



**Synchronous Aggregate Growth in an Abundant
New Ediacaran Tubular Organism**

Mary L. Droser, *et al.*
Science **319**, 1660 (2008);
DOI: 10.1126/science.1152595

***The following resources related to this article are available online at
www.sciencemag.org (this information is current as of July 25, 2008):***

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/cgi/content/full/319/5870/1660>

Supporting Online Material can be found at:

<http://www.sciencemag.org/cgi/content/full/319/5870/1660/DC1>

This article **cites 12 articles**, 3 of which can be accessed for free:

<http://www.sciencemag.org/cgi/content/full/319/5870/1660#otherarticles>

This article appears in the following **subject collections**:

Paleontology

<http://www.sciencemag.org/cgi/collection/paleo>

Information about obtaining **reprints** of this article or about obtaining **permission to reproduce this article** in whole or in part can be found at:

<http://www.sciencemag.org/about/permissions.dtl>

12. P. H. Wine, A. R. Ravishankara, *Chem. Phys. Lett.* **77**, 103 (1981).
13. S. P. Sander, et al., *Chemical Kinetics and Photochemical Data for Use in Stratospheric Modeling, Evaluation No. 14, JPL Publ. 02-25* (NASA Jet Propulsion Laboratory, Pasadena, CA, 2003).
14. C. M. Roehl et al., *J. Phys. Chem.* **98**, 7837 (1994).
15. C. G. Stevens, M. W. Swagel, R. Wallace, R. N. Zare, *Chem. Phys. Lett.* **18**, 465 (1973).
16. A. E. Douglas, *J. Chem. Phys.* **45**, 1007 (1966).
17. H. Okabe, *Photochemistry of Small Molecules* (Wiley, New York, 1978).
18. V. M. Donnelly, D. G. Keil, F. Kaufman, *J. Chem. Phys.* **71**, 659 (1979).
19. J. A. Thornton, P. J. Wooldridge, R. C. Cohen, *Anal. Chem.* **72**, 528 (2000).
20. J. N. Crowley, S. A. Carl, *J. Phys. Chem. A* **101**, 4178 (1997).
21. G. Dutton, R. J. Barnes, A. Sinha, *J. Chem. Phys.* **111**, 4976 (1999).
22. Materials and methods are available as supporting material on Science Online.
23. K. Shibuya, H. Nagai, T. Imajo, K. Obi, I. Tanaka, *J. Chem. Phys.* **85**, 5061 (1986).
24. G. V. Hartland, D. Qin, H. L. Dai, C. Chen, *J. Chem. Phys.* **107**, 2890 (1997).
25. B. J. Finlayson-Pitts, L. M. Wingen, A. L. Sumner, D. Syomin, K. A. Ramazan, *Phys. Chem. Chem. Phys.* **5**, 223 (2003).
26. K. A. Ramazan et al., *J. Phys. Chem. A* **110**, 6886 (2006).
27. L. S. Rothman et al., *J. Quant. Spectrosc. Radiat. Transf.* **82**, 5 (2003).
28. S. Madronich, S. Flocke, J. Zeng, I. Petropavlovskikh, J. Lee-Taylor, *Tropospheric Ultraviolet-Visible Model, version 4* (National Center For Atmospheric Research, Boulder, CO, 2006).
29. H. B. Singh et al., *J. Geophys. Res.* **112**, D12504 (2007).
30. We thank the Donors of the American Chemical Society Petroleum Research Fund and NSF Chemistry for partial support of this research.

Supporting Online Material

www.sciencemag.org/cgi/content/full/319/5870/1657/DC1

Materials and Methods

Figs. S1 to S4

References and Notes

9 October 2007; accepted 30 January 2008

10.1126/science.1151443

Synchronous Aggregate Growth in an Abundant New Ediacaran Tubular Organism

Mary L. Droser^{1*} and James G. Gehling²

The most abundant taxon of the Neoproterozoic soft-bodied biota near Ediacara, South Australia, occurs as clusters of similarly sized individuals, which suggests synchronous aggregate growth by spatfall. Tubes of *Funisia dorothea* gen. et sp. nov. were anchored within the shallow, sandy sea bed and lived in dense, typically monospecific concentrations. Tubes were composed of modular, serially repeating elements. Individuals grew by adding serial elements to the tubular body and by branching of tubes. Their construction and close-packed association imply likely affinity within the Porifera or Cnidaria. These data suggest that several of the most successful marine invertebrate ecological strategies known today were in place in Earth's oldest known metazoan ecosystems before the advent of skeletonization and widespread predation.

Both the structure and associations of Neoproterozoic Ediacaran fossils from near the Flinders Ranges, South Australia, provide information on the complex ecological makeup of Earth's first metazoan habitats (1). The fossil-bearing Ediacara Member of the Rawnsley Quartzite lies 50 to 500 m below a basal Cambrian disconformity and consists of shallow marine thin- to medium-bedded quartz sandstone (2). We excavated beds within the Ediacara Member of the Rawnsley Quartzite at the Ediacara Conservation Park (South Ediacara) and on Nilpena Station of South Australia (fig. S1) to reveal details of the form, diversity, and distribution of these taxa.

A large diversity of fossils in original growth position occurs on successive bedding planes within the more than 150 m² excavated. Tubular fossils, representing an undescribed structural organization, are more abundant than any other previously described element of the Ediacara biota (1). They occur on nearly all excavated beds and densely on 3 of the 10 beds excavated at Nilpena and 2 of the beds at South Ediacara.

Funisia dorothea gen. et sp. nov. (see supporting online material) is preserved exclusively on the base of beds, as are nearly all fossils in these strata (Fig. 1). Unlike most elements of the Ediacara Biota (3), *Funisia* is preserved in positive relief, either as flattened casts formed when sand entered the body cavity (Fig. 1, A and D), or as casts of the collapsed body that was impressed into the underlying biomat (Fig. 1, E and G). Collapse and casting is the most common preservation mode because sand rarely fills more than a few centimeters of each tubular body (Fig. 1A). Removal of internal casts leaves an external mold in the overlying bed. In the best-preserved specimens, individual serial units show faint, offset concentric wrinkles that suggest collapse of a thin integument during burial, rather than ornamentation (Fig. 1, E and G).

Funisia is up to 30 cm long and 12 mm in diameter and is divided longitudinally into serial units 6 to 8 mm in length throughout the length of the tube (Figs. 1 and 2). The serial units are defined by constrictions perpendicular or gently oblique to the axis of the tube. Particularly when tubes are bent or curved, constrictions give the tube the appearance of being a spiral, but examination of material preserved nearly in three dimensions (3D) (Fig. 1, D, E, and G) confirms serial segmented construction. In compacted and

poorly preserved tubes, or external molds, a scalloped-shaped tube outline, rather than the impression of individual segments, is typically preserved (Fig. 1, A, I, and J). Where *F. dorothea* covers the surface, the degree of overlapping is such that individual tubes are deformed by composite preservation (Figs. 1, I and J), and under very poor preservation, the sides of the tube appear as parallel lines (Fig. 1A).

Tube widths range from 2 to 12 mm and are consistent on individual bedding surfaces. These structures were originally interpreted to be strings of fecal pellets (4), but this has since been discounted on the basis of the presence of branching and orientation of specimens (5). Units within the tube taper progressively in width toward the axis, suggestive of growth by terminal addition (6) (Fig. 1, E and G). Individuals can occur within dense assemblages, sometimes greater than 1000/m² (Fig. 1, I and J). Here, individual tubes of similar size may radiate from a single area of origin (Fig. 1I). In such dense assemblages, tubes completely cover the surface and may overlap or crisscross in a felted manner (Fig. 1, I and J) but most commonly occur in parallel, close-packed groups of 5 to 15 individuals (Fig. 1, A and C). Such groups do not show alignment with current lineations or ripple crests that occur on top of the beds, which suggests that the position of these fossils is not a reflection of transport or reorientation by currents. Rather, they are the result of smothering by sandy event beds in the wake of storm activity (2). Branching is rare, but in such instances, the last common serial unit is expanded and branches remain tightly packed (Fig. 1H).

Tube attachment structures ranging in diameter from 1 to 8 mm are preserved as invaginate bosses on bed soles (Fig. 1, B, C, D, and I). Serially constricted tubes are directly connected to attachment structures (Fig. 1D). The marked modality of size and morphology suggest that different developmental cohorts are preserved (Fig. 1C). Attachment structures of a similar size and developmental stage are spatially clustered within individual bedding surfaces (Fig. 1C). Clustered attachment points are not typically closely packed, but three-dimensionally preserved examples recording the basal several millimeters of the tube demonstrate a hexagonal close packing

¹Department of Earth Sciences, University of California, Riverside, CA 92521, USA. ²South Australia Museum, North Terrace, Adelaide, South Australia 5000, Australia.

*To whom correspondence should be addressed. E-mail: Mary.droser@ucr.edu

within millimeters of vertical growth (Fig. 1, B and F). Individual attachments occur without close neighbors but are not common. The size and morphology of attachments range from small knobs 1 to 3 mm in width to well-developed structures that are casts of tube ends with concave hollows (Fig. 1, B, C, D, and I). These structures occur on both ripple crests and troughs and originally extended below the interface between water and substrate. They are clearly attachment discs rather than cross sections through the tubes. Ediacara preservation consists entirely of casts

and molds. Cross sections are confined to broken three-dimensionally cast specimens within a bed. Furthermore, there would be some ellipses preserved, and it would not be possible for the tube to be sectioned and still cast by sand.

Like the well-known Ediacaran fronds (7), *Funisia* tubes are typically preserved without holdfasts attached. In life position (Fig. 2), attachment structures are interpreted to have been situated within or beneath a microbial mat. Where they are cast by sand, the corresponding tube was ripped off by storm activity, allowing sediment to

enter the hollow holdfast (Fig. 1C). Alternatively, the holdfast was molded below the mat-bound sediment, and the tube was cast within the overlying sediment or preserved as a collapsed impression at the base of the sediment that engulfed the specimen (Fig. 1B).

The phylogenetic affinity of *F. dorothea* is problematic. The morphology is consistent throughout all well-preserved specimens and serial units are a 3D character rather than features of external ornamentation. However, the lack of evidence for polypoid openings or pores in the body wall limits our understanding of its taxonomic affinities. Although it is difficult to place these fossils within Metazoa, the morphology and ecology are suggestive of stem-group cnidarians or poriferans. The tightly packed nature of the tubes and attachment structures (Fig. 1I), as well as the rarity of branching, eliminates an algal origin because these characteristics are inconsistent with the maximization of surface area crucial for a photosynthetic habit.

The branching patterns and rarity of branching of *Funisia* is consistent with metazoan asexual budding. The consistency of tube widths on individual bedding surfaces (Fig. 1, A, I, and J), the densely packed nature of the attachment structures, and the clustering pattern of developmental stages of attachment structures on individual bedding planes suggests that the juveniles settled as aggregates in a series of limited cohorts.

These solitary organisms thus exhibit growth by addition of serial units to tubes and by the division of tubes, and dispersed propagation by the production of spats. Among living organisms, spat production is almost ubiquitously the result of sexual reproduction but is known to occur rarely in association with asexual reproduction (8). Hence, despite its morphological simplicity the Neoproterozoic *F. dorothea* provides evidence of a variety of growth modes and a complex arrangement for the propagation of new individuals. In living organisms, synchronous aggregate growth may result from a variety of factors—including response to competition, sediment disturbance, and heterogeneity of the substrate—and has the advantage of reducing competition for space between clones and can also decrease gamete wastage (9, 10). It may also reduce vulnerability to predation (9). Borings in the calcified *Cloudina* may demonstrate predation in the latest Ediacara (11). Furthermore, close

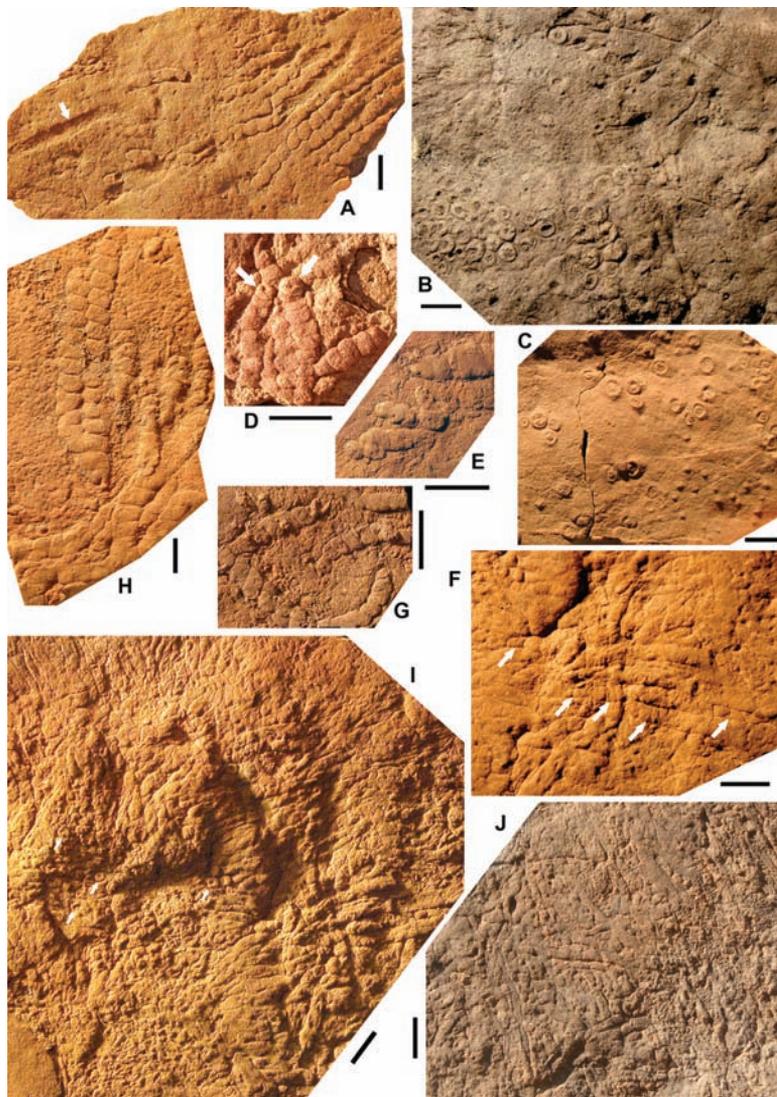


Fig. 1. *Funisia dorothea* gen. et sp. nov. preserved as external casts, internal casts, and external molds on bed bases. (A) Holotype set of subparallel tubes SAM P40725, internal casts, external mold where casts have separated, and as convex casts of collapsed specimens demonstrating various taphonomic variants, including well-preserved serial units, scalloped edge outlines (arrow), and parallel edged outlines. (B) Close-packed set of attachment points (lower left) showing typical convex rim and indented center with or without boss, one with cast of part of tube (arrow); SAM P42681. (C) Growth by branching; SAM P40726. (D) Attachment points with serially constricted tubes; field specimen E505. (E and G) Specimens showing growth by terminal addition; SAM P41508. (F) Two sets of attachment points demonstrating different stages of development. (H) Enlargement of lower right part of surface in Fig. 2I showing crossed tubes with serial constrictions (arrows). (I) Layered, close-packed specimens radiating from clusters of attachment points (examples marked by arrows); SAM P40309. (J) Densely packed surface with both scalloped and parallel edge preservation; part of very large field specimen, Nilpena. Scale bars, 2 cm.

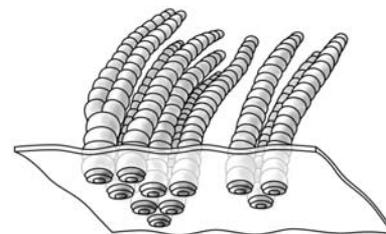


Fig. 2. Reconstruction of *Funisia* in life position with holdfast beneath mat substrate.

packing also imparts protection from current damage and/or high-energy events and allows for selection of most favorable sites for attachment and growth to adulthood (12).

Aggregation is not uncommon among some elements of the Ediacara biota and is present in the frond holdfast *Aspidella*. These typically occur in dense assemblages, but in contrast to *F. dorothea*, their size distribution is consistent with continuous recruitment (1, 13, 14) rather than periodic cohort growth. The terminal Neoproterozoic calcified tubes *Cloudina* and *Namacalathus* also show evidence of aggregation (15), but there is no indication of distinct cohorts.

These data demonstrate that even morphologically simple Ediacaran organisms had multiple modes of growth and propagation, reminiscent of several of the most successful marine invertebrate ecological strategies today (16). These systems were in place in Earth's oldest known metazoan ecosystems before the ecological pressures that

accompanied the advent of skeletonization and extensive predation.

References and Notes

- M. L. Droser, J. G. Gehling, S. R. Jensen, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **232**, 131 (2006).
- J. G. Gehling, *Precambrian Res.* **100**, 65 (2000).
- J. G. Gehling, *Palaios* **14**, 40 (1999).
- M. F. Glaessner, *Lethaia* **2**, 369 (1969).
- M. L. Droser, J. G. Gehling, S. R. Jensen, Eds., *Ediacaran trace fossils: Truth and false* (Peabody Museum of Natural History, New Haven, CT, 2005), pp. 125-138.
- D. K. Jacobs, N. C. Hughes, S. T. Fitz-Gibbon, C. J. Winchell, *Evol. Dev.* **7**, 498 (2005).
- J. G. Gehling, M. L. Droser, S. R. Jensen, B. N. Runnegar, Eds., *Ediacara Organisms: Relating Form to Function* (Yale Peabody Museum, New Haven, CT, 2005).
- D. G. Fautin, *Can. J. Zool.* **80**, 1735 (2002).
- J. B. C. Jackson, in *Biotic Interactions in Recent and Fossil Benthic Communities*, M. J. S. Tevesz, P. L. McCall, Eds. (Plenum Press, New York, 1983), vol. 3, pp. 39-120.
- D. J. Crisp, in *Biology and Systematics of Colonial Organisms*, G. P. Larwood, B. R. Rosen, Eds. (Academic Press, New York, 1979), pp. 319-327.
- S. Bengtson, Z. Yue, *Science* **257**, 1645 (1992).
- G. Wörheide, A. M. Solé-Cava, J. N. A. Hooper, *Comp. Biol.* **45**, 377 (2005).
- K. J. Peterson, B. Waggoner, J. W. Hagadorn, *Integr. Comp. Biol.* **43**, 127 (2003).
- J. G. Gehling, G. M. Narbonne, M. A. Anderson, *Palaeontology* **43**, 427 (2000).
- J. E. Amthor *et al.*, *Geology* **31**, 431 (2003).
- L. J. Holts, K. A. Beauchamp, *Mar. Biol.* **116**, 129 (1993).
- This research was supported by a National Science Foundation grant (EAR-0074021) and a NASA grant (NNG04G42G NASA Exobiology Program) and a NASA grant (NNG04G42G NASA Exobiology Program) to M.L.D. and an Australian Research Council Grant (DP0453393) to J.G.G. We are indebted to J. Fargher and R. Fargher for access to their property and permission to excavate fossiliferous beds. Fieldwork was facilitated by D. Rice, S. Jensen, J. Paterson, M. Dzaugis, M. E. Dzaugis, R. Droser, and members of the Waterhouse Club. N. Hughes, R. Wood and S. Xiao provided helpful comments. D. Garson constructed Fig. 2.

Supporting Online Material

www.sciencemag.org/cgi/content/full/319/5870/1660/DC1
SOM Text
Fig. S1

5 November 2007; accepted 1 February 2008
10.1126/science.1152595

Orrorin tugenensis Femoral Morphology and the Evolution of Hominin Bipedalism

Brian G. Richmond^{1,2*} and William L. Jungers³

Bipedalism is a key human adaptation and a defining feature of the hominin clade. Fossil femora discovered in Kenya and attributed to *Orrorin tugenensis*, at 6 million years ago, purportedly provide the earliest postcranial evidence of hominin bipedalism, but their functional and phylogenetic affinities are controversial. We show that the *O. tugenensis* femur differs from those of apes and *Homo* and most strongly resembles those of *Australopithecus* and *Paranthropus*, indicating that *O. tugenensis* was bipedal but is not more closely related to *Homo* than to *Australopithecus*. Femoral morphology indicates that *O. tugenensis* shared distinctive hip biomechanics with australopiths, suggesting that this complex evolved early in human evolution and persisted for almost 4 million years until modifications of the hip appeared in the late Pliocene in early *Homo*.

Bipedalism is one of very few human characteristics that appears to have evolved at the base of the hominin clade [species more closely related to modern humans than to any other living species (1)]. Recent fossil discoveries have apparently pushed back the origin of the hominin clade into the late Miocene, to 6 to 7 million years ago (Ma). The oldest known potential hominin fossils, attributed to *Sahelanthropus tchadensis*, come from Toros-Menalla in Chad and are biostratigraphically dated to ~7 Ma (2). Currently, *Sahelanthropus* is only known from craniodental evidence, and although the

position of the foramen magnum suggests that it was bipedal (3), postcranial fossils are needed to confirm this conclusion. The next oldest potential hominin remains were discovered in 2000 by Senut, Pickford, and colleagues (4) from localities (5.7 to 6.0 Ma) in the Lukeino Formation in Kenya (5, 6) and attributed to *Orrorin tugenensis*. Of the fossils assigned to *O. tugenensis*, three fragmentary femora (BAR 1002'00, 1003'00, and 1215'00) are critical pieces of evidence because they are interpreted as having derived characteristics indicating bipedalism (7). However, some of these features are also found in non-bipedal primates and are therefore inconclusive (8). Similarly, a study of the femora based on computerized tomography (9) suffered from poor image resolution and does not provide convincing evidence of bipedality (10). The discoverers have also cited the femora in formulating hypotheses about early hominin phylogenetic relationships (4), but these have been disputed (8, 11, 12). Thus, the morphology of the *O. tugenensis* femora

is critical to our understanding of the origin of bipedalism and phylogenetic relationships of the earliest hominin taxa, yet the functional and phylogenetic implications of their morphology remain highly controversial. We present here a quantitative, morphometric (shape) comparison of the most complete *O. tugenensis* femur, BAR 1002'00, of a young adult.

When compared to the proximal femora of a large and diverse sample of great apes, modern humans (including small-bodied adult individuals from African Pygmy and Andaman Island populations), as well as Plio-Pleistocene hominin femora (13), the *O. tugenensis* femur (BAR 1002'00) more closely resembles femora attributed to early hominin taxa (*Australopithecus* and *Paranthropus*) than do those of extant apes, fossil *Homo*, and modern humans. Multivariate analyses of shape (canonical variates, cluster analysis, and principal components analysis) reveal that modern human proximal femora are distinct from those of extant great apes primarily in having a relatively large head and short distance between the head and lesser trochanter. Canonical variates axis 1 (Fig. 1A) is a contrast vector driven by these distinguishing features of shape (table S1), and the non-*Homo* fossil hominins (including BAR 1002'00) occupy an intermediate position in this part of multivariate space. The second axis separates orangutans from African apes, modern humans, and all the fossils. Orangutans have relatively large femoral heads (related to mobility rather than more pronounced weight support) combined with narrow femoral shafts, a combination of features not seen in modern or fossil hominin femora. The third axis, driven by neck length and breadth, and shaft breadth, serves to separate early hominin femora from those of extant apes, modern humans, and fossil *Homo* taxa. BAR 1002'00 resembles the early hominin femora, which are characterized in this and previous analyses by a combination of long and

¹Center for the Advanced Study of Hominid Paleobiology, Department of Anthropology, The George Washington University, 2110 G Street, NW, Washington, DC 20052, USA.

²Human Origins Program, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA. ³Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY 11794-8081, USA.

*To whom correspondence should be addressed. E-mail: brich@gwu.edu