

Preliminary revision of the morphology of *Phyllozoon hanseni* from the Ediacaran of South Australia

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Resumen: En este trabajo se analiza la morfología de *Phyllozoon hanseni* Jenkins y Gehling, un organismo fósil con forma de fronde y de simetría deslizada del Ediacárico de la Sierra de Flinders, Australia del Sur. El estudio se centra en la medición de los parámetros básicos de estos fósiles con la intención de identificar tendencias que sean diagnósticas para *P. hanseni*, ayudar a definir su morfología funcional, y reconciliar esta información con el contexto paleobiológico. Los principales hallazgos han sido que el tamaño de los ejemplares presenta una distribución no-normal y de sesgo negativo, y que los extremos de *P. hanseni* son muy distintos. Uno lo denominamos ‘cuchara’, y es redondeado, con unidades anchas dispuestas en ángulo agudo respecto al eje sagital. Dicho ángulo es mayor hacia el ápice y le confiere a éste un aspecto de pimiento de rosa. La primera unidad consistentemente está en el lado izquierdo del epirelieve positivo. El otro extremo, el ‘cuchillo’, tiene un característico descenso lineal de anchura y longitud de sus unidades, que se mantienen perpendicular al eje del organismo. El área central, entre estas dos secciones, presenta bordes subparalelos, y lo denominamos ‘tronco’. Se ha detectado una fuerte correlación positiva entre la Longitud Mínima del Ejemplar y el Número Mínimo de Unidades, así como una moderada correlación positiva entre anchura y longitud de las unidades en la región central. Adicionalmente, los resultados sugieren un patrón de crecimiento asimétrico entre el incremento de tamaño y el número total de unidades desde el ápice del ‘cuchillo’. La morfología observada en *P. hanseni* se interpreta como un indicio de hábito bentónico postrado.

Abstract: We have investigated the morphology of *Phyllozoon hanseni* Jenkins and Gehling, a frond-like fossil organism with glide reflection symmetry from the Ediacaran of the Flinders Ranges, South Australia. The focus of this study was to measure some basic physical parameters of these fossils to identify some distinguishing trends, to help build a picture of the functional morphology of *P. hanseni*, and then to reconcile this information in a palaeobiological context. The main findings are that specimen length displayed a non-normal, negatively skewed distribution, and that *P. hanseni* possesses two distinct ends. One dubbed here the ‘spoon’, is rounded in profile, with steep-angled positioning of thicker units and a rosebud-like appearance at the terminus, found to always begin on the left bank of the positive hyporelief. The other end, the ‘knife’, displays instead a gradual decrease in both unit width and length with positioning of units perpendicular to the body axis. The area between these two sections, with sub-parallel edges, is referred to as the ‘trunk’. Specimen length was found to be positively associated with both unit number and specimen width. Additionally, the findings suggest a longitudinally asymmetrical growth pattern of increasing size and number of units, with serial addition of units at the knife terminus. The observed morphology of *P. hanseni* suggests a lifestyle as a benthic, prostrate organism.

Key words: *Phyllozoon*, Ediacara Biota, Flinders Ranges, Glide Symmetry, Longitudinal Asymmetry.

Palabras clave: *Phyllozoon*, Biota de Ediacara, Sierra de Flinders, Simetría deslizada, Asimetría longitudinal.

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Introduction

The Ediacara Biota, named after the Ediacaran Hills in the Flinders Ranges region of South Australia, were among the first multicellular organisms to inhabit the shallow coastal waters of our planet, some 555 million years ago. By studying the first emergence of complex creatures, with an assortment of shapes, sizes, and symmetries, we gain insights into the underlying natural processes behind the rise and evolution of early multicellular life and the ecosystems they were a part of. *Phyllozoon hansenii* was originally described by Jenkins and Gehling (1978) from three specimens collected at Devil's Peak, south of Quorn, in the Flinders Ranges of South Australia (Fossil site 3, Fig. 1A), and belongs to the White Sea Assemblage

of the Ediacara Biota (Droser *et al.*, 2017). Superficially, *P. hansenii* is frond-like in appearance, with a peculiar type of symmetry called 'glide reflection symmetry', where the two halves are roughly similar in shape and size but are slightly offset longitudinally (see Fig. 2). These two halves are made up of repeating long, rounded units, each based in a groove in a central corrugation that extends the length of the organism. Specimens range in length from as little as 45 mm to well over 300 mm, up to 60 mm in width, and can grow more than 125 units per side with many articulating interrupted off broken slab edges. *P. hansenii* also stands out due to its bizarre mode of preservation, in which it leaves positive hyporelief impressions, rather than the negative hyporelief preservation typical of many other fossils in this assemblage, such as

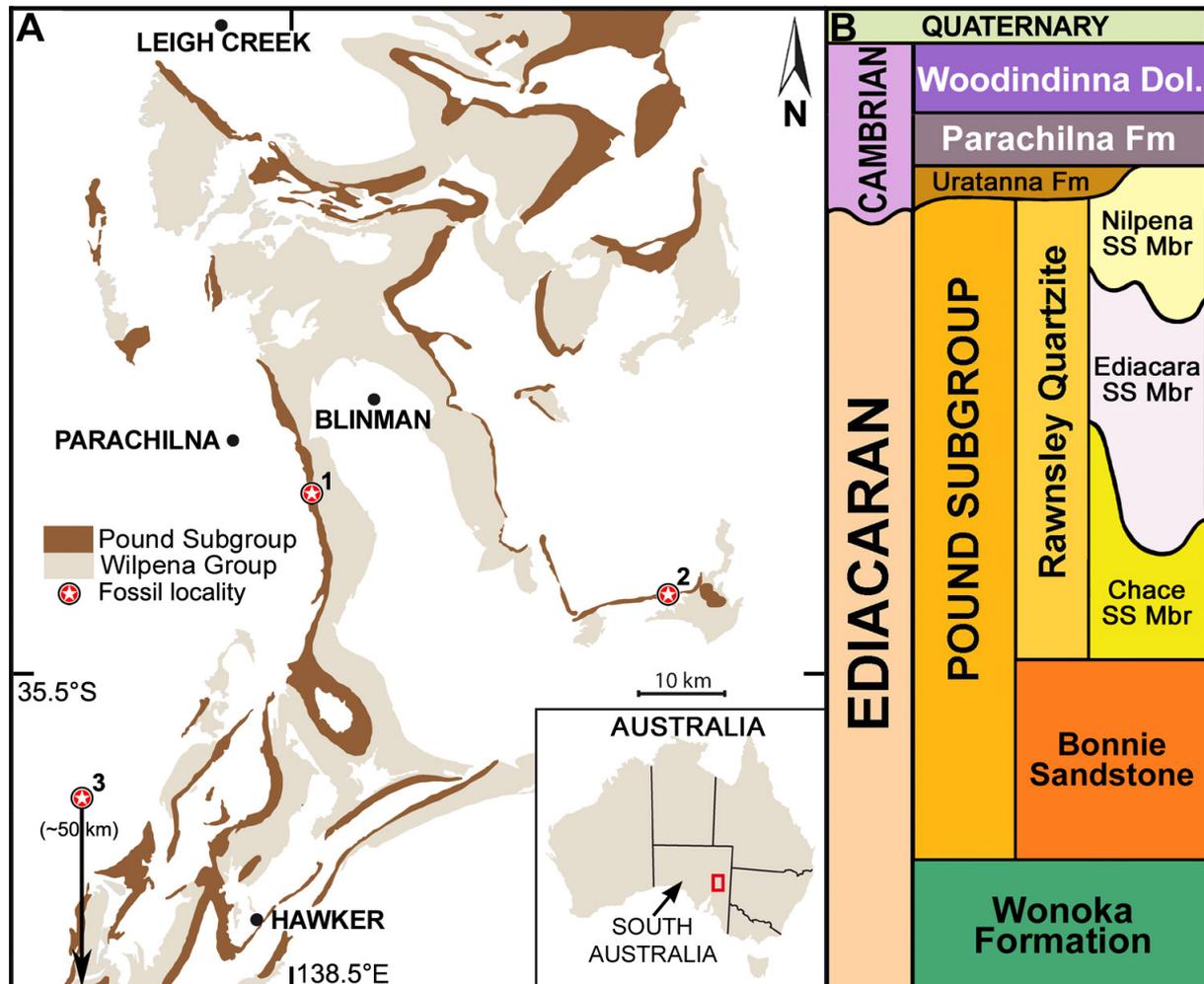


Figura 1. A) Mapa geológico de la Sierra de Flinders, Australia del Sur (Modificado de Reid *et al.* 2020). Localidades con especímenes de *Phyllozoon hansenii* marcados con estrellas numeradas 1, 2 y 3, que representan Bathtub Gorge, Tooth Knob y Devil's Peak respectivamente; **B)** Diagrama que muestra la sucesión estratigráfica simplificada en la Sierra de Flinders. / **Figure 1. A)** Geological map of the Flinders Ranges, South Australia (Modified from Reid *et al.* 2020). Sites bearing *Phyllozoon hansenii* marked by numbered stars 1, 2 and 3, representing Bathtub Gorge, Tooth Knob and Devil's Peak respectively; **B)** Diagram showing generalised stratigraphic succession in the Flinders Ranges.

Spriggina, *Dickinsonia* or *Tribrachidium* (Jenkins and Gehling, 1978). This has led some to suggest that this was a delicate, soft-bodied organism, made up of quilted, air-mattress like units, which quickly burst and decay after burial, but before the overlying sediment hardened (Gehling, 1999). It is known exclusively from the wave-base sands and sheet-flow sands facies, alongside two other taxa with the same preservation mode, ‘*Aulozoon*’ and *Funisia* (Reid *et al.*, 2020). Some have speculated that *P. hanseni* was a grazing trace fossil (Ivantsov, 2013), and it has even been suggested that it may be part of a terrestrial biota (Retallack, 2013). This last claim is widely disputed, as local sedimentary features imply large scale marine inundation at this time (Tarhan *et al.*, 2017). This report hopes to uncover any trends in morphological parameters of *Phyllozoon* and will attempt an accurate description of this organism. We will also briefly discuss the palaeoenvironment, but purely within the biological context of *P. hanseni*, as an in-depth investigation into the geological nature of this deposit has been addressed by other authors (Gehling and Droser, 2012).

Material and methods

The studied material is deposited at the South Australian Museum in Adelaide. A total of 15 slabs were studied, most containing multiple specimens. Thirty-one specimens chosen based on quality of preservation were measured and included in the data processed for this report. These came from the Bathtub Gorge, Tooth Knob and Devil’s Peak localities of South Australia (1–3, respectively in Fig. 1A), from beds of the recently-proposed Nilpena Sandstone Member (Gehling *et al.*, 2019), late Ediacaran Period (Fig. 1B). All fossil material is catalogued at the South Australian Museum Palaeontological Collections (specimen number prefix SAM P). Quantitative data was collected using digital callipers, protractor and a measuring string. Photography was done using low angle light with an Olympus D4 Tough digital camera and Canon EOS 50D SLR, with lenses EF-S 17–85 mm and EF 50 mm. Figures were produced with Adobe Photoshop CS3, Microsoft Excel and R (R Core Team, 2021).

Measured physical parameters were standardised, as illustrated by the simplified sketch in Figure 2, where we label the round end as the ‘spoon’ and the sharp end as the ‘knife’ and defined an arbitrary left and right bank when the

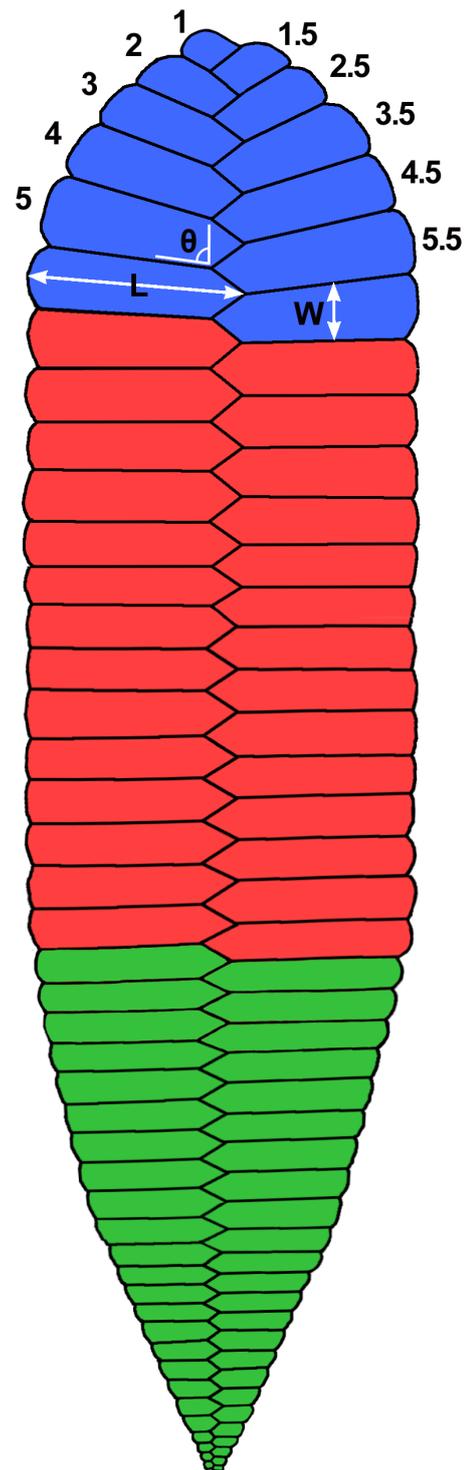


Figura 2. Diagrama esquemático de *Phyllozoon hanseni* indicando los parámetros biométricos investigados. Sistema de numeración de unidades desde el extremo. Código de colores: azul = región ‘cuchara’, rojo = región ‘tronco’ y verde = región ‘cuchillo’. / **Figure 2.** Schematic diagram of *Phyllozoon hanseni* outlining the biometric parameters investigated. Unit numbering system used from the terminus. Colour code: blue = ‘spoon’ region, red = ‘trunk’ region, and green = ‘knife’ region.

fossil is viewed from the latter to the former. Unit length *L* was taken in millimetres from central axis to the end of the unit, unit width *W* was taken in millimetres from lateral groove to lateral groove, and unit angle Θ was measured as degrees from the next knife-ward axial junction (0 degrees for reference). Minimum specimen length was measured in millimetres with string, and minimum units were counted along the impression's left bank and documented alongside. Both left and right banks were measured initially, as unit 1, 2, 3... and 1.5, 2.5, 3.5... respectively to represent the offset positions of the units, although for simplicity of data presentation, only left bank measurements were included in this report. An exception to this was for specimens measured from latex moulds, which were obviously inverted and so instead were measured along their right bank, serving as an inverted facsimile of the actual left bank. Due to the long, sometimes sinuous nature of *P. hanseni* fossils, along with fragmentary specimens and poor quality of preservation in some cases, only specimens showing clear units were measured for unit number and dimensions, and only complete specimens preserved in context were documented along their full profile. The spoon and knife of several specimens were measured for the first 25 units only, and only when preservation quality permitted. Measuring with such a close eye allowed a detailed view of some very small surface features, which were later investigated using putty. All the quantitative data was entered into Microsoft Excel and statistical analyses of the relationships between variables were conducted in R.

Systematic Palaeontology

Phyllozoon Jenkins and Gehling 1978

Type species: *Phyllozoon hanseni* Jenkins and Gehling 1978, by original designation and monotypy.

Phyllozoon hanseni Jenkins and Gehling 1978

figs 5–8, S1, S3–S4.

1978 *Phyllozoon hanseni* Jenkins and Gehling, p. 357–358, fig. 7.

1991 *Phyllozoon hanseni* Jenkins and Gehling; Gehling, pl. 3, fig. 2.

1992 *Phyllozoon* Jenkins and Gehling; Runnegar, fig. 3.10.

1994 *Phyllozoon hanseni* Jenkins and Gehling; Runnegar, fig. 3.

2003 *Phyllozoon hanseni* Jenkins and Gehling; Seilacher, Grazhdankin and Legouta, p. 45–46, fig. 5.

2005 *Phyllozoon* Jenkins and Gehling; Gehling, Dro-

ser, Jensen and Runnegar, p. 51, fig. 5.

2005 *Phyllozoon* Jenkins and Gehling; Seilacher, Bua-tois and Mángano, pp. 328–329, fig. 4.

2007 *Phyllozoon* Jenkins and Gehling; Seilacher, p. 178, pl. 62.

2007 *Phyllozoon hanseni* Jenkins and Gehling; Jenkins and Nedin, p. 209, fig. 8c.

2007 *Phyllozoon hanseni* Jenkins and Gehling; Retallack, p. 17, fig. 7.

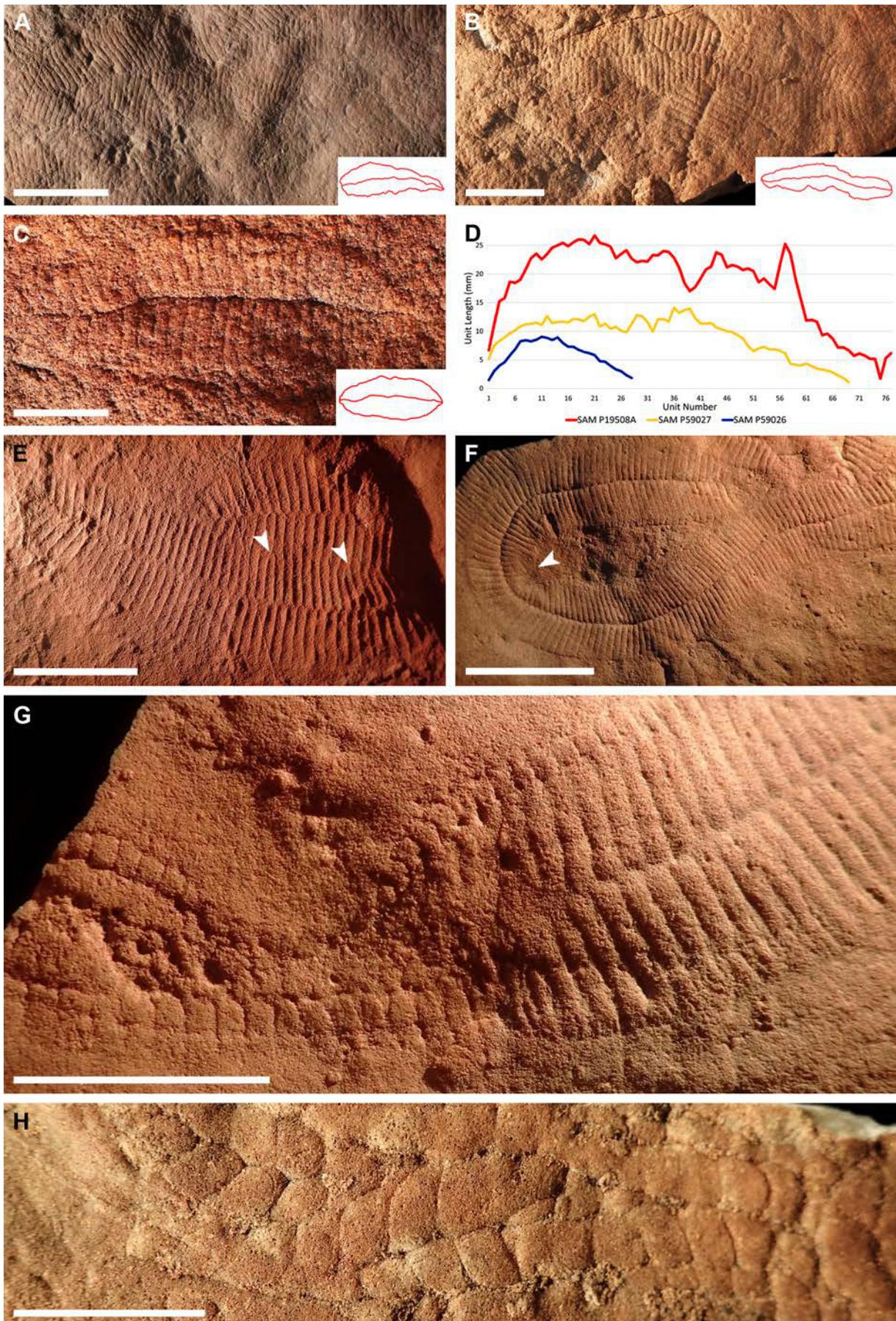
Material: SAM P19508A (holotype, Fig. 3A) and P19508B–C (paratypes), all on same slab, Nilpena Sandstone Member, Rawnsley Quartzite, Devil's Peak, south of Quorn, southern Flinders Ranges (Jenkins and Gehling 1978, fig. 7). Additional 30 specimens in the SAM collections from Bathtub Gorge, Tooth Knob, Nilpena Ediacara National Park and Chace Range (pers. obs.).

Diagnosis: “Fronde leaf-like, resembling *Pteridinium simplex* in its incised zig-zag median line and almost evenly-spaced, repetitive lateral grooves, but differing in that the organism was evidently more or less of planar or two dimensional form, not with three wings extending from the axis; incised axis and lateral grooves evidently representing a resistive skeleton which lay in foliate base of frond; lateral grooves extending from axis at about 70°, with their ends curved outwards; spacing of grooves tending to become less at (?) proximal end of frond.” (Jenkins and Gehling 1978, p. 357).

Description: *Phyllozoon hanseni* is an elongate, frond-like, soft-bodied fossil impression. Specimens range from just under 50 mm to more than 250 mm in length, and 20–40 mm wide, occasionally reaching up to 50 mm wide. The fossil generally consists of serially-arranged, hemicylindrical units that meet the axis at a regular sawtooth junction, displaying glide-reflection symmetry. *P. hanseni* has two termini that are morphologically distinct, with one made up of thicker units preserved at acute angles to the axis, transitioning gradually to the other end consisting of gradually thinner, shorter units arranged largely perpendicular to the axis.

Results

The holotype, South Australian Museum SAM P19508A (Fig. 3A), displays a complete specimen connected to what is here interpreted as an overlying partial specimen but could be mistaken for a case of branching, which is not observed in other specimens. Complete spe-



cimens where all the units are measurable are uncommon. The holotype was measured, along with another two complete and much smaller specimens, SAM P59027 (Fig. 3B) and SAM P59026 (Fig. 3C). From the measurement of these 3 full-length profiles (Fig. 3D), a consistent profile can be recognised, with unit length showing a steep increase at the spoon end, remaining similar for most of the trunk before showing a gradual decrease in unit length at about two thirds along the full profile to the knife.

Specimens SAM P35687–8 show what appears to be merging of units between the two adjacent individuals (arrows, Fig. 3E). On another slab, SAM P57687 is a significantly curved specimen that shows unit expansion and compression, with ‘lifting’ on the inside of the bend (arrow, Fig. 3F), in what appears to be a separation from the microbial mat in the seafloor, and thus lack of preservation. There is also one specimen that shows what could be interpreted as budding of globular chains at the edge of units along a consistent cleavage plane (SAM P59025, Fig. 3G) which has superficial resemblance to *Fumisia* (Fig. 3H).

A histogram of specimen lengths was produced (Fig. 4A) for 17 individuals that were objectively measurable along full length and width of the specimen, preserved in context. Using a Shapiro-Wilk normality test (Shapiro and Wilk, 1965) of the specimen lengths produces a non-normal distribution ($n = 17$, $M = 231$ mm, $W = 0.77$, $p = 0.0009$), with a negative skew. Other analyses found a positive relationship ($n = 17$, $R^2 = 0.58$, $p < 0.0001$) between the specimen length and unit number (Fig. 4B) when fitted to a robust generalised linear model with Poisson variance function. The plot in

Figure 4C displays a positive linear relationship between specimen length and specimen width ($n = 17$, $R^2 = 0.39$, $p = 0.007$) based on a reduced major axis (model II) regression. Further characterisation of the spoon and knife was pursued, so unit length, width, and Θ angle (Fig. 2) of ten of each were measured for 25 units from the terminus and plotted graphically (Fig. 5). Generalised additive mixed model analysis, with individual specimen variation characterised as random effects, demonstrated monotonic but non-linear patterns across units for each length or angle measure in both the spoon and knife. The exception was for the angle measurement for the knife (Fig. 5F), which decreased linearly across units, despite appearing to hold a lower angle threshold of around 90° to the axis.

Discussion

There is considerable literature on the environmental setting of the South Australian Ediacara Biota in general (e.g. Gehling and Droser, 2012; Reid *et al.* 2020), with some focused on the units where *Phyllozoon* has been collected (Gehling *et al.*, 2019). The consensus around these units is that it was a shallow marine environment where, despite abundant energy, there was enough time for the microbial mat to grow and upon burial, via early permineralization, replicate the soft-bodied organisms on those seafloors and its sedimentary structures, like ripples, which should otherwise be scoured away by the very currents that formed them (Tarhan *et al.*, 2017). Like with many other Ediacaran taxa, there is some debate as to what exactly *P. hanseni* was, although most seem to agree that it was closely related to *Pteridinium* Gürich, 1933

Figura 3. *Phyllozoon hanseni* Jenkins y Gehling 1978, del Ediacárico de la Sierra de Flinders, Australia del Sur. **A)** Vista completa del holotipo SAM P19508A (Escala: 50 mm); **B)** Vista completa de SAM P59027 y P59028 (Escala: 25 mm); **C)** Vista completa de SAM P59026 (Escala: 10 mm); **D)** Diagrama mostrando la variación de longitud de las unidades, a lo largo del perfil de los tres ejemplares de *P. hanseni* en Figs 3A, B y C; **E)** Molde de látex de SAM P35687 y SAM P 35688, mostrando las unidades fusionadas (flechas) entre estos dos ejemplares (Escala: 25 mm); **F)** Ejemplar SAM P57687, con unidades difusas (flecha, elevadas sobre el tapiz microbiano) en el borde interior (Escala: 50 mm); **G)** Gemas globulares concatenadas, formadas en el extremo distal de las unidades corporales del ejemplar SAM P59026 (Escala: 25 mm); **H)** Unidades globulares concatenadas de *Fumisia* SAM P42371, para comparación con Fig. 3G (Escala: 25 mm) / **Figure 3.** *Phyllozoon hanseni* Jenkins and Gehling 1978, from the Ediacaran of the Flinders Ranges, South Australia. **A)** Full length photograph of holotype SAM P19508A (Scale Bar: 50 mm); **B)** Full length photograph of SAM P59027 and P59028 (Scale Bar: 25 mm); **C)** Full length photograph of SAM P59026 (Scale Bar: 10 mm); **D)** Diagram illustrating unit length changes along the profile of the three specimens of *P. hanseni* from Figures 3A, 3B, and 3C; **E)** Latex mould of SAM P35687 and SAM P 35688, displaying merged units (arrows) between these two specimens (Scale Bar: 25 mm); **F)** Large, curved specimen SAM P57687, with diffuse units (arrow, lifted above the microbial mat) in the inside edge of the bend (Scale Bar: 50 mm); **G)** Chained budding features forming along the distal end of body units on specimen SAM P59026 (Scale Bar: 25 mm); **H)** Globular chained segments of *Fumisia* SAM P42371, for comparison with Fig. 3G (Scale Bar: 25 mm).

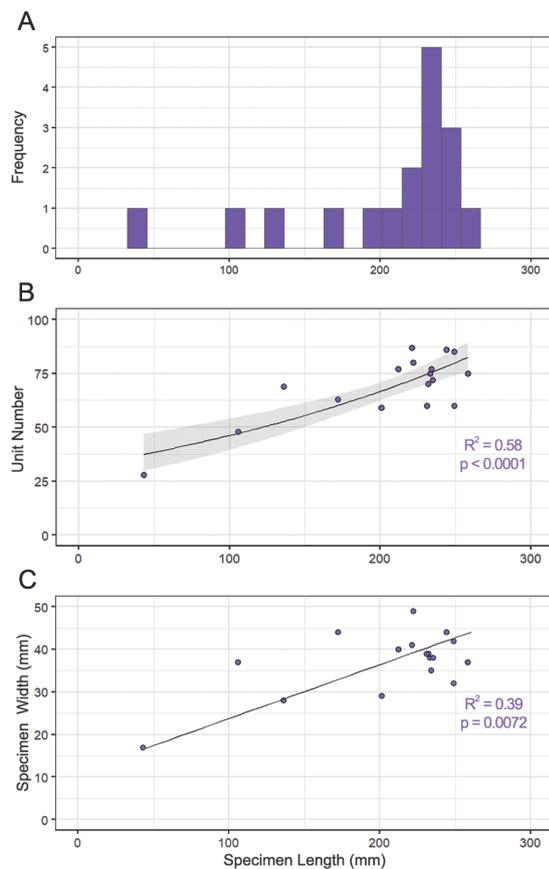


Figura 4. A) Histograma que muestra la distribución no-normalizada y de sesgo negativo ($M = 231$ mm, $W = 0.77$, $p = 0.0009$) de los 17 ejemplares completos medidos de *P. hanseni*; **B)** Gráfico de dispersión que muestra una correlación positiva entre la longitud del ejemplar y el número de unidades basado en modelo lineal generalizado robusto ($n = 17$, intervalo de confianza representado en gris); **C)** Gráfico de dispersión que muestra longitud frente a anchura de los ejemplares ($n = 17$) basado en una regresión de modelo II (errores en ambas variables). / **Figure 4. A)** Histogram displaying the non-normal, negative-skewed size distribution ($M = 231$ mm, $W = 0.77$, $p = 0.0009$) of the 17 *P. hanseni* specimens measured; **B)** Scatter plot showing a positive relationship between specimen length and unit number based on a robust generalised linear model ($n = 17$, 95% confidence interval represented in grey); **C)** Scatter plot mapping specimen length against specimen width ($n = 17$) based on a model II regression (errors in both variables).

and *Ernietta* Pflug, 1966, members of the Nama Assemblage from Namibia, partially due to the similarities in quilt-like units, and despite the 3-dimensional preservation mode of the latter (Elliott *et al.*, 2016). This would place *Phyllozoon* within the Erniettomorpha (Pflug, 1972). Higher-level phylogenetic affiliation for *Phyllozoon*, as with a number of Ediacara Biota members, remains undetermined, and falls outside the scope of this paper. However, an interesting

feature recognised here for the first time, which could be of some phylogenetic value, is that the body units in *P. hanseni* always start on the same side: left of the hyporelief fossil (right side in life), as we look from knife to spoon (Fig. 2), implying that *Phyllozoon* started from the spoon end and added units on the knife end.

There are some novel features of interest (Fig. 3) which may present several appropriate directions for future research. Firstly, the junction on SAM P19508A (Fig. 3A) should be investigated in detail, as although interpreted as a partial specimen overlap, further analysis should allow to totally refute a case of branching. Additionally, a study of new material as it becomes available could provide insight as to whether the merged units between specimens SAM P35687 and SAM P35688 (Fig. 3E) is an element of chance or a biological feature, where fusion of units from independent specimens occurs. The chains trailing from the edges of *Phyllozoon* on SAM P59025 (Fig. 3G) should also be further analysed and compared with specimens of the resembling *Funisia* (Fig. 3H). This taxon varies widely in size, and as mentioned earlier, shares the same positive hyporelief preservation, while also being known from wave-base and sheet-flow sands facies, in which *Phyllozoon* and ‘*Aulozoon*’ also occur (Reid *et al.*, 2020).

A negatively skewed, non-normal distribution was produced by the specimen length data (Fig. 4A), although some of this may be a result of preservation or collection bias, as larger specimens may have a better preservation potential. Figure 4B seems to suggest that *P. hanseni* grows by increasing both unit number and size which could prove useful as a predictor in similar future analyses of many more partial specimens and could be further developed upon recording more full-length specimens of different size ranges unearthed through future excavations. Figure 4C corroborates observations that it also grows only a fraction wider through its lifetime, but substantially longer. This information has the potential to yield further insights about mode of life. The spoon and knife generalised additive mixed model analyses (Fig. 5) illustrate a stark contrast between the spoon’s rounded form and the knife’s linearity, which could speak of physical or structural constraints within the body plan of these organisms. Perhaps some level of turgor or rigidity held smaller knife-ward units straight out perpendicular to the longitudinal axis. These trends could also hold functional implications: as *P. hanseni* was a benthic organism, the elongated teardrop sha-

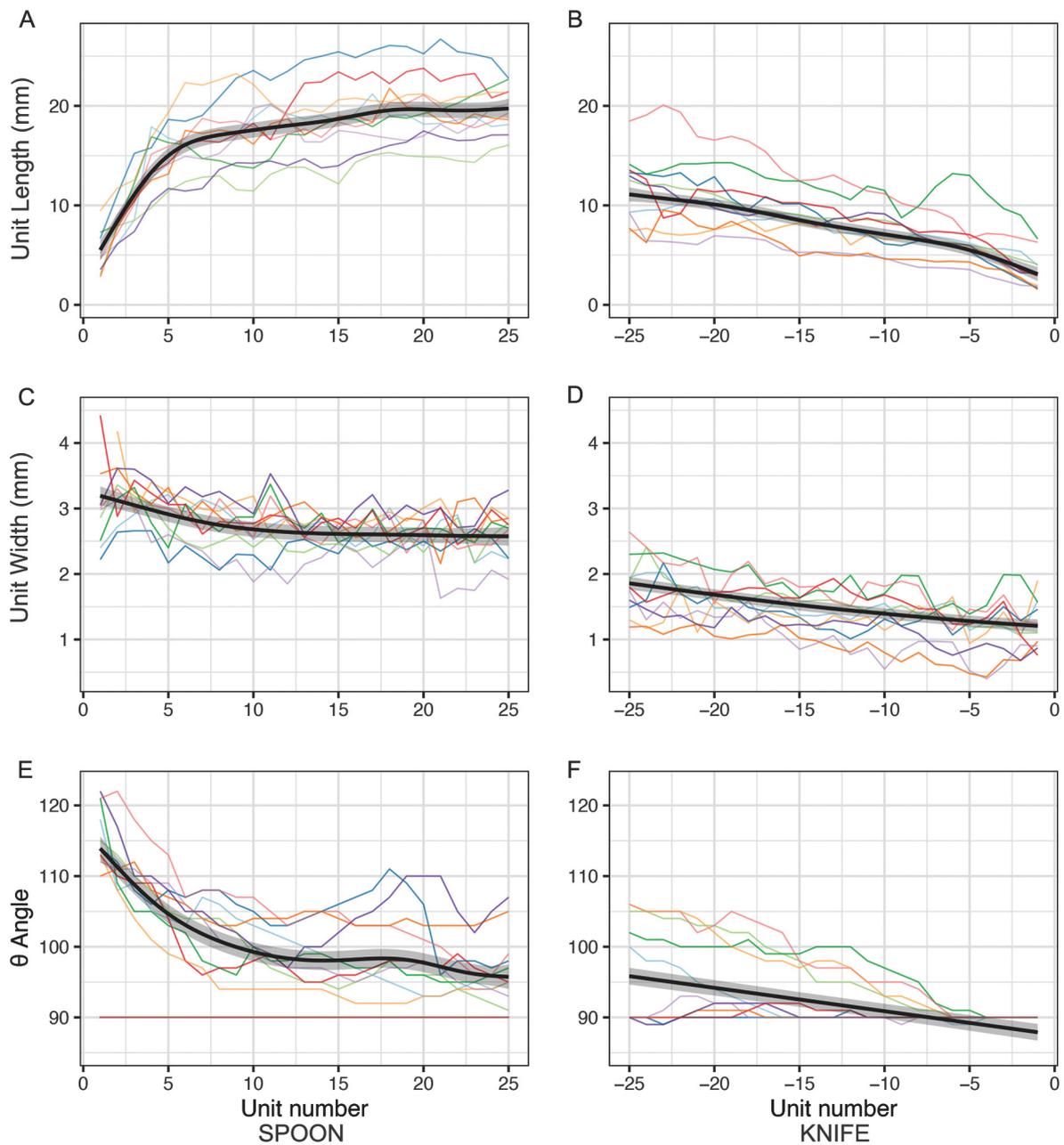


Figura 5. Gráficos del modelo mixto acumulativo generalizado de: **A)** Longitud de las primeras 25 unidades de la ‘cuchara’ de 10 ejemplares; **B)** Longitud de las últimas 25 unidades del ‘cuchillo’ de 10 ejemplares; **C)** Ancho de las primeras 25 unidades de la ‘cuchara’ de 10 ejemplares; **D)** Ancho de las últimas 25 unidades del ‘cuchillo’ de 10 ejemplares; **E)** Ángulo de las primeras 25 unidades de la ‘cuchara’ de 10 ejemplares; **F)** Ángulo de las últimas 25 unidades del ‘cuchillo’ de 10 ejemplares; línea marrón en E y F indica 90° respecto al eje sagital de *P. banseni*. / **Figure 5.** Generalised additive mixed model plot of: **A)** Length of the first 25 ‘spoon’ units of 10 specimens; **B)** Length of the last 25 ‘knife’ units of 10 specimens; **C)** Width of the first 25 ‘spoon’ units of 10 specimens; **D)** Width of the last 25 ‘knife’ units of 10 specimens; **E)** Angle of the first 25 ‘spoon’ units of 10 specimens; **F)** Angle of the last 25 ‘knife’ units of 10 specimens; brown line in E and F indicates 90° to the sagittal axis of *P. banseni*.

pe — the rounded spoon —, steadily tapering toward the knife could have reduced turbulence and pressure drag, so that currents had less chance of damaging delicate structures, while the bulbous spoon end could provide a larger surface area to serve as anchor.

Conclusion

This preliminary study on *Phyllozoon banseni* has provided new information on this relatively rare Ediacaran taxon, only known from Australia. From a literature review, first-hand

analysis of the fossils, to the features and measurements photographed and documented, this investigation posits that *P. hansenii* was possibly a benthic organism, despite lacking a singular central holdfast. It may have been made of a soft tubule matrix and may have reproduced by budding from these units/tubules. With the superficial similarities between these budding units with *Funisia*, their shared positive hyporelief preservation and shared presence in the wave-base and sheet flow sands facies, there may be some relationship between the two taxa yet to be realised. *Phyllozoon* grew from the oldest spoon region to the youngest knife region, adding units consecutively at the knife tip. Some individual specimens recorded more than 50 mm wide and longer than 300 mm, and as they grew in total length, they grew in unit number, and as units grew in length, they also grew slightly thicker. Most interestingly, the organism's width appears to be far more tightly constrained than its body length, with specimen widths appearing to grow towards a threshold. New material is being unearthed every year, particularly from the Nilpena site and will undoubtedly continue to provide further insights into the morphology of *Phyllozoon hansenii*.

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References

- Droser, M.L., Tarhan, L.G., Gehling, J.G. 2017. The Rise of Animals in a Changing Environment: Global Ecological Innovation in the Late Ediacaran. *Annual Review of Earth and Planetary Sciences*, 45: 593-617.
- Elliott, D.A., Trusler, P.W., Narbonne, G.M., Vickers-Rich, P., Morton, N., Hall, M., Hoffmann, K.H., Schneider, G.I.C. 2016. *Ernietta* from the late Ediacaran Nama Group, Namibia. *Journal of Paleontology*, 90 (6): 1017-1026.
- Gehling, J.G. 1991. The case for Ediacaran fossil roots to the metazoan tree. *Geological Society of India Memoir*, 20: 181-224.
- Gehling, J.G. 1999. Microbial Mats in Terminal Proterozoic Siliciclastics: Ediacaran Death Masks. *Palaiois*, 14: 40-57.
- Gehling, J.G., Droser, M.L., Jensen, S.R., Runnegar, B. 2005. Ediacaran organisms: relating form and function. In *Evolving Form and Function: Fossils and Development*, Proceedings of a symposium honoring Adolf Seilacher for his contributions to palaeontology, in celebration of his 80th birthday (ed. D.E.G. Briggs), pp. 43-67. New Haven: Peabody Museum of Natural History, Yale University.
- Gehling, J.G., Droser, M.L. 2012. Ediacaran stratigraphy and the biota of the Adelaide Geosyncline, South Australia. *Episodes*, 35 (1): 236-246.
- Gehling, J.G., García-Bellido, D.C., Droser, M.L., Tarhan, M.L. & Runnegar, B. 2019. The Ediacaran-Cambrian transition: sedimentary facies versus extinction. *Estudios Geológicos* (Madrid), 75 (2): 99.
- Gürich, G. 1933. Die Kuibis-Fossilien der Nama-Formation von Südwestafrika. *Paläontologische Zeitschrift* 15, 137-154.
- Ivantsov, A.Y. 2013. Trace Fossils of Precambrian Metazoans "Vendobionta" and "Mollusks". *Stratigraphy and Geological Correlation*, 21 (3): 252-264.
- Jenkins, R.J., Gehling, J.G. 1978. A review of the frond-like fossils of the Ediacara assemblage. *Records of the South Australian Museum*, 17: 347-359.
- Jenkins, R.J.F., Nedin, C. 2007. The provenance and palaeobiology of a new multi-vented, chambered frondose organism from the Ediacaran (later Neoproterozoic) of South Australia. *Geological Society of London, Special Publication*, 286: 195-222.
- Pflug, H.D. 1966. Neue Fossilreste aus den Nama-Schichten in Südwest-Afrika. *Paläontologische Zeitschrift*, 40: 14-25.
- Pflug H.D. 1972. Zur Fauna der Nama-Schichten in Südwest-Afrika. III. Erniettomorpha, Bau und Systematik. *Palaentographica* A139: 134-170.
- R Core Team 2021. R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*.

- Reid, L.M., Holmes, J.D., Payne, J.L., García-Bellido, D.C., Jago, J.B. 2020. Taxa, turnover and taphofacies: a preliminary analysis of facies-assemblage relationships in the Ediacara Member (Flinders Ranges, South Australia). *Australian Journal of Earth Sciences*, 67: 905-914.
- Retallack, G.J. 2007. Growth, decay and burial compaction of *Dickinsonia*, an iconic Ediacaran fossil. *Alcheringa: An Australasian Journal of Palaeontology*, 31: 215-240.
- Retallack, G.J. 2013. Ediacaran life on land. *Nature*, 493: 89-92.
- Runnegar, B. 1992. Evolution of the earliest animals. In *Major Events in the history of life* (ed. J.W. Schopf), pp. 65-93, Boston: Jones and Bartlett.
- Runnegar, B. 1994. Proterozoic eukaryotes: evidence from biology and geology. In *Early life on Earth*, Nobel Symposium No. 84 (ed. S. Bengtson), pp. 287-297. New York: Columbia University Press.
- Seilacher, A., Grazhdankin, D., Legouta, A. 2003. Ediacaran biota: the dawn of animal life in the shadow of giant protists. *Paleontological Research*, 7: 43-54.
- Seilacher, A., Buatois, L.A., Mángano, G. 2005. Trace fossils in the Ediacaran–Cambrian transition: behavioral diversification, ecological turnover and environmental shift. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 227: 323-356.
- Seilacher, A., 2007. *Trace Fossil Analysis*, Berlin and Heidelberg: Springer-Verlag, 226 pp.
- Shapiro, S.S., Wilk, M.B. 1965. An analysis of variance test for normality (complete samples). *Biometrika*, 52 (3–4), 591-611.
- Tarhan, L.G., Droser, M.L., Gehling, J.G., Dzaugis, M.P. 2017. Microbial Mat Sandwiches and other an-actualistic sedimentary features of the Ediacara Member (Rawnsley Quartzite, South Australia): Implications for interpretation of the Ediacaran sedimentary record. *Palaios*, 32: 181-194.

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