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The mtDNA Legacy of the Levantine Early Upper Palaeolithic in Africa

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Sequencing of 81 entire human mitochondrial DNAs (mtDNAs) belonging to haplogroups M1 and U6 reveals that these predominantly North African clades arose in southwestern Asia and moved together to Africa about 40,000 to 45,000 years ago. Their arrival temporally overlaps with the event(s) that led to the peopling of Europe by modern humans and was most likely the result of the same change in climate conditions that allowed humans to enter the Levant, opening the way to the colonization of both Europe and North Africa. Thus, the early Upper Palaeolithic population(s) carrying M1 and U6 did not return to Africa along the southern coastal route of the “out of Africa” exit, but from the Mediterranean area; and the North African Dabban and European Aurignacian industries derived from a common Levantine source.

An “out of Africa” dispersal of modern humans is now widely accepted, together with a model postulating a single “southern route” dispersal from the Horn of Africa to the Persian/Arabian Gulf and further along the tropical coast of the Indian Ocean to Southeast Asia and Australasia (1–3). Within this model, however, the delayed settlement of most parts of West Eurasia needs an explanation. In contrast

with South Asians, East Asians, and Australasians, West Eurasians have only a moderate amount of haplogroup-level diversity within mitochondrial DNA (mtDNA) haplogroups N and R (the early derivative of N) but lack almost completely haplogroup M, which is otherwise dominant in Asia (Fig. 1). The colonization of West Eurasia is thought to have been the result of an offshoot of the colonization along the southern

route, followed by a lengthy pause, perhaps at the Persian/Arabian Gulf, until the climate improved and the ancestors of West Eurasians were able to enter first the Levant and then Europe (2, 4, 5). Paleoenvironmental evidence is crucial to this argument, suggesting that an earlier migration toward the north >50 thousand years ago (ka) would have been impossible given the climate of the time, with desert extending from North Africa to Central Asia (6).

In contrast, a clade of M, referred to as M1, is present at high frequencies in the Horn of Africa and appears to be predominantly African-specific (Fig. 1 and table S1). This raises the possibility that M could have arisen in East Africa before the out of Africa exit (7, 8), or M1 might represent a back-migration into East Africa (9–11).

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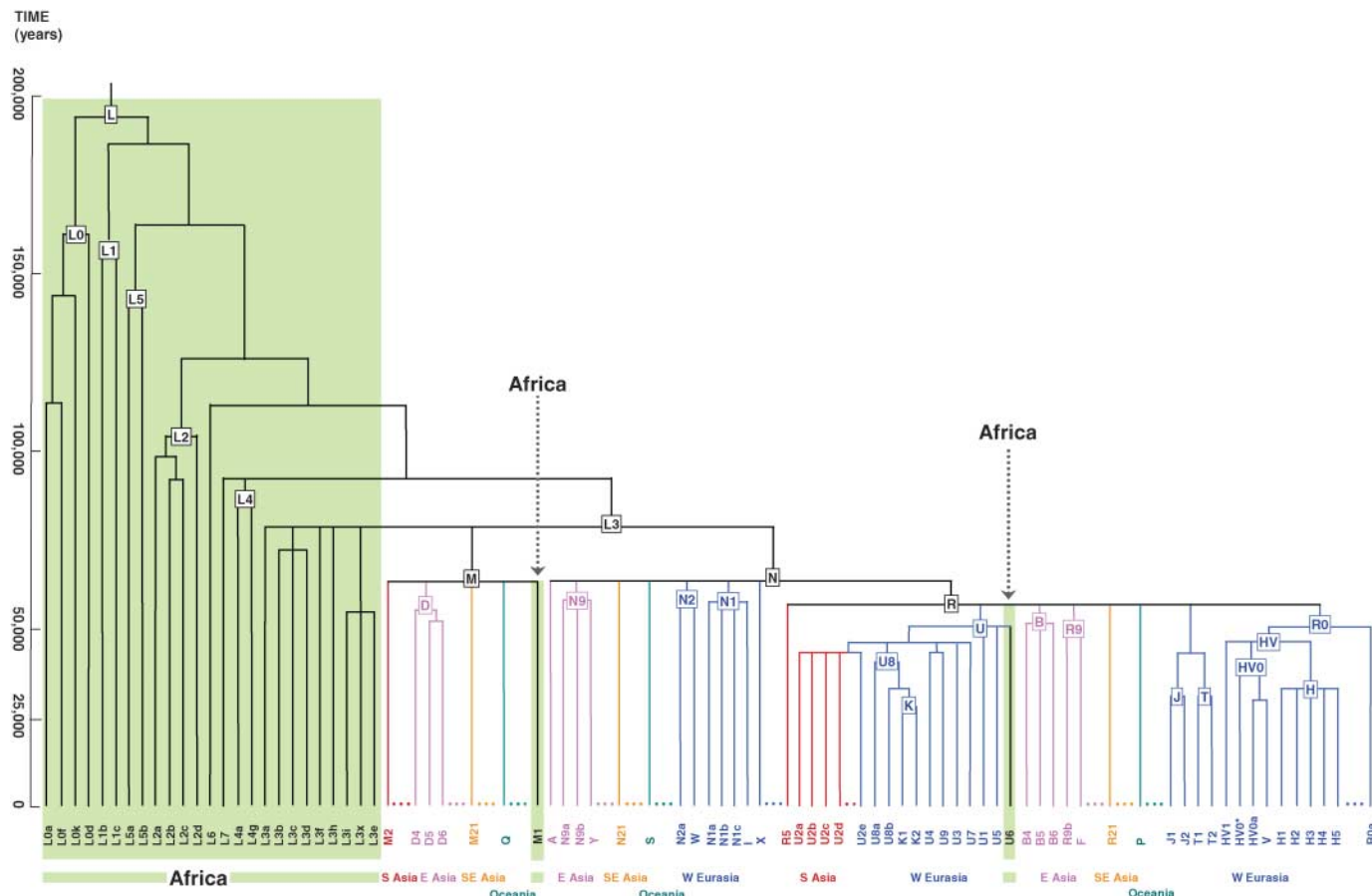


Fig. 1. Schematic representation of the worldwide phylogeny of human mtDNA. African haplogroups are in green and those of other geographical regions are in other colors.

The scenario of a back-migration into Africa is supported by another feature of the mtDNA phylogeny. Haplogroup M's Eurasian sister clade, haplogroup N, which has a very similar age to M and no indication of an African origin, includes R, which in turn embraces haplogroup U (Fig. 1). Haplogroup U is subdivided into numerous clades (U1 to U9) and is characterized by an extremely broad geographical distribution ranging from Europe to India and Central Asia (12). However, one of its clades—U6—is mainly found in northern Africans (13, 14) but is also observed in eastern Africans (11), a situation that parallels that of M1, with the only difference being that M1 is more common in East Africa than in North Africa.

The hypothesis of a back-migration from Asia to Africa is also strongly supported by the current phylogeography of the Y chromosome variation, because haplogroup K2 and paragroup R1b*, both belonging to the otherwise Asiatic macrohaplogroup K, have been observed at high frequencies only in Africa (15, 16). However, because of the relatively low molecular resolution of the Y chromosome phylogeny as compared to that of the mtDNA, it was impossible to come to a firm conclusion about the precise timing of this dispersal (15, 16).

To shed some light on haplogroups M1 and U6 in Africa, we sequenced mtDNA genomes belonging to M1 ($n = 51$) and U6 ($n = 30$) from populations distributed over the geographical range of the two haplogroups. The phylogenies of the M1 and U6 sequences are illustrated in Figs. 2 and 3, respectively.

The average sequence divergence [\pm standard error computed as in (17)] of the 51 M1 coding-region sequences from the root of haplogroup M1 is 7.16 ± 1.38 substitutions (disregarding indels and pathological mutations), which corresponds to a coalescence time estimate of 36.8 ± 7.1 thousand years (ky) for the entire haplogroup M1 (18). The M1 tree shows an initial deep split into two sister subclades, M1a and M1b, each containing several independent basal branches, at least seven within M1a and two within M1b (Fig. 2). The M1a branch shows a coalescence time of 28.8 ± 4.9 ky (5.60 ± 0.96 substitutions). The other major branch of the tree, M1b, is also ancient, with an estimated coalescence time of 23.4 ± 5.6 ky (4.55 ± 1.08 substitutions), but in contrast to M1a, which encompasses the entire geographical range of M1, M1b is present only in the Mediterranean area (fig. S1).

Haplogroup U6 is characterized by an overall coalescence time estimate of 45.1 ± 6.9 ky

(8.77 ± 1.34 substitutions) (Fig. 3), and U6a (the most represented of its clades) has a coalescence time of 37.5 ± 4.3 ky (7.29 ± 0.83 substitutions). It is worth emphasizing that U6 is a sister clade of the European haplogroup U5 (Fig. 1), which is dated 41.4 ± 9.2 ka (12) and was most likely carried by the first European settlers (19).

The overall coalescence age estimates for M1 (~37 ky) and U6 (~45 ky) are largely overlapping when standard errors are considered. This supports the scenario that M1 and U6 could have been involved in the same population expansion and dispersal events. Given that the origin of haplogroup U is West Asia and that the presence of U6 in Africa is due to gene flow from that area, the phylogeographic similarities between the two haplogroups indicate that M1 (or its molecular ancestor) is also of western Asian ancestry. This suggests that there was a migration event about 40 to 45 ka that concomitantly affected both haplogroups. An ancient arrival of M1 in Africa (or in its close proximity) is supported by the fact that none of the numerous M haplogroups in Asia (20, 21) harbors any of the distinguishing M1 root mutations, and by the lack of Asian-specific clades within M1 (and U6), as might be expected in the case of a more recent arrival. The arrival of

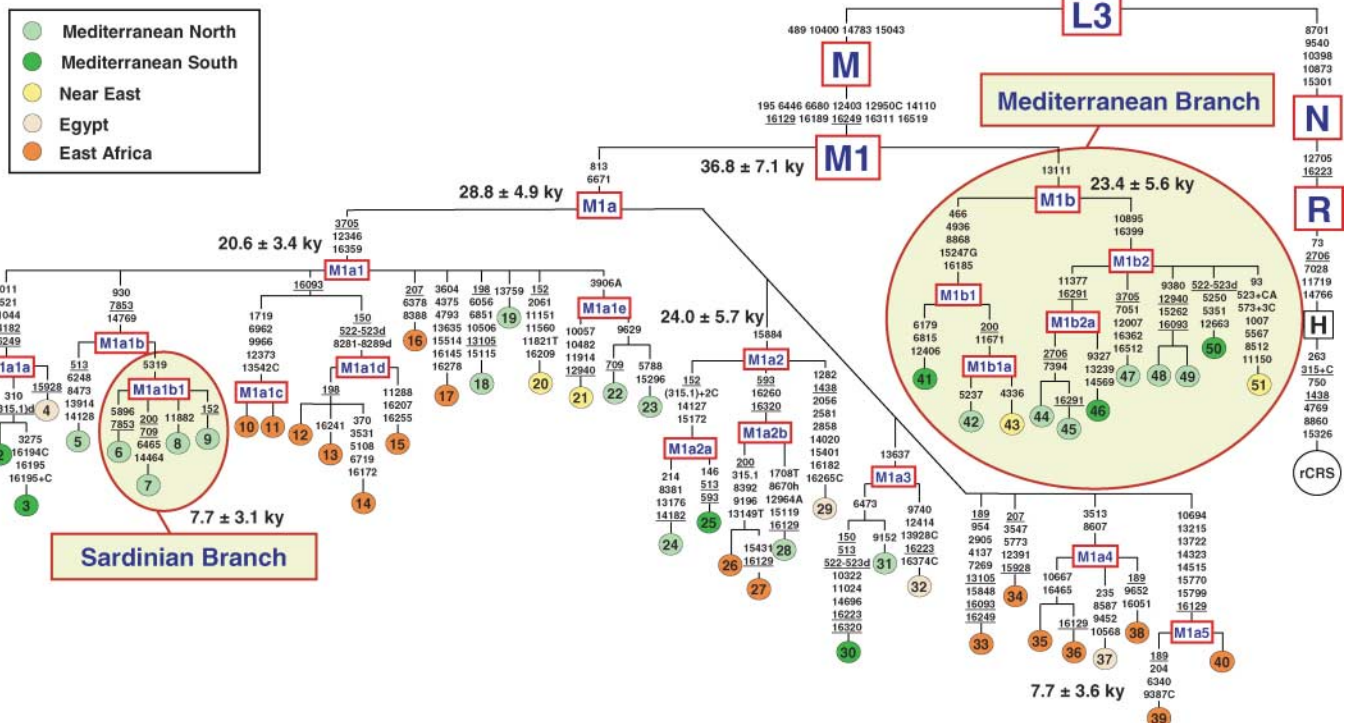


Fig. 2. Tree of 51 mtDNA sequences belonging to haplogroup M1. The tree is rooted using the reference sequence (rCRS) (27) as an outgroup. The sequencing procedure and phylogeny construction were performed as described elsewhere (4, 28, 29). mtDNAs were selected through a preliminary sequence analysis of the control region and a restriction fragment length polymorphism survey in order to include the widest possible range of internal variation of the haplogroup. All M1 sequences are new except for 17, which is the same sample as 25 in Torroni *et al.* (3). Mutations are shown on the branches; they are transitions unless a base is explicitly indicated. Suffixes indicate transversions (to A, G, C, or T), indels (+, d) or

heteroplasmy (h). Recurrent mutations are underlined; pathological mutations are in italics. The ethnic or geographic origins of mtDNAs are as follows: Italy (1, 5 to 9, 23, 24, 28, 31, 42, 44, 45, and 47 to 49); Berbers of Egypt (2 and 3); Egypt (4, 29, 32, and 37); Ethiopian Jews (10 and 11); Ethiopia (12 to 17, 26, 27, 33 to 35, 38, and 40); Greece (18 and 19); Iraqi Jew (20); Druze (21); American (USA) of European ancestry (22); Berbers of Morocco (25, 30, 46, and 50); Kenya (36); Somalia (39); Mauritania (41); Bedouin, southern Israel (43); and Iraqi (51). For additional information regarding the tree, see the supporting online material (SOM).

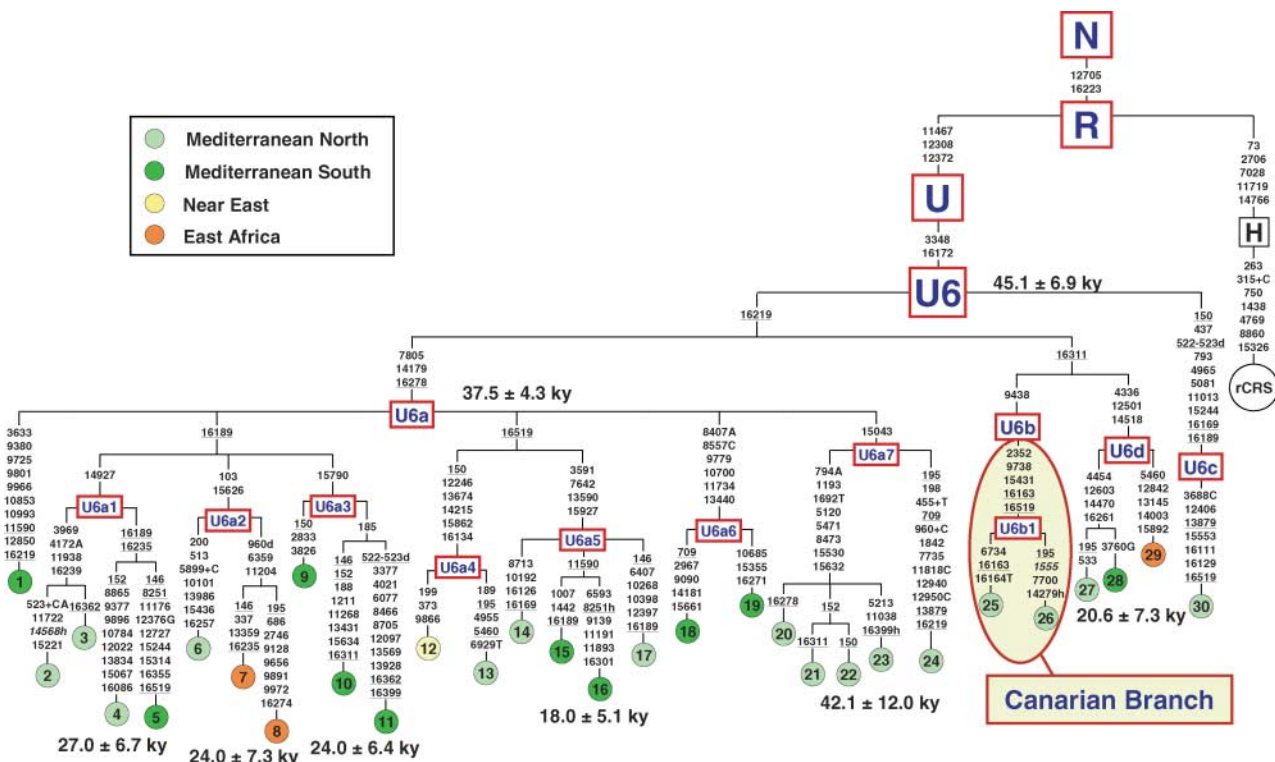


Fig. 3. Tree of 30 mtDNA sequences belonging to haplogroup U6. All U6 sequences are new except for 7 and 25, which are the same samples as 38 and 39 in Achilli *et al.* (12). Nomenclature is consistent with (24), except that U6a1 has now been narrowed and the motif for U6b1 has been completed. The ethnic or geographic origins of mtDNAs are as follows:

Berbers of Morocco (1, 10, 11, 19, and 28); Italy (2 to 4, 6, 13, 14, 17, 20 to 23, 27, and 30); Algeria (5); Ethiopia (7 and 8); Nigeria (9 and 15); Iraq (12); Tunisia (16 and 18); France (24); Dominican Republic (25); Spain (26); and Ethiopian Jew (29). For additional information regarding the tree, see the SOM.

M1 and U6 in Africa 40 to 45 ka would temporally overlap with the event(s) that led to the peopling of Europe by modern humans.

This raises the possibility that the population(s) harboring M1, U6, and U5 (or their close molecular ancestors) were all living in the same broad geographic area of southwestern Asia, possibly in separate regional enclaves, and that they all were affected by an event that led to their expansion and relocation. It has been proposed that a change in climate conditions, fragmenting and reducing the desert areas (6), allowed humans to enter first the Levant and then Europe (4). However, such a climatic change would also render North Africa equally accessible from the Levant. Thus, while populations bearing U5 took part in the colonization of Europe, populations with M1 and U6 entered North Africa. Such a scenario implies that the population(s) harboring M1 and U6 did not return to Africa along the southern coastal route of the out of Africa exit but from the Mediterranean area. The Greenland Interstadial 12, from ~44 to ~48 ka (22, 23), could have been the main period of dispersal into the Levant and subsequently into North Africa.

Furthermore, the distribution of M1b and most of the U6 clades only in Mediterranean regions indicates that both M1 and U6 differentiated into their major subclades while they were in the Mediterranean area, and only later

some subsets of M1a (including its derivatives M1a1 and M1a2), U6a2, and U6d diffused to East Africa, possibly along the Nile Valley. It cannot be excluded that a further late dispersal of M1 and U6 within North and East Africa might have been associated with the diffusion, after the Last Glacial Maximum, of the emerging Afro-Asiatic language family. Indeed, M1 and U6 in Africa are mostly restricted to Afro-Asiatic-speaking areas.

In the Holocene, some of the M1 and U6 clades were involved in subsequent migration and colonization events. For instance, M1a1b1 is found only in Sardinia (Fig. 2), where it is also fairly frequent (1.8%). Its estimated coalescence age of 7.7 ± 3.1 ky suggests that the founding M1a1b mtDNA was brought to Sardinia by the first modern humans that arrived to the island. A similar scenario can be envisioned for U6b1, which was typical of the Guanches (24), the ancestral population of the Canary Islands.

Our phylogeographic studies of mtDNA haplogroups reinforce the scenario that the first Upper Paleolithic cultures in North Africa (Dabban) and Europe (Aurignacian) had a common source in the Levant (14, 25, 26) and in fact spread by migration from some core area in the Levantine Corridor. The dispersal of Levantine people to Europe and North Africa was then marked by the mtDNA haplogroups U5 and U6/M1, respectively.

References and Notes

1. P. Forster, S. Matsumura, *Science* **308**, 965 (2005).
2. P. Mellars, *Science* **313**, 796 (2006).
3. A. Torroni, A. Achilli, V. Macaulay, M. Richards, H.-J. Bandelt, *Trends Genet.* **22**, 339 (2006).
4. V. Macaulay *et al.*, *Science* **308**, 1034 (2005).
5. M. Richards *et al.*, in *Human Mitochondrial DNA and the Evolution of Homo sapiens*, H.-J. Bandelt, V. Macaulay, M. Richards, Eds., vol. 18 of *Nucleic Acids and Molecular Biology* (Springer-Verlag, Berlin, Germany, 2006), pp. 225–265.
6. T. H. van Andel, P. C. Tzedakis, *Quat. Sci. Rev.* **15**, 481 (1996).
7. G. Passarino *et al.*, *Am. J. Hum. Genet.* **62**, 420 (1998).
8. L. Quintana-Murci *et al.*, *Nat. Genet.* **23**, 437 (1999).
9. M. Richards *et al.*, *Am. J. Hum. Genet.* **72**, 1058 (2003).
10. P. Forster, *Philos. Trans. R. Soc. London Ser. B* **359**, 255 (2004).
11. T. Kivisild *et al.*, *Am. J. Hum. Genet.* **75**, 752 (2004).
12. A. Achilli *et al.*, *Am. J. Hum. Genet.* **76**, 883 (2005).
13. J. C. Rando *et al.*, *Ann. Hum. Genet.* **62**, 531 (1998).
14. V. Macaulay *et al.*, *Am. J. Hum. Genet.* **64**, 232 (1999).
15. F. Cruciani *et al.*, *Am. J. Hum. Genet.* **70**, 1197 (2002).
16. J. R. Luis *et al.*, *Am. J. Hum. Genet.* **74**, 532 (2004).
17. J. Saillard *et al.*, *Am. J. Hum. Genet.* **67**, 718 (2000).
18. D. Mishmar *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 171 (2003).
19. M. Richards *et al.*, *Am. J. Hum. Genet.* **67**, 1251 (2000).
20. Q.-P. Kong *et al.*, *Hum. Mol. Genet.* **15**, 2076 (2006).
21. C. Sun *et al.*, *Mol. Biol. Evol.* **23**, 683 (2006).
22. N. J. Shackleton, R. G. Fairbanks, Tzu-chien Chiu, F. Parrenin, *Quat. Sci. Rev.* **23**, 1513 (2004).
23. W. J. Burroughs, *Climate Change in Prehistory: The End of the Reign of Chaos* (Cambridge Univ. Press, Cambridge, 2005).
24. N. Maca-Meyer *et al.*, *BMC Genet.* **4**, 15 (2003).

25. P. Van Peer, P. M. Vermeersch, in *The Emergence of Modern Humans: An Archaeological Perspective*, P. Mellars, Ed. (Edinburgh Univ. Press, Edinburgh, 1990), pp. 139–159.
26. O. Bar-Yosef, *Annu. Rev. Anthropol.* **31**, 363 (2002).
27. R. M. Andrews *et al.*, *Nat. Genet.* **23**, 147 (1999).
28. A. Torroni *et al.*, *Am. J. Hum. Genet.* **69**, 1348 (2001).
29. A. Achilli *et al.*, *Am. J. Hum. Genet.* **75**, 910 (2004).
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Supporting Online Material

www.sciencemag.org/cgi/content/full/314/5806/1767/DC1
SOM Text
Fig. S1
Table S1
References

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Nannoplankton Extinction and Origination Across the Paleocene-Eocene Thermal Maximum

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The Paleocene-Eocene Thermal Maximum (PETM, ~55 million years ago) was an interval of global warming and ocean acidification attributed to rapid release and oxidation of buried carbon. We show that the onset of the PETM coincided with a prominent increase in the origination and extinction of calcareous phytoplankton. Yet major perturbation of the surface-water saturation state across the PETM was not detrimental to the survival of most calcareous nannoplankton taxa and did not impart a calcification or ecological bias to the pattern of evolutionary turnover. Instead, the rate of environmental change appears to have driven turnover, preferentially affecting rare taxa living close to their viable limits.

Modern biodiversity studies predict huge losses of flora and fauna (*I*) associated with anthropogenic carbon emissions and projected climate change (up to ~35% of species by 2050) (2). Paleontological records from analog events in geologic history provide a way to test the ecological basis of these predictions. The Paleocene-Eocene Thermal Maximum (PETM) is attributed to a rapid increase in atmospheric CO₂ levels, perhaps caused by the exhumation and oxidation of methane from marine sediments (3–5). Within less than 10 thousand years (ky) (6, 7), ocean temperatures rose by 5° to 8°C, marine and terrestrial carbon isotope values ($\delta^{13}\text{C}$) decreased by 3 to 8 per mil, and the calcite compensation depth (CCD) (8) in the deep sea shoaled by up to 2 km (9–12). Subsequently, $\delta^{13}\text{C}$ values returned to near-background levels within 110 to 210 ky (6, 13). The PETM was accompanied by dramatic reorganization in marine and terrestrial ecosystems (9, 14–19), with the most extreme response being the catastrophic extinction of 35 to 50% of benthic foraminiferal species (17).

To understand biotic change across the PETM more fully, we estimate the rate of evolutionary change within the calcareous nannoplankton; i.e., the number of species that appeared and disappeared through time. Calcareous nannoplankton are ideal for testing the organismal response to the PETM because their surface-water habitat renders them highly sensitive to environmental change. Moreover, their fossil record is exceptionally complete during this time interval, both taxonomically and stratigraphically (18, 19). Our records are at a resolution of up to 10 ky, allowing us to resolve patterns on the time scale of environmental disturbance.

Our data come from open-ocean sites in the paleoequatorial Pacific and the Southern Ocean [Ocean Drilling Program (ODP) sites 1209 and 690] and two sections on the New Jersey paleoshelf (U.S. Geological Survey drill hole at Wilson Lake and ODP leg 174AX drill hole at Bass River) (fig. S1). By combining nannofloral data sets with cyclostratigraphic age models (6), we calculated species extinction and origination rates per unit depth and per unit time (20). Two methods were used to calculate evolutionary rates per unit time. First, we applied the widely used proportional rates method, dividing the number of originations or extinctions by time, normalized for diversity [(20), following (21)]. Second, per-capita rates were calculated using the natural log of the ratio of taxa that range through a time bin to either those that only cross the bottom boundary of the bin (for extinction) or

those that cross the top boundary (for origination) (20, 22, 23). This latter method has the advantage of removing spurious variation in rates created by unequal duration of time bins (22). Both methods return rates per unit time (24) and are thus not biased by variation in sediment accumulation (25).

At all sites, the pattern of change recorded across the PETM in evolutionary rates and species richness (Figs. 1 and 2 and table S1) is similar, pointing to global rather than local species turnover (26). In the ~70 ky before the PETM, origination was low and there were virtually no extinctions, resulting in a gradual increase in species richness. Origination and extinction rates increased during the first 70 ky of the PETM, defined by the interval from the onset to the peak of the carbon isotope excursion (CIE, dark shaded zone in Figs. 1 and 2). During this interval, the inferred rate of CO₂ absorption by the oceans was greatest, and up to 18 species (from a maximum of 84) appeared or disappeared. The synchronous increase in both per-unit-depth and per-unit-time rates demonstrates that the abrupt change in turnover cannot be attributed to changes in sedimentation rate (e.g., section condensation resulting from dissolution at the base of the PETM). At three locations [site 1209, Wilson Lake (WL), and Bass River (BR)], average proportional (per unit time) rates of origination and extinction were 1.6 and 1.7% per 10 ky, respectively (table S1), compared to an average of 0.5 and 0.1% per 10 ky in the pre-event background interval (Fig. 1). At site 690, Maud Rise, Southern Ocean, a more finely resolved record of the CIE is available (24), and the evolutionary rate data reveal that proportional origination and extinction rates were 11 and 5% per 10 ky, respectively, during the first 10 ky after the event onset (Fig. 2). During the remainder of the PETM, despite continued environmental perturbation (9, 10), origination and extinction rates rapidly returned to pre-event levels, with a maximum of 10 species appearing or disappearing over the next ~150 ky. Proportional rates of origination and extinction in the recovery interval remained low (averaging 0.2 and 0.5% per 10 ky, respectively, table S1) with a gradual drop in species richness (Fig. 1).

In Fig. 3, we compare the rates that we have measured for the PETM with long-term

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