High-precision ^{40}Ar/^{39}Ar geochronology and the advent of North America's Late Cretaceous terrestrial fauna

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ABSTRACT A densely sampled, diverse new fauna from the uppermost Cedar Mountain Formation, Utah, indicates that the basic pattern of faunal composition for the Late Cretaceous of North America was already established by the Albian-Cenomanian boundary. Multiple, concordant ^{40}Ar/^{39}Ar determinations from a volcanic ash associated with the fauna have an average age of 98.39 ± 0.07 million years. The fauna of the Cedar Mountain Formation records the first global appearance of hadrosaurid dinosaurs, advanced lizard (e.g., Helodermatidae), and mammal (e.g., Marsupialia) groups, and the first North American appearance of other taxa such as tyrannosaurids, pachycephalosaurs, and snakes. Although the origin of many groups is unclear, combined biostratigraphic and phylogenetic evidence suggests an Old World, specifically Asian, origin for some of the taxa, an hypothesis that is consistent with existing evidence from tectonics and marine invertebrates. Large-bodied herbivores are mainly represented by low-level browsers, ornithopod dinosaurs, whose radiations have been hypothesized to be related to the initial diversification of angiosperm plants. Diversity at the largest body sizes (>10^6 g) is low, in contrast to both preceding and succeeding faunas; sauropods, which underwent demise in the Northern hemisphere coincident with the radiation of angiosperms, apparently went temporarily unreplaced by other megaherbivores. Morphologic and taxonomic diversity among small, omnivorous mammals, multituberculates, is also low. A later apparent increase in diversity occurred during the Campanian, coincident with the appearance of major fruit types among angiosperms, suggesting the possibility of adaptive response to new resources.

Many groups of terrestrial vertebrates are believed to have either arisen or undergone significant radiations during the Early and medial Cretaceous (1–3). The biogeography and dynamics of these radiations are poorly understood, but it has been hypothesized that they are related, in part, to dramatic changes in the terrestrial flora, resulting from the evolution of flowering (angiosperm) plants (4–7). Unfortunately, the fossil record for the Early and early Late Cretaceous is exceedingly sparse (8); comparisons among the few known assemblages in North America are further hampered by a lack of absolute dates and poor temporal resolution in general (9). As a result, a great taxonomic, morphologic, and presumed paleoecologic hiatus separates the incomparably better known taxa and faunas of the Late Jurassic and Late Cretaceous. Herein we report on a densely sampled, diverse fauna of terrestrial vertebrates from a narrow stratigraphic interval in the Cedar Mountain Formation of Utah, present radiometric dates that establish the age of the fauna, and discuss its implications for interpretation of biotic change in the terrestrial Cretaceous of North America.

Geology, Geochronology, and Paleontology

The Cedar Mountain Formation, broadly exposed in central Utah (Fig. 1), includes two generally recognized units, a lower Buckhorn Conglomerate and an overlying, unnamed "shale" member (10). Fossils have not been recovered from the Buckhorn Conglomerate in the study area, west of the San Rafael Swell, though elsewhere it contains a distinctive dinosaur assemblage of possible Barremian age (11). The upper shale member is comprised of drab, variegated mudstones, deposited on alluvial floodplains, together with thin, discontinuous channel sandstones. The lower part of the upper member, which is characterized by abundant nodular zones representing paleosols, has produced dinosaurs of suspected Aptian-Albian age (11). The uppermost part of the unit includes some bentonitic mudstones and carbonaceous layers (Fig. 1); palynomorphs from this part of the section have been alternatively interpreted as of late Albian (12) or early Cenomanian (13) age. We conducted macrovertebrate and microvertebrate sampling techniques in a restricted stratigraphic interval of this uppermost part of the Cedar Mountain Formation, 10–20 m below the contact with the overlying Dakota Formation. The resulting fauna, known from 4,882 specimens representing 72 taxa (Table 1), was obtained from 31 sites, including several different depositional facies.

The uppermost part of the Cedar Mountain Formation also includes a number of local, smectitic ash horizons, one of which directly overlies the bone horizon at the most productive fossil locality. Three samples from this horizon (WS10A-C; Table 2), and one sample at the same level 6 km to the NE (1465–1+1; Table 2), were collected for dating; stratigraphic and compositional evidence suggests that they represent the same volcanic event. Sanidine phenocrysts from these samples were dated by the single-crystal, laser fusion ^{40}Ar/^{39}Ar method at the Berkeley Geochronology Center (BGC). Grain sizes varied from >75 mesh for samples WS10C and 1465–1+1 to considerable larger grains obtained from WS10B in the >40 mesh and from WS10A in the >30 mesh; crystals were washed in 5% hyrdrofluoric acid solution for 5 min, as is routine for volcanic K-feldspar (see ref. 15 for further details of the ^{40}Ar/^{39}Ar dating method in use at BGC). Samples were irradiated in two batches for 70 hr (WS10A) and 60 hr (all others) in the cadmium-lined in-core irradiation tube facility of the Oregon State University Training, Research, and Isotope production by General Atomics reactor. Sample holders consisted of aluminum disks with wells drilled out to accept the mineral concentrates. Sample WS10A was coirradiated with the commonly used standard, sanidine from the Fish Canyon Tuff (FCT) of Colorado [27.84 million years (Ma); ref. 16]. The error in *J* (the neutron flux parameter) assigned to the age

Abbreviation: Ma, mega-annum (millions of years).
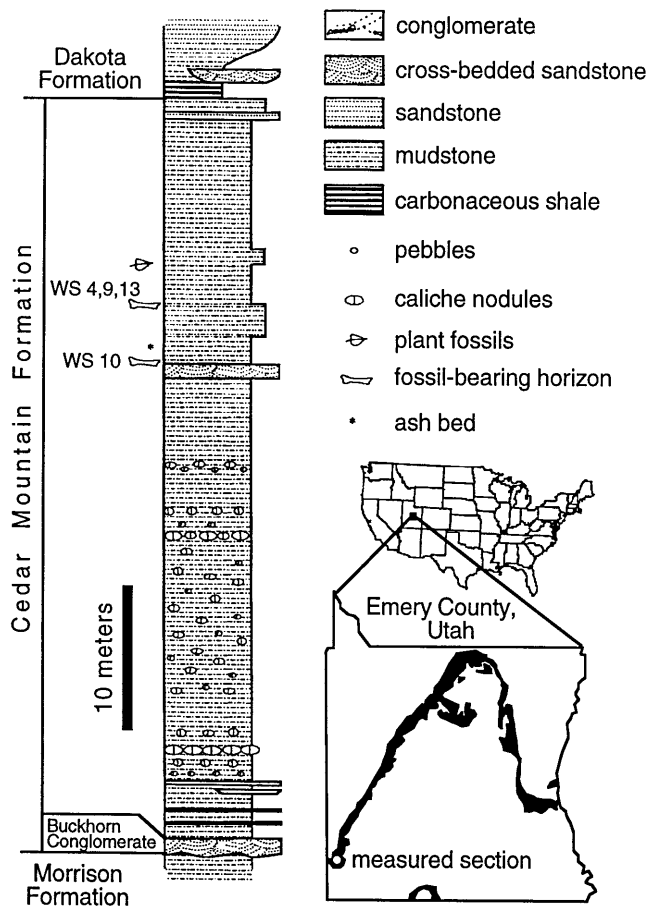†To whom reprint requests should be addressed.

FIG. 1.   Stratigraphic section including some of the paleontological and radiometric sampling sites in the upper Cedar Mountain Formation, Emery County, UT. Four of the principal fossil sites are in the section; an additional 27 sites (not shown) lie in the same part of the section and are interpreted as being of similar age. The three WS10 ash samples (Table 2, Fig. 2) were collected at the level of the asterisk; sample 1465–1+1 was collected from the same level in a measured section 6 km to the NE.

calculation of the unknown in this case is the SEM of the monitor analyses, 0.09%. The other three samples were irradiated within a single ring of 12 wells centered on an irradiation disk; FCT sanidine was distributed within every other well in this ring. All six monitor positions were analyzed, and planar least-square fit was calculated for the measured J values (adjusted $R^2 = 0.754$). Interpolations from this fit were used to determine values of J appropriate to the positions of the unknowns; the root mean square of the residuals of 2×10^{-5} (0.13%) was used as the error of predicted J values.

Analytical results are illustrated as age-probability diagrams (17) and compositional plots (Fig. 2). These plots demonstrate the high quality and uniformity of the sanidine grains measured: all are highly radiogenic, generally fall within a narrow (≈ 0.01–0.02) range of Ca/K ratio, and have similar analytical uncertainties. The age-probability diagrams indicate that all samples are composed of a single age population; summary statistics are provided in Table 2. The weighted mean ages of samples differ from each other by less than their analytical errors, with a maximum difference of 0.11 Ma (0.1%). Interestingly, the ages obtained from the modes of the populations are more tightly clustered than the weighted mean ages, due to slight skewness in several of the samples; modes are more robust to skewed populations than are means, but the differences are slight and within error of the mean. The best age of this ash horizon is taken as the weighted mean age of all four samples, yielding 98.39 $\pm$ 0.07 Ma (0.07%): this places the

Table 1.   Vertebrate fauna of the Cedar Mountain Formation*

Chondrichthyes	Hybodontifomes: Polyacrodontidae, *Polyacrodus parvidens*, *Lissodus* spp. (2) Orectolobifomes: Orectolobidae[†], n. gen. and spp. (2) Rajiformes: *Ischyrhiza*[‡] sp. Myliobatifomes: cf. *Baibisha*[‡] n. sp.
Osteichthyes	Lepisosteiformes[†]: Lepisosteidae[†], sp. indet. Semionotiformes: *Lepidotes* sp., n. gen. and spp. (2) aff. *Semionotus* Pycnodontiformes: Pycnodontidae, spp. (2) indet. Amiiformes: Amiidae, sp. indet. Dipnoi: Ceratodontidae, *Ceratodus* sp.
Lissamphibia	Inc. sedis: Albanerpetontidae, sp. indet. Caudata: Scapherpetontidae[‡], n. gen. and spp. (2) Anura: "Amphicoelous-grade", sp. indet.; "Discoglossoid-grade", 3 sp. indet.
Reptilia	Testudines: Baenidae, sp. indet.; Pleurosternidae, *Naomichelys*[¶] sp.; Glyptopsidae: *Glyptops*[§] sp. Squamata: Teiidae, cf. *Peneteius*[‡] sp., spp. (2) indet.; ?Paramacellodidae[§], n. gen. and sp.; Anguidae, spp. (2) indet.; Helodermatidae[‡], n. gen. and sp. Serpentes[†]: Aniliidae[†], *Coniophis*[†], sp. Crocodilia: Bernissartidae[§], *Bernissartia*[§] sp.; Goniopholidae, cf. *Dakotasuchus*[‡] sp., *Polydectes*[‡] sp.; Atoposauridae[§], sp. indet.; Teleosauridae[§], *Machimosaurus*[§] sp., sp. indet.; Pholidosauridae, sp. indet.
Dinosauria	Theropoda: Dromaeosaurinae[‡], sp. indet.; Velociraptorinae, sp. indet.; Troodontidae[‡], sp. indet., cf. *Paronychodon*[‡] sp.; Family indet., cf. *Richardoestesia*[‡] sp.; Tyrannosauridae[†], cf. *Alectrosaurus*[‡] sp. Sauropoda[‖]: Brachiosauridae[§], cf. *Astrodon*[§] sp. Ornithopoda: Hadrosauridae[‡], n. gen. and sp.; Hypsilophodontidae, cf. *Zephyrosaurus* sp.[§], spp. (2) indet. Ankylosauria: Nodosauridae, cf. *Pawpawsaurus*[‡] n. sp. Pachycephalosauria[†]: sp. indet. Ceratopsia: Neoceratopsia, sp. indet.
Avialae	Hesperornithiformes[†], sp. indet. Order indet: sp. indet.
Mammalia	Triconodonta: Triconodontidae, spp. (3) indet. Docodonta: Docodontidae[§], sp. indet. Multituberculata: Family indet., *Paracimexomys robisoni*[‡], *P. bestia*[‡], *P.* n. sp.[‡], gen. and sp. indet. Symmetrodonta: Spalacotheriidae, *Symmetrodontoides* spp. (2)[‡], *Spalacotheridium*[‡] sp. Tribotheria: Picopsidae[‡], spp. (2) indet; Pappotheriidae[§], n. gen. and spp. (2).; Family indet., n. gen and sp. Marsupialia[‡]: Family indet., gen. and spp. (2) indet., ?*Kokopellia juddi*

*Identifications based on 4,882 catalogued specimens in the Oklahoma Museum of Natural History.
[†]First or only occurrence in North America.
[‡]First occurrence.
[§]Last occurrence.
[¶]Listed by ref. 14 for the Aptian/Albian Cloverly and Trinity faunas; now known (R.L.C., unpublished data) from as late as the Campanian in UT.
[‖]Last occurrence in North America, before later reintroduction.

Table 2. Summary analytical and statistical data for sanidine samples from the uppermost Cedar Mountain Formation

Sample	$J \times 10^2$ $\pm$ 1 SD	Mode age, Ma	Weighted mean age, Ma	$\pm$Mean age, excl. $\pm J$	$\pm$Mean age, incl. $\pm J$
WS10A	1.675 ± 0.002	98.37	98.33	0.06	0.13
WS10B	1.517 ± 0.002	98.43	98.43	0.04	0.13
WS10C	1.522 ± 0.002	98.38	98.44	0.04	0.13
1365-1 + 1	1.521 ± 0.002	98.38	98.37	0.07	0.14

fauna of the uppermost Cedar Mountain Formation at the Albian-Cenomanian (Early-Late Cretaceous) boundary, which is estimated to be 98.5 ± 0.5 Ma (18).

Faunal Comparisons and Dynamics

The Cedar Mountain assemblage lies within an otherwise unrepresented interval in the terrestrial fossil record of North America. Unsurprisingly, only 26 genera of the 72 taxa reported (Table 1) are previously recorded. The fauna also includes 33 (46%) stratigraphic range extensions for North American taxa and 28 (39%) on a global scale. Most notable among last North American occurrences is that of Sauropoda, the large, perhaps high-browsing, herbivores that dominated faunas of the Late Jurassic (6) and reappeared briefly in the latest Cretaceous through immigration (19).

The vertebrate fauna of the uppermost Cedar Mountain Formation greatly resembles later Cretaceous assemblages, sharing 80% of taxa (at lowest identifiable level); by contrast, only 60% of Cedar Mountain taxa appear in earlier faunas. In this context, first appearances of groups that dominated North American faunas in the later Cretaceous are especially noteworthy. Hadrosaurs make their first global appearance in the

Cedar Mountain Formation; neoceratopsian dinosaurs, whose presence in an earlier fauna has been suggested (20), are also present, as are Tyrannosauridae, a first North American record. Several other dinosaur taxa (e.g., other theropods, Pachycephalosauria) make their first global or North American appearance in the fauna, as do a number of other lower vertebrate (e.g., snakes, helodermatid lizards, and hesperornithiform birds) and mammal groups, most notably advanced multituberculates and marsupials. The assemblage thus has a strong Late Cretaceous character.

Antecedents for a number of taxa appearing for the first time in the Cedar Mountain Formation are unknown from earlier North American faunas, such as that of the Aptian-Albian Cloverly Formation (14). Indeed, either the stratigraphic record, existing phylogenetic hypotheses, or both are suggestive of Old World, probably Asian, origins, for some of the most striking elements of the fauna: proximate sister taxa for ceratopsian dinosaurs are well documented from the Cretaceous of Asia (21); troodontid theropods first appear in the Aptian-Albian of Mongolia (22); a possible sister taxon of Tyrannosauridae has been described from the Early Cretaceous of China (23) and the oldest tyrannosaurid is from the Early Cretaceous of Thailand (24); primitive hadrosaurids and
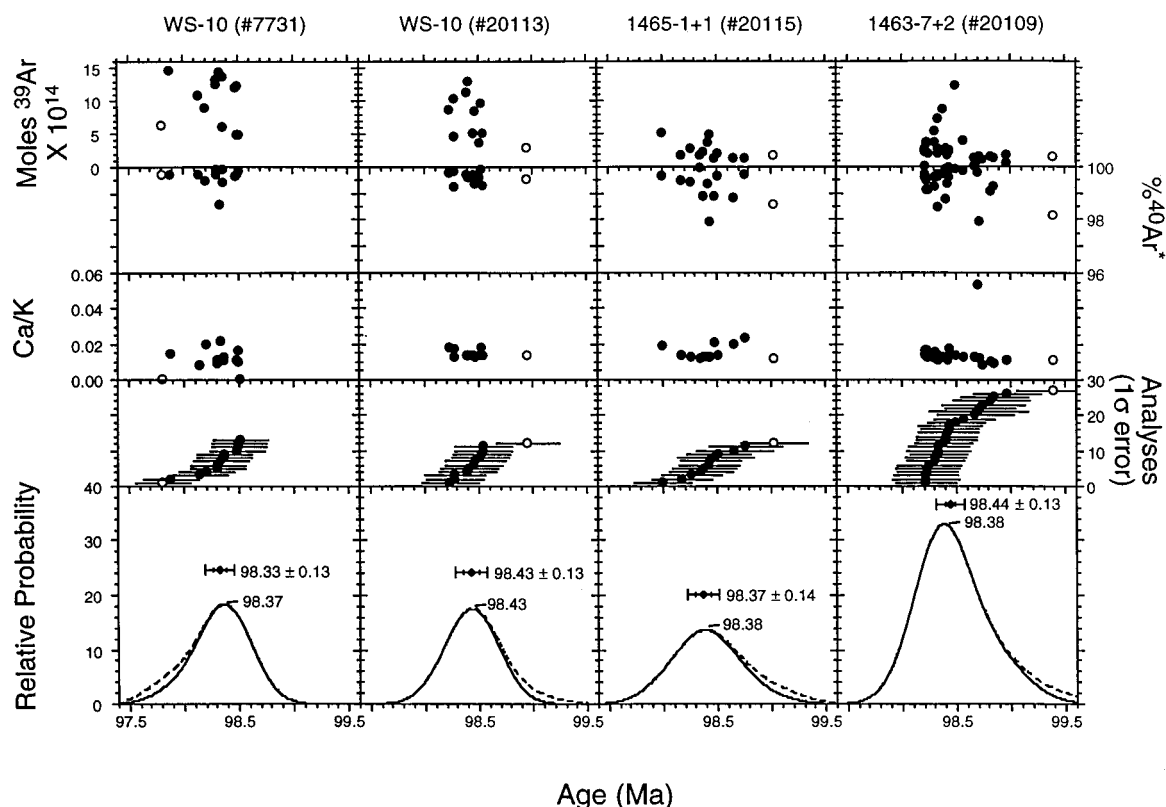

FIG. 2. Age-probability diagrams and auxiliary plots of $^{40}Ar/^{39}Ar$ analytical data. (*Top to Bottom*) mols ^{39}Ar, percent radiogenic ^{40}Ar of total argon ($^{40}Ar^*$), Ca/K ratio, and a display of individual ages. The age probabilities are calculated assuming a unit gaussian error for each analysis, followed by summation across all samples of probabilities within narrow age intervals. The dashed line in the age-probability plots represents the case where all analyses are included, whereas the solid line results from elimination of analyses falling more than two SDs beyond the mean. The omitted analyses (one from each of the four samples) are identified by ○ in the auxiliary plots above the probability diagrams. The names of samples are given at the top, with laboratory identification numbers in parentheses.

proximate sister taxa for Hadrosauridae are recorded from the Cretaceous of Kazakhstan, Europe, and Africa (21, 25). Of other notable first North American appearances, the earliest pachycephalosaur is from the Early Certaceous of England (26) and the earliest record of Serpentes is from the Early Cretaceous of Spain, whereas primitive anilioids similar to *Coniophis* from Utah are known from the Cenomanian of Africa (27).

Geologic evidence is consistent with the possibility of a transient, mid-Cretaceous highland connecting North America and Asia. The composite terrain of Wrangellia is believed to have collided with southern Alaska by the mid-Cretaceous (28), accompanied by intense deformation; penecontemporaneous magmatism occurred in a wide belt between the southern Brooks and Alaska ranges, locally extending into the southern margin of Wrangellia and westward into Siberia (29–30). During the same period, the Arctic composite terrain rotated into line with the Chukotsk Peninsula of Siberia, with stratigraphic and structural data indicating that rifting occurred mainly during the Albian to Cenomanian (31). Despite these combined tectonic events, Alaska may have been periodically isolated by inland seas from Asia, the remainder of North America, or both during parts of the Early and Late Cretaceous (32). Continuity of marine faunas on either side of Alaska was apparently disrupted by the end of the Albian, when North Pacific assemblages lose affinities with those to the north and east (33), suggesting that an intercontinental land bridge may have formed in the mid-Cretaceous. An Asian origin for North America's Late Cretaceous dinosaur fauna previously has been hypothesized, based on biogeographic considerations (34): the age and composition of the assemblage from the Cedar Mountain Formation, together with evidence from tectonics and marine invertebrates, place a temporal constraint on the proposed mid-Cretaceous immigration event and provide details on its nature.

The upper Cedar Mountain Formation is also of interest in that it dates from a time when flowering plants were radiating widely (35); some of the earliest angiosperm wood has been recovered from the Cedar Mountain Formation (5), and palynomorphs from the unit (12) include a diverse array of angiosperm taxa. Abundance of angiosperms in the unit is consistent with the depositional environment represented (floodplain) and with the hypothesis that early angiosperms were r-selected, rapid colonizers of disturbed habitat, and had achieved an important role in riparian communities by the mid-Cretaceous of mid-North America (36). Compositional changes in the flora of the Cretaceous, involving differences in plant stature and life history-reproductive strategies, have, in turn, been hypothesized to have had a reciprocal effect on vertebrate herbivores (4–7), including changes among large-bodied, foliage-eating animals (6). and later in radiations of small-bodied taxa using seeds and fruiting bodies (5).

The megaherbivore fauna (Fig. 3) of the uppermost Cedar Mountain Formation is comprised almost exclusively of ornithischian dinosaurs (e.g., ornithopods, nodosaurs, and ceratopsians), in marked contrast to earlier faunas, which are dominated by presumed high-level browsers, sauropods (6). This well established shift in terrestrial megaherbivores of the Mesozoic has been linked to reciprocal changes in the terrestrial flora, which came to be dominated, in certain habitats at least, by initially low-statured, rapid colonizing, angiosperms during the middle Cretaceous (36). Data from the upper Cedar Mountain Formation thus indicates that, on a local level at least, this process was well underway; the only sauropod recorded in the fauna is a small, extremely rare taxon. The megaherbivore fauna of the upper Cedar Mountain Formation is dominated by a hadrosaurid, characterized by a much more sophisticated masticatory apparatus (7) than that seen in the ornithopods of the Cloverly Formation (14) or older assemblages; Neoceratopsia, also characterized by advanced chewing mechanisms (7, 43), also are represented in the fauna. Domination of these groups in Late Cretaceous assemblages of North America suggests a greater degree of specificity in plant-herbivore interactions (4), but the implications of this are uncertain (44), and the exact diets of herbivorous dinosaurs remain controversial (45). Although very large ($>10^6$ g) ornithischian herbivores are diverse in North American faunas later in the Cretaceous, this size category is underrepresented in the upper Cedar Mountain Formation (Fig. 3), suggesting that sauropods—abundant and diverse in earlier faunas—may have gone temporarily unreplaced by other enormous herbivores, a situation somewhat analogous to that of ornithischians and mammals between the Late Cretaceous and Early Tertiary (5). Although results based on single faunas must be interpreted cautiously, we point out that the megaherbivore fauna of the Cedar Mountain Formation, like those of suspected Aptian-Albian age in North America (14), appears depauperate in comparison to earlier and later assemblages, suggesting that a profound reorganization of North America's terrestrial ecosystem occurred during the middle Cretaceous.
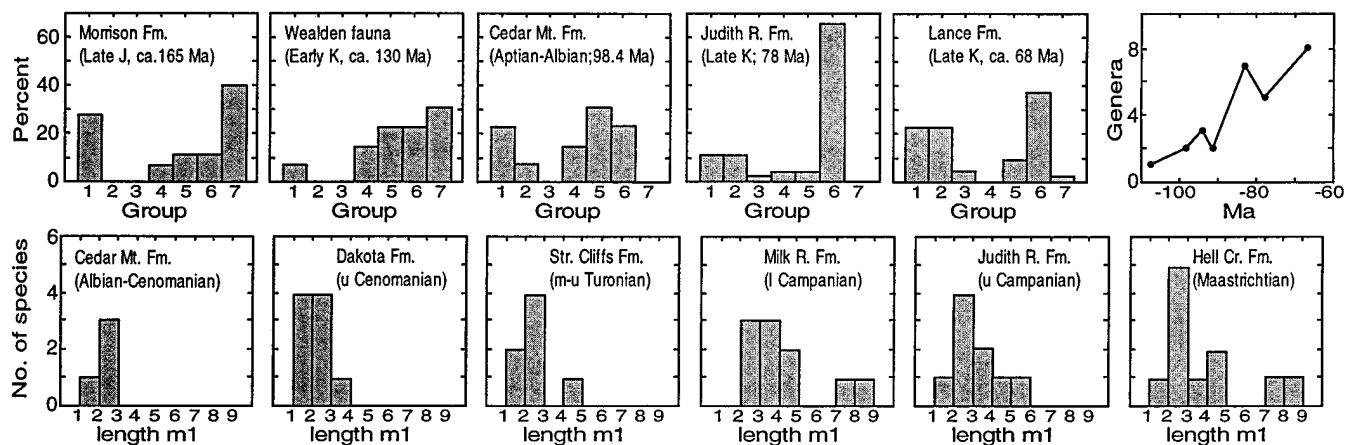

FIG. 3. Changes among Late Mesozoic vertebrate herbivores and omnivores. (*Top*, histograms) Body mass distribution of herbivorous vertebrates for Late Jurassic and Cretaceous terrestrial faunas; methodology and data for Morrison, Wealden, Judith River, and Lance faunas from ref. 6. Groups: 1, $<10^2$ g; 2, 10^2-10^3 g; 3, 10^3-10^4g; 4, 10^4-10^5 g; 5, 10^5-10^6 g; 6, 10^6-10^7 g; 7, 10^7-10^8 g. (*Top Right*) Generic diversity among multituberculate mammals through the Cretaceous: points based on (*Left to Right*) Trinity (37), Cedar Mountain (38), Dakota (39), Straight Cliffs (Smoky Hollow Member) (39), Milk River (40), Judith River (41), and Hell Creek (42) faunas; absolute ages from ref. 16. (*Bottom*) Multituberculate size distribution, based on length of m1, from the same faunas except Trinity (data unavailable). Length of m1 based on sample mean, where available, and estimated by proportional relationships in a closely related species, where not directly represented.

Because of constraints imposed by higher metabolic level, the diversification of small-bodied mammals generally is thought to be linked to the development of larger seeds and fruiting bodies among angiosperms; mammals, in turn, serve as biotic seed-dispersing mechanisms (5). These changes occurred, in part, with the diversification of angiosperms into larger statured, canopy-producing roles during the Late Cretaceous and Early Tertiary (46). In accordance with this hypothesis, multituberculate mammals, which are generally interpreted to be omnivorous, primary-users of plant parts (47), are neither morphologically nor taxonomically diverse in the Cedar Mountain Formation (Fig. 3). However, both taxonomic and size diversity increased markedly by the early Campanian in North America, somewhat earlier than previously suggested (5). Although average angiosperm diaspore size did not not increase appreciably until the Paleocene (46), it is notable that some major fruit types, including drupes and nuts, make their first appearance in the Campanian (48), suggesting the possibility that this observed pattern of taxonomic and morphologic diversification among multituberculates may reflect a response to the availability of such new food resources.

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