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Ancient ecology of 15-million-year-old browsing mammals within C3 plant communities from Panama

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Abstract Middle Miocene mammals are known from ~15 million-year-old sediments exposed along the Panama Canal of Central America, a region that otherwise has an exceedingly poor terrestrial fossil record. These land mammals, which represent a part of the ancient terrestrial herbivore community, include an oreodont *Merycochoerus matthewi*, small camel-like protoceratid artiodactyl *Paratoceras wardi*, two horses *Anchitherium clarencei* and *Archaeohippus* sp., and two rhinos *Menoceras barbouri* and *Floridaceras whitei*. Bulk and serial carbon and oxygen isotope analyses of the tooth enamel carbonate allow reconstruction of the ancient climate and ecology of these fossil mammals. Ancient Panama had an equable climate with seasonal temperature and rainfall fluctuations less than those seen today. The middle Miocene terrestrial community consisted predominantly, or exclusively, of C3 plants, i.e., there is no evidence for C4 grasses. Statistically different mean carbon isotope values for the mammalian herbivores indicate niche partitioning of the C3 plant food resources. The range of individual carbon isotope analyses, i.e., $\delta^{13}\text{C}$ from -15.9 to -10.1% , indicates herbivores feeding on diverse plants from different habitats with extrapolated $\delta^{13}\text{C}$ values of -29.9 to -24.2% , possibly ranging from dense forest to more open country woodland. The ecological niches of individual mammalian herbivore species were differentiated either by diet or body size.

Keywords Carbon isotopes · Diet · Fossils · Miocene · Oxygen isotopes

Introduction

In a global context, the modern-day Neotropics contain high biodiversity, yet relatively little is known about the

paleobiology and environmental history of this region in deep time, i.e. before the late Pleistocene, some 10,000 years ago. A debate currently exists (e.g., Knapp and Mallett 2003) about whether the Neotropics have been a stable region of high diversity (e.g., Colinvaux et al. 2000), or one of significant environmental and biotic change over geological time (i.e., thousands to millions of years), with the standing diversity preserved in isolated “refugia” (e.g., Haffer 1969). The ancient history of the Neotropics potentially could be clarified by paleontological evidence, but with a few exceptions this region has been “terra incognita” because of the paucity of known fossil localities (Ferrusquía-Villafrancha 1978; Rich and Rich 1983; Webb and Perrigo 1994; Kay et al. 1997). Until about 3 million years ago (Ma), the Neotropics were divided by an east-west trending seaway between the Atlantic and Pacific that then closed by the formation of the Isthmus of Panama (Coates and Obando 1996). Prior to 3 Ma the scant record of fossil land mammals indicates that the Neotropics had distinct northern and southern faunal provinces. After 3 Ma the Isthmus of Panama formed a dry land connection for corridor (sensu Simpson 1953a, 1965) dispersal during what is called the “Great American Biotic Interchange” (Stehli and Webb 1985).

In the 1960s and 1970s middle Miocene (15-million-year-old) land mammals were collected from exposures along the Panama Canal. Located some 2,000 km south of the nearest similar-aged North American mammal fauna (Oaxaca, Mexico; Ferrusquía-Villafrancha 1978) and 600 km west of the nearest similar-aged South American mammal fauna (La Venta, Colombia; Kay et al. 1997), the Miocene mammals from Panama are uniquely situated to elucidate the ancient terrestrial ecology and historical biogeography well before the Great American Biotic Interchange.

Stable isotope signatures archived in fossil mammal teeth can be used to reconstruct ancient ecology and local environmental parameters (e.g., Koch 1998; Kohn 1999; MacFadden 2000). This type of research has principally emphasized differentiation between ancient C3- versus C4-based communities (e.g., Cerling et al. 1997; Mac-

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Fadden 2000). Several recent papers have explored isotopic variation and niche partitioning of mammalian herbivores within modern C3 communities (Cerling and Harris 1999; Feranec 2003; Stewart et al. 2003; Cerling et al. 2004). These provide the framework from which ancient C3 terrestrial communities can be interpreted in deep time. Following on this theme, carbon and oxygen isotopes analyzed from Miocene mammal teeth from Panama will be used to understand the ancient terrestrial community and environment in what now is the Neotropics. Within this study, several specific questions will be addressed:

1. Were the plant foods eaten by the extinct mammalian herbivores principally C3-based, or is there evidence of C4 grasses during the Miocene in Central America?
2. Did the different mammalian herbivore species have different diets and therefore partition available plant food resources?
3. Relative to the present-day, was the climate seasonal or equable?
4. Is there isotopic evidence of a forest canopy during the Miocene in Panama?

These questions are addressed by either bulk or serial isotopic analyses presented below.

Previous work, geology, age, and ancient ecology

Pre-Pleistocene fossil mammals were essentially unknown from Panama until the 1960s when Canal Zone geologist R. Stewart made a collection from exposures along the southwestern banks of the canal (Fig. 1). These specimens were sent to the US National Museum (USNM) where they were deposited into the vertebrate paleontology collection and were the basis of the preliminary report on this fauna (Whitmore and Stewart 1965). This collection, subsequently referred to as the Gaillard Cut Local Fauna (L.F.; a geographically restricted fossil assemblage, Tedford 1970), has been listed in several publications (e.g., Ferrusquía-Villafrancha 1978; Rich and Rich 1983;

Tedford et al. 1987), but other than the description of the new extinct rodent *Texomys stewarti* (Slaughter 1981), these fossils have remained undescribed until recently (MacFadden 2004).

The vertebrates from the Gaillard Cut L.F. include miscellaneous fish, turtle, and crocodylian fragments, and the primary fossil assemblage representing four orders of mammals, including Rodentia, Carnivora, Artiodactyla, and Perissodactyla (Table 1). The geomyoid rodent *T. stewarti* has affinities with congeners known from fossil deposits in the Texas Gulf Coastal Plain (Slaughter 1981). The carnivores include a small dog-like canid *Tomarctus brevirostris* and postcranial fragments of a larger taxon, either pertaining to an extinct bear-dog, or true bear (MacFadden 2004). The artiodactyls include the oreodont *Merycochoerus matthewi*, also known from Wyoming (Schultz and Falkenbach 1940), and the small protoceratid *Paratoceras wardi*, previously described from the Texas Gulf Coastal Plain (Patton and Taylor 1973). The perissodactyls include two three-toed horses, *Anchitherium clarencei*, previously known from Florida (MacFadden 2001), and *Archaeohippus* sp. also known from North America and the rhinos *Menoceras barbouri* and *Floridaceras whitei*, both previously reported from Florida (Wood 1964; MacFadden 2004). The most striking paleobiogeographic aspect of this fauna is that despite being much closer to South America, which had a distinctive, endemic mammalian fauna during the Miocene, the Gaillard Cut L.F. is exclusively of North American affinities.

Given the above faunal assemblage, two aspects of the mammals of Gaillard Cut L.F. are relevant to this study: (1) The diversity represented in this assemblage, as it currently is known, seems depauperate relative to the actual mammalian diversity that potentially existed during the Miocene in Panama. The reason for this apparent lack of diversity (i.e., 9 mammalian species) could be sampling bias, where insufficient collecting was done in order to recover a more diverse fauna, including rare taxa. In contrast, comparable middle Miocene local faunas in North America have upwards of 30 mammal species from

Fig. 1 Map showing the general location from which the Gaillard Cut L.F. was collected

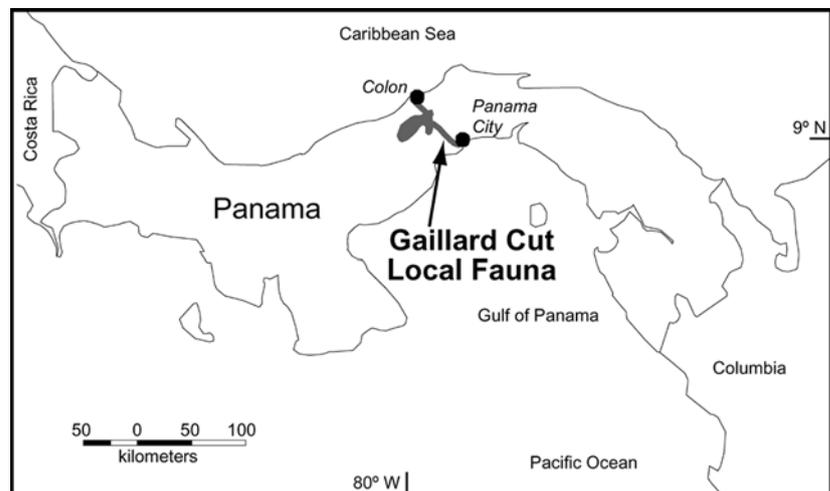


Table 1 Middle Miocene land mammals from the Gaillard Cut Local Fauna (L.F.), Panama, from MacFadden (2004)

Order Rodentia
Superfamily Geomyoidea (pocket gophers, pocket mice, kangaroo rats)
<i>Texomys stewarti</i>
Order Carnivora
Family Canidae (dogs, wolves, foxes)
<i>Tomarctus brevirostris</i>
Family Amphicyonidae (extinct bear-dogs) or Hemicyonidae (bears)
Indeterminant taxon
Order Artiodactyla
Family Oreodontidae (oreodonts; extinct primitive, non-ruminant artiodactyls)
<i>Merycochoerus matthewi</i>
Family Protoceratidae (protoceratids, extinct ruminant artiodactyls)
<i>Paratoceras wardi</i>
Order Perissodactyla
Family Equidae (horses)
<i>Anchitherium clarencei</i>
<i>Archaeohippus</i> sp.
Family Rhinocerotidae (rhinoceroses)
<i>Menoceras barbouri</i>
<i>Floridaceras whitei</i>

apparently well sampled localities, e.g., the late Hemingfordian Thomas Farm, Florida (Webb 1981) and early Barstovian Mascall of Oregon (Downs 1956). On the other hand, the paleobiogeography in Panama during the Miocene, consisting of islands and/or narrow isthmian lands (Coates and Obando 1996), may have resulted in lower diversity relative to continental North America. Elucidation of these possibilities could come from additional field collecting. (2) The mammalian herbivores all represent short-crowned forms, which are traditionally interpreted to represent forest or woodland browsers (e.g., Janis et al. 2000). In comparably aged local faunas from North America, short-crowned, presumed browsers, characteristically comprise a portion of overall mammalian herbivore diversity along with higher-crowned, presumed mixed feeders or grazers (Tedford et al. 1987). The high-crowned taxa are absent from the Gaillard Cut L.F. This may relate to the ancient terrestrial habitats that existed during the middle Miocene of Panama.

The fossil mammals were collected from outcrops of the Cucaracha Formation, a series of clastic sediments exposed along the excavations and cliffs of the Panama Canal. The Cucaracha conformably overlies the marine Culebra Formation of Oligocene/early Miocene age and is in turn conformably overlain by marine (La Boca) and volcanic (Pedro Miguel) sediments, mostly reported to be of early Miocene age (Woodring 1957). Given these maximum and minimum age constraints, the fossil mammals recovered from the Cucaracha Formation are inferred to be early Miocene, or within an age range between ~24 and 16 Ma (using the time chart of McKenna

and Bell 1997, compiled from Berggren et al. 1995). The stage of evolution of the taxa represented in the Gaillard Cut L.F. (Table 1) allows more precise age assignment of late Hemingfordian through early Barstovian North American Land Mammal age (MacFadden 2004), or middle Miocene, between ~15 and 17 Ma (Tedford et al. 1987; McKenna and Bell 1997). With Stewart and Whitmore's precisely documented field notes (available at the USNM Department of Paleobiology), their original localities were relocated in 2002 (MacFadden, personal observation). So far as can be determined from geological field relationships, the fossil mammals that comprise the Gaillard Cut L.F. were derived from a narrow stratigraphic interval assumed to represent a short duration of geological time. The ~15–17 Ma age determination for this local fauna represents the current uncertainty in dating and not an interpretation of a duration of 2 million years in which these animals lived. As such, these fossils are likewise interpreted to represent a single ancient fauna.

In addition to the vertebrate fossils, the total absence of marine fossils and presence of fragmentary land plants indicate a non-marine, terrestrial ecosystem during deposition of the Cucaracha Formation (Woodring 1957). Graham (1988) describes a very interesting assemblage of fossil pollen from the Cucaracha Formation from a locality less than 1 km to the south, and an apparent lateral equivalent, of the fossil mammal localities (MacFadden, personal observation). Graham (1988, p 1467) states that based on this evidence: "The paleocommunities include a fern marsh, with associated palms, fringed seaward by mangroves, and bordered on the surrounding uplands by versions of the tropical wet, tropical moist, and premontane forests. Evidence for higher-altitude vegetation and communities of drier to arid aspect (open forests, savannas) continues to be meager for Tertiary floras of the region." Graham (1988) also states that the fossil mammals described in Whitmore and Stewart (1965) indicate both browsers and grazers, the latter suggesting more open forest and grasslands. With regard the latter remark, so far as is known, and as will be discussed below, the Gaillard Cut L.F. actually does not contain herbivore species that would normally be interpreted as grazers.

Reconstructing the paleoecology of fossil mammalian herbivores: morphology and isotopes

Tooth morphology

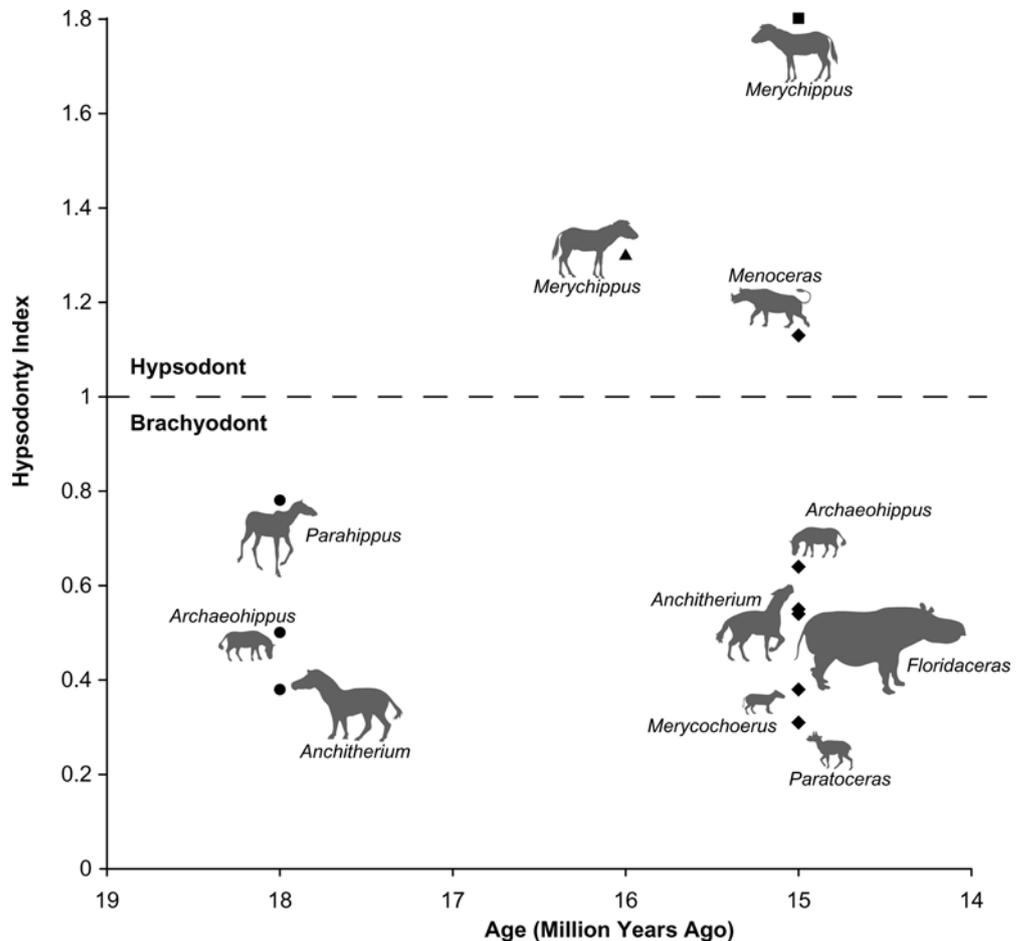
As a general rule, the morphological differences demonstrated in modern mammalian herbivore teeth are highly correlated to diet and habitat. Extant mammals such as white-tailed deer (*Odocoileus virginianus*) or the Brazilian tapir (*Tapirus terrestris*) have very short-crowned teeth that are known to be adapted to browsing mostly on soft, leafy vegetation in woodlands and forests (Nowak 1999). In contrast, mammals such as the zebra (e.g., *Equus burchelli*) or North American bison (*Bison bison*) have

high-crowned teeth known to be adapted to open-country grazing (Nowak 1999). Using these modern analogs, the tooth morphology of extinct herbivores can be used to interpret ancient diets and corresponding local plant communities in which these species lived (e.g., Janis 1988; MacFadden 2000).

A quantitative method of assessing relative crown height is determination of the “hypso-donty index” for a particular mammalian herbivore species. As used here, the hypso-donty index (HI) is simply the ratio of tooth length across the occlusal surface/unworn crown height. Extant species of browsing mammals generally have HIs < 1.0; a similar assumption is made for extinct species. Likewise, grazing mammals characteristically have HIs between 1 and 4, indicating very elongated tooth crowns (MacFadden 2000).

The Miocene was a time of major morphological transformation of mammalian herbivore teeth related to the global expansion of grassland biomes (Simpson 1953b). Using horses (Family Equidae) as an example, explosive evolution in crown height occurred between 15 and 18 Ma (MacFadden and Hulbert 1988), indicating the advent of grazing. After the middle Miocene, by 15–18 Ma, terrestrial mammalian faunas with open-country grassland components had a certain percentage of higher-crowned species, depending upon the relative amount of grass and browse available as food resources (Webb 1977).

Fig. 2 Hypso-donty Indices for several Miocene ungulate taxa. The horses from Thomas Farm, FL (18 Ma, circles) all have short-crowned (brachydont) teeth. By 2–3 million years later, middle Miocene North American terrestrial mammalian faunas have high-crowned, presumably grazing, taxa (e.g. the horses *Merychippus* from Nebraska (16 Ma, triangle; MacFadden 1988) and Oregon (15 Ma, square; Downs 1956, p 259, unworn M2). With the exception of the rhino *Menoceras barbourni*, the 15 Ma mammalian herbivores from Panama are characteristically short-crowned (diamonds)



Although the Gaillard Cut L.F. represents a limited sample of extinct mammalian herbivore biodiversity, similar-aged, poorly sampled (or low diversity) faunas from North America during this time characteristically have both short-crowned and some incipiently high-crowned species (e.g., the three-toed horse *Merychippus* from the middle Miocene of Florida; Bryant 1991; also Tedford et al. 1987). In contrast, the mammalian herbivores from the Gaillard Cut L.F. are, so far as is known, notably lacking in any higher-crowned taxa that would be interpreted to represent more open-country grazers (Fig. 2).

Stable isotopes: you are what you eat

Recent studies over the past decade have demonstrated that the stable isotope composition archived in fossil teeth can be used to reconstruct many aspects of the paleobiology as well as ancient ecology and environments of extinct vertebrates (e.g., Koch 1998; Kohn 1999; MacFadden 2000). Of relevance to the present study, analysis of the carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope composition of fossil herbivore teeth provide unique insight into the diets and environment of the extinct mammalian herbivores from Panama.

Carbon isotopes The stable isotopes of carbon are fractionated in different proportions depending upon the photosynthetic pathway used by specific plant species. These differences can be expressed relative to the amount of the ^{12}C and ^{13}C incorporated into plant biomass by the equation: $\delta^{13}\text{C} (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$, where R = ratio of $^{13}\text{C}/^{12}\text{C}$ of an unknown sample relative to the known standard V-PDB (Coplen 1994).

C3 plants, which photosynthesize carbon using the Calvin Cycle, comprise ~85% of terrestrial plant biomass, and include most trees, shrubs, and high-elevation, high-latitude, and other cool-growing season grasses, have a mean $\delta^{13}\text{C}$ value of -27‰ , with a wide range from about -32 to -24‰ (Dienes 1980; Farquhar et al. 1989; Boutton 1991). This range is important because it can have ecological significance: More negative $\delta^{13}\text{C}$ values, i.e., less than -30‰ , are frequently found in modern forested habitats with closed canopies (van der Merwe and Medina 1989; Cerling and Harris 1999; Cerling et al. 2004). C3 plants in more open country, and/or arid environments can have more positive $\delta^{13}\text{C}$ values (Farquhar et al. 1989; Cerling et al. 2004). In contrast, C4 plants, which photosynthesize carbon using the Hatch-Slack cycle, comprise about 5–10% of the terrestrial plant biomass and consist predominantly of temperate, sub-tropical, and tropical grasses. C4 grasses characteristically have a mean $\delta^{13}\text{C}$ value of -13‰ with a narrow range between -15 and -11‰ . CAM plants, which in terrestrial communities include succulents (Cactaceae) and consist of a minor percentage (~5%) of global plant terrestrial biomass, exhibit a wide range of $\delta^{13}\text{C}$ values that can overlap between those seen in C3 and C4 plants (Dienes 1980; Farquhar et al. 1989; Boutton 1991). Because CAM plants represent a minor fraction of overall plant biomass, and are not significantly represented in studies of Miocene pollen from Panama (Graham 1988), they are not considered to be of great importance in the discussion of plants eaten by fossil herbivores from Panama described below.

Of relevance to the fossil mammals studied here, the carbon isotopic signature of plant foods is incorporated into the biological apatite mineral phase of vertebrate teeth. Whereas the mean values of C3 and C4 plants are -27 and -13‰ , respectively, the corresponding mean $\delta^{13}\text{C}$ values of tooth enamel carbon are enriched relative to plant foods. The exact amount of enrichment has received considerable attention in the literature (e.g. Ambrose and Norr 1993; Lee-Thorp et al. 1989; Koch et al. 1992). There may be intrinsic physiological factors that result in different $\delta^{13}\text{C}$ enrichment within different groups of mammals. We nevertheless use the enrichment factor (ϵ^*) of $14.1 \pm 0.5\text{‰}$ reported for medium sized terrestrial herbivores (Cerling and Harris 1999). As such, a browser feeding on C3 plants will have a mean $\delta^{13}\text{C}$ tooth enamel carbonate value of $\sim -13\text{‰}$ whereas a C4 grazer will have a corresponding $\delta^{13}\text{C}$ value of $\sim +1\text{‰}$.

Oxygen isotopes Traditionally, variation in oxygen isotope ratios studied from terrestrial environments have been ascribed to environmental temperature changes, where

warmer weather results in an enrichment of ^{18}O and cooler weather results in depletion of ^{18}O in meteoric water (McCrea 1950; Bryant et al. 1996). From this, the $^{18}\text{O}/^{16}\text{O}$ ratios are compared by the equation: $\delta^{18}\text{O} (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$, where R = $^{18}\text{O}/^{16}\text{O}$ of an unknown relative to the standards V-PDB or V-SMOW (Coplen 1994). In terrestrial ecosystems, seasonal variation archived in progressively mineralized teeth will demonstrate more positive $\delta^{18}\text{O}$ values interpreted to represent summer high temperatures and more negative $\delta^{18}\text{O}$ values indicating winter low temperatures (Fricke and O'Neil 1996; MacFadden et al. 1999; Feranec and MacFadden 2000). However, other factors also clearly influence the oxygen isotopic archive in terrestrial settings. One of these, the "Amount Effect," is an important relationship between precipitation/humidity, temperature, and $\delta^{18}\text{O}$ (Dansgaard 1964). The main result of the amount effect is that when environmental temperatures rise above a threshold of $\sim 20^\circ\text{C}$, and there is significant precipitation and/or high humidity, $\delta^{18}\text{O}$ decreases (Rozanski et al. 1993; Bard et al. 2002; Straight et al. 2004). Both the temperature effect and the amount effect may be recorded in the isotopic signature of teeth (Higgins and MacFadden 2004).

Materials and methods

A total of 24 bulk (Appendix 1) and 15 serial (Appendix 2) enamel samples were analyzed from the available teeth of mammalian herbivores from the Gaillard Cut L.F. Although optimally we would have increased the statistical pool of sample analyses for each species, the small number of specimens in the collection does not allow additional sampling. Likewise, one potential herbivore species, the tiny three-toed horse *Archaeohippus* sp., is only represented from this locality by one pristine molar tooth, which we decided did not warrant isotopic sampling. As will be discussed below, despite the limited sample size, the isotopic data produced significant results that could be interpreted in a meaningful paleoecological context.

Bulk sampling for all taxa was done by removing enamel parallel the apparent growth axis for the full available height of the tooth. Isotopic analysis was done using between 5 and 10 mg of powdered enamel collected from the teeth using a low speed FOREDOM dental drill and carbide dental burs. Care was taken to avoid collecting any dentine underlying the enamel. Serial samples were collected from two rhino (*Floridaceras whitei*) tusks by drilling grooves perpendicular to the apparent growth axis of the tooth, following growth or hypoplasia lines when visible (Balasse 2003). A sample was taken every 2–3 mm, to also allow discrimination of the seasonal signal based on the known growth rate of the teeth (Goddard 1970) and to maximize the amount of powdered enamel that is collected, resulting in seven to eight samples per tooth. The position of each groove is recorded in millimeters starting with the groove closest to the root (assigned a value of 0). The samples were analyzed and data plotted against the height of the tooth.

Powdered samples were chemically treated to ensure that only pure biological apatite was analyzed. Samples were first treated with H_2O_2 to remove any organic contaminants, and then with weak (0.1 N) acetic acid to remove any secondary carbonate. About 1–2 mg of sample is needed for each analysis. The treated samples were analyzed using the VG Prism mass spectrometer in the Center for Isotope Geoscience, Department of Geological Sciences at the University of Florida.

Unknown sample analyses were calibrated to either an internal laboratory standard (MEme) or NBS-19, and ultimately back to the

V-PDB (PeeDee Belemnite), following Vienna convention, hence “V-,” (e.g., Coplen 1994). Following Hoefs (1997), $\delta^{18}\text{O}$ data calibrated to V-PDB were corrected to V-SMOW as follows: $\delta^{18}\text{OV-SMOW} = 1.03091(\delta^{18}\text{OV-PDB}) + 30.91$.

Results

Bulk isotope analyses

The individual carbon isotopic analyses demonstrate a range from -15.8‰ to -10.1‰ (Appendix 1, Table 2, Fig. 3). Both ANOVA and nonparametric Kruskal-Wallis tests indicate that the mean carbon isotopic values for five species of mammalian herbivores are statistically different. Given the possibility that the horse *Anchitherium clarencei*, with $n = 1$, might affect the overall statistics, the same statistical tests for the remaining four species still indicates highly significant differences in mean $\delta^{13}\text{C}$ values. Further statistical analyses indicates three groups, i.e., (1) the oreodont *Merychochoerus matthewi* with the most negative mean $\delta^{13}\text{C}$ value of -14.6‰ ; (2) the horse *Anchitherium clarencei*, and rhinos *Menoceras barbouri*, and *Floridaceras whitei*, all with statistically indistinguishable mean $\delta^{13}\text{C}$ values of, respectively -12.1‰ , -12.8‰ , and -12.8‰ ; and (3) the protoceratid artiodactyl *Paratoceras wardi* with the relative most positive mean $\delta^{13}\text{C}$ value of -11.3‰ .

The individual oxygen isotopic values have a narrower range from -5.9 to -2.1‰ (Appendix 1, Table 2). ANOVA and Kruskal-Wallis tests indicate that the mean $\delta^{18}\text{O}$ values (-5.5 , -4.4 , -4.4 , -3.9 , and -3.8‰) for all five (or four, with *Anchitherium clarencei* removed because $n = 1$) species do not differ significantly.

Serial isotope analyses

The serial isotope analyses of two different teeth, i.e., a tooth fragment (USNM 23176) and a right lower molar (USNM 23190) of the large rhino *Floridaceras whitei* yielded similar results, i.e. relatively little variation among individual serial samples within the same tooth (Fig. 4) and between the two teeth analyzed. The $\delta^{13}\text{C}$ demonstrates a very small range from -13.5 to -13.0‰ in USNM 23176 and -12.8 to -12.3‰ in USNM 23190 (Appendix 2). Likewise, the $\delta^{18}\text{O}$ demonstrates a relatively small range from -6.3 to -4.7‰ in USNM 23176 and -4.6 to -2.8‰ in USNM 23190.

The results of the serial sampling are of relevance to an interpretation of the bulk isotopic data. In extinct vertebrates that lived in highly variable climates, migrated long distances, or fed on isotopically different, e.g., seasonally available plant foods, annual variation in carbon and oxygen isotopic values can be as great as 4‰ (or more; Higgins and MacFadden 2004). Many teeth mineralize over a relatively short time, a few months to a year. A single bulk isotopic analysis from one such tooth reflects the average environmental variation during the period while that tooth mineralized. Since we cannot be certain of the length of time over which the teeth used in this study mineralized, and therefore whether the differences in values among bulk analyses represent niche partitioning or different parts of the year, we conducted serial analyses of two rhino teeth known to have taken more than 2 years to fully mineralize (Goddard 1970). The relatively little variation demonstrated in the serial sections, as well as identical values obtained for the bulk sample ($\delta^{13}\text{C} = -13.3\text{‰}$; $\delta^{18}\text{O} = -5.3\text{‰}$; Appendix 1) versus the mean of the serial samples ($\delta^{13}\text{C} = -13.3\text{‰}$, $\delta^{18}\text{O} = -5.3\text{‰}$; Appendix 2) for the rhino *Floridaceras whitei* (USNM 23176) allow a more insightful interpretation of the bulk isotopic data presented here.

Table 2 Univariate statistics, ANOVA, and nonparametric analyses for carbon and oxygen isotopic bulk analyses for the middle Miocene mammals from Panama. Individual data analyses are presented in Appendix 1. n number of specimens analyzed

Taxon	Common names(s)	n	$\delta^{13}\text{C}$ (‰)a			$\delta^{18}\text{O}$ (‰)b		
			Mean	SD	Range	Mean	SD	Range
<i>Merychochoerus matthewi</i>	Oreodont (artiodactyl)	5	-14.6	0.8	-15.8 to 13.7	-3.8	1.3	-5.3 to -2.0
<i>Paratoceras wardi</i>	protoceratid (artiodactyl)	8	-11.3	0.3	-12.9 to 10.1	-4.4	0.3	-5.9 to -3.0
<i>Anchitherium clarencei</i>	Horse (Family Equidae)	1	-12.1	–	–	-5.5	–	–
<i>Menoceras barbouri</i>	Rhino (Rhinocerotidae)c	3	-12.8	0.9	-14.2 to -11.2	-3.9	0.9	-4.9 to -2.1
<i>Floridaceras whitei</i>	Rhino (Rhinocerotidae)c	5	-12.8	0.3	-13.5 to -12.0	-4.4	0.3	-5.3 to -3.7

a ANOVA indicates significant differences in $\delta^{13}\text{C}$ among five species analyzed ($F=10.69$; $F_{\text{crit}}=2.96$; $P=0.0002$) and among four species ($F=14.11$; $F_{\text{crit}}=3.20$; $P=0.00007$; i.e., *A. clarencei* removed because $n = 1$). Likewise the nonparametric Kruskal-Wallis test indicates significant difference both among the same five ($H_{\text{obs}}=15.624$, $H_{\text{crit}}=9.488$, $P=0.004$) and four ($H_{\text{obs}}=14.967$, $H_{\text{crit}}=7.815$, $P=0.002$) species analyzed

b ANOVA indicates no significant differences in $\delta^{18}\text{O}$ among five species analyzed ($F=0.80$; $F_{\text{crit}}=2.96$; $P=0.54$) and among four species ($F=0.57$; $F_{\text{crit}}=3.20$; $P=0.65$; i.e., *A. clarencei* removed because $n=1$). Likewise the nonparametric Kruskal-Wallis test indicates no significant difference both among the same five ($H_{\text{obs}}=2.723$, $H_{\text{crit}}=9.488$, $P=0.605$) and four ($H_{\text{obs}}=0.492$, $H_{\text{crit}}=7.815$, $P=0.921$) species analyzed

c Two other specimens of tooth enamel fragments assigned to “rhino, indeterminate” (Appendix 1) are not included here

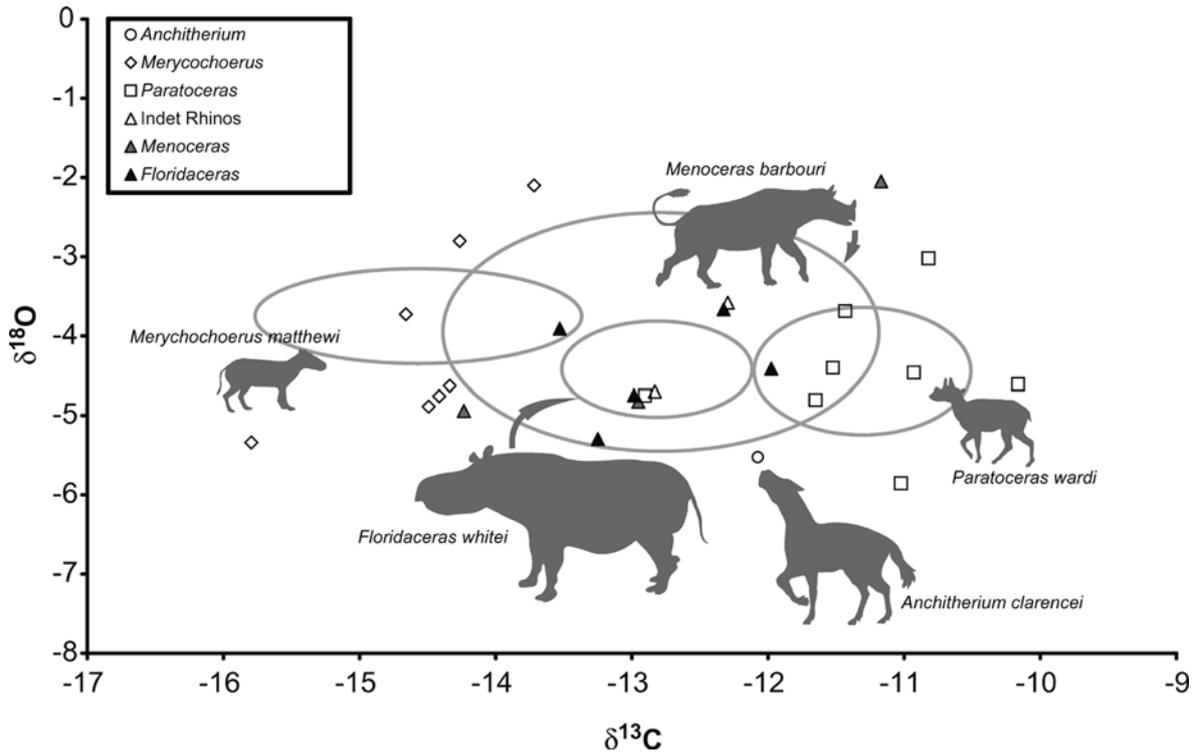


Fig. 3 Bivariate plot of $\delta^{13}\text{C}$ versus $\delta^{18}\text{O}$ for tooth samples from available mammalian herbivores from the Gaillard Cut L.F. The ellipses indicate one standard deviation around the mean for the four samples with $n > 1$

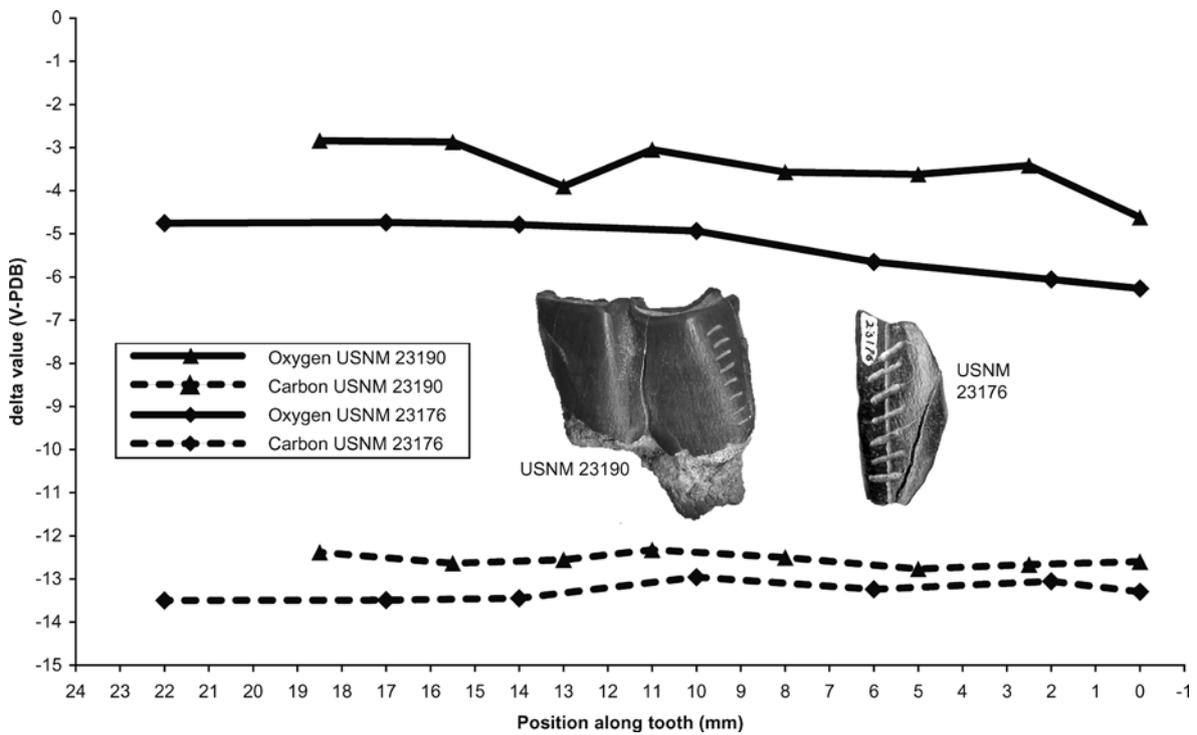


Fig. 4 Isotopic values from serial samples of two middle Miocene teeth of the rhino *Floridaceras whitei* plotted against the sample position along the tooth. Sample positions are measured in millimeters starting with zero at the sample closest to the root of the tooth. Images of the actual teeth are shown for reference

Discussion: life in an ancient C3 terrestrial ecosystem

A few important assumptions guide the interpretations of the data presented below. Firstly, in the absence of evidence to the contrary, we assume that the tooth enamel $\delta^{13}\text{C}$ enrichment factor of 14.1‰ (Cerling and Harris 1999) is applicable to all of the five species of mammalian herbivore taxa analyzed here. Secondly, relatively little is known, nor is there agreement, about levels of atmospheric CO_2 and related plant fractionation in terrestrial communities during the Miocene. We assume that these processes and relationships were similar in deep time to what we know about the present-day. We realize, however, that as more data on ancient levels of atmospheric CO_2 and direct measurements of ancient plant $\delta^{13}\text{C}$ in relevant paleocommunities become available, our interpretations might require modification. In short, the current carbon and oxygen isotope data presented below for the fossil mammals are interpreted within a framework of what we know about modern-day plant photosynthesis and isotopic enrichment of tooth enamel.

Presence/absence of C4 grasses in ancient Panama

In the geological context of deep time, grasslands are relatively recent arrivals on the global ecological landscape. Although the first grass fossils are known from about 50 Ma (Paleocene/Eocene) from Tennessee, USA (Crepet and Feldman 1991), grasslands do not become globally widespread until the Miocene (Jacobs et al. 1999). Based on analysis of fossil mammal teeth and ancient soil carbonates, Cerling et al. (1993, 1997, 1998) have asserted that unlike today, during most of the Miocene, low-latitude, low-elevation C3 grasses predominated during the early spread of grasslands. The modern-analog C4 grasses did not become common in global ecosystems until the late Miocene, about 7 Ma. Fox and Koch (2003) demonstrated that although C3 grassland ecosystems dominated prior to late Miocene, evidence from isotopic studies of paleosol carbonates from the ancient Great Plains of North America indicate the presence of a minor component (12–34%) of C4 grasses prior to the global shift to temperate/tropical C4-based grasslands after 7 Ma. Likewise, within ancient North America, fossil C4 grasses with diagnostic Krantz micro-anatomy are described from ~10 Ma deposits in southern California (Tidwell and Nambudiri 1989) and Nebraska (Thomasson et al. 1986). Given the presence, albeit in low proportions, of C4 grasses in the predominantly C3 grassland ecosystems of North America during the Miocene prior to 7 Ma, the question can rightly be asked if there is any isotopic evidence of C4 plant foods that were eaten by the mammalian herbivores from the Gaillard Cut L.F. of Panama? Given the mean $\delta^{13}\text{C}$ value of ~12‰ for C4 grasses (Dienes 1980; Farquahar et al. 1989; Boutton 1991), and with a reported enrichment factor of 14.1‰ between plant foods and tooth enamel carbon (Cerling and Harris 1999), one would expect a

$\delta^{13}\text{C}$ signature of ~+2‰ for an ancient mammalian grazer that fed principally on C4 grasses.

There is significant variation of $\delta^{13}\text{C}$ tooth enamel signatures of the extinct middle Miocene mammalian herbivores from Panama (Table 2; Appendices 1, 2). The small artiodactyl *Paratoceras wardi* demonstrates the most positive $\delta^{13}\text{C}$ values, i.e., with a mean of -11.3‰ and a range of -12.9 to -10.1‰ (Table 2). Although *P. wardi* could have been a mixed feeder with a small proportion of C4 grass in its diet, there is no definitive carbon isotopic evidence of C4 grasses in ancient Panama during the middle Miocene. Thus, we conclude that this ancient terrestrial ecosystem was fundamentally C3-based in plant photosynthesis.

Niche partitioning within a C3-based terrestrial ecosystem

Most previous studies of isotopic differences in the diets of ancient mammalian herbivores have concentrated on whether or not a particular species had a C3, C4, or mixed diet. From studies of modern plant communities, however, we know that there are clear patterns and differences of isotopic fractionation (sometimes exceeding 10‰) even within C3 plant communities (Dienes 1980; Farquahar et al. 1989; Boutton 1991). Until recently, however the sample sizes for particular extinct species that have been analyzed isotopically did not allow for statistical discriminations of different C3 plant foods. As the results indicate above, there are statistically significant differences in the mean isotopic values for the mammalian herbivores from Panama that are interpreted to fall into three groups. These differences almost certainly can be interpreted to represent differences in diets.

Most negative: oreodont Merycochoerus matthewi (mean $\delta^{13}\text{C}$ value of -14.6‰)

The paleoecology of oreodonts as a group is poorly known, and probably was fairly diverse considering the morphological variation represented in this family. Janis (1982) considered these primitive artiodactyls to be open-country woodland browsers with a seasonally variable diet similar to that of the modern peccary (e.g., *Tayassu tajacu*) and white-tailed deer (*Odocoileus virginianus*) from North America (and present-day Panama) and Asian cervids, like the chital (*Axis axis*). Schultz and Falkenbach (1968) believed that the Panama oreodont (which they called *Brachycrus*) did not represent a typical restricted plains or grassland species as might be characteristic for oreodonts in the ancient North American Great Plains. In contrast, they speculated that the Panama oreodonts may have been “river-valley-forest living animals” (p 371). With a mean $\delta^{13}\text{C}$ value of -14.6‰ and a range between -15.8 and -13.7‰, the carbon isotopic evidence for *Merycochoerus matthewi* is the most negative of all of the taxa analyzed during this study. Subtracting the enrichment factor (ϵ^*

sensu Cerling and Harris 1999) of 14.1‰, the mean $\delta^{13}\text{C}$ value of the plants eaten by the oreodonts would have been -28.7‰ , slightly more negative than the mean value of -27‰ generally reported for C3 plants (Dienes 1980; Farquahar et al. 1989; Boutton 1991). Similarly, the most negative individual bulk sample of *M. matthewi* indicates a plant food with a $\delta^{13}\text{C}$ value of -29.9‰ , approaching values reported for present-day Neotropical forests of Amazonia (van der Merwe and Medina 1989) and Panama (Sternberg et al. 1989). However, none of the carbon isotopic values for *M. matthewi* are as negative as has been reported for present-day dense closed-canopy folivores, such as the okapi (*Okapia johnstoni*) from the Ituri rainforest, Democratic Republic of the Congo, with a mean tooth enamel $\delta^{13}\text{C}$ of -21.1‰ (Cerling and Harris 1999; Cerling et al. 2004). Closed-canopy understory plants from the modern-day forests of Panama have $\delta^{13}\text{C}$ values that are about -35‰ (Sternberg et al. 1989). Thus, although the Miocene Panama oreodont has tooth enamel $\delta^{13}\text{C}$ values approaching those that would be expected from forest-dwelling browsers, there is no definitive evidence of closed canopy.

Intermediate: horse Anchitherium clarenci (-12.1‰)
and rhinos *Menoceras barbouri* (-12.8‰) and
Floridaceras whitei (-12.8‰)

The three-toed horse *A. clarenci* and rhinos *M. barbouri* and *F. whitei* have indistinguishable $\delta^{13}\text{C}$ values (Table 2). Based mostly on its low-crowned dentition (HI < 1.0; data from MacFadden 1988), *Anchitherium* is generally reconstructed as a browser, inhabiting forests

(Webb 1977) or open woodlands (Janis 1982). There is little direct paleoecological evidence for *A. clarenci* from Panama other than a HI of 0.55 for a single relatively unworn upper molar (USNM 23156). This species is also known from Florida and possibly several other localities in North America, where it is interpreted as a forest-dwelling browser (MacFadden 2001). Given the ϵ^* of 14.1‰, with a single $\delta^{13}\text{C}$ value of -12.1‰ , this individual of *A. clarenci* from Panama had a diet with a $\delta^{13}\text{C}$ isotopic signature of -26.2‰ , close to the accepted mean value of C3 plants (Dienes 1980; Farquahar et al. 1989; Boutton 1991). Given this limited evidence based on morphology and isotopic signature, it is likely that *A. clarenci* from Panama was a forest or woodlands browser.

It should be noted here that although no isotopic analyses were done on *Archaeohippus* from Panama (due to lack of suitable specimens), this tiny, three-toed horse does occur in the Gaillard Cut L.F. Because of its low-crowned teeth, with a hypsodonty index of 0.6 based on a single little worn upper molar (USNM 23157; MacFadden 2004) from Panama and HI of 0.5 based on a large sample of *A. blackbergi* from Thomas Farm, Florida (data from MacFadden 1988), *Archaeohippus* is likewise interpreted as a short-crowned browser. The question can rightly be asked how did these two closely related, coexisting equids divide up resources within their ancient communities if they both were browsers? In addition to their considerably different body sizes, with estimates of 44 kg for *Archaeohippus* and 132 kg for *A. clarenci* (MacFadden 1987), they also could have been selective browsers feeding on different C3 plants.

The two rhinos from Panama, *M. barbouri* and *F. whitei* have identical mean $\delta^{13}\text{C}$ values of -12.8‰ . Janis (1982)

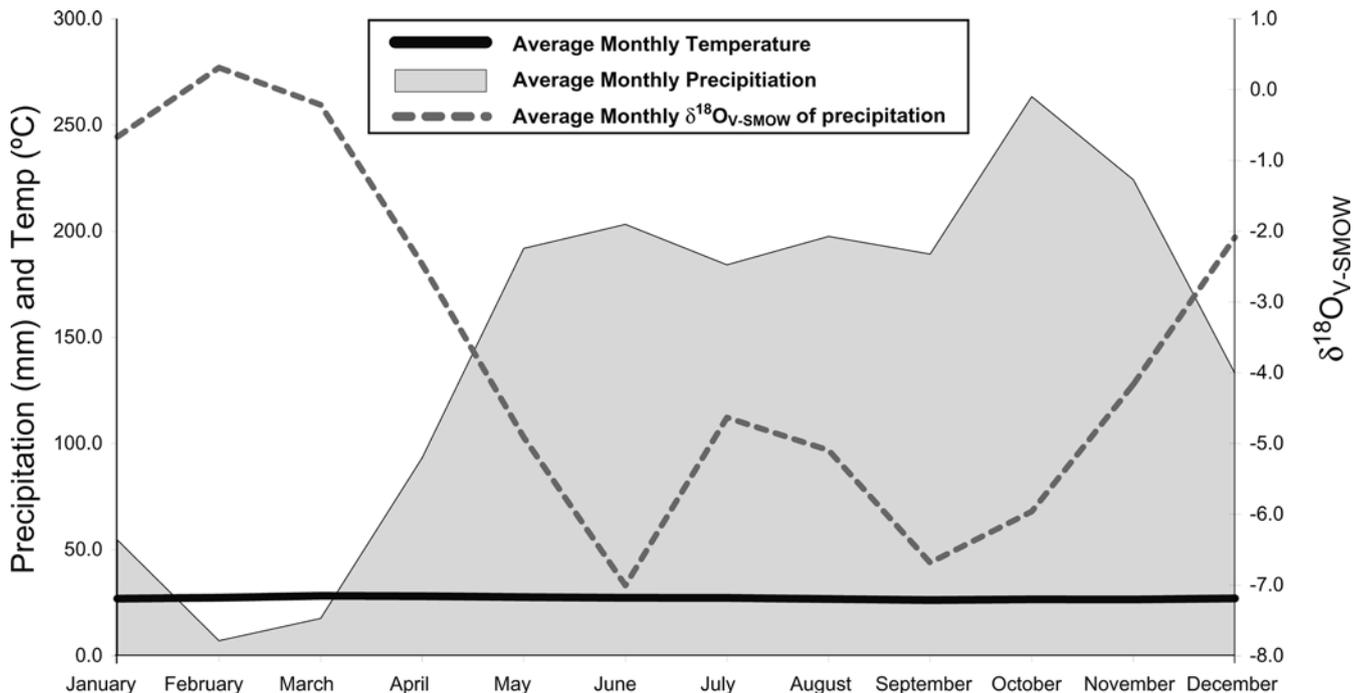


Fig. 5 Plot showing 26-year monthly average of temperature, precipitation, and $\delta^{18}\text{O}$ of precipitation in present-day Panama (from IAEA/WMO 2001)

interpreted middle Tertiary short-crowned rhinos to be browsers, possibly feeding on both higher- and lower-level trees and shrubs. Subtracting the enrichment factor ϵ^* of 14.1‰ yields a plant food source of 26.9‰, close to the mean for C3 plants (Dienes 1980; Farquahar et al. 1989; Boutton 1991). The serial sectioning of two *F. whitei* teeth (Fig. 5) demonstrates little variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, indicating an isotopically monotonous diet within an equable climate. Like the horses, the rhinos from the Gaillard Cut L.F. are of significantly different body sizes, with *M. barbouri* being medium sized (~250 kg; Janis 1982, for similar-sized *Diceratherium*) and *F. whitei* being much larger, perhaps approaching 1,000 kg (similar to the modern black rhino *Diceros bicornis*; Janis 1982). Thus, both rhinos fed on C3 plants, probably browse, and they partitioned their environment by differences in body size, which is well-known to be highly predictive of the ecology of particular species (Eisenberg 1981).

Most positive: protoceratid artiodactyl Paratoceras wardi (−11.3‰)

Protoceratids were an extinct group of New World ruminant artiodactyls that were initially widespread, but became restricted to southeastern USA by the middle Miocene (Patton and Taylor 1973), perhaps within the ancient subtropical “Gulf Coastal Savannah Corridor” (Webb 1977). A variety of diets and habitats has been suggested for protoceratids, ranging from feeding on semiaquatic vegetation to open-country browser (Janis 1982; Prothero 1998). Little is known about the paleoecology of *P. wardi*, a species that in addition to Panama is otherwise known from the Texas Gulf Coastal Plain. It was a small, short-crowned form with a body size probably similar to, or slightly smaller than, the small equid *Archaeohippus* sp. in the Gaillard Cut L. F.

The mean $\delta^{13}\text{C}$ value of −11.3‰ for *P. wardi* indicates an animal feeding principally on C3 plants with an extrapolated mean value of −25.4‰, only slightly more enriched than the overall mean for these plants (Dienes 1980; Farquahar et al. 1989; Boutton 1991). There are several possible explanations for the slightly more positive values seen in this artiodactyl: (1) *P. wardi* could have had a specialized diet of xeric adapted C3 browse, or (2) there may have been a minor (<20%) component of C4 grass in its diet. While neither of these possibilities can be ruled out, its low-crowned dentition and mean $\delta^{13}\text{C}$ value nevertheless suggest a C3 browser.

In summary, the tooth morphology and statistically significant differences in mean values for the mammalian herbivores are interpreted to indicate a community of predominantly C3 browsers. At one end of the isotopic spectrum there is some suggestion of forest canopy based on a single individual bulk analysis of −15.9‰ for the oreodont *M. matthewi*. At the other end of the spectrum, a single bulk isotopic analysis of −10.1‰ for the artiodactyl *P. wardi* could suggest either feeding on xeric-adapted C3 browse, or with a small component of C4 grass in its diet.

So far as can be reconstructed with the available evidence, these mammalian herbivores partitioned the environment within a predominantly, if not exclusively C3 community, by differences in plant diets and/or body size.

Ancient climate reconstruction

Tooth enamel mineralizes incrementally, beginning at the crown with a mineralization front moving toward the root of the tooth as enamel formation proceeds (Fricke and O’Neil 1996; Gadbury et al. 2000; Hoppe et al. 2004). As enamel mineralizes, it incorporates oxygen with a $\delta^{18}\text{O}$ value in equilibrium with body water. The isotopic value of body water, in turn, is affected by the total water budget of the animal. For terrestrial herbivores (and more so as the mass of the animal increases), body water $\delta^{18}\text{O}$ tracks the $\delta^{18}\text{O}$ value for surface drinking water (Bryant and Froelich 1995; Bryant et al. 1996), which maximizes the isotopic effects of temperature and precipitation changes in tooth enamel.

High-crowned mammal teeth provide a long isotopic record because mineralization occurs over several months to years. However, total mineralization of any point along the growth axis of the tooth is not instantaneous. An isotopic analysis at any point along a tooth crown usually represents the average of several weeks or months of tooth growth (Passey and Cerling 2002; Balasse 2003; Hoppe et al. 2004). Passey and Cerling (2002), however, showed that although there is some averaging of the isotopic signal, the original incremental signal is not lost.

The serial samples analyzed from two rhino (*F. whitei*) teeth provide insight about the interpretation of the bulk data and seasonality in ancient Panama. There is little variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ serial isotopic values, suggesting that likewise bulk analyses of the other teeth and tooth fragments analyzed from the Gaillard Cut L.F. are a valid method for examining overall patterns of ecological partitioning. Thus, the $\delta^{13}\text{C}$ bulk data do not represent chance outliers at the extremes of large overall seasonal variation in diet. Furthermore, the lack of significant overall variation in $\delta^{18}\text{O}$ provides insight into the annual pattern of climate variation.

Figure 5 illustrates the mean values of temperature, precipitation, and $\delta^{18}\text{O}$ measured over the past 26 years from Panama (IAEA/WMO 2001). While mean temperature throughout the year shows very little variation (averaging around 27°C), precipitation shows a strong seasonal pattern in which January, February, and March are often relatively dry. The result is a strong annual variation in $\delta^{18}\text{O}$ values of precipitation (about 7.3‰), with the lowest values occurring during the rainy season (the Amount Effect; Dansgaard 1964). Strong seasonal changes in precipitation and/or temperature are expected to produce strong seasonal changes in $\delta^{18}\text{O}$ recorded in tooth enamel. Without independent knowledge of temperature or precipitation amount, it may not be possible to distinguish the two. Nevertheless, if seasonal changes are not apparent in the isotopic record, it may be assumed that

seasonal changes in precipitation and temperature are negligible.

Assuming that the amount of variation of $\delta^{18}\text{O}$ in tooth enamel is dampened with respect to the variation present in meteoric water (Passey and Cerling 2002; Balasse 2003; Higgins and MacFadden 2004), then the pattern from serial sampling of tooth enamel from a hypothetical modern rhinoceros living in modern Panama would be expected to have a range of around 3.5‰ (reduced from the annual range of 7.3‰ for meteoric water; Fig. 5). Plots of $\delta^{18}\text{O}$ versus tooth height for the two rhinos that were serially sampled are shown in Fig. 4. Teeth were sampled along a length that probably encompasses at least 1 year of development, and possibly 2 (based on a comparison to the modern black rhinoceros, *Diceros bicornis*; Goddard 1970). The values for USNM 23176 and USNM 231990 vary over a range of about 1.5 and 1.8‰, respectively. Values tend to decrease toward the root of the tooth (Fig. 4), but there is no clear annual pattern. The limited range of variability suggests only minor seasonal changes in temperature and/or precipitation compared to the modern climate of Panama. Without an independent proxy either for amount of precipitation or for temperature, it is not possible to know which was the dominant factor in Miocene Panama.

Conclusions

Evidence from stable isotope analyses of the tooth enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ provides insight about the community paleoecology of the mammalian herbivores from the Gaillard Cut L.F., middle Miocene of Panama. With regard to the questions to be answered posed above:

1. So far as indicated by the carbon isotope evidence, the Miocene of Panama was characterized by predominantly, or exclusively, C3 plants. There is no definitive evidence for C4 grasses.
2. The different species of mammalian herbivores analyzed here partitioned their available resources by either feeding on different kinds of C3 plants, or by difference in body size.
3. The oxygen isotope evidence indicates an ancient climate that was considerably more equable than is seen in present-day Panama.
4. Although there is some suggestion of isotopically negative values that might be interpreted as indicating a tropical rainforest canopy, there is no definitive isotopic evidence for this from the data produced from the mammalian herbivores from ancient Panama.

The mammalian herbivores from the middle Miocene of Panama provide a rare opportunity to better understand terrestrial plant and animal communities and interactions in the ancient Neotropics. Our knowledge of this important region will be enhanced as additional fossil mammals are

Table 3 Data for individual bulk carbon and oxygen isotopic analyses

Taxon	USNM No.	Lab no.	Tooth	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
<i>Merycochoerus matthewi</i>	23163	PH 02-146	m3 talonid	-14.4	-4.8
<i>M. matthewi</i>	171016	PH 02-288	Lower tusk	-13.7	-2.1
<i>M. matthewi</i>	23162	PH 02-158	Molar	-15.8	-5.3
<i>M. matthewi</i>	23159	PH 03-68	Lower molar	-14.3	-2.8
<i>M. matthewi</i>	23158	PH 03-69	Tooth fragment	-14.7	-3.7
<i>Paratoceras wardi</i>	23172	PH 03-100	Lm3	-11.4	-3.7
<i>P. wardi</i>	23179	PH 03-102	M 1 or 2	-10.2	-4.6
<i>P. wardi</i>	23152	PH 03-101	Lm3	-11.0	-5.9
<i>P. wardi</i>	171025	PH 03-103	Lm2	-10.8	-3.0
<i>P. wardi</i>	23154	PH 03-179	Rm3	-12.9	-4.8
<i>P. wardi</i>	23155	PH 03-180	Rm3	-10.9	-4.5
<i>P. wardi</i>	23170	PH 03-181	Lm3	-11.5	-4.4
<i>P. wardi</i>	171006	PH 03-182	Lp4	-11.7	-4.8
<i>Anchitherium clarencei</i>	494438	PH 03-70	p3	-12.1	-5.5
<i>Menoceras barbouri</i>	494439	PH 02-132	P2	-11.2	-2.1
<i>M. barbouri</i>	23188	PH 02-140	L upper cheek tooth	-14.2	-4.9
<i>M. barbouri</i>	23187	PH 03-178	Incisor	-13.0	-4.8
<i>Floridaceras whitei</i>	183060	PH 03-183	Tusk	-14.0	-4.9
<i>F. whitei</i>	183060	PH 03-184	m3	-13.1	-4.0
<i>F. whitei</i>	23176	PH 03-104	Tooth fragment	-13.2	-5.3
<i>F. whitei</i>	23185	PH 02-139	L upper tooth fragment	-13.0	-4.7
<i>F. whitei</i>	23179	PH 02-142	M 1 or 2	-12.3	-3.7
<i>F. whitei</i>	23190	PH 03-72	R lower molar	-12.0	-4.4
Rhino, indeterminate	171009	PH 03-71	Tooth fragment	-12.8	-4.7
Rhino, indeterminate	23167	PH 02-141	Tooth fragment	-12.3	-3.6

Table 4 Serial isotopic analyses for two teeth of the large rhino *Floridaceras whitei* from the Miocene of Panama

Lab no.	Distance from base (mm)	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
USNM 23176—lower molar fragment			
PH 03-105	0	-13.3	-6.3
PH 03-106	2	-13.1	-6.1
PH 03-107	6	-13.2	-5.7
PH 03-108	10	-13.0	-4.9
PH 03-109	14	-13.4	-4.8
PH 03-110	17	-13.5	-4.7
PH 03-111	22	-13.5	-4.8
USNM 23190—right lower molar			
PH 03-73	0	-12.6	-4.6
PH 03-74	2.5	-12.7	-3.4
PH 03-75	5	-12.8	-3.6
PH 03-76	8	-12.5	-3.6
PH 03-77	11	-12.3	-3.0
PH 03-78	13	-12.6	-3.9
PH 03-79	15.5	-12.6	-2.9
PH 03-80	18.5	-12.4	-2.8

collected from the Gaillard Cut L.F. in Panama, and when new fossil localities are discovered elsewhere in Central America, a region that up to now has been terra incognita in deep time.

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Appendix 1

Table 3 shows data for individual bulk carbon and oxygen isotopic analyses.

Appendix 2

Table 4 shows serial isotopic analyses for two teeth of the large rhino *Floridaceras whitei* from the Miocene of Panama.

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