Intraspecific variation in an early skeletal metazoan: Namacalathus from the Ediacaran Nama Group, Namibia

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Intraspecific variation in an early skeletal metazoan: *Namcalathus* from the Ediacaran Nama Group, Namibia.
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ABSTRACT

*Namacalathus hermanastes* is one of the oldest known skeletal metazoans, found in carbonate settings of the terminal Ediacaran (~550-541 Million years (Ma) ago). The palaeoecology of this widespread, goblet-shaped, benthic organism is poorly constrained yet critical for understanding the dynamics of the earliest metazoan communities.

Analysis of in-situ assemblages from the Nama Group, Namibia (~548-541 Ma), shows that *Namacalathus* exhibited size variation in response to differing water depths, hydrodynamic conditions, and substrate types. In low energy, inner ramp environments, *Namacalathus* attains the largest average sizes but grew in transient, loosely-aggregating, monospecific aggregations attached to microbial mats. In high energy mid-ramp reefs, *Namacalathus* spatially segregated into different palaeoecological habitats with distinct size distributions. In outer ramp environments, individuals were small and formed patchy, dense, monospecific aggregations attached to thin microbial mats. Asexual budding is common in all settings.

We infer that variations in size distribution in *Namacalathus* reflect differences in habitat heterogeneity and stability, including the longevity of mechanically stable substrates and oxic conditions. In the Nama Group, long-lived skeletal metazoan communities developed within topographically heterogeneous mid-ramp reefs which provided diverse mechanically stable microbial substrates in persistently oxic waters, while inner and outer ramp communities were often ephemeral, developing during fleeting episodes of either oxia and/or substrate stability. We conclude that *Namacalathus*, which forms a component of these communities in the Nama Group, was a generalist that adapted to various palaeoecological habitats within a
heterogeneous ecosystem landscape where favourable conditions persisted, and was also able
to opportunistically colonise transiently hospitable environments. These early skeletal
metazoans colonised previously unoccupied substrates in thrombolitic reefs and other
microbial carbonate settings, and while they experienced relatively low levels of inter-
specific competition, they were nonetheless adapted to the diverse environments and highly
dynamic redox conditions present in the terminal Ediacaran.

INTRODUCTION

Ediacaran (580–541 million years ago) strata yield diverse non-skeletal and skeletal
macrofossils which record the emergence of metazoans and complex ecosystems. Many of
these forms have unresolved phylogenetic relationships, reproductive modes, and ecologies,
even though an understanding of these is critical to investigating the origins of the modern
biosphere.

Ediacaran macroorganisms may have been capable of multiple reproductive modes,
implying the presence of correspondingly complex developmental systems (Mitchell et al.,
2015). The terminal Ediacaran (~550-541 Ma) skeletal taxa Cloudina and Namacalathus
reproduced clonally through budding (Hua et al., 2005; Cortijo et al., 2010; Zhuravlev et al.,
2015a), but their broad geographic distribution suggests that like many extant benthic
invertebrates, they also possessed a dispersive, planktonic larval stage (Zhuravlev et al.,
2012, fig. 7; Cortijo et al., 2015). Size distributions, and bedding plane-scale spatial
distributions have further been used to distinguish reproductive style. For example, the
unmineralised taxa Funisia and Tribrachidium cluster into groups of similar size, suggesting
episodic larval settlement (Droser & Gehling, 2008; Hall et al., 2015), and Fractofusus shows
a recurring pattern of smaller individuals clustered around larger ones suggestive of clonal
reproduction via stolons (Mitchell et al., 2015).
Namcalathus has a goblet-like morphology, consisting of a hollow stem which flares to form a ‘cup’. The cup generally has 6 or 7 lumens in the side walls imparting a polygonal cross-section, and a larger opening at the top whose edges curl in towards a central cavity (Grotzinger et al., 2000; Watters & Grotzinger, 2001). On the basis of this distinctive but simple morphology, Namcalathus has been assigned various affinities. It has been interpreted as a possible cnidarian because of its goblet-shaped morphology and hexaradial cross-section (Grotzinger et al., 2000), a protozoan due to its small size and an apparent lack of accretionary growth (Seilacher et al., 2003), and a stem eumetazoan based on its symmetrical, stalked morphology and sessile, benthic life habit (Wood, 2011). More recently, a lophophorate affinity has been suggested, based on the presence of bilaterally symmetrical budding and a distinctive skeletal ultrastructure of a tripartite microlamellar construction with columnar deflections (Zhuravlev et al., 2015a).

Namcalathus occurs associated with thrombolitic reefs in carbonate inner, mid- and outer ramp settings in the Nama Group, Namibia (Grotzinger et al., 2000; Wood, 2011), and thrombolitic reefs in western Canada and Oman (Hofmann & Mountjoy, 2001; Amthor et al., 2003). Some fossils putatively attributed to Namcalathus are reported from in a mixed clastic-carbonate environment in West Siberia (Kontorovich et al., 2008; Grazhdankin et al., 2015) and in reefs associated with calcimicrobes in the Altay Sayan Foldbelt, South Siberia, Russia (Terleev et al., 2011). Siberian Namcalathus differs from all other fossils ascribed to this genus in possessing a phosphatic skeleton, and pores which are much more numerous than the lumens of Namcalathus and are distributed randomly across the cup, while in Namcalathus they are fairly uniform in number and position on the cup facets (Grazhdankin et al., 2015, fig.4g, h, l). It is also an order of magnitude smaller than the smallest Namcalathus from the type locality in Namibia, and from other localities globally (0.2 mm against 2 mm), and so its assignment to this genus is questionable.
To date, published studies on Namacalathus are mostly restricted to its morphology and biostatigraphic significance while its reproduction, relationship to substrate, environmental preferences, and other ecological traits have received comparatively little attention. Size distribution data may help constrain some of these uncertainties as Namacalathus shows notable size variation between localities both locally and globally. In the Nama Group, Namibia, cup diameters range from 2 to 35 mm (Grotzinger et al., 2000; Wood, 2011). Maximum cup diameters of 30 mm are reported from Oman (Amthor et al., 2003), and 17 mm from Canada (Hofmann & Mountjoy, 2001), giving a global size range from 2 - 35 mm, excluding Siberian forms. In assemblages from the Byng Formation of western Canada, size differences have been used to infer variation between environmental settings, with larger individuals (modal value ~12 mm) occurring in pockets betweenstromatolite columns and smaller individuals (modal size ~6 mm) in channel fills (Hofmann & Mountjoy, 2001).

Grotzinger et al. (2000) observed that Namacalathus was more abundant on thrombolites than on other substrates, and suggested that Namacalathus preferred the firm, elevated substrates provided by thrombolites in the Nama Group of Namibia. Wood (2011) noted that such habitats also appeared to support the largest individuals.

Metazoans, particularly skeletal ones, are strongly influenced by oxygen levels in their environments. The size and abundance of metazoans in modern benthic communities declines with bottom-water oxygen levels, as does biodiversity (e.g. Rhoads & Morse, 1971). Oxygen levels also have an impact on benthic community structure, with communities under sub-oxic conditions showing reduced pelagic-benthic coupling and suppressed community succession (Nilsson & Rosenberg, 2000; Broman et al., 2015). At reduced oxygen levels, communities also consist of smaller, shorter-lived species with opportunistic life histories and few predators (Diaz & Rosenberg, 1995; Sperling et al., 2013; 2015), and only very few metazoan taxa may live under permanently anoxic conditions (Danovaro et al., 2010). In addition to
oxygen level, redox stability plays a role: some metazoans tolerate temporary, but not permanent, anoxia (Bernhard et al., 2000; Müller et al., 2012). Consequently, both $pO_2$ and redox stability are likely to have been important controls on the structure of early metazoan communities (Johnston et al., 2012; Wood et al., 2015).

The terminal Ediacaran Nama Group, Namibia, was deposited under highly dynamic redox conditions, where shallow, inner ramp settings experienced transient oxygenation (Wood et al., 2015). These environments supported short-lived and monospecific skeletal metazoan communities of either Cloudina or Namacalathus. By contrast, microbial (thrombolite) reefs, found in deeper inner- and mid-ramp settings, support more diverse communities of organisms which constructed reefs and aggregations, may have had distinct environmental preferences, and could attain large sizes (Wood et al., 2002; Wood & Curtis, 2015). These long-lived reef communities, as well as Ediacaran soft-bodied biotas, are found particularly within transgressive systems, where oxygenation was persistent. A mid-ramp position may have enabled physical ventilation mechanisms for water column oxygenation to operate during flooding and transgressive sea-level rise. In the Nama Group it appears that the stability of oxygenated conditions may have controlled both the distribution and ecology of Ediacaran skeletal metazoan communities (Wood et al., 2015).

Here we explore Namacalathus size data and substrate relationships in the Nama Group, Namibia, in order to better constrain its environmental preferences and relationship to its substrate. Among other skeletal metazoans, Namacalathus colonized carbonate habitats where microbial mats were abundant, in the diverse environments presented by the late Ediacaran Nama Group. This raises the question of whether the earliest skeletal metazoans were generalists able to colonise a range of environments, or specialists requiring a narrow range of environmental conditions. We place size data within the context of hydrodynamic setting, substrate type and relative redox stability to explore local environmental controls on
early metazoan life habits and ecosystems. Such an analysis contributes to the ongoing
discussion of the role of environmental conditions and substrate types in controlling the
evolution and palaeoecology of Ediacaran metazoans.

**GEOLOGICAL SETTING**

The Nama Group (~550 – 541 Ma) is a terminal Ediacaran succession comprising a
foreland basin infill of marine shelf and fluvial deposits (Saylor *et al*., 1995). Fossiliferous
successions consist of mixed clastics and carbonates ranging from supratidal to outer ramp
settings with varying hydrodynamic conditions (Germs, 1995; Jensen *et al*., 2000; Geyer,
2005; Grotzinger & Miller, 2008).

The Nama Group was deposited across the Zaris and Witputs sub-basins (Fig. 1), which
have been correlated using a combination of sequence stratigraphy and chemostratigraphy
(Figs. 2 and 3) (Saylor *et al*., 1995; 1998). Carbon isotope measurements indicate that the
lower Nama Group was deposited during the final stages of the Shuram-Wonoka carbon
isotope excursion (Kaufman *et al*., 1991; Wood *et al*., 2015).

Zircons from ash beds in the Nama Group have provided radiometric dates (Fig. 2). The
earliest, dated to 547.32 ± 0.65 Ma, is in the Hoogland Member of the Kuibis Subgroup
(Grotzinger *et al*., 1995; revised by Schmitz, 2012), and provides a minimum age for the base
of the Nama Group. The age of the underlying base of the Nama Group is less certain, but is
estimated at around 550 – 553 Ma based on assumed sedimentation rates (Ries *et al*., 2009).
An intermediate date of 542.68 ± 1.245 Ma was obtained from an ash bed in the lower
Spitskopf Member of the Urusis Formation of the Schwarzrand Subgroup (Grotzinger *et al*.
1995; Schmitz, 2012). The youngest Ediacaran ash bed in the Nama Group, 130 m below the
youngest *Cloudina* and unmineralised Ediacaran fossils, but above the stratigraphically
highest *Namacalathus* assemblage in this study gave U-Pb dates of 540.61 ± 0.67 Ma in the
upper Spitskopf Member (Grotzinger et al., 1995 as 543.3 ± 1 Ma; date recalculated by Schmitz, 2012). A fourth ash bed in the lower Nomtsas Formation, above the unconformity that includes the Precambrian-Cambrian boundary, gave an estimated date of 538.18 ± 1.24 Ma, giving a minimum age for the Precambrian-Cambrian boundary in the Nama Group (Grotzinger et al., 1995; Schmitz, 2012). The localities in this study therefore span ≥ 6 Myr from the Lower Omkyk Member (> 547 Ma) to the Spitskopf Member (~ 541 Ma).

Environmental and redox settings of localities

Namacalathus assemblages were studied at five localities which represent three environments: Low energy inner ramp, high energy mid-ramp thrombolitic reefs, and low energy outer ramp (Table 1, Figs. 2 and 3, for locality coordinates, see Table SM 1). Below, we briefly document the sedimentology, and outline the redox dynamics of each setting.

Redox conditions for each of these localities has been inferred by Wood et al. (2015) based on a multiproxy approach using iron speciation (Fe$_{HR}$/Fe$_T$), total iron (Fe$_T$), and Fe/Al ratios, summarised in Table 1; for an explanation of the proxies see Table SM 2.

The use of geochemical proxies to explain biological patterns requires reconciliation of markedly different time scales of integration. Biological time scales, such as the time between successive generations are often short compared with the geological timescales over which sediment accumulates and geochemical signatures develop (Wood et al., 2015). In addition, iron speciation may not be sufficiently sensitive to detect whether pO$_2$ was above or below the crucial thresholds for metazoan life (Sperling et al., 2013). With care, however, geochemical proxies may be used to make inferences on local-scale palaeoenvironmental dynamics (Hall et al., 2013; Wood et al., 2015; Sperling et al., 2015; Jin et al., 2016).

The low energy inner ramp setting in the Omkyk Member is dominated by dolomitised micritic, laminated lithologies, with thinly bedded (~10-100 mm thickness) mudstones,
wackestones and packstones, which accumulated mainly during sea level highstands. Thin, closely-spaced, undulating laminae suggest that thin microbial mats developed regularly, binding fine grained sediment. $\text{Fe}_{\text{HR}}/\text{Fe}_T$, $\text{Fe}_T$ and $\text{Fe}/\text{Al}$ data show that such settings experienced only intermittent oxia, and benthic metazoan communities developed during these fleeting oxic episodes (Wood et al., 2015). Some beds with clearly in-situ $\text{Namcalathus}$ assemblages nonetheless present an anoxic iron speciation signature, even when microsampled (Wood et al., 2015). From this it has been inferred that the transient populations exploited brief periods of oxia in otherwise dominantly and more persistently anoxic settings, which may have been caused by periodic upwelling of anoxic deep waters (Wood et al., 2015).

Mid-ramp thrombolitic reefs in the Omkyk Member are associated with packstones, cross-bedded grainstones and breccias that developed during transgressive systems tracts in relatively energetic waters. These microbial reef complexes range from a few metres to kilometres in extent. Variable $\text{Namcalathus}$ ecology has been documented from these reefs, and includes attachment to thrombolite heads (Grotzinger et al., 2000; Wood, 2011), growth as monospecific sheet-like aggregations, intergrowth with $\text{Cloudina riemkeae}$ thickets, and growth within primary cavities (crypts) in thrombolitic reefs (Wood & Curtis, 2015). The very low $\text{Fe}_T$ of mid-ramp reef settings suggest that these were probably persistently oxic, especially during transgressive systems tracts, when large microbial reefs with calcified metazoan communities developed.

Swartpunt locality from the Spitskopf Member of the Schwartzrand Subgroup is interpreted as an outer ramp setting. Although the succession shallows to inner ramp environments, the sampled lower part of the succession is dominated by laterally continuous to discontinuous thin- to medium bedded (50-150 mm) wackestones and packstones. Some units show scoured bases and low relief channels. We infer deposition below fair weather
wave base, under weak current activity and occasional disturbance by storms. Thin, undulating, irregularly spaced laminae suggest that thin microbial mats developed intermittently, binding fine micritic or fine grain sediment. Very low Fe\text{\textasciitilde} suggests that these settings were probably deposited in oxic waters (Wood et al., 2015).

Size data were sub-divided by locality and setting, and individuals from mid-ramp reefs were further sub-divided into three palaeoecological habitats: those found adjacent to thrombolite heads, those in low-relief sheets on open surfaces, and those found within reef crypts. On the basis of these differing habitats, we infer that \textit{Namacalathus} occupied different specific areas within the overall metazoan-microbial ecosystem. In sum, we identify five palaeoecological habitats: Low energy inner ramp, Mid-ramp reef: Thrombolite association, Mid-ramp reef: Open surface sheet, Mid-ramp reef: Cryptic (occupying reef crypts), and Outer ramp.

\textbf{METHODS}

\textit{Namacalathus} fossils were identified as in life position on the basis of intact skeletons with an upwards growth \textit{perpendicular} to bedding planes. Some show skeletal deformation due to close-packed growth, or show the base of the stem anchored in sediment or attached to microbial mats. Measurements were taken from scans of rock samples, and from field photographs, and the cup diameter of in-situ \textit{Namacalathus} individuals was recorded (see Table SM 7).

Because of the three-dimensional preservation of \textit{Namacalathus} in the Nama Group, exposed or cut rock surfaces present a variety of different sections through the skeleton due to variations in the orientation of individuals relative to exposed rock surfaces. Consequently, a complete set of measurements is impossible on most \textit{Namacalathus} individuals. However, cup diameter is commonly measurable, so has been used as a size indicator. Field
photographs and scans of rock specimens were imported into ImageJ for data collection, and measurements were made from all clearly visible individuals in each image; specimens where cup diameter could not be measured or identification as *Namcalathus* was not certain were excluded.

Different sections through the skeleton were categorised into ‘vertical’, ‘horizontal’ and ‘oblique’ as the type of section measured can alter the apparent size. ‘Vertical’, ‘horizontal’ and ‘oblique’ sections are defined as follows: ‘vertical’ sections represent a slice parallel to the growth axis of the fossil which includes both the apical opening in the cup and the hole at the base of the stem. ‘Horizontal’ sections through the cup are perpendicular to the growth axis and preserve the outer wall of the cup together with the 5-7 lateral lumens. ‘Oblique’ sections are any other section through the apical cup. An oblique section through a goblet shape is likely to show a smaller cup diameter than a vertical or horizontal section.

Vertical and horizontal sections are most useful as they permit a consistent comparison of measurements between individuals. However, oblique sections are also useful as they provide a minimum size constraint, so they have been included in this analysis. Maximum measured cup diameter at each site may also usefully reflect size differences between palaeoecological habitats, although is not amenable to statistical testing. When describing *Namcalathus* assemblages, we therefore use the median for statistical purposes (for a justification of this, see the Shapiro-Wilk normality test in Results section), but also quote the maximum cup diameter.

Where vertical sections were available, both cup diameter and cup height measurements were taken (see Table SM 8), to determine whether *Namcalathus* individuals in different settings shared a growth trajectory. Since vertical sections, which are required for cup height measurements, are much rarer than oblique ones, this dataset is much smaller than the cup diameter dataset and consequently has not been subjected to the same statistical analyses. In
total, 398 sections were measured, of which 97 were vertical; there are five vertical sections for which cup height was not measured due to breakage at the apical part of the cup. For all statistical tests, p-values lower than 0.05 were taken as significant. Statistical tests were performed in PAST, version 3.02 (Hammer, 2014), and in R.

To determine whether the cup diameter data were normally distributed, and inform further statistical tests, a Shapiro-Wilk test was applied to the data from each of the five palaeoecological habitats, and to the dataset as a whole. The Shapiro-Wilk test was selected due to its statistical power, and was first applied to the raw data, then to the log-transformed dataset. In the Shapiro-Wilk test, the null hypothesis ($H_0$) is that the data were taken from an assemblage with a normal distribution.

The Kolmogorov-Smirnov test was used to compare the overall cup diameter distribution across all data with the distributions in each of the five palaeoecological habitats (Table SM 5). The Kolmogorov-Smirnov test is a pairwise non-parametric test which detects differences in both the shape and position of a distribution, and was selected because it makes no assumptions about the distribution of the data, and its application in this way avoids multiple comparisons problems which can lead to Type 1 errors. In the Kolmogorov-Smirnov test, the null hypothesis ($H_0$) is that the two samples under comparison come from assemblages with the same distribution.

To compare the median cup diameter values from each dataset, a Kruskal-Wallis test was performed. The Kruskal-Wallis test is a multiple samples test whose null hypothesis ($H_0$) is that there is no statistically significant difference between the medians of the samples. The test was selected because it does not require an assumption that the data are normally distributed.

Although the results of the Kruskal-Wallis test do not identify the sources of statistically significant differences in the median between samples, this can sometimes be ascertained by
visually comparing the data distributions of the samples. However, Mann-Whitney tests were also carried out on all possible pairs of palaeoecological habitats to ascertain where statistically significant differences in the median lay, as data from some palaeoecological habitats gave visually similar distributions. In the Mann-Whitney test, the null hypothesis ($H_0$) is that there is no significant difference between the medians of two samples. A Bonferroni correction was applied to remedy the potential problem of multiple comparisons leading to Type 2 errors (i.e. falsely identifying significant differences). A linear regression was used to determine if the cup diameter and cup height of all vertical sections correlated, with the aim of determining if they had a shared growth trajectory. A Spearman’s Rank correlation coefficient ($r_s$) was also calculated to quantify the correlation, and was selected because it makes no assumptions about data distribution. If $r_s = 1$ or -1, there is a perfect monotonic relationship between the two variables (in this case, cup height and cup diameter).

**RESULTS**

**Aggregation Style**

*Namacalathus* commonly occurs in densely aggregated assemblages which range from decimetre to metre scale. In the inner ramp setting, some in-situ *Namacalathus* occur as isolated individuals (Fig. 4A, C), but most are found in aggregations of up to 0.5 m diameter (Fig. 4B).

In mid-ramp reefs, small (<0.5 m) aggregations are associated with thrombolite heads. These close-packed aggregations contain individuals of up to 35 mm cup diameter, though a range of individual sizes occurs (Fig. 5A, B, F). Some of these large individuals also have external spines, though the sample contains too few individuals with this feature to statistically analyse its occurrence (Fig. 5B). On open surfaces in mid-ramp reefs, *Namacalathus* aggregates to form sheets of up to 5 m in diameter (Fig. 5D, G), and also
intergrow with extensive (> 20 m in diameter) thickets of *Cloudina riemkeae* (Fig. 5E, D, Wood & Curtis, 2015). One open surface aggregation appeared to contain individuals whose cups are slightly ellipsoidal, with a preferential orientation to their long axes, though the sample is small (Figs. SM 1, 2); however, oblique sectioning of a uniformly oriented assemblage of in-situ fossils cannot be discounted. The small available sample size for the cryptic habitat does not permit an assessment of aggregation style (Fig. 5C).

In the low energy outer ramp, small lenticular aggregations (<0.3 m diameter) occur (Fig. 6A, C, D). These aggregations develop very little topographic relief, and may occupy scours produced by periodic storms.

**Cup Diameter**

In total, 398 individuals were measured, and of these 97 were represented by a vertical section through the skeleton, 12 by horizontal sections, and 289 by oblique sections. Cup diameter data are given in Table SM 7.

The Shapiro-Wilk test returned a p-value of 9.156E-16 when applied to the whole cup diameter dataset, and 0.003318 when applied to the log-transformed dataset, implying that the data do not show a normal or log-normal distribution overall. Histograms of the cup diameter data were also plotted to give a visual indication of the data distribution (Fig. 7). These show a highly non-normal distribution, with most individuals tending towards the smaller end of the size scale. This distribution persists whether the whole cup diameter dataset is plotted, or just data from vertical and horizontal sections, which we might expect to reflect true cup diameter more accurately.

The results of the Shapiro-Wilk test on cup diameter datasets from each of the five palaeoecological habitats are given in the Supplemental Material (Table SM 3). All returned p-values below 0.05, so we reject the null hypothesis that the cup diameter data are normally
distributed. In the case of the outer ramp locality, the p-value returned was 0.049, very close to the critical value but still below it.

The Shapiro-Wilk test was repeated on the log-transformed cup diameter data for each palaeoecological habitat, returning p-values over 0.05 (Table SM 4), so we cannot reject the null hypothesis that the log-transformed data from each palaeoecological habitat are normally distributed.

Since the untransformed cup diameter data are not normally distributed, the median was used for comparison of central tendency between habitats (Fig. 8A). Inner ramp individuals have the largest median cup diameter (8.0 mm) and also show a larger range of cup diameters than the outer ramp. The outer ramp showed the smallest median cup diameter (4.4 mm), and the smallest range. In mid-ramp reefs, individuals from the three distinct habitats have different cup diameter ranges. Individuals associated with thrombolite heads have a median cup diameter of 7.7 mm. Those growing on open surfaces or intergrown with Cloudina riemkeae had a median cup diameter of 6.9 mm, and individuals in reef crypts have a median cup diameter of 5.8 mm.

Non-parametric tests were applied to the untransformed cup diameter data to assess the statistical significance of differences between size distributions. Kolmogorov-Smirnov tests were applied to Namacalathus cup diameter datasets from each palaeoecological habitat, to compare them with the overall cup diameter distribution for all data. Results are tabulated in Supplementary Materials (Table SM 5). For all palaeoecological habitats except for the mid-ramp reef open surface, the Kolmogorov-Smirnov test returned a p-value lower than 0.05, so we may reject the null hypothesis that cup diameter distributions within the other palaeoecological habitats match the overall distribution of the data.

The Kruskal-Wallis test returned a p-value of 2.9E-19, so we reject the null hypothesis that there is no significant difference in the median cup diameter of samples from each of the
five palaeoecological habitats. Bonferroni corrected p-values resulting from the Mann-Whitney tests on all pairs of samples are given in Table SM 6, and vary from $p = 1.43 \times 10^{-15}$ (for the comparison of the outer ramp with low energy inner ramp palaeoecological habitats) to $p = 1$ (for the comparison of the low energy inner ramp and mid-ramp reef thrombolite associated samples).

According to the Mann-Whitney tests, the median cup diameter in the low energy inner ramp palaeoecological habitat was significantly different to that of all other palaeoecological habitats ($p$-values of $1.43 \times 10^{-15}$ to $0.01665$) except to that of the mid-ramp reef thrombolite association, which returned a $p$-value of 1. Within the mid-ramp reef setting, there was no significant difference between the median cup diameters of the open surface, thrombolite-associated and cryptic palaeoecological habitats ($p$-values of 0.1195 to 0.4417), though the open surface and cryptic palaeoecological habitats hosted *Namacalathus* with a significantly different median cup diameter to the low energy inner ramp and outer ramp habitats ($p$-values of $6.07 \times 10^{-14}$ to $0.01665$). Finally, the outer ramp *Namacalathus* assemblage had a significantly different median cup diameter to the assemblages from all other palaeoecological habitats ($p$-values of $1.43 \times 10^{-15}$ to $0.005758$).

Though not amenable to statistical analysis, maximum cup diameter may also be informative due to the prevalence of oblique sections in our dataset. Inner ramp individuals have a maximum cup diameter of 23.7 mm, while in the mid-ramp reef environment, individuals in cryptic environments had a maximum cup diameter of 12 mm, those on open surfaces 18.4 mm, and in thrombolite associations 35.1 mm. Outer ramp settings show the smallest maximum cup diameter at 8.9 mm.

To check whether all individuals in the dataset shared a growth trajectory, cup height was plotted against cup diameter for 92 vertical sections from the entire dataset, regardless of habitat. Spearman’s Rank correlation coefficient ($r_s$) returned a value of 0.84506, suggesting
a correlation between the two. A major axis linear regression model was fitted to the data and
visual inspection shows that that cup height appears to be proportional to cup diameter across
all data (See Fig. 8B).

**Relationship to substrate**

In the inner and outer ramp settings, *Namacalathus* is anchored to or within thin microbial
laminae by the base of the stem, occupying small primary depressions in the surface of the
microbial laminae (Figs. 4C and 6B, D). By contrast, mid-ramp settings provided
thrombolitic substrates. While direct contact between the bases of stems and thrombolite
surfaces was not observed in the mid-ramp reefs, early cements encase the erect
*Namacalathus* individuals, suggesting that they are in life position. Forms in reef crypts are
also attached to thrombolitic substrates (Fig. 5C). The attachment of the sheet-like
aggregations is not clear, but these may be attached to *Cloudina riemkeae* thickets intergrown
with thrombolite (Wood & Curtis, 2015).

**Budding distribution**

Regular bilateral budding in *Namacalathus* was reported in the outer ramp (Figs. 6D and
E) and inner ramp (Fig. 4B) (Zhuravlev et al. 2015a). In contrast, smaller individuals are
sometimes apparently randomly attached to the inner or outer cup surfaces of larger
individuals in mid-ramp thrombolites (Fig. 5A). This may reflect attachment to the pre-
existing abandoned skeletons of other individuals.

In the inner ramp, budding is common (Fig. 4B) and smaller individuals also frequently
occur within larger forms. In the mid-ramp setting the skeletal continuity between individuals
observed in open surface assemblages is suggestive of budding. In the thrombolite-associated
setting, one or more small individuals are observed inside the cup of larger individuals,
apparently attached (Fig. 5A). Individuals in reef crypts exhibited no budding, though the sample size here is small.

In the outer ramp, *Namacalathus* forms small, dense aggregations with individuals commonly displaying budding. Here, two possible generations of buds are noted on some individuals (Fig. 6D, E)

**DISCUSSION**

*Namacalathus* occupied diverse carbonate settings in terms of water depth, hydrodynamic energy, and variable microbial substrate types (Fig. 9), and *Namacalathus* from different palaeoecological habitats show distinct size distributions (Fig. 8B). However, cup diameter and cup height data correlate across all settings, suggesting that all *Namacalathus* individuals shared the same growth trajectory (Fig. 8B). This implies that they belong to one taxon showing considerable intraspecific size variation, rather than *Namacalathus* in different settings representing different species with distinct environmental preferences. Since size in metazoans is influenced by a variety of factors, many of which are not amenable to explanation using the environmental factors discussed identified here, we will not attempt to assign particular environmental causes to the differences in median cup diameter between palaeoecological habitats. Quantifying size and comparing size distributions can, however, yield information on the adaptations of metazoans to their environments.

*Namacalathus* attains the largest median cup diameter and a large size range (3.6 – 23.7 mm) within aggregations in the low energy inner ramp environment, though does not attain the maximum sizes found in mid-ramp reef thrombolite-associated individuals (35.1 mm). Statistically, there is no significant difference between the median cup diameters of *Namacalathus* assemblages in the low energy inner ramp and the mid-ramp reef. In the inner ramp settings, thin microbial mats were preferentially colonised, and despite geochemical
evidence for only transient oxygenation on geological timescales, there is evidence of budding which implies that multiple generations developed on the same sites.

In the mid-ramp reef setting, *Namacalathus* occupied at least three palaeoecological habitats, though these assemblages show no statistically significant differences in cup diameter. *Namacalathus* assemblages from each habitat do however show substantial differences in maximum cup diameter and differing size distributions, as well as occupying differing substrates. Individuals in depressions between microbialite mounds attained the largest maximum sizes (Grotzinger et al. 2000; Hofmann & Mountjoy, 2001; Wood, 2011), while individual sizes show a large range and the attachment of smaller individuals to larger ones suggests that multiple generations were present. The low-relief open surface assemblages do not show a cup diameter distribution that differs significantly from the cup diameter distribution across the whole dataset, but the cup diameter distribution of the assemblage in reef crypts does differ significantly from the overall distribution, likely because of their smaller cup diameters and smaller size range (Fig. 8A). We suggest that persistently oxic conditions and the range of varied, mechanically stable substrates in such topographically complex habitats may have allowed occupancy of a wider range of substrates over longer timescales.

By contrast, the inner and outer ramp environments lack any differentiation into different habitats, which may in part reflect the lack of topographic heterogeneity offered in these settings compared with mid-ramp reefs. The outer ramp *Namacalathus* individuals are generally much smaller than those in the inner or mid-ramp, though the presence of budding or multiple generations suggests that the outer ramp hosted assemblages of mature, reproducing individuals. Nonetheless, *Namacalathus* in transiently hospitable inner and outer ramp settings may still have experienced early mortality or shown high growth rates. This may be compared to modern populations which show an adaptive response to stressful
conditions resulting in early growth cessation and reproductive onset combined with early
and high adult mortality (Perry & Dominy, 2009; Whiteman et al., 2012). Regardless, it
appears that *Namacalathus* was adapted for life in transiently hospitable environments.

In modern ecosystems, species that first colonise newly available heterogeneous
landscapes in the absence of strong intra-specific competition, e.g., fishes in postglacial lakes,
often establish co-existing sympatric morphotypes (Rundle et al., 2000; Klemetsen, 2010).
These can show remarkably different sizes, mouth parts, and behaviour within single lakes
even in the absence of reproductive isolation because such morphs are adapted to different
resource niches (Klemetsen, 2010). While there are few studies on low-competition benthic
metazoan communities, high rates of sympatric speciation are observed among benthic
cacenogastropods of the East African Great Lakes due to phenotypic plasticity which in turn
reflect a rising opportunity for ecophenotypes to occupy different substrates (Salzburger et
al., 2014). It is possible that carbonate settings in the late Ediacaran presented a similar
landscape of low competition with a limited number of metazoan species forming low
diversity communities. This may have promoted the intraspecific size variation of
*Namacalathus* noted here, allowing differentiation into morphs of different sizes due to
adaptation to various substrates, relative redox stability or variable hydrodynamic conditions.
This is particularly evident in the difference in median cup diameter between the outer ramp
*Namacalathus* and those in the rest of the dataset.

Size differentiation may indicate intraspecific niche partitioning, particularly in mid-ramp
reefs, whereby natural selection drives members of a species into different sub-groupings
according to different patterns of resource use or niches. Alternatively, the differences in size
distribution may represent intraspecific ecophenotypic variation - a phenomenon well-
documented in sessile benthic metazoans (e.g. Alexander, 1975; Scrutton, 1996; Gittenberger
& Hoeksema, 2006; Zieritz & Aldridge, 2009).
Namaclathus appears to have been an environmental generalist, occupying a range of
different settings from inner ramp lagoons to more distal ramp environments, and both open
surface and cryptic habitats in mid-ramp reefs. It was capable of high intraspecific size
variation, and may have differentiated into size morphs. Variable redox conditions and
otherwise transiently available habitats appear not to have been a barrier to growth and
reproduction despite Namaclathus’ presumed reliance on oxygen for maintenance of
metabolism. A tendency towards opportunistically colonising areas during transient periods
of oxia would have served Namaclathus well in the Nama Group in the late Ediacaran, and
it is possible that this was a widespread ecological strategy among Ediacaran skeletal
metazoans.

This highly generalist behaviour whereby Namaclathus occupied different
microenvironments via intraspecific variation and possibly the development of different size
morphs adapted to local conditions contrasts with the next phase of sessile calcified metazoan
development, represented by the lower Cambrian Stage 2 (~535 – 525 Ma) archaeocyathan
reefs of the Siberian Platform. Here, different microenvironments were occupied by
specialised representatives of different species and genera (Zhuravlev & Wood, 1995;
Debrenne & Zhuravlev, 1996; Zhuravlev, 2001; Zhuravlev et al., 2015b). As such, we may
infer an escalation in levels of inter-specific competition in sessile skeletal metazoans from
~548 to 535 Ma.

CONCLUSIONS

Namaclathus occupied a variety of palaeoenvironments in the Nama Basin, and exhibited
intraspecific size variation between settings. The largest individuals lived in association with
mid-ramp reef thrombolites, while the smallest lived in cryptic habitats in mid-ramp reefs,
and in more distal ramp environments. In mid-ramp reefs, Namaclathus occupied a range of
habitats, and formed large, persistent aggregations in association with other early skeletal metazoans. This is likely to be due to the mechanical stability of substrates and persistence of oxic waters in this habitat.

We conclude that *Namacalathus* was an environmental generalist that colonised both persistently and transiently oxic habitats, and spatially differentiated into populations with differing size distributions. As such, *Namacalathus* was adapted to the various substrates and sometimes highly dynamic redox environment that characterized the late Ediacaran Nama Group. This contrasts with the situation in early Cambrian metazoan reefs, whereby individual taxa were specialised for particular microenvironments, and may reflect a trend from generalist to specialist in the earliest sessile metazoans of shallow marine carbonate settings.

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**TABLE AND FIGURE CAPTIONS**

Table 1. Table showing localities sampled, stratigraphic position, dominant lithology and inferred ramp setting. Redox data and interpretations from Wood et al. (2015).

Figure 1. Geological map showing the Nama Group, Namibia (after Grotzinger et al., 2000).


Abbreviations: U. Mbr = Urikos Member; Z. Fm = Zaris Formation; OS1 = Zaris Subbasin
Sequence Boundary OS1; K1 = Witputs Subbasin Sequence boundary K1; S1 = Witputs Subbasin Sequence boundary S1, PC-C = Precambrian-Cambrian boundary.

Figure 3. Fossil occurrences and inferred redox conditions at the five study localities in the Nama Group. Redox conditions inferred from iron speciation, total iron and total organic carbon measurements in carbonates and shales. Modified from Wood et al. (2015).

Figure 4. *Namacalathus* in low energy inner ramp settings in the Nama Group. A – View on a bedding plane showing *Namacalathus*. Lack of breakage suggests little or no transport, and these may be in life position, with vertical sections provided by toppled individuals. B – View on a bedding plane showing an aggregation. Rare wall deflections may result from close-packed growth, and suggest that these individuals are in growth position. Occasionally smaller individuals occur within larger ones, which may be a result of asexual budding (white arrow). C – Two small *Namacalathus*. The individual to the right shows a stem embedded in thin, undulating laminae.

Figure 5. *Namacalathus* in mid-ramp reefs in the Nama Group. A – Transverse section of the cup of a large *Namacalathus* individual containing at least four smaller individuals, one of which has an apparent attachment to the inner cup surface of the larger individual (arrow). B = Botryoidal early cement, S = Sparry late cement. B – View down on a bedding plane showing *Namacalathus* occupying depressions between thrombolite heads, in the ‘thrombolite associated’ palaeoecological habitat. C – Small *Namacalathus* attached to the ceiling of a reef crypt (white arrows). The original crypt is defined by large crystals of dark, early aragonite cement, now neomorphosed to calcite (Wood & Curtis, 2015). D – Closely aggregated *Namacalathus* of uniform size, forming a metre-scale aggregation on an open surface (Wood

Figure 6. *Namacalathus* from an outer ramp setting. A - Aggregated individuals in the outer ramp. B – Two small *Namacalathus* with geopetal infills showing that these examples remained in-situ while micrite was deposited within them. A well-preserved stem is anchored within microbial mat (arrow). C – Small, monospecific, lenticular aggregation enclosed in microbially bound micrite in outer ramp setting. D – Enlargement of C showing *Namacalathus* stems attached to other individuals or to the substrate (white arrows). E – Enlargement of C showing *Namacalathus* individuals attached to each other by their stems, possibly indicating budding (arrows).

Figure 7. Cup diameter distributions for the entire size dataset and for vertical and horizontal sections only. Both show a near-lognormal distribution.

Figure 8. A - Box and whisker plots of cup diameter data for *Namacalathus* from three settings, with the mid-ramp reef setting subdivided into three palaeoecological habitats. “Thromb. Association” = Thrombolite association. Whiskers show the range of the data, while upper and lower boundaries of the boxes show the first and third quartiles. Medians are 8.0 mm for inner ramp; 6.9mm for mid-ramp open surfaces, 7.7mm for *Namacalathus* in thrombolite associations, 5.8 mm in cryptic environments; and 4.4 mm for outer ramp. B - Cup height against cup diameter for all individuals in the three settings, with a major axis linear model suggesting a linear relationship. $R^2 = 0.89867$. Data are given in Table SM 7.
Figure 9. Composite schematic transect placing *Namalathus* palaeoecologies within a palaeoenvironmental context. Scale bars represent 10mm. A – Inner ramp monospecific aggregations of large *Namalathus* on a microbially bound micritic substrate. These have the largest median cup diameter of any palaeoenvironment in this study, but not the largest maximum cup diameter. B-E, mid-ramp reef settings. B – Large *Namalathus* in association with thrombolites. C – Small *Namalathus* pendant from primary crypt ceilings. D – Thrombolite association of individuals of various cup diameters, with long stems. Smaller individuals appear to be attached to the inner cup surfaces of the larger individuals. E – *Namalathus* intergrowing with *Cloudina riemkeae* to form metre-scale reefs on open surfaces. F – Small aggregations of small *Namalathus* on a microbially bound substrate in outer ramp setting, with small individuals attached to, or budding from, pre-existing ones.
<table>
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<tr>
<th>Locality</th>
<th>Stratigraphy</th>
<th>Dominant Lithology</th>
<th>Ramp Setting</th>
<th>Redox Data</th>
<th>Redox State</th>
</tr>
</thead>
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<td>Omkyk Farm</td>
<td>Omkyk Member</td>
<td>Flaggy limestone and dolomites and wackstone and packstone</td>
<td>Inner Ramp</td>
<td>Fe/Al 0.612-4.198</td>
<td>Predominantly anoxic, with fleeting oxia</td>
</tr>
<tr>
<td>Zebra River</td>
<td>Omkyk Member</td>
<td>Flaggy limestone and dolomites and wackstone and packstone, microbialite reefs</td>
<td>Inner Ramp</td>
<td>Fe$_T$ 0.02-2.66</td>
<td>Predominantly anoxic, with fleeting oxia</td>
</tr>
<tr>
<td>Pinnacle Reefs</td>
<td>Feldschuhhorn</td>
<td>Microbialite reefs</td>
<td>Mid-Ramp</td>
<td>Fe$<em>T$/Fe$</em>{Al}$ 0.032-0.876</td>
<td>Probably persistently oxic</td>
</tr>
<tr>
<td>Driedoornvlakte</td>
<td>Upper Omkyk Member</td>
<td>Microbialite reefs</td>
<td>Mid-Ramp</td>
<td>No data</td>
<td>Not measurable as Fe$_T$ &lt; 0.5%</td>
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<tr>
<td>Swartpunt</td>
<td>Spitzkopf Member</td>
<td>Lenses of wackstone and packstone</td>
<td>Outer Ramp</td>
<td>No data</td>
<td>Probable oxic conditions predominate at level of Namacalathus; possible brief episodes of anoxia towards top of section (above Namacalathus occurrence).</td>
</tr>
</tbody>
</table>

**TABLE 1**
Figure 1
Figure 7
For Review Only
Figure 9