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Exceptional soft-tissue preservation reveals the oldest evidence for tube feet and their ecological significance in crinoids

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Tube feet are extensions of the echinoderm water vascular system that play essential roles in feeding and ecology in living crinoids. However, only a single instance of tube foot preservation has been described across the 485-million-year fossil record of crinoids, which limits our understanding of soft-tissue morphology and functional ecology within this major clade of echinoderms. Here, we report on the earliest example of tube feet preserved in the crinoid *Dendrocrinus simcoensis* from the Late Ordovician Neuville Lagerstätte of Québec, Canada. The tube feet are preserved as pyrite films and exhibit morphology that is broadly similar to that of extant comatulid crinoids, but with combinations of length and spacing that differ from those documented in any extant crinoid. Spacing of tube feet in *D. simcoensis* is significantly similar to that inferred for other fossil crinoids based on ambulacral cover plates, especially other eucladid crinoids, and reveals a strong relationship between tube foot spacing, phylogeny and palaeoecology. The unique combination of tube foot length and spacing in *D. simcoensis* suggests this crinoid may have fed with the arms oriented in a multidirectional or conical posture, unlike most modern stalked crinoids.

1. Introduction

The fossil record is overwhelmingly dominated by biomineralized hard parts, but non-mineralized tissues may be preserved in rare cases. By revealing details of soft tissues that are typically lost during the fossilization process, instances of exceptional preservation provide important windows into the anatomy, ecology and evolution of ancient organisms. Soft-tissue preservation is particularly informative when it occurs in entirely extinct groups that lack modern representatives [1,2] or in the early members of clades where the preservation of non-mineralized tissues can clarify aspects of ecology, functional morphology, behaviour, evolution and character acquisition that would otherwise be impossible to infer from fossilized hard parts or living organisms alone [3,4].

Echinoderms are a major phylum of marine invertebrates with a rich fossil record that ranges from the Cambrian period to the present day [5,6]. Despite their exceptional abundance and diversity over more than 500 million years, only a small portion of the echinoderm tree of life is extant, and very little is known about the soft-tissue anatomy of most fossil echinoderms. The water vascular system is a critical part of the soft-tissue anatomy of all echinoderms that performs key functions including movement, respiration and feeding [7,8]. Most of the water vascular system is internal, but perforations in the ambulacral regions of the skeleton allow tube feet, extensions of the water vascular system, to penetrate through the skeleton. The anatomy of tube feet varies depending on the specific functions for which they are used (e.g. [9–12]), which makes them informative for understanding many aspects of echinoderm ecology and evolution. Because tube feet are rarely preserved, each discovery of these structures in the fossil record has revealed new information on ancient echinoderms, such as anatomical and ecological insights [13–15], the nature of the water vascular system in entirely extinct groups (e.g. edrioasteroids and ophiocistioids [16,17]), affinities of enigmatic taxa [18] and the evolutionary steps leading to development of crown-group body plans [19].

Within class Crinoidea (sea lilies and feather stars), tube feet play an essential role in feeding as the primary structures that are used for direct food capture during passive suspension filter feeding [20,21]. In extant crinoids, tube feet exhibit variations in length, width and spacing that reflect aspects of environmental conditions and feeding posture [9,12]. However, across the thousands of crinoid species known from the fossil record, only a single example of tube foot preservation has been recognized [14], which limits our understanding of feeding mechanics and anatomy in extinct crinoids.

Here, we report the oldest evidence of tube feet in the crinoid fossil record from newly discovered specimens of *Dendrocrinus simcoensis* Wright *et al.* 2019 [22] collected from the Upper Ordovician (Katian) Neuville Lagerstätte of Québec, Canada (approx. 452 Ma). The occurrence of tube feet in an Ordovician fossil provides a rare opportunity to document the soft-tissue anatomy and palaeobiology of extinct crinoids. Based on its phylogenetic position within total-group Crinoidea [23], this species is confidently assigned to the Eucladida, a major clade that includes both crown-group crinoids (superorder Articulata) and their closest Palaeozoic stem groups [24]. Comparative analysis of the tube feet anatomy of *D. simcoensis* with other members of the total-group Crinoidea provides significant, independent support for our interpretation of these morphological structures as tube feet and reveals new insights into understanding the feeding ecology and functional diversity of early crinoid communities.

2. Material and methods

2.1. Geologic setting and taphonomy

The Neuville Formation (uppermost Trenton Group) from the Québec City region of Québec, Canada, preserves a diverse but sparsely distributed Upper Ordovician (early Katian) fauna that includes echinoderms, trilobites, brachiopods, bryozoans, conulariids, graptolites and other typical Lower Palaeozoic marine invertebrates [25–29]. The unit is composed of argillaceous and micritic limestones with thin interbedded shales and is interpreted to have been deposited in a deep carbonate ramp setting with minimal storm influence [26]. Black shales dominate at some locations, such as the Saint-Joachim Quarry (approx. 3 km northeast of Beaupré, Québec) that exposes the upper Grondines Member of the Neuville Formation [25,26]. Several fossil medusozoan cnidarians have been described from the Saint-Joachim Quarry that exhibit Burgess Shale-type preservation of soft tissues through carbon impressions [29], which has led to its recognition as a Konservat-Lagerstätte. Other fossils from the Saint-Joachim Quarry commonly exhibit pyritization, but to date, soft-tissue preservation has not been described in other taxa from this or any other locality within the Neuville Lagerstätte.

Echinoderms have primarily been recovered from the upper Grondines Member of the Neuville Lagerstätte. The Neuville echinoderm fauna is dominated by crinoids, but also includes rhombiferans, solutes, stylophorans, cyclocystoids, asterozoans and paracrinoids [28,30]. The deep-water setting of the Neuville Formation promoted the preservation of fully articulated echinoderms, with many specimens preserving complete columns, holdfasts and feeding structures. Although the majority of echinoderm specimens are preserved as original calcite, many also exhibit partial pyritization that ranges from minor to nearly complete replacement by pyrite. Disseminated pyrite is also common throughout the surrounding matrix in horizons where pyrite replacement of fossils occurs.

2.2. Fossil material and imaging

The most significant collection of fossil material from the Neuville Formation is housed at the Musée de paléontologie et de l'évolution (MPE) in Montréal, Québec, Canada. During a survey of the crinoids in this collection, two specimens of *D. simcoensis* Wright *et al.* 2019 [22] (MPEP700.56a and MPEP700.56b) from the Saint-Joachim Quarry (Neuville Formation, Grondines Member) were identified that exhibit soft-tissue preservation of the tube feet through partial pyritization. These specimens were prepared prior to donation to the MPE using air abrasion. Specimens were photographed under alcohol, and tube foot measurements were taken from photographs using ImageJ. Interpretive diagrams were drawn using a camera lucida and photo tracings to better visualize the anatomy of the preserved tube feet. Although geochemical methods such as scanning electron microscope (SEM) imaging or X-ray fluorescence (XRF) can further confirm the presence of pyrite versus calcite in soft-tissue preservation (e.g. [31,32]), it was deemed unnecessary to employ these methods here, given the clear distinction between calcite and pyrite material based on textural relationships and optical properties observed under microscopy.

2.3. Comparative study of tube feet in fossil and living crinoids

A comparative study was conducted to evaluate the tube foot anatomy of *D. simcoensis* compared with that of other living and fossil crinoids. Data for tube foot length (in mm) and spacing (in mm^{-1}, the number of tube feet per 1 mm) were collected for *D. simcoensis* and for the Lower Devonian crinoid *Codiacrinus schultzei* Follmann 1877 [33], which is the only other known fossil crinoid that preserves tube feet [14].

To compare tube foot anatomy of fossil taxa with extant species, we conducted a survey of published literature and identified publications from which data on the length and/or spacing of extant crinoid tube feet could be compiled from reported values and photographs [9,12,34]. Meyer [9] presented data for tube foot length and spacing for comatulid crinoids from Lizard Island (Great Barrier Reef, Australia) and Palau Islands. Because some species were sampled at both localities, we calculated mean values for tube feet measurements of these species. Messing *et al.* [12] documented an approximate tube foot length of 2.0 mm in a stalked, deep-sea hyocrinid (Hyocrinidae sp.) but did not document tube foot spacing or width or include photographs from which these data could be collected. Byrne & Fontaine [34] reported the mean primary tube foot length in *Florometra serratissima* but did not report tube foot spacing. To add tube foot spacing data for this species, we collected novel measurement data from a scaled photograph of pinnules with tube feet from Byrne & Fontaine [34, fig. 4], which were used to calculate mean tube foot length and spacing. A total of 17 extant crinoid species were included in the final dataset, of which 16 included tube foot spacing data and all included tube foot length data (electronic supplementary material, table S1 [35]).

Although tube foot anatomy is not directly preserved in other known fossil specimens, Brower [36] proposed a model to infer tube foot spacing based on the configuration of associated ambulacral cover plates and inferred tube foot spacing distributions for 15 extinct species spanning major subclades of Ordovician taxa. To evaluate how values of tube foot spacing measured from *D. simcoensis* specimens compare with other members of the total-group Crinoidea, we used simple Gaussian modelling to generate tube foot spacing distributions for subclades based on the mean and standard deviation of tube foot spacing measurements in fossil ($n = 16$) and extant ($n = 16$) taxa. Measurements for tube foot spacing were gathered from our literature compilation of extant species and Brower's [36] inferred values for fossil taxa. Data were analysed and visualized in R v. 4.3.1 using custom scripts and the base R MASS package [37] to evaluate patterns of morphological variation in tube feet of fossil and living crinoids. Additional analytical details are outlined in the R script that is provided in the electronic supplementary material [35].

3. Results

3.1. Description

The skeletal morphology of *D. simcoensis* was previously described in detail [22], so this description focuses on the new details of soft-tissue anatomy and associated features that can be observed in the Neuville Formation specimens. The two specimens of *D. simcoensis* are preserved adjacent to each other on a single bedding surface in association with three partially complete solute echinoderms (figure 1*a*). Both *D. simcoensis* specimens consist of small, crushed calyces with partial arms and stems. The calyx of MPEP700.56b is 3.7 mm high and 3.3 mm wide with a maximum arm length of 14.9 mm. The calyx of MPEP700.56a is crushed but of a similar size, with a maximum complete arm length of 17.9 mm. Tube feet are best preserved along two of the medial to distal arms of MPEP700.56a (figure 1*b*) and one of the medial to distal arms of MPEP700.56b (figure 1*f*). Additional structures are present on some of the other arms of both specimens that may be tube feet, but they are very poorly defined or indistinct due to heavy pyritization.

The tube feet are essentially indistinguishable from the surrounding matrix when observed or photographed dry under direct light. Under strongly angled light, the tube feet are visible as reflective, slightly raised structures that are similar in colour and texture to the surrounding matrix (figure 1*c*). When immersed in alcohol, the preservation of tube feet by pyrite is apparent due to increased contrast between pyritized structures and the surrounding matrix, and the boundaries of most tube feet are more distinctive. However, extensive pyritization obscures details of the tube feet in some instances (e.g. figure 1*d*). As a result, tube feet are best viewed using a combination of different lighting angles and immersion in alcohol versus dry photography.

The best-preserved tube feet project from the secundibrachials and tertibrachials in both specimens. Each tube foot consists of a short, smooth structure with a bluntly rounded tip (figure 1*c,e,g,h*). Tube feet of *D. simcoensis* average 0.41 mm long and 0.15 mm wide in MPEP700.56a ($n = 17$) and 0.48 mm long and 0.16 mm wide in MPEP700.56b ($n = 9$) for an overall mean tube foot size of 0.45 mm long and 0.15 mm wide. Spacing of tube feet is approximately 4 mm^{-1} in both MPEP700.56a and MPEP700.56b. Each brachial plate of the arms corresponds to two pairs of tube feet.

In both specimens, additional structures are preserved adjacent to some parts of the arms that superficially resemble tube feet (figure 1*a,f,i,j*). However, submersion in alcohol reveals that these features are preserved as calcite plates rather than pyrite films (e.g. figure 1*j*). As a result, these structures are interpreted as partially disarticulated biserial ambulacral cover plates rather than tube feet. This interpretation is further supported by the fact that these plates are substantially larger and have more equant dimensions than the tube feet (mean width = 0.39 mm, mean length = 0.41 mm), and in MPEP700.56a, they are roughly divided into two columns of plates (figure 1*i*), which is consistent with the typical morphology and biserial arrangement of crinoid cover plates.

3.2. Comparative anatomy

In all living crinoids, tube feet occur in groups of three, called podial triplets, that flank the ambulacra. The primary tube feet are the longest within each triplet and are used for particle capture, whereas the shorter secondary and tertiary tube feet are used to transfer particles down the ambulacra and compact them into boluses, respectively [20]. Due to their small size, the secondary and tertiary tube feet are typically not visible in living crinoids unless examined under a microscope and thus are not expected to be readily detectable in fossil specimens. Surveys of modern crinoids have shown that primary tube foot length, width and spacing are variable across modern species. Tube foot length ranges from approximately 0.45–0.9 mm in unstalked feather stars from order Comatulida and up to at least 2 mm in stalked crinoids from the order Hyocrinida [9,12,34]. Although tube foot spacing has not been well-documented for living stalked crinoids in the literature, comatulids show variable spacing, with mean values between 4.59 and 9.49 tube feet per mm [9].

A specimen of the Lower Devonian crinoid *C. schultzei* preserves three partial tube feet that are at least 7.0 mm in length [14] and approximately 1.4 mm wide. These structures are substantially longer than the tube feet documented in *D. simcoensis* or in any living crinoids. The bases of the tube feet are obscured, but spacing is approximately 0.3 mm^{-1}, which reflects the large size of the tube feet.

Other than *C. schultzei* and the specimens of *D. simcoensis* documented here, no other fossil crinoids have been identified that preserve tube feet, which limits the data available for tube foot length. However, Brower [36] inferred the spacing of primary tube feet in fossil taxa based on the arrangement

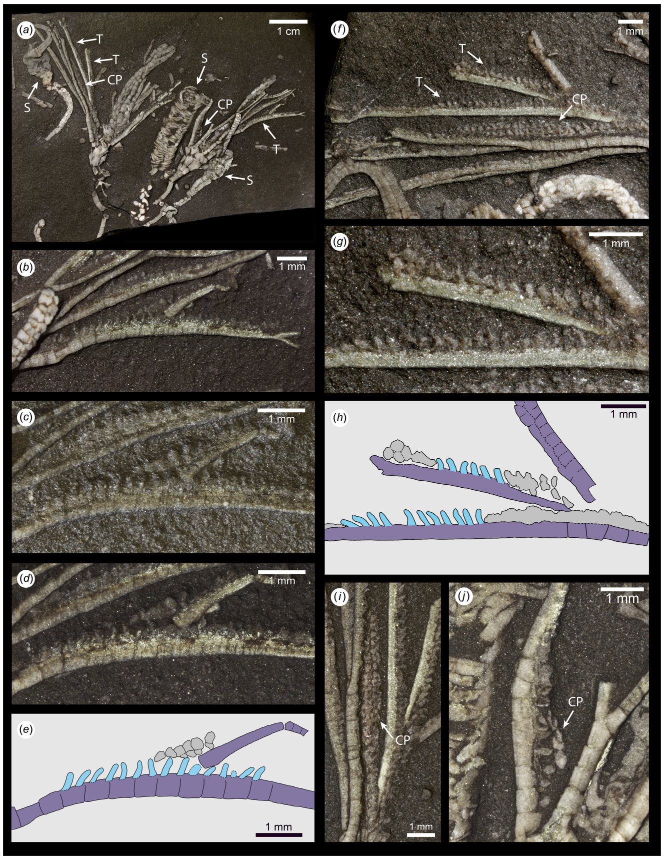

Figure 1. *Dendrocrinus simcoensis* photographs taken under alcohol (*a, b*, *e*, *f*, *h*, *i*) or dry (*c*) and interpretive diagrams of tube feet (*d*, *g*). (*a*) MPEP700.56a (left specimen) and MPEP700.56b (right specimen), noting the location of arms bearing tube feet, cover plates and associated solutes. (*b*) Arms of MPEP700.56b showing the location of tube feet. (*c*) Close-up of tube feet on MPEP700.56b photographed dry. (*d*) Close-up of tube feet on MPEP700.56b photographed under alcohol. (*e*) Interpretive drawing of tube feet preserved in MPEP700.56b. (*f*) Arms of MPEP700.56 a showing the location of tube feet and cover plates. (*g*) Close-up of tube feet on MPEP700.56a. (*h*) Interpretive drawing of tube feet preserved in MPEP700.56a. (*i*) Biserial column of ambulacral cover plates preserved in MPEP700.56a. (*j*) Ambulacral cover plates preserved in MPEP700.56b. Abbreviations: T, tube feet; CP, cover plates; S, solutes. Scale bars: (*a*) is 1 cm; (*b*–*j*) are 1 mm.

of ambulacral cover plates that cover the food grooves of the arms. In this model, each cover plate is assumed to correspond to one podial triplet, which is consistent with the configuration observed in extant crinoids [38]. In the fossil species sampled, inferred tube foot spacing ranges from 2.24 to 13.70 mm^{-1}, which reveals that spacing is much more variable across fossil taxa compared with spacing in extant comatulid crinoids (figure 2a). Tube foot spacing in fossil species also shows a close relationship with clade membership across crinoid phylogeny, where mean spacing is closest in camerate crinoids, widest in porocrinoids and intermediate in disparids and eucladids. Tube foot spacing measured from *D. simcoensis* specimens falls within the theoretical distribution predicted for fossil Eucladida (figure 2b) but is significantly outside the distributions for all other crinoid subclades (electronic supplementary material, table S2 [35]).

4. Discussion

4.1. Tube foot interpretations and comparative anatomy

Preservational differences provide one major line of evidence that supports the interpretation of these structures as crinoid tube feet. The soft tissues that make up the tube feet are preserved as slightly raised, lightly pyritized structures, whereas biomineralized skeletal elements of the crinoid are preserved as calcite. Calcite structures interpreted as cover plates exhibit these preservational differences and also have different dimensions compared with the tube feet.

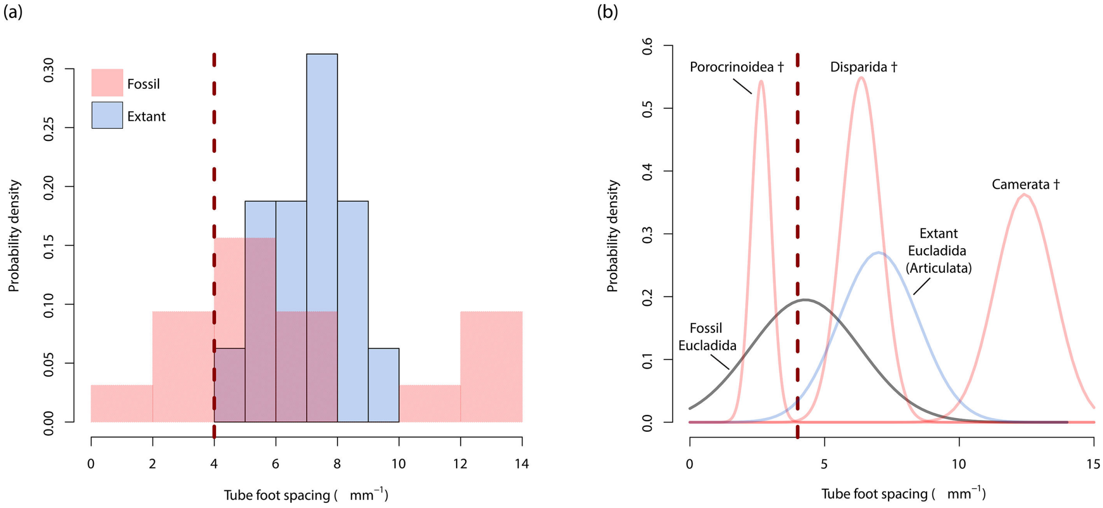

Figure 2. Distributions of tube foot spacing in extant versus fossil specimens and by clade membership. Tube foot spacing measured from specimens of the eucladid *D. simcoensis* is indicated by dashed lines. (a) A comparison of tube foot spacing values measured in extant crinoid species with inferred values for fossil taxa [36]. (b) Empirically derived Gaussian distributions of tube foot spacing for major subclades of crinoids. Specimen measurements for *D. simcoensis* are consistent with the predicted theoretical distribution for Eucladida taxa but well outside the distributions of other subclades.

A second major line of evidence that these structures are tube feet relates to their overall morphology and measurements compared with tube feet of other fossil and extant crinoids. Tube foot length and spacing in *D. simcoensis* are consistent with previously documented measurements for tube feet in extant crinoids [9,34], as well as inferred tube foot spacing in fossil crinoids [36]. Compared with extant crinoids for which both length and spacing data are available, *D. simcoensis* tube feet have the same spacing as *F. seratissima* A.H. Clark 1907 [39] (4 mm^{-1}) and the same length as *Himerometra robustipinna* Carpenter 1881 [40] (0.45 mm), which has the shortest tube feet of the extant crinoids sampled (electronic supplementary material, figure S1 [35]). The short tube feet of *D. simcoensis* may be attributed to several possible factors, including the very small size of both *D. simcoensis* specimens as well as substantial differences in the overall structure of the arms and filtration fan (e.g. *D. simcoensis* is apinnulate, whereas all living crinoids possess pinnules).

An additional line of evidence supporting these structures as tube feet comes from our comparative analysis of tube foot spacing in *D. simcoensis*. Tube foot spacing in *D. simcoensis* is very consistent overall with fossil crinoids for which tube foot spacing has been inferred based on cover plates, which ranges from 2.24 to 13.7 mm^{-1} in the Ordovician dataset compiled by Brower [36] (figure 2b). Furthermore, *D. simcoensis* is taxonomically assigned to the Eucladida based on whole-body skeletal anatomy, and three of the eucladid species sampled by Brower [36] have tube foot spacing similar to *D. simcoensis* (4.59, 4.96 and 5.61 mm^{-1}). In our analysis of tube foot spacing, *D. simcoensis* falls within the statistical expectation for Eucladida but is significantly outside the distributions for other extinct taxa (figure 2b and electronic supplementary material, table S2 [35]). Although it is possible that fossil species could exhibit morphological variation outside of a subclade's known distribution, we are unaware of any bias that could account for a spurious recovery of tube foot spacing measurements closely matching its expected subclade distribution while also statistically outside the distributions of other clades (figure 2b).

Given the limited data that are currently available, the breadth of morphological variation in tube foot anatomy is probably underestimated in both fossil and living crinoids. However, new data from *D. simcoensis* suggest that fossil crinoids may exhibit more extensive variation in tube foot morphology compared with living crinoids. The range of tube foot length in the fossil crinoids *C. schultzi* (7 mm) and *D. simcoensis* (0.45 mm) is much greater than that reported for living crinoids (0.45–2.0 mm), and tube foot spacing ranges from 0.3 to 13.7 mm^{-1} in fossil crinoids compared with only 4.0–9.49 mm^{-1} in living crinoids (figure 2 and electronic supplementary material, figure S2 [35]). The higher morphological disparity of tube feet in fossil crinoids may reflect a number of differences between fossil and living crinoids, including variations in arm number, structure and branching [12], tiering height and the presence or absence of a stalk [41], body size [42] and phylogenetic diversity [24]. Although living crinoids show extensive variation in the number and branching of arms [12], fossil crinoids show greater variability in arm structure, often within a single fauna (e.g. [36,43]). Additionally, all living crinoids are pinnulate, whereas fossil lineages include both pinnulate and apinnulate forms; as a result, apinnulate forms might be expected to have substantial differences in tube foot length and spacing to accommodate differences in arm morphology. As an example, *C. schultzi* is a very large, stalked, apinnulate crinoid from the Devonian with arm morphology that is unlike any living species, which may explain the unusually large tube feet that it possesses. Finally, all living crinoids belong to a single superorder, Articulata, whereas the fossil record includes many distantly related, entirely extinct lineages. Given that tube foot spacing is strongly correlated with taxonomic affinity (figure 2b), the greater phylogenetic diversity among fossil forms may also contribute to greater tube foot disparity in the fossil record.

4.2. Ecological implications

Because tube feet play an essential role in feeding, there are several ecological implications for the discovery of tube feet in *D. simcoensis*. Meyer [9] established that the length and spacing of tube feet directly correspond to feeding posture and habitat type in reef-dwelling comatulids. For example, comatulids with shorter, more closely spaced tube feet live and feed in more exposed areas with higher flow velocities (i.e. perched on reef prominences) and orient their arms into filtration fans. By contrast, reef-dwelling comatulids with longer, more widely spaced tube feet are semi-cryptic and live within the reef infrastructure where lower-energy microhabitats with slower, multidirectional currents dominate. Arm orientation of these crinoids is multidirectional in order to maximize particle capture while feeding in weak currents. Non-reef-dwelling comatulids like *F. seratissima*, which have tube feet that are widely spaced but intermediate in length [34], also live in environments with low currents, which suggests wider spacing of tube feet may be an adaptation for low-energy environments. Arm orientation of *F. seratissima* shifts from a cone posture when currents are absent to a partial fan when a measurable current flow is present [9]. Because the tube feet of *D. simcoensis* are short but widely spaced compared with other extant crinoids, there is no living analogue that can serve as a direct ecological model for this species. However, the relationship between wide tube foot spacing and low-current environments is consistent with the interpretation that the Neuville Formation was deposited in a deep-water, low-energy environment. This may also suggest that *D. simcoensis* fed with the arms oriented in a multidirectional or conical posture, rather than the fan orientations that are observed in modern stalked crinoids and assumed for most stalked crinoids in the fossil record [12,44]. However, because few studies have linked tube foot morphology to posture and habitat, and tube foot data for both fossil and extant species are limited, further studies are needed to confidently establish these relationships. Investigating links between tube foot morphology, habitat parameters and feeding posture in living crinoids presents a promising avenue for future study that could allow more robust inferences of ecology in extinct crinoid species.

5. Conclusion

Small, pyritized structures projecting from the arms of two specimens of *D. simcoensis* from the Neuville Lagerstätte of Québec (Upper Ordovician, Katian) are interpreted as tube feet and represent an example of exceptional soft-tissue preservation. These are the earliest known examples of crinoid tube foot preservation and only the second documented instance of these features preserved in fossil crinoids. The interpretation of these structures as tube feet is supported by (i) preservational differences compared with adjacent skeletal features, (ii) morphological differences compared with cover plates preserved in the same specimens, and (iii) striking similarities in tube foot anatomy compared with tube foot data from fossil and living crinoids. Comparative analysis of the tube foot anatomy of *D. simcoensis* reveals that fossil taxa exhibit much higher morphological disparity of the tube feet than extant crinoids, and that tube foot spacing is significantly correlated with clade membership. Relationships between tube foot anatomy, feeding posture and habitat in living crinoids suggest that *D. simcoensis* fed using a multidirectional or conical arm posture that was optimized for low-energy environments. These findings highlight the important role of tube feet in crinoid feeding ecology and the need for additional studies of living crinoids to further clarify relationships between tube foot morphology and ecological factors.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data, R scripts and supplementary data used in this study are freely available online at Figshare [35].

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

Authors' contributions. S.R.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft, writing—review and editing; D.F.W.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft, writing—review and editing; W.I.A.: conceptualization, investigation, methodology, writing—review and editing; M.E.C.: conceptualization, methodology, resources, 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. Kraft P, Vaškaninová V, Mergl M, Budil P, Fatka O, Ahlberg PE. 2023 Uniquely preserved gut contents illuminate trilobite palaeophysiology. *Nature* **622**, 545–551. (doi:10.1038/s41586-023-06567-7)
2. Sutton MD, Briggs DEG, Siveter DJ, Siveter DJ. 2011 A soft-bodied lophophorate from the Silurian of England. *Biol. Lett.* **7**, 146–149. (doi:10.1098/rsbl.2010.0540)
3. Nadhira A, Sutton MD, Botting JP, Muir LA, Gueriau P, King A, Briggs DEG, Siveter DJ, Siveter DJ. 2019 Three-dimensionally preserved soft tissues and calcareous hexactins in a Silurian sponge: implications for early sponge evolution. *R. Soc. Open Sci.* **6**, 190911. (doi:10.1098/rsos.190911)
4. Siveter DJ, Briggs DEG, Siveter DJ, Sutton MD. 2024 Preserved appendages in a Silurian binodicope: implications for the evolutionary history of ostracod crustaceans. *Biol. Lett.* **20**, 20240097. (doi:10.1098/rsbl.2024.0097)
5. Nanglu K, Cole SR, Wright DF, Souto C. 2023 Worms and gills, plates and spines: the evolutionary origins and incredible disparity of deuterostomes revealed by fossils, genes, and development. *Bio. Rev.* **98**, 316–351. (doi:10.1111/brv.12908)
6. Rahman IA, Zamora S. 2024 Origin and early evolution of echinoderms. *Annu. Rev. Earth Planet. Sci.* **52**, 295–320. (doi:10.1146/annurev-earth-031621-113343)
7. Boolootian RA. 1966 *Physiology of Echinodermata*. New York, NY: Interscience Publishers (Wiley).
8. Byrne M, O'Hara T. 2017 *Australian echinoderms: biology, ecology and evolution*. Clayton, Australia: CSIRO Publishing.
9. Meyer DL. 1979 Length and spacing of the tube feet in crinoids (Echinodermata) and their role in suspension-feeding. *Mar. Biol.* **51**, 361–369. (doi:10.1007/BF00389214)
10. Smith AB. 1979 Peristomial tube feet and plates of regular echinoids. *Zoomorphologie* **94**, 67–80. (doi:10.1007/BF00994057)
11. Warner G. 1982 Food and feeding mechanisms: Ophiuroidea. In *Echinoderm nutrition* (eds M Jangoux, JM Lawrence), pp. 161–181. Boca Raton, FL: CRC Press. (doi:10.1201/9781003078920-7)
12. Messing CG, Ausich WI, Meyer DL. 2021 Ch. 16 Feeding and arm postures in living and fossil crinoids. In *Treatise online no.150, part t*, pp. 1–45, vol. 1, Revised. Lawrence, KS: The University of Kansas, Paleontological Institute. (doi:10.17161/to.vi.15390)
13. Glass A, Blake DB. 2004 Preservation of tube feet in an ophiuroid (Echinodermata) from the Lower Devonian Hunsrück Slate of Germany and a redescription of *Bundenbachia beneckei* and *Palaeophiomyxa grandis*. *Paläontol. Z.* **78**, 73–95. (doi:10.1007/BF03009131)
14. Ausich WI, Bartels C, Kammer TW. 2013 Tube foot preservation in the Devonian crinoid *Codiacrinus* from the Lower Devonian Hunsrück Slate, Germany. *Lethaia* **46**, 416–420. (doi:10.1111/let.12023)
15. Clark EG, Bhullar BAS, Darroch SAF, Briggs DEG. 2017 Water vascular system architecture in an Ordovician ophiuroid. *Biol. Lett.* **13**, 20170635. (doi:10.1098/rsbl.2017.0635)
16. Briggs DEG, Siveter DJ, Siveter DJ, Sutton MD, Rahman IA. 2017 An edrioasteroid from the Silurian Herefordshire Lagerstätte of England reveals the nature of the water vascular system in an extinct echinoderm. *Proc. R. Soc. B.* **284**, 20171189. (doi:10.1098/rspb.2017.1189)
17. Rahman IA, Thompson JR, Briggs DEG, Siveter DJ, Siveter DJ, Sutton MD. 2019 A new ophiocistioid with soft-tissue preservation from the Silurian Herefordshire Lagerstätte, and the evolution of the holothurian body plan. *Proc. R. Soc. B.* **286**, 20182792. (doi:10.1098/rspb.2018.2792)
18. Sutton MD, Briggs DEG, Siveter DJ, Siveter DJ, Gladwell DJ. 2005 A starfish with three-dimensionally preserved soft parts from the Silurian of England. *Proc. R. Soc. B.* **272**, 1001–1006. (doi:10.1098/rspb.2004.2951)
19. Smith AB, Reich M. 2013 Tracing the evolution of the holothurian body plan through stem-group fossils: origins of the holothurian body plan. *Biol. J. Linn. Soc.* **109**, 670–681. (doi:10.1111/bij.12073)
20. Byrne M, Fontaine AR. 1983 Morphology and function of the tube feet of *Florometra serratissima* (Echinodermata: Crinoidea). *Zoomorphology* **102**, 175–187. (doi:10.1007/BF00310346)

21. Holland ND, Strickler JR, Leonard AB. 1986 Particle interception, transport and rejection by the feather star *Oligometra serripinna* (Echinodermata: Crinoidea), studied by frame analysis of videotapes. *Mar. Biol.* **93**, 111–126. (doi:10.1007/BF00428660)
22. Wright DF, Cole SR, Ausich WI. 2020 Biodiversity, systematics, and new taxa of cladid crinoids from the Ordovician Brechin Lagerstätte. *J. Paleontol.* **94**, 334–357. (doi:10.1017/jpa.2019.81)
23. Wright DF. 2017 Bayesian estimation of fossil phylogenies and the evolution of early to middle paleozoic crinoids (Echinodermata). *J. Paleontol.* **91**, 799–814. (doi:10.1017/jpa.2016.141)
24. Wright DF, Ausich WI, Cole SR, Peter ME, Rhenberg EC. 2017 Phylogenetic taxonomy and classification of the Crinoidea (Echinodermata). *J. Paleontol.* **91**, 829–846. (doi:10.1017/jpa.2016.142)
25. Globensky Y, Jauffred JC. 1971 Upper Trenton conodonts from the Grondines section of Quebec. *Can. J. Earth Sci.* **8**, 1473–1479. (doi:10.1139/e71-134)
26. Harland TL, Pickerill RK. 1982 A review of middle ordovician sedimentation in the St. Lawrence Lowland, eastern Canada. *Geol. J.* **17**, 135–156. (doi:10.1002/gj.3350170205)
27. Harper DAT, Pickerill RK. 1996 Mid Ordovician commensal relationships between articulate brachiopods and a trepostome bryozoan from eastern Canada. *Atl. Geol.* **32**, 181–187. (doi:10.4138/2087)
28. Brower JC, Cournoyer M, Iellamo J, Wright D, Cole S, Ausich WI. 2022 Diversity and paleoecology of a new Ordovician (Katian) crinoid fauna from the Neuville Formation, Southern Québec, Canada. In *Joint 56th Annual North-Central/ 71st Annual Southeastern Section Meeting*. The Geological Society of America. (doi:10.1130/abs/2022NC-374841)
29. Ramirez-Guerrero G, Alghaled H, Bateman LP, Cournoyer M, Cameron CB. 2026 Thecate stem medusozoan polyp from the upper Ordovician of Québec. *J. Paleontol.* 1–11. (doi:10.1017/jpa.2025.10211)
30. Baldwin J, Limbeck M, Cournoyer M, Deline B. A new exceptionally preserved paracrinoid from the Neuville Formation of Québec, Canada. In *Joint 56th Annual North-Central/ 71st Annual Southeastern Section Meeting*. The Geological Society of America. (doi:10.1130/abs/2022NC-374757)
31. Lefebvre B *et al*. 2019 Exceptionally preserved soft parts in fossils from the Lower Ordovician of Morocco clarify stylophoran affinities within basal deuterostomes. *Geobios* **52**, 27–36. (doi:10.1016/j.geobios.2018.11.001)
32. Zamora S, Rahman IA, Sumrall CD, Gibson AP, Thompson JR. 2022 Cambrian edrioasteroid reveals new mechanism for secondary reduction of the skeleton in echinoderms. *Proc. R. Soc. B.* **289**, 20212733. (doi:10.1098/rspb.2021.2733)
33. Follmann O. 1887 Unterdevonische crinoidea. In *Verhandlungen des naturhistorischen vereins der preussischen rheinlande, westfalens, and des regierungs-bezirks osnabruck*, pp. 113–138. Bonn, Germany: Naturhistorischer Verein der Rheinlande und Westfalens.
34. Byrne M, Fontaine AR. 1981 The feeding behaviour of *Florometra serratissima* (Echinodermata: Crinoidea). *Can. J. Zool.* **59**, 11–18. (doi:10.1139/z81-003)
35. Cole SR, Wright DF, Ausich WI, Cournoyer ME. 2026 Supplementary material from: Exceptional soft-tissue preservation reveals the oldest evidence for tube feet and their ecological significance in crinoids. *Figshare* (doi:10.6084/m9.figshare.c.8476600)
36. Brower JC. 2006 Ontogeny of the food-gathering system in Ordovician crinoids. *J. Paleontol.* **80**, 430–446. (doi:10.1666/0022-3360(2006)80%5B430:OOTFSI%5D2.0.CO;2)
37. R Core Team. 2024 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.
38. Brower JC. 2007 The application of filtration theory to food gathering in Ordovician crinoids. *J. Paleontol.* **81**, 1284–1300. (doi:10.1666/05-034.1)
39. Clark AH. 1907 Descriptions of new species of recent unstalked crinoids from the North Pacific Ocean. *Proc. US Natl. Mus.* **33**, 69–84. (doi:10.5479/si.00963801.33-1559.69)
40. Carpenter PH. 1880 On the genus *Solanocrinus*, Goldfuss, and its relations to recent *Comatulae*. *J. Linn. Soc. London Zool.* **15**, 187–217. (doi:10.1111/j.1096-3642.1880.tb00356.x)
41. Ausich WI. 1980 A model for niche differentiation in lower Mississippian crinoid communities. *J. Paleontol* **54**, 273–288. https://www.jstor.org/stable/1304062
42. Salamon MA, Brachaniec T, Kołbuk D, Saha A, Gorzelak P. 2021 Shared patterns in body size declines among crinoids during the Palaeozoic extinction events. *Sci. Rep.* **11**, 20351. (doi:10.1038/s41598-021-99789-6)
43. Cole SR, Wright DF, Ausich WI. 2019 Phylogenetic community paleoecology of one of the earliest complex crinoid faunas (Brechin Lagerstätte, Ordovician). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **521**, 82–98. (doi:10.1016/j.palaeo.2019.02.006)
44. Macurda DB, Meyer DL. 1974 Feeding posture of modern stalked crinoids. *Nature* **247**, 394–396. (doi:10.1038/247394a0)