**EVOLUTIONARY BIOLOGY**

**Ediacaran metazoan reveals lophotrochozoan affinity and deepens root of Cambrian Explosion**

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Through exceptional preservation, we establish a phylogenetic connection between Ediacaran and Cambrian metazoans. We describe the first three-dimensional, pyritized soft tissue in *Namacalathus* from the Ediacaran Nama Group, Namibia, which follows the underlying form of a stalked, cup-shaped, calcitic skeleton, with six radially arranged lobes projecting into an apical opening and lateral lumens. A thick body wall and probable J-shaped gut are present within the cup, and the middle layer of the often-spinose skeleton and skeletal pores are selectively pyritized, supporting an organic-rich composition and tripartite construction with possible sensory punctae. These features suggest a total group lophotrochozoan affinity. These morphological data support molecular phylogenies and demonstrate that the origin of modern lophotrochozoan phyla, and their ability to biomineralize, had deep roots in the Ediacaran.

**INTRODUCTION**

Exceptional preservation of fossils from the Ediacaran-Cambrian, ca. 570 to 500 million years (Ma) ago, provides great insight into the first radiation of metazoans. While the oldest putative skeletal metazoans known are from the terminal Ediacaran, the general absence of both definitive skeletal characteristics and soft-tissue preservation has precluded clear assignment of affinity and, hence, an understanding of the origin of major metazoan groups. Here, we describe the first, three-dimensional, pyritized preservation of soft tissue in the Ediacaran skeletal metazoan *Namacalathus hermanastes*, from the Nama Group, Namibia, where new features support a bilaterian, lophotrochozoan affinity. In so doing, we also establish a strong evolutionary link between terminal Ediacaran and early Cambrian taxa.

*Namacalathus* is a sessile, benthic skeletal organism with a widespread distribution known from diverse carbonate settings, including thrombolite reefs and shallow lagoons, ca. 550 to 540 Ma ago. *Namacalathus* has a goblet-like skeletal morphology formed by a hollow stalk expanding into a calyx from ca. 3 to 35 mm in diameter with an apical central opening and five to seven, but generally six, lateral lumens (1–3). Spines are present on the outer surface of the stem and cup in some individuals (2), and adjacent individuals have been found with shared cavities, interpreted as representing potential bilateral, asexual, external budding (3). Present skeletal mineralogy is generally low-Mg calcite, but the original mineralogy may have been either Mg calcite or aragonite (1,4). Preserved plastic deformation implies that skeletal walls were flexible and, therefore, organic rich (1). Skeletal microstructure has been described as a diagenetic, tufa-like cement (5), but well-preserved specimens display foliated outer and inner skeletal layers, with a middle layer inferred to have been organic rich (3).

*Namacalathus* has been proposed to be a cnidarian because of its hexaradial symmetry and a goblet-like morphology, as found in some hydrozoan polyps, scyphozoan scyphistomae, and stauromedusae (1). Others have suggested a protozoan affinity because of the absence of accretionary growth (6) or a total group lophophorate based on foliated skeletal microstructure and bilateral budding (3). Recently, a stem group ctenophore affinity has been proposed on the basis of phylogenetic analyses and a general morphological similarity to sessile, Cambrian skeletonized “dinomischids” and scleroctenophores (7).

**RESULTS**

Here, we report exceptionally preserved *Namacalathus* individuals found within the uppermost Upper Omkry Member of the Nama Group, Namibia, from a low-energy, very shallow, dominantly carbonate, inner ramp setting, just below an ash bed dated at 547.32 ± 0.65 Ma old (see fig. S1) (8). *Namacalathus* individuals range from 4 to 12 mm in diameter, although many are partially covered with sediment and are preserved as reddish brown to yellow (oxyhydr) oxide minerals, FeOx [“FeOx” here denotes unspecified iron (oxyhydr) oxide] resulting from oxidation of pyrite (FeS2), or as raised gray limestone casts that sometimes reveal weathered sections through the calcified skeleton (Fig. 1 and figs. S2A and S3). Seventy-three individuals (numbered 1 to 73) are found on a bedding plane sample, some with stalks (fig. S2, A and D), with 29% preserved upright in inferred growth position, 48% slightly toppled, and 23% of undetermined orientation (fig. S3). The host lithology is finely laminated micrite that grades from a mud-rich packstone with some silt-grade quartz and recrystallized bioclasts, often with a stylolitic contact (fig. S2C). *Namacalathus* individuals are immediately overlain by a thin (<1 mm) micritic carbonate with silt-grade, angular lithic fragments of quartz, albite, clays, and phosphatic minerals (figs. S4 and S5).

The best-preserved individuals show a raised pin cushion–like form, which surrounds the central, apical, opening. The central apical opening ranges from 1.3 to 12.3 mm (n = 37, mean = 3.6 mm) in diameter and can either be circular (Fig. 1, E and F, and fig. S3, K to N) or show five to seven, but generally six, isoceinal folds that radiate outward (Fig. 1, A to D and F, and fig. S3, A to J, P, and Q). Fold height ranges from 0.18 to 2.78 mm and width ranges from 0.43 to 4.66 mm (table S1). Both types of opening are preserved either as an FeOx crust (Fig. 1, A to D and F, and fig. S3, A to G and M to Q) or as casts of limestone (Fig. 1, E and I, and fig. S3, H to L and W to X). In cups where the central opening and lumens are visible, central opening folds oppose folds across the lumens (Fig. 1D). Full lumens are
CT images reveal the uppermost structure within the cup (Fig. 2, E, J, and O), sometimes decreasing in width to lastly disappear without attachment (fig S12.). FeOx and an outer area of nonzoned, dark dull luminescent, blocky neomorphic sparry calcite (Fig. 4, F and R), where crystals differing in orientation are present on either side of the pyritized pores (Fig. 4F).

A tube-like structure, often defined by a central area of frambooidal FeOx and an outer area of nonzoned, dark dull luminescent, sparry calcite (also present as a later-stage cement infill within the carbonate sediment), is found within three of four Namacalathus cups analyzed and can be distinguished in polished serial sections, as well as imaging via CL and backscatter SEM (Figs. 2, D, I, and N; 3, A and D; and 4, L and M; and figs. S4, S9, S13, and S14) and μCT (Fig. 2, E, G, H, J to M, and O). This structure has an elliptical cross section of up to 400 μm in diameter and may connect with a thin layer of FeOx 100 to 400 μm thick draped across the central opening of the cup (Figs. 2, D, I, and N; 3D; and 4, N and O). The tube then descends into the cup moving toward the inner wall, inflating to a circular section up to 600 μm, and then curves to form a J-shaped structure within the cup (Fig. 2, E, J, and O), sometimes decreasing in width to lastly disappear without attachment (fig S12.).

FeOx frambooids are abundant in both the soft tissue (Fig. 3C and figs. S11 and S12) and skeleton (Fig. 3J and figs. S5 and S12). There...
are no framboids in the wider sediment. The neomorphic sparry calcite skeleton of *Namacalathus* also contains extensive FeOx framboids. These often occur within a well-defined, straight-edged middle layer (Fig. 3G), where pyritization extends to almost the full width of the skeleton in the uppermost parts of the cup, thinning toward the base of the cup where the calcitized outer and inner skeletal layers thicken (Fig. 3, G and H). Thin accumulations of FeOx framboids also occur in patches along the inner and outer skeletal surfaces and additionally pick out inverted V-shapes within the calcitic parts of the skeleton (Fig. 3, G and J). CL imaging shows zoned calcite cements growing around uncompacted sediment, which project into the neomorphic calcite skeleton of *Namacalathus* and other neomorphic bioclastic grains (Fig. 4F). The dominant bright CL zone of early calcite cements associated with sediment within the upper part of cups (S2), is indicative of high-Mn and low-Fe pore water conditions (Fig. S4). The sediment of S2 is also characterized by FeOx staining, which is inferred to derive from the oxidation of pyrite. This confirms the coincidence of both early

**DISCUSSION**

We therefore infer that early precipitation of both pyrite and calcite cements is responsible for this exceptional, three-dimensional preservation (10). This type of preservation occurs in sulfate-reducing environments with high concentrations of highly reactive iron but low or very localized availability of organic carbon available during early diagenesis, where pyrite precipitation is only associated with labile tissues and cellular structure is destroyed (10) and where the form of pyrite may reflect the relative susceptibility to decay of the original material (11,12). Pyrite framboidal pyrite formation can occur within hours to days on organic matter under these conditions (13). We infer that framboidal pyrite formed very early and replaced both soft tissue and the inferred organic-rich parts of the skeleton. The occurrence of pyritized bacteria, here found alongside *Namacalathus*, is highly unusual in the fossil record and confirms that pyritization was rapid enough to replicate soft tissue.

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pyrite and early calcite cementation. Early carbonate cement formation is known to be facilitated by cell walls, extracellular polymeric substances, organic matter degradation, and other metabolic or microbial processes where peloids may form [e.g., (14)]. Local dissolution around pyritized soft tissue, perhaps induced by limited oxidation of pyrite, led to the formation of molds that later became infilled with a burial spar cement.

Similar three-dimensional preservation of soft tissues in pyrite is found in the terminal Ediacaran Gaojiashan Member of the Dengying Formation, China (15), the Early Cambrian Chengjiang and Guanshan Lagerstätten from China (11), the Lower Ordovician Fenxiang Formation (16), and the Lower Cretaceous Santana Formation (12), often created by rapid entombment via storms. In the Nama Group, the proximal, very shallow, low-energy environment provided both a fine-grained medium and sufficient calcium carbonate saturation to facilitate early cementation. The Namacalathus individuals may also have been rapidly buried, in life, by a thin incursion of terrigenous sediment containing the so-called “Namacalathus horizon” (17). Internal digestion is otherwise completely unknown from the Ediacaran record although common in Cambrian Lagerstätten (17). In sum, the processes operating in this preservational setting have created a taphonomically unique Lagerstätte.

The pyrite-rich middle layer within the Namacalathus skeleton confirms the presence of a tripartite skeleton with an organic-rich central portion (3). FeOx framboids in thin layers within other parts of the skeleton also suggest the presence of thinner organic-rich layers, parallel to potential accretionary growth lines. The additional presence of framboids that traverse the wall, as well as neomorphic calcite of differing orientations on either side of the pores, suggests that these are primary biological features, such as pores piercing the walls and the longer channels penetrating the spines. The thickness of the pyritized middle layer increases toward the upper part of the skeletal cup, suggesting that this may have been the area of initial skeletalogenesis in contact with other soft tissue. This middle layer may have formed an organic template upon which the outer and inner calcareous layers formed and, as such, was the area of active skeletal growth, as observed in modern corals and lophophorates [e.g., (18)]. The FeOx staining noted extensively within the cup and lumens, and in

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**Fig. 3. Backscatter SEM images of N. hermanastes.** Museum No. F1547, Museum of the Geological Survey of Namibia. (A) to (F), no. 32, slices D and D’ (Fig. 2N). (G) to (J), no. 68. (A) Scanning electron microscopy (SEM) image showing CS and Fl with L, pyritized/FeOx soft tissue of lobes (FeOx) and CT, with S. (B) Inset of (A), soft-tissue lobe of Namacalathus at the bedding surface infilled by FeOx framboids (Fr). (C) Inset of (B), showing FeOx Fr. (D) Inset of (A), showing line of FeOx Fr (arrowed) across the CO, which attach to CT. (E) Inset of (A), spine with perpendicular pore infilled with FeOx Fr. (F) Inset of (E), showing FeOx Fr. (G) FeOx Fr within the central area of the skeleton and CT. (H) Inset of (G), showing the middle layer of FeOx Fr (FeOx) in CS widening toward the bedding surface, and S2 peloidal sediment with FeOx (arrowed) partially replacing peloids (P). SC, burial sparry calcite. (I) Inset of (G), FeOx cement around angular calcitic and lithic grains of S3. (J) Inset of (G), FeOx Fr within the CS.
thinner patches inside and outside the cup, suggests the presence of soft tissue.

In sum, *Namacalathus* has a goblet-shaped calcareous skeleton with a hollow stalk and central opening, generally hexaradial symmetry with lateral facets bearing large lumens, a foliate microstructure with concordant columnar inflections and a middle organic-rich layer, and asexuality reproduction expressed by bilateral budding (1,3). Soft tissue faithfully follows the internal skeleton, and the lumens do not have a localized, diagentic, dissolution origin as previously suggested (1). In addition, we note the presence of folds formed between radially arranged lobes that extend from the central apical opening to lateral lumens, organic-rich pores, and channels within the skeletal wall; an internal, asymmetric, J-shaped tube-like structure, soft tissue adhering to the inner skeletal wall; an internal membrane that traverses the apical opening of *Namacalathus* (Fig. 2A, D, I, and N) can be interpreted as a frontal membrane, and so the position of the presumed gut below would correspond to the coelomic cavity following a lophophorate model. A retraction mechanism can also be inferred in *Namacalathus*, where muscle bundles may connect the frontal membrane and body wall (Fig. 2, D, I, and N).

This set of features, together with those seen in other specimens [bilateral budding and columnal inflections in the skeletal laminae (3)], excludes assignment of *Namacalathus* to protists, coralline algae, porifera, cnidarians, and echinoderms (table S3). While hexaradial symmetry might favor an affinity within the Cnidaria, and some extinct Paleozoic corals have a foliated microstructure (22), the presence of skeletal columnar punctae, channels, a J- or U-shaped inferred gut, and a frontal membrane rather than a large, central, pharynx, as well as an absence of mesentery-like structures, does not support a cnidarian affinity.

Skeletal representatives of the Lophophorata, including stem and crown group brachiopods, bryozoans, and extinct microconchids, have very similar foliated microstructures with columnar inflections...
in places extending into spines. A consensus tree for 54 lopho-
trchozoan taxa where Namacalathus occupies a basal position reveals
that such “canaliculate” microstructure and “punctae” have multi-
ple origins across the brachiozoan total group (23). The absence
of any traces of a gastral cavity and the discovery of possible organic-
rich punctae and channels within the skeletal walls further emph-
size a similarity with the sensory porosity observed in lophophorates
(brachiopods, tommotiids, and microconchids) (21,24), as does the
presence of a possible J- or U-shaped gut. The generally six, large lat-
eral lumens point to either a colonial organization for Namacalathus
or a solitary organism in which lumens might correspond to brood
chambers formed by external body wall invaginations, as found in
bryozoans (19). Invaginations of the body wall are observed within
the lumens in Namacalathus (fig. S10, B and C).

The confirmation of total group lophotrochozoans in the Ediacar-
an is supported by molecular phylogenies (25) and has implications
for the earliest evolution of lophotrochozoans. The fossil record of
biomineralized stem group lophotrochozoans is abundant from the
early Cambrian onward where the possession of a calcareous skeleton
or external sclerites likely represents the independent acquisition of
skeletons of variable mineralogy in sessile, attached benthic fossil
taxa, which have features shared with Namacalathus. These include
tommotiids (26) and hyoliths, which were pedunculate and ten-
taculate organisms lacking a lophophore (23). Some goblet-shaped
Cambrian forms that resemble Namacalathus, such as Cotyle-
dion tylodes from the Chengjiang deposits, may represent stem lophophor-
ates and also show an upper calyx and elongate stalk, with a central
canal interpreted as an extension of the calycal cavity, a U-shaped
gut with a mouth and aboral anus ringed by retractable marginal
tentacles, and an outer surface covered by external sclerites, which
may have been mineralized (27).

Cotyledion and some other Cambrian stalked fossils, namely,
Dinomischus and Siphusauctum, have been compared with entoprocts
(27–29). These fossils are relatively large (over 15 mm in height),
while extant entoprocts are extremely small (less than 1 mm) and
nonbiomineralized.

The Entoprocta are an enigmatic monophyletic acelomate group
that occupies a phylogenetically basal position among lophotro-
chozoans, close to molluscs (30). Namacalathus displays some notable
similarities with the entoprocts, including the goblet-shaped overall
morphology (a body divided into distinct stalk and calyx), hexara-
dial symmetry, the position of both mouth and anus within the pre-
sumable tentacle collar, and bilateral buds emerging from frontal
area of the parental individual. Hence, we are now able to reconstruc-
Namacalathus as a total group lophotrochozoan, capable of asexual
budding with an organic-rich, foliated calcareous skeleton and an
open, apical J- or U-shaped gastric cavity within the apical opening
potentially accommodating a retractable collar of tentacles and with
brood chambers around the lumens (Fig. 5).

Sessile extant lophotrochozoan phyla such as annelids, molluscs,
brachiopods, and phoronids have been suggested to have their ori-
gins in the earliest Cambrian small skeletal fauna [e.g., (26)], which
are iconic representatives of the Cambrian Explosion. However, now,
we can extend the origin of these modern lophotrochozoan phyla fur-
ther back still into the terminal Ediacaran. In so doing, we establish
a phylogenetic connection between Ediacaran and early Cambrian
taxa, faunas that were previously thought distinct. We hence ex-
tend the roots of the Cambrian Explosion itself into the Ediacaran,
where total group lophotrochozoans such as Namacalathus show a
combination of features that became typical of both later lopho-
phorates and representatives of the entoproctan-molluscan-annelidan
branch.

MATERIALS AND METHODS
One float sample (237 mm by 194 mm by 33 mm) was collected from
Zwartmodder Farm. A single-lens reflex camera and a binocular micro-
scope were used to photograph and document each Namacalathus,

Fig. 5. Reconstruction of N. hermanastes as a total group lophotrochozoan.
SUPPLEMENTARY MATERIALS

Namacalathus imaging and EDX analysis. No. 68 for backscatter electron transverse sections of Namacalathus polished, uncovered thick sections (200 to 2000 \( \mu \)m increments, which were also imaged through binocular microscope (fig. S9). These sections were serially sectioned to 26-\( \mu \)m increments, which were also imaged through binocular microscopy and CL. Two highly polished thin sections were made of the slab to describe the lithology using petrographic microscopy. Three highly polished, uncovered thick sections (200 to 2000 \( \mu \)m) were cut from transverse sections of Namacalathus no. 68 for backscatter electron imaging and EDX analysis. Two samples (nos. 66 and 68) were serially sectioned and highly polished at 1-mm and 500-\( \mu \)m increments, respectively; to understand the distribution of iron oxide and its relationship to the calcitic skeleton using light microscopy and CL imaging. Serial sectioning at 1 mm of a core plug containing Namacalathus no. 66 allowed us to observe the relationship between the iron oxide and the calcite skeleton. A CanoScan LiDE 210 flatted scanner was used to scan each section (4000 dots per inch for both sections).

SUPPLEMENTARY MATERIALS
Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/1/eabf2933/DC1

REFERENCES AND NOTES


conditions control late Ediacaran metazoan ecosystems in the Nama Group, Namibia. 


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