complete gene elimination per 5 to 10 My during the divergence of these two *B. aphidicola* species. The evidence for reduced effectiveness of selection and lability at the nucleotide sequence level (*12*) makes the stability of gene inventory and gene arrangements in *B. aphidicola* all the more striking.

These seemingly contradictory patterns can be explained by two kinds of losses during genome reduction of obligate host-associated bacteria (*13*). First, eliminated sequences include elements that normally mediate genome dynamics and gene mobility, such as phages, plasmids, repeated sequences, and transposons. Indeed, a survey of the repeat contents in microbial genomes has revealed a decreased density of repeated sequences in obligate intracellular bacteria with genomes in the 1 Mb range (*14*). Here, *B. aphidicola* is the extreme, containing no prophages, a single rRNA operon, and no repeated sequences longer than 30 base pairs (bp). Second, gene losses also include loci that facilitate recombination and incorporation of foreign DNA. Here, the two *B. aphidicola* genomes are also distinct in their lack of *recA* and *recF*; the absence of the corresponding gene functions is expected to lower the incidence of genome rearrangements (*5*, *15*).

If the mutational input of rearrangements is extremely low due to these losses, the frequency of such events that are beneficial or selectively neutral will approach zero, resulting in genomic stasis during lineage evolution. Also, selection on gene content and gene order may be unusually restrictive in small symbiont genomes, further reducing the fixation rate of rearrangements. It is unlikely that sequestering resulting from the symbiotic lifestyle prevents gene uptake, because other bacteria regularly coinfect aphids (*16*).

This leads to the testable hypothesis that the reduction of genome size caused by transitions to obligate host-associated lifestyles is ultimately halted by a corresponding increase in genome stability because of the loss of genetic elements that mediate recombination events. Scaling genome divergence by nucleotide substitutions of orthologous genes reveals a dramatic positive relation between the frequencies of rearrangements and indels and the genomic content of repeats (Fig. 2, C and D). This relation is expected because the number of recombination sites is $n(n-1)/2$, where n represents the number of identical repeats per genome. Thus, the number of possible genome variants that can be generated will decrease rapidly as the repeat content and genome size are reduced. The result is a correlation between genome rearrangements and lifestyle, because obligate host-associated bacteria tend to have smaller genomes with lower content of repeats and less efficient recombination systems than free-living bacteria.

Reconstruction of the ancestor shared with *E. coli* shows that the *B. aphidicola* lineage eliminated at least 2000 genes and underwent multiple chromosomal inversions before the divergence of *B. aphidicola* (Sg) and *B. aphidicola* (Ap) (*17*). This degree of reduction would have required over 10^{10} years if gene disappearance in the early *B. aphidicola* lineage occurred at the rate (14 genes per 50 My) estimated for the period in which these two genomes diverged. Thus, more rapid genomic changes must have been characteristic of the early stages of *B. aphidicola* evolution. This may be attributable to both more repeats and a greater proportion of expendable genes in the ancestor of *B. aphidicola*, allowing deletions of multigene fragments (*17*).

Although the original acquisition of a bacterial symbiont enabled aphids and other sap-feeding insects to exploit food resources that would be otherwise nutritionally unsuitable, the dependence on *B. aphidicola* has not conferred continued evolutionary plasticity in nutritional capabilities and diet breadth. Rather, our study has shown that *B. aphidicola* remains stable in genome content and architecture and has even lost pathways that may affect the ecological range of the aphids. This stability, particularly the complete absence of gene acquisition, implies effectively invariant or diminishing biosynthetic capabilities of the symbionts over periods that span many evolutionary shifts in the diet and life cycles of hosts. Within the clade of aphids, including *S. graminum* and *A. pisum*, there are about 3000 different species living on a wide range of monocots, dicots, and even ferns; yet the corresponding lineages of *B. aphidicola* have not obtained new genes or novel capabilities. Thus, the ecological diversification of aphids cannot be attributed to the genetic diversity of *B. aphidicola*.

References and Notes

1. The complete annotated genome sequence, methods, and all supporting online material are available at *Science* Online at www.sciencemag.org/cgi/content/full/296/5577/2376/DC1. The GenBank accession number is AE013218.
2. S. Shigenobou, H. Watanabe, H. Masahira, Y. Sakaki, H. Ishikawa, *Nature* **407**, 81 (2000).
3. M. A. Munson, P. Baumann, M. A. Clark, L. Baumann, N. A. Moran, *J. Bact.* **173**, 6321 (1991).
4. M. A. Clark, N. A. Moran, P. Baumann, *Mol. Biol. Evol.* **16**, 1586 (1999).
5. M. Suyama, P. Bork, *Trends Genet.* **17**, 10 (2001).
6. E. U. Brynnel, C. G. Kurland, N. A. Moran, S. G. E. Andersson, *Mol. Biol. Evol.* **15**, 574 (1998).
7. O. G. Berg, M. Martelius, *J. Mol. Evol.* **41**, 449 (1995).
8. J. Sandström, A. Telang, N. A. Moran, *J. Insect Physiol.* **91**, 33 (2000).
9. C. Girousse, J.-L. Bonnemain, S. Delrot, R. Bournoville, *Plant Physiol. Biochem.* **29**, 41 (1991).
10. K. Komaki, H. Ishikawa, *J. Mol. Evol.* **48**, 717 (1999).
11. E. Boye, A. Lobner Olesen, K. Skarstad, *EMBO Rep.* **1**, 479 (2000).
12. N. A. Moran, *Proc. Natl. Acad. Sci. U.S.A.* **93**, 2873 (1996).
13. S. G. E. Andersson, C. G. Kurland, *Trends Microbiol.* **6**, 263 (1998).
14. A. C. Frank, H. Amiri, S. G. E. Andersson, *Genetica*, **115**, 1 (2002).
15. J. Courcelle, A. K. Ganesan, P. C. Hanawalt, *BioEssays* **23**, 463 (2001).
16. J. P. Sandström, J. A. Russel, J. P. White, N. A. Moran. *Mol. Ecol.* **10**, 217 (2001).
17. N. A. Moran, A. Mira, *Genome Biol.* **54**, 1 (2001).
18. D. Dalevi, N. Eriksen, K. Eriksson, S. G. E. Andersson. *J. Mol. Evol.*, **55**, 23 (2002).

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A Tropical Rainforest in Colorado 1.4 Million Years After the Cretaceous-Tertiary Boundary

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An extremely diverse lower Paleocene (64.1 million years ago) fossil leaf site from Castle Rock, Colorado, contains fossil litter that is similar to the litter of extant equatorial rainforests. The presence of a high-diversity tropical rainforest is unexpected, because other Paleocene floras are species-poor, a feature generally attributed to the Cretaceous-Tertiary (K-T) extinction. The site occurs on the margin of the Denver Basin in synorogenic sedimentary rocks associated with the rise of the Laramide Front Range. Orographic conditions caused by local topography, combined with equable climate, appear to have allowed for the establishment of rainforests within 1.4 million years of the K-T boundary.

The Cretaceous-Tertiary (K-T) boundary in North America is characterized by the extinctions of plant (*1*, *2*), insect (*3*), and vertebrate (*4*) species and the restructuring of terrestrial ecosystems because of the loss of large-bodied herbivores and overall biodiversity. Extensive paleobotanical sampling over the past 150 years has produced hundreds of Paleocene floras with low numbers of species per site (*5*–*9*) that exhibit the foliar physiognomy of temperate deciduous forests (*10*). This suggested that floral recovery from the K-T event may have taken up to 10 million years. In marked contrast to this

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pattern, we present data from the Denver Basin, Colorado, of an early Paleocene, high-diversity fossil flora that has the foliar physiognomy of modern tropical rainforests.

Extant tropical rainforests are restricted to low-latitude areas with high rainfall and equable temperature (*11*). They share dominance by angiosperm trees and vines, high species diversity, and spatial heterogeneity. Many rainforest angiosperms exhibit large leaf size, smooth leaf margins, and elongate drip tips, presumably in response to high moisture and temperature (*12*). The origin of tropical rainforests is poorly known (*13*). Because the leaf litter of modern forests preserves the physiognomic and spatial heterogeneity of the source plants (*14*), it is reasonable to assume that properly collected fossil litter would allow for the recognition of ancient rainforests.

The Castle Rock site [Denver Museum of Nature & Science (DMNH) locality 1200] was discovered in 1994 on the east side of Interstate 25 in the town of Castle Rock, 40 km south of Denver, Colorado (Fig. 1). The site represents the burial of minimally transported forest-floor leaf litter and is unusual because of its high species diversity, large numbers of new species, and large size of the fossil leaves (up to 1280 cm^2) (*15*). Multiple tree trunk casts (up to 1.8 m diameter) and a nearly complete and in situ cycad plant (compare *Dioonopsis*), including numerous 1-m-long fronds, trunk, and roots, support the interpretation that this site is a buried forest floor (*16*).

A variety of data shows that the Castle Rock site is 64.1 million years old (early Paleocene) (*17–19*). The site occurs just below the top of the Denver Formation, an andesitic unit deposited during uplift of the Front Range. Recent work has defined two sequences of synorogenic strata (D1 and D2) that are separated by a 9- to 11-million-year hiatus containing a distinctive paleosol series (*20*). The Castle Rock site occurs at the top of the Upper Cretaceous–lower Paleocene D1 sequence, which is overlain by the lower Eocene D2 sequence. Based on correlation to the Castle Pines well (*21*), the Castle Rock site is ~280 m above the K-T boundary.

In synorogenic rocks, where older units are eroded to form younger ones, the youngest zone indicator palynomorphs in the assemblage provide the most reliable age estimate. This leaf site contains a mixed assemblage of Late Cretaceous and early Paleocene palynomorphs, including several species indicative of Paleocene pollen zone P3 (*18*). Dated P3 palynofloras in the Williston Basin, North Dakota, occur between 64.4 and 61.2 million years ago (Ma) (*22*).

Paleomagnetic analysis of the Castle Pines and Kiowa wells (8 and 35 km from Castle Rock, respectively) and from the Castle Rock site itself show that the upper portion of the D1 sequence is of normal polarity (*17*, *19*). Palynology and magnetostratigraphy of these wells identify this interval as polarity subchron C28N (*17–20*). Radiometric analysis of a sanidine-bearing bentonite just below the top of the D1

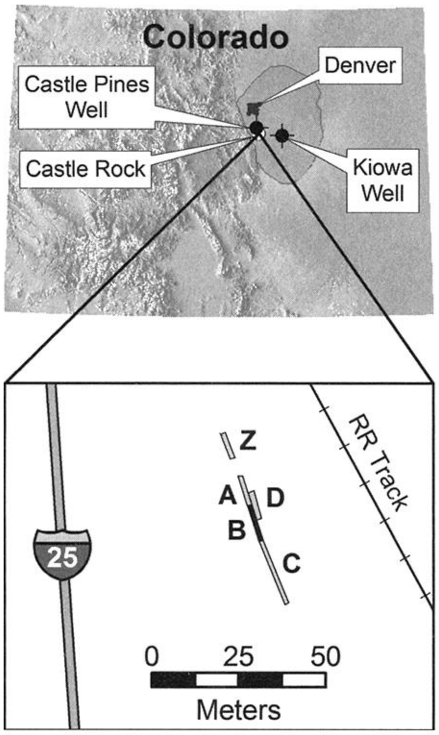

Fig. 1. Map of the Castle Rock fossil site (DMNH locality 1200; 39°23′N, 104°51′W) and the locations of the Castle Pines and Kiowa cored wells in the Denver Basin. The inset depicts the location and size of the five fossil leaf quarries.

Table 1. Climatic parameters of the Castle Rock flora compared to fossil forests. A dash indicates that the data were not available. The MAT, calculated (Calc.) using leaf margin analysis, has a minimum error of ±2°C (*12*, *27*, *28* and errors greater than 3°C are listed). The MAP was calculated using leaf area analysis (*29*). Supporting data for this table are in tables S1 to S6. Values for dicot species and specimens do not include fruits and seeds.

Site	Jimmy Camp	West Bijou (*40*)	Castle Rock	Bison Basin (*31*)	Big Multi (18-m level) (*31*)	Sourdough (*31*)	15 Mile Creek (*30*)
Formation	Denver	Denver	Denver	Fort Union	Fort Union	Wasatch	Willwood
Ma	65.9	65.4	64.1	60–56.2	55.6	52.8	52.8
Age	Late Cretaceous	Early Paleocene	Early Paleocene	Late Paleocene	Late Paleocene	Early Eocene	Early Eocene
No. of quarries	2	4	5	10	3	5	11
No. of dicot species	36	23	90	21	12	32	31
No. of total species	46	26	104	23	–	–	41
No. of dicot specimens	167	1502	855	4308	1617	3295	2030
No. of total specimens	208	1547	937	5659	–	–	3612
Calc. MAT (°C)	20.6	18.5 ± 3.2	22.2	11.7	18.6 ± 3.3	21.3	22.2
Calc. MAP (cm/year)	192	157	225	147	137	140	–
MAP range (cm/year)	134–215	110–225	157–322	103–211	90–185	98–201	–

Table 2. Climatic parameters of the Castle Rock flora compared to extant forests. A dash indicates that the data were not available. The MAT, calculated using leaf margin analysis, has a minimum error of ±2° C (*12*, *27*, *28*). The MAP was calculated using leaf area analysis (*29*). Supporting data for this table are in tables S1 and S7 to S9.

Site	Castle Rock	Rio Cueiras, Brazil	Rio Negro, Brazil	Manu, Peru (*33*)	Yasuní, Ecuador (*41*)	Wharton Brook, Connecticut (*9*)
Age	64.1	Modern	Modern	Modern	Modern	Modern
No. of quarries	5	2	2	4	3	13
Sample type	Fossil	Litter	Litter	Voucher	Voucher	Litter
No. of species	104	43	63	292	50	17
No. of specimens	937	647	599	–	–	10441
Calc. MAT (°C)	22.2	29.6	28.8	24.2	25.5	6.9 ± 3.0
Actual MAT (°C)	–	26.7	26.7	24	26.6	9.5
Calc. MAP (cm/year)	225	204	153.4	243	300	–
MAP range (cm/year)	157–322	143–292	107–220	170–348	209–429	–
Actual MAP	–	191	191	210	320	126

sequence, 46 km east of Castle Rock, yielded a weighted average age of 64.13 ± 0.21 Ma (*17*). All lines of evidence are consistent with the deposition of the uppermost D1 sequence and the enclosed Castle Rock leaf assemblage about 64.1 Ma, or 1.4 million years after the K-T boundary at 65.51 Ma (*23*). This correlates with the first part of the Torrejonian "North American Land Mammal Age" (NALMA) (*24*).

We collected leaf specimens between 1994 and 1999 from five separate quarries (Fig. 1) (*25*). The flora contains 104 morphotypes: 96 dicotyledons (90 leaf types and 6 fruit types), 3 ferns, 3 cycads, and 2 conifers (*26*) (Fig. 2). Most of the species of dicotyledonous leaves are new to science but include recognizable families such as Platanaceae, Lauraceae, Elaeocarpaceae, Tiliaceae, Sterculiaceae, and Urticaceae. Dominant species vary between the quarries, suggesting that the leaf samples reflect tree position in the source forest (table S1).

The physiognomy of the Castle Rock flora is similar to that of modern tropical rainforest litter. Of the 90 dicot species found, 69% are entire-margined, 39.5% of the 48 species that preserve intact apexes have drip tips (acuminate apexes) (Fig. 3), and the average leaf size is 67 cm^2 (mean of the averages for each leaf morphotype). Leaf margin analysis (*12*, *27*, *28*) gives an estimated mean annual temperature (MAT) of 22.2° ± 2°C. Mean annual precipitation (MAP) is estimated as 225 cm (the standard error range is 157 to 322 cm) (*29*).

The Castle Rock flora is the richest fossil plant site known from the Late Cretaceous and Paleogene of the Western Interior (Fig. 4A). When compared to sites where multiple quarries have been excavated from a single horizon (Fig. 4B and Table 1), the Castle Rock flora is dramatically richer, producing nearly three times the number of dicotyledonous species found at sites deposited during the early Eocene thermal maximum (*30*, *31*).

The pattern of spatial heterogeneity between quarries of the Castle Rock flora was evaluated with Sorenson's coefficient of similarity (*32*). Values ranged from 0.35 to 0.60. Coefficients for nontransported litter from a modern rainforest at Manu, Peru, range from 0.15 to 0.65 (*33*), whereas those from a temperate deciduous forest in Connecticut range from 0.67 to 1.0 (*9*).

On the basis of leaf physiognomy, diversity, and spatial heterogeneity, the Castle Rock flora

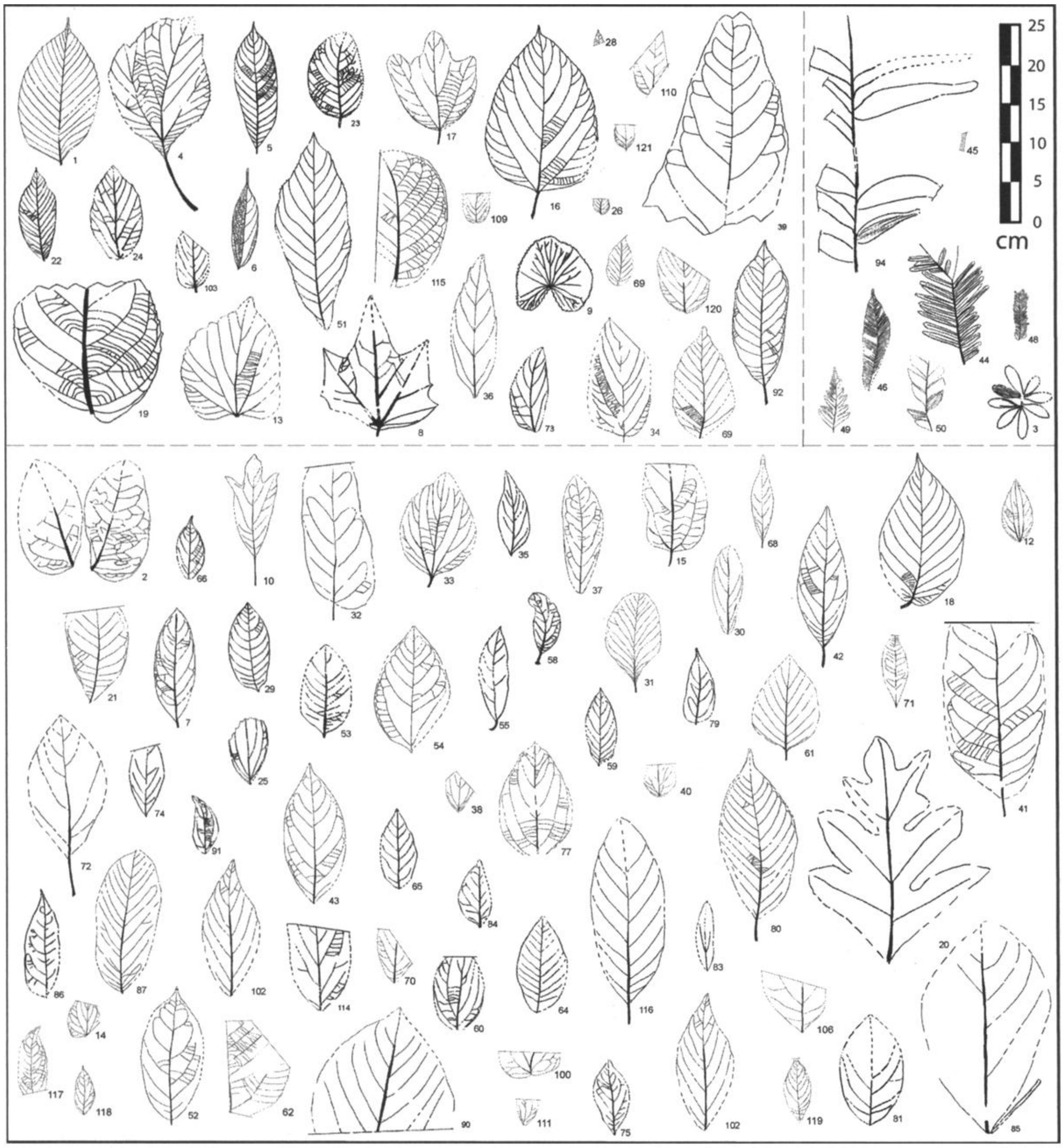

Fig. 2. Scale line drawings of the 98 early Paleocene Castle Rock leaf morphotypes. The numbers next to each leaf identify specific morphotypes. Dotted lines indicate areas that are missing on the primary reference specimens but are available on other specimens of the same morphotype. The upper left area contains the toothed dicot species. The upper right contains all the nondicots (ferns, cycads, and conifers). The lower group contains the entire-margined dicot species.

is more similar to modern tropical rainforest floras than it is to well-sampled Paleocene or Eocene floras or to modern temperate floras (Tables 1 and 2). Of the sites we compared, the Castle Rock flora is most similar to the leaf litter of Manu, Peru, which is located at the base of the Andes on the western margin of the Amazon Basin. Castle Rock occupied an analogous position relative to the Laramide Front Range during the Paleocene. Although Paleocene topographic relief is unknown, at least 4500 m of Laramide structural relief was in place 2 million years before the K-T boundary (*20*, *34*).

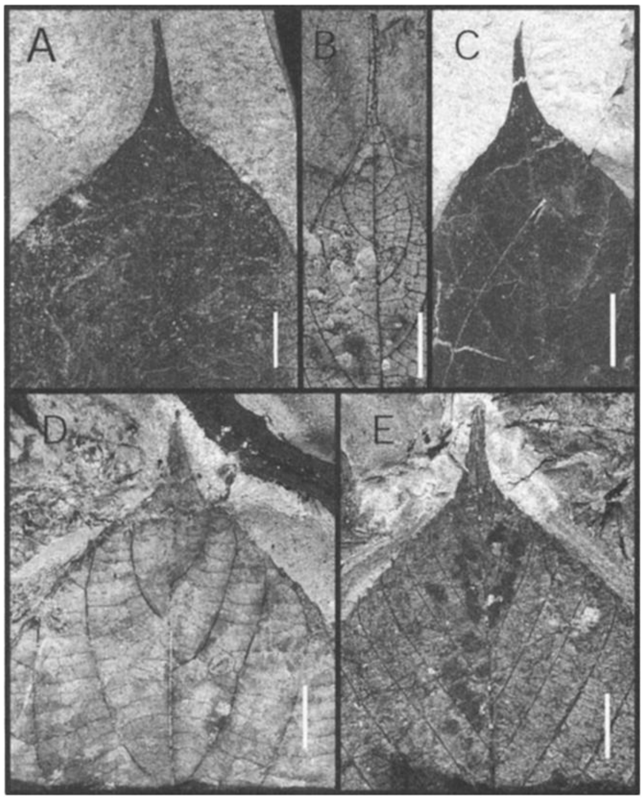

Fig. 3. Examples of leaf morphotypes with acuminate apexes, also known as drip tips, from the Castle Rock site. (**A**) Example CR 23, (**B**) CR6, (**C**) CR5, (**D**) CR 16, and (**E**) CR1. All of the illustrated leaves have toothed margins. Scale bars equal 1 cm.

A plausible reason for the existence of the Castle Rock rainforest is that the Laramide Front Range had a substantial orographic effect, resulting in heavy rains on the eastern slopes of the mountains. The source of this moisture may have been monsoons generated in either the Gulf of Mexico or the Cannonball Sea, which was then present in North Dakota (*35*). Supporting evidence for this hypothesis comes from the occurrence of coal in three pairs of Rocky Mountain basins separated by north-south ranges (the Raton–San Juan Basins, Colorado-New Mexico; the Denver–South Park Basins, Colorado; and the Powder River–Bighorn Basins, Wyoming). In each case, the eastern basin accumulated extensive Paleocene coal measures, and the western basin did not (*36*). An early Paleocene forest with rainforest physiognomy but only moderately high diversity (27 dicotyledons) has also been reported from the Raton Basin (*37*). The regression of the Cannonball Sea by 61 Ma may explain the absence of Castle Rock–style rainforests later in the Paleocene.

Most previous work on Paleocene floral diversity occurred in Wyoming, Montana, and the Dakotas, where post–K-T levels of floral diversity did not begin to increase until the late Paleocene–early Eocene (*6*, *8*, *30*). Although usually associated with late Paleocene global

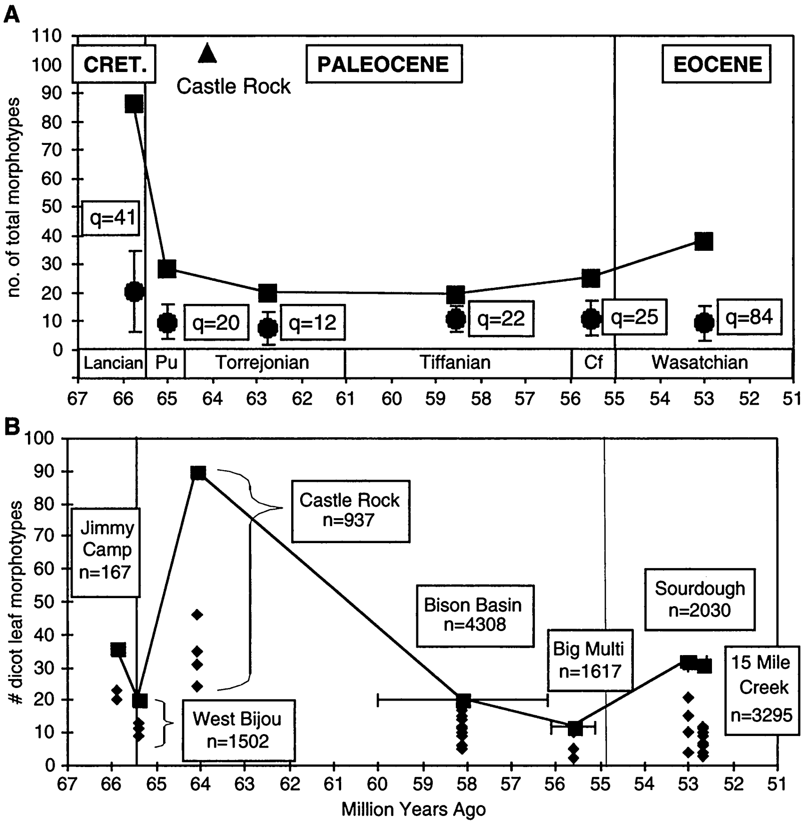

Fig. 4. Comparison of late Cretaceous and Paleogene megafossil localities from the Rocky Mountain region. (**A**) Circles represent the average number of plant morphotypes per quarry for each NALMA from Wyoming, Montana, and the Dakotas. The vertical error bars indicate 1 SD. q, number of quarries sampled. The Lancian and Puercan samples represent quarries that yielded more than 50 specimens (*7*, *9*); the number of specimens for the remaining quarries is unknown (*8*). Squares represent the maximum number of morphotypes from a single quarry for each NALMA. The triangle shows the number of morphotypes found at the Castle Rock site. The K-T boundary is placed at 65.51 Ma (*23*). The duration of the NALMAs is from (*24*). Pu, Puercan; Cf, Clarkforkian. (**B**) Number of dicotyledonous leaves from quantitatively sampled fossil sites in Colorado and Wyoming, where multiple quarries have been collected from a single stratigraphic level, compared to the Castle Rock site. Most of these sites represent floodplain lakes or swamps and may not be completely comparable to the forest floor deposit at Castle Rock. *n* = total number of dicotyledonous leaves collected. Diamonds represent the number of dicot morphotypes found in each individual quarry; squares represent the total number of dicot morphotypes from all quarries. Horizontal error bars represent uncertainty in the age of the site.

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. Raynolds *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. Raynolds, 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(number of species in common between the two samples)]/(number of species in sample 1 + 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).

→ R. J. Burnham, N. C. A. Pitman, K. R. Johnson, P. Wilf, *Am. J. Bot.* **88**, 1096-1102 (2001).

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

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Proterozoic Modular Biomineralized Metazoan from the Nama Group, Namibia

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We describe a Proterozoic, fully biomineralized metazoan from the Omkyk Member (~549 million years before the present) of the northern Nama Group, Namibia. *Namapoikia rietoogensis* gen. et sp. nov. is up to 1 meter in diameter and bears a complex and robust biomineralized skeleton; it probably represents a cnidarian or poriferan. *Namapoikia* encrusts perpendicular to the walls of vertical synsedimentary 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