# The ecology of *Dickinsonia* on tidal flats

## *Ecología de* Dickinsonia *en llanuras mareales*

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## ABSTRACT

Specimens of *Dickinsonia* from the Central Urals are characterised by clear bilateral symmetry. Taking into account observations from Australian specimens, we consider that the so called 'glide reflection symmetry' in these fossils is a taphonomic phenomenon. The size frequency distribution plot shows the predominance of smaller individuals in the studied population of *Dickinsonia* from the Central Urals. Assuming that the age of an individual is manifested in the body size, there is a significant predominance of juvenile individuals in the population. Three possible scenarios can be envisaged: (i) the population has a large number of juvenile individuals as the result of high survivorship rate in the intertidal zone; (ii) the population teems with juvenile forms because it is buried immediately after hatching; (iii) assuming that *Dickinsonia* was an actively motile organisms, that abundance of juvenile individuals could be explained by their inability to escape burial (although it is difficult to imagine that some of the mature individuals are buried with signs of escape behaviour); and (iv) the population could be interpreted as a fossilised 'nesting ground' for *Dickinsonia* in the intertidal zone where juvenile forms underwent maturation before migrating back to the subtidal zone. The study population can be characterised as expanding or stable; therefore, the intertidal setting can be described as favourable for these organisms.

**Keywords:** *Dickinsonia*; Tidal-flat; Central Urals; Ediacaran; Russia.

## RESUMEN

Los ejemplares de *Dickinsonia* de los Urales Centrales se caracterizan por una clara simetría bilateral. Tomando en cuenta las observaciones de especímenes australianos, consideramos que la llamada'simetría de reflexión por deslizamiento' en estos fósiles es un fenómeno tafonómico. El gráfico de distribución de frecuencias de tamaño muestra el predominio de individuos juveniles en la población estudiada de *Dickinsonia* de los Urales Centrales. Asumiendo que la edad de un individuo se manifiesta por su tamaño, existe un predominio significativo de individuos juveniles en la población. Se pueden prever tres escenarios posibles: (1) la población tiene un gran número de individuos juveniles como resultado de la alta tasa de supervivencia en la zona intermareal; (2) la población está dominada por formas juveniles porque está enterrada inmediatamente después

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de la eclosión; (3) suponiendo que *Dickinsonia* fuera un organismo móvil activo, la abundancia de individuos juveniles podría explicarse por su incapacidad para escapar del enterramiento (aunque es difícil imaginar que algunos de los individuos maduros estén enterrados con signos de comportamiento de escape); y (4) la población podría interpretarse como un "lugar de nidificación" fosilizado para *Dickinsonia* en la zona intermareal, donde las formas juveniles maduraron antes de migrar a la zona submareal. La población de estudio puede caracterizarse como en expansión o estable; por lo tanto, el entorno intermareal puede describirse como favorable para estos organismos.

**Palabras clave:** *Dickinsonia*; Llanura mareal; Urales centrales; Ediacárico; Rusia

## Introduction

Few, if any, Ediacaran organisms have so many alternative interpretations with regards to their position on a phylogenetic tree than does *Dickinsonia*. Originally described as a jellyfish by Sprigg (1947), it was subsequently regarded as a rhizarian protist (Seilacher *et al.*, 2003), a lichenised fungus (Retallack, 2007), a stem-group placozoan (Sperling & Vinther, 2008), a sister-group eumetazoan (Buss & Seilacher, 1994), a stem-group bilaterian (Gold *et al.*, 2015), and even as a acoelomorph (Fedonkin, 1981), a polychaete (Glaessner & Wade, 1966), and a direct chordate ancestor (Dzik, 2015). In addition to comparison of morphological similarities, different specialists have attempted implementing novel approaches such as studying taphonomic processes, ontogenetic patterns and chemical composition in these organisms. In addition to resolving the course of evolution, the new methods could elucidate so far unnoticed and not fully appreciated processes of modern Metazoan development and ecology. It is well established that *Dickinsonia* represents a benthic organism with a flattened body, but poor fossil preservation is the crucial problem that paleontologists deal with. The imprints of soft bodies in sedimentary rocks can be subsequently altered by various tectonic processes, and unknown paleobiological information can be lost during excavation, rock splitting, fossil collection and preparation processes. Furthermore, in-situ preservation of large populations of individual specimens from the same bedding surface are rarely found, collected, and studied. Hence, even the assignment of morphologically similar fossils to the same biological species often remains an unsolvable task.

## Results

Over a period of several years (2016-2018) our team gradually excavated a vertically standing bedding surface dropping off into the rapid mountain river Sylvitsa, western slope of the Central Urals. The bedding surface yielded an exceptionally preserved life association of *Dickinsonia*. In terms of local stratigraphy, it belongs to the Konovalovka Member of the Cherny Kamen Formation, Sylvitsa Group of supposedly terminal Ediacaran age. The fossils are preserved in negative hyporelief in a package of finely alternating sandstone, siltstones and mudstones. The fine-grained texture of the casting material provided an unparalleled resolution of the fossil preservation. Most important, nine square meters of the surfaces preserved over a hundred of exquisitely preserved *Dickinsonia* specimens in life association. The sedimentary environment of this fossil assemblage has been reconstructed as a restricted coastal lagoon surrounded by tidal flats (Bobkov *et al.*, 2019), which seems very unusual compared to other fossil localities conventionally regarded as representing shallow marine settings.

Previous studies reported a good correlation between the length and the width of the body in these organisms (Evans *et al.*, 2017; Reid *et al.*, 2018); however, the correlation between these two parameters in our collection showed a weaker trend ($R^2 = 0.58$; $p<2.2e-16$). All of the specimens from the Central Urals appear to be deformed in one direction as a result of tectonic activity (rather than taphonomic or soft sediment deformation processes). This distortion is likely to be the cause of the observed poor correlation between the length and the width of the body in the studied specimens, and it most likely would affect other conclusions. To compensate for this deformation, we developed a method for accurate estimation of direction and degree of surface deformation based on pure geometric calculations depending of orientation of the axis of the specimens. The method has shown consistent results, the constructed hypothetical curve has been confirmed with actual measurement of the specimens. Once we received a coefficient of deformation and determined the angle of deformation, we recalculated the coordinates and the length and width values for

each specimen. The length-width correlation in the retrodeformed specimens is stronger ($R^2 = 0.84$; $p<2.2e-16$) compared to undeformed material.

The age structure of the population was estimated based on size frequency distribution. The plot (Fig. 1) shows log-normal distribution for the population (Shapiro-Wilk; $W = 0.98$, $p = 0.27$). In contrast, a population of *Dickinsonia costata* studied from coeval strata in the Crisp Gorge locality, South Australia shows normal distribution (Reid *et al.*, 2018), quite dissimilar from the population studied in the Central Urals. Furthermore, the population of *Dickinsonia* from the Konovalovka Member can be
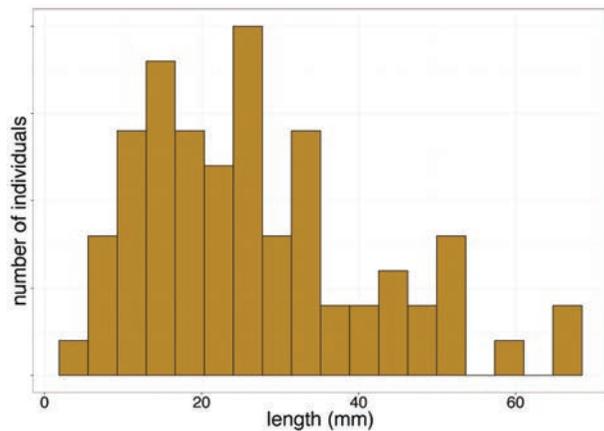
divided into two cohorts by size ($< 20$ mm and 21–67 mm); for this purpose we used Bayesian Information Criterion (Fraley & Raftery, 2006, 2007). The analysis of spatial distribution shows different behaviour between the larger and smaller individuals. The larger individuals show spatial segregation (greater distance then expected by random distribution with PCF value is placed under lower bound for random distribution), but smaller individuals tend to form denser aggregations (Fig 2). These spatial patterns are found in extant populations where larger organisms require more food resources than smaller ones, so avoid competing with others by moving away from other individuals.

## Conclusions

This study demonstrates the importance of tectonic and post-depositional processes that can negatively affect morphological analyses of fossil material leading to misidentification of species. Specimens of *Dickinsonia* from the Central Urals are characterised by clear bilateral symmetry (i.e. modules of the left side extend across the axial structure of the body with no offset). Taking into account observations from Australian fossil localities (Reid *et al.*, 2018; Evans *et al.*, 2017) we consider that the so called 'glide reflection symmetry' in these fossils is a taphonomic phenomenon. The size frequency



Figure 1.—Size-frequency histogram showing log-normal distribution in *Dickinsonia* sp. population.
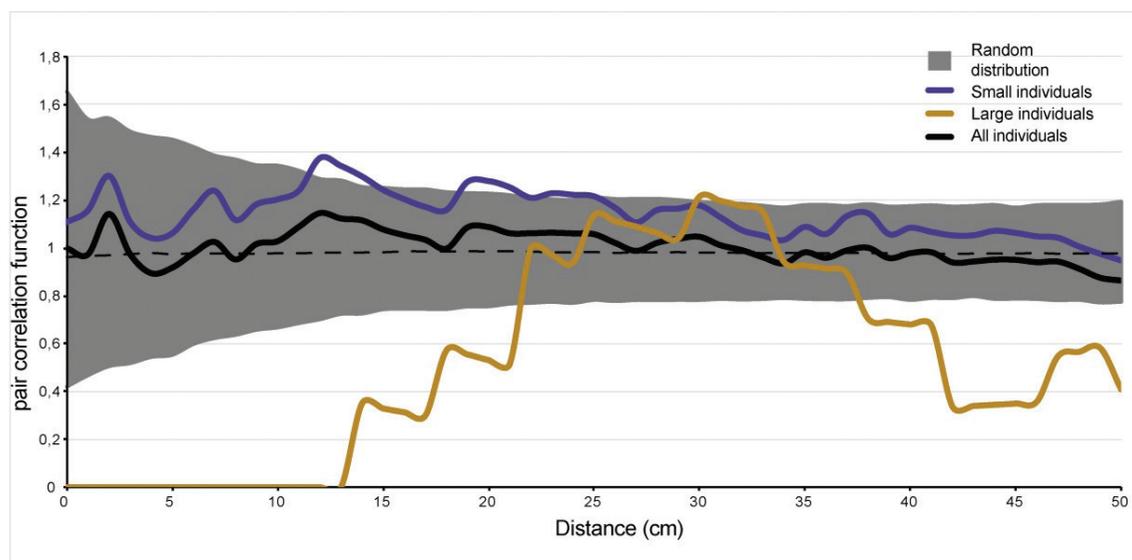


Figure 2.—Pair correlation function for the entire population and two distinct age groups in comparison with the random distribution.

distribution plot shows the predominance of smaller individuals in the studied population of *Dickinsonia* from the Central Urals (Fig. 1). Assuming that the age of an individual is manifested in the body size, there is a significant predominance of juvenile individuals in the population. Three possible scenarios can be envisaged: (i) the population has a large number of juvenile individuals as the result of high survivorship rate in the intertidal zone; (ii) the population teems with juvenile forms because it is buried immediately after hatching; (iii) assuming that *Dickinsonia* was an actively motile organisms, that abundance of juvenile individuals could be explained by their inability to escape burial (although it is difficult to imagine that some of the mature individuals are buried with signs of escape behaviour); and (iv) the population could be interpreted as a fossilised 'nesting ground' for *Dickinsonia* in the intertidal zone where juvenile forms underwent maturation before migrating back to the subtidal zone. Our data is most consistent with the latter hypothesis because it explains the high proportion of juveniles in a single population in the intertidal zone, their low proportion in populations preserved in subtidal settings and their spatial behaviour. The studied population can be characterised as expanding or stable; therefore, the intertidal setting can be described as favourable for these organisms.

## ACKNOWLEDGEMENTS

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