubril R, Whitaker A, Schiffbauer J, Kimmig J. 2021 First palaeoscolecoid from the Cambrian (Miaolingian, Drumian) Marjum Formation of western Utah. *Acta Palaeontol. Pol.* **66**. (doi:10.4202/app.00875.2021)
45. Huang D, Chen J, Zhu M, Zhao F. 2014 The burrow dwelling behavior and locomotion of palaeoscolecoidian worms: new fossil evidence from the Cambrian Chengjiang fauna. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **398**, 154–164. (doi:10.1016/j.palaeo.2013.11.004)
46. Morris SC, Peel JS. 2010 New palaeoscolecoidian worms from the lower Cambrian: Sirius Passet, Latham Shale and Kinzers Shale. *Acta Palaeontol. Pol.* **55**, 141–156. (doi:10.4202/app.2009.0058)
47. Hu S, Steiner M, Zhu M, Luo H, Forchielli A, Keupp H, Zhao F, Liu Q. 2012 A new priapulid assemblage from the early Cambrian Guanshan fossil lagerstätte of SW China. *Bull. Geosci.* 93–106. (doi:10.3140/bull.geosci.1238)
48. Martin ELO, Lerosey-Aubril R, Vannier J. 2016 Palaeoscolecoid worms from the lower Ordovician Fezouata lagerstätte, Morocco: palaeoecological and palaeogeographical implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **460**, 130–141. (doi:10.1016/j.palaeo.2016.04.009)
49. Germs GJB. 1983 Implications of a sedimentary facies and depositional environmental analysis of the Nama Group in South West Africa/Namibia. *Spec. Publ. Geol. Soc. South Afr.* **11**, 89–114.
50. Germs GJB. 1995 The Neoproterozoic of southwestern Africa, with emphasis on platform stratigraphy and paleontology. *Precambrian Res.* **73**, 137–151. (doi:10.1016/0301-9268(94)00075-3)
51. Stanistreet IG, Kukla PA, Henry G. 1991 Sedimentary basinal responses to a Late Precambrian Wilson Cycle: the Damara Orogen and Nama Foreland, Namibia. *J. Afr. Earth Sci.* **13**, 141–156. (doi:10.1016/0899-5362(91)90048-4)

52. Gresse PG, Germs GJB. 1993 The Nama foreland basin: sedimentation, major unconformity bounded sequences and multisided active margin advance. *Precambrian Res.* **63**, 247–272. (doi:10.1016/0301-9268(93)90036-2)
53. Saylor BZ, Grotzinger JP, Germs GJB. 1995 Sequence stratigraphy and sedimentology of the Neoproterozoic Kuibis and Schwarzrand subgroups (Nama Group), southwestern Namibia. *Precambrian Res.* **73**, 153–171. (doi:10.1016/0301-9268(94)00076-4)
54. Saylor BZ, Kaufman AJ, Grotzinger JP, Urban F. 1998 A composite reference section for terminal Proterozoic strata of southern Namibia. *J. Sediment. Res.* **68**, 1223–1235. (doi:10.2110/jsr.68.1223)
55. Grotzinger JP, Miller R. 2008 *The geology of Namibia, vol. 2, Geological Society of Namibia special publication*, (ed. R Miller), pp. 13 229–13 272. Windhoek, Namibia: Geological Survey of Namibia.
56. Saylor BZ. 2003 Sequence stratigraphy and carbonate-siliciclastic mixing in a terminal proterozoic foreland basin, Uruis Formation, Nama Group, Namibia. *J. Sediment. Res.* **73**, 264–279. (doi:10.1306/082602730264)
57. Turk KA, Maloney KM, Laflamme M, Darroch SAF. 2022 Paleontology and ichnology of the late Ediacaran Nasep–Huns transition (Nama Group, southern Namibia). *J. Paleontol.* **96**, 753–769. (doi:10.1017/jpa.2022.31)
58. Saylor BZ, Grotzinger JP. 1996 Reconstruction of important Proterozoic–Cambrian boundary exposures through the recognition of thrust deformation in the Nama Group of southern Namibia. *Commun. Geol. Surv. Namib.* **11**, 1–12.
59. Narbonne GM, Saylor BZ, Grotzinger JP. 1997 The youngest Ediacaran fossils from Southern Africa. *J. Paleontol.* **71**, 953–967. (doi:10.1017/S0022336000035940)
60. Wilson JP *et al.* 2012 DEEP-water incised valley deposits at the Ediacaran–Cambrian boundary in southern Namibia contain abundant *Treptichnus pedum*. *Palaios* **27**, 252–273. (doi:10.2110/palo.2011.p11-036r)
61. Linnemann U *et al.* 2019 New high-resolution age data from the Ediacaran–Cambrian boundary indicate rapid, ecologically driven onset of the Cambrian explosion. *Terra Nova* **31**, 49–58. (doi:10.1111/ter.12368)
62. Grotzinger JP, Bowring SA, Saylor BZ, Kaufman AJ. 1995 Biostratigraphic and geochronologic constraints on early animal evolution. *Science* **270**, 598–604. (doi:10.1126/science.270.5236.598)
63. Darroch SAF *et al.* 2015 Biotic replacement and mass extinction of the Ediacara biota. *Proc. R. Soc. B* **282**, 1–10. (doi:10.1098/rspb.2015.1003)
64. Hammond RA. 1970 The burrowing of *Priapulius caudatus*. *J. Zool.* **162**, 469–480. (doi:10.1111/j.1469-7998.1970.tb01281.x)
65. Elder HY, Hunter RD. 1980 Burrowing of *Priapulius caudatus* (Vermes) and the significance of the direct peristaltic wave. *J. Zool.* **191**, 333–351. (doi:10.1111/j.1469-7998.1980.tb01463.x)
66. Turk KA, Wehrmann A, Laflamme M, Darroch SAF. 2024 Priapulid neoichnology, ecosystem engineering, and the Ediacaran–Cambrian transition. *Palaeontology* **67**, e12721. (doi:10.1111/pala.12721)
67. Streng M, Ebbestad JOR, Berg-Madsen V. 2017 Cambrian palaeoscolecid (Cycloneuralia) of southern Scandinavia. *Pap. Palaeontol.* **3**, 21–48. (doi:10.1002/spp2.1067)
68. Parry LA *et al.* 2017 Ichneological evidence for meiofaunal bilaterians from the terminal Ediacaran and earliest Cambrian of Brazil. *Nat. Ecol. Evol.* **1**, 1455–1464. (doi:10.1038/s41559-017-0301-9)
69. Chen Z, Chen X, Zhou C, Yuan X, Xiao S. 2018 Late Ediacaran trackways produced by bilaterian animals with paired appendages. *Sci. Adv.* **4**, eaao6691. (doi:10.1126/sciadv.aao6691)
70. Turk KA, Pulsipher MA, Bergh E, Laflamme M, Darroch SAF. 2024 *Archaeichnium haughtoni*: a robust burrow lining from the Ediacaran–Cambrian transition of Namibia. *Pap. Palaeontol.* **10**, e1546. (doi:10.1002/spp2.1546)
71. Peng SC, Babcock LE, Ahlberg P. 2020 The Cambrian Period. In *Geologic time scale 2020* (eds FM Gradstein, JG Ogg, MD Schmitz, GM Ogg), pp. 565–629. Amsterdam, The Netherlands: Elsevier. (doi:10.1016/B978-0-12-824360-2.00019-X)
72. Nelson LL, Crowley JL, Smith EF, Schwartz DM, Hodgins EB, Schmitz MD. 2023 Cambrian explosion condensed: high-precision geochronology of the lower Wood Canyon Formation, Nevada. *Proc. Natl Acad. Sci. USA* **120**, e2301478120. (doi:10.1073/pnas.2301478120)
73. Germs GJB. 1972 Trace fossils from the Nama Group, south-west Africa. *J. Paleontol.* **46**, 864–870.
74. Geyer G, Uchman A. 1995 Ichnofossil assemblages from the nama group (neoproterozoic-lower cambrian) in namibia and the proterozoic-cambrian boundary problem revisited. In *Beringeria special issue 2* (eds G Geyer, E Landing), pp. 175–202.
75. Jensen S. 2003 The Proterozoic and earliest Cambrian trace fossil record; patterns, problems and perspectives. *Integr. Comp. Biol.* **43**, 219–228. (doi:10.1093/icb/43.1.219)
76. Babcock LE, Grunow AM, Sadowski GR, Leslie SA. 2005 *Corumbella*, an ediacaran-grade organism from the late Neoproterozoic of Brazil. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **220**, 7–18. (doi:10.1016/j.palaeo.2003.01.001)
77. Pacheco MLAF *et al.* 2015 Insights into the skeletonization, lifestyle, and affinity of the unusual Ediacaran fossil *Corumbella*. *PLoS One* **10**, e0114219. (doi:10.1371/journal.pone.0114219)
78. Van Iten H *et al.* 2016 Origin and early diversification of phylum Cnidaria: key macrofossils from the Ediacaran system of North and South America. In *The Cnidaria, past, present and future: the world of Medusa and her sisters* (eds S Goffredo, Z Dubinsky), pp. 31–40. Cham, Switzerland: Springer International Publishing. (doi:10.1007/978-3-319-31305-4_3)
79. Walde DHG, Weber B, Erdtmann BD, Steiner M. 2019 Taphonomy of *Corumbella weneri* from the Ediacaran of Brazil: sinotubulitid tube or conulariid test? *Alcheringa* **43**, 335–350. (doi:10.1080/03115518.2019.1615551)
80. Zhang XG, Hou XG, Bergström J. 2006 Early Cambrian priapulid worms buried with their lined burrows. *Geol. Mag.* **143**, 743–748. (doi:10.1017/S0016756806002445)
81. García-Bellido DC, Paterson JR, Edgecombe GD. 2013 Cambrian palaeoscolecid (Cycloneuralia) from Gondwana and reappraisal of species assigned to *Palaeoscolex*. *Gondwana Res.* **24**, 780–795. (doi:10.1016/j.gr.2012.12.002)

82. Wang W, Muir LA, Botting JP, Feng H, Servais T, Li L. 2014 A Tremadocian (early Ordovician) palaeoscolecidan worm from graptolitic shales in Hunan Province, South China. *Palaeontology* **57**, 657–671. (doi:10.1111/pala.12083)
83. Wills MA, Gerber S, Ruta M, Hughes M. 2012 The disparity of priapulid, archaeopriapulid and palaeoscolecid worms in the light of new data. *J. Evol. Biol.* **25**, 2056–2076. (doi:10.1111/j.1420-9101.2012.02586.x)
84. Brett CE, Walker SE. 2002 Predators and predation in paleozoic marine environments. *Paleontol. Soc. Pap.* **8**, 93–118. (doi:10.1017/S1089332600001078)
85. Huang DY, Vannier J, Chen JY. 2004 Anatomy and lifestyles of early Cambrian priapulid worms exemplified by *Corynetis* and *Anningvermis* from the Maotianshan Shale (SW China). *Lethaia* **37**, 21–33. (doi:10.1080/00241160410005088)
86. Vannier J, Chen J. 2005 Early Cambrian food chain: new evidence from fossil aggregates in the Maotianshan Shale biota, SW China. *PALAIOS* **20**, 3–26. (doi:10.2110/palo.2003.p03-40)
87. Vannier J. 2012 Gut contents as direct indicators for trophic relationships in the Cambrian marine ecosystem. *PLoS One* **7**, e52200. (doi:10.1371/journal.pone.0052200)
88. Hua H, Pratt BR, Zhang LY. 2003 Borings in *Cloudina* shells: complex predator-prey dynamics in the terminal Neoproterozoic. *Palaios* **18**, 454–459. (doi:10.1669/0883-1351(2003)018<0454:BICSCP>2.0.CO;2)
89. Gehling JG, Droser ML. 2018 Ediacaran scavenging as a prelude to predation. *Emerg. Top. Life Sci.* **2**, 213–222. (doi:10.1042/ETLS20170166)
90. Erwin DH, Tweedt S. 2012 Ecological drivers of the Ediacaran-Cambrian diversification of Metazoa. *Evol. Ecol.* **26**, 417–433. (doi:10.1007/s10682-011-9505-7)
91. Cribb AT, van de Velde SJ, Berelson WM, Bottjer DJ, Corsetti FA. 2023 Ediacaran-Cambrian bioturbation did not extensively oxygenate sediments in shallow marine ecosystems. *Geobiology* **21**, 435–453. (doi:10.1111/gbi.12550)
92. Buatois LA, Mángano MG. 2011 *Ichnology: organism-substrate interactions in space and time*. Cambridge, UK: Cambridge University Press.