

had the cumulative effect of destroying most older, subduction-related structures. Inferences of subduction polarity in other ancient orogens drawn from either reflection geometry or surface structures therefore need to be critically reviewed. A fundamental characteristic is the predominance of structures extending throughout the crust (for example, detachment 'DT', Fig. 3b; Archaean-cored culmination, Fig. 3c), suggesting that collisional and/or intracontinental deformation was principally 'thick-skinned'<sup>1,20,28</sup>. Clearly, interpretations of crustal structure and tectonic history in collisional orogens based solely on surface geology can be flawed. Furthermore, crustal growth rate<sup>11</sup> based on the surface area of juvenile crust preserved in orogens such as THO need to be reconsidered<sup>12</sup>. □

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- Green, A. G. *et al.* *Geology* **16**, 788–792 (1988).
- Meissner, R. *et al.* (eds) *Am. geophys. Un. Geodynam. Series* **22**, 1–450 (1991).
- Frei, W. *et al.* *Nature* **340**, 544–548 (1989).
- Klemperer, S. *et al.* *Nature* **348**, 34–38 (1990).
- Scott, D. J., Helmstaedt, H. & Bickle, M. J. *Geology* **20**, 173–176 (1992).
- McCarthy, J. & Thompson, G. A. *Geol. Soc. Am. Bull.* **100**, 1361–1374 (1988).
- Keen, C., Peddy, C., de Voogd, B. & Matthews, D. *Geology* **17**, 173–176 (1989).
- Nelson, K. D. *Geophys. J. int.* **105**, 25–35 (1991).
- Hoffman, P. F. in *The Geology of North America—An Overview* (eds Bally, A. W. & Palmer, A. R.) 447–512 (Geol. Soc. Am., Boulder, 1989).
- Lewry, J. F. & Collerson, K. D. in *The Early Proterozoic Trans-Hudson Orogen of North America* (eds Lewry, J. F. & Stauffer, M. R.) 1–14 (Geol. Assoc. Can. spec. Pap. 37, 1990).

- Patchett, P. J. & Arndt, N. T. *Earth planet. Sci. Lett.* **78**, 329–338 (1986).
- Bickford, M. E., Collerson, K. D., Lewry, J. F., Van Schmus, W. R. & Chiarenzelli, J. R. *Geology* **18**, 14–18 (1990).
- Hoffman, P. F. *Geology* **17**, 135–138 (1989).
- Green, A. G., Hajnal, Z. & Weber, W. *Tectonophysics* **116**, 281–322 (1985).
- Clowes, R. M. *et al.* *Can. J. Earth Sci.* **29**, 1813–1864 (1992).
- Lewry, J. F. *Nature* **294**, 69–72 (1981).
- Bleeker, W. in *The Early Proterozoic Trans-Hudson Orogen of North America* (eds Lewry, J. F. & Stauffer, M. R.) 57–73 (Geol. Assoc. Can. spec. Pap. 37, 1990).
- Lewry, J. F., Thomas, D. J., Macdonald, R. & Chiarenzelli, J. in *The Early Proterozoic Trans-Hudson Orogen of North America* (eds Lewry, J. F. & Stauffer, M. R.) 75–94 (Geol. Assoc. Can. spec. Pap. 37, 1990).
- Meyers, M. T., Bickford, M. E. & Lewry, J. F. *Geol. Soc. Am. Bull.* **104**, 1073–1085 (1992).
- St-Onge, M. R., Lucas, S. B. & Parrish, R. *Can. J. Earth Sci.* **29**, 746–764 (1992).
- Gordon, T. M., Hunt, P. A., Bailes, A. H. & Syme, E. C. in *The Early Proterozoic Trans-Hudson Orogen of North America* (eds Lewry, J. F. & Stauffer, M. R.) 177–199 (Geol. Assoc. Can. spec. Pap. 37, 1990).
- Machado, N. in *The Early Proterozoic Trans-Hudson Orogen of North America* (eds Lewry, J. F. & Stauffer, M. R.) 433–441 (Geol. Assoc. Can. spec. Pap. 37, 1990).
- Nelson, K. D. *et al.* *Geology* (in the press).
- Fuente, F. & Robin, P.-Y. *Can. J. Earth Sci.* **26**, 1976–1989 (1989).
- Goodwin, E. B. & Thompson, G. A. *Geol. Soc. Am. Bull.* **100**, 1616–1626 (1988).
- Cook, F. A. *et al.* *Tectonics* **11**, 12–36 (1992).
- Collerson, K. D., Lewry, J. F., Bickford, M. E. & Van Schmus, W. R. in *Modern Exploration Techniques*, 150–165 (Saskatchewan Geol. Soc., Regina, 1991).
- Goleby, B. R., Shaw, R. D., Wright, C., Kennett, B. L. N. & Lambeck, K. *Nature* **337**, 325–330 (1989).
- Syme, E. C. in *Report of Field Activities*, 20–34 (Manitoba Energy and Mines, 1988).
- Leclair, A., Scott, R. & Lucas, S. B. in *Geol. Surv. Can. Pap.* 93–1C, 249–258 (1993).

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## Implications of an exceptional fossil flora for Late Cretaceous vegetation

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**THE rapid radiation of angiosperms during the Late Cretaceous has been thought to reflect their rise to vegetational dominance<sup>1–3</sup>. The number of species in a clade and its vegetational importance are not necessarily related, however. Quantitative studies of the recently discovered Big Cedar Ridge flora, found preserved *in situ* in a mid-Maastrichtian volcanic ash in central Wyoming, USA, reveal that dicotyledonous angiosperms accounted for 61% of the species but constituted just 12% of vegetational cover. Dicots, many of which appear to have been herbaceous, were abundant only in areas disturbed just before burial. By contrast, free-sporing plants were 19% of the species but 49% of cover. The only abundant and ubiquitous angiosperm was a single species of palm (about 25% of cover). A comparably low abundance of dicots was found in two other nearly contemporaneous floras buried by volcanic ash, whereas coeval floras from fluvial environments are dominated by dicots<sup>4</sup>. This shows that, even as late as the mid-Maastrichtian, in northern mid-latitudes there were areas away from streams that were not yet dominated by dicots. Despite vigorous taxonomic diversification during the previous 30 Myr<sup>3</sup>, dicots played a subordinate role in these areas of fern-dominated vegetation.**

The Big Cedar Ridge (BCR) fossil flora consists of three-dimensional organic films preserved in the basal 10–20 cm of a 4–5-m-thick bentonitic tuff. When discovered, the tuff had been mapped as part of the Paleocene Fort Union Formation<sup>5</sup>, but

<sup>40</sup>Ar/<sup>39</sup>Ar analysis of single crystals of euhedral biotite from the basal part of the BCR tuff resulted in a weighted mean age of 71.77 ± 0.16 Myr (Table 1). Subsequently it has been shown that the BCR tuff lies within 8 m of a magnetic polarity reversal correlated biostratigraphically with the top of Chron C32N, which also implies an age of about 71.7 Myr<sup>6,7</sup> (J. F. Hicks, personal communication). Stratigraphically, the BCR tuff belongs to the Meeteetse Formation, an upper Cretaceous deltaic and coastal plain unit deposited on the western shore of the North American epicontinental seaway during the Campanian and Maastrichtian<sup>4</sup> (Fig. 1a). Meeteetse palaeoclimate was subtropical and wet<sup>4,8</sup>.

The BCR tuff overlies a highly variable, generally organic-rich palaeosol formed on muddy to sandy fluvial sediments. These units are exposed in three long outcrops over a total distance of 4 km (Fig. 1b). There is strong evidence for *in situ* preservation of the flora: a number of palmetto and tree fern trunks rooted in the soil project 10–20 cm into the tuff; leaves frequently are found attached to axes and compound fronds are generally articulated; and the composition of the flora changes radically across distances of a few metres.

Five features of the BCR flora show that it was derived from open fern and palmetto-dominated vegetation with minor dicot herbs and scattered conifers, rather than the dicot-dominated, canopied forest that would be expected to occur in a similar climate today (Fig. 1c–e). First, within-site species richness is very high (Table 2), especially considering the assemblage represents an instant in time and the census sites are small. The upper levels of richness recorded at BCR (30–34 spp. per census site) are rare even in the autochthonous litter of diverse tropical forests, because the latter show strong dominance of leaves from a few local canopy species<sup>9,10</sup>. Second, there is a very high abundance and diversity of pteridophytes (mean of 6.5 species per census; 28 species known from the BCR tuff), which is consistent with a diverse and abundant herb layer. Preliminary examination of the palynoflora shows it too is dominated by ferns. Third, many of the dicot species have leaf features that suggest they were herbs or scramblers (for example, funnel-form bases, deeply cordate bases, or small leaves attached to small upright stems). Fourth, provisional determinations of the dicots

TABLE 1  $^{40}\text{Ar}/^{39}\text{Ar}$  laser total fusion analyses of selected biotite grains from the BCR bentonite of the Meeteetse Formation

Sample	$^{40}\text{Ar}/^{39}\text{Ar}$	$^{37}\text{Ar}/^{39}\text{Ar}$	$^{36}\text{Ar}/^{39}\text{Ar}$	$^{40}\text{Ar}^*/^{39}\text{Ar}$	% $^{40}\text{Ar}^*$	Age (Myr)	±s.d.
3601-01	2.2460	0.0300	0.0005	2.1074	93.8	71.765	0.293
3601-02	2.3660	0.0169	0.0009	2.1099	89.2	71.848	0.518
3601-03	2.2691	0.0333	0.0005	2.1073	92.9	71.760	0.767
3601-04	2.4449	0.0042	0.0011	2.1105	86.3	71.868	0.762
3601-05	2.4233	0.0016	0.0011	2.1058	87.0	71.827	0.718
3601-06	2.2121	0.1071	0.0004	2.0978	95.2	71.711	0.464
3601B-01	2.2564	0.0564	0.0005	2.1047	93.3	71.673	1.015
3601B-02	2.2543	0.0247	0.0005	2.1073	93.5	71.761	0.765
3601B-03	2.3018	0.0458	0.0007	2.1032	91.4	71.625	0.441
3601B-05	2.6124	0.0304	0.0017	2.1051	80.6	71.688	0.891
3601B-06	2.4516	0.0073	0.0012	2.1078	86.0	71.779	0.803
3601B-08	2.3253	0.0272	0.0007	2.1110	90.8	71.886	0.429
				Weighted mean		71.768	0.155 (s.e.)
Contaminant grains?							
3601B-04	7.4410	0.0058	0.0007	7.2465	97.4	235.658	0.774
3601B-07	2.6111	0.0161	0.0015	2.1699	83.1	73.849	0.552

Analysis procedures followed ref. 15.  $\text{Ca}^{2+}$  and  $\text{K}^+$  corrections were determined from laboratory salts:  $(^{36}\text{Ar}/^{37}\text{Ar})_{\text{Ca}} = 2.557 \times 10^{-4} \pm 4.6 \times 10^{-6}$ ,  $(^{39}\text{Ar}/^{37}\text{Ar})_{\text{Ca}} = 6.608 \times 10^{-4} \pm 2.53 \times 10^{-5}$ , and  $(^{40}\text{Ar}/^{39}\text{Ar})_{\text{K}} = 2.4 \times 10^{-3} \pm 7.0 \times 10^{-4}$ . The irradiation coefficient ( $0.019256 \pm 0.000009$  ( $\pm 0.05\%$ )), is based on replicate single-crystal analyses of the monitor mineral Fish Canyon Sanidine, with a reference age of 27.84 Myr as recommended in ref. 16, but slightly modified as a result of in-house intercalibration at the Geochronology Center with MMhb-I with a published age of  $520.4 \pm 1.7$  Myr<sup>17</sup>. Mass discrimination during this study, determined by replicate air aliquots delivered from an on-line pipette system, was  $1.007 \pm 0.002$ . Decay constants are from refs 18 and 19. The uncertainties (s.d.) associated with the individual  $^{40}\text{Ar}/^{39}\text{Ar}$  ages are  $1\sigma$  errors; that for the calculated weighted mean age of the replicate analyses is a standard error (s.e.) following ref. 20.

\* Radiogenic  $^{40}\text{Ar}$ .

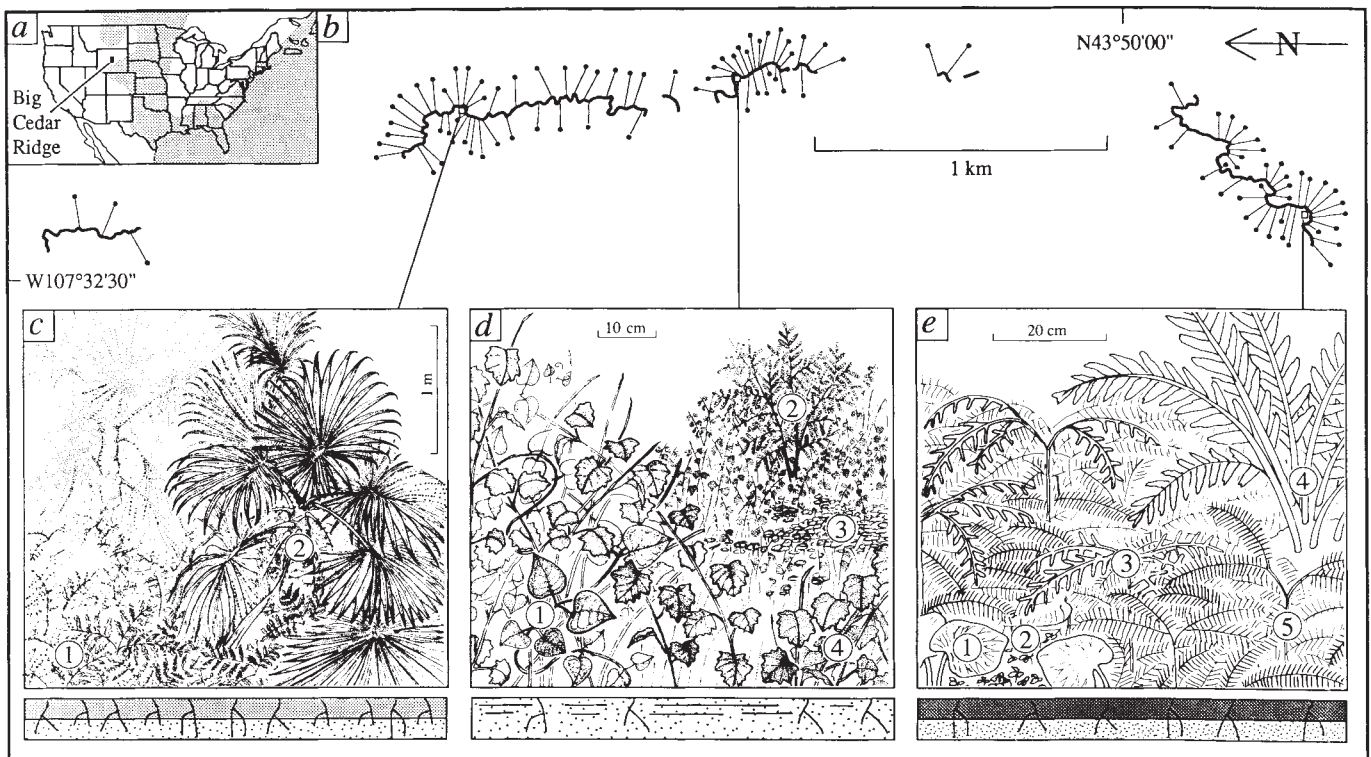


FIG. 1 a, Map of North America shows location of the BCR site with respect to the mid-Maastrichtian (*Baculites grandis* zone) shoreline of the epicontinental seaway; shoreline position from ref. 22. b, Dark line shows outcrop of BCR tuff; small crossing lines show positions of 100 census sites, which were determined largely by accessibility. c–e, Sketches of three types of vegetation found in the BCR tuff, based on outcrop censuses and *in situ* specimens, with soil profiles underneath; scale bars apply to foreground vegetation: c, vegetation on an organic silt substrate dominated by (1) a

fern cf. *Anemia fremontii* and (2) coryphoid palms; d, vegetation of a recently disturbed site on fine sandy substrate dominated by (1) '*Ficus*' *planicostata*, a probable scrambler, (2) an undescribed magnoliid dicot, (3) a peltate-leaved dicot, and (4) cf. '*Acer*' *cretaceum*; e, a peat substrate community with (1) *Hausmannia* (Dipteridaceae), (2) a small dicot similar to *Thalictrum*, (3) an undescribed dipteridaceous or matoniaceous fern, (4) the cycad *Ctenis*, and (5) abundant gleicheniaceus ferns.

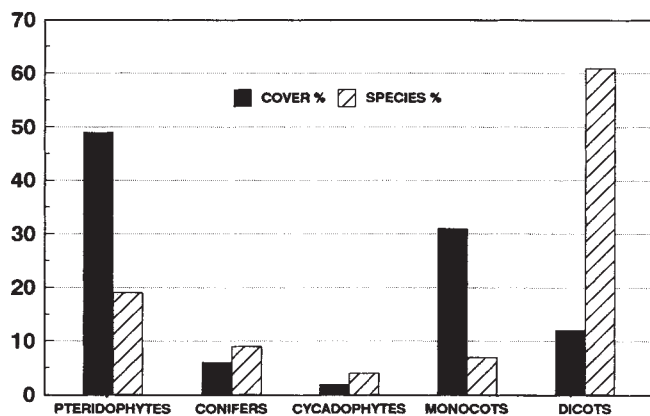


FIG. 2 Comparison of cover and species richness for major groups of plants in the 100 censuses. Pteridophytes (ferns and a few lycopsids) and monocots (mostly palms) are abundant but not particularly diverse. Dicots are extremely diverse but not very abundant. See Table 2 legend for data and details of sampling procedure, and Fig. 1b for spacing of localities.

indicate many have affinities with the ranunculid and palaeoherb groups<sup>11,12</sup>. Fifth, some of the most ubiquitous groups of Late Cretaceous dicot trees (platanoids, cercidiphylloids) are rare in the BCR tuff, suggesting that the ash preserves a type of vegetation not recorded in more typical fluvial depositional environments.

The taxonomic distribution of BCR species is close to the global average for the Maastrichtian<sup>13</sup>: 19% free-sporing lycopsids and ferns, 9% conifers, 4% cycadophytes and 68% angiosperms. But comparison of megafossil richness and abundance data at BCR shows no correlation between the two (Fig. 2). Dicots were 61% of the species recovered even though they were relatively uncommon. The mean census richness of dicots (6.9; s.d. = 3.5) is essentially the same as that of ferns, but the ratio of total richness to mean census richness is much higher for dicots (12.9) than for pteridophytes, conifers, cycads and monocots (4.3). These ratios reflect greater heterogeneity in species composition across the landscape for dicots than for other groups; this difference in distribution is consistent with the hypothesis that insect-pollinated dicots were able to exist in highly dispersed populations<sup>12</sup>.

At only 3 of the 100 sites did dicots exceed 50% of identified plant cover, and at only 18 did they exceed 30%. At all sites where dicots exceeded 20% of cover there was sedimentological evidence for physical disturbance shortly before the deposition of the BCR tuff: either the underlying soil was relatively coarse, or primary sedimentary structures indicating recent deposition are preserved just below the soil/tuff interface (Fig. 1d).

In spite of evidence for local disturbance in a few areas along the outcrop, the soil underlying the BCR tuff generally is rooted and has high levels of dispersed organic matter or a 4–8 cm coal

TABLE 2 Summary statistics on major plant groups at BCR

	Species per census			Total spp.	Line intercept per census (cm)		
	Mean	Max	Min		Mean	Max	Min
Pteridophytes	6.5	12	0	28	375.6	1,166	0
Conifers	3.0	7	0	13	43.6	444	0
Cycadophytes	0.6	3	0	6	12.0	170	0
Monocots	2.3	4	1	10	240.0	1,127	18
Dicots	6.9	15	0	89	94.8	363	0
Totals	19.3	34	8	146	766.0	1,701	184

All figures are derived from 100 roughly equal-sized censuses along the BCR outcrop (Fig. 1b). A modified line intercept method was used to estimate the area of bedding plane covered by each species; cover is commonly used as a measure of importance in living herbaceous vegetation<sup>21</sup>. Census excavations were roughly square, with a mean size of 3.4 m<sup>2</sup> (s.d. = 3.0). Fossiliferous tuff was removed as blocks, and all bedding surfaces displaying at least one identifiable plant fragment were included in the census. A frame strung with parallel threads spaced 2 cm apart and marked off in 2-cm segments was placed over each block. All 2-cm segments were recorded as touching a particular species, an unidentifiable plant fragment, or blank rock. If a single segment touched both identifiable and unidentifiable remains, the whole segment was assigned to the identified species. Segments that touched two species were scored 1/2 for each species. If multiple segments touched a single leaf they were all scored for that species. Each census consisted of four replicate samples of 500 segments (10 m of line). The mean amount of intercept per site was 4,190.6 cm (s.d. = 727.4), of which 766 cm (s.d. = 315.8) were identifiable plant fragments. Our tests of this line intercept method on simulated fossil assemblages showed that the relative area of different 'species' of paper leaves could be estimated to within ±2% (manuscript in preparation).

deposit at its top. These features indicate a substantial period of soil formation, and imply that the fern–palm dominated vegetation preserved in the BCR tuff does not represent early primary succession. There is also no fusain concentrated in the upper part of the soil to suggest a fire shortly before the preservational event, nor are there footprints or bioturbation that indicate dinosaur feeding. Furthermore, censuses of plants preserved in two other Meeteetse tuffs of similar age over 100 km away resemble the BCR flora in having low cover of dicots; they are dominated either by ferns or conifers. Together these sites provide direct evidence for the hypothesis<sup>14</sup> that in spite of high species numbers, dicots played a minor role in the vegetation of northern mid-latitude stable land surfaces as late as the mid-Maastrichtian.

The BCR flora reveals the possible pitfalls of inferring ecological dominance from taxonomic lists, as well as the 'mega-biases' associated with a plant fossil record derived mainly from areas disturbed by frequent sedimentation. Quantitative analyses of assemblages such as BCR that represent instantaneous preservation of an entire local vegetation can help calibrate interpretations based on more abundant fluvial assemblages, and greatly amplify our understanding of the ecological setting of plant evolution. □

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- Niklas, K. J., Tiffney, B. H. & Knoll, A. H. in *Phanerozoic Diversity Patterns: Profiles in Macroevolution* (ed. Valentine, J. W.) 97–128 (Princeton Univ. Press, New Jersey, 1985).
- Knoll, A. H. in *Community Ecology* (eds Diamond, J. & Case, T. J.) 126–141 (Harper & Row, New York, 1986).
- Crane, P. R. in *The Origins of Angiosperms and their Biological Consequences* (eds Friis, E. M., Chaloner, W. G. & Crane, P. R.) 107–144 (Cambridge Univ. Press, UK, 1987).
- Hickey, L. J. *Am. J. Bot.* **78**, 115 (1991).
- Love, J. D. & Christiansen, A. C. *Geological Map of Wyoming* (US Geological Survey, 1985).
- Harland, W. B. et al. *A Geologic Time Scale 1989* (Cambridge Univ. Press, UK, 1990).
- Cande, S. C. & Kent, D. V. *J. geophys. Res.* **97**, 13917–13951 (1992).
- Horrell, M. A. *Palaeogeogr. Palaeoclimat., Palaeoecol.* **86**, 87–138 (1991).
- Burnham, R. J., Wing, S. L. & Parker, G. G. *Paleobiology* **18**, 34–53 (1992).
- Greenwood, D. R. *Rev. Paleobot. Palyn.* **71**, 149–190 (1992).
- Taylor, D. W. & Hickey, L. J. *Pl. Syst. Evol.* **180**, 137–156 (1992).
- Doyle, J. A. & Hickey, L. J. in *Origin and Early Evolution of Angiosperms* (ed. Beck, C. B.) 139–206 (Columbia Univ. Press, New York, 1976).
- Lidgard, S. & Crane, P. R. *Paleobiology* **16**, 77–93 (1990).

- Wing, S. L. & Tiffney, B. H. *Rev. Paleobot. Palyn.* **50**, 179–210 (1987).
- Swisher, C. C. et al. *Science* **257**, 954–958 (1992).
- Cebula, G. T. et al. *TERRA Cognita* **6**, 139–140 (1986).
- Samson, S. D. & Alexander, E. C. *Chem. Geol. Isot. Geosci. Sect.* **66**, 27–34 (1987).
- Steiger, R. H. & Jager, E. *Earth planet. Sci. Lett.* **36**, 359–362 (1977).
- Dalrymple, G. B. *Geology* **7**, 558–560 (1979).
- Taylor, J. R. *An Introduction to Error Analysis* (University Science, Mill Valley, California, 1982).
- Greig-Smith, P. *Quantitative Plant Ecology* (Univ. California Press, Berkeley, 1983).
- Lillegraven, J. A. & Ostresh, L. M. Jr in *Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America* (eds Bown, T. M. & Rose, K. D.) 1–30 (Geol. Soc. Am., Special paper **243**, Boulder, 1990).

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