Proc. Natl. Acad. Sci. USA
Vol. 84, pp. 5096–5100, August 1987
Geology

Leaf assemblages across the Cretaceous–Tertiary boundary in the Raton Basin, New Mexico and Colorado

(paleobotany/quasisuccession/extinction/"impact winter")

JACK A. WOLFE AND GARLAND R. UPCHURCH, JR.*

Paleontology & Stratigraphy Branch, U. S. Geological Survey, MS-919, Federal Center, Denver, CO 80225

Communicated by Estella B. Leopold, May 6, 1987 (received for review September 4, 1986)

ABSTRACT Analyses of leaf megafossil and dispersed leaf cuticle assemblages indicate that major ecologic disruption and high rates of extinction occurred in plant communities at the Cretaceous–Tertiary boundary in the Raton Basin. In diversity increase, the early Paleocene vegetational sequence mimics normal short-term ecologic succession, but on a far longer time scale. No difference can be detected between latest Cretaceous and early Paleocene temperatures, but precipitation markedly increased at the boundary. Higher survival rate of deciduous versus evergreen taxa supports occurrence of a brief cold interval (<1 year), as predicted in models of an "impact winter."

Vegetational and floristic studies of pollen and leaf assemblages across the Cretaceous–Tertiary (K–T) boundary generally have presented evidence against major long-term effects of possible bolide impact(s). Although pollen data indicate major short-term disruption of the terrestrial ecosystem at the K–T boundary, low levels of extinction are reported (1, 2). In regard to leaf assemblages, vegetational change from the Lancian (late Maestrichtian) through the early Paleocene in the northern high plains of Wyoming and Montana was attributed to general Late Cretaceous cooling (3). Extinction levels across the K–T boundary were suggested to be comparable to those across the Paleocene–Eocene boundary in North America (3), although Krasilov (4) noted that extinction rates appeared to be much higher in northeastern Asia. These previous studies of extinction in leaf assemblages across the K–T boundary are based on assemblages (*i*) from sections that lack the iridium-rich boundary clay and (*ii*) that are stratigraphically widely spaced. Such studies cannot address rates of extinction or of climatic and ecologic changes.

That major ecologic disruption occurred throughout the western interior of North America, including the Raton Basin, cannot readily be disputed. Fern spores make up <25% of individual samples (including samples from swamp environments) during the latest Cretaceous in the Raton Basin, but fern spores reach abundances of 96–99% immediately above the iridium-rich boundary clay (1). This anomalous abundance of fern spores has been likened to mass-kill of land plants from known volcanic catastrophes such as the 1883 eruption of Krakatau (1), providing strong evidence for mass-kill of the angiosperm-dominated latest Cretaceous vegetation. However, mass-kill may not necessarily result in mass extinction.

This report is based on detailed sampling in the Raton Basin of Colorado and New Mexico (Fig. 1), where the iridium-rich boundary clay occurs in 15 local sections (5, 6). Almost all the fossil samples were obtained from sections that can be physically related to boundary clay. This clay also contains abundant shocked minerals (7), which are considered as strong evidence that the boundary clay represents fallout from a bolide impact. Palynological correlations (5, 6) indicate that the boundary clay in the Raton Basin is the same age as the iridium-rich clay in areas such as Hell Creek, Montana, where vertebrate data (8) also indicate that the clay approximates the K–T boundary. A previous report (9) of the Raton K–T boundary clay occurring in a zone of normal magnetic polarity is erroneous; the boundary occurs, as elsewhere, in a zone of reversed magnetic polarity (10).

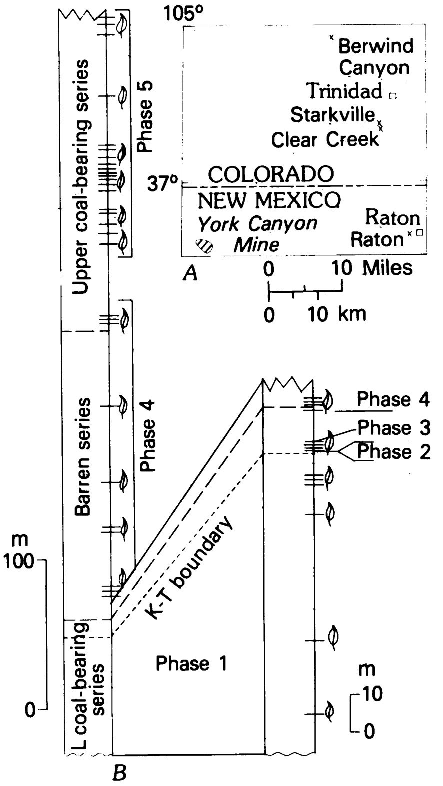

FIG. 1. (*A*) Map of part of Raton Basin and (*B*) generalized section of Raton Formation. Megafossil localities shown by leaf symbol have measured or estimated stratigraphic distances from the K–T boundary clay, which contains high amounts of iridium and shocked minerals.

METHODS OF ANALYSIS

High percentages of extinct plant genera and families in K–T boundary assemblages preclude accurately interpreting veg-

---

Abbreviations: K–T, Cretaceous–Tertiary; aff., affinity.

*Present address: University Museum, Campus Box 315, University of Colorado, Boulder, CO 80309.

etation on the basis of ecologic tolerances of related extant taxa; general taxonomic affinities can yield only general concepts of ecologic and climatic change. Analyses of foliar physiognomy (e.g., leaf size, overall shape, apical shape, and characters of margin) offer a more precise method of inferring vegetational and climatic change because, in extant vegetation, changes in foliar physiognomy parallel overall changes in vegetation and thus climate (refs. 11–15; see particularly ref. 13, which discusses some of the prior critiques of foliar physiognomy). Various physiognomic characters of leaves, in conjunction with taphonomy, can also indicate probable ecologic preference within vegetation—e.g., whether streamside, understory, or early or late successional (14).

The analysis of cuticle—the waxy covering that preserves anatomical details of the leaf surface—adds a significant dimension to our data base. Individual cuticle morphology may be identified to leaf type on megafossils; subsequently, dispersed cuticle can be used to infer the presence of the whole-leaf taxon. Further, many additional groups can be recognized in the dispersed cuticle record by their diagnostic features. Like pollen, cuticle offers the potential of recovering many data from a small sample volume, including samples from stratigraphic intervals where megafossil assemblages are absent. This affords (*i*) a tighter stratigraphic sampling and control, (*ii*) increased accuracy in determining the ranges of whole-leaf taxa, and thus (*iii*) the potential to analyze vegetational change on a near-ecological time scale. Cuticles also have physiognomic characters (e.g., thickness, hairiness) that allow climatic inferences independent of their systematic affinities, thus affording additional physiognomic characters from which climate can be inferred (16, 17). Sampling in proximity to the K–T boundary was at intervals of 1–2 cm.

RATON LEAF SEQUENCE

Phase 1. Five vegetational–floristic phases are recognized (Fig. 2) in the Raton Basin. Phase 1, of Lancian age (about 66–68 million years), is represented by assemblages from the upper part of the Vermejo Formation (18) and from the base of the Raton Formation up to the K–T boundary clay. Leaf megafossil assemblages from the Lancian part of the Raton indicate high spatial heterogeneity as well as high specific diversity. The two main leaf localities in the Lancian Raton, each about 6 m below the boundary clay, produced 450–500 specimens and 36 species from excavations each <1 m^3; few species are common to the two localities. At least 75 species are known from the dispersed cuticle record.

The phase-1 flora contains palms and diverse dicots, including extinct relatives of Lauraceae (protolauraceans) and other Laurales (Fig. 2 *A, F, G, H, CC, DD, FF*), Illiciales (Fig. 2*EE*) and extinct relatives (protoillicialeans), Euphorbiaceae [extinct genera of Acalyphoideae such as "*Ficus*" *leei*, "*Cissites*" *panduratus* (Fig. 2*B*), and "*Zizyphus*" *fibrillosus* (Fig. 2*C*)], and Menispermaceae (Fig. 2*I*). One of the numerous extinct lauralean genera includes "*Artocarpus*" *dissecta* (Fig. 2 *G, FF*) and occurs as dispersed cuticle in the Mississippi Embayment, Atlantic Coastal Plain, and Western Interior during the late Campanian and Maestrichtian; this genus has a highly characteristic foliar morphology and cuticular anatomy and was obviously a major component of latest Cretaceous vegetation. Another common extinct lauralean group has lateral primary veins decurrent into the petiole [e.g., "*Ficus*" *praetrinervis* (Fig. 2*F*) and "*Cinnamomum*" *linifolium* (Fig. 2A)]. Many common Lancian dispersed-cuticle species occur up to the boundary but not above it; for example, immediately below (0–1 cm) the

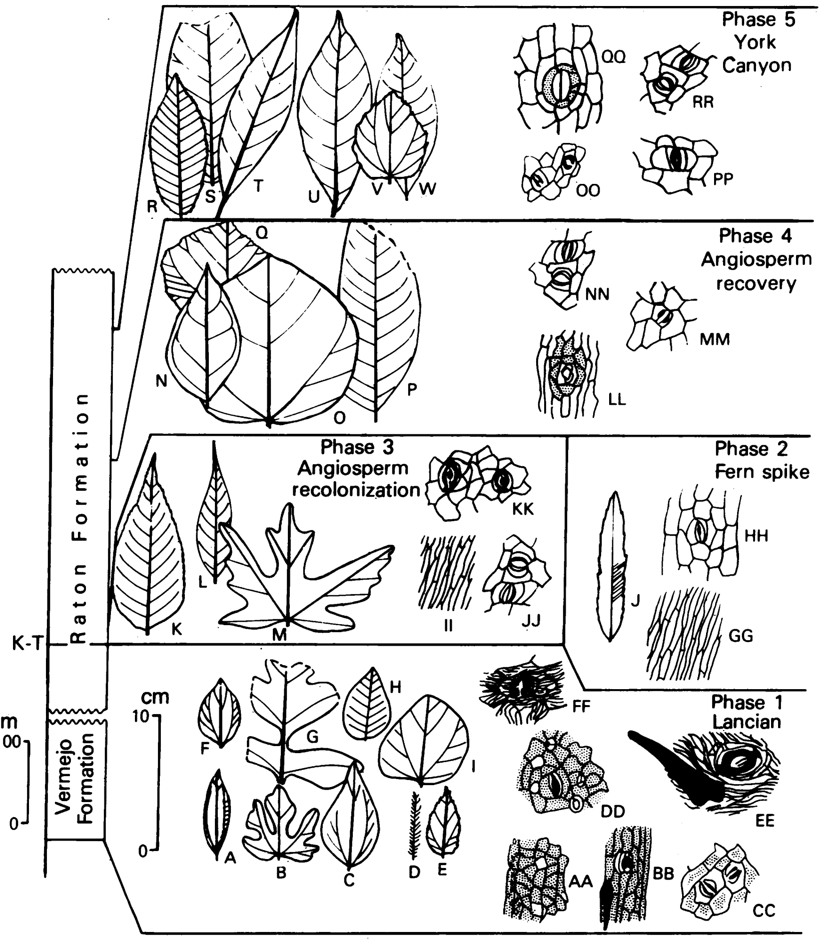

FIG. 2. Changes in leaf physiognomy from the latest Cretaceous to the early Paleocene in the Raton Basin. Phase 1 is characterized by a high-diversity flora and leaves (and leaf cuticles) indicative of warm subhumid climate. The iridium-rich clay interpreted as the K–T boundary occurs between phase 1 and phase 2. Immediately above the boundary (phase 2), the vegetation was dominated by a fern and probably represents vegetation following a mass-kill. Angiosperms again became dominant in phase 3 but were not diverse and were of early successional morphology; the leaves and cuticles indicate a warm, wet climate. Diversity gradually increased during phases 4 and 5, but even in phase 5 (about 1.5 million years after the K–T boundary), diversity was low compared to phase 1; leaves and cuticles indicate a warm rain-forest environment. *AA–RR*, cuticles (approximately ×120).

boundary clay at Berwind Canyon are the highest occurrences of dispersed cuticles of "*Cinnamomum*" *linifolium*, affinity (aff.) "*Ficus*" *praetrinervis*, "*Artocarpus*" *dissecta* and two closely related species, and two species groups of monocots.

Evergreen conifers are moderately diverse in the Vermejo. In the Lancian Raton, the highest megafossil assemblages contain *Geinitzia* (Fig. 2*D*) and a *Sequoia*-like plant; a dispersed-cuticle type allied to extant Australian–New Caledonian Cupressaceae (especially *Neocallitropsis* and *Callitris*) occurs 2 m below but not above the boundary (Fig. 2*AA*). Presumably conifers were emergents, analogous to extant vegetation of the Southern Hemisphere (15).

The plants of phase-1 megafossil assemblages were overwhelmingly broad-leaved evergreen, as indicated by thick, coriaceous leaves and robust cuticles. The high percentage of entire-margined leaves (Table 1) indicates that Lancian temperatures were megathermal (>20°C), as on lowland Taiwan or New Caledonia (15). Strong variation in taxonomic composition between coeval dispersed-cuticle assemblages from a given lithology indicates high spatial heterogeneity, characteristic of megathermal vegetation. Precise temperature assignment based on leaf-margin percentage is difficult and depends on whether analogies are made to extant east Asian or Southern Hemisphere vegetation (15). Occurrences of evergreen conifers and a low-diversity deciduous (thin-leaved) element suggest a Southern Hemisphere analog; if so, Lancian mean annual temperature was probably 21–22°C.

Elongated foliar apices (drip-tips) are uncommon and leaf size is small. Many taxa have dense hairs, some of which are cutinized (Fig. 2 *BB, EE*). Leaves of extant rain forest plants, if pubescent, typically have hairs only on the lower surface (11), but phase-1 leaves can have hairs on both surfaces, a condition that characterizes leaves of dry, sunny habitats (16, 17). In modern megathermal climates, such characters indicate only moderate precipitation. Such dry-adapted characters of both whole leaves and cuticles continue to the highest megafossil assemblages of the Lancian. Dispersed-cuticle assemblages immediately below the boundary are also characterized by adaptations to dryness, suggesting no significant change in precipitation during the Lancian.

Phase 2. Phase 2 occurs immediately above the iridium-rich boundary clay and includes the palynological "fern spike," in which fern spores are overwhelmingly dominant (1). Abundant fern fronds and rare specimens of a bryophyte occur <1 m above the clay in the Starkville and Clear Creek sections. The sterile fern fronds (Fig. 2*J*) represent an extinct genus related to the extant *Stenochlaena*, a primary colonizer in vegetation of Indomalaya and Africa. In open situations, *Stenochlaena* produces sterile fronds, while as a climber in closed forests, it produces fertile fronds. All cuticle assemblages are dominated by cuticles that have cells in files (Fig. 2*GG*), typical of herbaceous stems, monocot leaves, or fern rachises; in many samples, these cuticles are thin. Rare dicot cuticles also occur, all of which are smooth; we have been unable to identify most of these as any known Cretaceous leaf-species. Because of the limited assemblage, no temperatures are inferred for phase 2.

Phase 3. Phase 3 is characterized as the angiosperm recolonization phase. The first evidence of phase 3 occurs at the Starkville locality, where fragments of "*Cissites*" *panduratus* (Fig. 2*M*) occur directly above phase 2. This same species is well represented at Berwind Canyon, the best phase-3 locality. Here, >400 leaves were collected. Dominants are "*Cissites*" *panduratus* and a celastracean (Fig. 2*K*), with lesser abundances of a protolauracean (Fig. 2*L*), a fern similar to *Stenochlaena*, and a second fern. Only 8 megafossil and 10 dispersed-cuticle entities are known in phase 3. Although herbaceous-type cuticle is less dominant than in phase 2, all dispersed-cuticle assemblages are typically dominated by a single taxon. Dispersed-cuticle taxa include species of Laurales (Fig. 2*JJ*), a protoillicialean (Fig. 2*KK*), and a palm (Fig. 2*LL*); the last two have not been found below the boundary. Monocot, including palm, cuticle types in phases 3–5 typically represent different species than in phase 1.

The physiognomy and general affinities of the phase-3 flora indicate disturbed conditions. Phase 3 "*Cissites*" *panduratus* is large- and wide-leaved, palmately veined, and unlobed to deeply lobed; this morphology is found in extant megathermal colonizing species, including members of Acalyphoideae of the family Euphorbiaceae. The megafossil protolauracean and celastracean taxa are stenophyllous (narrow-leaved) as in extant stream-side plants. Although both taxa occur in carbonaceous shales during phase 3, both are restricted to fluviatile sandstones during phase 4, and the protolauracean occurs in fluviatile sandstones in phase 1. Stream-side plants are, of course, early successional, and the occurrence of such early successional plants in swamp habitats during phase 3 suggests ecologic disruption and extinction that allowed opportunistic species to invade stable habitats. All phase-3 taxa either indicate, or are consistent with, early successional

Table 1. Physiognomy of Vermejo and Raton leaf assemblages and lithologies sampled

	Megafossils							
Phase	Total localities	Total species	Total dicot species	Leaf-size index*	% entire-margined species	% drip-tips	Cuticle foliar hairs	Lithologies sampled for dispersed cuticle and/or megafossils
5 (York Canyon)	20	35	27	68	74	55	Noncutinized, lower surface	Coal, carbonaceous shale, overbank sandstone
4 (angiosperm recovery)	14	25	21	72	71	42	Noncutinized, lower surface (see text)	Coal, carbonaceous shale, overbank sandstone, channel sandstone
3 (angiosperm recolonization)	5	8	5	70	80	40	Absent	Coal, carbonaceous shale, overbank sandstone
2 (fern-spike)	3	2	0	—	—	—	Absent	Coal, carbonaceous shale
1 (Lancian)								
Raton	6	47	43	34	72	9	Cutinized and noncutinized, lower and upper surfaces	Coal, carbonaceous shale, overbank sandstone, channel sandstone
Vermejo	19	86	63	34	71	9	(Inadequately sampled)	Carbonaceous shale, overbank sandstone

*Leaf-size index is that of ref. 19; an assemblage composed entirely of mesophyllous and larger species has an index of >100, and an assemblage composed entirely of microphyllous and smaller species has an index of <0.

vegetation. The 2 m of coal and carbonaceous shales at Berwind Canyon that contain phase 3 have four rooted horizons, which we interpret as soil-forming stages; no lithologic evidence of flood events is present that would suggest periodic disruption of the environment. Although no precise estimates of duration of these soil-forming stages can be presently made, phase 3 apparently persisted for a considerably longer period than does extant early successional megathermal vegetation.

The low diversity of phase 3 yields a small statistical sample, but the dominance of large leaves in the flora, the abundance of large leaves at outcrops, and the highly attenuated apices probably indicate high precipitation. Species such as "*Cissites*" *panduratus* show a marked increase in leaf size and apical attenuation from the Lancian (Fig. 2*B*) into phase 3 (Fig. 2*M*). Dense, cutinized hairs are not known from phase-3 cuticle types, even when present on related taxa from phase 1; this condition characterizes leaves of wet megathermal vegetation (11).

Phase 4. The angiosperm recovery phase extends from just below the barren series (so named for the scarcity of coal) and into the lower part of the upper coal-bearing series, about 200 m above the K–T boundary (Fig. 1). Phase 4 contains leaf species in swamp environments that have physiognomy characteristic of late successional (or "climax") vegetation. Specimens of "*Cissites*" *panduratus* (Fig. 2*O*) are all unlobed, and these, along with stenophylls, are restricted to stream-side or near-stream depositional environments. Two deciduous dicots are also found in channel and overbank facies: the platanoid "*Cissus*" *marginatus* (Fig. 2*Q*) and the archaic rosid *Averrhoites affinis*. The leaves typically have drip-tips, and leaf-margin percentage and leaf size index are high (Table 1). Phase 4 is not diverse, although it is richer than phase 3 (Table 1). Dominants are palms (Fig. 2*LL*) and evergreen dicots: Lauraceae (Fig. 2*MM*), "*Ficus*" *praetrinervis*, aff. *Picramnia* (Fig. 2*N*), and Celastraceae. Cuticles from most samples are thick and smooth, as in megathermal rain forests. However, four samples from a 5-m interval in the upper part of phase 4 contain some cuticles that have cutinized hairs, suggesting a possible drier interval.

Phase 5. Phase 5 is distinguished by the first appearances in the Raton sequence of numerous taxa and is best represented in the upper coal-bearing series at York Canyon Mine in an interval 270–420 m above the K–T boundary (Fig. 1). Extensive commercial stripping over an area of about 6 km^2 allowed examination of many thousands of specimens at many sites in the field and large collections through a stratigraphic interval of about 50 m. The megafossil flora is of low diversity: if old collections from coal mine dumps elsewhere in the upper coal-bearing series are included (18), the phase-5 flora contains only 45–50 species from throughout the Raton Basin (>4000 km^2). Dispersed-cuticle assemblages show comparable low diversity. Palms (both fan and feather) are present, and evergreen dicots include protolauraceans, other lauraleans [including "*Magnolia*" *lesleyana* (Fig. 2*U*)], Euphorbiaceae, and Tiliaceae [aff. *Grewia* (Fig. 2*V*), aff. *Heliocarpus*, and aff. *Triumfetta*]; the "*Magnolia*" and Tiliaceae are not known lower in the Raton sequence. Phase 5 also contains the earliest Raton occurrence of the deciduous dicotyledons "*Carya*" *antiquorum* (Fig. 2*R*) and "*Eucommia*" *serrata* and a deciduous conifer (aff. *Glyptostrobus*, Fig. 2*QQ*).

The foliar (including cuticular) physiognomy of phase 5 is indicative of megathermal rain forest. Most leaf-megafossil species have marked drip-tips. The leaf species in phase 5 tend to have a similar gross morphology, unlike the morphologic diversity in phase 1.

CONCLUSIONS

Extinction and Floristic Change. Studies of leaf megafossils and dispersed cuticles from the Raton Basin corroborate palynological studies (1) in suggesting rapid extinction at the end of the Cretaceous. For example, archaic Laurales such as "*Artocarpus*" *dissecta*, "*Cinnamomum*" *linifolium*, and their allies disappear at the K–T boundary, as do other groups characteristic of the Lancian.

However, the amount of extinction in the Raton leaf record is apparently much greater than in the Raton pollen record, from which the regional extinctions of only three pollen genera and few pollen species were inferred (2). For example, acalyphoid Euphorbiaceae and archaic Laurales, which were diverse in the Lancian, are each represented by a single species in the early Paleocene. Although palms and other monocots occur both above and below the boundary, cuticular anatomy indicates that the latest Cretaceous taxa are distinct specifically, if not generically, from the early Paleocene taxa. Archaic conifers (e.g., *Geinitzia*) also disappear. Although some taxa that are rare below the boundary are common above the boundary and vice versa, about 75% of phase-1 leaf species are unknown in Paleocene floras either in the Raton Basin or elsewhere.

The inferred high level of extinction in the leaf flora contrasts with the low level based on pollen studies (1). Although the reasons for this discrepancy are not certain, the foliar studies indicate that many extinctions occurred in groups (*i*) that have pollen that rarely fossilizes (e.g., Laurales; see also ref. 20) or (*ii*) that have generalized pollen that is typically not diagnostic to specific or generic levels (e.g., Acalyphoideae and Palmae; see also refs. 2 and 20).

Most Raton phase-5 dominants are typically unknown in phase 1, but some have records prior to the K–T boundary. *Grewia*-type Tiliaceae have a Maestrichtian record in the Mississippi Embayment region (21), and the thin-leaved (deciduous) *Glyptostrobus*, "*Carya*" *antiquorum*, and "*Eucommia*" *serrata* have been reported from the Maestrichtian of Montana (22). The deciduous element in phases 4 and 5 appears to be derived largely from the north. Some broad-leaved evergreen dominants in phase 5, however, may have been derived from a southern source—e.g., "*Magnolia*" *lesleyana*, which is also abundant in the Paleocene of the Mississippi Embayment region (23).

Vegetational and Climatic Change. The dominance of ferns immediately above the K–T boundary in phase 2 is analogous to the abundance of ferns on Krakatau after the 1883 eruption (11), as has been emphasized in Raton pollen studies (1). Phase-3 foliar physiognomy is typical of early successional vegetation in modern megathermal climates but occurred over a much longer time period than in "normal" vegetational succession. Rate of recovery of diversity on Krakatau contrasts markedly with that following the K–T boundary. On Krakatau, angiosperm species numbered 15 after 3 years, 49 after 14 years, 73 after 23 years, and 219 after 51 years (11). Although the 45–50 species represented in phase-5 collections probably do not represent all taxa actually present during phase 5 in the Raton Basin, this factor is countered by (*i*) the variety of depositional environments sampled, (*ii*) the large number of localities, (*iii*) the large area sampled (>4000 km^2 in the Raton Basin versus 45 km^2 for Krakatau), (*iv*) the long time period represented by phase 5, and (*v*) the large number of specimens examined. Even assuming incomplete sampling of the phase-5 flora, recovery in diversity of early Paleocene vegetation was on an evolutionary, not ecological, time scale. Such long-term change (whether floristic or physiognomic) that mimics short-term ecologic succession is here termed *quasisuccession* (from Latin *quasi*, appearing as if or simulating).

Vegetation, except during phase 2, was primarily broad-leaved evergreen. The uniformity of leaf-margin percentages in the Vermejo–Raton sequence indicates no general temperature difference between the latest Maestrichtian and the early Paleocene. However, selective extinction could bias some aspects of physiognomic analyses. Nonentire margins are partially correlated with thin deciduous leaves (14). Selective extinction of evergreen versus deciduous taxa could lower the apparent paleotemperature derived from the leaf-margin analysis. Our data indicate that a higher percentage of evergreen taxa than deciduous taxa became extinct (see below), and thus the temperature for the early Paleocene could have been higher than indicated by the leaf-margin analysis.

Changes in foliar features such as leaf size, apical attenuation, and hairiness of cuticles indicate a major increase in precipitation at the K–T boundary in the Raton Basin. Because dispersed-cuticle samples 0–1 cm below the K–T boundary have physiognomy characteristic of other phase-1 samples, subhumid climate is inferred to have persisted up to the boundary. Samples immediately above the boundary and higher in the early Paleocene section have cuticular physiognomy characteristic of humid climate, thus suggesting that high precipitation had a rapid onset at the K–T boundary and continued through the early Paleocene.

Only 12 of 75 (16%) phase-1 evergreen dicots are known in the Paleocene, in contrast to 8 of 12 (67%) phase-1 deciduous dicots; most evergreen conifers also became extinct, with deciduous Taxodiaceae first appearing above the boundary. Higher survival rate of deciduous versus evergreen taxa suggests an event favoring plants that had dormancy mechanisms. Dormancy mechanisms would be triggered by drought, darkness, or low temperature. Given the observed major increase in precipitation at the boundary, which eliminates the drought factor, the event would probably have been a brief period (<1 year) of darkness, low temperature, or both, as predicted in models of an "impact winter" (24). The survival of ferns is also significant because rhizomes of ferns can withstand thermal shock (25), as shown on El Chichón. Moreover, the overall high rate of extinction indicates that both reproductive and vegetative organs of vascular plants were destroyed. As in the present tropics, latest Cretaceous megathermal plants that had never been exposed to low temperatures (19) would be particularly vulnerable to a low-temperature excursion (3, 26).

We thank C. L. Pillmore for assistance in stratigraphic problems. T. M. Bown, W. A. Clemens, L. J. Hickey, A. W. Knoll, E. B. Leopold, D. J. Nichols, C. B. Officer, P. H. Raven, R. A. Spicer, B. H. Tiffney, and S. L. Wing offered critiques of the manuscript.

1. Tschudy, R. H., Pillmore, C. L., Orth, C. J., Gilmore, J. S. & Knight, J. D. (1984) *Science* **225**, 1030–1032.
2. Tschudy, R. H. & Tschudy, B. D. (1986) *Geology* **14**, 667–670.
3. Hickey, L. J. (1981) *Nature (London)* **292**, 529–531.
4. Krasilov, V. A. (1983) *Paleontol. Zh.*, 93–95.
5. Orth, C. J., Gilmore, J. S., Knight, J. D., Pillmore, C. L. & Tschudy, R. H. (1982) *Geol. Soc. Am. Spec. Pap.* **190**, 423–433.
6. Pillmore, C. L., Tschudy, R. H., Orth, C. J., Gilmore, J. S. & Knight, J. D. (1984) *Science* **223**, 1180–1183.
7. Bohor, B. F., Foord, E. E., Modreski, P. J. & Triplehorn, D. M. (1984) *Science* **224**, 867–869.
8. Clemens, W. A. (1982) *Geol. Soc. Am. Spec. Pap.* **190**, 407–413.
9. Payne, W. A., Wolberg, D. L. & Hunt, A. (1983) *New Mexico Geol.* **5**, 41–44.
10. Shoemaker, E. M., Pillmore, C. L. & Peacock, E. W. (1987) *Geol. Soc. Am. Spec. Pap.* **209**, 131–150.
11. Richards, P. W. (1952) *The Tropical Rain Forest* (Cambridge Univ. Press, London).
12. Wolfe, J. A. (1971) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **9**, 27–57.
13. Wolfe, J. A. (1981) in *Paleobotany, Paleoecology, and Evolution*, ed. Niklas, K. J. (Praeger, New York), Vol. 2, pp. 79–101.
14. Givnish, T. (1979) in *Topics in Plant Population Biology*, eds. Solbrig, O. T., Jain, S., Johnson, G. B. & Raven, P. H. (Columbia Univ. Press, New York), pp. 375–407.
15. Wolfe, J. A. (1979) *U. S. Geol. Surv. Prof. Pap.* **1106**.
16. Coley, P. D. (1983) *Ecol. Monogr.* **53**, 209–233.
17. Fahn, A. (1967) *Plant Anatomy* (Pergamon, Oxford).
18. Knowlton, F. H. (1917) *U. S. Geol. Surv. Prof. Pap.* **101**.
19. Wolfe, J. A. & Upchurch, G. R. (1987) *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, in press.
20. Muller, J. (1981) *Bot. Rev.* **47**, 1–142.
21. Berry, E. W. (1916) *U. S. Geol. Surv. Prof. Pap.* **91**.
22. Hickey, L. J. (1980) *Univ. Mich. Mus. Paleontol. Pap.* **24**, 33–49.
23. Berry, E. W. (1925) *U. S. Geol. Surv. Prof. Pap.* **136**.
24. Alvarez, W., Alvarez, L. W., Asaro, F. & Michel, H. V. (1982) *Geol. Soc. Am. Spec. Pap.* **190**, 305–315.
25. Spicer, R. A., Burnham, R. J., Grant, P. & Glicken, H. (1985) *Am. Fern J.* **75**, 1–5.
26. Ehrlich, P. R., Harte, J., Harwell, M. A., Raven, P. H., Sagan, C., Woodwell, G. M., Berry, J., Ayensu, E. S., Ehrlich, A. H., Eisner, T., Gould, S. J., Grover, M. P., Herrera, R., May, R. M., Mayr, E., McKay, C. P., Mooney, M. A., Myers, N., Pimentel, D. & Teal, J. M. (1983) *Science* **222**, 1293–1300.