

Growth of the enigmatic Ediacaran *Parvancorina minchami*

Andrey Ivantsov¹ , Andrew H. Knoll², Maria Zakrevskaya¹ ,
Mikhail Fedonkin³ and Daniel Pauly⁴ 

Article

Cite this article: Ivantsov, A., A. H. Knoll, M. Zakrevskaya, M. Fedonkin, and D. Pauly (2025). Growth of the enigmatic Ediacaran *Parvancorina minchami*. *Paleobiology* **51**, 356–363. <https://doi.org/10.1017/pab.2024.55>

Received: 06 May 2024
Revised: 03 November 2024
Accepted: 04 November 2024

Handling Editor:
Carl Simpson

Corresponding authors:
Andrey Ivantsov and Daniel Pauly;
Emails: ivancov@paleo.ru; d.pauly@oceans.ubc.ca

¹Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow 117647, Russia

²Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

³Geological Institute of the Russian Academy of Sciences, Moscow 119017, Russia

⁴Sea Around Us, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

Abstract

Analysis of length-frequency data using the ELEFAN (Electronic Length-Frequency Analysis) approach and software is widely used to quantify the growth, mortality, longevity, and related parameters of Recent marine animals. Here we analyze a sample ($n = 211$) of the Ediacaran metazoan *Parvancorina minchami* Glaessner, 1958, from the Vendian siliciclastic marine deposits of the southeastern White Sea region, Russia. The results fit a von Bertalanffy equation with the parameters $L_{\infty} = 2$ cm, $K = \text{yr}^{-1}$ (with t_0 not estimated) and an instantaneous rate of mortality (M) of 1.44 yr^{-1} , implying $M/K \approx 2$, as commonly occurs in Recent small invertebrates. These parameter values also imply a longevity for *P. minchami* of about 4 yr. The concepts and approach used here, previously applied to an Ordovician trilobite and a Cambrian radiodont, suggest that inferences on growth, mortality, longevity, and related parameters can be obtained from suitable size-frequency samples of long-extinct metazoans, opening new vistas on their growth dynamics and functional roles in ancient ecosystems.

Non-technical Summary

Macrofossils in Ediacaran sedimentary rocks provide our earliest known evidence of animal morphology. In recent years, much has been learned about the diversity and phylogenetic relationships of Ediacaran metazoans, but many basic aspects of organismic function remain poorly understood. ELEFAN, a statistical package for analyzing length-frequency data, has been shown to provide quantitative insights into the growth dynamics and longevity of living marine invertebrates. Study of a large population of the Ediacaran metazoan *Parvancorina minchami*, preserved on a single bedding surface exposed in the White Sea region of Russia, permits the inference that despite their unusual morphology and uncertain phylogenetic relationships, these organisms were similar to many living marine invertebrates in terms of their growth and expected longevity of about 4 years. Thus, ELEFAN brings us closer to understanding early metazoans as functioning organisms in Ediacaran ecosystems.

Introduction

Ediacaran macrofossils are simultaneously among the most celebrated and least understood remains known from the fossil record. Although many of these fossils are widely, if not universally, accepted as metazoans (e.g., Narbonne 2005; Fedonkin et al. 2007; Xiao and Laflamme 2009; Sperling and Vinther 2010; Erwin et al. 2011; Droser and Gehling 2015; Dunn et al. 2018; Hoyal Cuthill and Han 2018; Bobrovskiy et al. 2022; Stephenson et al. 2024), much remains unknown about their anatomy, phylogenetic relationships, and functional biology. Here we employ a method of length-frequency (L/F) analysis known as ELEFAN (Electronic Length-Frequency Analysis) to investigate patterns of growth and mortality in *Parvancorina minchami* Glaessner, 1958. ELEFAN was originally developed from first principles to study the growth dynamics of Recent water-breathing ectotherms (WBE; Pauly and David 1981), and it was successfully applied to numerous (sub)phyla—here illustrated by one example each—such as fishes (Hikmawansyah et al. 2019), crustaceans (Dwiponggo et al. 1986), cephalochordates (Vergara et al. 2012), echinoderms (Chan et al. 2018), mollusks (Djan et al. 2022), polychaetes (Omena and Amaral 2000), cnidarians (Palomares and Pauly 2009), and poriferans (Pauly et al. 2022). ELEFAN has also been shown to illuminate the growth of extinct marine invertebrates known only through fossils (Pauly and Holmes 2022; Wu et al. 2024).

© The Author(s), 2025. Published by Cambridge University Press on behalf of Paleontological Society. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

PALEO BIOLOGY
A PUBLICATION OF THE
 PALEONTOLOGICAL SOCIETY

 **CAMBRIDGE**
UNIVERSITY PRESS

The Organisms: *Parvancorina minchami*

Parvancorina minchami is a distinctive Ediacaran taxon first described by Martin Glaessner (1958) from sandstone bedding surfaces of the Pound Quartzite in South Australia. Millimeter- to centimeter-scale individuals have a bilaterally symmetric shield-like morphology, rounded at one end and bluntly pointed at the

other. *Parvancorina*'s most distinctive feature is an anchor-like ridge system, one end curving along the rounded margin and the other running along the central axis of the body (Fig. 1). The only other salient features are fine, parallel lineations of uncertain origin that extend from the axial ridge outward toward the lateral margins (Glaessner 1980: plates 1,2; Paterson et al. 2017: fig. 4). In addition

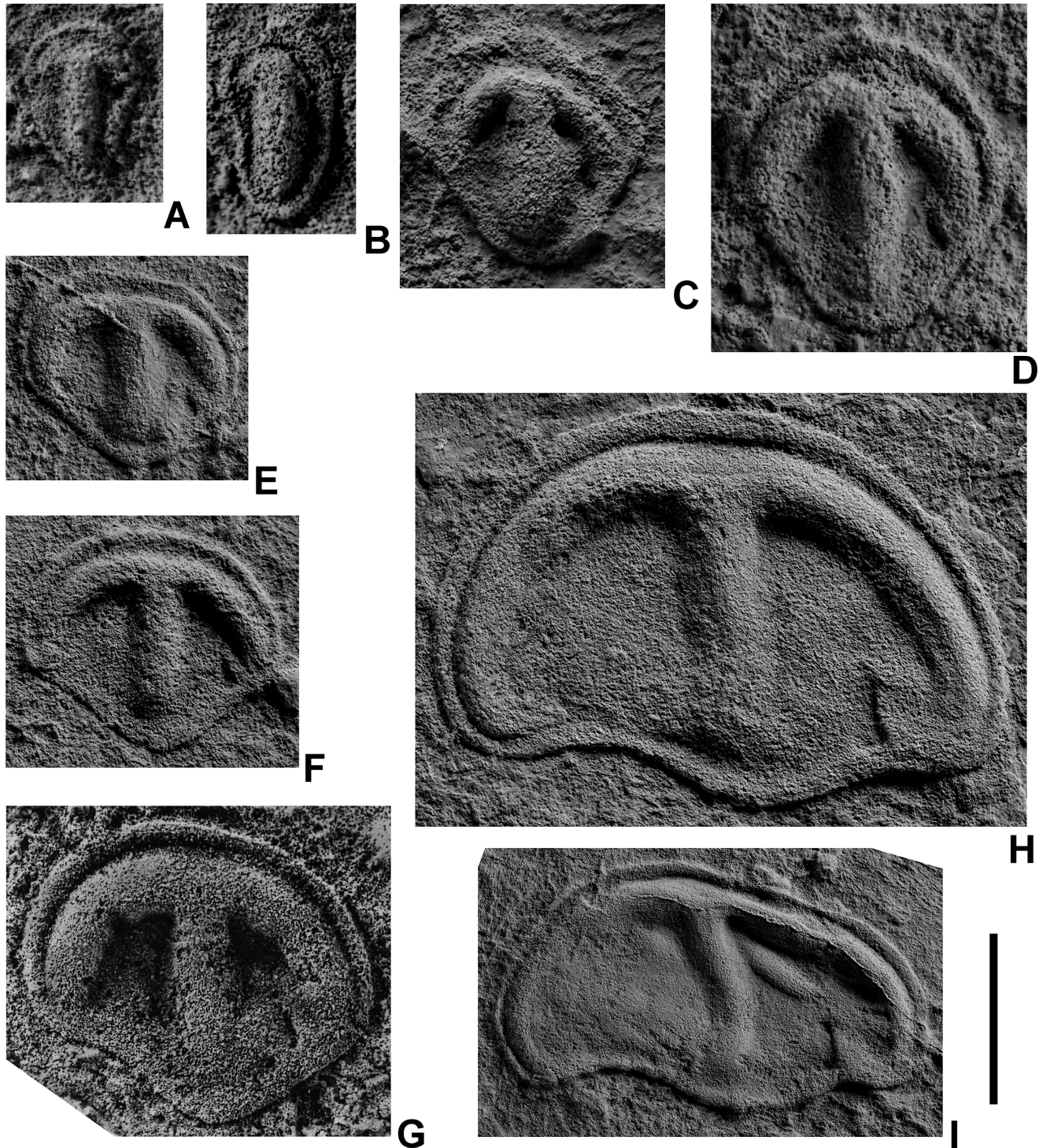


Figure 1. *Parvancorina minchami* Glaessner, 1958; late Ediacaran (Vendian), southeastern White Sea region, Zimnie Gory locality, burial event horizon Z11(XXII); latex casts from natural imprints with preliminary spraying with ammonium chloride: **A**, specimen PIN no. 3993/6214; **B**, specimen PIN no. 3993/6156; **C**, specimen PIN no. 3993/6286; **D**, specimen PIN no. 3993/6255; **E**, specimen PIN no. 3993/9040; **F**, specimen PIN no. 3993/9021; **G**, specimen PIN no. 3993/6382; **H**, specimen PIN no. 3993/8940; **I**, specimen PIN no. 3993/9019. Scale bar, 2.5 mm (**A–D**); 0.5 mm (**E–H**); 10 mm (**I**).

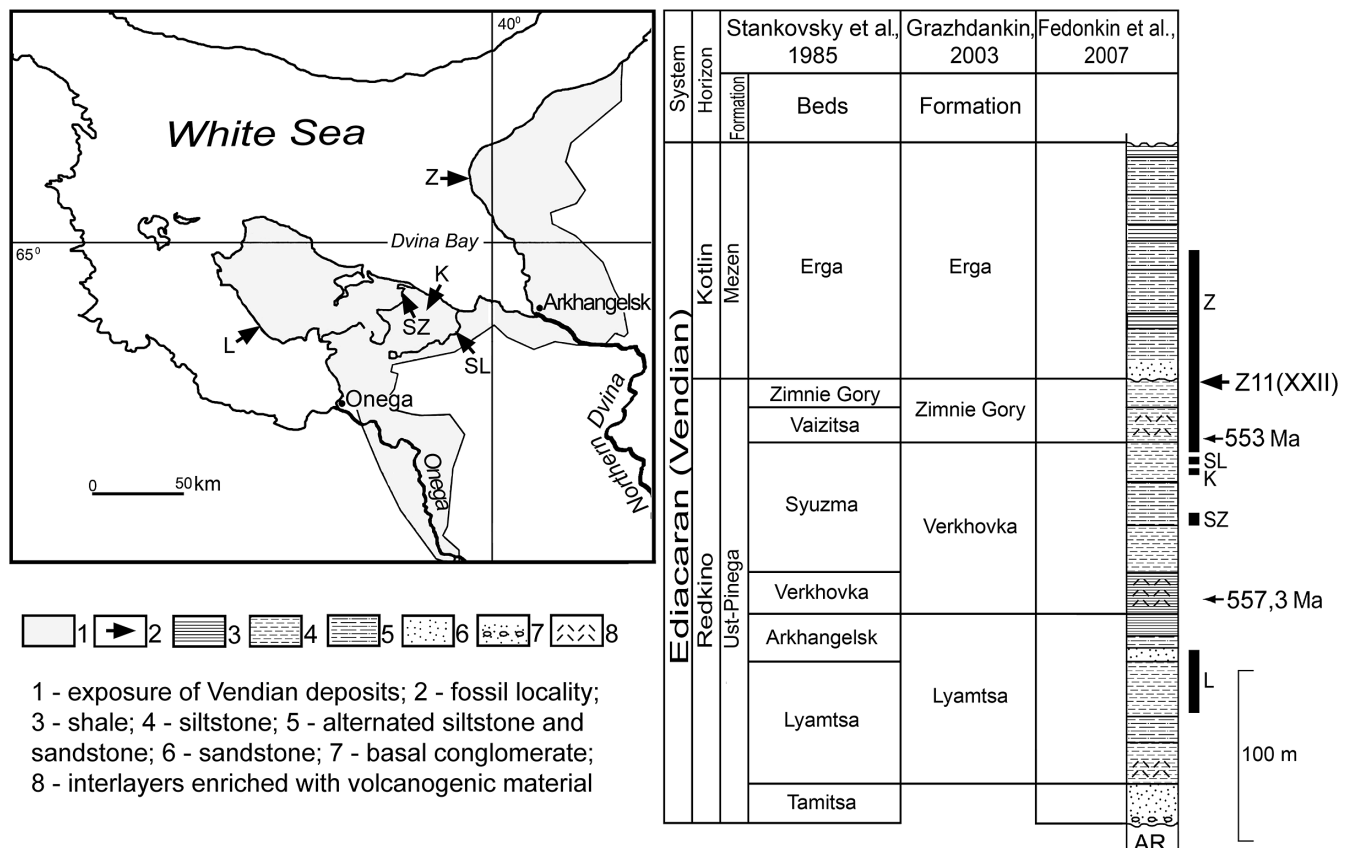


Figure 2. Geographic and stratigraphic position of the burial event horizon Z11(XXII) in the Ediacaran (Vendian) succession of the southeastern White Sea region. Wide vertical stripes to the right of the stratigraphic column correspond to intervals containing macrofossil localities. Letters indicate: L, Lyamtsa; SZ, Syuzma; K, Karakhta; SL, Solza; Z, Zimnie Gory (localities); AR, metamorphic rocks of the Archean and Paleoproterozoic. Stankovsky et al. 1985; Grazhdankin 2003; Fedonkin et al. 2007.

to Australian occurrences, *P. minchami* has also been found in Ediacaran sandstones of the Zimnie Gory and Erga Beds along the White Sea coast of Russia (Fig. 2), where it occurs stratigraphically higher than a second, more elongated species, *Parvancorina sagitta* (Ivantsov et al. 2004; Naimark and Ivantsov 2009). The first appearance of *Parvancorina* in the White Sea section occurs in the underlying Lyamtsa Beds, where it is most likely represented by a new, as yet undescribed species.

Glaessner (1958) originally viewed *Parvancorina* as problematic, but later (Glaessner 1980) interpreted it as an early arthropod, somewhat distantly related to trilobites. Arthropod affinities were also championed by others, informed by comparisons with marrellomorph and other fossils in Cambrian rocks (e.g., Zhang et al. 2003; Lin et al. 2006). Careful analysis, however, shows that purported similarities between *Parvancorina* and arthropods are superficial at best (e.g., Legg 2015 and references therein). Like many other Ediacaran macrofossils, *Parvancorina* shows no evidence of external gills, no mouth or digestive system, and no limbs. Thus, as originally intuited by Glaessner (1958), *Parvancorina* remains problematic, an early macroorganism that exchanged gases by diffusion and likely gained nutrition via phagocytosis by individual epidermal cells, perhaps augmented by osmotrophy.

Several authors have argued that *Parvancorina* individuals could sense and align themselves with prevailing water movements (Paterson et al. 2017; Coutts et al. 2018). Employing innovative simulations, Darroch et al. (2017) made a strong case that such movements would have facilitated the intake of suspended food

particles. That said, no trackways document more sustained locomotion, consistent with the absence of limbs or other locomotory structures.

In summary, then, *P. minchami* was a macroscopic organism capable of orienting itself relative to predominant currents, likely using at least simple muscle fibers. The case is also strong that it gained nutrition by means of suspension feeding. Macroorganisms capable of movement that feed by suspension feeding occur only in the Metazoa, justifying, we believe, the interpretation that *P. minchami* most likely falls within this kingdom. Even if *P. minchami* were simply convergent with animals, its structure, habitat, and inferred function would require a physiology not unlike those of unambiguous animals and so amenable to ELEFAN analysis.

Materials and Stratigraphic Setting

This study is based on 211 measured individual *Parvancorina minchami* out of 651 identified specimens from a single burial event horizon and from a single bedding plane, exposed in outcrops along the White Sea. All specimens are deposited in the Borissiak Paleontological Institute of the Russian Academy of Sciences. The age of this succession is constrained by U-Pb zircon dates for ash layers near the top and bottom of the Zimnie Gory Beds of 550.2 ± 4.6 and 553.0 ± 0.7 Ma, respectively, as well as a date of 557.3 ± 0.6 Ma for the underlying Verkhovka Beds (Martin et al. 2000; Grazhdankin 2016; Yang et al. 2021). The measured population

comes from a single event horizon, Z11(XXII), that preserves an assemblage fossilized in place by instantaneous burial. Such rapid events preserve our closest available approximation to biological populations.

The event horizon Z11(XXII) is found within the Zimnie Gory locality, the northernmost and largest locality among the outcrops of late Ediacaran (Vendian) rocks in the southeastern White Sea region. Stratigraphically, the horizon occurs at the top of the Zimnie Gory Beds of the Ust'-Pinega Formation, or Zimnie Gory Formation in the meaning of Grazhdankin (2003) (Fig. 2). The burial event horizon can be traced along the southern group of Zimnie Gory outcrops for a distance of at least 2 km. The fossil impressions occur at the base of a lens-shaped layer (0–3.5 cm in thickness) of light gray, fine-grained, cross-bedded sandstone with well-developed ripples on the top. The fossiliferous surface is flat to tuberculate, with a network of thin depressions between the mounds, covered with numerous rounded negative impressions of *Aspidella terranova* (which we interpret as attachment structures of the frondose *Charniodiscus* sp.), with an average diameter of 1–1.5 cm (Fig. 3).

The Z11(XXII) assemblage is unparalleled for its sheer abundance of benthic Ediacaran biota, including body imprints of *Armillifera parva*, *Charniodiscus* sp., *Cyanorus singularis*, *Dickinsonia costata*, *D. cf. tenuis*, *Keretsa brutoni*, *Kimberella quadrata*, *Cephalonega stepanovi*, *Ovatoscutum concentricum*, *Paleophragmodictya* sp., *Paravendia janae*, *P. minchami*, *Tamga chamulifera*, *Tribrachidium heraldicum*, *Vavilovskia vanaas*, and *Yorgia wagneri*, as well as enigmatic tubes assigned to *Harlaniella ingriana* and feeding traces of *Dickinsonia*, called *Epibaion costatus* (Ivantsov 2013, 2017; Zakrevskaya 2014; Ivantsov and Zakrevskaya 2022). Based on many years (1996–2012) of excavations of burial event horizon Z11(XXII), the average concentration of macrofossils is 171 individuals m⁻², but in some places, the concentration of *Aspidella* attachment disks alone reaches 200 individuals m⁻² (Zakrevskaya 2014). Three genera—*Kimberella*, *Dickinsonia*, and *Parvancorina* (e.g., see Ivantsov 2009; Naimark and Ivantsov 2009;

Ivantsov and Zakrevskaya 2022)—are represented in the collection by several dozens, even hundreds of imprints. *Kimberella* collected from the burial event horizon Z11(XXII) numbers 770 specimens, ranging from 1.2 to 18.8 mm in width; it had a head section that was rarely preserved. The body of *Kimberella* was soft, and muscular contraction upon burial led to changes from its generally ribbon-like morphology to an oval or rounded shape. The same is true for *Dickinsonia*, of which 78 individuals were found, ranging in length from 4 to 145 mm, but which, apparently, also reflect postmortem shape distortion. Thus, the L/F distributions of *Kimberella* and *Dickinsonia* cannot be used straightforwardly for reliable inferences about their growth. In contrast, the sharp outline of *Parvancorina* can be measured accurately and so provides our focus in this study.

The benthic community of the White Sea region lived in and was buried beneath hydrodynamically active shallow waters between fair weather and storm wave bases (Grazhdankin 2004). In general, local burial event horizons extend for several tens, or rarely hundreds, of meters along strike, apparently reflecting the limited volume and trajectory of suspended sediments. In contrast, burial event horizon Z11(XXII) can be traced along strike for 2 km, and we can assume that its area reached several square kilometers. Microbial mat textures are common on bedding plane surfaces (Zakrevskaya 2014).

All individuals under consideration were buried in place by a single event, facilitating the collection of reliable data on the growth dynamics and average life span of *P. minchami*. The lengths and widths of the fossils were measured using plasticine casts of natural imprints using the built-in scale of an MBS-2 binocular microscope, with measured specimens ranging in length from 1.9 to 18.7 mm (Fig. 4). Previously studied populations in White Sea burial horizons commonly demonstrate division into two or more size groups (Zakrevskaya 2014), presumably reflecting distinct age cohorts and reproductive cycles (Zakrevskaya 2014; see also Darroch et al. 2013; Coutts et al. 2018). This certainly applies to *Parvancorina* from the burial horizon Z11(XXII), which fall into two, possibly three, size groupings (Fig. 5A). A clear predominance of small, presumably young individuals may indicate increased mortality of middle-aged and older individuals.

Methods

Ediacaran organisms had no gills or other identifiable dedicated respiratory surfaces. Still, thus, their growth rate (d_w/d_l) can be

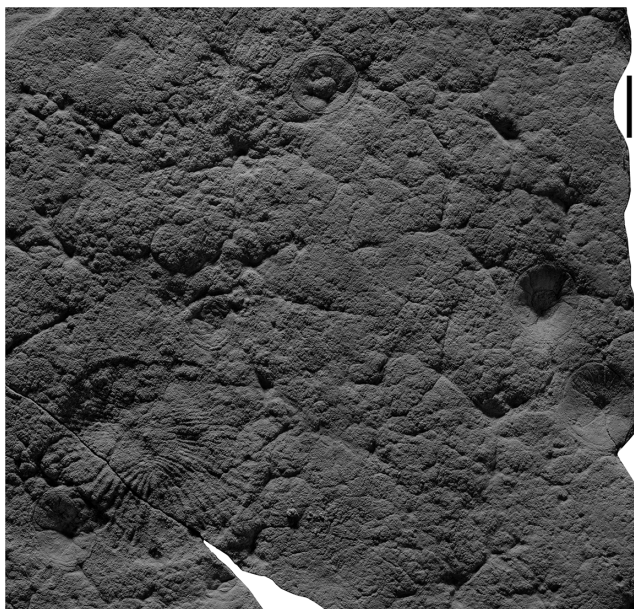


Figure 3. Fossiliferous surface of the burial horizon Z11(XXII), showing an imprint of *Dickinsonia costata* and five imprints of the attachment disks of *Aspidella terranova*. Scale bar, 10 mm.

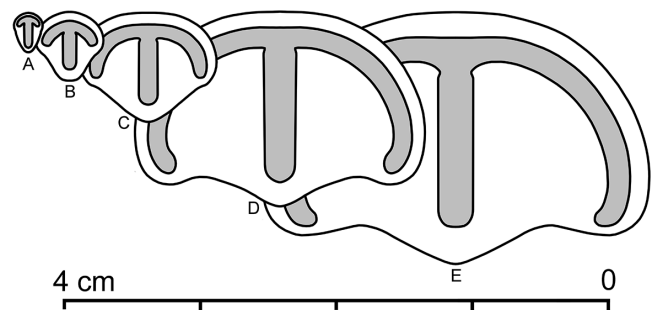


Figure 4. *Parvancorina minchami* Glaessner, 1958 from the burial event horizon Z11(XXII); note the change in proportions with increasing size: **A**, “juvenile” specimen 2.6 mm long, 1.8 mm wide; **B**, specimen 4.7 mm long, 4.6 mm wide; **C**, specimen 9.1 mm long, 10.2 mm wide; **D**, specimen 14.6 mm long, 20.5 mm wide; **E**, “adult” specimen, 11.8 mm long, 24.6 mm wide. Note allometry, i.e., the width grew faster than the length; see also Naimark and Ivantsov (2009).

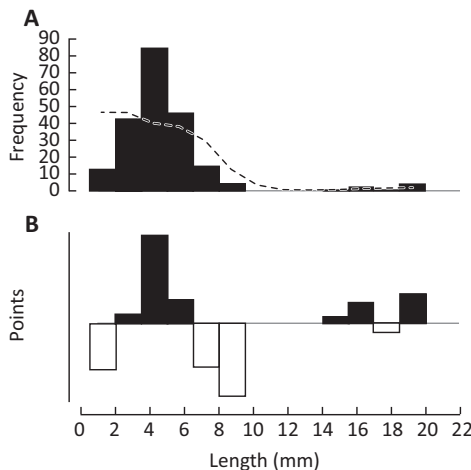


Figure 5. Length-frequency (L/F) data for *Parvancorina minchami* Glaessner, 1958 from the burial event horizon Z11(XXII), southeastern White Sea region, Russia. **A**, L/F data of 211 specimens ranging from 2.0 to 18.6 mm, grouped in classes or “bins” of 1.5 mm, with a running average of five classes (dotted line); **B**, the original L/F data, in each bin, divided by the corresponding running average and 1 subtracted from the quotient. This generates positive (black) points representing peaks in the original L/F data, and negative (white) points, representing the troughs between peaks. Such restructured L/F data are used in ELEFAN (Electronic Length-Frequency Analysis) to estimate the parameters of a best growth curve (see text).

conceived as having consisted, as in Recent WBE, of two processes with opposing tendencies, as proposed by Pütter (1920), yielding

$$dW/dt = HW^d - kW \quad (1)$$

where W is the weight (i.e., mass), H is the rate of synthesis of body proteins, d is the exponent of a relationship of the form $S \propto W^d$, where S is the surface of their bodies exposed to the water that supplied the oxygen required for protein synthesis, and k is the net rate of spontaneous protein denaturation (Pauly and Lam 2023).

The integration of equation (1) with $d = 2/3$, that is, assuming that the exposed body surface grew such that $S \propto L^2$ while body weight grew according to $S \propto L^3$ leads to the von Bertalanffy growth function (VBGF), which is widely used in fisheries and aquatic research (see FishBase, www.fishbase.ca, for fish; SeaLifeBase, www.sealifebase.ca, for marine invertebrates). This has the form:

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)} \right) \quad (2)$$

where L_t is the predicted length at age t , L_∞ is the asymptotic length, that is, the mean length the individuals of a given population would reach if they grew indefinitely, K is the rate, of dimension over time (here: yr^{-1} ; with $k=3K$) at which L_∞ is approached, and t_0 is the hypothetical age at zero length. The parameter t_0 is ignored here, as it is usually very small, and plays no role in the equations that follow.

Note that in Recent WBE, L_∞ is usually slightly larger than $L_{\max}$, the largest individual in a population, and also that longevity ($t_{\max}$) is related to K via the relationship

$$t_{\max} \approx 3/K \quad (3)$$

Once an estimate of L_∞ is available, K can be estimated by first reconstructing the available length-frequency (L/F) sample using ELEFAN software originally developed by Pauly and David (1981), which multiple applications show is appropriate for WBE reaching up to 10–12 yr, through a procedure involving the following steps:

1. selecting a class interval that results in grouping the individual length measurements into 12–15 length classes or “bins” (Fig. 5A);
2. calculating the running average of the L/F data over five bins (dotted line in Fig. 5A); and
3. dividing the frequency in each bin by the corresponding running average frequency and subtracting 1 from each quotient.

The resulting reconstructed L/F data are shown in Figure 5B, in which the peaks of the original distribution are black positive points, with the troughs originally separating peaks becoming white negative points.

The ELEFAN procedure then selects, from thousands of growth curves generated by a wide range of K values and a single set value of L_∞ , the single value of K associated with the growth curve that best links (most of) the peaks while avoiding (as much as possible) the trough of a reconstructed L/F sample, based on the assumption that the sought-after growth pattern repeats itself from one year to the next.

This single best value of K maximizes the number of points that are “hit” by the resulting growth curve. The sum of the positive and negative points that are hit is the explained sum of peaks (ESP), because the curve explains their positions by analogy to the “explained” variance in statistics. The ESP is then related to the available sum of peaks (ASP), that is, the sum of the peaks (i.e., of the highest bins in runs of positive point values, analogous to total variance) via $R_n = 10^{(ESP/ASP)}/10$, here used as a goodness-of-fit index.

Once an optimal value of K has been estimated, a length-converted catch curve (Pauly et al. 1995) can be used to estimate the instantaneous mortality rate (M) defined by

$$N_2 = N_1 \cdot e^{-M \cdot t_2 - t_1} \quad (4)$$

and where estimates of M can be obtained from the regression

$$\ln(N/\Delta t) = a - Mt' \quad (5)$$

applied to the descending arm of a plot of $\ln(N/\Delta t)$ versus t' values.

Here, N is the number of specimens in bin i , Δ is the time needed for the organisms to grow from the lower (L_{1i}) to the upper (L_{2i}) limit of bin i as estimated for successive values of

$$t_i = -(1/K) \cdot \ln[(L_\infty - L_{2i})/(L_\infty - L_{1i})] \quad (6)$$

where t_i is the relative age (i.e., the age ignoring t_0) corresponding to successive lengths.

Finally, the age t' is estimated from

$$t' = -\ln[1 - (L_{mr}/L_\infty)]/K \quad (7)$$

where L_{mr} is the midrange of a bin.

Table 1 summarizes the parameter definitions and spells out the acronyms used in this contribution. Also note that several versions of ELEFAN versions exist that implement the equations and logic presented above (e.g., Pauly and Greenberg 2013; Taylor and Mildnerberger 2017); the version used here is that of Gayanilo et al. (2005), available from the Food and Agriculture Organization of the United Nations (www.fao.org/fishery/en/topic/16072/en).

Results

For an asymptotic length set at 20 mm, that is, slightly longer than the maximum reported length of 18.6 mm, and a bin width of

Table 1. Parameters and acronyms used and corresponding definitions.

Item (units)	Definition
$\propto$	Proportional to...
Δ	Δ , a time increment, i.e., $t_2 - t_1$ (see eq. 7)
ASP	Available sum of peaks, used in ELEFAN as a measure analogous to the total variance in parametric statistics
d	Exponent of a relationship linking respiratory surface (S) and weight (W), i.e., $S \propto W^d$
d_w/d_t	Growth rate
ELEFAN	Electronic Length-Frequency Analysis, a software approach for analyzing L/F data
ESP	Explained sum of peaks, used in ELEFAN as a measure analogous to the explained variance in parametric statistics
H	Rate of protein synthesis (see eq. 1)
k	Rate of spontaneous denaturation of proteins (see eq. 1)
K (yr^{-1})	Parameter of the VBGF expressing the rate at which L_∞ is approached
$L_{\max}$ (mm)	Maximum length in a population; usually slightly lower than asymptotic length (L_∞)
L_∞ (mm)	Asymptotic length in a population; usually slightly higher than maximum length ($L_{\max}$)
L_t	Length at age t predicted by a growth curve, such as the VBGF
L/F	Length-frequency data, i.e., length measurements grouped in classes or “bins”
$\ln$	Natural, or base e logarithms
M (yr^{-1})	Instantaneous rate of (natural) mortality, usually caused by predation
N_1, N_2	Number of WBE in a population at times t_1 and t_2 (see eq. 4)
R_n	$= (10^{ESP/ASP})/10$, ELEFAN's measure for the goodness of fit of the VBGF to an L/F dataset
S (mm^2)	Respiratory surface, e.g., gills in many WBE; $S \propto W^d$
t_0 (year)	The (usually negative and small) “age” that WBE would have at $L = 0$ if WBE always grew according to the VBGF (which they do not, because it does not reflect the growth of early stages)
$t_{\max}$ (year)	Longevity of WBE, roughly the time needed to reach 95% of asymptotic length (L_∞)
VBGF	von Bertalanffy growth function (eq. 2)
W (g)	Body weight (usually wet, or live weight)
WBE	Water-breathing ectotherms (fish and invertebrates that breathe water)

1.5 mm, the K value associated with the highest R_n is $K = 0.77 \text{ yr}^{-1}$ (Fig. 6A). This implies, given equation (3), that the longevity of *P. minchami* was about 4 yr (Fig. 6C). Also, the growth of *P. minchami* in term of its length was not slower than that of small Recent invertebrates randomly selected as a function of their size from multiple options, such as *Thysanoessa longipes* (Euphausiacea: Euphausiidae; $L_\infty = 17.7 \text{ mm}$, $K = 0.72 \text{ yr}^{-1}$), *Plesionika martia* (Decapoda: Caridae; $L_\infty = 24 \text{ mm}$, $K = 0.71 \text{ yr}^{-1}$), and *Macoma balthica* (Mollusca: Bivalvia; $L_\infty = 17.1 \text{ mm}$, $K = 0.42 \text{ yr}^{-1}$), as can

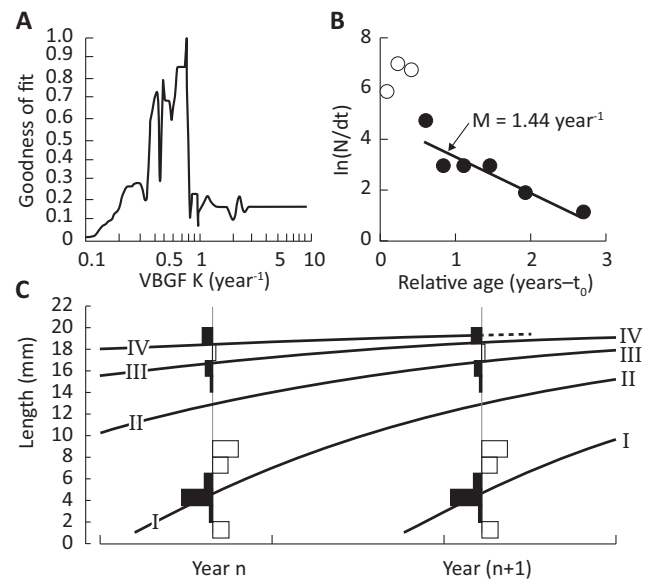


Figure 6. Growth and mortality of the Ediacaran *Parvancorina minchami* Glaessner, 1958. **A**, Goodness-of-fit of growth curves featuring asymptotic length (L_∞) of 20 mm, and K -values ranging from 0.1 to 10 yr^{-1} , suggesting that 0.77 yr^{-1} is the best estimate. **B**, Catch curve, whose slope for larger “adult” specimens allows the estimation of instantaneous mortality rate $M = 1.44 \text{ yr}^{-1}$, which suggests a much higher mortality rate for juveniles. **C**, Growth curve, as estimated by ELEFAN (Electronic Length-Frequency Analysis) based on the restructured length-frequency data of Fig. 6B, with the Roman numerals referring to various age groups (see text). VBGF, von Bertalanffy growth function.

be ascertained from SeaLifeBase (www.sealifebase.ca), based on Iguchi and Ikeda (2004), Vafidis et al. (2004), and Bachelet (1980). The catch curve, constructed with a bin width of 2 mm to generate L/F data that did not contain zeroes), estimated M at 1.14 yr^{-1} for the specimens larger than 8 mm (Fig. 6B).

Discussion

Darroch et al.’s (2017) elegant study of the relationship of *Parvancorina* to flowing water was based on digital models of three morphs, *P. sagitta*, *P. minchami* from South Australia, and *P. minchami* from Russia (White Sea). The results indicate that the orientation of these morphs to the direction of the water flow impacted on the turbulence behind their dorsal ridges and thus on the amount of food particles potentially available for deposition and ingestion by phagocytic cells on the rear surface. This simulation therefore strongly suggests that *Parvancorina* spp. could orient themselves relative to the direction of variable tidal currents and, perhaps, move to places where the water speed and the richness of suspended particles were optimal.

Ineffective as it may seem, this feeding mode, along with the oxygen obtained by diffusion from flowing waters, generated enough metabolic energy for their growth parameters to be comparable to those of small Recent invertebrates (e.g., Apostolidis and Stergiou 2008; see also SeaLifeBase, www.sealifebase.ca), as illustrated in Figure 7. Note, however, that growth, as defined in equation (1), is a process involving mass, and that *P. minchami* may have been lighter than Recent invertebrates with the same asymptotic length. This, however, would still result in *P. minchami* having Recent analogues in terms of growth and, hence, metabolic rate. Moreover, these analogue species would also feed on phytoplankton and suspended detritus, the same food that Darroch et al.

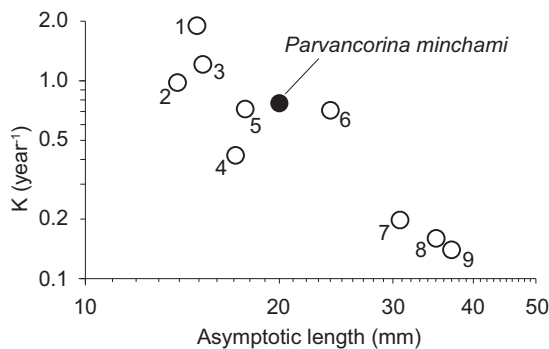


Figure 7. An auximetric plot, allowing the growth parameters of Recent invertebrates whose growth was described by the von Bertalanffy growth function (VBGF; eq. 2) to be compared with *Parvancorina minchami*. They are: 1, *Alpheus armillatus*; 2, *Plesionika antgai*; 3, *Alpheus estuariensis*; 4, *Macoma balthica*; 5, *Thysanoessa longipes*; 6, *Plesionika martia*; 7, *Lithophaga patagonica*; 8, *Arca noae*; and 9, *Hiatella arctica* (see also www.sealifebase.org). This illustrates that *P. minchami* had a growth performance comparable with that of small Recent invertebrates, at least when their “length” is considered.

(2017) suggested for *P. minchami*. Possibly, *P. minchami* was also able to phagocytize organic particles in the underlying sediment on which they rested (M. Laflamme, University of Toronto, personal communication 15 August 2024), which would increase the relative importance of detritivory.

The estimated mortality rate of $M = 1.14 \text{ yr}^{-1}$ implies $M/K \approx 2$, a common ratio in Recent small invertebrates. However, it is clear from Figure 6C that specimens of lengths representing age group II are missing, presumably because of a failure of annual recruitment of young *P. minchami* to the population represented by the *L/F* sample (see Houde [2016] for possible causes). Thus, our mortality estimates remain tentative. Nonetheless, our estimates dovetail with longevity estimates for a *Parvanocorina* population from Australia, based on multiple peaks in a size-frequency curve interpreted in terms of seasonal reproduction (Weyland and Droser 2023).

Conclusions

Length-frequency analysis using the ELEFAN method suggests that *Parvancorina minchami* had growth and mortality dynamics comparable to those of many small marine invertebrates living today. Thus, despite continuing uncertainties surrounding function and phylogenetic relationships, this brings us a bit closer to an understanding of *P. minchami*, and by extension other Ediacaran metazoans, as living organisms. More broadly, as demonstrated by previous applications to Paleozoic fossils, the ELEFAN methodology holds the promise of connecting many animal fossils to the huge literature on the dynamics of Recent WBE, enriching our understanding of the paleobiology and ecology of ancient animals and ecosystems.

Acknowledgments. We thank C. Simpson, M. Laflamme, and an anonymous reviewer for helpful comments. We also thank E. Chu for drafting Figs. 5–7. This study was supported by a grant of the Russian Science Foundation (project no. 24-27-00253; <https://rscf.ru/project/24-27-00253/>) to A.I. and M.A.Z.

Competing Interests. The authors declare no competing interests.

Literature Cited

Apostolidis, C. A., and K. I. Stergiou. 2008. A preliminary compilation of life-history data for Mediterranean marine invertebrates. Pp. 102–121 in M. L. D.

Palomares and D. Pauly, eds. *Von Bertalanffy growth parameters of non-fish organisms*. Fisheries Centre Research Reports 16(10). Fisheries Centre, University of British Columbia, Canada. <https://open.library.ubc.ca/soa/cIRcle/collections/facultyresearchandpublications/52383/items/1.0074762>, accessed 19 August 2024.

- Bachelet, G. 1980. Growth and recruitment of the tellinid bivalve *Macoma balthica* at the southern limit of its geographical distribution, the Gironde estuary (SW France). *Marine Biology* 59:105–117.
- Bobrovskiy, I., A. Nagovitsyn, J. M. Hope, E. Luzhnaya, and J. J. Brooks. 2022. Guts, gut contents, and feeding strategies of Ediacaran animals. *Current Biology* 32:5382–5389.
- Chan, Y. K. S., T. C. Toh, and D. Huang. 2018. Distinct size and distribution patterns of the sand-sifting sea star, *Archaster typicus*, in an urbanised marine environment. *Zoological Studies* 57:e28.
- Coutts, F. J., C. J. A. Bradshaw, D. C. García-Bellido, and J. C. Gehling. 2018. Evidence of sensory-driven behavior in the Ediacaran organism *Parvancorina*: implications and autecological interpretations. *Gondwana Research* 55:21–29.
- Darroch, S. A., M. Laflamme, and M. E. Clapham. 2013. Population structure of the oldest known macroscopic communities from Mistaken Point, Newfoundland. *Paleobiology* 39:591–608.
- Darroch, S. A., L. A. Rahman, B. Gibson, R. A. Racicot, and M. Laflamme. 2017. Inference of facultative mobility in the enigmatic Ediacaran organism *Parvancorina*. *Biology Letters* 13:20170033.
- Djan, P. S., J. A. Fynn, and N. Lazar. 2022. Habitat distribution, growth and mortality of giant African cuttlefish *Sepia hierredda* (Rang, 1835) in Ghana waters. *Journal of Fisheries and Coastal Management* 3:1–9.
- Droser, M. L., and J. G. Gehling. 2015. The advent of animals: the view from the Ediacaran. *Proceedings of the National Academy of Sciences USA* 112:4865–4870.
- Dunn, F. S., A. G. Liu, and P. C. J. Donoghue. 2018. Ediacaran developmental biology. *Biological Reviews* 93:914–932.
- Dwiponggo, A., T. Hariati, S. Banon, M. L. D. Palomares, and D. Pauly. 1986. Growth, mortality and recruitment of commercially important fishes and penaeid shrimps in Indonesian waters. *ICLARM Technical Reports* 17.
- Erwin, D. H., M. Laflamme, S. M. Tweedt, E. A. Sperling, D. Pisani, and K. J. Peterson. 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* 334:1091–1097.
- Fedonkin, M. A., J. G. Gehling, K. Grey, G. Narbonne, and P. Vickers-Rich. 2007. *The rise of animals. evolution and diversification of the kingdom Animalia*. Johns Hopkins University Press, Baltimore, Md.
- Gayanilo, F. C., P. Sparre, and D. Pauly. 2005. *FAO-ICLARM Sock Assessment Tool II (FiSAT II)—User Guide*, Revised version. FAO Computerized Information Series (Fisheries), no. 8. Food and Agriculture Organization of the United Nations, Rome.
- Glaessner, M. F. 1958. New fossils from the base of the Cambrian in South Australia. *Transactions of the Royal Society of South Australia* 81:185–188.
- Glaessner, M. F. 1980. *Parvancorina*—an arthropod from the late pre-Cambrian (Ediacaran) of South Australia. *Annalen des Naturhistorischen Museums in Wien* 83:83–90.
- Grazhdankin, D. V. 2003. Stratigraphy and depositional environment of the Vendian Complex in the Southeast White Sea area. *Stratigraphy and Geological Correlation* 11:313–331.
- Grazhdankin, D. V. 2004. Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution. *Paleobiology* 30:203–221.
- Grazhdankin, D. V. 2016. Forbidden fruits in the Garden of Ediacara. *Paläontologische Zeitschrift* 90:649–657.
- Hikmawansyah, Y., Y. Andriani, A. M. Khan, and L. P. Dewanti. 2019. Stock estimates of white pomfret (*Pampus argenteus*) based on length and weight data in Pangdaran waters. *Asian Journal of Fisheries and Aquatic Research* 5:1–13.
- Houde, E. D. 2016. Recruitment variability. Pp. 98–187 in T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness, eds. *Fish reproductive biology: implications for assessment and management*, 2nd ed. Wiley, Hoboken, N.J.
- Hoyal Cuthill, J. F., and J. Han. 2018. Cambrian petalonamid *Stromatoveris* phylogenetically links Ediacaran biota to later animals. *Palaeontology* 61:813–823.
- Iguchi, N., and T. Ikeda. 2004. Vertical distribution, population structure and life history of *Thysanoessa longipes* (Crustacea: Euphausiacea) around Yamato Rise, central Japan Sea. *Journal of Plankton Research* 26:1015–1023.

- Ivantsov, A. Yu. 2009. New reconstruction of *Kimberella*, a problematic Vendian Metazoan. *Paleontological Journal* 43:601–611.
- Ivantsov, A. Yu. 2013. New data on Late Vendian problematic fossils from the genus *Harlaniella*. *Stratigraphy and Geological Correlation* 21:592–600.
- Ivantsov, A. Yu. 2017. The most probable Eumetazoa among late Precambrian macrofossils. *Invertebrate Zoology* 14:127–133.
- Ivantsov, A. Yu., and M. A. Zakrevskaya. 2022. *Dickinsonia costata* of the Winter Mountains: features of morphology and ontogenesis. *Precambrian Research* 379:106788.
- Ivantsov, A. Yu., Y. E. Malakhovskaya, and E. A. Serezhnikova. 2004. Some problematic fossils from the Vendian of the southeastern White Sea Region. *Paleontological Journal* 38:1–9.
- Legg, D. A. 2015. The morphology and affinities of *Skania fragilis* (Arthropoda) from the middle Cambrian Burgess Shale. *Bulletin of Geosciences* 90:509–518.
- Lin, J.-P., S. M. Gon, J. G. Gehling, L. E. Babcock, Y.-L. Zhao, X.-L. Zhang, S.-X. Hu, J.-L. Yuan, M.-Y. Yu, and J. Peng. 2006. A *Parvancorina*-like arthropod from the Cambrian of South China. *Historical Biology* 18:33–45.
- Martin, M. W., D. V. Grazhdankin, S. A. Bowring, D. A. D. Evans, M. A. Fedonkin, and J. L. Kirschvink. 2000. Age of Neoproterozoic bilaterian body and trace fossils, White Sea, Russia: implications for metazoan evolution. *Science* 288:841–845.
- Naimark, E. B., and A. Yu. Ivantsov. 2009. Growth variability of the late Vendian Problematics *Parvancorina* Glaessner. *Paleontological Journal* 43:12–18.
- Narbonne, G. M. 2005. The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annual Review of Earth and Planetary Sciences* 33:421–442.
- Omena, E. P., and A. C. Z. Amaral. 2000. Population dynamics and secondary production of *Laeonereis acuta* (Treadwell, 1923) (Nereididae: Polychaeta). *Bulletin of Marine Science* 67:421–431.
- Palomares, M. L. D., and D. Pauly. 2009. The growth of jellyfishes. *Hydrobiologia* 616:11–21.
- Paterson, J. R., J. G. Gehling, M. L. Droser, and R. D. C. Bicknell. 2017. Rheotaxis in the Ediacaran epibenthic organism *Parvancorina* from South Australia. *Scientific Reports* 7:45539.
- Pauly, D., and N. David. 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. *Berichte der Deutschen wissenschaftlichen Kommission für Meeresforschung* 28:205–211.
- Pauly, D., and A. Greenberg, eds. 2013. *ELEFAN in R: a new tool for length-frequency analysis*. Fisheries Centre Research Reports 21(3). Fisheries Centre, University of British Columbia, Canada.
- Pauly, D., and J. D. Holmes. 2022. Re-assessing growth and mortality estimates for the Ordovician trilobite *Triarthrus eatoni*. *Paleobiology* 49:120–130.
- Pauly, D., and M. E. Lam. 2023. Too hot or too cold: the biochemical basis of temperature-size rules for fish and other ectotherms. *Environmental Biology of Fishes* 106:1519–1527.
- Pauly, D., J. Moreau, and N. Abad. 1995. Comparison of age-structured and length-converted catch curves of brown trout *Salmo trutta* in two French rivers. *Fisheries Research* 22:197–204.
- Pauly, D., N. Smith, and M. Butler. 2022. Growth and related traits of the wool sponge *Hippospongia lachne*: practical and theoretical considerations. *Fisheries Bulletin* 120:99–112.
- Pütter, A. 1920. Studien über physiologische Ähnlichkeit. VI. Wachstumsähnlichkeiten. *Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere* 180:293–340.
- Sperling, E. A., and J. Vinther. 2010. A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evolution and Development* 12:201–209.
- Stankovsky, A. F., E. M. Verichev, and I. P. Dobeiko. 1985. The Vendian of Southeastern White Sea region. Pp. 67–76 in B. Sokolov and A. Iwanowski, eds. *The Vendian System, stratigraphy and geological processes*, Vol. 2. Nauka, Moscow. [In Russian.]
- Stephenson, N. P., K. M. Delahooke, N. Barnes, B. W. T. Rideout, C. G. Kenchington, A. Manica, and E. G. Mitchell. 2024. Morphology shapes community dynamics in early animal ecosystems. *Nature Ecology and Evolution* 8:1238–1247.
- Taylor, M. H., and T. K. Mildenberger. 2017. Extending electronic length-frequency analysis in R. *Fisheries Management and Ecology* 24: 330–338.
- Vafidis, D., P. K. Leontarakis, A. Dailianis, and A. Kallianiotis. 2004. Growth parameters of the most abundant pandalid shrimps (Decapoda: Caridae) from the Northern Aegean Sea. *Rapports et procès-verbaux des réunions Commission internationale pour l'exploration scientifique de la Mer Méditerranée* 37:453.
- Vergara, M., M. E. Oliva, and J. M. Riascos. 2012. Population dynamics of the amphioxus *Branchiostoma elongatum* from northern Chile. *Journal of the Marine Biological Association of the United Kingdom* 92: 591–599.
- Weyland, W., and M. Droser. 2023. *Parvancorina*: the next generation, a growth model of how an Ediacaran organism lives long and prospers. *Geological Society of America Abstracts with Programs* 55(6). doi: 10.1130/abs/2023AM-392205.
- Wu, Y., S. Pates, D. Pauly, X. Zhang, and D. Fu. 2024. Rapid growth in a large Cambrian apex predator. *National Science Review* 11:nwad284.
- Xiao, S., and M. Laflamme. 2009. On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends in Ecology and Evolution* 24:31–40.
- Yang C., A. D. Rooney, D. J. Condon, X.-H. Li, D. V. Grazhdankin, F. T., Bowyer, C. Hu, F. A. Macdonald, and M. Zhu. 2021. The tempo of Ediacaran evolution. *Science Advances* 7:eabi9643.
- Zakrevskaya, M. A. 2014. Paleoeological reconstruction of the Ediacaran benthic macroscopic communities of the White Sea (Russia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 410:27–38.
- Zhang, X.-L., J. Han, Z.-F. Zhang, H.-Q. Liu, and D.-G. Shu. 2003. Reconsideration of the supposed Naraoiid larva from the early Cambrian Chengjiang Lagerstätte, South China. *Palaeontology* 46:447–465.