TITLE

Predator-prey scaling laws support a suspension-feeding lifestyle in Cambrian lobopodians

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AUTHOR CONTRIBUTIONS

Jared Richards conducted the literature search and data analysis. Jared Richards and Javier Ortega-Hernández contributed to the interpretation of results, discussion, and writing. All authors approved the final manuscript.

COMPETING INTEREST STATEMENT

There are no competing interests.

ABSTRACT

The early Paleozoic saw a dramatic diversification of shelly epibenthic metazoans adapted to suspension and filter-feeding, but the extent to which these radiations affected the evolution of non-biomineralized suspension-feeding taxa is uncertain because these organisms are not typically well represented in the fossil record. Luolishaniids are a highly derived and disparate clade of (typically) armoured lobopodians widely interpreted as having a suspension-feeding ecology based on the presence of five or six anterior pairs of setulose appendages. Luolishaniids are globally widespread and represent the only Cambrian non-biomineralized free living epibenthic bilaterians regarded as having a suspension feeding mode of life, but their proposed ecology only relies on a qualitative interpretation of their functional morphology. Here we test the hypothesis that the setulose appendages of luolishaniids were adapted for a suspension feeding function. Quantitative morphological comparisons reveal a positive and statistically significant relationship between body length and the mesh spacing of the setulose anterior limbs of luolishaniids. This pattern correlates with suspension-feeding scaling in extant aquatic organisms, and suggests that luolishaniids primarily fed on mesoplanktonic seston. We provide quantitative evidence for suspension-feeding in luolishaniids, which represents the first statistically supported example of modern-like predator-prey scaling patterns observed in Cambrian soft-bodied metazoans.

Keywords: lobopodians, plankton, macroecology, niche ecology, functional morphology, comparative zoology

INTRODUCTION

Suspension feeding is a widespread life strategy in which animals capture food particles such as phytoplankton, zooplankton, and organic detritus from the water column in aquatic environments [1–3]. Suspension feeding is found throughout diverse animal clades, and may be further subcategorized based on precise habitat, mode of life and locomotory capabilities of the organisms [1]. Given that the feeding strategy of these organisms fundamentally involves extracting organic matter from large volumes of water, they play a key ecological role as primary consumers in aquatic food webs where they help cycle nutrients, transport biomass from small particles into higher trophic levels in the water column, increase light penetration and alter the distribution of planktonic lifeforms in space and time [1,4–7].

Suspension feeding among the earliest animal-dominated communities is particularly well represented during the early Paleozoic among biomineralizing organisms with high preservation potential such as sponges, brachiopods, echinoderms and bivalved molluscs [8–13]. By contrast, our understanding of the evolution of non-biomineralizing suspension-feeding organisms is much more precarious due to their comparatively low preservation potential in the conventional fossil record [14–19] (Fig. 1). Radiodonts, typically large-bodied nektonic stem-group euarthropods typified by the presence of arthropodized frontal appendages, represent the most widespread suspension-feeding soft-bodied metazoans found in sites with exceptional preservation around the world during the early Paleozoic [20,21]. Suspension-feeding radiodonts include the hurdiids (Fig. 1C) , which become increasingly diverse after the middle Cambrian and extended into the Devonian [22–26,26,27] and the rarer tamisiocaridids (Fig. 1B), which are restricted to the early Cambrian [28–30]. Other Cambrian soft-bodied organisms with a likely suspension-feeding mode of life based on comparisons with modern analogues include groups such as hemichordates, tunicates, vertebrates, ctenophores, and bivalved euarthropods [31–35] (Fig. 1D, 1E). However,

suspension feeding has also been proposed to be expressed in lobopodians, a diverse group of ecdysozoans resembling worms with legs found in several major Cambrian sites with exceptional preservation around the world, particularly the clade Luolishaniidae [36–43] (Fig. 1A). The general body plan of luolishaniids consists of a tubular trunk with five or six pairs of differentiated setulae anterior appendages, followed by a variable number of clawed walking legs on the trunk (Fig. 1). Other aspects of their morphology vary substantially, such as extent of spinose dorsal amour ranging from absent (e.g. *Facivermis, Ovatiovermis*) to nearly baroque (e.g. *Collinium, Collinsovermis, Acinocricus*), as well as their body size (roughly 10 to 100 mm in length) and lifestyle (e.g. free living or tube dwelling). Luolishaniids differ from other suspension-feeding organisms because most of them had a vagile epibenthic mode of life and lack obvious extant analogues, with phylogenetic analyses suggesting affinities as either early relatives of velvet worms (Onychophora), water bears (Tardigrada), or even panarthropods more broadly [39,42,44,45]. However, the view of luolishaniids as suspension feeders is exclusively based on the qualitative interpretation of the functional morphology of their anterior setulose appendages, and thus this ecological hypothesis remains to be critically tested, particularly since the peculiar morphology and variable lifestyle of these bizarre organisms.

In this study we quantitatively test the hypothesis that Cambrian luolishaniids were suspension feeders by examining the relationship between body size and sieving potential of the setulose anterior appendages. Based on comparative statistical methods, we provide the first quantitative evidence for suspension-feeding in luolishaniids and demonstrate that these lobopodians follow the same predator-prey and suspension feeder–seston size scaling laws observed in modern ecosystems.

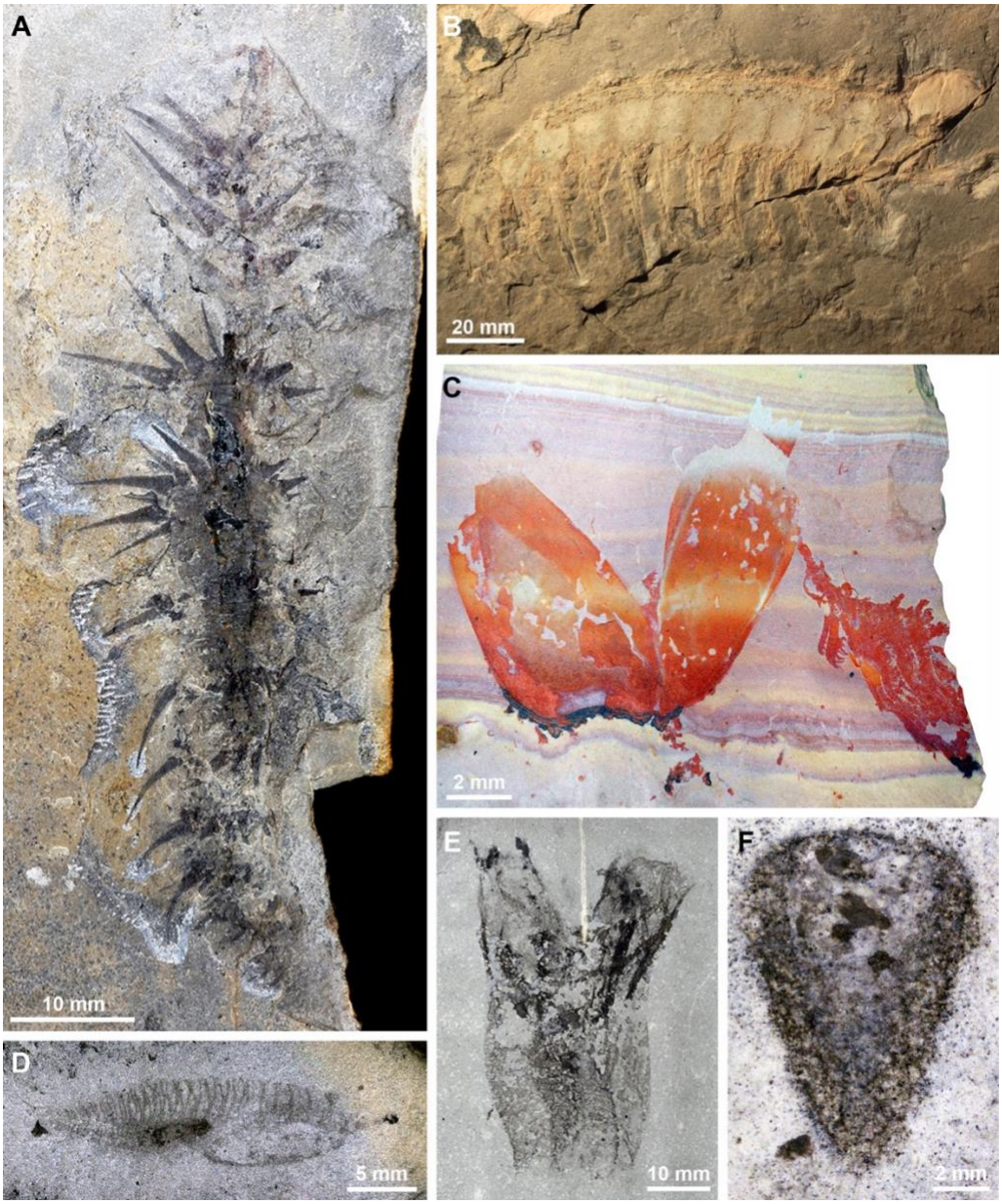

Figure 1. Diversity of exceptionally preserved suspension feeding organisms from Cambrian deposits. A. The luolishaniid lobopodian *Acinocricus stichus* from the middle Cambrian (Wuluian) Spence Shale, Utah (Kansas University Museum Invertebrate Paleontology collection; KUMIP 204353). **B.** Frontal appendage of the tamisiocaridid radiodont *Echidnacaris briggsi* [30] from the early Cambrian (Stage 4) Emu Bay shale, South Australia (South Australian Museum, Adelaide Paleontological collection; SAMA P40180). **C.** Carapace elements and frontal appendage of the hurdiid radiodont *Pahvantia hasta* [24] from the middle Cambrian (Drumian) Wheeler Shale, Utah (KUMIP 314089). **D.** The vertebrate *Nuucicthys rhynchocephalus* [35] from the mid-Cambrian (Drumian) Marjum Formation, Utah (Utah Museum of Natural History; UMNH.IP.6084). **E.** The tunicate *Megasiphon thylakos* [32] from the mid-Cambrian (Drumian) Marjum Formation, Utah (UMNH.IP.6079). **F.** The hexactinellid-like sponge *Polygoniella turrelli* [13] from the mid-Cambrian (Drumian) Marjum Formation, Utah (Museum of Comparative Zoology Invertebrate Paleontology collection, Harvard University; MCZ.IP.199049).

MATERIAL AND METHODS

Data collection

High-resolution digital images from all previously described luolishaniid taxa were loaded into Adobe Illustrator 28.2 (2024) (see Table 1). We measured the spacing between the setae (mesh spacing) on the anterior limbs for each taxon, as this is generally considered a proxy for determining the seston (i.e. particles suspended in water) size of suspension feeders [28,46,47]. The average mesh spacing (mm) and the body size for each taxon were plotted on a logarithmic scale (mm). Given the paucity of complete specimens and the widespread likelihood of morphological distortion via diagenesis, we used the maximum recorded body size (maximum length) in the original description (Table 1). In cases where the specimen with the best preservation of the setulose structures is also complete, we would collect the body size measurement from the same specimen.

Data Analysis

Given the smaller sample size of the available data (*e.g.*, multiple mesh spacing values imposed onto only one body size measurement per species), we employed a variety of analytical tools to extract as much information as possible from our limited dataset while being methodologically conservative. First, we ran an Ordinary Least-Squares (OLS) linear regression on unaggregated mesh size values versus body size to determine if there was a similar correlation between these predators (suspension-feeders) and their potential prey size (seston) as seen in other animal clades [46–48]. Next, we performed an Ordinary Least-Squares (OLS) linear regression examining the relationship between aggregated (mean) mesh size values and body size. This

summarized view of the data would be used later for further examination of the ecology of each luolishaniid species. The former OLS model, which has a higher degree of freedom, was *a priori* assumed to have higher statistical power than any analysis of aggregated data [49]. To compare the goodness of fit of the two OLS models and verify our *a priori* assumption, we calculated the second-order Akaike Information Criterion (AICc) for each OLS regression. This unitless metric can be calculated to determine and compare the quality of various statistical models, in this case, linear regressions [50]. The AICc is a specific instance of the Akaike information criterion (AIC) specifically designed to handle data with smaller sample sizes [51]. We report the F-statistic, the adjusted coefficient of determination (adjusted R^2), and the p-value recovered from the t-test of the regression's slope coefficient of both OLS models. We also ran a Harvey-Collier test on the aggregated mesh spacing dataset to check the linearity assumption before use in estimating the seston prey size of luolishaniids [52]. Finally, using the relationship that exists between mesh spacing and estimated prey size for a variety of extant metazoans [28] and our aggregated mean mesh spacing values for each luolishaniid genus, we calculated the minimum and maximum estimated prey size (μm) of all known luolishaniids to examine the lifestyles of this rare clade even further.

RESULTS

Luolishaniid Macroecological Scaling and Seston Prey Size Estimate

We find a positive and statistically significant relationship between body size and mesh spacing on the log-log scale for both disaggregated mesh spacing data ($F(1,152) = 90.87$, p-value < 0.001, adjusted $R^2 = 0.37$, AICc = -199.58) and aggregated mean mesh spacing data ($F(1,5) =$

7.72, p-value < 0.05, adjusted $R^2 = 0.53$, AICc = 0.65) (Fig. 2). The corresponding sublinear power functions are Mesh Spacing (mm) = 0.061*Body Length(mm)$^{0.33}$ and Mesh Spacing (mm) = 0.052*Body Length(mm)$^{0.37}$, respectively. The linearity assumption was met in the OLS of aggregated mesh spacing data on the logarithmic scale (Harvey-Collier statistic = 0.36, degrees of freedom = 4, p-value > 0.05).

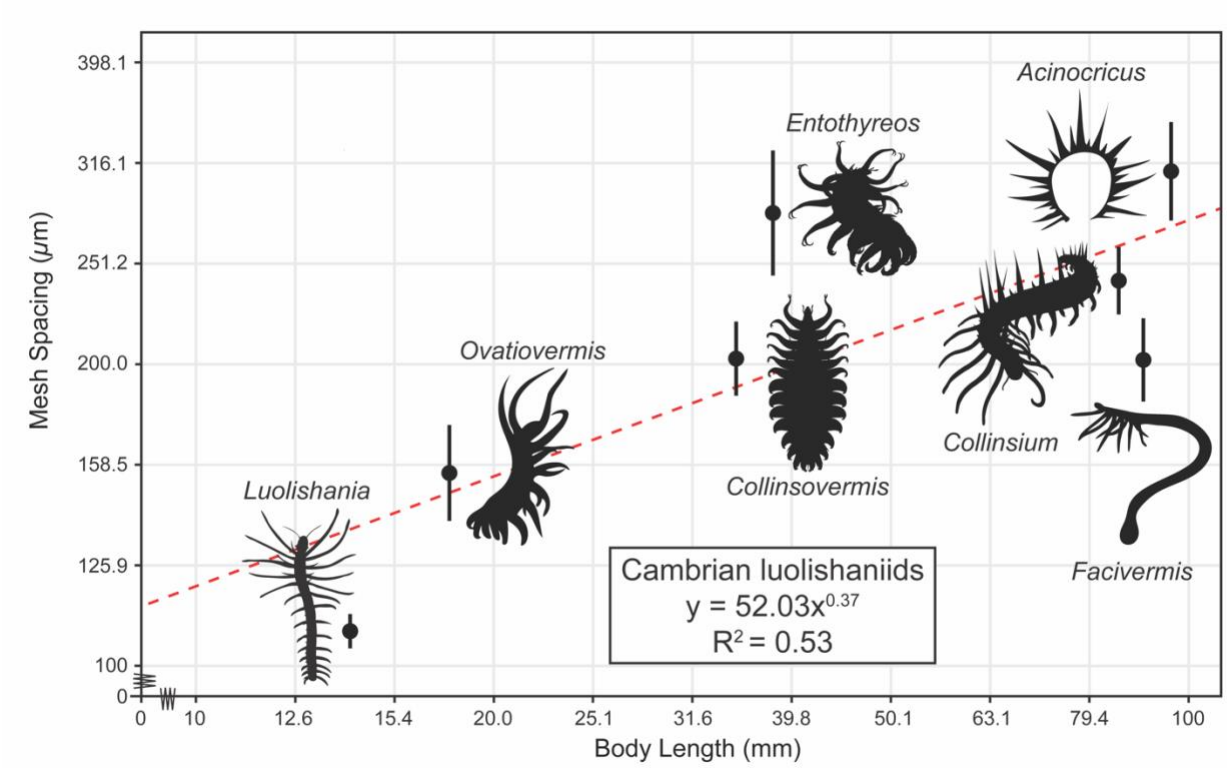

Figure 2. Comparison of body scaling proportions in Cambrian luolishaniids. Relationship between body length (mm) and appendage mesh spacing (μm) showing a significant positive trend (red dashed line; $y = 52.03x^{0.37}$, $R^2 = 0.53$, $p < 0.05$, $F(1,5) = 7.72$). Each point represents a species with a 95% CI around the mean mesh spacing.

Using the OLS regression of mean mesh spacing versus body size, we find that the estimated minimum particle diameters would have enabled most luolishaniids to capture suspended prey/particles on the lower end of the mesoplanktonic scale (~230 μm — 460 μm) (Fig. 3; Table 1). *Luolishania* is the only luolishaniid estimated to have been able to collect

suspended prey and particles that were on the microplanktonic spectrum (~150 µm). Given that our knowledge of the Emu Bay luolishaniids is based on a single incomplete specimen that obstructs our ability to measure its body size, we can use the previously derived power laws to calculate its estimated maximum body size.

Table 1. Autoecological metrics for all Cambrian luolishaniid lobopodians. Note that body size in the Emu Bay Shale luolishaniid (*asterisk*) is estimated from the statistically significant scaling pattern established amongst other Cambrian luolishaniids.

Taxa	Number of Mesh Spacings (N)	Average Mesh Spacing (µm)	Minimum Estimated Prey Diameter (µm)	Maximum Estimated Prey Diameter (µm)	Body Size (mm)
Acinocricus stichus [41]	21	319.3	457.1	4248.5	96.0
Collinsium ciliosum [39]	52	250.6	358.0	3421.5	85.0
Collinsovermis monstruosus [41]	25	206.2	294.1	2875.1	~35.0
Enthothyreos synnaustrus [43]	14	290.4	415.4	3902.8	~38.12
Facivermis yunnanicus [42]	8	202.7	289.1	2831.3	90.0
Luolishania longicruris [37]	8	108.4	153.8	1619.4	14.30
Ovatiovermis cribratus [40]	26	161.1	229.3	2305.8	18.0
Collins' monster, Emu Bay [38]	12	272.0	389.0	3681.6	87.5*

DISCUSSION

Luolishaniid Macroecological Scaling

The strong relationship between body size and mesh spacing in the setulose appendages of Cambrian luolishaniids (Figure 1) recapitulates macroecological scaling patterns observed in extant suspension-feeding aquatic invertebrates [46,47]. Given that mesh size closely correlates with estimated prey size in modern suspension feeders (Fig. 2; Table 1), these results provide direct quantitative evidence that different Cambrian luolishaniids species exploited various types of meso-planktonic food sources through suspension-feeding [28,53]. The sublinear relationship between body size and mesh size, represented by a slope value less than one recovered in both linear regressions (Fig. 2; Supplementary Figure 1), indicates that mesh spacing does not scale uniformly with body size in luolishaniids. For a given unit of increase in body size, there is a proportionally smaller increase in mesh spacing. These observations concur with neontological data on predator-prey scaling laws for numerous suspension feeding and obligate predatory aquatic and terrestrial invertebrates, which also feature a similar sublinear relationship [46,47,54]. In the context of luolishaniid macroecology, the correlation between body size and mesh size would have had direct implications for the planktonic prey items that would be targeted by the different species. We find that the smallest Cambrian luolishaniids also had the finest mesh size, estimated at 108.4 µm for *Luolishania* (body length = 14 mm) and 161.1 µm for *Ovatiovermis* (body length = 18 mm) (Fig. 3), which would have allowed them to capture microplankton (e.g. acritarchs), as well as the smaller cohorts of mesoplankton (e.g. chitinozoans, radiolarians). All other larger bodied luolishaniids, ranging from *Collinsovermis* (body length = 35 mm) to *Acinocricus* (body length = 96 mm), show a progressive increase in the mesh size on the setulose appendages, ranging from ca. 200 µm to 450 µm. This mesh size range would have allowed

medium to large bodied luolishaniids to feed on all types of mesoplankton but would be less suitable for targeting microplankton as it would fall below the minimum seston capture size (Figure 2). More broadly, it is interesting to note that the estimated minimum particle size of luolishaniids suggests that they targeted smaller plankton than the radiodonts *Tamisicaris borealis (~700* µm) and *Aegirocassis benmoulai (~800* µm), but larger prey items than *Pahvantia hastata (~100* µm). These comparisons indicate that most luolishaniids, except for the small bodied *Luolishania* and *Ovatiovermis*, fed on larger prey items than *Pahvantia,* which has an estimated body length of 24 cm [24], making it more than twice the size of the largest luolishaniid *Acinocricus* (body length ca. 95 mm; [41]). We hypothesize that this pattern might reflect autecological differences in terms of suspension-feeding preferences for luolishaniids as epibenthic and vagile organisms, relative to the nektonic lifestyle of suspension-feeding radiodonts. We also notice that the few suspension feeding radiodonts with enough quantitative data on their body length and mesh size, namely *P. hastata* (estimated body length = 24 cm; mesh spacing = 0.07 mm), *T. borealis* (estimated body length = 34 cm; mesh spacing = 0.49*), and A. benmoulai* (body length = 200 cm; mesh spacing = 0.56 mm) also follow a comparable scaling pattern to that of luolishaniids in which body size increases faster than mesh size [21,24,28]. However, the number of radiodont taxa that fulfill these requirements is too small to properly analyze quantitatively and make further extrapolations of the available data.

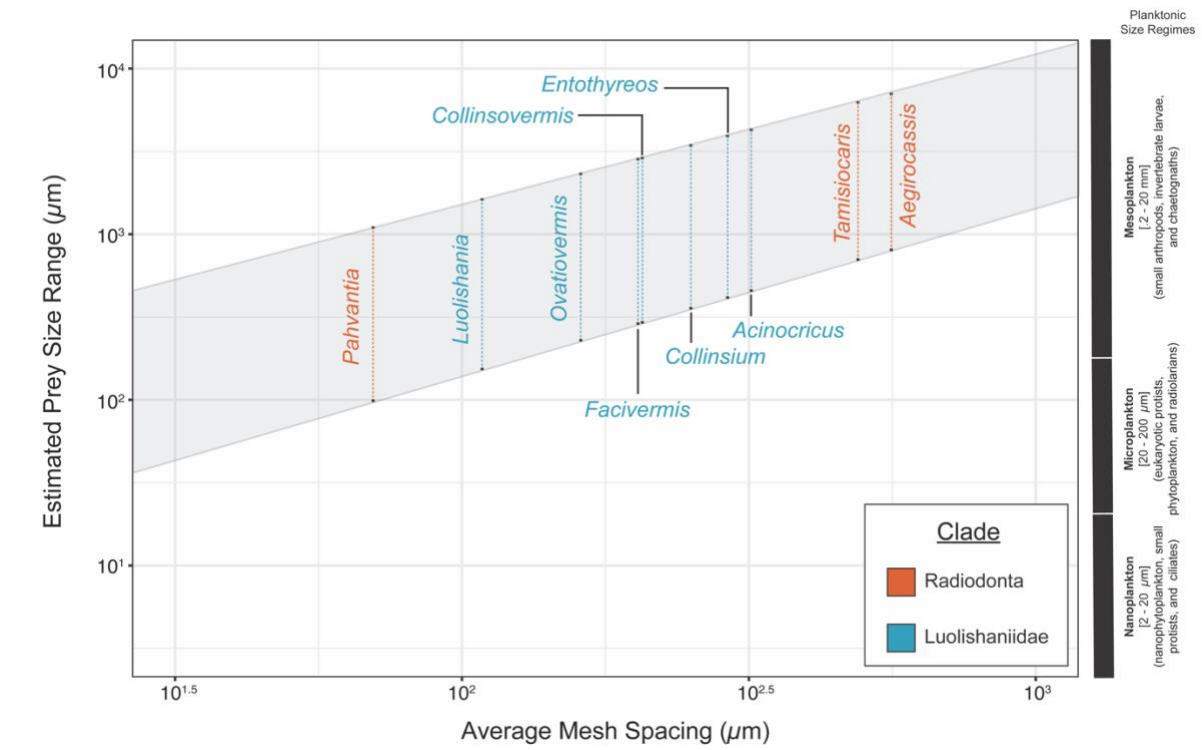

Figure 3. Relationship between mesh size and planktonic prey size in Cambrian luolishaniids and radiodonts. Estimated planktonic prey size for Cambrian luolishaniids (blue) based on the relationship between mesh size and seston size in modern suspension feeding metazoans. Radiodont (orange) quantitative data based on refs [24,28].

Modern Analogs

Cambrian luolishaniids have been directly compared in terms of their autecology with extant suspension-feeding invertebrates, particularly caprellid amphipod crustaceans, based on suggested similarities in their morphology including an elongate tubular body, anterior setulose appendages with a sieving function, and clawed walking legs on body trunk or posterior for grasping onto the substrate [40,41,55–57]. However, these represent qualitative comparisons and interpretations, and these taxa differ in important aspects of their functional morphology with direct implications for their precise mode of life and feeding strategies. Caprellid amphipods employ their cilia-laden,

228 mucus-covered antennae to initiate suspension-feeding [40,55]. After detecting a substantial
229 accumulation of seston on the antennae, caprellids use their raptorial gnathopods to cleanse these
230 appendages from food particles, form a ball of mucus and seston, and pass it to their mouth for
231 consumption [55].

232 Although luolishaniids and caprellid amphipods employ setulose anterior appendages to
233 capture plankton, the former differs in the absence of specialized cleaning limbs or complex
234 mouthparts employed in suspension feeding [39,40,42,55,56,58,59]. These differences suggest
235 that luolishaniids most likely employed a different strategy to consume the seston, with suction
236 feeding being a suitable option as it is widely employed by aquatic invertebrates where a negative
237 pressure vacuum is produced to draw nearby water, and therefore any suspended materials, into
238 the buccal cavity [60,61]. Experimental work on the fluid dynamics of extant suction feeders has
239 shown that no modern invertebrates with hydrostatically supported bodies can create the same
240 suction forces seen in aquatic vertebrates such as fish [62]. However, we hypothesize that the
241 suction feeding capacity of luolishaniids would have been comparatively low, just enough so that
242 a low-pressure difference between the buccal cavity and the environment would suffice to consume
243 the seston captured by the sieving apparatus on the anterior setulose appendages of these
244 lobopodians [40].

245

246 *Broader Paleoecological Implications*

247 Luolishaniids differ from other Cambrian suspension feeding soft-bodied animals, particularly
248 free-swimming radiodonts such as *Tamisiocaris*, *Pahvantia* or *Hurdia*, in that the former
249 lobopodians had a slow-moving epibenthic habitus, which means they would not be able to force

water over their sieving apparatus by simply moving against the water column [21,28]. Instead, luolishaniids most likely sought after microhabitats with low to intermediate water flow rates facing their anterior setulose limbs perpendicular to the oncoming water current to collect suspended food items [1,63–65]. The water flow speeds necessary for stationary suspension-feeding of mesoplankton in modern ecosystems ranges from 5 to 10 centimeters per second based on experiments involving modern suspension feeders feeding on mesoplankton [64,66]. Assuming that luolishaniids would require a similar flow speed necessary for effective suspension feeding, the role of the robust sclerotized terminal claws on the posterior trunk appendages becomes critical as it would allow these lobopodians to maintain a secure attachment to hard substrates during food capture without becoming dislodged [1,39,64,66,67].

The feeding ecology of luolishaniids also has implications for better understanding their mode of life considering their peculiar morphology, particularly the presence of extensive dorsal spinose defensive armature in most species [39,41,43]. Neontological behavioural work has shown that free living animals that bear some type of external body armor (e.g. epidermal spines, plates or scales) display a higher threat tolerance or threshold before they flee or take refuge from potential predators when compared to unarmored forms, both in aquatic and terrestrial environments [68,69]. Applied in the context of luolishaniid paleobiology, this generalized behaviour would suggest that smaller-bodied species and/or those in which dorsal armor is relatively light (*Luolishania*) or non-existent (*Ovatiovermis*) would be more hasty to seek refuge compared to larger bodied and more heavily armored forms, such as *Acinocricus, Collinsium, Collinsovermis,* and *Entothyreos* [38,39,43]. *Facivermis* is a notable exception in this regard because it is large-bodied (ca. 90 mm long) but completely lacks dorsal armor [42]. In this case, the unique tube-dwelling mode of life of *Facivermis* most likely represents a tradeoff that allowed

it to attain a large body size despite the absence of dorsal armor by shifting to a different defensive strategy that instead relies on the protection of the secreted tube, facilitating a readily accessible refuge if disturbed. It is notable that the extent of dorsal armature in luolishaniids closely follows their overall body size, with *Acinocricus, Collinsium, Collinsovermis, Entothyreos* featuring the heaviest coverage within the clade based on the number of dorsal spines per appendage pair. The heavy armature of these forms would have likely made their movements cumbersome due to excessive resistance against the water column and thus caused a tradeoff against their ability to swiftly escape from potential predators, as also observed in modern species. Heavily armored luolishaniids would have primarily relied on their body size and impressive arrays of dorsal spines as primary deterrents, particularly when actively engaging in suspension feeding against the water current [68–74].

In conclusion, our results support the widespread interpretation of luolishaniids as effective epibenthic suspension feeders that follow comparable macroecologial patterns observed in modern species with a suspension feeding autecology. The findings demonstrate that the fundamental requirements for a suspension-feeding lifestyle were already in place by the early and middle Cambrian based on a comparative quantification of luolishaniid morphology. This study also provides the first estimates of planktonic prey sizes for luolishaniids and provides further insights into their most likely behavior based on modern analogues. Although luolishaniids are among some of the most unconventional organisms that evolved during the Cambrian Explosion, hence their initial moniker as Collin's monsters [38,41], we posit that their main adaptations and mode of life can be readily explained through the lens of a modern suspension feeding ecology.

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