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UNIVERSITY OF CALIFORNIA
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First to Float: Investigating the Taphonomy and
Morphology of *Attenborites janae* From the Nilpena
Ediacara National Park

A Thesis submitted in partial satisfaction of the
requirements for the degree of

Master of Science

in

Earth and Planetary Sciences

by

Heather Kaitlin McCandless

June 2022

Thesis Committee:
Dr. Mary Droser, Chairperson
Dr. Richard Minnich
Dr. Nigel Hughes

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The Thesis of Heather Kaitlin McCandless is approved:

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This research was conducted on land that lies within the Adnyamathanha Traditional Lands. Thank you to Ross and Jane Fargher who own the property housing the Nilpena Ediacara National Park for access to the fossil site and for support during field work. Field work for this project was facilitated by M.L. Droser, S. Evans, P.C. Boan, I. Hughes, and E. Hughes. Thank you to R.L. Surprenant and P.C. Boan for reviewing the presentations of this research, both written and oral, and for being such supportive labmates. Thank you also to S. Srivastava for providing moral support both on campus and during conversations over the kitchen counter. I would also like to acknowledge my committee members for their reviews and their mentorship over the past two years.

Dedication

This manuscript is dedicated to my parents, Bob and Cari McCandless, who always believed that I could be a scientist.

ABSTRACT OF THE THESIS

First to Float: Investigating the Taphonomy and
Morphology of *Attenborites janae* From the Nilpena
Ediacara National Park

by

Heather Kaitlin McCandless

Master of Science, Graduate Program in Earth and Planetary Sciences
University of California, Riverside, June 2022
Dr. Mary Droser, Chairperson

The Ediacaran fossil taxon *Attenborites janae* was originally excavated in 2017 from the Ediacara Member of the Nilpena Ediacara National Park (Nilpena, Droser et al, 2018). *Attenborites* was described as a potentially pelagic organism that had undergone deflation during preservation. This thesis tests this hypothesis by examining the taphonomy and preservational morphology of *Attenborites* using an additional 55 specimens recently excavated from Nilpena. The life habit of *Attenborites* is determined by comparing the characteristics of known benthic Ediacaran organisms and evaluating the preservational morphology and taphonomy of *Attenborites* according to criteria for the preservation of early soft-bodied pelagic forms put forth by Young and Hagadorn (2010). It is concluded that *Attenborites* was most likely a pelagic organism, consistent

with findings in the original description of *Attenborites*. This taxon is thus the first known macroscopic inhabitant of the pelagic realm. In identifying the life habit of *Attenborites*, criteria for identifying the preservation of Ediacaran pelagic taxa in the fossil record were created.

This thesis was focuses on developing methods for the retrodeformation of deflated taxa and characterization of the *in vivo* morphology of *Attenborites janae*. Laser scans taken of the fossils in the field were simulated to inflate using the 3D modeling software Blender. This is a novel effort because no soft-bodied fossil taxon has ever been retrodeformed. This approach led to the characterization of then-living *Attenborites* as ellipsoid forms with relatively smooth surfaces and confirmed that the ridges found within the fossils are taphonomic features formed during deflation rather than true morphological features.

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Chapter 1: Characterizing the taphonomy and life habit of *Attenborites janae*

I. Introduction

Fossils of the Ediacara Biota (575-542ma) represent the oldest macroscopic, multicellular organisms on Earth, and their record is replete with abundant specimens and diverse taxa that provide evidence on the evolution of key metazoan developments such as mobility, scavenging, bilateral symmetry, and sexual reproduction (Darroch et al, 2018; Erwin et al, 2011; Xiao and LaFlamme, 2009; Evans et al, 2019A; Evans et al, 2020; Gehling and Droser, 2018; Droser and Gehling, 2008). The Ediacara Biota also contains the first macroscopic community-forming taxa and thus represents the first step in the development of modern-style ecosystems (Darroch et al 2018; Erwin et al, 2011; Coutts et al, 2016). Because the Ediacara Biota represent such a fundamental evolutionary step between simple and complex ecosystems, characterizing the advent and fate of these early organisms and their communities in the Ediacaran Period is critical to understanding the development of Phanerozoic-style ecosystems and the phylogenetic origin of metazoan life.

While multiple major evolutionary innovations are documented during the Ediacaran Period, there has been debate and uncertainty surrounding whether the origin of pelagic macrofauna occurred during the Ediacaran Period (Gehling, 1991; McCall, 2006). The pelagic ocean is volumetrically the largest ecosystem on Earth and is filled with diverse organisms adapted for life within the water column, and the development of the pelagic realm played a major role in establishing Earth's biogeochemical cycles (Henehan et al, 2016; Logan et al, 1995; Logan et al, 1997). Although the pelagic realm

comprises a large portion of Earth and its life history, the nature of early macroscopic pelagic life remains elusive. It is known that a diverse metazoan pelagic fauna was present by the Cambrian Period (541mya), as recorded by carbonaceous compression lagerstätten, including the Burgess Shale, but the nature of pelagic ecosystems during the late Ediacaran Period (574-541mya) is unknown (Hagadorn et al, 2002; Vinther et al, 2014; Cartwright et al, 2007; Conway Morris, 1979).

Wide geographic ranges and settlement patterns of some benthic Ediacaran organisms strongly suggest that microscopic dispersive larvae were likely inhabiting the pelagic realm during the Ediacaran Period (Mitchell et al, 2020; Zakrevskaya, 2014; Peterson, 2005; Darroch et al, 2013). Many of the Ediacaran biota are interpreted as suspension feeders; hence life in the water column was sufficient to serve as a dependable food source (Gibson et al, 2019; Raham et al, 2015; Cracknell et al, 2021; Clapham and Narbonne, 2002; Jenkins et al, 2007). Moreover, the presence of a well-developed Cambrian pelagic macrofauna along with molecular clock placement of the origin of pelagic medusoids in the Ediacaran have created pressure to identify which of the Ediacaran biota were the first large pelagic organisms (Gold et al, 2018; Peterson et al, 2005; Peterson et al, 2004; Peterson et al, 2008). These disparate lines of evidence have led many to conjecture about the ecological affinity of multiple members of the Ediacara Biota that share morphological similarities to Cambrian medusoids, but no such pelagic taxa have been definitively described.

Members of the Ediacara Biota are fundamentally difficult to characterize based solely on morphology due to their enigmatic and non-analogous form compared to

modern organisms (Tarhan et al, 2010; Hall et al, 2015; Darroch et al, 2017; Meyer et al, 2012). Investigations of ecological affinity must therefore be based in both taphonomy, functional interpretation, and sedimentology rather than morphological similarity to Cambrian taxa. Because taphonomy has been largely ignored in the identification of potentially pelagic taxa, several Ediacaran organisms have been proposed as pelagic, only to be later be classified as benthic (Sprigg, 1947; Signor and Vermeij, 1994; Glaessner, 1984; Gehling et al, 2003). For example, *Aspidella* and *Mawsonites*, circular Ediacaran fossils ranging in size from centimeters to tens of centimeters in diameter, have both been assigned to multiple taxonomic affinities, including pelagic medusoids, based on morphological similarity to jellyfish (Hsu, 1972; Glaessner and Wade, 1966). *Aspidella* was later described as the holdfasts of a frondose benthic organism, and the ecological affinity of *Mawsonites* remains contested (Tarhan et al, 2010; Gehling et al, 2003; Runnegar and Schopf, 1992). The lack of established methods for using taphonomic and associated sedimentological data of Ediacaran fossils to interpret ecological modes has led to a research landscape of continuous debate over the life habits Ediacaran organisms based on non-uniform and often non-comparable lines of evidence, with focus on morphological similarity to Cambrian medusoids (Tang et al, 2011; Zhu et al, 2008; Gehling, 1991; McCall, 2006).

An Ediacaran fossil that was recently proposed to represent a soft-bodied pelagic organism (Droser et al, 2018). This thesis presents a detailed examination of the taphonomy, associated sedimentology, and morphology of *Attenborites janae* to determine this taxon's life habit. Investigations into the ecological affinity of *Attenborites*

are informed by the initial paper describing *Attenborites* (Droser et al, 2018), criteria developed for the preservation of pelagic Cambrian medusoids (Young and Hagadorn, 2010), and comparison of the taphonomy of *Attenborites* to known benthic Ediacaran organisms whose taphonomy has been well-characterized (Hall et al, 2015; Evans et al, 2019A). Developing methods to characterize the life habit of *Attenborites* led to the creation of Ediacaran-specific criteria describing the preservation of Ediacaran pelagic taxa. These Ediacaran-specific criteria are necessary due to the unique preservation style of the Ediacaran facilitated by widespread organic mats that largely disappeared by the Cambrian (Gehling, 1999; Buatois et al, 2014). The ongoing debate and uncertainty surrounding the identity of the oldest pelagic organisms speaks to the exigency in the development of such criteria founded in taphonomic examinations rather than in morphological similarity to Cambrian pelagic forms. This thesis aims to resolve the lack of established methods for using the preservation and enclosing sedimentology of Ediacaran fossils in conjunction with their fossil morphology to interpret their life habit. In additions, methods are created to constrain the origin of the first pelagic macrofauna and give insight into the origin and development of both complex Phanerozoic-style macroscopic communities and the pelagic realm.

II. *Attenborites janae*

Attenborites specimens are preserved as irregular, discoidal, fossil that range from 3-17mm in length (Figure 1.1). This fossil represents a monospecific taxon and is only found in the Ediacara Member in South Australia. It is always preserved as a cast in

negative hyporelief on the base of fine-grained sandstone beds from the Ediacara Member of the Rawnsley quartzite at the Nilpena Ediacara National Park (Nilpena).



Figure 1.1. Fossil *Attenborites janae* from the Nilpena Ediacara National Park. A-C show specimens with converging, non-uniform ridges. D shows a specimen with no ridges preserved. E shows a specimen with parallel ridges. Scale bar 5mm.

The bedding plane preserving all but 2 specimens of *Attenborites* was first excavated in 2017, leading to the discovery of this fossil. The description of *Attenborites* was subsequently published in 2018 (Droser et al, 2018). After additional excavation in 2018, a total of 89 *Attenborites* specimens were documented on bed TB-ARB, with 13 more of those specimens preserved on float pieces associated with this bed. There are only two other *Attenborites* fossils known from Nilpena, one each on bedding planes 1T-F and 1T-F Annex.

The original description of *Attenborites* focuses describing the then newly-discovered taxon, paying specific attention to the unique parallel and subparallel longitudinal internal ridges that typically converge towards one end of the specimens (Figure 1.1A-C). The ridges are confined within the outer margin of all specimens, and preserved cast tissue of *Attenborites* is smooth between ridges and does not reflect detail

or topography of underlying textured organic surface (TOS) created by the fossilized organic mat.

There is no consistent external or internal symmetry among *Attenborites* as the outline shape, number of ridges, and orientation of ridges within *Attenborites* specimens lacks consistent uniformity of preservation (Figure 1.1). Some specimens exhibit ridges that converge towards one end of the specimen while others have parallel, non-converging ridges (Figure 1.1E). Additionally, the number of ridges preserved ranges from 0-19, with some not displaying ridges at all (Figure 1.1D). The degree of variation in ridges across samples led previous researchers to hypothesize that these structures may be evidence of deflation of *Attenborites* upon death and/or burial; hence this fossil represents a deflated version of the living organism's morphology (Droser et al, 2018).

Consistent with this hypothesis, the initial descriptive study suggests that *Attenborites* may represent a pelagic organism (Figure 1.2A) rather than a benthic organism (Figure 1.2B) based on preliminary data describing its taphonomy and morphology (Droser et al 2018). Using an additional 55 *Attenborites* specimens excavated since the initial descriptive study, this thesis examines the morphology and taphonomy of the taxon in greater detail, retesting the proposed hypothesis of a pelagic life habit for *Attenborites* with 104 specimens of *Attenborites jane*, effectively doubling the original sample size.

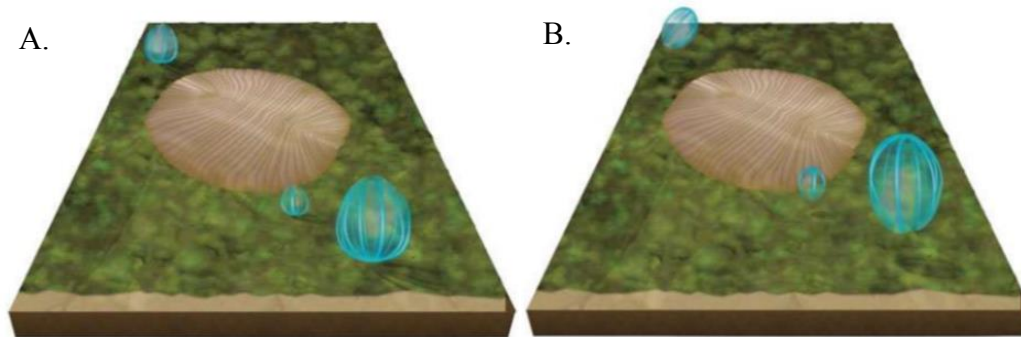


Figure 1.2. A: *Attenborites janae* reconstructed as a benthic organism with the long-axis oriented orthogonal to the mat. B: *Attenborites janae* reconstructed as a pelagic organism in the water column above the mat.

III. Geologic Setting

a. Nilpena Ediacara National Park

Specimens are from the Nilpena Ediacara National Park fossil site, South Australia, located West of the South Australian Flinders Ranges in the Ediacara member of the Rawnsley Quartzite (Figure 1.3; Coutts, 2009). The Rawnsley Quartzite is part of the Pound Subgroup, which contains a sandstone dominated siliciclastic sequence representing a shallow marine depositional environment (Figure 1.3B). The fossils are all ca.550my old, placing them within the White Sea assemblage of the Ediacara Biota (Droser et al, 2019).

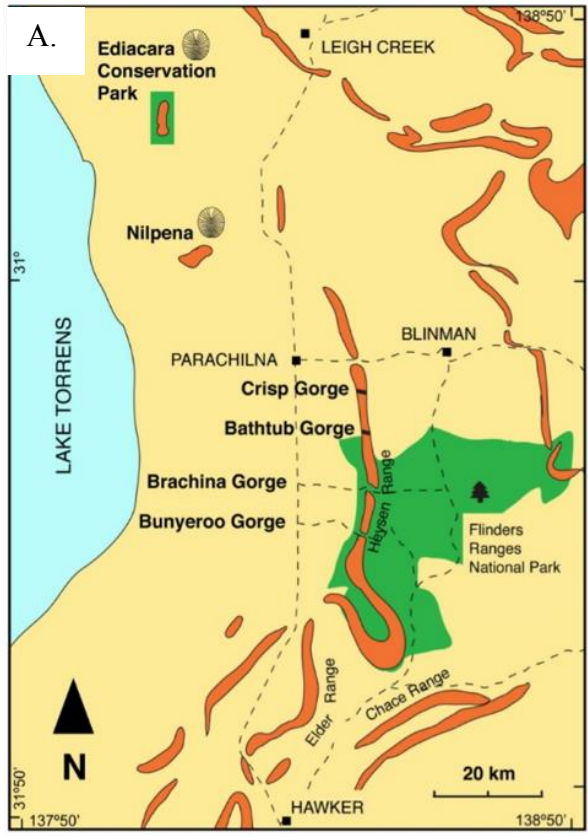
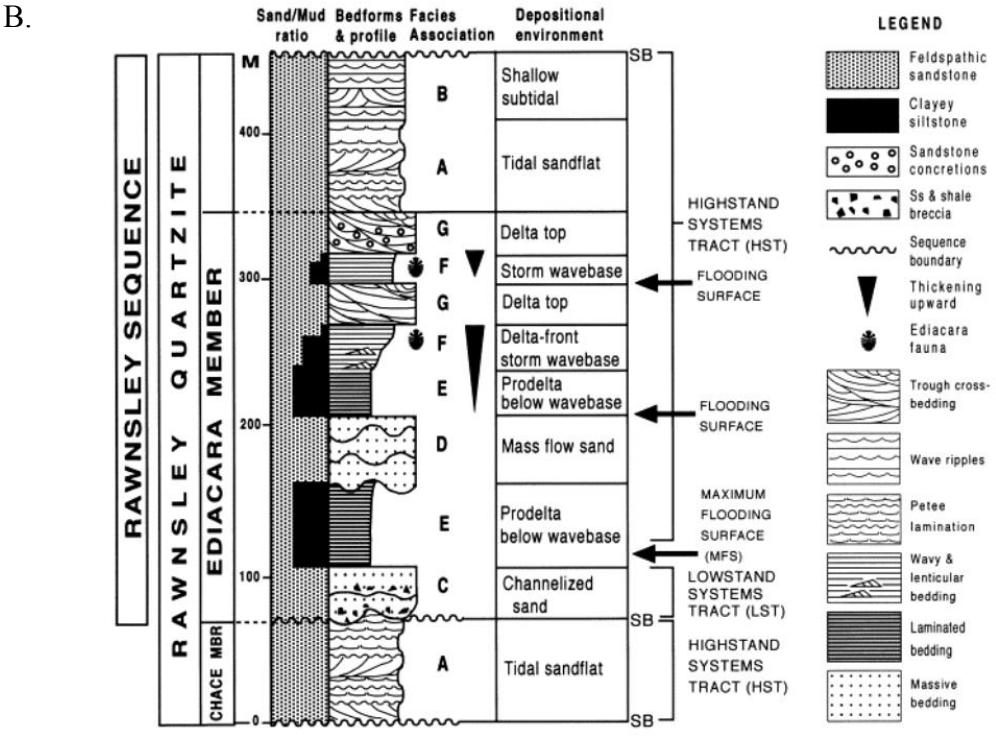
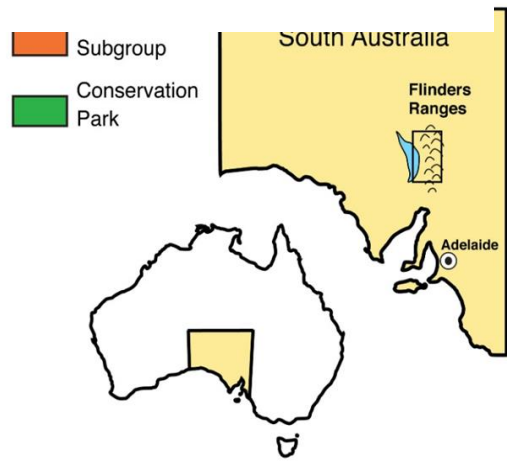


Figure 1.3. A: Flinders Ranges in South Australia denoting the Nilpena Ediacara National Park and the Pound subgroup in orange. Modified from Coutts, Gehling, and García-Bellido, 2009.

B: Stratigraphic column of the Rawnsley sequence showing the Ediacara Member (Gehling, 2000)



Fossils at Nilpena are preserved *in situ* as casts and molds on the underside of successive beds representing sediment deposited during individual storm events that smothered whole Ediacaran seafloor communities at once (Droser et al, 2019). These successive sandstone beds that remained distinct from one another due to the widespread organic mats covering the seafloors during the Ediacaran that grew over newly deposited sediment after each storm (Gehling, 1999). Forty of these discrete sandstone beds have been excavated and reconstructed, revealing successive snapshots of the Ediacaran organisms, their communities, and the widespread textured organic surface (TOS) representing a fossilized organic mat in ecological context.

The pelagic realm of the Ediacaran is difficult to characterize as modes of bed preservation at Nilpena are biased to preserve only the benthic environment in detail. It is therefore likely that preservation of pelagic Ediacaran organisms would only be rarely preserved in instances where they were swept up and buried during sediment deposition to be fossilized on the seafloor. Moreover, those rare preserved pelagic Ediacaran organisms must be distinguished from surrounding benthic taxa. Although the dearth of preserved soft-bodied pelagic taxa is not an issue unique to the Ediacaran Period (Valentine and Grubb, 1990; Hagadorn et al, 2002), identifying Ediacaran pelagic taxa is further complicated by the enigmatic nature of the Ediacara Biota that makes it difficult to distinguish pelagic organisms from their benthic fossil neighbors.

The extensive bedding planes at Nilpena facilitate the investigation of potential pelagic taxa because fossil preservation is in-tact and representative of the taxonomic and ecological record. Over the last 20 years, approximately 350m² of Ediacaran seafloor has

been uncovered through the excavation of 40 bedding planes from 4 distinct facies. An impression of the Ediacaran seafloor as it was 550mya is revealed by excavating the sandstone beds one at a time, flipping them over to reveal the fossiliferous surface underneath, and then piecing the beds back together. This excavation process keeps fossils in their original placement, allowing fossils to be examined through an ecological lense (Droser et al, 2019). Because this site has been extensively studied and documented, the overall taphonomy and sedimentology of the beds are well-constrained, providing the ideal opportunity to test the proposed hypotheses.

b. Fossil Bed Tb-ARB

Eighty-nine specimens of *Attenborites janae* are preserved on the singular bedding plane TB-ARB with 13 additional specimens preserved on discontinuous rock, or float, associated with that bedding plane. The mature mat growth on bed TB-ARB resulted in muted ripples on the bed surface, preventing clear interpretation of current direction. Additionally, taxa that usually indicate current direction, such as anchored, flexible macroalgae informally referred to as “Bundle of Fibers” (BOF) are not oriented in a consistent direction (Xiao et al, 2013). Lifted *Dickinsonia* do not exhibit consistent orientation (Evans et al, 2019B), and the taxon *Parvancorina* that is hypothesized to orient itself preferentially with the current are not aligned (Paterson et al., 2017). Thus, homogenous current direction cannot be determined (Evans et al, 2018).

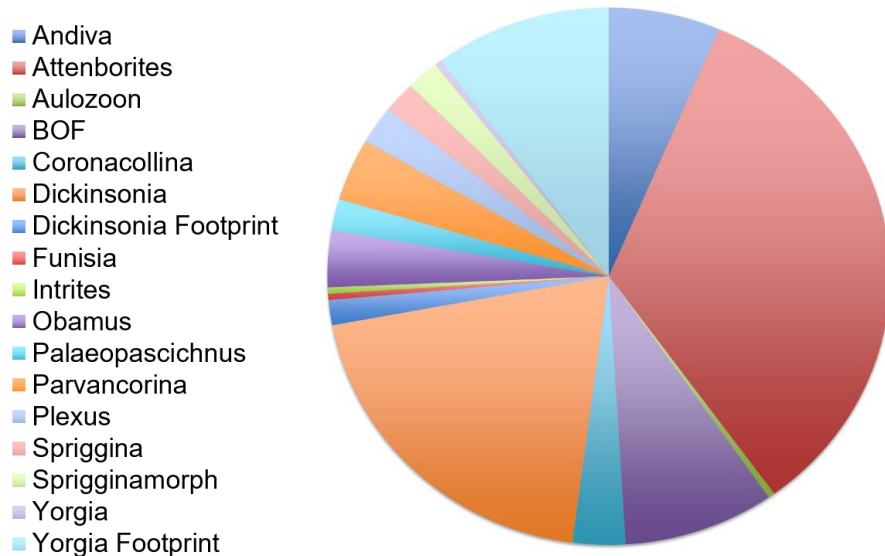


Figure 1.4. Pie chart showing the number and abundance of taxa preserved on TB-ARB. *Attenborites* dominates the bed, as shown in red.

An area of 8.62m² of bed TB-ARB was excavated from the TB site bedding sequence in 2017, including 49 specimens of *Attenborites*. The remaining portions of bed TB-ARB were excavated in 2018 for a total excavated bedding place area of 13.1m² (Evans et al, 2018). This bed preserves a mature Ediacaran community with well-developed TOS and little taphonomic disturbance. This bed also documents one of the most diverse Ediacaran ecosystems at Nilpena (Evans et al, 2018). Fifteen taxa preserved comprise a total of 265 specimens, 89 of which are *Attenborites* (Figure 1.4). This bed also has extraordinary preservational quality, allowing for the identification of sub-millimeter-scale features (Evans et al, 2018). The preservation of *Attenborites* at this level of detail, and the preservation of those specimens *in situ*, provides an ideal opportunity to characterize the taphonomy of *Attenborites janae*.

IV. Materials and Methods

a. Comparison with the initial descriptive study on *Attenborites*

The initial study describing *Attenborites* (Droser et al, 2018) also began characterizing and deciphering the taxon's life habit as put forth in two potential scenarios: a benthic organism with its long axis oriented orthogonally to the seafloor or a pelagic organism. This thesis examines an additional 55 specimens to test the likelihood of a pelagic life habit, and novel data collection techniques not employed in the initial description of *Attenborites* are used to develop more detailed and fine scale taphonomic investigations.

This study characterizes the taphonomy of *Attenborites* and tests whether the conclusions drawn in the initial descriptive paper have efficacy with a doubled sample size. The original 49 *Attenborites* specimens were found to be distinct from other Ediacaran taxa because they had an irregular morphology with no internal or external symmetry but were all consistently preserved with a sharply defined outer margin (Droser et al, 2018). Their preservation include *en masse* fossilization, lack of tentacles and lack of holdfast structures. The intent of the original descriptive study of *Attenborites* relied strictly on observations of the characteristics and variation of *Attenborites* specimens to put forth hypotheses about the taxon's likely life habit. With the inclusion of a newly excavated 55 specimens, the original pelagic hypothesis is tested here by empirically and thoroughly evaluating the properties of *Attenborites*.

b. Evaluation based on criteria for the preservation of Cambrian medusae

Young and Hagadorn (2010) developed criteria for recognizing preserved pelagic medusae specimens in the Cambrian fossil record by examining *bona fide* specimens of Cambrian medusae. This study marked the first attempt to develop criteria for the preservation of soft-bodied, pelagic organisms. While not all these criteria are relevant to the Ediacara Biota and the paleoenvironment of Nilpena, this study employs criteria relevant to the paleoenvironments and preservation of the Ediacara Biota to inform a determination of ecological affinity among Ediacaran organisms. These criteria include (1) rare preservation of tentacles, (2) variable preservational morphology when specimens are preserved via cast and mold, (3) appropriate paleoenvironment for pelagic organisms, (4) preservation of several individuals on a single horizon, (5) and evidence that specimens are body fossils rather than fossilized abiotic processes or trace fossils (Young and Hagadorn, 2010).

Criteria excluded due to differences between the Ediacaran and Cambrian include: pelagic organisms orienting dorsal side up, having partial sediment coverage oriented seaward, and shrinking due to dehydration resulting in distinctive wrinkle marks on the surrounding sediment (Young and Hagadorn, 2010). These preservational observations and criteria were created for intertidal preservational settings and are inapplicable to the subtidal preservational setting of Nilpena. Despite these differences, the relevant criteria for the preservation of Cambrian, pelagic, soft-bodied forms were used to investigate *Attenborites* and characterize its life habit.

c. Comparison with benthic Ediacaran taxa

This study compares *Attenborites* to known benthic Ediacaran organisms *Tribrachidium* and *Dickinsonia*. *Tribrachidium heraldicum* is a trilateral, circular, sessile benthic organism that ranges from 3-38mm in diameter (Hall et al, 2015). There are close to 300 total specimens of this taxon documented at Nilpena (Hall et al, 2015; Droser et al, 2019). *Tribrachidium* possesses an indistinct outer margin that lacks definition from the surrounding microbial mat, especially on beds with well-developed TOS (Figure 1.5A). The blurred outer margin indicates that *Tribrachidium* specimens spent enough time in one location that the mat grew up over the edges of the specimen. An indistinct outer margin is thus a taphonomic indicator of a sessile life habit for members of the Ediacara Biota.

Dickinsonia is a mobile benthic organism with modular morphology that ranges from 6.4-94.4mm in length (Droser et al, 2019). There are over 1,300 known specimens of *Dickinsonia* at Nilpena (Evans et al, 2019B; Droser et al, 2019). It is consistently preserved with a sharp outer margin that clearly distinguishes it from the surrounding TOS (Figure 1.5B). This sharp boundary shows that *Dickinsonia* was not sessile, but mobile upon the mat (Evans et al, 2019A). While the sharp margin characterizes *Dickinsonia*'s mobility, its benthic affinity is based mainly in the presence of "footprints", or positively preserved impressions of similar size to the body fossil, left by *Dickinsonia* on the microbial mat as it moved. Both the sharp outer margin and the preservation of footprints serve as evidence for a mobile lifestyle on top of the microbial mat. The footprints of *Dickinsonia* have been used in conjunction with modern microbial

mat analogues to infer the growth rates of the Ediacaran microbial mat. Modern organic mats grow vertically on the scale of a few mm per year (Evans et al, 2019; Buffan-Dubau et al, 2001; Sanchez-Cabeza et al, 1999). *Dickinsonia* footprints average less than 0.5mm in depth and thus would have been obscured by mat regrowth in a matter of weeks at maximum (Evans et al, 2019). This data suggests that if an Ediacaran organism spent significant time on one spot on the mat, on the scale of weeks to months, it would likely exhibit blurred outer margins.

Dickinsonia and *Tribrachidium* are well-represented in the Ediacaran fossil record at Nilpena, and their taphonomy, sedimentology, and morphology have been extensively studied and characterized (Hall et al, 2015; Droser et al, 2019; Evans et al, 2019A; Evans et al, 2019B). They are therefore particularly suited for use as comparative taxa to assist the understanding and interpretation of preservation of *Attenborites* specimens. The outer edges of *Attenborites* are compared to those of *Dickinsonia* and *Tribrachidium* to determine if *Attenborites* specimens spent significant time on the mat before burial. We also searched for evidence indicating attachment to or movement upon the mat, including the presence of positively preserved footprints of *Attenborites*.

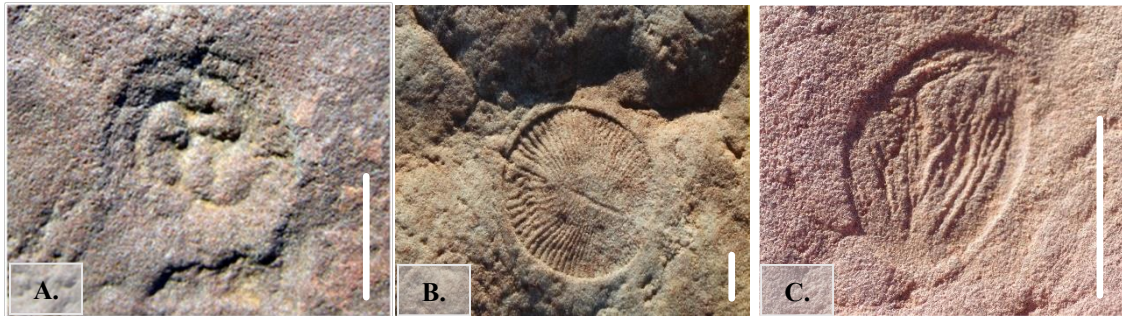


Figure 1.5. A: *Tribrachidium heraldicum* specimen exhibiting a blurred outer margin. B: *Dickinsonia* specimen exhibiting a sharp outer margin. C: *Attenborites janae* for comparison. Scale bar 1cm.

d. Field Data Collected

In the field, the length and width of all 104 specimens of *Attenborites* were measured to the nearest tenth of a millimeter using calipers, and the number of ridges displayed on each specimen was recorded. The uniformity, orientation, and degree to which the ridges converged or remained parallel was also noted. Specimen outlines were categorized as very sharp, somewhat sharp, or less sharp based on clarity of the boundary between the fossil and surrounding TOS. Silly putty was used to both create a cast of the fossil, representing what the organism would have looked like when buried, and assess the outer margin clarity (Figure 1.6). Additionally, the overall specimen shape was noted as circular, ovate, or triangular. Circular specimens are those where length and width measurements were within 1mm of each other, ovate specimens are those with longer length than width but similarly rounded ends, and triangular specimens possess one end that is relatively flat and the other more rounded. These categories define the three taphomorphs recognized within *Attenborites* (Figure 1.10).



Figure 1.6. A specimen of *Attenborites* captured in positive relief on a piece of silly putty being used to observe the clarity of the outer margin of the specimen. Scale bar 1 cm.

The long axis of *Attenborites* was defined as the longest line through opposite ends of the organism, regardless of internal ridge orientation. The long axis typically aligned at least partially with the internal morphology of the organism. Thus, in round specimens, the long axis was oriented in line with the parallel internal morphology. Orientations of the long axes of all *Attenborites* specimens were measured using a protractor to find the angle of the long axis compared to the North-South grid line marked on the bed. Since no top or bottom of the organism was assumed, angles were only measured across a range of 180 degrees. Orientations were then plotted in a rose diagram with the specimen abundances plotted proportionally to the area using the program PAST (<https://past.en.lo4d.com/download>).

Due to the small size of *Attenborites* specimens, laser scans of the fossils were taken using the HDI Compact C506 3D laser scanner that has a reported accuracy to 12 μ m. This laser scanner has sufficient resolution to make observations necessary to understand the details of the taxon's morphology and preservation. The 3D mesh processing software MeshLab (<https://www.meshlab.net/>) was then used to measure the surface area of these scans, remeasure the length and width of specimens, and recount the ridges on each specimen to ensure accuracy of the original measurements (Figure 1.7).

The scaling of the laser scans was automatically registered by MeshLab and required no manual scaling.

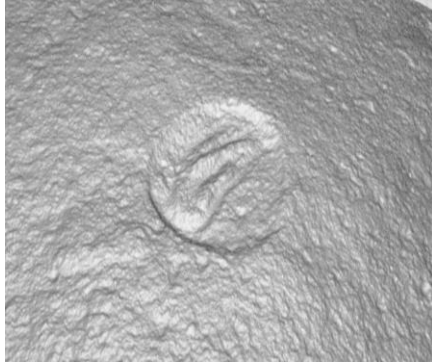


Figure 1.7. A specimen of *Attenborites* captured by the HDI Compact laser scanner. These scans have an accuracy up to 12 μ m – note the preservational detail of the fossil shown here. Scale bar 5mm.

We note details on the broad-scale preservation of *Attenborites*, including the preservation *en masse* of all but 2 specimens on a single continuous bedding plane and associated float pieces of that bedding plane. A crucial factor on the taphonomy of the Ediacara Biota is how they interacted in life with the mat. Taxa such as “Bundle of Fibers” show pulled out holdfasts that anchored them to the mat in life (Xiao et al, 2013). *Dickinsonia* and *Yorgia* left distinct footprints behind on the mat as they moved around (Evans et al, 2018). Signatures of interaction with the mat like these were sought out for *Attenborites* specimens, especially those recently excavated as they had not been investigated yet.

V. Results

Specific aspects of *Attenborites* taphonomy, sedimentology, and morphology were considered as relevant in the characterization of the taxon’s life habit. Previous conclusions made about *Attenborites*, established criteria for the preservation of soft-bodied pelagic forms, and characteristics indicative of a benthic lifestyle in Ediacaran

organisms guided selection of the characters described and evaluated more deeply in this thesis. These characters include (1) the outer margin of *Attenborites*, (2) its internal characteristics, (3) the presence of taphomorphs, (4) the long-axis orientation of specimens on bed TB-ARB, (5) the distribution of *Attenborites* at Nilpena, and (6) any evidence of movement on or attachment to the microbial mat.

a. Outer margin

The outer margin was examined on the newly excavated 55 specimens. These new specimens were also found to have a sharp outer margin, indicating that the presence of this taphonomic feature is a unifying characteristic of *Attenborites*. This well-defined margin can be found preserved independently of morphological characteristics like ridges (Figure 1.8). Of the 89 specimens preserved on TB-ARB, there was slight variation in the preservation of the outer margin within the total population. Most *Attenborites* specimens (n = 52) possess an extremely sharp margin, 31 possess a somewhat sharp margin, and only 6 have less sharp margins. However, less well-preserved specimens displayed clearer outer margins than the blended outer margins seen on sessile taxa.



Figure 1.8. A: *Attenborites* with a well-defined and sharp outer margin. B: *Attenborites* with a less well-defined outer margin. Scale bar is 5mm.

b. Internal Characteristics

Within the sharp boundaries of *Attenborites* fossils, the forms were all found to be internally distinct from the surrounding TOS. No features of the underlying TOS impinged upon the specimens, indicating that these fossils possessed thick enough tissues to resist total collapse and maintained their integrity on an uneven surface, even with deflation. The relatively smooth internal surface of *Attenborites* specimens was disturbed only by distinct, sub-parallel ridges that typically extended the length of the specimen. The spacing between ridges varies widely and does not correlate with the size of the fossil. There is also variable orientation of the ridges among specimens, with some specimens even exhibiting ridges oriented in multiple directions (Figure 1.9). These variable internal structures are unique to *Attenborites* alone and are not found in any other taxa at Nilpena.

The number of ridges also display significant variation, ranging from 0-19 across all 104 specimens. Fourteen specimens do not preserve ridges at all (Figure 1.9C). Of the 89 *Attenborites* preserved on TB-ARB, 42 of them are preserved with crisp, well-defined ridges. 17 have less crisp but still distinguishable ridges, and 16 of the specimens have ridges that are barely visible. These data show little uniformity among the preserved ridges as the number, orientation, spacing, and definition of the ridges appears to be random and exhibits large variation across specimens.

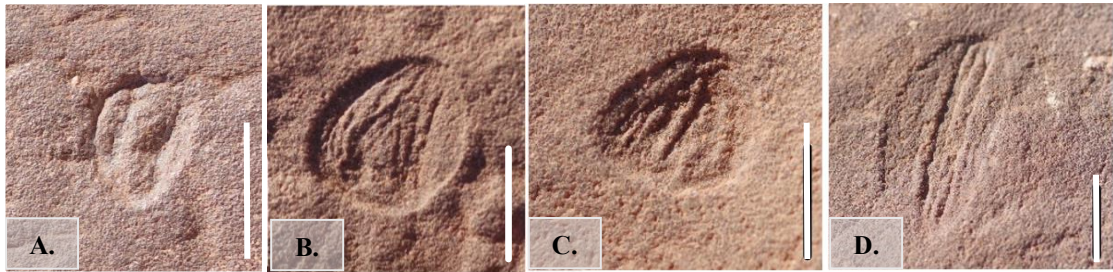


Figure 1.9. *Attenborites* specimens with a wide variety of ridge patterns. A: spaced out ridges, B: dense ridges, C: converging ridges, D: parallel ridges. Scale bar 5mm.

c. Taphomorphs of *Attenborites*

While the three taphomorphs of *Attenborites* are visually distinct and easy to categorize, there are individuals that fall in between these endpoints of morphology (Figure 1.10). Once these taphomorphic groups were identified, tests were performed to determine if they represented distinctive morphotypes within *Attenborites*. Because the widths of ovate and triangular taphomorph populations were not found to be statistically different from one another ($p = 0.2321$), they were considered as one population in these tests. When this group's widths were compared to the width of circular taphomorphs, these two groups were found to be statistically significant from one another ($p = 0.000836$, Figure 1.10B).

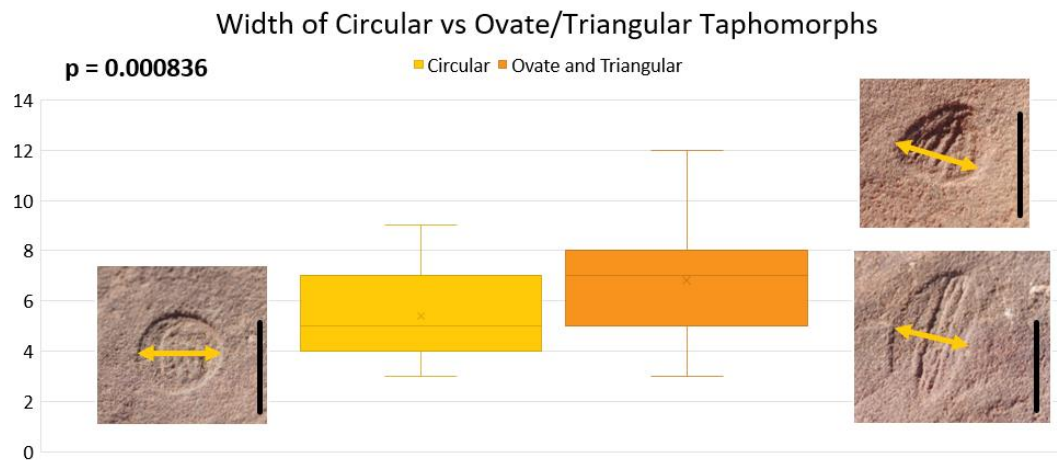
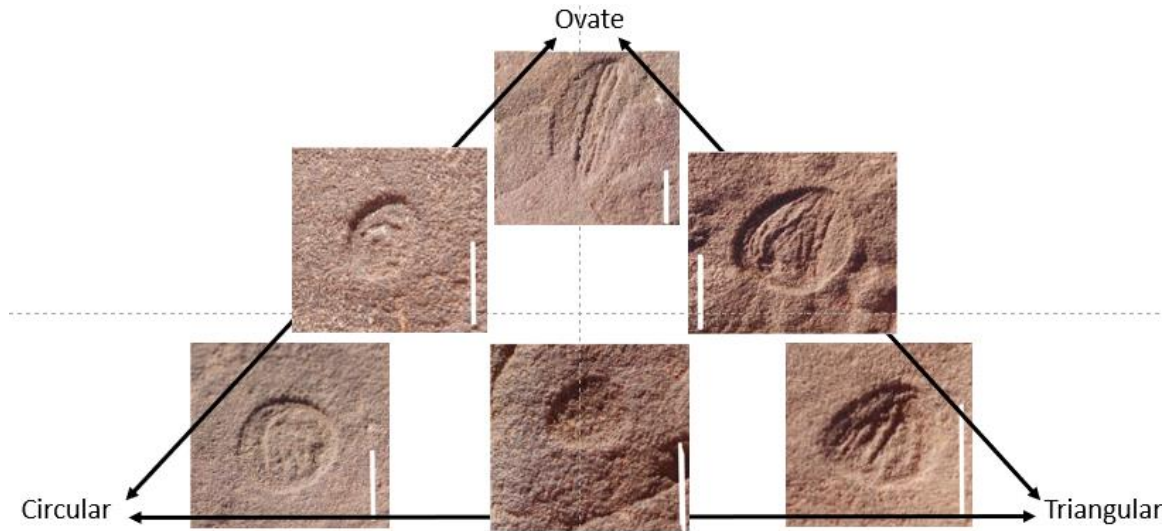


Figure 1.10. A: taphomorphic groups circular, ovate, and triangular are at the endpoints of this triangle. Specimens that do not cleanly assign to one category are shown as transitional between the taphomorphic endpoints. B: Width distributions of circular taphomorphs versus ovate and triangular taphomorphs. Scale bar 5mm.

d. Long-axis orientation

The long-axis orientation of each *Attenborites* specimen preserved on TB-ARB was measured against a North-South grid and plotted on a Rose diagram with

measurements ranging from 0-180 degrees using the software PAST. A Rayleigh's R test of circular uniformity was then performed, where a value of 0 indicates an evenly spread circular distribution and a value of 1 indicates a unidirectional distribution (Figure 1.12). The Rayleigh's R test resulted in a value of 0.1913, indicating that there was a slight orientation but that the long axes are statistically evenly and randomly oriented.

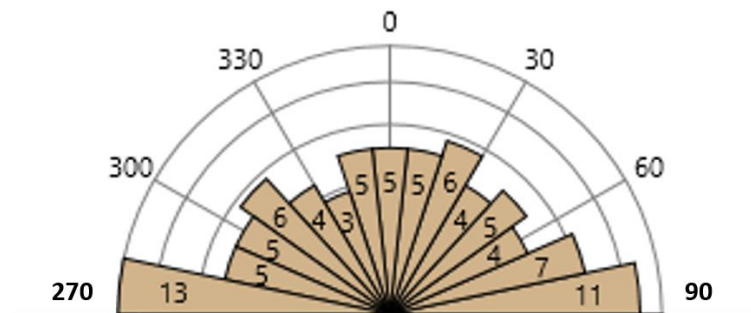


Figure 1.11. Rose diagram plotting the orientations of the long axis of *Attenborites* specimens. Plots are mirrored across the East-West line. Integers are specimen counts.

e. Preservation *en masse*

The 102 specimens of *Attenborites* are found preserved on or in association with bed TB-ARB. Eighty-nine of these are preserved on the continuous bedding plane in ecological context (Figure 1.13). This preservational distribution concentrated almost exclusively on one bed is not described in any other taxon at Nilpena. Benthic organisms that occur in high abundance are found in high numbers across bedding planes and seldom as single individuals. For example, 53 individuals of *Dickinsonia* are preserved on TB-ARB, but *Dickinsonia* is commonly found in relatively high abundance on other bedding planes. TB-ARB represents the most abundant and well-documented facies at

Nilpena, so the abundant preservation of *Attenborites* on TB-ARB can be considered a true signal and not a taphonomic overprint.

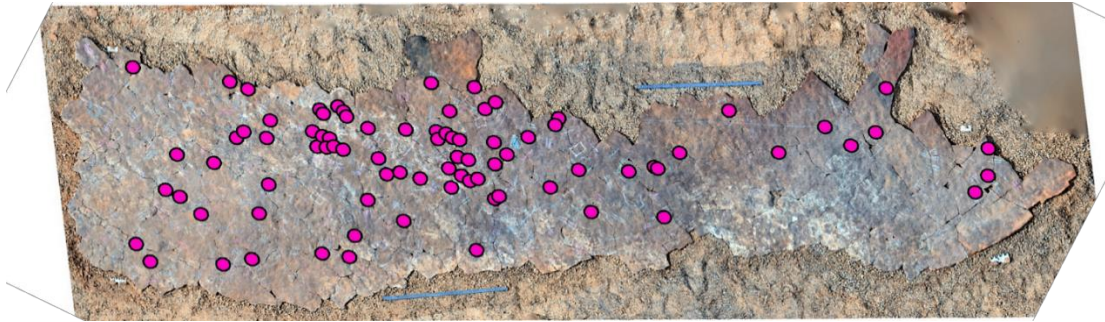


Figure 1.12. Bed TB-ARB with pink dots denoting the location of all 89 *Attenborites* specimens. Figure created by P.C. Boan.

f. Benthic attachment or motility

Attenborites fossils show no evidence of either being anchored to the mat or having moved upon it. There are no holdfast structures present on any of the 104 specimens or “footprint” marks distinguishable, similar to those found with *Dickinsonia*, despite the well-developed TOS and exceptional preservation of TB-ARB. The original paper describing *Attenborites* noted that the rounded ends of specimens are not morphologically consistent with taxa that stick into the mat with a pointed end like the Ediacaran organism *Thectardis* (Droser et al, 2018; Clapham et al, 2004). There is no evidence that *Attenborites* might represent a pull-out structure from part of a larger organism such as *Aspidella* (Tarhan et al, 2010; Droser et al, 2019; Gehling et al, 2003). If *Attenborites* were a pull-out structure, we would expect it to be preserved in positive relief, but all specimens are preserved in negative relief.

VI. Discussion

a. Outer margin

The newly excavated 55 specimens of *Attenborites* were found to have a sharp outer margin, making this a characteristic feature of *Attenborites*, consistent with the conclusion drawn in Droser et al, 2018. Comparisons to known benthic organisms reveal that the clarity of the outer fossil margin on *Attenborites* is much more similar to that of *Dickinsonia* than *Tribrachidium*, signifying that *Attenborites* was well-defined from the underlying microbial mat and not embedded or incorporated into the mat during life. *Attenborites* had thus not spent much time, if any, in the same location on the microbial mat prior to burial. This evidence precludes a sessile life habit for *Attenborites*.

b. Internal characteristics

Additional evidence for a pelagic life habit for *Attenborites* comes from the lack of uniformity in its preservation. The large variation in the internal preservational morphology can be considered true morphological preservation as there is no evidence of taphonomic distortion on TB-ARB (Droser et al, 2018; Evans et al, 2018). The large degree of variation is consistent with the criterion by Young and Hagadorn (2010) that pelagic soft-bodied taxa will exhibit variable preservational morphology when specimens are preserved via cast and mold, as they are at Nilpena.

The variable frequency of ridges across supports the original hypothesis (Droser et al, 2018) that ridges may have formed during the biostratinomic deflation of living organisms. Still, the subparallel orientations and triangular convergence of the ridges on 40 specimens suggests that these ridges preferentially formed in non-random and non-

uniform patterns. Features formed purely from deflation would not be expected to form with directionality and would be discontinuous and sinuous. Ridges on *Attenborites* are typically continuous and straight across the length of the specimen. While there are exceptions (Figure 1.10), the internal features of *Attenborites* are clearly forming along certain planes of the organism rather than at random. These ridges are therefore assumed to be taphonomic features reflecting underlying organization of *Attenborites* tissues without being biological characteristics.

c. Taphomorphic groups

If circular specimens had the same or slightly larger width as ovate and triangular specimens, it would be possible that circular specimens were simply top-down preservation of ovate and triangular specimens. However, circular specimens have a statistically smaller width than ovate and triangular specimens, suggesting that some circular specimens are potentially smaller forms of *Attenborites*. Despite the statistically significant difference between the width of circular specimens compared to the widths of the ovate and triangular group, there is still overlap in the widths of the two populations. Consequently, we could not rule out that larger circular taphomorphs are top-down preservations of ovate or triangular organisms.

Although the preservational morphology of *Attenborites* can be categorized into three taphomorphic groups, all specimens possess the sharp outer margin, preservation in negative hyporelief, and ridge-like internal morphology. Therefore, it appears much more likely that these taphomorphs all represent variable preservation of a single taxon rather than the preservation of multiple taxa. This finding is also consistent with the criterion

that soft-bodied pelagic forms will not have a single preservational morphology (Young and Hagadorn, 2010).

d. Long-axis orientation

The long-axis orientations of *Attenborites* on bed TB-ARB (Figure 12) resulted in a Rayleigh's R test result confirming the null hypothesis that the long axes of specimens are randomly oriented on the bed. This is expected on bed TB-ARB because there is no clear paleocurrent direction. Additionally, if *Attenborites* were a pelagic taxon, we would expect that it was swept out of the water column and buried during an extreme storm event. Because this would only happen during instances of turbulent flow rather than laminar flow, we would expect pelagic organisms to never be oriented unidirectionally on a bedding plane. The Rayleigh's R test resulting in a value of 0.1913 is consistent with the turbulent, non-oriented flow expected in a burial event powerful enough to foul a pelagic organism.

e. Preservation *en masse*

If *Attenborites* were benthic, we would expect the taxon to occur on other bedding planes at Nilpena and in similar relative abundances on those bedding planes. The selective *en masse* preservation of *Attenborites* on TB-ARB, exclusively, is a true signal of preservation *en masse* as abundant benthic taxa like *Dickinsonia* are present on TB-ARB but also on almost 30 other beds at Nilpena and in high abundance on those beds. The mass preservation of *Attenborites* on TB-ARB is therefore not likely to represent preservation of a benthic taxon in abundance; it is more likely coincident with *Attenborites* being driven out of the water column and buried by a singular storm event

that fouled and buried them. Regarding the two single specimens not preserved on ARB, it is improbable that these *Attenborites* occurred as isolated individuals within the populations documented on 1T-F and 1T-F Annex. An alternative conclusion is that only a few, larger specimens of *Attenborites* sank to the seafloor to be preserved on these beds, and that the environmental conditions that facilitated the burial and preservation of *Attenborites* on TB-ARB were not present when the sediment comprising 1T-F and 1T-F Annex was deposited.

The possibility that *Attenborites* specimens are just only recognizable on bedding plane TB-ARB because of its exceptional preservation, as evidenced by its fine-grained lithology, must also be considered. The presence of larger specimens on bedding planes 1T-F and 1T-F Annex suggests that random preservation of larger specimens on other beds should be expected on coarse-grained beds if this were the case though. Because the specimens on 1T-F and 1T-F Annex fall within the size frequency range exhibited by the population on ARB we would also expect to find more larger, single specimens preserved on other beds if they too were dominated by *Attenborites*. Specimens as small or smaller than *Attenborites* can also be found on less well-preserved, coarser grained beds. We therefore conclude that *en masse* preservation of *Attenborites* on bed TB-ARB is not a taphonomic artifact of exceptionally detailed preservation, but a direct indicator of rare preservation. The preservation of abundant specimens on a singular bedding plane is therefore inconsistent with the preservation of known benthic organisms but is consistent with the criterion proposed by Young and Hagadorn (2010) that soft-bodied pelagic taxa should be preserved *en masse* during stranding or storm events (Droser et al, 2019).

f. Benthic attachment or motility

While it cannot be ruled out that *Attenborites* were globular forms that rolled around on the mat surface, such a life mode not yet described in the Ediacara Biota. Even if this life habit was plausible, we would not expect the preservation *en masse* on one bedding plane with extremely rare preservation on all other excavated bedding planes. Although there is no evidence of neither tentacles nor holdfasts for *Attenborites*, Young and Hagadorn (2010) suggested in their criteria that tentacles are very rarely preserved in cast and mold fossils of pelagic forms due to their fragile nature. Therefore, the lack of tentacles does not preclude a pelagic life habit, but the lack of a holdfast provides evidence against mat attachment. There are no footprints preserved in positive relief that could indicate periodic mobility upon the mat (Droser et al, 2018; Evans et al, 2019A). Taphonomic data on *Attenborites* indicates that this taxon was not interacting with the mat at all during life, meaning that a pelagic life habit is most parsimonious.

VII. Conclusion

The conclusion that *Attenborites* was pelagic rather than benthic is based in the taphonomy, sedimentology, and fossil morphology of this taxon and not in its similar appearance to early pelagic taxa. Although it is difficult to draw definitive conclusions about the ecological affinities of Ediacaran organisms, we can exclude the possibility that *Attenborites* was a sessile organism due to its sharp outline distinguishing it from the surrounding TOS. Multiple lines of evidence indicate that *Attenborites* was pelagic, including preservation on only 3 of 40 excavated bedding planes, preservation *en masse*

on one of those beds, a lack of external and internal symmetry, and a lack of evidence for interaction with or attachment to the microbial mat.

The placement of *Attenborites* within the water column during the White Sea interval of the Ediacaran Period also fits within the known greater context of the development of the pelagic realm. Studies documenting the significant presence of acritarchs during this time is evidence of ample food sources of algae and microplankton in the water column that *Attenborites* could have exploited (Yin et al, 2011; Moczyłowska, 2005; Jenkins et al, 2009; Xiao et al, 2014). Benthic members of the Ediacara Biota are also hypothesized to have fed from this abundant food source including *Corumbella* (Babcock et al, 2005), *Tribrachidium* (Rahman et al, 2015), *Ernietta* (Gibson et al, 2019), and *Arkarua* (Cracknell et al, 2021). Larvae of some benthic Ediacaran taxa are also predicted to have had a pelagic stage to aid in dispersal (Mitchell et al, 2020; Zakrevskaya, 2014; Peterson, 2005; Darroch et al, 2013). This represents that an evolutionary leap to a pelagic lifestyle was potentially achievable for Ediacaran taxa. Molecular clock data has also placed the origin of pelagic microorganisms within the Ediacaran Period, and a well-developed pelagic ecosystem is present by the early Cambrian (Gold et al, 2018; Peterson et al, 2005; Peterson et al, 2004; Peterson et al, 2008; Hagadorn et al, 2002; Vinther et al, 2014; Cartwright et al, 2007; Conway Morris, 1979). These data all provide important context that pelagic macroorganisms like *Attenborites* had likely evolved by the White Sea interval of the Ediacaran Period.

The taphonomic examination of *Attenborites* described heretofore along with the taxon's parsimonious characterization as pelagic have been considered in conjunction with the criteria for the preservation of Cambrian medusoids put forth by Young and Hagadorn (2010) and comparisons to known benthic Ediacaran taxa to form the basis for the development of criteria for the preservation of Ediacaran pelagic organisms. The 5 criteria developed to describe the preservation of pelagic Ediacaran organisms include (1) sharp definition of the fossil's outline against surrounding textured organic surface, (2) random orientation and positioning on a bedding plane, (3) rare preservation on an individual bedding plane and/or preservation *en masse*, (4) lack of evidence for holdfast onto or movement on the mat, and (5) a body plan that lends itself to a pelagic life habit (Martindale et al, 2002).

These Ediacaran-specific criteria were developed by considering how the Ediacaran environment affected taphonomy – i.e., how an organism from the water column would be preserved on the microbial mat-covered seafloor in comparison to how mobile or sessile benthic organisms would likely be preserved in the same environmental setting – specifically considered through the taphonomic lense of *Attenborites janae*. These are the first holistic criteria for determining if an organism was pelagic based on ecological, sedimentological, morphological, and taphonomic evidence. Armed with these criteria, future studies can investigate other potentially pelagic early metazoan taxa and begin to address the significant knowledge gap regarding the origins of complex metazoan life and the beginnings of Earth's largest and most ecologically relevant ecospace.

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Chapter 2: Using 3D modeling to retrodeform *Attenborites janae*

I. Introduction

Attenborites specimens contain ridges that are presumed to be preservational rather than biological as they follow no symmetrical pattern, display multiple orientations even within the same specimen, are inconsistent in length and degree of curvature, and do not always span the full specimen. These data indicate that *Attenborites* was potentially deformed or deflated during death and burial (Figure 2.1). Results from previous investigations of the preservation of *Attenborites* agree with this conclusion (Droser et al, 2018). Thus, the morphology of *Attenborites* remains poorly understood.

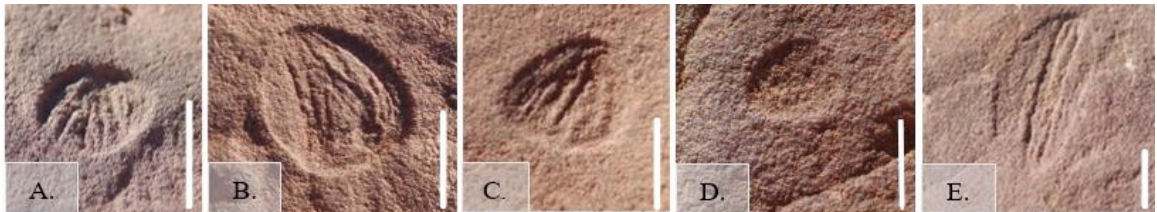


Figure 2.1. Variations in internal morphology displayed within specimens of *Attenborites* at Nilpena.

The goal of this study was to determine whether the ridges originated biologically or taphonomically and use this information and 3D modeling tools to effectively reconstruct the original morphology of *Attenborites* as a living organism.

The simulated reconstruction of *Attenborites* was performed by importing 3D laser scans taken of the fossils in the field into the open-source 3D modeling software, Blender (<https://www.blender.org/download/>). These scans were taken using the HDI Compact C506 3D laser scanner, which has a reported accuracy of 12 μ m (Figure 2.2).

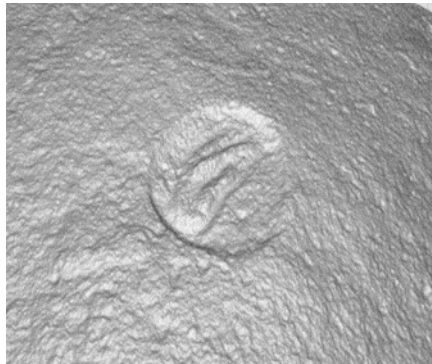


Figure 2.2. A specimen of *Attenborites* captured by the HDI Compact laser scanner. These scans have an accuracy up to 12 μ m – note the preservational detail of the fossil shown here. Scale bar 5mm.

Blender has become a well-used tool for paleontologists when reconstructing the original morphology of fossils (Garwood and Dunlop, 2014; Lautenschlager, 2015; DeVries et al, 2022). The ability of laser scanners to capture fine detailed models that can be used with Blender also allows fossils to be characterized with unprecedented accuracy and visualized in three dimensions. Because Blender is open source, easily accessible, possesses accurate physical simulation capabilities and has advanced animation features, it has become a useful tool applicable in a broad range of paleontological investigations. Using digital analysis tools like Blender also expand the reproducibility of analyses, improve accessibility to specimens, and prevent damage and displacement of original specimens.

The implementation of 3D visualization techniques has opened the door for a suite of functional morphology investigations that were previously inaccessible (Cunningham et al, 2014). Garwood and Dunlop (2014) used Blender to reconstruct the gait of extinct trigonotarbid arachnids after the discovery of limb articulations in exceptionally well-preserved specimens from the Rhynie Chert. Blender has also been used to perform 3D retrodeformations and reconstructions of fossilized elements with

distinct symmetry or a known original morphology (Rushton and Smith, 1993; DeVries et al, 2022; Peri et al, 2021; Cunningham et al, 2014). DeVries et al (2022) used Blender to retrodeform the dorsal rib and frontal bone of a thyreophoran dinosaur that had undergone brittle deformation, fracturing, swelling, and plastic deformation. Peri et al (2021) reconstructed missing elements of a *Zygophyseter varolai* cranium using Blender along with comparisons to the documented morphology of related species. While many studies have used Blender to retrodeform fossils with known symmetry and/or morphology, no such attempt has been made to reconstruct or retrodeform a soft-bodied asymmetric fossil. While it is typically impossible to retrodeform a soft-bodied taxon without a known outline or symmetry, the potential deflation of *Attenborites* during preservation makes this taxon specifically suited for investigations aimed at reinflating the specimens and modeling *in vivo* morphology. This study thus represents the first retrodeformation of a soft-bodied fossil taxon using 3D modeling, and reconstructing *Attenborites* will give insight into the morphology of the living organism.

II. Materials and Methods

a. Determining the origin of the ridges

The first test to determine if the ridges preserved within *Attenborites* specimens were formed during deflation or if they were morphological structures involved tallying the number of ridges on each specimen and comparing that tally to the size measurements of *Attenborites*. To do so, the original scans were trimmed to isolate the fossil and the MeshLab program was used to measure length, width, and surface areas of each specimen (Figure 2.3). These size values were then plotted against the number of ridges

to determine if ridges increased with size and could potentially be added on during growth of *Attenborites*.

To further test if the ridges of *Attenborites* were morphological or taphonomic in origin, I compared the size data from the previous slide to that of *Dickinsonia*, which is known to have modular morphology that varies consistent with growth, which has been well documented. Lastly, overall features of the ridges and their patterns were examined to determine if they originated biologically or taphonomically due to deflation.

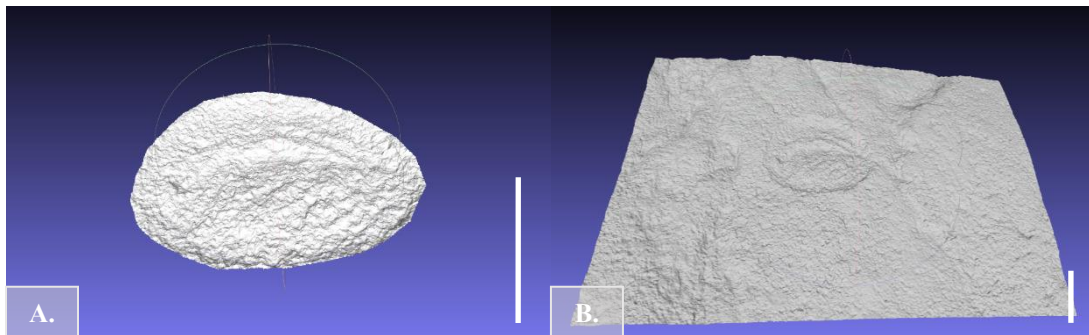


Figure 2.3. A: Original fossil scan of an *Attenborites* specimen imported into MeshLab. B: Isolated scan of *Attenborites* specimen used in the inflation simulation. Scale bar 5mm.

b. Inflating *Attenborites*

Laser scans of *Attenborites* were manipulated using 3D modeling software MeshLab and Blender to construct a data-driven reconstruction of *Attenborites* if the ridges originated taphonomically. To reverse potential preservational effects of deflation and reconstruct the morphology of *Attenborites* as a living organism,

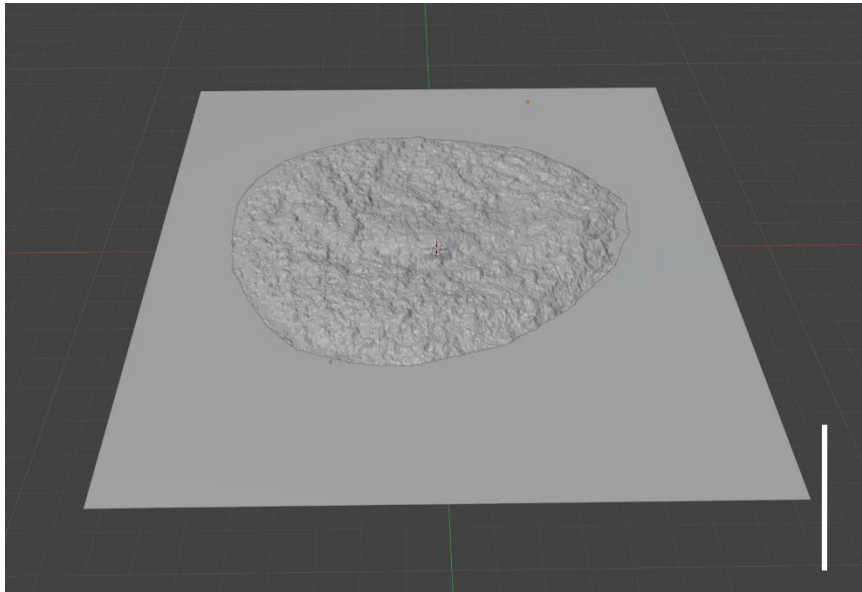


Figure 2.4. Isolated fossil scan of *Attenborites* in Blender. Scan and its normal have been flipped to be convex rather than concave. Scan has also been decimated and a 2D plane has been added underneath the scan. The edges of the scan are pinned to this plane. Scan has also been filled on the bottom to create an airtight shape. Scale bar 5mm.

Scans of the isolated fossil were imported into Blender and remeshed to reduce the number of vertices while preserving the shape and resolution of the 3D scan (Figure 2.4). Typically, the unreduced scans contain 200,000 vertices or more. Thus, scans were reduced to have around 25,000 faces to reduce the amount of RAM necessary for manipulation. After reducing the meshes, each scan was rotated on the y-axis so that it was convex instead of concave, flipping the mesh so it represents a positive model of a living specimen of *Attenborites* on the seafloor rather than a negative impression of the organism left on the casting sediment (Figure 2.4). Once the scan was flipped, the normals, or assigned directions of the faces, were reversed so that the scan did not register as inverted, with its inner surface shown as the outside. A 2D plane mesh was then added underneath the mesh so that the edges of the fossil scan mesh could be pinned

to this plane (Figure 2.4). This anchors the fossil scan when pressure is virtually applied to it.

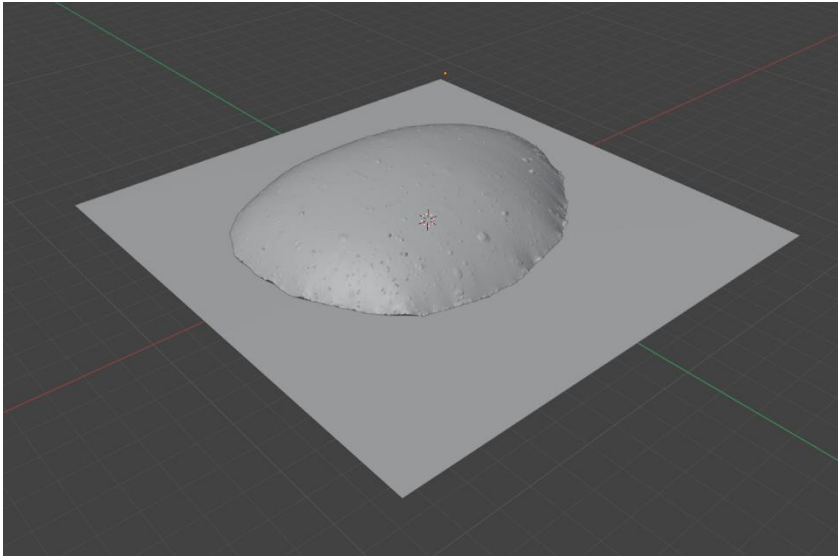


Figure 2.5.
Inflated scan of
Attenborites janae
in Blender. Scale
bar 5mm.

To begin inflating *Attenborites*, a Cloth Modifier was applied to only the fossil scan and an internal pressure setting of 50 was applied to the scan to fill the volume of the mesh and inflate the 3D scan of the fossil. The simulation was allowed to run until completion (Figure 2.5), and the inflated *Attenborites* scan was exported as a .stl file. The inflated scans of *Attenborites* were then imported into MeshLab where Surface Area and Volume measurements were taken using the “Compute Geometric Measures” tool (Figure 2.6). An in-depth step-by-step guide for cleaning the original scans, importing them into Blender, and simulating their inflation is provided as a supplemental file to this manuscript. This methodology effectively reconstructs what the organism looked like as a living body if the ridges originated during deflation.

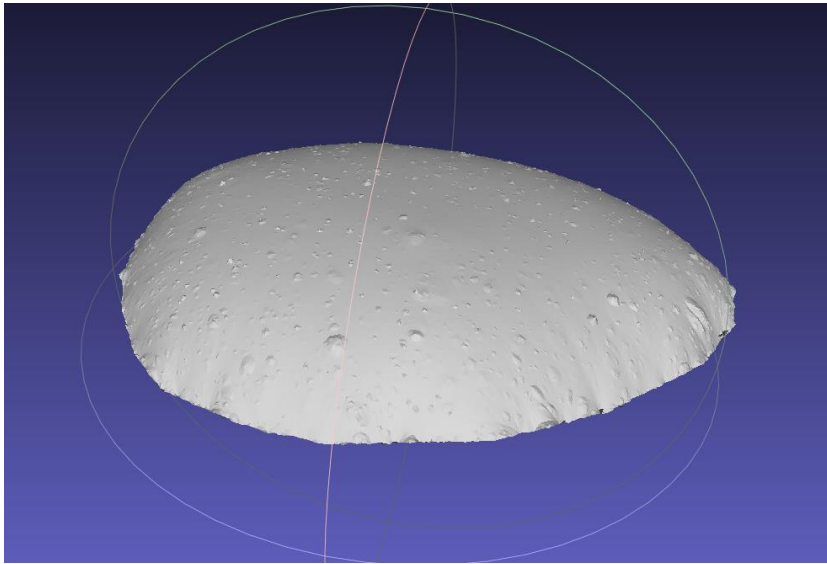


Figure 2.6. Isolated scan of inflated *Attenborites* fossil in MeshLab. Scale bar 5mm.

c. Ensuring the accuracy of the inflations

To test if the simulation inflating *Attenborites* had been performed properly, the surface areas of the original scans of the isolated fossils were compared to the surface areas of the inflated scans. Both were measured in MeshLab using the “Compute Geometric Measures” tool. The surface area measurements were also compared to the volume measurements to test if the volume, measured in mm^3 , in fact increased faster than the surface area, measured in mm^2 .

III. Results

a. Determining the origin of the ridges

A tally of the number of ridges on each specimen compared to specimen size data reveals that ridge density and frequency on individual specimens did not correlate to the length, width, or surface area. While the number of ridges generally increased with the overall area of the specimen, this trend did not apply to all specimens and was generally

weak ($R^2 = 0.2533$, Figure 2.7A). If ridges were being added with growth, it could be expected that these distributions would plot with a distinct correlation, like that observed between the length and number of modules on *Dickinsonia* specimens, which has an R^2 value of 0.85 (Figure 2.7B). The weak correlation between the number of ridges and surface area of *Attenborites* compared to *Dickinsonia* rules out the conclusion that ridges are added with growth. Also, based on observations of *Attenborites*, the width between ridges does not correlate with size of the fossil and there is no way to predict where the ridges will form. This is opposite of what we see in *Dickinsonia* modules though, which do increase in size as the specimen size increases and the modules have a predictable size and shape based on their location on *Dickinsonia* (Evans et al, 2017). Thus, ridges are most likely taphonomic in origin rather than biological.

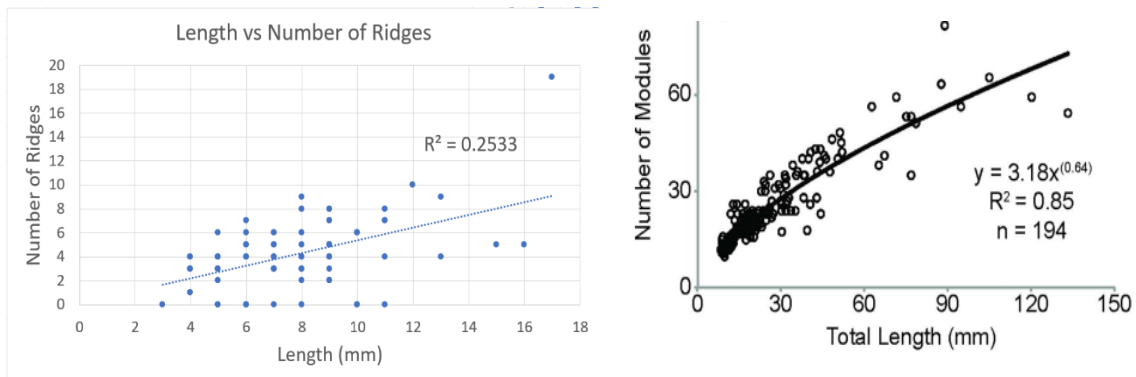


Figure 2.7. A: The relationship between the length of the isolated laser scans of *Attenborites* fossils and the number of ridges those fossils possess. Note the R^2 value of only 0.2533. B: The relationship between the length of *Dickinsonia* specimens and their number of modules. $R^2 = 0.85$ (Evans et al, 2017)

b. Testing the accuracy of the inflation technique

Plotting the surface areas before and after inflation demonstrated that the surface areas remained unchanged through the inflation process as these data plotted linearly with

a slope of 0.99 and an R^2 value of 0.999 (Figure 2.8). The agreement between the surface areas before and after inflating the specimens indicates that the simulation did not overinflate the specimens or stretch the initial scanned material.

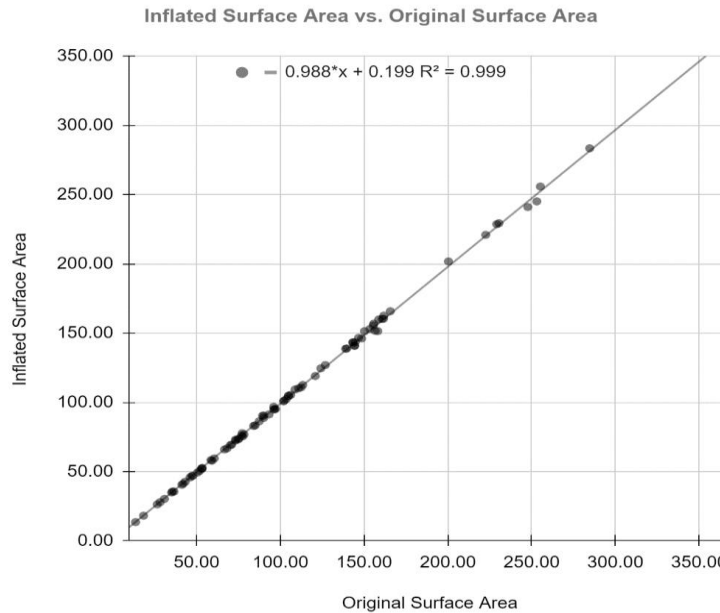


Figure 2.8. Surface area measurements of original and inflated scans of *Attenborites* measured in mm^2 .

To further confirm that the inflations had been performed correctly, the surface areas and volumes of the inflated scans were measured in MeshLab and then plotted against one another. This resulted in a graph where the volume increased more rapidly than the surface area, which is expected as volume measurements are cubed, and surface area measurements are squared (Figure 2.9). These data plotted as a curved line with a changing slope, signifying accelerated motion that is characteristics of surface area versus volume plots. Lastly, if the surface areas and volumes correlated correctly, we would expect the best fitting line of regression to be that of a power series, where measurements

increase at a certain rate. This plot has an R^2 value of 0.989 when fit with a power series line of regression, so we can conclude that the scans were inflated correctly (Figure 2.9).

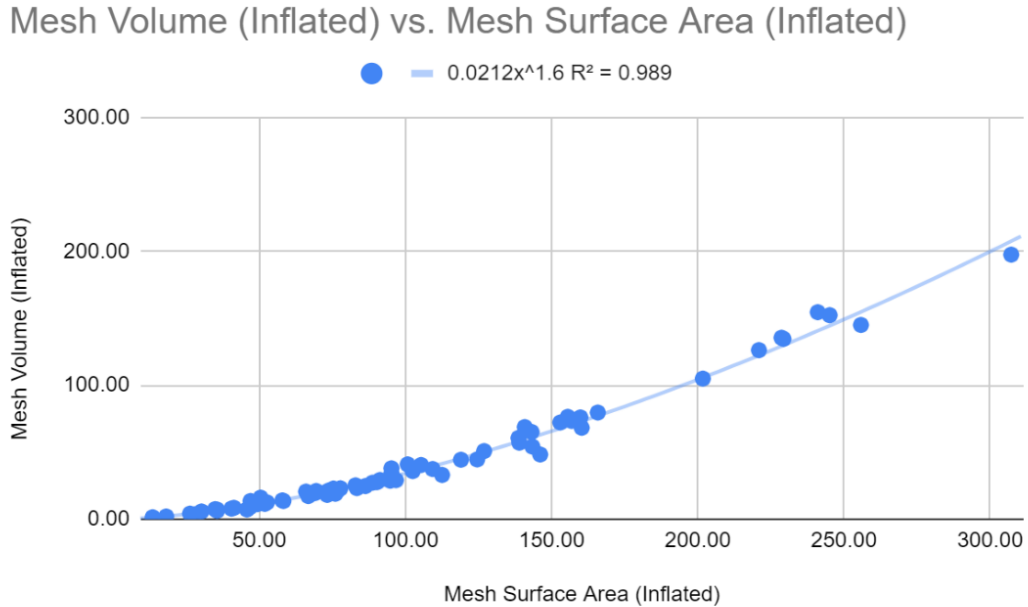


Figure 2.9. Relationship between the surface area (mm^2) and volume (mm^3) of inflated *Attenborites* scans with regression line of a power series, $R^2 = 0.989$.

IV. Discussion

a. Determining the origin of the ridges

Because the ridges of *Attenborites* were not being added on with growth, did not correlate to the size of the fossil, did not exhibit any predictable patterns, and display a huge range of variation, the ridges were determined to originate taphonomically due to deflation of the original organism and do not represent biological structures. If a biological hypothesis for the ridges could be confirmed, we might predict that these ridges reflect structure or symmetry of the organism. For example, ctenophores have 8-

part symmetry and often possess 8 comb rows that traverse the length of the organism and are present and unchanging in number throughout the adult life stage (Martindale, 1986). These 8 comb rows are distinctly well-preserved in fossil ctenophores (Parry et al, 2021; Conway Morris and Collins, 1996). *Attenborites* ridges do not reflect any kind of stability or symmetry though, further refuting the hypothesis of a biological origin. Because the results of tests aimed at determining the origin of the ridges are consistent with the ridges forming during the deflation of the living organism prior to burial, the methods created to use 3D modeling tool Blender to inflate *Attenborites* can be confirmed as methods to retrodeform a deflated, soft-bodied taxon.

b. Establishing methods for the retrodeformation of soft-bodied fossils

Because the surface areas of the isolated fossil scans remain essentially unchanged before and after simulating inflations of the specimens, we can be confident that the scans of *Attenborites* are not being stretched or overinflated. This is crucial to the success of the simulation and its interpretations as the material properties of *Attenborites* and its tissues remain unknown. Even if the tissue of this taxon was elastic and could stretch, resulting in higher volume measurements, we would still expect volumes to increase uniformly and proportionally. Therefore, any elastic properties of *Attenborites* are not expected to affect the results of this study, but precautions have been taken to maintain the original surface area of the preserved fossil. The methods of inflation have therefore ensured that the surface areas of the scans remain consistent throughout the simulation.

Because the comparisons of surface area to volume also corroborated the accuracy of the inflation simulations, and because the ridges were determined to originate taphonomically due to deflation, the methods used to inflate the scans of *Attenborites* are therefore confirmed to accurately reconstruct the *in vivo* morphology of *Attenborites*. *Attenborites* can therefore be reconstructed as an ellipsoidal form, completing the retrodeformation of this soft-bodied taxon (Figure 2.10).



Figure 2.10. Fully reconstructed *Attenborites janae* as an ellipsoidal form. Scale bar 5mm.

V. Conclusion

The enigmatic nature of the Ediacara Biota often precludes an understanding of their true nature (Tarhan et al, 2010; Hall et al, 2015; Darroch et al, 2017; Meyer et al, 2012). Characterizing Ediacaran taxa is especially complicated by taphonomic features incurred during the burial and fossilization process (Droser et al, 2018; Surprenant et al, 2020; Hall et al, 2015). The methods described in this study represent an avenue to better understand the original nature of the Ediacara Biota despite the overprint of taphonomic

features on fossilized organisms. 3D modeling tools have already become an indispensable tool for understanding the original morphology of fossil taxa with known symmetry and form (Cunningham et al, 2014; Garwood and Dunlop, 2014; DeVries et al, 2022; Peri et al, 2021), but the methods established in this thesis allow 3D modeling technique to also be applied to understand the morphology of amorphous, soft-bodied forms. Specifically, this study has resulted in a novel technique for using 3D modeling to retrodeform and reconstruct a soft-bodied taxon from the Ediacara Biota, representing the first soft-bodied retrodeformation and the oldest taxon to be retrodeformed. Establishing these methods has given valuable insight into the true morphology of *Attenborites janae*, further characterizing the nature of the first pelagic macroscopic organism.

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Appendices and Supplemental Material

Appendix I. Methods for Inflating *Attenborites janae* scans

Preparing scans in MeshLab

1. Download MeshLab (<https://www.meshlab.net/>) and open the application.
2. Once in MeshLab, select **File, Import Mesh**, and select your scan file. Then wait for it to load. This may take a few moments depending on the size of your Mesh.
3. Use the left click tool to manipulate the scan so you can see the edges of the fossil. Try not to angle the scan too much so you can see as much of the edge as possible.
4. The next step is to isolate the *Attenborites janae* fossil and delete the surrounding mesh. Do this by selecting the **Select Faces/Vertices Inside the Polyline Area Tool** at the toolbar at the top of the page. Then click around the shape you want to select. This works a bit like a freeform selection tool. Next, hit **Q** on your keypad to select inside the line you just created, then hit **I** to invert the selection. You should now have everything except the *Attenborites* fossil selected. Go ahead and hit delete now to isolate your scan.
5. Export your scan by hitting **File, Export mesh as...**, and save your scan as an STL file.

Inflating Scans in Blender

1. Download and open Blender (<https://www.blender.org/download/>). Then import your newly saved STL file by selecting **File, Import, .stl** and select the STL file you just saved from MeshLab.
2. Go ahead and delete everything preexisting in the scene by selecting it and hitting delete.
3. The next step is to move your mesh to the proper position to inflate it. First, you'll want to rotate your scan on the y-axis so that it is convex instead of concave. To do this, select your mesh, then hold down **R, Y**, and move your mouse until the scan has flipped over. Then, rotate your scan so it's flat with the X-Y plane using **R, X; R, Y; or R, Z** until your scan is flat. Then position your scan so it's just above the X-Y plane in the middle of your screen by holding down **G, X; G, Y; or G, Z** until your scan is positioned where you want it. Now it should be concave, just barely above the X-Y axis, and centered at the origin.
4. Now that we've flipped our mesh so it represents the organism rather than the imprint, we need to flip the normals of the scan so that it inflates properly. To do this, select the mesh by left clicking on it, then hit **tab** to go into edit mode rather than object mode. Now hit **A** to select your mesh, then go to **Mesh**, at the top, then **Normals**, then **Flip**, and your normals will now be correctly oriented! Make sure to hit **Tab** again to go back into Object mode now. You can check that this worked in Object mode by hitting the drop down menu from the two linking

circles in the top right, and checking the box for **Face Orientation**. Your scan should light up blue! Not red.

5. Next we'll want to insert a plane so that our mesh doesn't fall into the void when we run our simulation. To do this, just hit **Shift+A, Mesh**, and select **Plane** to get the plane into the scene. It should automatically be centered at the origin. Then, hit **S** and scale your plane so that it's larger than the scan. Make sure that your mesh is almost touching but not intersecting the plane. Use **G, Z** to move up your scan if necessary.
6. Give both your scan and the plane a collision by hitting the blue wrench on the right side menu and selecting Collision from the physics modifiers. You'll do this once with the plane selected and once with the scan selected. To apply these changes, just hit **CTRL+A** with the modifier selected for each object.
7. Next, to make sure our mesh doesn't fly away when we try to inflate it, we'll pin down the outside of our mesh to our plane. To do this, start by hitting **Tab** to go into Edit mode and using **ALT+LMB** to select the edges of the mesh. Hold **Shift** as you do this to select additional segments of the edge if the full edge doesn't select the first time. To deselect if you incorrectly select something, just hold shift and click it again. Once the whole edge is selected, hit the green triangle button on the right edge of the screen, hit **+**, then double click on the highlighted **Group** section to rename your pin group. Now hit **Assign** with your edge still selected. We'll officially pin this once we use our cloth modifier!

8. Next, make the scan a closed, watertight object. Still in edit mode with the edge you just made the Pin group selected, go ahead and hit **F** to fill the space and close the scan. It will look bad now, but don't worry. Hit **TAB** to go back into Object mode.
9. Follow the steps under the section, **Measuring scans in MeshLab** in this document to measure and record the measurements of the non-inflated mesh. Now, you'll want to reduce the size of the mesh so that it's easier to manipulate and is less taxing on your machine. To do so, make sure you're in Object Mode, displayed at the top toolbar, and then click on your Mesh to select it. Now, go to **Modifier Properties**, the little blue wrench on the right side of your screen, and then navigate to **Add Modifier** and select **Decimate** from the drop down menu. Make sure your mesh is still selected as you're doing so. Select the **Collapse** option, and then enter the ratio you'd like to collapse it by. For example, if you enter 0.5, you'll reduce your mesh from 50,000 faces to 25,000 faces. To apply these changes, just hit **CTRL+A** with the modifier selected. Now that you've reduced the size of your mesh, it will load faster and be easier to work with.

**Make sure that the shape and detail of the mesh does not visually change too much when you do this!
10. Now we'll begin the process of inflating our mesh - to do this, select your imported mesh, not the plane. Next go to **Modifier Properties** with the little blue wrench on the right side, and this time select **Cloth Modifier**. Now go down to the **Physics Properties** tab, represented by the blue circle surrounded by the blue

line. I like to increase the number of quality steps to at least 7 to prevent inaccurate model results. I also like to take the speed modifier down to at least 0.5 so that I can watch it inflate more slowly. Next, make sure you're using the Linear bending model instead of the Angular bending model. Under the **Stiffness** tab, raise Tension, Compression, and Shear to 300. Under **Damping**, make sure all are set to 50. I also like to keep Internal Springs off. Next, check the **Pressure** box and increase the Pressure to 50. Next, under the Shape tab, hit Pin Group and select the vertex group you created earlier for our edge of the scan. Lastly, increase your Collision quality to at least 8 under the Collisions tab. Now make sure to save your model as **Blender_scan name_your initials**, and then your *Attenborites* should be ready to inflate! Set your playback frame all the way to 0, and then hit **Play** and watch *Attenborites* inflate! Let it run until 250 frames to stabilize.

11. Choose the keyframe where *Attenborites* is the most stable, probably around frame 250. Note this keyframe in Excel.
12. Delete the plane by selecting it (in Object mode) and pressing delete.
13. Save your mesh and then export your mesh at the most inflated keyframe.
14. Follow the steps under the section, **Measuring scans in MeshLab** in this document to measure and record the measurements of the inflated mesh. Make sure you're importing/measuring the inflated version in MeshLab!

Measuring scans in Meshlab

1. Import STL from Blender into MeshLab again.
2. Use **Select Faces in a Rectangular Region** and highlight the entire scan.
3. Next, go to **Filters**→ **Quality Measures and Computations**→ **Compute Geometric Measures** and paste all the measurements into the Sheets page.
4. If it says it's not watertight, select the scan, then go to **Filters**→ **Cleaning and Repairing**→ **Repair non-manifold edges**.
5. Then go to **Filters**→ **Remeshing, Simplification, and Reconstruction**→ **Close Holes**, and then try again.

Supplemental Material I. Video of *Attenborites* scan being inflated in Blender.