

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.

References and Notes

1. R. Sweet, *Geosci. Canada* **28**, 127 (2001).
2. K. R. Johnson, *Cretaceous Res.* **13**, 91 (1992).
3. C. C. Labandeira, K. R. Johnson, P. Wilf, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 2061 (2002).
4. D. A. Pearson, T. Schaefer, K. R. Johnson, D. J. Nichols, *Geology* **29**, 36 (2001).
5. R. W. Brown, *U. S. Geol. Surv. Prof. Pap.* 375 (1962), p. 119.
6. L. J. Hickey, in *Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming*, P. D. Gingerich, Ed. (University of Michigan Pap. Paleontol. Ann Arbor, MI, 1980), vol. 24, pp. 33–49.
7. K. R. Johnson, L. J. Hickey, *Geol. Soc. Am. Spec. Paper* 247 (1990), p. 433.
8. S. L. Wing, J. Alroy, L. J. Hickey, *Palaeogeogr. Paleoclimatol. Paleoecol.* **115**, 117 (1995).
9. K. R. Johnson, thesis, Yale University, New Haven, CT (1989).
10. J. A. Wolfe, *Paleobiology* **13**, 215 (1987).
11. P. W. Richards, *The Tropical Rainforest: an Ecological Study* (Cambridge Univ. Press, Cambridge, ed. 2, 1996).
12. J. A. Wolfe, *U. S. Geol. Surv. Prof. Pap.* 1106 (1979), p. 37.
13. R. J. Morley, *Origin and Evolution of Tropical Rainforests* (Wiley, Chichester, UK, 2000).
14. R. J. Burnham, *Rev. Palaeobot. Palynol.* **81**, 99 (1994).
15. The fossil leaves are preserved as cuticle-bearing compressions in a medium gray andesitic mudstone with relictual ripple cross-stratification, suggesting that the matrix was a muddy sand at the time of deposition. Two 5-cm-thick leaf-bearing layers, separated by 10 cm of massive mudstone, lie directly above a rooted mudstone interpreted as a gley paleosol.
16. D. J. Hopkins Jr., K. R. Johnson, *Am. J. Bot.* **84**, 135 (1997).

17. R. G. Reynolds et al., "The Kiowa Core, a Continuous Drill Core Through the Denver Basin Bedrock Aquifers at Kiowa, Elbert County, Colorado," *U. S. Geol. Surv. Open-File Rep. 01-0185* (2001).
18. D. J. Nichols, R. F. Fleming, *Rocky Mountain Geol.*, in press.
19. J. F. Hicks, K. R. Johnson, L. Tauxe, *Rocky Mountain Geol.*, in press.
20. R. G. Reynolds, in *Geologic History of the Colorado Front Range, 1997 RMS-AAPG Field Trip #7*, D. W. Bolyard, S. A. Sonnenberg, Eds. (Rocky Mountain Association of Geologists, Denver, CO, 1997), pp. 43–48.
21. S. G. Robson, E. R. Banta, *U.S. Geol. Surv. Open-File Rep. 93-442* (1993).
22. P. D. Warwick, R. M. Flores, D. J. Nichols, E. C. Murphy, in *Coal-Bearing Strata: Sequence Stratigraphy, Paleoclimate, and Tectonics*, J. C. Pashin, R. A. Gastaldo, Eds. (American Association of Petroleum Geology Studies in Geology, Tulsa, OK, in press).
23. J. F. Hicks, K. R. Johnson, L. Tauxe, D. Clark, J. D. Obradovich, in *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. Hartman, K. R. Johnson, D. J. Nichols, Eds. (Geological Society of America, Boulder, CO, 2002, in press), vol. 361.
24. J. D. Archibald et al., in *Cenozoic Mammals of North America*, M. O. Woodburne, Ed. (Univ. of California Press, Berkeley, CA, 1987), pp. 24–76.
25. Quarry 1200A produced 33 morphotypes from 176 identified specimens; 1200B produced 36 from 180; 1200C produced 50 from 193; 1200D produced 39 from 185; and 1200Z produced 50 from 203. A total of 937 specimens were identified from a collection of 1490 (the remaining leaves are too poorly preserved to be definitively identified). Although most of the well-preserved and identifiable specimens were collected, poorly preserved and unidentifiable specimens were common and many were not collected, suggesting caution when quantitatively comparing this flora with other unbiased samples.
26. *LAWG, Manual of Leaf Architecture—Morphological Description and Categorization of Dicotyledonous and Net-Veined Monocotyledonous Angiosperms* (Smithsonian Institution Press, Washington, DC, 1999).
27. S. L. Wing, D. R. Greenwood, *Philos. Trans. R. Soc. London Ser. B* **341**, 243 (1993).

28. P. Wilf, *Paleobiology* **23**, 373 (1997).
29. P. Wilf, S. L. Wing, D. R. Greenwood, C. L. Greenwood, *Geology* **26**, 203 (1998).
30. S. L. Wing, in *Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records*, M.-P. Aubry, S. P. Lucas, W. A. Berggren, Eds. (Columbia Univ. Press, New York, 1998), pp. 380–400.
31. P. Wilf, *GSA Bull.* **112**, 292 (2000).
32. The formula used was $[2(\text{number of species in common between the two samples})/(\text{number of species in sample 1} + \text{number of species in sample 2})]$.
33. R. J. Burnham, in *Manu: The Biodiversity of Southeastern Peru*, D. E. Wilson, A. Sandoval, Eds. (Smithsonian Institution, Washington, DC, 1996), pp. 127–140.
34. R. M. Kirkham, L. R. Ladwig, *Coal Resources of the Denver and Cheyenne Basins, Colorado* (Resource Series 5, Colorado Geological Survey, Denver, CO, 1979).
35. V. B. Cherven, A. R. Jacob, in *Cenozoic Paleogeography of the West-Central United States*, R. M. Flores, S. S. Kaplan, Eds. (Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists, Denver, CO, 1985), pp. 127–170.
36. W. R. Dickinson et al., *Geol. Soc. Am. Bull.* **100**, 1023 (1988).
37. J. A. Wolfe, G. R. Upchurch Jr., *Proc. Natl. Acad. Sci. U.S.A.* **84**, 5096 (1987).
38. G. I. Omar, T. M. Lutz, R. Giegengack, *Geol. Soc. Am. Bull.* **106**, 74 (1994).
39. R. S. Barclay, D. L. Dilcher, K. R. Johnson, *Geol. Soc. Am. Abstr. Program* **33**, A-198 (2001).
40. R. S. Barclay, thesis, Univ. of Florida, Gainesville, FL (2002).
41. R. J. Burnham, N. C. A. Pitman, K. R. Johnson, P. Wilf, *Am. J. Bot.* **88**, 1096–1102 (2001).
42. We acknowledge funding from NSF (grant EAR-9805474) and in-kind support from the Colorado Department of Transportation. R. Burnham, P. Wilf, D. Nichols, S. Wallace, R. Barclay, K. Benson, R. Dunn, R. Ellis, S. Manchester, R. Reynolds, M. Reynolds, and A. Kropp provided useful comments and help on various aspects of the project.

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

21 March 2002; accepted 24 May 2002

Proterozoic Modular Biomineralized Metazoan from the Nama Group, Namibia

Rachel A. Wood,^{1,2*} John P. Grotzinger,³ J. A. D. Dickson²

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 syndimentary 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

REPORTS

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 siliciferous 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 stylolitization (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 actiniarian and corallomorphariid 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.

¹Schlumberger Cambridge Research, High Cross, Madingley Road, Cambridge CB2 0EL, UK. ²Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK. ³Department of Earth, Atmospheric, and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139, USA.

*To whom correspondence should be addressed. E-mail: rwood2@cambridge.scr.slb.com

REPORTS

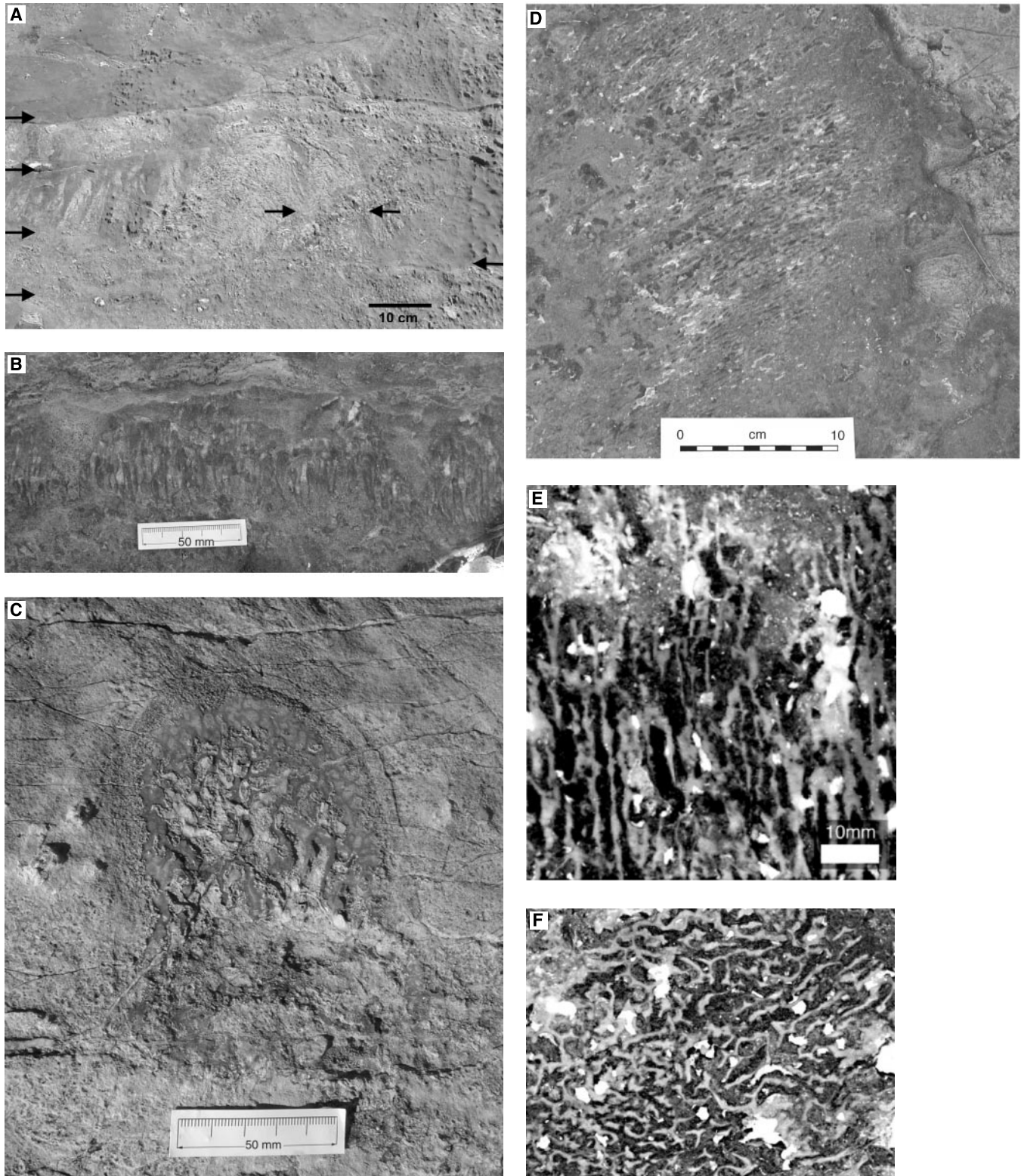


Fig. 1. *Namapoikia rietoogensis* gen. et sp. nov.; Omkyk Member, Zaris Formation, Nama Group, Driedoornvlagte; southern Namibia. (A to D) Outcrop photographs; (E and F) holotype (F 623), polished surfaces. (A) Three intersecting neptunian dykes (walls indicated by arrows) within a thrombolitic-stromatolitic 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.

References and Notes

1. S. Bengtson, S. Conway Morris, *Top. Geobiol.* **20**, 447 (1992).
2. M. D. Brasier, *The Precambrian-Cambrian Boundary* (Clarendon, Oxford, UK, 1989), pp. 117–165.
3. S. A. Bowring *et al.*, *Science* **261**, 1293 (1993).
4. S. W. F. Grant, *Am. J. Sci.* **290A**, 261 (1990).
5. G. B. H. Germs, *Am. J. Sci.* **272**, 752 (1972).
6. W. A. Watters, J. P. Grotzinger, *Paleobiology* **27**, 159 (2001).
7. H. J. Hofmann, E. W. Mountjoy, *Geology* **29**, 1091 (2001).
8. B. Z. Saylor, A. J. Kaufman, J. P. Grotzinger, F. Urban, *J. Sediment. Res.* **68**, 1223 (1998).
9. G. M. Narbonne, B. Z. Saylor, J. P. Grotzinger, *J. Paleontol.* **71**, 953 (1997).
10. J. P. Grotzinger, S. A. Bowring, B. Z. Saylor, A. J. Kaufman, *Science* **270**, 598 (1995).
11. J. P. Grotzinger, *Commun. Geol. Surv. Namibia*, in press.
12. C. T. Scrutton, *Proc. Yorks. Geol. Soc.* **51**, 177 (1997).
13. A. Yu. Zhuravlev, *Palaeontol. J.* **33**, 502 (1999).
14. D. R. Kobluk, *Can. J. Earth Sci.* **16**, 2040 (1979).
15. ———, *J. Paleontol.* **58**, 703 (1984).
16. J. R. Reitner, *Berliner Geowissenschaft. Abh. E.* **1**, 1 (1992).
17. D. Bridge, C. W. Cunningham, R. DeSalle, L. Buss, *Mol. Biol. Evol.* **12**, 679 (1995).
18. J. H. Gehling, J. K. Rigby, *J. Paleontol.* **70**, 185 (1996).
19. M. D. Brasier, O. Green, G. Sheilds, *Geology* **25**, 303 (1997).
20. S. Xiao, X. Yuan, A. H. Knoll, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 13684 (2000).
21. S. Conway Morris, *Palaeontology* **36**, 593 (1993).
22. C. T. Scrutton, in *The Origin of Major Invertebrate Groups*, M. R. House, Ed. (Academic Press, London, 1979), pp. 161–207.
23. S. Jensen, B. Z. Saylor, J. G. Gehling, G. J. Germs, *Geology* **28**, 143 (2000).
24. R. Wood, *Am. Sci.* **78**, 224 (1990).
25. S. L. Romano, S. D. Cairns, *Bull. Mar. Sci.* **67**, 1043 (2000).
26. G. D. Stanley Jr., D. G. Fautin, *Science* **291**, 1913 (2001).
27. R. Wood, *Reef Evolution* (Oxford Univ. Press, Oxford, UK, 1999).
28. Supported by the Geological Survey of Namibia, NSF, Petroleum Development Oman, and Schlumberger. We thank C. Husselmann for access to Driedoornvlagte; D. McCormick and S. Schroeder for assistance in the field; D. Simons for photographic expertise; S. Conway Morris, C. Scrutton, A. Knoll, S. Bengtson, M. Brasier, M. Droser, and an anonymous reviewer for comments on the manuscript; R. Duncan-Jones and A. Brett for etymological expertise; and R. Swart (National Petroleum Corporation of Namibia) for permission to publish the LANDSAT image shown in fig. S1B.

Supporting Online Material
www.sciencemag.org/cgi/content/full/296/5577/2383/DC1
 Figs. S1 and S2
 Appendix S1

4 March 2002; accepted 15 May 2002

Pollen-Mediated Movement of Herbicide Resistance Between Commercial Canola Fields

Mary A. Rieger,^{1,2*} Michael Lamond,³ Christopher Preston,^{1,2} Stephen B. Powles,³ Richard T. Roush¹

There is considerable public and scientific debate for and against genetically modified (GM) crops. One of the first GM crops, *Brassica napus* (oilseed rape or canola) is now widely grown in North America, with proposed commercial release into Australia and Europe. Among concerns of opponents to these crops are claims that pollen movement will cause unacceptable levels of gene flow from GM to non-GM crops or to related weedy species, resulting in genetic pollution of the environment. Therefore, quantifying pollen-mediated gene flow is vital for assessing the environmental impact of GM crops. This study quantifies at a landscape level the gene flow that occurs from herbicide-resistant canola crops to nearby crops not containing herbicide resistance genes.

Data on pollen dispersal has mostly been obtained from small-scale field trials of limited sample size (1–5). Canadian experiments with GM canola found less than 0.03% pollination at 30 m into conventional varieties (6). However, Hall *et al.* (7) suggested GM canola pollen moved over greater distances. Therefore, we examined pollen movement between herbicide-resistant canola and conventional varieties on a commercial scale, testing over 48 million individual plants. This was possible because canola resistant to acetolactate synthase (ALS)-inhibiting herbicides was grown commercially in Australia for the first time in 2000. These first commercial fields served as the herbicide resistance gene source in an uncontaminated environment. This variety has a two-gene

system—one herbicide resistance gene on each genome—and is homozygous for both genes. Therefore, any crosses to a conven-

tional variety will contain one copy of each gene.

To assess gene flow, seeds were collected from 63 conventional canola fields growing near herbicide-resistant fields in New South Wales, Victoria, and South Australia. These three states represent over half of the canola-growing area in Australia as well as a wide and diverse range of environments. Source and sink fields were of similar sizes, ranging from 25 to 100 ha. At crop maturity, 10 stratified samples totaling at least 100,000 seeds were taken from each of three locations in each field of conventional canola. These were parallel to the source field and taken at the edge nearest to the source field, the middle, and the edge furthest from the source field. Collected seed samples (500 g) were planted as separate plots, in an irrigated field, along with two resistant and two susceptible canola controls. To determine whether pollen-mediated gene flow from source to sink fields had occurred, we screened the seedlings with a lethal discriminating dose of the ALS-inhibiting herbicide chlorsulfuron, and any sur-

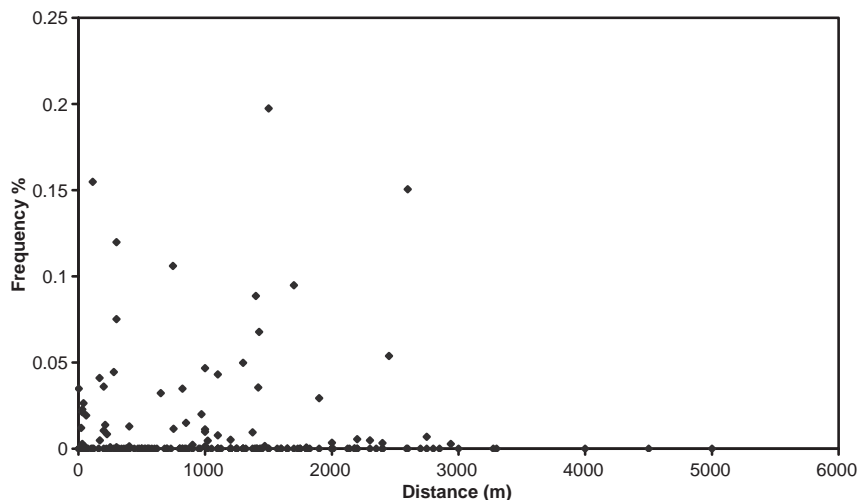


Fig. 1. Percentage of ALS herbicide-resistant individuals in seed from nonresistant varieties in relation to distance from the source field. Three individual samples were collected per field, with 190 individual collection locations.

¹Cooperative Research Center for Australian Weed Management, ²Department of Applied and Molecular Ecology, University of Adelaide, PMB1, Glen Osmond SA 5064, Australia. ³Western Australian Herbicide Resistance Initiative, University of Western Australia, Nedlands WA 6907, Australia.

*To whom correspondence should be addressed. E-mail: mary.rieger@adelaide.edu.au