Palaeogeography, Palaeoclimatology, Palaeoecology xxx (2012) xxx–xxx

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Northward range extension of a diminutive-sized mammal (*Ectocion parvus*) and the implication of body size change during the Paleocene–Eocene Thermal Maximum

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ARTICLE INFO

Article history:
Received 12 March 2012
Received in revised form 6 August 2012
Accepted 11 September 2012
Available online xxxx

Keywords:
Paleocene
Eocene
Global warming
Biogeography
Piceance Creek
Carbon isotopes

ABSTRACT

An abrupt global warming event marks the Paleocene–Eocene boundary, known as the Paleocene–Eocene Thermal Maximum (PETM). The event is distinguished in the strata globally by a significant negative excursion of δ^{13}C ratio values. The response of the terrestrial biota to the abrupt climatic change has been well studied in northern Wyoming in the Bighorn Basin, where it has been observed that the mammalian fauna during the global warming event is represented by smaller, but morphologically similar species to those found later in the Eocene. Various hypotheses have been proposed to explain the observation smaller body sizes during the global warming event. In this article, evidence is presented to support the hypothesis that the observed body size decrease during the PETM was influenced by the appearance of smaller southern species who extended their geographic range northward during the abnormal global warming event. Using disperse organic carbon isotopic ratios of bulk sediment, the negative excursion of δ^{13}C was located in the Piceance Creek Basin of western Colorado, 400 km to the south of the Bighorn Basin. Below the stratigraphic level marking the negative carbon excursion in the Piceance Creek Basin are five specimens of the phenacodontid mammal (*Ectocion parvus*), a diminutive species of the genus *Ectocion* restricted to the basal Eocene (Wa-0 Biozone) in northern Wyoming. The five specimens of *E. parvus* are associated with a late Paleocene (Clarkforkian) mammalian fauna in Colorado, implying that the diminutive species extended its geographic range northward during the global warming event. This evidence supports biogeographic models that assume poleward biogeographic shifts during global warming events, and will have modern day implications for the conservation of species as global temperatures rise in the near future.

1. Introduction

Stable isotopic ratios of oxygen in marine sediments indicate an abrupt global warming event at the Paleocene–Eocene boundary (Kennett and Stott, 1991), referred to as the Paleocene–Eocene Thermal Maximum (PETM; Aubry et al., 2003; McInerney and Wing, 2011). Estimates indicate global temperatures rose upward 8° Celsius (Zachos et al., 2006), within a single precession cycle of Earth's orbit (less than 24,000 years; Röhl et al., 2007).

Terrestrial strata crossing the Paleocene–Eocene boundary is well documented in the Bighorn Basin of northern Wyoming, where it is recognized by a significant negative excursion of δ^{13}C ratio values (Koch et al., 1992; Magioncalda et al., 2004), and an abrupt turnover of mammalian species (Gingerich, 2003). In the Bighorn Basin, the interval of the Paleocene–Eocene Thermal Maximum is represented by a unique mammalian fauna referred to as the Wa-0 biozone; the first biozone of the Eocene Wasatchian North American Land Mammal Age (NALMA). Gingerich and Smith (2006) have further divided the Wa-0 biozone, by recognizing a Wa-M biozone which characterizes the lower several meters. The Wa-M is distinguished by the additional presence of the mammal *Meniscotherium priscum* (hence the suffix M) and lack of primates and artiodactyls.

In its entirety, the Wa-0 mammalian fauna is characterized by diminutive and novel species (Gingerich, 2001, 2003; Strait, 2001; Secord et al., 2012). Diminutive species include the early equid *Sifrhippus sandrae* (Froehlich, 2002; Secord et al., 2012) (also referred to either the genus *Eohippus* or *Hyracotherium*), the phenacodontids *Ectocion parvus* (Gingerich and Smith, 2006) and *Copecion davisi* (Gingerich, 2003) as well as the small hyposodontid *Hapomylus zalmouti* (Gingerich and Smith, 2006). Novel species, such as the earliest artiodactyl *Diacodexis*, euprimate *Teilhardina*, and perissodactyl *S. sandrae*, all make their first appearance during this interval. Similar genera co-occur in the earliest Eocene rock units in Asia and Europe. In fact, in the northern hemisphere early Eocene mammalian faunas are much more cosmopolitan and homogenous than faunas known from the late Paleocene (Krause and Maas, 1990; Beard, 2002; Bowen et al., 2002; Hooker and Dashzeveg, 2003; Beard, 2008).

Two proposed hypotheses attempt to explain the diminutive body size of mammals during the Wa-0 biozone in the Bighorn basin. The first hypothesis is that mammal species underwent a phenotypic change. Populations decreased the average body-size in response to

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0031-0182/$ – see front matter © 2012 Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.palaeo.2012.09.008

Please cite this article as: Burger, B.J., Northward range extension of a diminutive-sized mammal (*Ectocion parvus*) and the implication of body size change during the Paleoc..., Palaeogeogr. Palaeoclimatol. Palaeoecol. (2012), http://dx.doi.org/10.1016/j.palaeo.2012.09.008

the environmental conditions that existed during the PETM global warming event. This hypothesis favors an intrinsic response of the population to cope with the new selection pressure of a warmer climate, such as the possible decreased availability of food, shelter and habitat which led to their smaller size. The second hypothesis is that the observed decrease in the average body-size was the result of extrinsic forces, such as the range extension of small species into the Bighorn Basin, displacing larger species. This second hypothesis explains the observation by invoking biogeographical shifts in the geographic range of species during the PETM rather than an *in situ* evolutionary response. Both hypotheses invoke Bergmann's rule, in which smaller species occur in warming climates (or lower latitudes), but the mechanism for the body-size shift in each hypothesis differs. In the first hypothesis, the response is evolutionary driven, while the second hypothesis the response is ecologically driven.

In order to test these two hypotheses, an intense fossil collecting effort was undertaken in the more southerly located Piceance Creek Basin, 400 km to the south of the Bighorn Basin in western Colorado. The purpose of the collecting effort was to build a comparative collection of late Paleocene and early Eocene fossil mammals to gain a better sense of the wider biogeographical occurrences of species across North America.

2. Methods and materials

The Piceance Creek Basin flanks the western margin of the southern Rocky Mountains and encompasses 26,000 km^2 of rugged topography. Following the advent of the Laramide Orogeny during the late Cretaceous and early Paleocene, the basin formed as eroded sediment was shed off the recently uplifted Sawatch and Park Mountain Ranges to the southeast and east. Sediment was deposited throughout the Eocene until the mid-Tertiary ignimbrite flare-up resulted in the uplift of the White River Plateau and magmatism in the San Juan volcanic field, which significantly altered the physiography of the basin.

Paleocene and Eocene fossils were first reported from the basin as early as 1916, but museum led collections were not made until the 1920s by Carnegie Museum, and 1930s and 1940s by the Field Museum in Chicago. One of the largest collections of fossil mammals was made by Allen Kihm while a student at the University of Colorado, with his advisor Peter Robinson (Kihm, 1984). The fossil collection at the University of Colorado has further increased in size by the continued research efforts of Peter Robinson, James Honey and Jaelyn Eberle, as well as collections made since 2004 as part of this ongoing study. One hundred and fifty-five mammal species are now recognized from the Paleocene and Eocene strata in the basin, making the fossil collection one of the most complete records of late Paleocene and early Eocene mammals in North America outside of the Bighorn Basin. The biostratigraphic record of the recovered fossil mammals identifies the location of the Paleocene–Eocene boundary within a roughly 70 meter section of strata that includes the lithological contact between the Atwell Gulch Member of the Fort Union Formation and Molina Member of the Wasatch Formation.

A more precise stratigraphic location of the Paleocene–Eocene boundary was determined using carbon isotope analysis of dispersed organic carbon (DOC) across the identified 70 meter interval of strata likely to contain the Paleocene–Eocene boundary. The carbon isotope excursion that characterizes the PETM has been identified by analysis of DOC at four separate locations in the Bighorn Basin: Polecat Bench (Magioncalda et al., 2004), Sand Creek Divide (Rose et al., 2012), Cabin Fork (Wing et al., 2005), and Castle Gardens (Yans et al., 2006). The major benefit to analyzing DOC is that a greater range of lithologies can be sampled than carbon isotope ratios derived from rare and frequently absent carbonate nodules or fossilized mammalian teeth. A number of investigators (e.g., Benner et al., 1987) criticized DOC analyses because the carbon originates from a variety of plant material sources that can exhibit different values of δ^{13}C (Hedges et al., 1985; Budd et al., 2002). The influence of changing plant communities also can have an effect on the magnitude of the observed δ^{13}C values in the rock record (Wing et al., 2005; Smith et al., 2007). The δ^{13}C values calculated from DOC represent an average δ^{13}C from numerous sources, some of which may be derived from resistant carbon from older sedimentary rocks. Although mixing (and reworking) is possible, all of these sources were directly influenced by the δ^{13}C in the atmosphere, and the CIE has been identified using this method elsewhere in the world (Collinson et al., 2003; Harrington et al., 2005; Domingo et al., 2009). Organic-poor sandstone units tend to have greater variance in δ^{13}C values. This greater variance of δ^{13}C values is likely due to the combined effects of mixing and reworking, and the smaller amounts of organic carbon found in sandstones. In contrast, organic rich rocks, such as coals, contain in-situ organic matter sourced from fallen plant matter that was not transported and exhibit δ^{13}C values with low variance.

Rock samples were collected from each rock unit at approximately one-meter intervals (from each lithologic rock unit) in Sulfur Gulch, along the southern face of South Shale Ridge near the town of DeBeque Colorado. Samples were powdered and subjected to a treatment of 10–33% HCl for several hours to remove diagenetic carbonate. While most samples dried at room temperature, very fine-grained samples required additional heating to remove excess moisture. Roughly 20 milligrams of dried powdered rock was added into each tin capsule. Samples were combusted at 1050 °C in a Eurovector elemental analyzer at the Colorado School of Mines. A continuous flow system on the GV Instruments IsoPrime mass spectrometer then measured the δ^{13}C value on the combusted CO_2 gas, with He as the carrier gas. Calibration was performed using the IAEA-C-6 sucrose stable isotope reference standard, with an external precision of 0.5‰. Additional samples were combusted at Washington State University, with an ECS 4010 Costech elemental analyzer, and analyzed with a Delta PlusXP Termofinnigan mass spectrometer. Calibration was performed using the RM 8542 sucrose stable isotope reference standard. Isotopic compositions were calculated using Craig's (1957) correction for ^{17}O and reported using the δ^{13}C notation normalized by the reference standards to the international PDB standard (V-PDB, Vienna Peedee Belemnite). Both labs gave similar results.

2.1. Results of carbon isotopic analysis

The measured section is 168.3 meters thick, 125.3 m of which is the Fort Union Formation, and 43 m in the Wasatch Formation. Across the sampled portion of the section (70 m), δ^{13}C ratios ranged between −22.46‰ to −26.40‰, with a mean value of −23.54‰ (Fig. 1).

The basal 12.7 m of the Wasatch Formation show significant negative δ^{13}C ratios below −24.53‰, and is interpreted as the negative carbon isotope excursion that is used widely for correlating to the Global Boundary Stratotype Section and Point (GSSP) for the Paleocene–Eocene boundary located in Luxor, Egypt (Fig. 1). The basal contact between the Fort Union and Wasatch Formations is formed by a sharp erosional contact between a tan to yellow medium grained sandstone, and a dark red smectic claystone. Thus the 12.7 m likely does not represent the entire duration of the carbon-isotope excursion as has been inferred for the Bighorn Basin (Magioncalda et al., 2004). However, an estimated comparative sedimentation rate derived from biostratigraphic correlation between the two basins indicates a sedimentation rate in the Piceance Creek Basin roughly one forth that observed in the Bighorn Basin, where the Wa-0 biozone is 36 meters thick (Gingerich, 2003). In the Piceance Creek Basin, no fossils, either mammal or otherwise, has been reported within the 12.7 meter stratigraphic interval.

Lithologically, the 12.7 m at the base of the Wasatch Formation is composed of 2.9 m of dark red smectic claystone (−24.92‰), a 1.9 m-thick light gray white siltstone to very fine sandstone (−24.63‰), a 0.2 m thick green siltstone (−24.70‰), a 2.4 m thick olive green to dark gray flakey claystone (−26.40‰); a 0.8 light brown fine grained

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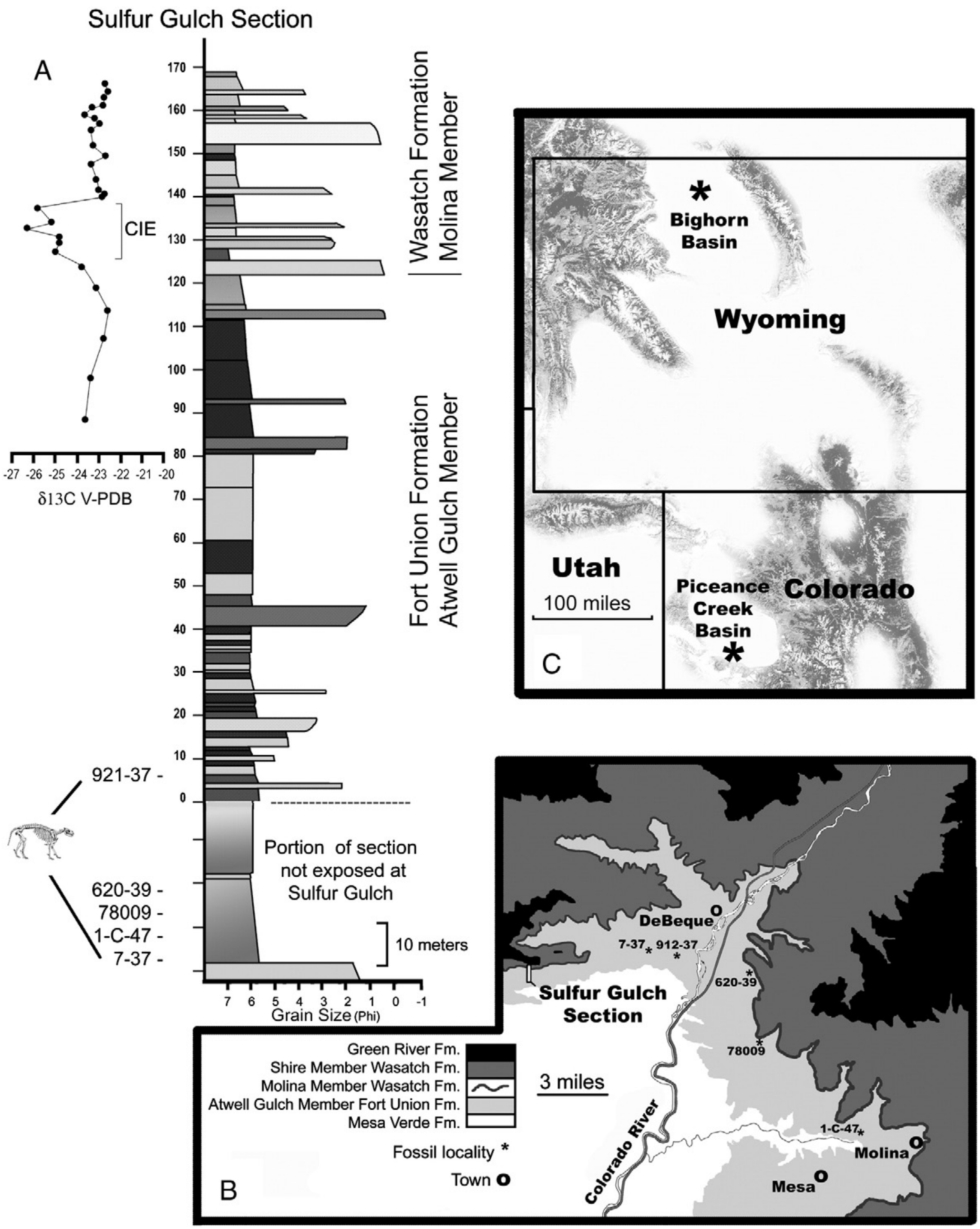

Fig. 1. A, Stratigraphic column of the Sulfur Gulch stratigraphic section, with measured Carbon Isotope Ratios (V-PDB: Vienna Pee Dee Belemnite Standard) and stratigraphic positions of *Ectocion parvus* localities. CIE indicates the negative carbon isotopic excursion that marks the Paleocene–Eocene boundary in the section. B, Map of the southern Piceance Creek Basin showing location of *Ectocion parvus* localities (geology after Hail and Smith, 1997). C, Map showing the location of the Bighorn Basin in Wyoming relative to the Piceance Creek Basin in Colorado.

sandstone (−25.03‰), and 4.5 m thick gray to red mottled, blocky mudstone (−25.79‰), the top contact of the upper unit is locally covered. As a reference stratigraphic section, the Sulfur Gulch section exhibits discernible marker beds (such as the boundary between the dark gray units of the Fort Union Formation and reddish pink units of the Wasatch Formation) that can be used to correlate fossil localities in the general area of the Plateau Valley region (Fig. 1).

2.2. Results of paleontological findings

Biostratigraphic ranges for the 155 mammal species were established based on measured stratigraphic sections, and correlation of rock units across the basin. A few mammals are endemic to the Piceance Creek Basin; these include *Chiromyoides giga*, *Pulverflumen magnificum*, the two known species of the early horse *Xenicohippus*, and the primate

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Pelycodus schidelerorum. Mammals display similar biostratigraphic ranges as documented in the Bighorn Basin, with several important differences.

The small terrestrial condylarth *Meniscotherium*, which is confined to the basal Eocene (Wa-M) in the northern portion of the Bighorn Basin, has been found in later early Eocene strata in southern Wyoming, northern New Mexico, as well as in the Piceance Creek Basin in western Colorado (Kihm, 1984; Burger, 2009).

The second difference, and the subject of this article, is the appearance of the small condylarth species *E. parvus* in the late Paleocene strata of western Colorado. *Ectocion parvus* was previously restricted to the Wa-0 biozone (earliest Eocene) in the Bighorn Basin. Five specimens of *E. parvus* were found to occur below the recognized Paleocene–Eocene boundary.

Among these specimens, *E. parvus* is best represented by the fragmentary skull FMNH P15536, and left and right dentaries from the Field Museum locality 7-37, located 173 m below the identified Paleocene–Eocene boundary (Fig. 2).

The left dentary preserves the two most posterior lower teeth (m2, m3), while the right dentary preserves the four most posterior lower teeth (p4, m1, m2, m3). The molariform right p4 lacks a paraconid and the cristid obliqua runs anteriorly toward the notch between the subequal metaconid and protoconid. There is no entoconid or hypoconulid on the p4. The lower molars feature strong cristid obliqua crossing to the metaconid, small entoconid and hypoconulid that are close together, and a reduced hypoconulid on the m3, (contrasting the moderately-developed m3 hypoconulid in *Ectocion osbornianus*).

The right maxillary bone preserves the five most posterior upper teeth (P3, P4, M1, M2, M3). The P3 contains a parastyle and large paracone closely appressed to a small metacone, and a reduced protocone. The P4 bears a large parastyle, paracone and metacone, reduced protocone encircled by a cingulum, and distinct metaconule and paraconule. The M1 has a large anteriorly-projecting parastyle and a slightly reduced hypocone. The M2 exhibits a large parastyle and distinct mesostyle along the buccal margin of the tooth. The posterior shelf of the cingulum forms the hypocone on the M1 and M2, whereas the M3 lacks a hypocone and possesses a large parastyle that is nearly as large as the paracone, and exhibits an anteriorly-flaring cingulum. Four additional specimens compare with the dental anatomy of the more complete FMNH P15536. These additional specimens include isolated teeth, one M2 and M3 and two M3s.

The most distinguishing feature of *E. parvus* is its relative small size. The natural log of the length multiplied by the width of the m1 preserved in specimen FMNH P15536 equals 3.09, which within the range of specimens of *E. parvus* from the Bighorn Basin (Gingerich, 2003); ranging from 2.90 to 3.55; Fig. 3. With a first lower molar length of 5.36 mm, FMNH P15536 is also near the mean average length of m1s of *E. parvus* reported by Thewissen (1990: Table A-13; mean of 5.47 mm; Fig. 3). Tooth size is also within the range reported by Rose et al. (2012) for specimens of *E. parvus* from the Sand Creek Divide locality in the Bighorn Basin. Wood et al. (2007) found no significant difference in tooth shape between *E. parvus* and the larger *E. osbornianus* in the Bighorn Basin sample, indicating that only its smaller size distinguishes *E. parvus* from *E. osbornianus*. Table 1 shows the tooth dimensions of the referred specimens of *E. parvus* from Colorado. An unpaired *t*-test comparing tooth areas resulted in P values of less than 0.0001, indicating that the sample of *E. parvus* is significantly different from the specimens of the two larger species *E. osbornianus* and *Ectocion mediotuber* from the late Paleocene of Colorado.

Comparison with specimen UM 77202 from the Wa-0 fauna of the Bighorn Basin shows only minor morphological differences (Fig. 2). These include a more pronounced parastyle on the M3, a very slight decrease in separation of the entoconid and hypoconulid, likely due to differences in wear on the m1, and the cingula on the lingual margin of the M2 is slightly more rugose (Fig. 2). These differences are not adequate for separate species designation between the two samples and likely are variable within a more widespread population. Examination of other specimens from Wyoming indicates similar slight variations in morphology. Given the similarities in size and morphology these specimens represent the species *E. parvus*.

Specimens of *E. parvus* are represented from five different localities in the Plateau Valley area of the Piceance Creek Basin (Fig. 1). The localities are well documented (Kihm, 1984; Burger, 2009). Correlation to the Sulfur Gulch section utilized previous stratigraphic sections (Kihm, 1984), and recent measured stratigraphic sections in the area (Burger, 2009). Marker beds include the upper-most coal layer of the Atwell Gulch

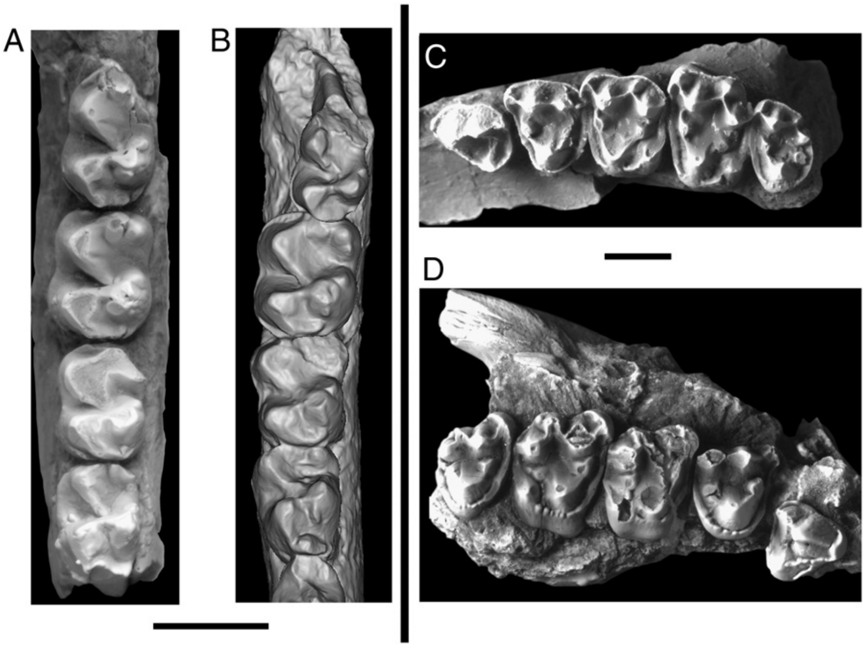

Fig. 2. Specimens of *Ectocion parvus*. A, occlusal view of FMNH P15536 right p4–m3 from the late Paleocene of the Piceance Creek Basin compared to B, occlusal view (reversed) of UW 77207 left p4–m3 from the early Eocene of the Bighorn Basin (from Strait et al., 2010). (Scale is 5 mm.) C, occlusal view of UM 77202 left P3–M3 from the early Eocene of the northern Bighorn Basin, in comparison to D, occlusal view of FMNH P15536 right P3–M3 from the late Paleocene of the Piceance Creek Basin (scale is 5 mm).

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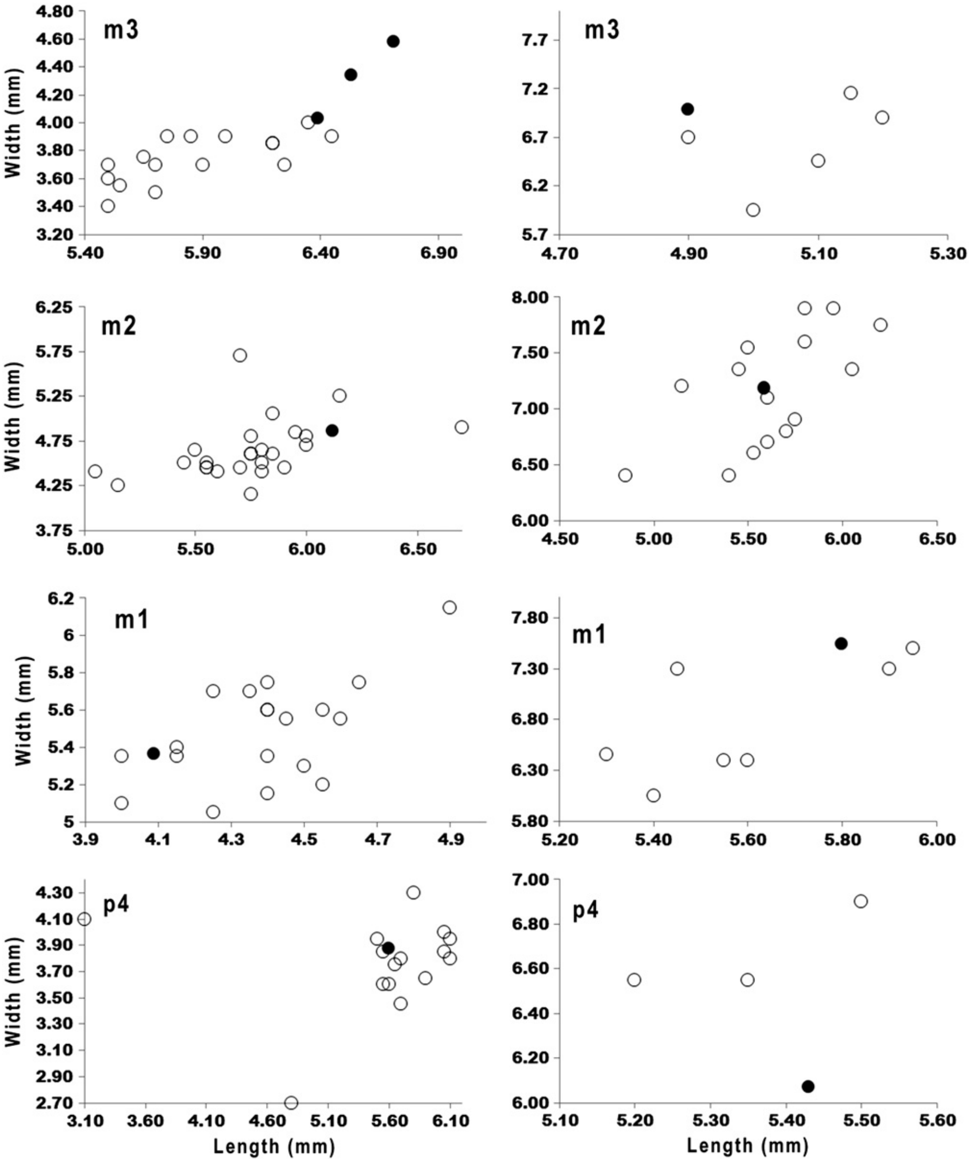

Fig. 3. Measurements of *Ectocion parvus* specimens. White circles indicate early Eocene specimens from the Bighorn Basin, Sand Creek Divide reported in Rose et al., 2012. Black circles indicate late Paleocene specimens from the Piceance Creek Basin.

Member and the lower contact of the Molina Sandstone, both of which are widespread and well exposed in the Plateau Valley area. Both units can be traced in the exposed bedrock along the sides of the hills and ridges in the Plateau Valley area. Locally, beds are near horizontal, and there are no major structural faults or folds in the area. Stratigraphically fossil localities containing *E. parvus* were found to be between 120 and 173 m below the Paleocene–Eocene boundary, as defined at the base of the carbon isotopic excursion in the Sulfur Gulch section (base of the dark red smectic claystone).

Wood et al. (2008) noted the occurrence of down slope contamination of fossil mammal teeth of the larger *E. osbornianus* from the erosion of a younger fossiliferous conglomerate that cut down into the older Wa-0 (*E. parvus*-bearing) stratigraphic interval in the Bighorn Basin. Such down slope contamination is unlikely to have occurred in the Piceance Creek Basin. Given the great distance of the *E. parvus* localities to the nearest early Eocene locality (Fig. 1), fossils would have had to travel long distances. The comparatively complete material of a partial skeleton (FMNH P15536) indicates no pre-discovery exhumation and transportation, which would cause breakage and dissociation of the specimen. Isolated teeth (FMNH 14938a, FMNH P26107, FMNH P26125, and FMNH PM209) may have incurred some transportation, but the associated fauna shows no component of typical Eocene fossils other than these specimens (Table 2).

Each *E. parvus* bearing locality represents a characteristically late Paleocene mammalian fauna (Table 2). In fact, two of the localities (UMC loc. 78009 and FMNH loc. 7-37) contain *Plesiadapis dubius*, an index species of the Clarkforkian (late Paleocene; Burger and Honey, 2008). The stratigraphic separation of *E. parvus* from the larger *E. osbornianus* in the Polecat Bench section was not found in the Piceance Creek Basin, as both species co-occur at UMC loc. 78009 (Table 2).

3. Discussion and conclusion

Revisiting the two hypotheses presented earlier, the presence of *E. parvus* in late Paleocene strata in the southern Piceance Creek Basin gives support to the idea of a northward biogeographic extension of the species' range during the global warming event that marks the Paleocene–Eocene boundary. These new fossils and their stratigraphic

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Table 1
Measurements of specimens.

Specimen		Width (mm)	Length (mm)
FMNH P26107	Right M3	7.06	5.20
FMNH P26125	Right M3	6.78	5.10
FMNH P14938a	Left M3	6.98	4.90
FMNH PM209	Right m3	4.58	6.71
FMNH P15536	Right P3	4.93	5.34
FMNH P15536	Right P4	6.07	5.43
FMNH P15536	Right M1	7.54	5.80
FMNH P15536	Right M2	7.19	5.58
FMNH P15536	Right M3	7.02	5.14
FMNH P15536	Right p4	3.88	5.59
FMNH P15536	Right m1	4.09	5.36
FMNH P15536	Right m2	4.86	6.19
FMNH P15536	Right m3	4.34	6.53
FMNH P15536	Left m2	Unmeasurable	Unmeasurable
FMNH P15536	Left m3	4.03	6.39

position supports the importance of the ecological response to climate change.

While northward habitat range extension may have played a role in the observed diminutive-sized *E. parvus*, the contemporaneous Wa-0 species *S. sandrae* an evolutionary response to climate change may represent the best explanation of the resulting smaller body size. Secord et al., 2012 noted a slight decrease (~30%) in the molar size of *S. sandrae* during the basal few meters of the Wa-0 biozone in the Big Horn Basin in northern Wyoming, indicating a possible evolutionary response occurring within the population. Indeed no specimen of *S. sandrae* has been found in the late Paleocene of Colorado or elsewhere. Thus, the size shift observed in *S. sandrae* may have resulted from evolutionary change in response to selective pressures due to temperature change (Secord et al., 2012). Thus, a combination of both ecological and evolutionary responses likely worked together to produce the diminutive sized mammals that characterize the Wa-0 biozone in the Big Horn Basin.

Studies on modern populations of mammals demonstrate how complex the issue of body size and geographic range can be. The pocket gopher *Thonomys bottae* demonstrates that mammal species are more adaptable and readily hybridize with other species, within the totality of their geographic ranges. Patton and Brylski (1987) found that body-size is a function of both interbreeding and habitat difference within different races of the population. Studying the northward range expansion of the coyote (*Canis latrans*) in North America Thurber and Peterson (1991) documented that the species became larger in its more northern range, citing differences in food supply as the cause, although hybridization has also been cited. Indeed more complex interactions may ultimately explain the results for the change in body size in *Ectocion*. The two hypotheses of ecological expansion of the habitat range and *in situ* evolutionary change are not necessarily mutually exclusive.

This study has important implications for predicting biotic responses to climate change by supporting studies that rely on modeling biogeographic ranges under different climatic scenarios (summarized by Bellard et al., 2012). This study also highlights the importance of considering shifting ecological biogeographic ranges during times of abrupt climatic change. The mammalian turnover observed at the Paleocene–Eocene boundary was dominated by the sudden appearance of many invasive species and marked by extinction of older endemic species. The cumulative effects of biogeographic range extensions and invasive species during the PETM was the driving force behind the observation that across the northern hemisphere earliest Eocene mammalian faunas become cosmopolitan and homogenous in their makeup, and exhibited more diminutive body sizes.

In the search for the origin of modern mammalian groups that suddenly appear at the base of the Eocene (Euprimates, Artiodactyla, and Perissodactyla), more southern basins may provide a location to discover additional examples of northward species range extensions across the late Paleocene and early Eocene.

Acknowledgments

I thank my advisor J. Eberle and committee members H. Covert, M. Kraus, H. Fricke, and M. Pranter. I thank W. Simpson, O. Rieppel, J. Holstein, and W. Turnbull for their hospitality during my visit to the FMNH, and allowing me further study of the specimens of *E. parvus*. I would like to thank R. Secord at the University of Nebraska for sending me casts from northern Wyoming and Suzanne Strait at Marshall University for allowing me to use specimen images hosted on the website paleoview3d.marshall.edu. Special thanks go to J.D. Humphrey at the Colorado School of Mines and B. Harlow at Washington State University for their aid in the stable isotope analysis, and P. Robinson for his encouragement of my study. A. Dutchak, I. Sweeney, T. Culver, J.G. Honey, K. Lloyd, P. Monaco, J. Armstrong, A. Bair, A. Matthias, L. McWhinney, Z. Jolley-Burger, L. Jolley, and R. Burger assisted me in the field. The Field Museum of Natural History visiting researcher fellowship, University of Colorado Museum William H. Burt Fund, Colorado Scientific Society Ogden Tweto Fund, Shell Petroleum, a Geological Society of America research grant and the Jeff Deen memorial scholarship provided funding for this research. Research was

Table 2
Associated mammalian fauna from each locality containing *Ectocion parvus*.

			Localities				
Order	Family	Species	78009	912-37	620-39	1-C-47	7-37
Multituberculata	Eucosmodontidae	*Neoliotomus conventus*					X
	Ptilodontidae	*Prochetodon kihmi*	X				
Taeniodonta	Stylinodontidae	*Ectoganus gliriformis*	X				X
Procreodi	Arctocyonidae	*Lambertocyon ischyrus*	X		X		
	Oxyclaenidae	*Thryptacodon australis*	X				X
Carnivoramorpha	Viverravidae	*Protictis proteus*	X		X		
Condylarthra	Phenacodontidae	*Ectocion osbornianus*	X				
		Ectocion parvus	X	X	X	X	X
		Phenacodus primaevus	X		X	X	X
		Phenacodus vortmani	X		X		
	Apheliscidae	*Haplomylus simpsoni*	X				
Dinocerata	Prodinoceratidae	*Probathyopsis harrisorum*	X			X	
Mesonychia	Mesonychidae	*Dissacus navajovius*			X		
Pantodonta	Barylambdidae	*Barylambda faberi*	X		X		X
	Titanoideidae	*Titanoides primaevus*	X				X
Primates	Plesiadapidae	*Chiromyoides caesor*	X				
		Plesiadapis dubius	X				

Please cite this article as: Burger, B.J., Northward range extension of a diminutive-sized mammal (*Ectocion parvus*) and the implication of body size change during the Paleoc..., Palaeogeogr. Palaeoclimatol. Palaeoecol. (2012), http://dx.doi.org/10.1016/j.palaeo.2012.09.008

conducted under United States Department of Interior, Bureau of Land Management paleontology permit #C-60170 issued to the University of Colorado.

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