The first animals: ca. 760-million-year-old sponge-like fossils from Namibia

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One of the most profound events in biospheric evolution was the emergence of animals, which is thought to have occurred some 600–650 Ma. Here we report on the discovery of phosphatised body fossils that we interpret as ancient sponge-like fossils and term them *Otavia antiqua gen. et sp. nov*. The fossils are found in Namibia in rocks that range in age between about 760 Ma and 550 Ma. This age places the advent of animals some 100 to 150 million years earlier than proposed, and prior to the extreme climatic changes and postulated stepwise increases in oxygen levels of Ediacaran time. These findings support the predictions based on genetic sequencing and inferences drawn from biomarkers that the first animals were sponges. Further, the deposition and burial of *Otavia* as sedimentary particles may have driven the large positive C-isotopic excursions and increases in oxygen levels that have been inferred for Neoproterozoic time.

Introduction

Evidence for the early evolution of animals has been documented from three main fossil assemblages of Ediacaran age (635–542 Ma). The first assemblage consists of phosphatised embryos, recovered principally from sedimentary successions in South China.[1,2,3] The second is defined by large, complex fossils known collectively as the Ediacaran, of worldwide occurrence, which arose and largely went extinct through the last third of that geological period.[4,5] The last is a group of small biomineralisers that first evolved about 550 Ma.[6,7] These fossil discoveries reveal a relatively rich assemblage of organisms preserved in strata that predate by several tens of millions of years the base of the Cambrian at 542 Ma.[8,9,10] Although older trace fossils have been assigned an animal origin,[11,12] no undisputed body fossils of animals are known from rocks older than about 650 Ma. Nevertheless, molecular clock estimates place the origin of metazoans much deeper in time and predict that a major split in animal evolution occurred some 100 to 300 million years prior to the Cambrian explosion[13,14,15] – an event that is thought to define the advent of sponges and subsequent divergence of all other animals. An exciting discovery in Australia in rocks 650–635 million years old of inferred animal-body fossils thought to be sponges[16] supports the contention that Porifera may form the oldest group of animal lineages.

Ediacaran-age sponge embryos and/or siliceous spicules have been documented in the Doushantuo Formation in south China,[17] Tsagaan Gol Formation in south-western Mongolia[18] and the Ediacara fauna of south Australia (Palaeophragmodictya).[19] These fossils are interpreted as either Demospongiae or Hexactinellida. In the Nama Group from southern Namibia, *Namapoikia rietoogensis*, a biomineralised metazoan that grew to as much as 1 m in diameter, is thought to have had a cnidarian or poriferan affinity.[20] Molecular biomarkers of marine demosponges that are somewhat older than 635 Ma have been found in rocks of the Huqf Supergroup in south Oman.[21] The forms reported herein and described below are interpreted as animal fossils but are much older than any yet reported: time constraints indicate that the organism evolved at least 760 Ma in the Cryogenian.

The marine carbonate rocks that formed in the Neoproterozoic oceans in which these organisms lived are marked by C-isotopic compositions much more enriched in ^{13}C than found in the previous billion years, or in the subsequent half billion years of the Phanerozoic; these long-lived high $\delta^{13}C$ plateaux were themselves punctuated by shorter-lived, large-amplitude excursions.[22] Although some workers have concluded that such patterns are as a result of diagenetic effects,[23,24] the systematic nature and coherence of C-isotopic trends from numerous sections worldwide is not easily accommodated in such a model. We offer an additional and alternative idea: that the evolution of the organisms described herein, with an exterior shell, initiated a global-scale burial of organic matter that was encased in hard parts. This sedimentation would have removed

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isotopically light organic matter from the oceans, thereby contributing to enrichment of marine carbonates in ^{13}C; such a perturbation of the global C cycle could also have influenced oxygen budgets.

Methods

Individual hand-sized samples of black limestones from the Otavi and Nama Groups in Namibia (Figure 1) were collected and dissolved in acetic acid. More than 800 thin sections of rock were examined and over 1000 *Otavia* specimens were hand-picked from the acid residues.[25] Representative *Otavia* were picked for analyses using scanning electron microscopy (SEM), electron probe imaging (BSE), cathode luminescence microscopy (CL) and X-ray microtomography (XMT) (see Box 1 for details). In addition, 153 rock samples spanning the lithologies and stratigraphy in which *Otavia* fossils have been found were analysed for carbonate C–O stable isotope ratios at the Scottish Universities Environmental Research Centre; those data will be reported in a separate article.

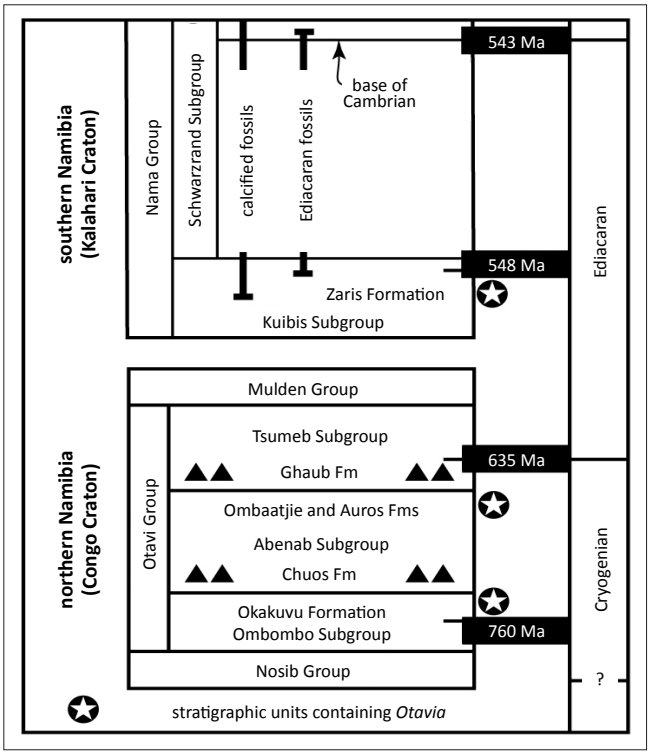
Results

Prior to a detailed discussion of the inferred fossil, we pose and answer two fundamental methodological questions related to our underlying assumptions:

1. Is there any evidence that the ensemble of objects (i.e. the inferred microfossils) is derived from one or more genetically related populations?
2. Is there a priori quantitative evidence *against* biogenicity of the objects?

The measured size distribution of the objects recovered at two of the richest sampling sites (both in Etosha National Park, Namibia) provides an answer to the first question. The null hypothesis is that the objects are not genetically related, and so no internally consistent size distribution is expected at either site. In Figure 2a the diameter X (defined as the midpoint of the observed range of sizes) is plotted against the percentage of the observed population with diameter less than X. A linear relationship in this log-probability plot is usually taken as *prima facie* evidence of a log-normal distribution of sample sizes.[26] Data from each site are, to first order, impressively linear and so the null hypothesis is rejected. This result deals satisfactorily with the issue of the ensembles of observed objects being part of a genetically related population at each locality. We remain uncertain as to why there are size differences, but it likely reflects an environmental control in that the larger specimens are recovered from a locality that represents relatively deeper, quieter conditions. Work is continuing on this issue.

We also stress that this conclusion provides no evidence of biogenicity: for example, Fallick et al.[27] demonstrated convincing evidence for a truncated lognormal distribution of sizes for a suite of iron droplets in lunar soil 10084. Given that our positive size–distribution analysis cannot be taken as *prima facie* evidence of biogenicity, we then address the second of the above questions and ask: is a lognormal distribution of object sizes *consistent* with biogenicity? That the answer to this question is positive is proved by data derived from Javaux et al.[28] and plotted in Figure 2b. Those workers described specimens that are believed to be 3.2-billion-year-old organic-walled microfossils, and are thus accepted as biogenic. The scatter about the line in the log–probability plot is not distinctly different from the scatter associated with the objects we propose herein as biogenic fossils.



Sources: Radiometric age constraints: 760 Ma,[22] 635 Ma,[25] 548 Ma and 543 Ma.[8]
Note: Please see the full reference list of the article, Brain CK, Prave AR, Hoffmann KH, et al. The first animals: ca. 760-million-year-old sponge-like fossils from Namibia. S Afr J Sci. 2012;108(1/2), Art. #658, 8 pages. http://dx.doi.org/10.4102/sajs.v108i1/2.658, for more information.

FIGURE 1: Generalised Cyrogenian and Ediacaran stratigraphy of the Neoproterozoic Otavi and Nama Groups of northern and southern Namibia, respectively. Triangle symbols denote the glacigenic Chuos and Ghaub Formations. Timing of calcifying and Ediacaran fossils is shown. Note that the Congo and Kalahari cratons were landmasses separated by an ocean during much of Neoproterozoic time.

BOX 1: Details of techniques used to image representative *Otavia* specimens.

Scanning electron microscopy	High-energy electrons are focussed into a beam and targeted onto the surface of an object. The surface morphology can thus be examined at very high resolution to obtain detailed images of the object.
Electron probe imaging	Backscattered electrons are high-energy electrons that rebound from the sample surface with high mean atomic number areas appearing brighter than lower areas and, when combined with spectrometers, compositional images can be produced.
Cathodoluminescence	Some minerals emit characteristic visible light or cathodoluminescence when bombarded by an electron beam, and differing amounts and types of trace elements and structural defects within a mineral produce different wavelengths and intensities of light, thereby providing information on composition and growth histories of mineral grains and cements.
X-ray microtomography	A non-destructive method of visualising and characterising objects in three dimensions in which a series of X-ray projections are recorded as the sample is rotated through 360°; variations in the contrast of the projection images relate to the density of the sample material and images are reconstructed to create a three-dimensional digital structure of the sample using specialised software.

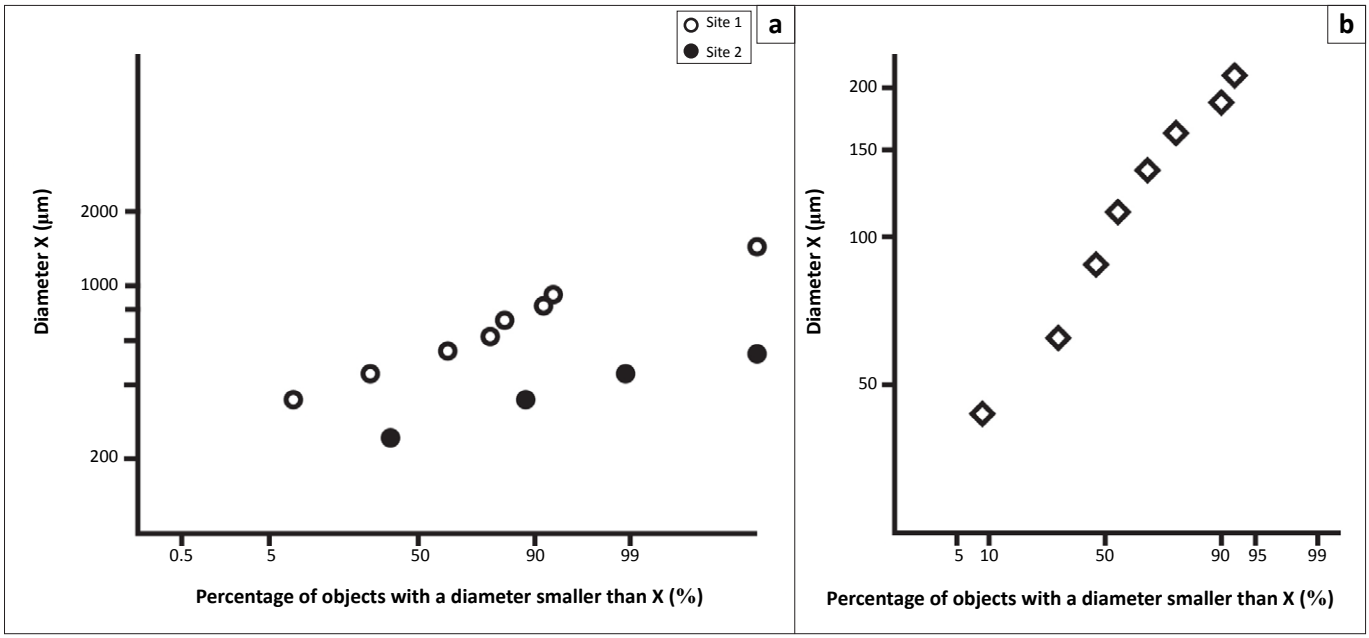


FIGURE 2: (a) Plot of the percentage of objects that have a diameter less than X µm versus the diameter X µm (defined as the midpoint of the range; from observations by CK Brain) for two fossil-bearing sites in Etosha National Park, Namibia. For Site 1 the population was 200 objects and for Site 2 the total was 90. A straight line in this plot is usually considered as *prime facie* evidence for a lognormal size distribution. (b) Log-log plot as in 2a, but for the size distribution data on 3.2 Ga organic-walled microfossils[28] (compare with Figure 2a for linearity).

Hence, our fundamental questioning of core assumptions has been satisfactorily dealt with. What follows is a detailed description of the putative fossils themselves.

Otavia fossils: Stratigraphy

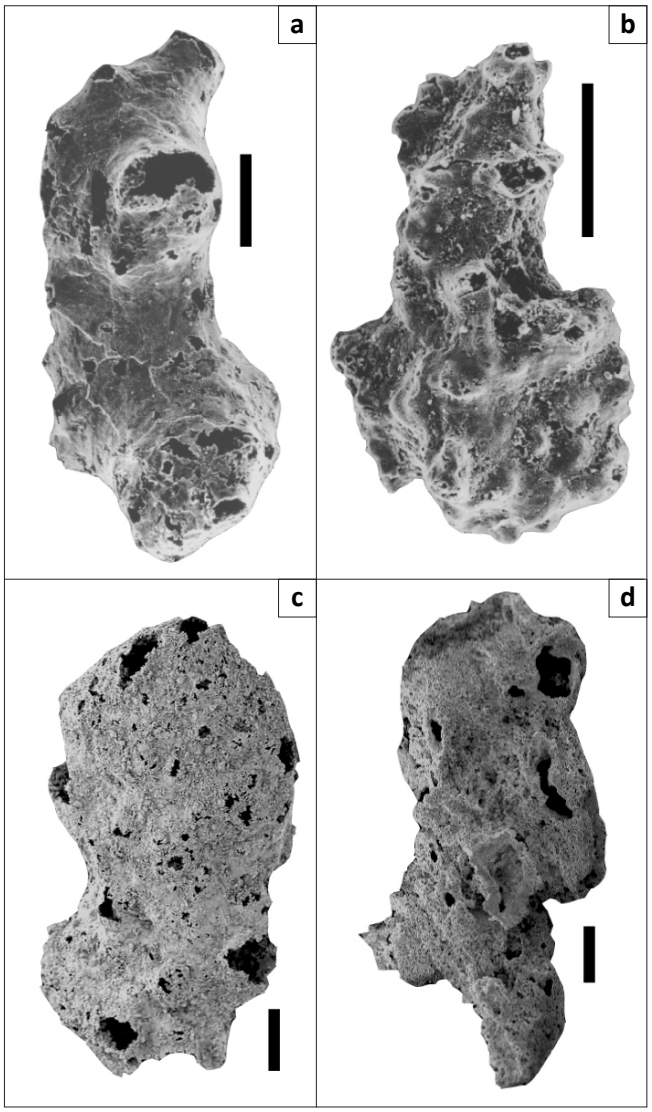
We term the putative fossils *Otavia*, because they have been recovered most abundantly from black limestone units of the Otavi Group of Namibia (Figure 1). *Otavia* have also been found in the Nama Group of Namibia. Both Otavi and Nama Groups are several kilometres thick and comprised of siliciclastic and carbonate rocks deposited in shallow marine shelf and slope environments. High precision U-Pb ages on zircons from syndepositional volcanic ash beds provide geochronological constraints on these rocks. The oldest *Otavia* to have been discovered come from the Otavi Group, in units correlative with upper Ombombo Subgroup strata (Okakuyu Formation) that occur above an ash bed dated at 760±1 Ma and which lies beneath the glacigenic Chuos Formation of ca. 710 Ma.[22] *Otavia* were also found in Otavi Group rocks (Ombaatjie and Auros Formations) underlying the glacigenic Ghaub Formation, the meltback phase of which is dated at 635.5±1.2 Ma.[29] The stratigraphically youngest known *Otavia* come from rocks in the Nama Group (Zaris Formation, Mara Member) that are correlative with units beneath an ash bed dated at 548.8±1 Ma.[8]

Otavia fossils: Description

The general shape of *Otavia* is elongate ovoid to globular and, although individuals vary, the overall form of each remains similar (Figure 3). Sizes range from as small as 0.3 mm to as large as 5 mm in the longest dimension. The outer surface of *Otavia* is perforated and pierced by numerous small holes, typically 5 µm – 20 µm across, as well as a number of larger openings that form raised turrets or mounds several to many tens of microns in diameter (Figure 3).

The internal character of *Otavia* provides evidence for its biological origin. SEM, BSE, CL and XMT images show that *Otavia* consists of three components (Figures 4 and 5): (1) an exterior wall that is several to many microns thick, pierced by numerous holes and comprised mostly of calcium phosphate and minor dolomite (secondarily silicified *Otavia* have been found in Nama Group limestones[25]); (2) a peripheral labyrinth (so termed because it encloses a large inner cavity) a few to many tens of microns in thickness, and composed of calcium phosphate (minor areas of calcite and replacement dolomite are also present); and (3) an irregularly shaped inner cavity that runs much of the length of *Otavia* and which is now filled with fine-grained carbonate sediment. In effect, *Otavia* resembles an elongate, irregularly shaped, hollow container (Figures 4 and 5).

The larger openings, which form raised turrets on the outer walls of *Otavia*, are linked to passageways that transect the peripheral labyrinth and open directly into the internal cavity; these openings provide a direct communication between the cavity and the outside (Figure 4a, i, j; Figure 5a, b). The smaller holes or pores that pierce the exterior wall open into the peripheral labyrinth (Figure 4e; Figure 5c, d). The labyrinth consists of layered galleries of interlinked chambers bounded by several-micron-thick tabular to wavy-parallel mineralised (mostly phosphatised) walls (Figure 4c, d, e, f; Figure 5d). The inner portion of the labyrinth adjacent to the internal cavity displays wavy to cuspate surfaces with many openings that link the chambers of the labyrinth to the internal cavity (Figure 4c, d, e, f; Figure 5b, d). The internal cavity can comprise lesser or greater volumes of the interior of *Otavia* and XMT reconstructions show that it can be complex in shape (XMT software can be programmed to eliminate solid material and highlight void spaces), reflecting the irregular form of the inner bounding surfaces of the peripheral labyrinth (Figure 5e, f).



All scale bars are 100 µm.

FIGURE 3: Scanning electron microscopy images of *Otavia*. These are representative of more than 1000 specimens examined and show the consistent globular to ovoid shape and external bounding surface pierced by numerous small pores and larger openings commonly forming raised mounds: (a) and (b) are from the Auros Formation in Etosha National Park, northern Namibia; (c) is from the upper part of the Ombombo Subgroup near Opuwa, north-western Namibia and (d) is from the Kuibis Subgroup (Mara Member of the Zaris Formation) near Kliphoek, southern Namibia.

The mechanism of phosphate concentration and fixation remains to be ascertained. Phosphate preferentially occurs in the interior portions of *Otavia*, implying a genesis linked to conditions internal to *Otavia* and not as a result of an externally precipitated, microbially mediated layering, coating or binding. Parts of the walls and labyrinth are calcite and it is assumed that *Otavia* was originally composed of calcium carbonate and, to a lesser extent, dolomite.

Regardless of what original mineralogy *Otavia* used to construct itself, its overall structure indicates that it developed the capability to control mineral precipitation. The walls and peripheral labyrinth reveal sharp boundaries between internal and external areas and their surfaces show repeated patterns and complex shapes (Figure 4c, d). That *Otavia* was a hollow container is evident from the fact that its internal cavity can be filled with sediment different from the encompassing sedimentary matrix (i.e. a geopetal sediment) (Figure 4f, g, i, j). In some *Otavia*, especially near to large external openings, the sediment within the interior cavity is mottled, having characteristics of both the internal (geopetal) and external sediment. This finding indicates that both sediment types were able to mix, additionally confirming that *Otavia* was hollow during life. In these cases, the cavities of *Otavia* were filled after death and then transported as a bioclast (fragments of *Otavia* can be seen in Figure 4i, j). In other cases, no distinction can be made between the internal and external sediment (Figure 4f), implying that those *Otavia* remained largely *in situ* after death and burial.

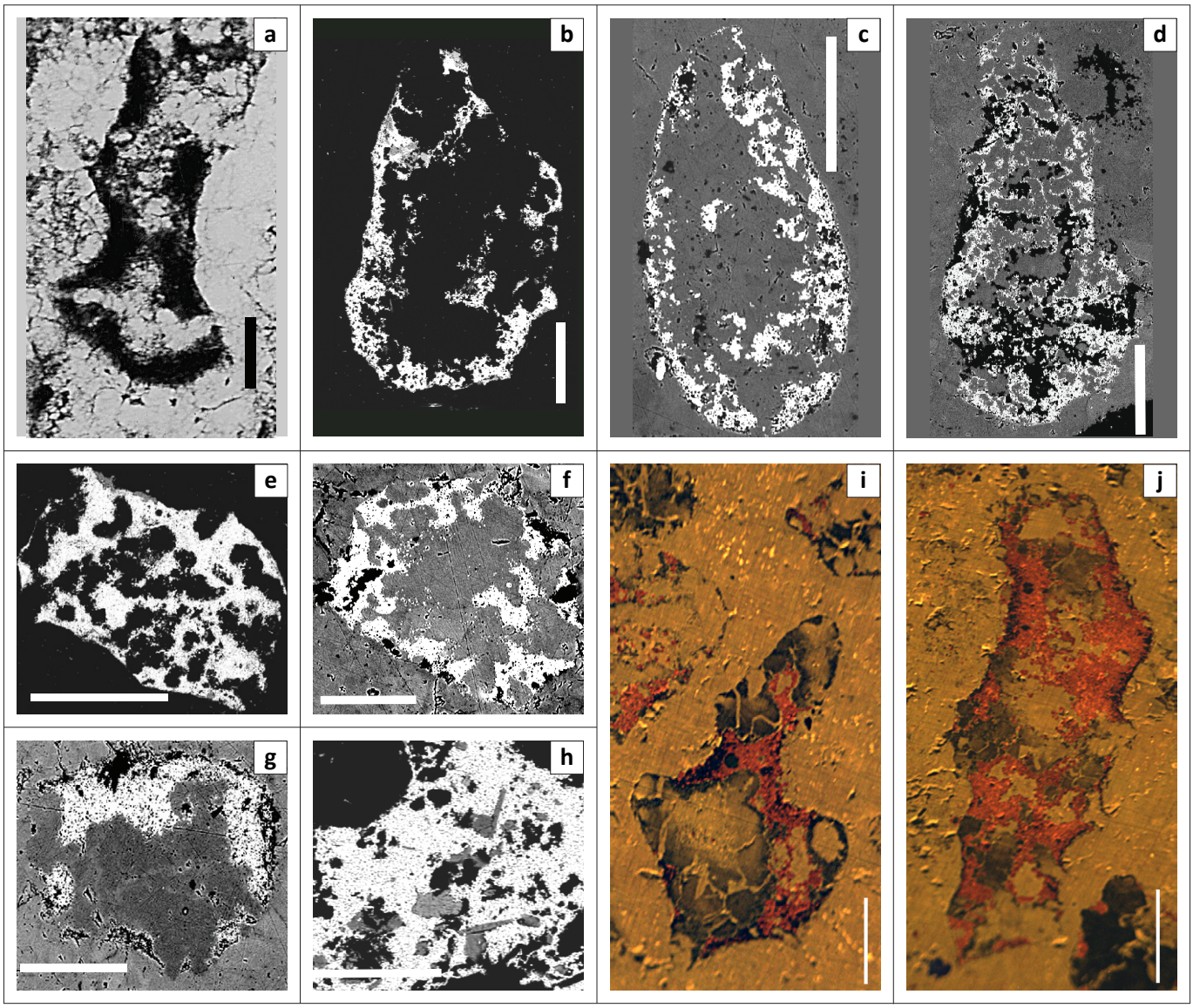
Otavia fossils: Interpretation

In describing the features that characterise *Otavia*, it is also important to stress what features have not been observed. To do so is important because microbial sedimentary structures such as thrombolites (mottled textures) and stromatolites (layered textures) are common in the Otavi and Nama Group rocks and it is necessary to reduce, and perhaps eliminate, the possibility that *Otavia* are bacterially mediated and/or influenced structures.

In the hundreds of *Otavia* specimens examined, not a single example of micron-scale globular clusters, botryoidal surfaces, or even singular ovoid (coccoid) forms was observed which would suggest an origin by bacteria or bacterial communities. *Otavia* do not display micron-scale layering and thus cannot be attributed to microbial sheets, veneers, coatings, layered cortices around clasts and grains, or to crystal shapes. Furthermore, the cavities and layered chambered labyrinths of *Otavia* are typically tens of microns in size and thus are not the micron-scale tubules of cyanobacteria. Nor is *Otavia* an aggregate or cluster of detrital grains and allochems (secondarily reworked and transported carbonate or other types of grains) bounded by microbial sheets (i.e. microphytollites). Irregularly shaped filamentous sheaths that trap and bind particles are readily distinguishable from *Otavia* (Figure 4j).

We have also considered the possibility that the *Otavia* organisms could have been foraminifera. However, documented examples of Cryogenian-age foraminifera (Amoebozoa) display agglutinated tests comprised of abundant Al-K-Mg silicate minerals embedded in carbonaceous matter.[30] *Otavia*, in contrast, has a phosphatic shell. Further, the foraminifera are typically smaller (generally < 200 µm[30]) than *Otavia* and do not display the variably sized wall-piercing openings and passageways that seem to be diagnostic of *Otavia*. Hence, Neoproterozoic foraminifera are both compositionally and morphologically dissimilar to *Otavia*, and we thereby discount the possibility that *Otavia* could be a form of Amoebozoa.

Synthesising all of the above, the most parsimonious interpretation of *Otavia* is that it was a sponge-like organism. The small openings represent incurrent pores or ostia,

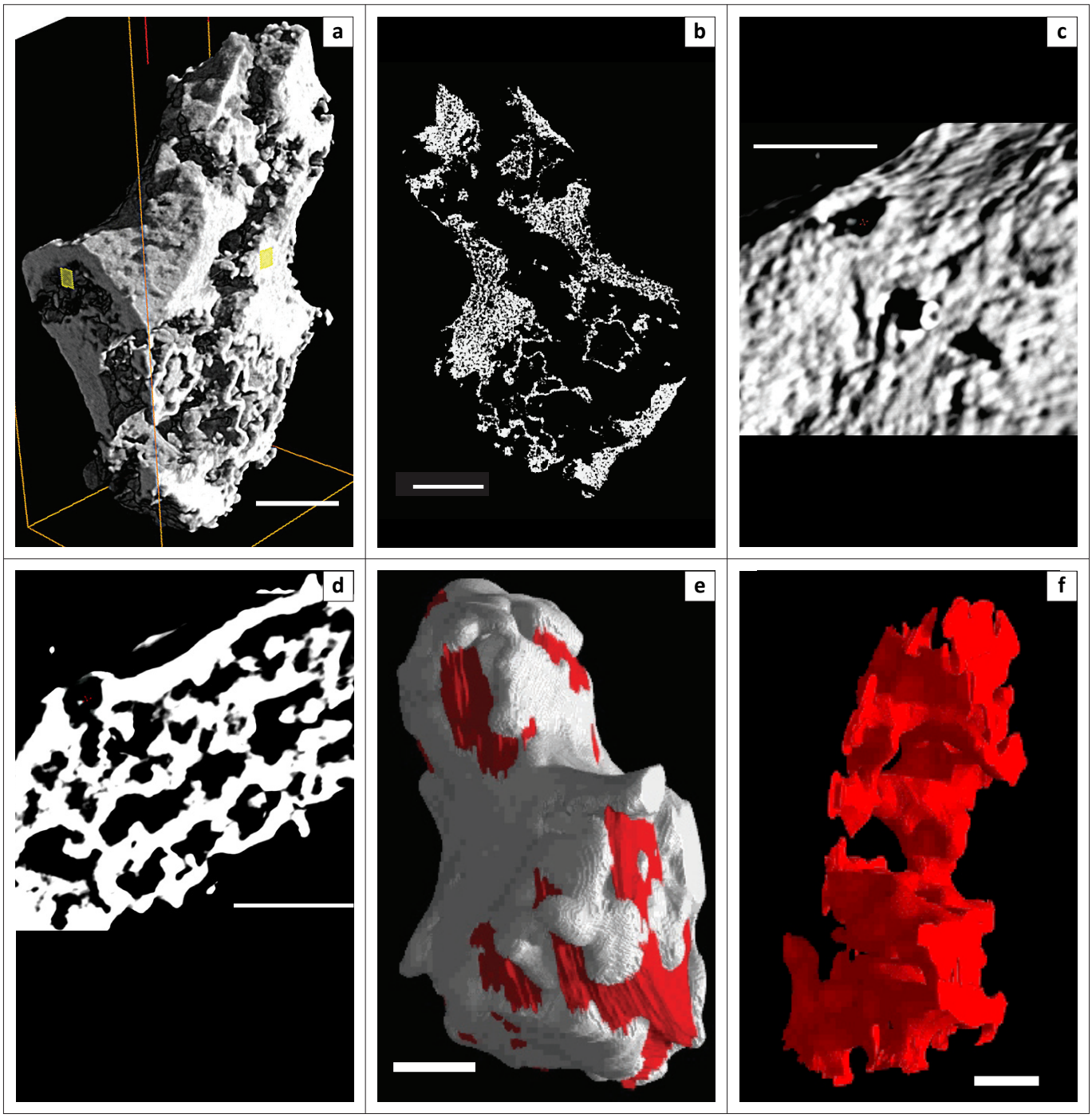


Scale bars in a-j are 100 µm, except for in c and d, which are 50 µm.

FIGURE 4: Images of the internal characteristics of *Otavia* revealing the diagnostic feature of an interior cavity enclosed within phosphatised walls of a peripheral labyrinth and pierced by passages leading to the outside. (a) Petrographic thin section (plane-polarised light) showing large passageways that pass through the walls into the interior void; the phosphatised peripheral labyrinth appears black. (b–g) Backscattered electron images reveal an internal cavity surrounded by the complexly shaped bounding surfaces of the interior peripheral labyrinth. Bright areas are calcium phosphate in composition; dull and dark grey areas are composed of calcite and dolomite, respectively. (b, e) are from acetic acid residues and mounted in resin, other images are from polished rock slabs (black areas in these are holes through the slide). The complex structure of the peripheral labyrinth is well shown in (d) and (f) and its chambered character is evident in (e). (f, g) reveal that the internal cavity is filled with different types of sediment: in (f) the matrix and internal sediment have the same brightness and hence are compositionally similar whereas the internal sediment in (g) is darker and thus compositionally distinct from the matrix. (h) Backscattered electron image of a phosphatised sheath in which mineral grains (feldspars and micas) have been trapped and bound (note how the sheath frays at the margins). (i, j) Cathodoluminescence images show the interior cavity connected to the outside via large openings, filled with geopetal sediment that differs in composition from the encompassing matrix; medium grey (red in the online version) areas are phosphatic, lighter grey (yellow in the online version) are calcitic and darker grey (grey in the online version) are dolomitic in composition. Broken *Otavia* bioclasts are visible in both images. All examples are from the Auros Formation, Etosha National Park, northern Namibia.

the larger ones exhalent oscula, and the internal cavity a paragastric chamber (Figure 6). The limestones containing *Otavia* vary from grainstones to micrites and exhibit a variety of shallow-water features including oolitic lenses, tidal bundles, cross-stratification, stromatolitic and microbial laminites, intraclastic rip-up beds, hummocky cross-stratified bedforms and wave ripples. Hence, *Otavia* lived in normal marine conditions.

Otavia occur as unabraded fossils, as well as reworked bioclasts. The unabraded fossils are largely found in finely laminated micritic limestones representing relatively calm depositional conditions free from agitation and implying a setting of quiet, low-energy conditions. The reworked forms are recovered from intraclastic packstones and grainstones, indicating stronger current activity and transport of *Otavia* as part of the tractive bedload. As such, *Otavia*'s skeleton was resilient enough to survive abrading during transport. Thus, the classification proposed here is that *Otavia* belong to the phylum Porifera. A prolonged search has been undertaken for spicules, as these would clarify the taxonomic relationship, but no unquestionable example has been found. The etymology of the name *Otavia antiqua gen. et sp. nov.* is derived from the Otavi Group in which the fossils occur and their age.



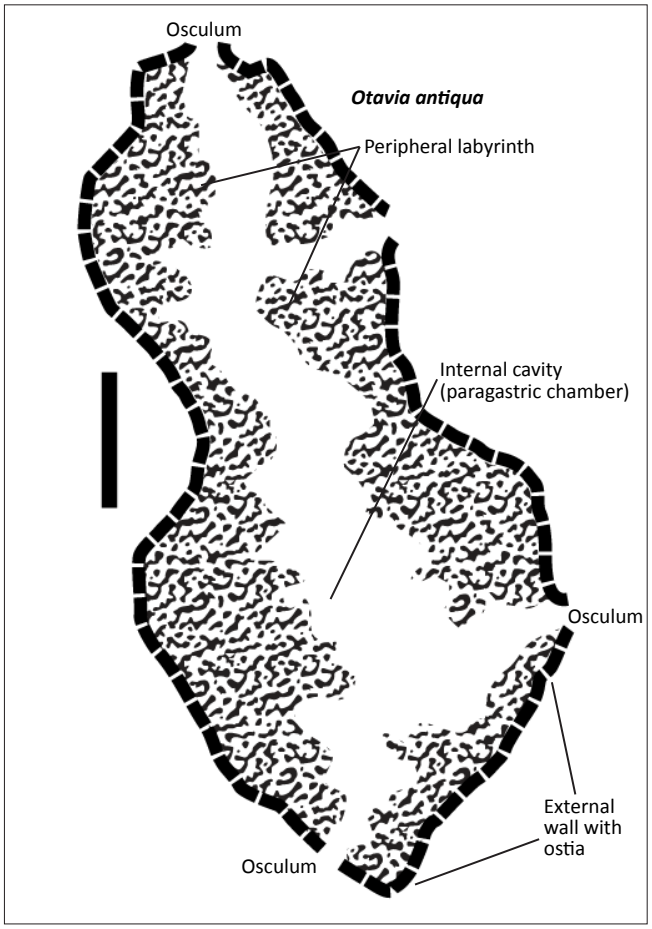
Scale bars in a–d are 100 µm and in e and f are 50 µm.

FIGURE 5: X-ray microtomography images show: (a, b) the internal cavity of *Otavia* connected to passages linked to large openings on the external surface; (c) small pores on the outer surface of *Otavia* opening into the multilayered chambered peripheral labyrinth (d) and (e, f) the irregular shape of the internal cavity of *Otavia* (shaded medium grey; note that in the online version it is coloured red). All examples are from the Auros Formation, Etosha National Park, northern Namibia.

Discussion

Sponges require their ostia to be large enough to allow the entry of water drawn inwards by beating flagellae in the peripheral labyrinth and paragastric chambers. Assessing the efficiency at which *Otavia* would have been able to draw fluid into their bodies is speculative. However, if models are broadly correct in inferring that Neoproterozoic oceans were characterised by large pools of micron-scale particulate and dissolved organic matter,[31] then the amount of fluid *Otavia* needed to filter for nutrition would have certainly been considerably less than that required for modern sponges.

Neoproterozoic time was marked by severe climatic conditions and widely fluctuating marine C-isotopic compositions.[22,32] The pattern of C-isotopic values recorded in Neoproterozoic carbonate rocks worldwide has been well documented, with most workers interpreting the positive and negative excursions as globally generated secular variations that are useful in establishing correlations between regions



Scale bar ~100 µm.

FIGURE 6: Diagnostic features of *Otavia* (based on images in Figures 4 and 5): (1) overall ovoid to globular shape; (2) external wall pierced with ostia and (3) interior peripheral labyrinth surrounding an irregularly shaped internal void connected to the outside by large oscula.

and continents.[22] As noted previously, others have concluded that such large-magnitude fluctuations are diagenetic overprints, post-depositional phenomena largely unrelated to original seawater compositions.[23] Ascertaining which of these two opposing views is more correct is beyond the scope of this paper. However, it is interesting to consider the effect that the development of mineralogical hard parts enclosing organic matter would have had on the global C cycle. In effect, the genesis of hard parts would have made *Otavia* behave, particularly upon death, like any other sedimentary particle – it would have undergone transport and burial, thereby removing isotopically light organic C from the global oceanic reservoir.

The amount of biomass *Otavia* represented is unknown. However, the number of *Otavia* fragments that can be observed in thin section (e.g. see Figure 4i, j) and recovered from residues is impressive; if this number is representative of *Otavia*'s global distribution, then the likelihood is that *Otavia* was abundant. The widespread burial of *Otavia* would have removed organic matter from the water column, driving $\delta^{13}C_{carbonate}$ towards the high values that typify the Neoproterozoic[22] and helping generate the inferred rise in Neoproterozoic oxygen levels.[33,34] Until the evolution of burrowing metazoans, re-entrainment of sedimented *Otavia* would have been at the whim of physical processes stirring bottom layers. However, once metazoans evolved, their behavioural activities (such as burrowing and digging) would have reworked the sedimented organic matter back into the water column where it would have oxidised, driving C-isotopic values back towards 'normal'.

Given the existing time and stratigraphic constraints, *Otavia* predated and lived through the extreme environmental changes of later Neoproterozoic time – the snowball Earth events.[32] *Otavia* evolved prior to the earliest of the documented Neoproterozoic global glaciations, survived through the repeated icehouse–greenhouse states, and existed at least to the dawn of metazoans at the end of the Precambrian. Hence, *Otavia* could not have been adversely affected by the severe environmental fluctuations and associated changing conditions. It is often postulated that the cessation of the climatic extremes concomitant with an inferred, stepwise global rise in oxygen levels near the close of Proterozoic time[33,34] set the stage for the emergence of animals. The presence of *Otavia* in rocks 760 million years old requires this view to be revised. If our interpretation of *Otavia* is correct, then the early lineages of animals go back considerably further in time on the basis of molecular evidence and, now, on fossil evidence.

Conclusions

Microfossils, termed *Otavia antiqua gen. et sp. nov.*, have been recovered from Cryogenian–Ediacaran successions in Namibia (the Otavi and Nama Groups) in rocks as old as 760 Ma to as young as 550 Ma. They are interpreted as calcareous sponges and occur as ovoid to irregularly elongate globular forms, ranging in size from 0.3 mm to 5 mm in the longest dimension. The outer surface of *Otavia* is perforated by numerous small and large openings (several to many tens of microns in size), with the latter commonly forming raised mounds. The outer wall of *Otavia* is thin (many microns to a few tens of microns thick), typically calcium phosphate in composition, and interior to the wall is a peripheral labyrinth, so named because it encases an irregularly shaped, longitudinally running inner cavity that is connected via irregular pathways through the peripheral labyrinth to the outer-wall openings. Combined, these features are interpreted as the ostia, oscula and paragastric chamber of an ancient calcareous sponge. The evolution of hard parts, effectively encasing organic matter, made *Otavia* a sedimentary particle. It is speculated that sedimentation and burial of *Otavia* helped drive the increase in the $\delta^{13}C$ composition of Neoproterozoic oceans, and perhaps even contributed to the inferred rise in oxygen levels. *Otavia* evolved prior to the first known Neoproterozoic global (snowball Earth) glaciation, and survived through the climatic extremes associated with the repeated snowball Earth episodes.

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Competing interests

We declare that we have no financial or personal relationships which may have inappropriately influenced us in writing this article.

Authors' contributions

C.K.B. was the project leader. A.P. and K.H. were responsible for fieldwork and A.F., A.B., D.A., C.S. and I.Y. performed the various analyses. C.K.B., A.P., K.H., A.F., D.A., D.C. and S.A. made conceptual contributions. C.K.B., A.P. and A.F. wrote the manuscript.

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