

warming, this floral diversification also coincides with the uplift of the Bighorn and Beartooth mountain ranges (38). The results from Castle Rock suggest that local topography may be related to floral diversification. Conversely, the Castle Rock flora may represent a previously unidentified warm interval in the early Paleocene.

Our results imply that, in certain settings, floral diversity recovered soon after the mass extinction at the K-T boundary in North America. Another possibility is that the Laramide Front Range provided a K-T refugium for Cretaceous plants and that the early Paleocene rainforest was stocked with Cretaceous survivors from the uplands. We do not favor this hypothesis for four reasons: (i) The Castle Rock palynoflora, although unusually rich, is more similar to typical Paleocene palynofloras than to Cretaceous ones; (ii) earliest Paleocene floras (pre-Castle Rock floras) from the Denver Basin are of low diversity (Fig. 4B) and resemble coeval post-K-T boundary recovery floras to the north (2, 5–7, 39, 40); (iii) Cretaceous floras in the Denver Basin share only a few species in common with Castle Rock; and (iv) no known Cretaceous floras exhibit rainforest physiognomy.

The presence of the Castle Rock flora argues that orographic effects on local climate can be recognized in the fossil record and that the recovery of plant diversity after the K-T boundary occurred at different rates, depending on physiographic location.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/296/5577/2379/DC1
Tables S1 to S9

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Proterozoic Modular Biomineralized Metazoan from the Nama Group, Namibia

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We describe a Proterozoic, fully biomineralized metazoan from the Omkyk Member (~549 million years before the present) of the northern Nama Group, Namibia. *Namapoikia rietoogensis* gen. et sp. nov. is up to 1 meter in diameter and bears a complex and robust biomineralized skeleton; it probably represents a cnidarian or poriferan. *Namapoikia* encrusts perpendicular to the walls of vertical symsedimentary fissures in microbial reefs. This finding implies that large, modular metazoans with biologically controlled mineralization appeared some 15 million years earlier than previously documented.

The appearance and rapid diversification of metazoans with fossilizable hard parts around the Precambrian-Cambrian boundary [~543 million years (My) before the present (B.P.)] marks one of the most dramatic events of evolution (1–3). Only five

calcified taxa have been recorded from terminal Proterozoic (Vendian) strata. These taxa are solitary, weakly biomineralized, of uncertain affinity, and with only generally constrained ecological preferences (4–7). Here, we describe a Late Proterozoic

fully biomineralized metazoan from Namibia.

The fossil is from the Omkyk member of the terminal Proterozoic–early Cambrian Nama Group (>3000 m) in southern Namibia (fig. S1A). These host rocks are fossiliferous shallow marine carbonate and siliciclastic rocks (8, 9). An ash bed that immediately overlies the Omkyk Member has been dated as 548.8 ± 1 My B.P. (10).

Many specimens of *Namapoikia* gen. nov. were found associated with thrombolitic and stromatolitic bioherms within the Driedoornvlagte pinnacle reef complex, near Rietoog (23° S, 51.50'; 16° E, 39.38') (fig. S1B). The reef complex is over 300 m thick and at least 7 km long (6, 11). Bioherms individually form elliptical mounds that reach up to 20 m in diameter, 5 to 10 m in width, and 5 m in height, but coalesce to produce near-continuous structures with their long axes displaying a strong orientation parallel to the inferred paleoshoreline (now about northeast-southwest). Bioherm cores were constructed by massive thrombolites, often with entrapped *Namacalathus*; the outer (younger) layers consist of stromatolites up to 0.75 m thick. *Namapoikia* gen. nov. encrusts the walls of vertical syndimentary fissures, which formed perpendicular to bedding (Fig. 1, B and C), and more rarely open reef surfaces. Fissures are abundant and occur with a spacing of up to three per meter. Individual fissures can reach at least 5 m in length and 0.3 m in width (Fig. 1A). Fissure systems form in reefs as a result of early lithification, and many became filled with cement and sediments; such fissures are common in modern and ancient reefs. *Namapoikia* individuals may partially or completely fill the fissure void, although details of the original basal attachment sites have been destroyed by stylolization (Fig. 1C). Some *Namapoikia* were subsequently encrusted by thin rinds of stromatolites (now dolomitized) (Fig. 1C). Remaining void space is filled with large neomorphosed aragonitic botryoids up to 15 mm in radius that represent early marine aragonite cements (now calcite); bioclastic-rich packstone with abundant *Cloudina* debris, which may form geopetal infills; and lateburial calcite spar (Fig. 1D).

Namapoikia gen. nov. begins as nodular or domal individuals that either coalesce or extend laterally, similar to a sheet (Fig. 1, B

to D). Several *Namapoikia* specimens are up to 1 m in width and 0.25 m in height (Fig. 1D). The skeleton is modular and consists of multiple, incomplete, continuously conjoined tubules ranging from 1.5 to 5 mm in diameter (Fig. 1, C and D), which in transverse section appear labyrinthine to occasionally polygonal (Fig. 1F). The tubules do not appear to have expanded with growth. Skeletal elements are 0.5 to 3.5 mm in diameter. Longitudinal partition walls are present, and tubules grew by longitudinal fission. Growth annulae occur with a spacing of 0.5 to 2.5 mm. Skeletal filling tissue, such as tabulae or dissepiments, is absent, although some structures resemble incomplete tabulae. The skeleton of all collected specimens is totally recrystallized to blocky calcite (~20 μ m in diameter). The distinction of skeletal from pore cement calcite is difficult in transmitted light (fig. S2A). We examined several sections using cathodoluminescence but could not identify any original internal microstructure (fig. S2, B and C). Systematic paleontology is given in Appendix S1.

Diverse skeletal fossils variously described as coralomorphs or corals are known from the Lower Cambrian (12, 13). *Namapoikia* shows similarities to the small Lower Cambrian (Botomian) cerioid coralomorphs, in particular *Yaworipora* from Siberia (13) and the cryptic, encrusting taxa *Labyrinthus* (14) and *Rosellatana* (15) from eastern North America and British Columbia, respectively. *Yaworipora* and *Labyrinthus* grew as conjoined, thick-walled, polygonal tubes, <5 mm in diameter, with an open, labyrinthine transverse section. *Rosellatana* shows a more regular tubular construction, with polygonal to rounded lumens up to 1.5 mm in diameter. All three genera lack tabulae.

These forms and *Namapoikia* show a clear modular organization, suggesting affinity with some calcified protozoans or lower invertebrates (Porifera and Cnidaria). Their tubular construction is particularly similar to that of chaetetids [a polyphyletic group of calcified sponges (16)], known from the mid-Ordovician to Recent, and tabulate corals (Lower Ordovician to Permian). The tube diameter of *Namapoikia*, however, considerably exceeds that of all described skeletal protozoans and algae and, to a lesser degree, chaetetid sponges. Recrystallization of the skeleton precludes identification of either a lamellar microstructure or a central wall (indicative of biomineralization through a cnidarian epithelium), which would provide unequivocal placement within the Cnidaria. Recrystallization of the original microstructure is, however, suggestive of an original aragonitic mineralogy for *Namapoikia*. *Labyrinthus*, *Rosellatana* (12), and *Namapoikia* share

some characteristics with tetradiids, a group otherwise known from the Ordovician, but lack the distinctive quadripartite longitudinal fission of corallites. Tetradiids are aragonitic coralomorphs, but their precise position within the Cnidaria is unclear (12).

Molecular phylogenies for the divergence of the phyla Porifera and Cnidaria differ widely but can be conservatively placed at ~670 My B.P. or earlier (17). The oldest sponge body fossils (~560 My B.P.) are known from both soft-bodied Ediacaran biota (18) and spicule clusters (19). What appear to be soft-bodied cnidarians are known from phosphatized material in the Doushantuo Formation of China (20), and more generally in the Ediacaran biotas (21). Unequivocal body fossils of actinarian and corallomorphiid sea anemones are described from the Ordovician (22), but supposed trace fossils of resting sites are known from the early Cambrian (23).

Calcified skeletons have evolved multiple times in the history of the Porifera (24), and molecular data suggest that, for example, the scleractinian coral skeleton alone may have evolved at least four times (25). Poriferans and Cnidarians can acquire or lose hard parts with relative ease (24, 26). Many of the putative Lower Cambrian calcified cnidarians show no obvious affinity to the two main groups of corals (the orders Tabulata and Rugosa) that dominated the Paleozoic record and so have been proposed to represent a series of independently skeletalized clades of anemone (12). We suggest here that *Namapoikia* represents a further calcified, modular clade of probable cnidarian or poriferan affinity.

Terminal Proterozoic reefs have been thought to be ecologically simple and of low biodiversity (27); but the presence of *Namapoikia* implies that there was a common metazoan component to these communities and that a differentiation of reef metazoans into distinct open surface and cryptic inhabitants, so characteristic of Phanerozoic reefs, had taken place by the end of terminal Proterozoic time.

Fossilizable hard parts were thought to have first appeared as weakly skeletal, solitary organisms in the terminal Proterozoic, followed by an array of small, mainly calcareous, shelly fossils in the earliest Cambrian (Nemakit-Daldyn to Tommotian); large metazoans with heavily biomineralized skeletons were not known previously before the Tommotian (1–7). The skeleton of *Namapoikia* is notably robust, and its large size is reminiscent of coral and poriferan organizations that do not otherwise appear in the fossil record until the mid-Paleozoic. *Namapoikia* thus demonstrates that large, modular, skeletal metazoans appeared some 15 million years earlier than previously documented (1–7), and complex reef ecologies even earlier.

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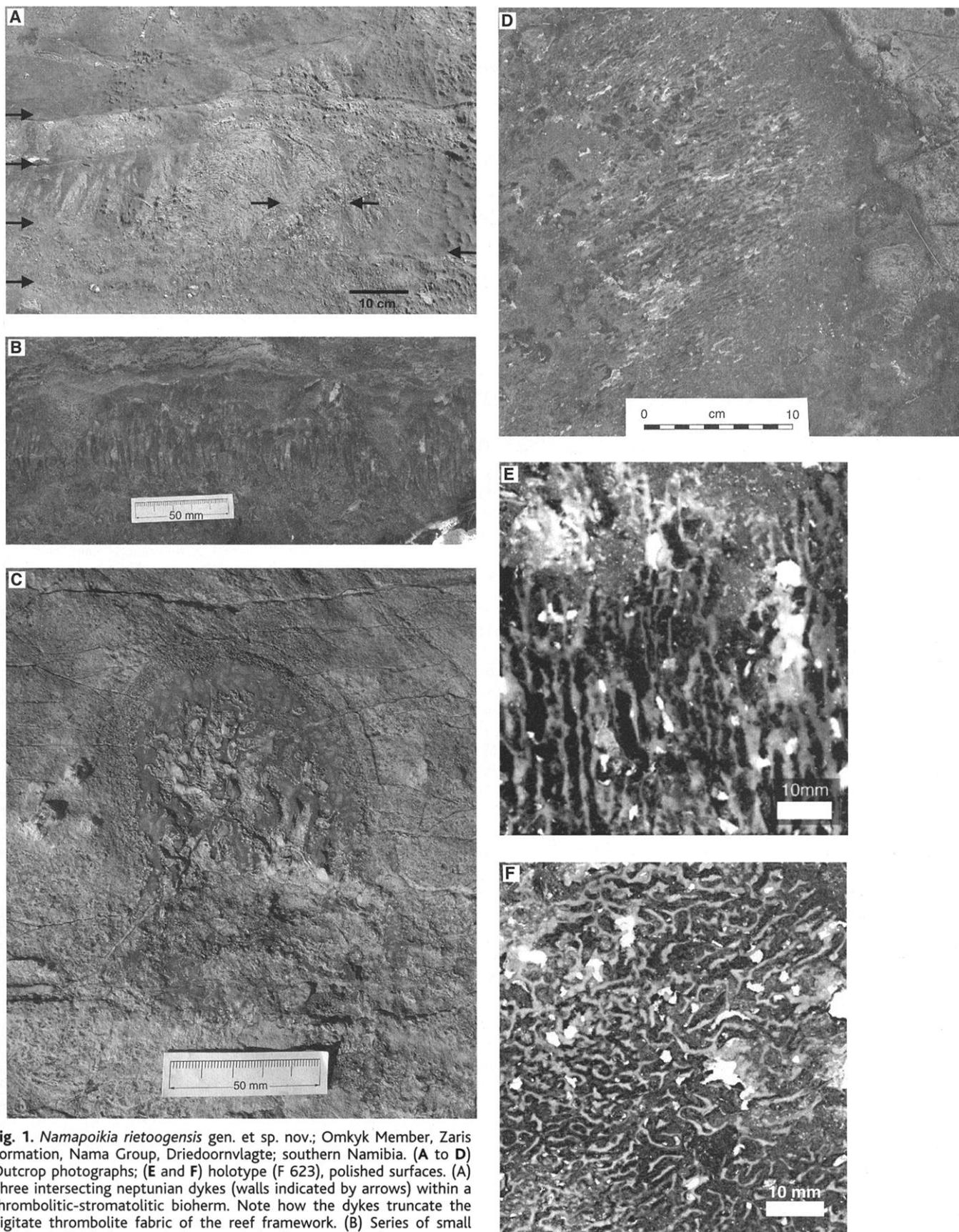


Fig. 1. *Namapoikia rietoogensis* gen. et sp. nov.; Omkyk Member, Zaris Formation, Nama Group, Driedoornvlagte; southern Namibia. (A to D) Outcrop photographs; (E and F) holotype (F 623), polished surfaces. (A) Three intersecting neptunian dykes (walls indicated by arrows) within a thrombolitic-stromatolitic bioherm. Note how the dykes truncate the digitate thrombolite fabric of the reef framework. (B) Series of small nodular individuals attached to a single fissure wall. The contact is stylolitized. (C) Nodular individual growing perpendicular to a fissure wall, encrusted by a rind of dolomitized stromatolite (arrows). (D) Tangential section of a single, extensive individual, with some early botryoidal (dark) and late burial spar (white) cements. (E) Longitudinal section, showing open, tubular construction. (F) Transverse section showing labyrinthine tubule cross sections.

