mm. Using these data, we obtain from Fig. 4 cooling rate ~2 to 4 K/Ma, which is in excellent agreement with that of ~2 K/Ma deduced independently (*3*). For very slowly cooled rocks, the retrieved cooling rate is quite insensitive to errors in Δt. However, for relatively rapidly cooled rocks (for example, $dT/dt > 50$ K/Ma for $T_o = 800°C$), small error in Δt leads to very large error in dT/dt. Thus, for these rocks, it would be more appropriate to define a minimum cooling rate, taking into account the error in Δt.

References and Notes

1. F. J. Humphries and R. A. Cliff, *Nature* **295**, 515 (1982).
2. A. S. Cohen, R. K. O'Nions, R. Siegenthaler, W. I. Griffin, *Contrib. Mineral. Petrol.* **98**, 303 (1988).
3. K. Mezger, E. J. Essene, A. N. Halliday, *Earth Planet. Sci. Lett.* **113**, 387 (1992).
4. K. Burton, M. J. Kohn, A. S. Cohen, R. K. O'Nions, *ibid.* **133**, 199 (1992).
5. B. J. Hensen and B. Zhou, *Geology* **23**, 225 (1995).
6. H. Becker, *Contrib. Mineral. Petrol.* **127**, 224 (1997).
7. J. Ganguly, W. Cheng, S. Chakraborty, *ibid.* **131**, 171 (1998).
8. The isotope-enriched solution was prepared by first dissolving metals of Sm and Nd, enriched in the isotopes ^{149}Sm and ^{145}Nd, respectively, in 2 N HCl, evaporating it to almost dryness, and then adding triply distilled water. The nearly aqueous solutions were analyzed by inductively coupled plasma–mass spectrometry (ICP-MS) and found to have ^{145}Nd and ^{149}Sm concentrations varying between ~100 and 200 ppm in two different stock solutions used in this work.
9. H. St. C. O'Neill, *Am. Mineral.* **73**, 470 (1988)
10. The analyses were obtained in a Cameca ims 3f SIMS using a primary beam of mass-filtered $^{16}O^{-}$ accelerated to 10 keV. The samples were held at ~+4.5 kV, resulting in an impact energy of ~14.5 keV. Two approaches were used to avoid contribution of secondary ions from the crater walls. For some of the samples, a 50-nA primary beam was focused onto a spot and rastered over a 200 μm by 200 μm area. An aperture inserted into the path of the ions allowed only those originating from a 60-μm-diameter circular area in the center of the crater into the mass spectrometer. For other samples, a 15- to 20-nA primary beam was focused by Kohler illumination to generate a circular, flat-bottomed crater ~120 μm in diameter (*24*). Secondary ions from the central 10 or 20 μm of the crater were allowed into the mass spectrometer by selecting either a 100- or 200-μm field aperture. In both cases a 75-V offset was applied to the sample voltage to minimize the contribution of molecular ions to the mass spectrum (*25*). Crater depths were determined with a Dektak surface profilometer and varied as a function of primary beam current and analysis time (1 to 2 hours) between ~3000 and 7000 Å.
11. J. Crank, *The Mathematics of Diffusion* (Clarendon, Oxford, 1975).
12. F. James and M. Ross, *Comput. Phys.* **10**, 343 (1975).
13. D. S. Tannhauser, *Appl. Phys.* **27**, 662 (1956).
14. R. D. Shannon and C. T. Prewitt, *Acta Crystallogr.* **B25**, 925 (1969).
15. S. Chakraborty and J. Ganguly, in *Diffusion, Atomic Ordering and Mass Transport*, J. Ganguly, Ed. (Advances in Physical Geochemistry 8, Springer-Verlag, New York, 1991), pp. 120–175.
16. M. Morioka and H. Nagasawa, in (*15*), pp. 176–197.
17. D. J. Cherniak, J. M. Manchar, E. B. Watson, *Chem. Geol.* **134**, 289 (1997).
18. W. J. Harrison and B. J. Wood, *Contrib. Mineral. Petrol.* **72**, 145 (1980).
19. R. A. N. Coghlan, thesis, Brown University, Providence, RI (1990).
20. S. Chakraborty and J. Ganguly, *Contrib. Mineral. Petrol.* **111**, 74 (1992).
21. M. H. Dodson, *ibid.* **40**, 259 (1973).
22. ———, *Mat. Sci. Forum* **7**, 145 (1986).
23. J. Ganguly, in preparation. The geometric parameter A in the expression of mean T_C in Dodson's (*21*) eqn. 23 equals exp(G), where G is the spatially averaged value of the closure function $G(x)$ of his (*22*) eqn. 20. In deriving the expression for $G(x)$, Dodson (*22*) assumed that the dimensionless quantity $M \gg 1$, which implies removal of the composition of the crystal from its initial composition in all parts. The closure function has been modified so that it is valid for any arbitrary value of M, numerically evaluated as a function of the normalized radial distance from the center of a grain, and then spatially averaged to yield average closure function versus M; for example, $G(M = 0.001) = 0.9018$, $G(0.01) = 2.7603$, $G(0.10) = 3.8693$, $G(0.4) = 4.0041$, as compared to Dodson's (*22*) $G = 4.0066$.
24. S. W. J. Clement, W. Compston, G. Newstead, in *Proceedings International Secondary Ion Mass Spectrometry Conference*, A. Bennighoven, Ed. (Wiley, Münster, Germany, 1991), pp. 289–293.
25. E. K. Zinner and G Crozaz, *Int. J. Mass Spectrom Ion* **69**, 17 (1986).

26. We thank M. H. Dodson and J. Ruiz for helpful discussions and for providing some of the isotope-enriched solutions, respectively. This research was supported by U.S. National Science Foundation grant EAR 9418941 and EAR 9805232.

30 April 1998; accepted 30 June 1998

Decoupled Temporal Patterns of Evolution and Ecology in Two Post-Paleozoic Clades

Frank K. McKinney,* Scott Lidgard, J. John Sepkoski Jr., Paul D. Taylor

Counts of taxonomic diversity are the prevailing standards for documenting large-scale patterns of evolution in the fossil record. However, the secular pattern of relative ecological importance between the bryozoan clades Cyclostomata and Cheilostomata is not reflected fully in compilations of generic diversity or within-fauna species richness, and the delayed ecological recovery of the Cheilostomata after the mass extinction at the Cretaceous-Tertiary boundary is missed entirely. These observations demonstrate that evolutionary success and ecological dominance can be decoupled and profoundly different, even over tens of millions of years.

Taxonomic diversity, or richness (*1, 2*), is the current paradigm used to describe how Earth's biota has changed over time. An alternative approach examines patterns in biological activity or habitat structure (*3, 4*), but this has rarely been associated with taxonomic diversity. Here, we describe a different approach. We compiled data on skeletal mass of two coexisting marine bryozoan clades (Cyclostomata and Cheilostomata) to measure one aspect of relative local ecological dominance over geological time (*5*). Dominance is usually measured by the abundance of a group of organisms relative to co-occurring groups, or less often by the relative effect of a group on energy flow within a community (*6*). Species are not equally abundant or important energetically, so lists of species alone may not reflect dominance. Moreover, despite calls for recognizing the importance of abundance in large-scale evolutionary patterns (*7*), there have been few applications (*4, 8*).

We compared bryozoan abundance data spanning the past 150 million years with two measures of taxonomic diversity to assess the degree of correspondence between the evolutionary success and ecological importance, or dominance, of the two clades on continental shelves, where they have similar ecological distributions (*9*). During the past 150 million years, cheilostome bryozoans radiated to an extent comparable with the euteleost fishes, neogastropods, and echinoids (*2*), whereas diversification of cyclostome bryozoans was arrested.

Cyclostome bryozoans survived the severe crises at the end-Permian and Triassic mass extinctions that removed the other stenolaemate bryozoan clades that had much higher Paleozoic diversities (*10*). Cyclostome genera increased from four in the Early Jurassic [Hettangian; 206 to 202 million years ago (Ma)] to a maximum of 176 in the latest Cretaceous (Maastrichtian; 71 to 65 Ma). Cheilostomes did not appear until the Late Jurassic and increased from four genera in the mid-Cretaceous (Aptian; 121 to 112 Ma) to a maximum of 178 in the Maastrichtian. The Cretaceous-Tertiary (K-T) extinction resulted in a decrease to 111 genera of cheilostomes and to 83 of cyclostomes by the late Paleo-

---

F. K. McKinney, Department of Geology, Appalachian State University, Boone, NC 28608–2067, USA. S. Lidgard, Department of Geology, Field Museum, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605, USA. J. J. Sepkoski Jr., Department of the Geophysical Sciences, University of Chicago, Chicago, IL 60637, USA. P. D. Taylor, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

*To whom correspondence should be addressed. E-mail: mckinneyfk@appstate.edu

cene (Thanetian; 61 to 55 Ma). Cheilostome diversity recovered during the Eocene, and the number of genera exceeded that of the Maastrichtian by mid-Eocene (Lutetian; 49 to 41 Ma). Cyclostome generic diversity, on the other hand, never rebounded after the Paleocene. On the basis of global generic diversity, the later originating cheilostomes had become as species rich as cyclostomes by the Maastrichtian, and through the Cenozoic the proportion of cheilostome species continued to increase (Figs. 1 and 2).

To assess the ecological consequences of changing diversity, we determined the skeletal mass of cyclostome and cheilostome bryozoans for samples from 70 Jurassic-to-Holocene marine continental shelf deposits (*11*). The sampled faunas were mostly from Europe and eastern North America and have about the same geographic concentration as the taxonomic databases (*12, 13*). Despite the noise potentially introduced by taphonomic bias (*11*), a distinct temporal pattern in relative skeletal mass of cyclostomes and cheilostomes emerges that cannot be attributed to local taphonomic effects.

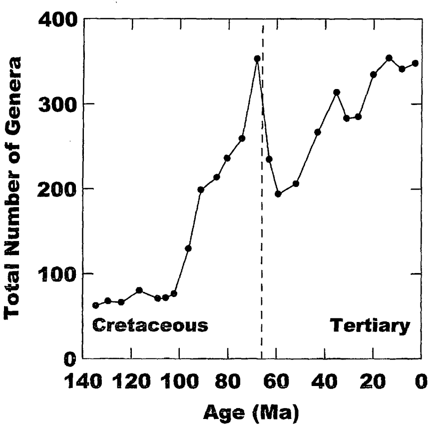

Fig. 1. Early Cretaceous to Quaternary global generic diversity of the bryozoan clades Cyclostomata and Cheilostomata.

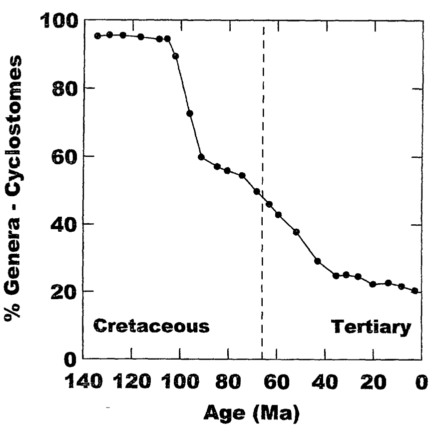

Fig. 2. The proportion of global bryozoan generic diversity constituted by cyclostomes from Early Cretaceous to Quaternary.

The within-fauna skeletal mass of cyclostomes declined steeply relative to the skeletal mass of cheilostomes from the mid- through Late Cretaceous (Fig. 3) so that cyclostomes constituted an average of only 28% of total bryozoan skeletal mass by the Maastrichtian. However, relative mass abundance reversed abruptly to 72% cyclostomes immediately above the K-T boundary, and in terms of skeletal mass the cyclostomes dominated to the end of the Danian (65 to 61 Ma) (*14*). Thanetian through Ypresian (Early Eocene; 55 to 49 Ma) faunas are underrepresented in our data. Therefore, we cannot distinguish adequately whether the Danian cyclostome peak (i) is a relatively short-lived spike of abundance (about 4 million years), similar to but of greater duration than abundance spikes seen in ferns and some foraminifers in the recovery biota (*15*), or whether (ii) the ecological replacement of cyclostomes by cheilostomes was reset such that tens of millions of years were required for cheilostomes to regain their Late Cretaceous ecological dominance over cyclostomes. Regardless, the long-term pattern in relative skeletal mass of cheilostomes and cyclostomes departs substantially from the generic diversity pattern (Fig. 2) and from patterns at higher taxonomic levels (13).

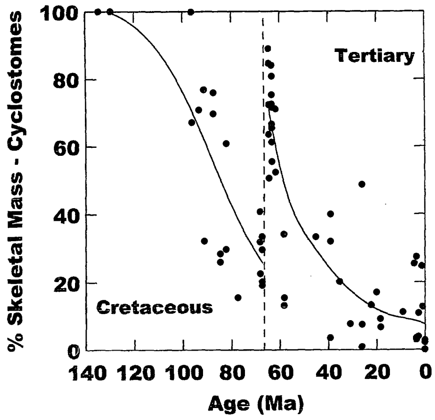

Fig. 3. Cretaceous and Cenozoic (Tertiary-Quaternary) within-fauna relative skeletal mass of the bryozoan clades Cyclostomata and Cheilostomata, plotted as percent cyclostomes. The moving average curves were fitted by a distance-weighted least squares method (*19*).

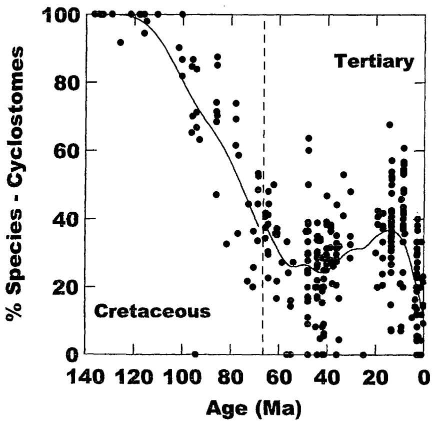

Fig. 4. Cretaceous and Cenozoic (Tertiary-Quaternary) curves for within-fauna relative species richness of cyclostomes and cheilostomes, plotted as percent cyclostomes. The moving average curves were fitted by a distance-weighted least squares method (*19*).

Mean within-fauna species richness of both cheilostomes and cyclostomes declined from the Late Cretaceous into the Paleocene (*13*). The decline in species richness of cyclostomes appears to have begun in the Cenomanian (99 to 93 Ma), whereas cheilostomes reached maximum species richness in the Maastrichtian and then declined at the K-T boundary. When the cheilostomes began to diversify in the mid-Cretaceous, the ratio of cyclostome to cheilostome species in local communities began a long-term decline that lasted across the K-T boundary through to the early Oligocene (Fig. 4).

The two measures of taxonomic diversity summarized above differ in detail but both imply that the cheilostomes were more resilient than the cyclostomes during the end-Cretaceous crisis. Among total calcified bryozoans the global proportion of cyclostome genera declined slightly from the Maastrichtian (~50%) to the Danian (~46%), and the proportion of within-fauna cyclostome species richness declined from ~37% in the Maastrichtian to ~30% in the Danian. The abrupt Danian increase in relative skeletal mass of cyclostomes contrasts sharply with these trends in global generic and within-fauna species diversities. This Danian spike could not have been determined from taxonomic databases, and it demonstrates that macroecological and macroevolutionary patterns can be decoupled even within a well-delimited suite of ecologies, such as the overlapping ecological range occupied by both cyclostome and cheilostome bryozoans on marine shelves. This is not unlike some patterns of global morphological disparity relative to taxonomic diversity (*16*).

The overall Mesozoic and Cenozoic histories of relative within-fauna species richness and skeletal mass of cyclostomes and cheilostomes also demonstrate that macroevolutionary and macroecological patterns can correspond qualitatively but differ quantitatively. As shown in Figs. 3 and 4, the relative skeletal mass of cyclostomes declined much more precipitously than did relative species richness through the Late Cretaceous and again during the post-Paleocene after the Danian spike in cyclostome skeletal mass. The lack of quantitative correspondence of the within-fauna species richness and skeletal mass curves through geologic time indicates that, in the absence of major perturbations, there is a long-term trend for the average cheilostome species to generate a progressively greater skeletal mass than the average cyclostome species. This could result from a gradual trend toward relatively larger colony sizes within cheilostomes (*17*), a greater number of colonies per cheilostome species, or both.

These data suggest that multiple measures of biotic change through time are necessary for a rich understanding of biospheric evolution. As in contemporary biotic communities, taxonomic diversity captures only limited aspects of the complexity of the biota (*18*). Multiple measures of biotic systems provide greater insight into history and processes and a better basis for predicting future biodiversity.

Reference and Notes

1. P. W. Signor, *Annu. Rev. Ecol. Syst.* **21**, 509 (1990); J. J. Sepkoski Jr., *Paleobiology* **19**, 43 (1993); in *Global Events and Event Stratigraphy in the Phanerozoic*, O. H. Walliser, Ed. (Springer-Verlag, Berlin, 1995), pp. 35–51; M. J. Benton, *Science* **268**, 52 (1995).
2. J. J. Sepkoski Jr. and M. L. Hulver, in *Phanerozoic Diversity Patterns*, J. W. Valentine, Ed. (Princeton Univ. Press, Princeton, NJ, 1985), pp. 11–39.
3. W. I. Ausich and D. J. Bottjer, *Science* **216**, 173 (1982); G. J. Vermeij, *Evolution and Escalation* (Princeton Univ. Press, Princeton, NJ, 1987); J. J. Sepkoski Jr., *Paleobiology* **14**, 221 (1988); R. K. Bambach, *ibid.* **19**, 372 (1993).
4. C. W. Thayer, in *Biotic Interactions in Recent and Fossil Benthic Communities*, M. J. S. Tevesz and P. O. McCall, Eds. (Plenum, New York, 1983), pp. 480–625.
5. Counts of individuals are inappropriate for skeletalized colonial organisms because of modularity and fragmentation, and the sizes of sexually mature bryozoan colonies range over several orders of magnitude. Therefore, skeletal mass was taken as an appropriate proxy for abundance or biomass [W. I. Ausich, *Ohio J. Sci.* **81**, 268 (1981); G. Staff, E. N. Powell, R. J. Stanton Jr., H. Cummins, *Lethaia* **18**, 209 (1985)]. We stress that this proxy is potentially subject to taphonomic bias and is strictly empirical. Competitive dominance in the once-living community requires different bases of inference.
6. S. J. McNaughton and L. L. Wolf, *Science* **167**, 131 (1970); R. H. Whittaker, *Communities and Ecosystems* (Macmillan, New York, ed. 2, 1975); J. H. Brown and B. A. Maurer, *Nature* **324**, 248 (1986); E. O. Wilson, *The Diversity of Life* (Belknap, Cambridge, MA, 1992).
7. J. B. C. Jackson, *Paleobiology* **14**, 307 (1988); S. L. Wing, L. J. Hickey, C. C. Swisher, *Nature* **363**, 342 (1993); M. L. Droser, D. J. Bottjer, P. M. Sheehan, *Geology* **25**, 167 (1997).
8. T. L. Phillips and R. A. Peppers, *Int. J. Coal Geol.* **3**, 205 (1984); D. W. Krause, *Univ. Wyoming Contrib. Geol. Spec. Pap. 3* (1986), pp. 95–117; S. Lidgard and J. B. C. Jackson, *Paleobiology* **15**, 255 (1989); B. E. Berglund, H. J. B. Birks, M. Ralska-Jasiewiczowa, H. E. Wright, Eds., *Paleoecological Events During the Last 15,000 Years* (Wiley, Chichester, UK, 1996); R. Lupia, P. R. Crane, S. Lidgard, in *Biotic Response to Global Change: The Last 145 Million Years*, S. J. Culver and P. F. Rawson, Eds. (Chapman & Hall, London, in press).
9. F. K. McKinney and J. B. C. Jackson, *Bryozoan Evolution* (Unwin Hyman, Boston, 1989).
10. P. D. Taylor and G. P. Larwood, in *Extinction and Survival in the Fossil Record*, G. P. Larwood, Ed. (Clarendon, Oxford, 1988), pp. 99–119.
11. All bryozoan fragments retained on 0.5-mm and larger screens were picked from 60 entire disaggregated 0.3- to 3.0-kg samples or, where bryozoans were extraordinarily abundant, from subsamples; fragments were sorted on the basis of clade, and total mass for each clade was determined directly or calculated on the basis of subsamples. Species that produce colony fragments typically smaller than 0.5 mm have not been included in most previous studies *of bryozoan species diversity [summarized in (13)]*. We have excluded such small size fragments from our calculations of relative skeletal mass as well; these fractions are subject to winnowing in many recent bryozoan habitats and are rarely derived from the ecologically dominant taxa. Nonetheless, small colonies of cyclostomes and cheilostomes may be numerous in some environments (E. Håkansson, personal communication). Our data were supplemented by data in O. Berthelsen, *Danmarks Geol. Unders.* **83**, 1 (1962) and A. H. Cheetham, *Smithsonian Contrib. Paleobiol.* **6**, 1 (1971). Some variation in the data inevitably results from variable amounts of cement or of matrix or shell fragments. Cyclostomes tend to have thinner walls than do cheilostomes, and raw cheilostome mass was weighted by 1.26 on the basis of a thin-section determination of the ratio of skeleton to cement plus adherent material in control samples [33 cheilostomes ($\bar{X}$ = 0.62, SD = 0.147) and 35 cyclostomes ($\bar{X}$ = 0.51, SD = 0.151) from four representative collections]. Additional "noise" in the data may be due to different taphonomic responses of cyclostome and cheilostome bryozoans in different environments. However, dissolution and abrasion rates of mineralized bryozoans are dependent upon diverse factors that cut across clade assignment [A. M. Smith, C. S. Nelson, P. J. Danaher, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **93**, 213 (1992); A. M. Smith and C. S. Nelson, in *Biology and Palaeobiology of Bryozoans*, P. J. Hayward, J. S. Ryland, P. D. Taylor, Eds. (Olsen & Olsen, Fredensborg, Denmark, 1994), pp. 177–180; in *Bryozoans in Space and Time*, D. P. Gordon, A. M. Smith, J. A. Grant-Mackie, Eds. (National Institute of Water & Atmospheric Research Ltd., Wellington, New Zealand, 1996), pp. 213–226.
12. J. J. Sepkoski Jr., *J. Paleontol.* **71**, 533 (1997).
13. S. Lidgard, F. K. McKinney, P. D. Taylor, *Paleobiology* **19**, 352 (1993).
14. The skeletal mass of cyclostomes was 70% in middle Danian and 62% in late Danian.
15. G. R. Upchurch, in *Mass Extinctions Process and Evidence*, S. K. Donovan, Ed. (Columbia Univ. Press, New York, 1989), pp. 195–216; S. J. Fowell and P. E. Olsen, *Tectonophysics* **222**, 361 (1993); R. P. Speijer and G. J. Van der Zwan, in *Biotic Recovery from Mass Extinction Events*, M. B. Hart, Ed. (The Geological Society, London, 1996), pp. 343–371.
16. M. Foote, *Palaeontology* **34**, 461 (1991); *Univ. Michigan Mus. Paleontol. Contrib.* **28**, 101 (1991); *Proc. Natl. Acad. Sci. U.S.A.* **89**, 7325 (1992); *Paleobiology* **19**, 185 (1993); *ibid.* **21**, 273 (1995); *Science* **274**, 1492 (1996).
17. The mean size of encrusting cyclostomes is 4.7 mm^2 and of cheilostomes is 10.1 mm^2 on shell debris in the Mainstreet Limestone Member of the Grayson Formation (Albian), Roanoke, Texas; the mean size of encrusting cyclostomes is 5.8 mm^2 and of encrusting cheilostomes is 51.8 mm^2 on shell debris in the northern Adriatic off Rovinj, Croatia (F. K. McKinney, unpublished data). The two faunas are qualitatively judged to represent colony size of contemporaneous faunas, and the major change has been an increase in mean size of cheilostome colonies.
18. K. J. Gaston, Ed., *Biodiversity: A Biology of Numbers and Difference* (Blackwell, Oxford, 1996).
19. L. Wilkinson, *SYSTAT: The System for Statistics* (Systat, Evanston, IL, 1990).
20. Supported by the NSF (DEB 9306729 to S.L.; EAR 9117289 to F.K.M.), U.S.-U.K. Fulbright program (F.K.M.), National Geographic Society (F.K.M.), Petroleum Research Fund of American Chemical Society (F.K.M.), NASA (NAGW-1963 to J.J.S.J.), and Global Change and the Biosphere Programme of the National History Museum/University College London (P.D.T.). We thank S. Hageman, R. Lupia, and two anonymous reviewers for evaluating the manuscript and numerous colleagues who served as guides to field localities.

16 April 1998; accepted 26 June 1998

In Situ Observations of a High-Pressure Phase of H_2O Ice

I-Ming Chou,* Jennifer G. Blank,† Alexander F. Goncharov,
Ho-kwang Mao, Russell J. Hemley

A previously unknown solid phase of H_2O has been identified by its peculiar growth patterns, distinct pressure-temperature melting relations, and vibrational Raman spectra. Morphologies of ice crystals and their pressure-temperature melting relations were directly observed in a hydrothermal diamond-anvil cell for H_2O bulk densities between 1203 and 1257 kilograms per cubic meter at temperatures between −10° and 50°C. Under these conditions, four different ice forms were observed to melt: two stable phases, ice V and ice VI, and two metastable phases, ice IV and the new ice phase. The Raman spectra and crystal morphology are consistent with a disordered anisotropic structure with some similarities to ice VI.

The manifold ways in which the water molecules may link through hydrogen bonding give rise to a remarkably rich phase diagram (*1–5*). Enhancing this complexity is the existence of both proton-ordered and -disordered forms as well as metastable crystalline and amorphous phases (*3, 6*). Though evidence for additional phases in the system has been obtained in the past [for example, (*7*)], information about them has been very sparse, if not controversial, because previous studies have relied principally on quench techniques or limited in situ probes (*7–10*). Here we document the existence of another H_2O phase from in situ microscopy and Raman spectroscopy at 0.7 to 1.2 GPa. The phase exhibits an

---

I. Chou, 955 National Center, U.S. Geological Survey, Reston, VA 20192, USA. J. G. Blank, A. F. Goncharov, H. Mao, R. J. Hemley, Geophysical Laboratory and Center for High Pressure Research, Carnegie Institution of Washington, 5251 Broad Branch Road, NW, Washington, DC 20015, USA.

*To whom correspondence should be addressed.

†Present address: Department of Geology and Geophysics, University of California, Berkeley, CA 94720, USA.