

Identifying forested environments in Deep Time using fossil tapirs: evidence from evolutionary morphology and stable isotopes

With 6 figs, 2 tabs

Larisa R. G. DeSANTIS & Bruce MacFADDEN

Abstract

Despite dramatic global environmental changes during the Cenozoic, fossil tapirs have demonstrated morphologically conservative, bradytelic evolution. Through time their masticatory morphology is consistent with browsing dietary niches as compared to closely related, fast-evolving equids. Similarly, stable carbon isotope analyses indicate that tapirs have consistently had diets of C_3 vegetation in denser canopied environments than most other sympatric mammalian herbivores. Thus, tapirs are robust indicators of ancient forested habitats. After a relatively widespread distribution during the Eocene, declines in tapiroid latitudinal ranges during the Oligocene are consistent with paleobotanical evidence for contracting mesothermal and megathermal vegetation. Tapirs increased their latitudinal ranges from the Miocene through the Pleistocene, and recently retreated to occupy only southern distributions below $21^\circ N$ by $\sim 10,000$ years ago. Maps of tapiroid (i.e., tapirids and close relatives) fossil distributions in continental North America provide spatial and temporal proxy evidence for the presence of associated forested environments.

Key words: Cenozoic, forest distributions, canopy density, stable isotopes, $\delta^{13}C$, Tapiroidea, Tapiridae, tapirs, North America

Introduction

Modern tapirs occupy densely-canopied forests throughout southern Mexico, Central America, South America, and southeast Asia (SALAS 1996, BROOKS et al. 1997, FOERSTER & VAUGHAN 2002, TOBLER 2002, HOLDEN et al. 2003). Living tapirs are browsers and possess morphological features that are present in diverse clades of browsing mammals (e.g., low-crowned teeth, short mandibular diastema; MacFADDEN & SHOCKEY 1997, MENDOZA et al. 2002). The masticatory morphology (morphological characters associated with the oral processing of food) of tapirs is interpreted to be highly conservative, retaining plesiomorphic characters through time (COLBERT & SCHOCH 1998). In addition to the conservative nature of morphological characters of browsers, tapiroids also appear to have browsed through time, as inferred from the stable carbon isotopes of their tooth enamel (MacFADDEN & CERLING 1996, MacFADDEN & SHOCKEY 1997, KOCH

et al. 1998, KOHN et al. 2005, FERANEC & MacFADDEN 2006). Thus, if tapiroids are morphologically conservative and maintain stable carbon isotope values consistent with browsing, then their distributions can be used to identify forested environments in Deep Time.

The four extant tapirs, Baird's tapir (*Tapirus bairdii*), the lowland tapir (*Tapirus terrestris*), the mountain tapir (*Tapirus pinchaque*), and the Malaysian tapir (*Tapirus indicus*) occupy forested environments, including: lowland forests, primary and secondary forests, Amazonian floodplains, and montane cloud forests (BROOKS et al. 1997). TOBLER (2002) also noted that tracks of *T. bairdii* were almost exclusively found in areas with dense vegetation and were rare in more open habitats. While *T. bairdii*, *T. terrestris*, and *T. indicus* inhabit forested environments (SALAS 1996, BROOKS et al. 1997, FOERSTER & VAUGHAN 2002, TOBLER 2002, HOLDEN et al. 2003), even the most ecologically divergent species, *T. pinchaque* (capable of occupying treeless paramo environments of greater than 3800 m elevation) lives in dense Andean forests more

Authors' addresses: Larisa R. G. DeSANTIS (corresponding author), Department of Zoology, University of Florida and Florida Museum of Natural History, PO Box 118525, Gainesville, Florida 32611, USA, <lgrawe@ufl.edu>; Bruce J. MacFADDEN, Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA, <bmacfadd@flmnh.ufl.edu>

frequently than any other habitat type (DOWNER 2001). Additionally, the Andean forests are necessary habitats for *T. pinchaque* as their canopies offer protection from predators and icy storms (DOWNER 1996, 2001). Since living tapirs are consistently found either within, or in close proximity to, dense closed-canopy forests, they are model organisms for inferring forested environments of the past.

The diets of living tapirs generally consist of leaves, twigs, fiber, and fruit (BODMER 1991, HENRY et al. 2000, DOWNER 2001, GALETTI et al. 2001, TOBLER 2002, LIZCANO & CAVELIER 2004). Despite seasonal flooding, there is little variation in the diet of *T. terrestris* in Peru's Amazon floodplain (BODMER 1990). In contrast, *T. terrestris* in French Guiana consume fewer fruits and greater fiber seasonally, after peak fruiting (HENRY et al. 2000). Even with potential seasonal variability in diet corresponding with fruiting events, living tapirs predominantly browse and forage for food throughout the year in forested environments (BODMER 1990, SALAS 1996, TOBLER 2002, HENRY et al. 2000, FOERSTER & VAUGHAN 2002).

Stable carbon isotope signatures of mammalian tooth enamel can be used to reconstruct the diet of extinct herbivores, including tapirs (DENIRO & EPSTEIN 1978, QUADE et al. 1992, CERLING et al. 1997, MACFADDEN et al. 1999). Since the stable carbon isotope signatures of mammalian tooth enamel reflects the diet consumed (with a dietary enrichment rate, ϵ^* , of approximately 14.1 ‰ for medium to large bodied mammalian herbivores; CERLING & HARRIS 1999), the diet of fossil tapirs can likewise be reconstructed through time. All previous studies of extinct mammals have demonstrated that within a given herbivore fauna, tapirs consistently have among the most negative $\delta^{13}\text{C}$ values (along with camelids; MACFADDEN & CERLING 1996, KOCH et al. 1998, KOHN et al. 2005, FERANEC & MACFADDEN 2006). Based on modern analogues (e.g., CERLING et al. 2004), these values are interpreted to represent ancient forested habitats. In addition to their known ecological preference for forests, tapirs are model organisms for comparisons through Deep Time due to low intra-population variation of enamel stable carbon isotope values (DESANTIS 2005). Given that a recent adult population of *T. bairdii* from Acapulco, Mexico was isotopically homogeneous in diet, with $\delta^{13}\text{C}$ variation of only 3 ‰, the carbon isotope values of adult fossil tapir specimens are likely to reflect those of a "fossil population" (DESANTIS 2005). Thus, comparisons of carbon isotope values of fossil tapirs through time will elucidate their dietary niche and proximity to forested environments.

Throughout the Cenozoic, North America underwent dramatic environmental transformations, as evident from anomalously warm tropical forests in high latitude North America during the Paleocene-Eocene Thermal Maximum (PETM) (WING et al. 2005), dramatic declines in browsing taxa throughout the middle to late Miocene (JANIS et al. 2000), and the expansion of C_4 grasslands during the late Miocene/early Pliocene (WANG et al.

1994, CERLING et al. 1997, KOCH et al. 2004, RETALLACK 2001, STROMBERG 2005). Because the expansion and contraction of forested environments are likely to affect the distributions of resident taxa, the presence of obligate forest dwellers can help reconstruct the distributions of their corresponding forested habitats in the past. COLBERT & SCHOCH (1998) suggested that tapiroids have always resided in humid, mesothermal areas and that declining clade diversity during the Oligocene and Miocene reflects the contraction of these areas in comparison to Eocene distributions.

The primary objective of our study is to reconstruct the distribution of forested environments through time using fossil tapiroids as indicator taxa. While plant macrofossils and pollen are usually analyzed to understand ancient forest distributions, mammalian herbivores potentially provide another line of evidence typically not available to paleobotanists. In order to use tapirs this way, we will first document their conservative morphology through time and compare them to the closely related horses (Equidae), a family with a considerably different evolutionary and adaptive history. Secondly, we will compare stable isotope values of tapirid tooth enamel through time to confirm their occupation as forest dwelling browsers. Lastly, we will use the Paleobiology Database (2006) to map tapiroid distributions through time, therefore, reconstructing forest distributions in Deep Time.

Materials and Methods

Morphology

Selected dental measurements were taken to quantify the evolution of crown height and body size proxies in relevant tapir specimens, ranging in age from early Eocene (Wasatchian, North American Land Mammal Age) to Recent. These measurements include: greatest anterior-posterior length of M1, m1, and m3; greatest transverse width of M1, m1, and m3; and greatest enamel crown height of M1, m1, and m3 (Mx, upper molar position; mx, lower molar position; Px, upper premolar position; px, lower premolar position). Relative ontogeny (based on tooth wear) was coded for each specimen as unworn, little wear, intermediate wear, and heavily worn. Individuals in the latter category were not used to calculate hypsodonty index (ratio of molar length to crown height).

Other measured characters that were taken, as available on individual specimens, include: greatest length of i1; greatest length of i3; length of mandibular diastema (i.e., from posterior to the canine to the anterior point of the p2); lower premolar row length (PRL); and lower molar row length (MRL).

Following SOLOUNIAS & MOELLEKEN (1993), MACFADDEN & SHOCKEY (1997), and MENDOZA et al. (2002),

several cranial characters were coded to describe morphological evolution related to browsing and grazing adaptations: glenoid fossa height above occlusal plane (low, high), paracondylar process length (short, long), anterior zygomatic arch (poorly or well developed), position of anterior most part of the orbit (dorsal to P3, P4, M1, M2, M3, or posterior to M3); shape of incisor arcade (curved, straight), and masseteric process above M1 (absent, present).

Specimens measured were from: the American Museum of Natural History (AMNH) Vertebrate Paleontology and Mammalogy collections in New York, New York, USA; the University of Florida/Florida Museum of Natural History (UF) Vertebrate Paleontology and Mammalogy collections in Gainesville, Florida, USA; and, the Yale Peabody Museum (YPM) Vertebrate Paleontology and Vertebrate Zoology collections in New Haven, Connecticut, USA. Data from the Paleobiology Database (2006) were also included, when available.

Stable Isotopes

Stable isotopic evidence was compiled from all available publications dealing with fossil tapirs from North America (MACFADDEN & CERLING 1996, KOCH et al. 1998, KOHN et al. 2005, FERANEC & MACFADDEN 2006). To this we have added previously unpublished data produced in our laboratory for specimens from the late Miocene McGehee and early Pliocene Palmetto Fauna localities in Florida and extant tapirs from Acapulco, Mexico.

All carbon isotope data are reported in the standard convention:

$$\delta^{13}\text{C} \text{ (per mil, ‰)} = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1,000$$

where R is the ratio of $^{13}\text{C}/^{12}\text{C}$ and the standard is VPDB (Pee Dee Belemnite, Vienna Convention; COPLEN 1994). All newly analyzed data were prepared using standard pre-treatment techniques (e.g., KOCH et al. 1997, MACFADDEN & HIGGINS 2004) and then analyzed on a VG Prism stable isotope ratio mass spectrometer with an inline ISOCARB automatic sampler in the Department of Geological Sciences at the University of Florida. The analytical precision based on replicate analyses is ± 0.1 ‰.

Inferred Forest Distributions

The locations and therefore known geographic distributions were plotted for all tapiroid taxa (Tapiroidea; classification based on MCKENNA & BELL 1997 and COLBERT 2005) compiled in the Paleobiology Database (2006). These data were used to produce the range maps for the Eocene through Recent. Present tapir distributions as determined from the International Union for Conservation

of Nature and Natural Resources (IUCN) and the Species Survival Commission-Tapir Specialist Group's (SSC), "Tapir Status Survey and Conservation Action Plan" (BROOKS et al. 1997), were added to the Present map.

Results and Interpretations

Morphology

"For tapirs, all the evolutionary action was over after the Eocene." – Radinsky (Paraphrased comment, L. Radinsky to B. MacFadden, mid 1970's).

The superfamily Tapiroidea has a fossil record extending back into the early Eocene, ~55 million years ago (MCKENNA & BELL 1997, COLBERT 2005, PALEOBIOLOGY DATABASE 2006, fig. 1). Here we present both qualitative and quantitative morphological results demonstrating the conservative nature of fossil tapirs as compared to a more rapidly evolving clade within the Perissodactyla, i.e., the classic example of fossil horses (family Equidae; e.g., SIMPSON 1953, MACFADDEN 1992). As we assert above, the bradytelic (i.e., very slow, *sensu* SIMPSON 1953) evolution in Cenozoic tapirs allows ecological interpretations relative to modern *Tapirus* far back into the fossil record.

Several previous studies have demonstrated that there are suites of qualitative morphological characters of the cranium and mandible in mammalian herbivores that represent adaptations for either browsing or grazing (SOLOUNIAS & MOELLEKEN 1993, MACFADDEN & SHOCKEY 1997, MENDOZA et al. 2002, tab. 1). Based on the distribution of these characters in the fossil record, it is known that browsing adaptations are primitive (plesiomorphic), whereas grazing characters are derived (apomorphic). These morphologies are illustrated (fig. 2) in four representative examples, the Oligocene tapiroid *Protapirus* and modern *Tapirus* as compared to the Oligocene equid *Mesohippus* and modern *Equus*. As can be seen in both table 1 and fig. 2, primitive morphologies of the cranium and mandible are demonstrated in *Protapirus*, *Mesohippus*, and *Tapirus*, whereas derived morphologies are demonstrated in *Equus*. This indicates that the adaptive morphology of *Tapirus* has evolved little since the early Cenozoic when both the Tapiroidea and Equidae had browsing adaptations (tab. 1, fig. 2). While the Equidae subsequently underwent explosive evolution in cranial and mandibular morphology, particularly since the Miocene (SIMPSON 1953, RADINSKY 1984, MACFADDEN 1992), tapirs demonstrate bradytelic evolution. The comparative evolution and analysis of multiple characters that are associated with dietary strategies strengthens our dietary interpretations through time.

Most of the evolution described above results from major morphological changes to the masticatory com-

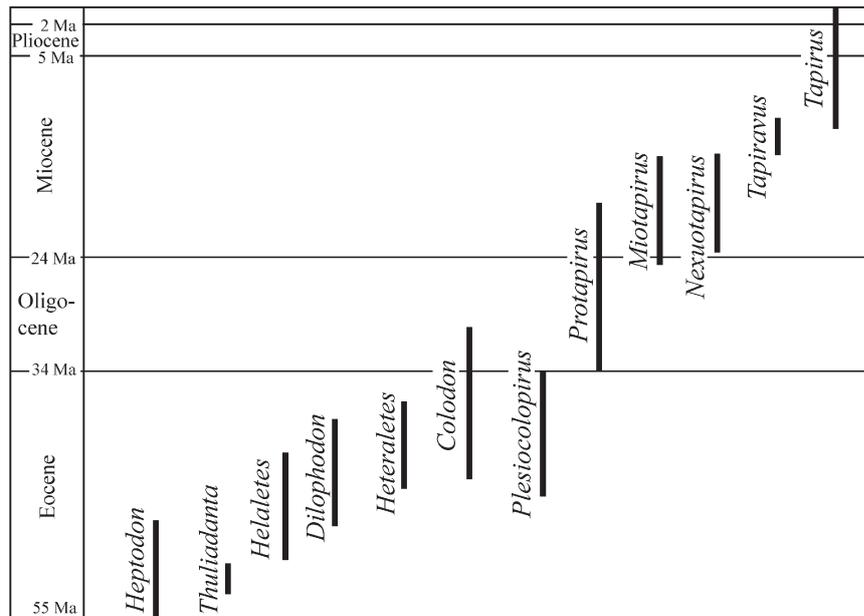


Fig. 1: Temporal distributions of the tapiroid genera analyzed in this study. The ranges are taken from the Paleobiology Database. Following MCKENNA & BELL (1997) and COLBERT (2005), *Heptodon* is included in the Tapiroidea.

plex, including the great expansion of cheek tooth crown heights observed in advanced horses (SIMPSON 1953, RADINSKY 1984, MACFADDEN 1992). Given the relatively common occurrence of fossil horse teeth, as opposed to the rarely preserved cranial and mandibular morphology, equid dentitions are frequently cited as prime examples of macroevolution. One such dental character, hypsodonty index (HI), is an informative means of comparing the evolutionary morphology in clades of mammalian herbivores. Previous studies have shown that extinct mammal species with HIs < 1 are primarily browsers and those with HIs > 1, although classically interpreted as primarily grazers (e.g., SIMPSON 1953, MACFADDEN 1992), actually have the evolutionary capacity to be either browsers or grazers (MACFADDEN et al. 1999, FERANEC 2003, MACFADDEN 2005). Horses were primitively short-crowned, with HIs all < 1 until about 20 million years ago. Thereafter, several clades of horses underwent explosive, rapid evolution of crown heights, resulting in HIs ranging from > 1 to 3 (fig. 3); although one equid clade, the browsing anchitheres, retained the primitive morphology. The explanation for this rapid increase in HIs during the Miocene is initially to exploit a new food resource, grasses, which were spreading over many continental landscapes. This “Great Transformation” (SIMPSON 1953, STROMBERG 2005) fundamentally affected both the morphological and ecological evolution of the Equidae. In contrast to the Equidae, a very different pattern is seen in the evolution of HIs in Tapiroidea (fig. 3). All tapiroid taxa measured for this study ranging in age from ~53 Ma to the present have HIs < 0.7. Thus, while horses were rapidly evolving in response to the changing environments, the bradytelic tapirs are characterized by stasis in crown heights.

Body size is a fundamentally important character in understanding ecological adaptations of individual species

(e.g., EISENBERG 1981). Although body size is difficult to estimate in extinct species, molar dimensions can serve as a proxy for relative body size (e.g., MACFADDEN 1986, DAMUTH & MACFADDEN 1990). In this paper, we use m1 length as a relative indicator of tapir body size. With the exception of the three modern species *T. terrestris*, *T. bairdii*, and *T. pinchaque* and the fossil taxon *Tapirus polkensis* that have declined in m1 length since the late Miocene, the m1 length within other species within the Tapiroidea has increased in size by about 2.5 times in approximately 50 million years (fig. 4). This increase in m1 length, and corresponding inferred body size increase, appears to be linear and relatively gradual, interpreted to represent relative stasis, both in morphology and diet. This is in contrast to the explosive pulse of evolution seen in fossil horses during the Neogene after about 20 million years ago (MACFADDEN 1986). As will be seen below, the conservative morphology and browsing diet demonstrated here for fossil tapirs are also corroborated by evidence from stable isotopes.

Stable Carbon Isotopes

In addition to the traditional method of interpreting extinct mammalian herbivores as grazers or browsers using morphological characters, stable carbon isotope ratios can be used to interpret ancient diets (CERLING et al. 1993, 1997, WANG et al. 1994, MACFADDEN & SHOCKEY 1997, MACFADDEN et al. 1999, ZAZZO et al. 2000). Stable carbon isotope analysis of fossil tooth enamel provides dietary information about the respective taxon, because carbon is incorporated into the lattice of enamel hydroxylapatite retaining an isotopic signal that is reflective of plants consumed (KRUEGER 1991, LEE-THORP & VAN DER MERWE 1991, CERLING et al.

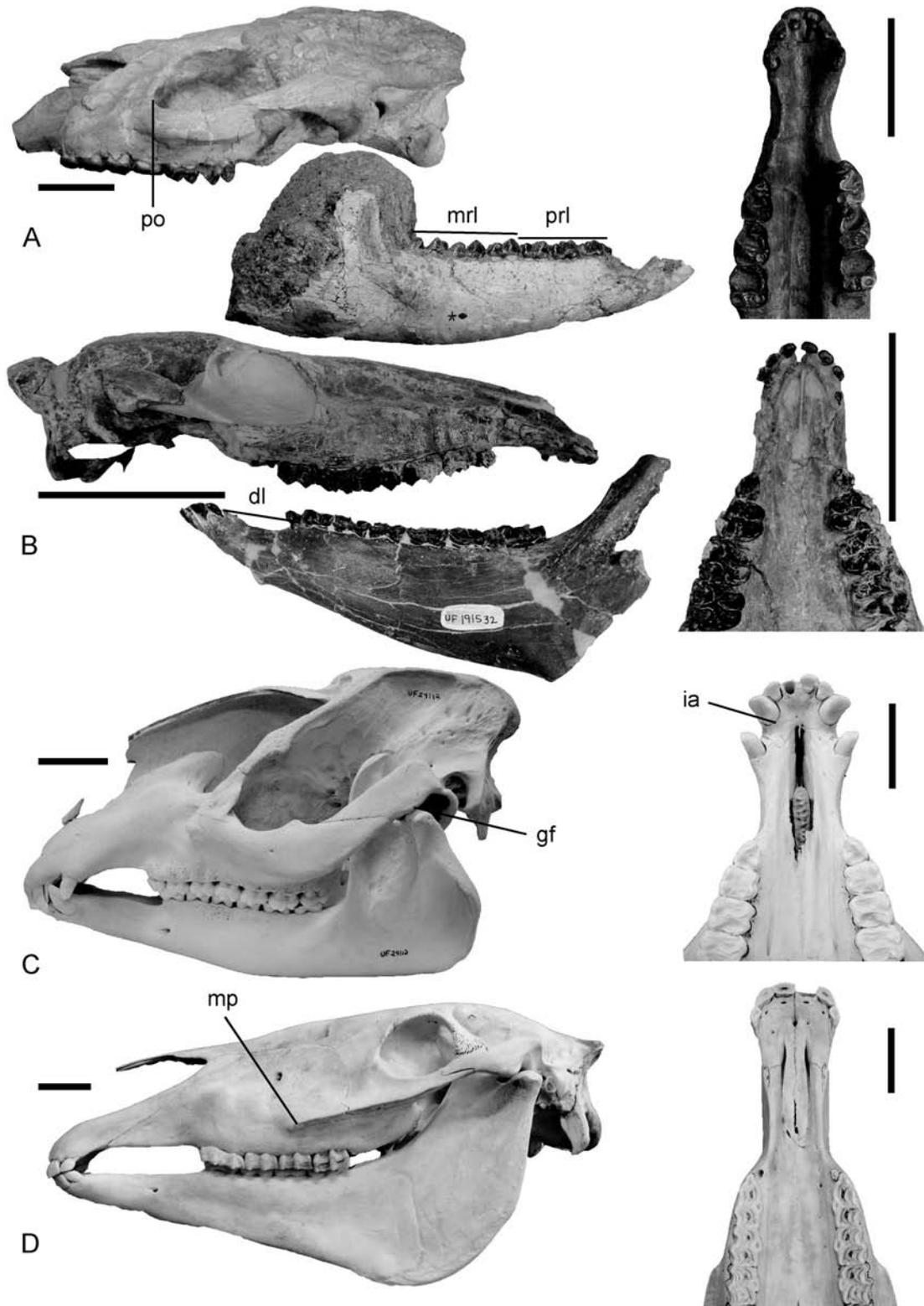


Fig. 2: Fossil specimens of the (A) tapirid *Protapirus* (left: YPM 11165; right: AMNH 661) from the middle Oligocene (“Protoceras beds”), South Dakota, and (B) equid *Mesohippus* (cranium, UF 201941, and UF 191532, mandible) from the late Eocene/early Oligocene White River Group, western Nebraska. Modern (C) tapir (*Tapirus*; UF 24112) and (D) horse (*Equus*; UF 225366) specimens are from the UF/FLMNH collection. Abbreviations are, as follows: dl=diastema length; gf=glenoid fossa; ia=incisor arcade; mrl=molar row length; mp=masseteric prominence; po=position of orbit; and, prl=premolar row length. All scale bars equal 5 cm.

Table 1: Comparison of craniodental features between the Oligocene tapiroid *Protapirus*, modern *Tapirus*, the Oligocene equid *Mesohippus*, and modern *Equus*. The craniodental features were modified from those compiled by MENDOZA et al. (2002). PRL=pre-molar row length, and MRL=molar row length.

Craniodental feature	<i>Protapirus</i> (Oligocene)	<i>Tapirus</i> (Modern)	<i>Mesohippus</i> (Oligocene)	<i>Equus</i> (Modern)
Hypsodonty Index	< 1	< 1	< 1	> 1
Relative size of incisors	I1 > I3	I1 > I3	I1 > I3	I1 ≈ I3
Shape of Incisor arcade	curved	curved	curved	straight
Relative length of premolar tooth row	PRL < MRL	PRL < MRL	PRL < MRL	PRL > MRL
Length of mandibular diastema	short	short	short	long
	<2 x m1 length	<2 x m1 length	<2 x m1 length	>2 x m1 length
Masseteric prominence above M1	absent	absent	absent	present
Position of the orbit	above or anterior to M2	above or anterior to M2	above or anterior to M2	posterior to M3
Anterior extension of the zygomatic arch	poorly developed	poorly developed	poorly developed	well developed
Height of the glenoid fossa above the occlusal plane	low	low	low	high

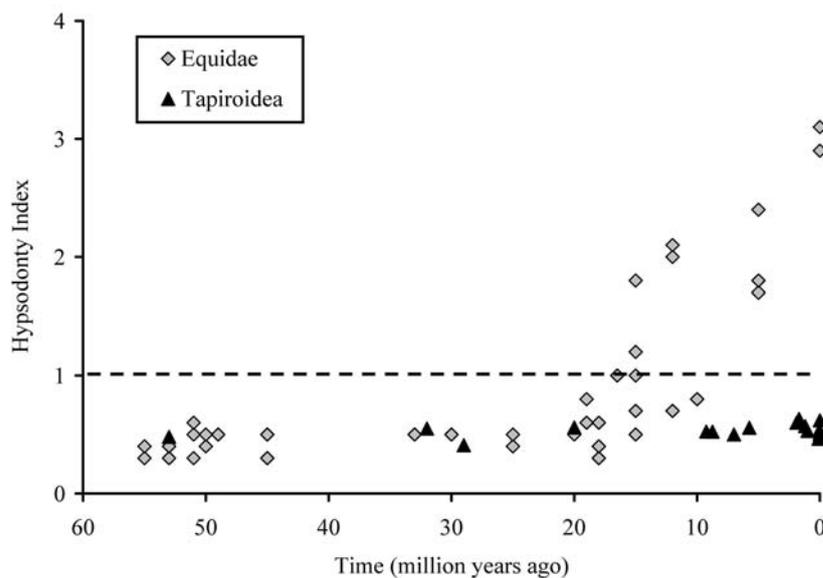


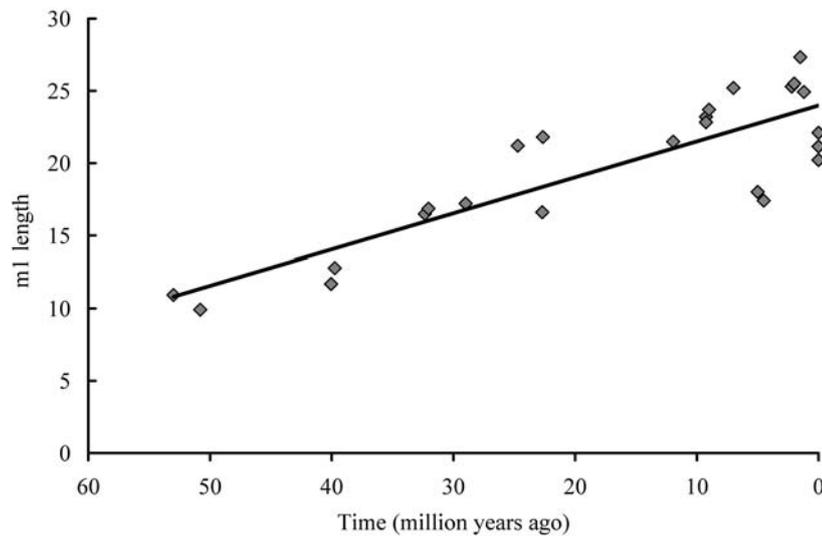
Fig. 3: Hypsodonty index of two contrasting clades of perissodactyls, i.e., Equidae and Tapiroidea, throughout the past 55 million years. Data for Equidae are taken from MACFADDEN (1992, fig. 11.6). Tapiroid values were measured from collections at the AMNH, YPM, and FLMNH. Mean values of the following taxa are included: *Colodon* (including *C. occidentalis*), *Heptodon*, *Miotapirus*, *Protapirus* (including *P. simplex*), *Tapiravus* (including *T. validus*), and *Tapirus* (including *T. bairdii*, *T. haysii*, *T. indicus*, *T. johnsoni*, *T. pinchaque*, *T. simpsoni*, *T. terrestris*, *T. veroensis*).

1997, CERLING & HARRIS 1999). Because $^{13}\text{C}/^{12}\text{C}$ ratios in plants vary depending on plant photosynthetic pathways and stable carbon isotopes do not decay with time (EHLERINGER & MONSON 1993) in the absence of diagenesis (postmortem chemical alteration), we can look at ^{13}C and ^{12}C ratios of the past similarly to ratios of ^{13}C and ^{12}C today (CERLING et al. 1997). The $\delta^{13}\text{C}$ values of medium to large-bodied ungulates are enriched by approximately 14.1 ‰ (although non-ruminants, such as tapirs, may be enriched by 12–13 ‰), as compared to plants consumed (CERLING & HARRIS 1999). Therefore, enamel $\delta^{13}\text{C}$ values ≤ -9 ‰ (possibly as enriched as -7 ‰ due to modern atmospheric CO_2 enrichment; CERLING et al. 1997, PASSEY et al. 2002) reflect a pure C_3 diet and $\delta^{13}\text{C}$ values ≥ -2 ‰ indicate a

predominantly C_4 diet (MACFADDEN et al. 1996, CERLING et al. 1997, 1999, 2004, CERLING & HARRIS 1999).

Stable carbon isotopes of extinct/extant taxa can also be used to reconstruct forest canopy density due to greater ^{13}C discrimination occurring in dense closed canopies as compared to less dense/open C_3 environments (VAN DER MERWE & MEDINA 1989, CERLING et al. 2004). Since $\delta^{13}\text{C}$ values increase with decreasing canopy density and/or increasing distance from dense forest edges (VAN DER MERWE & MEDINA 1989, KAPOS et al. 1993, WEST et al. 2001), more depleted $\delta^{13}\text{C}$ values of mammalian herbivores reflect the consumption of browse in denser canopied forests (VAN DER MERWE & MEDINA 1991, CERLING et al. 2004). By examining the stable isotopes of

Fig. 4: North American fossil tapiroid and extant Central American and South American tapir m1 lengths through time as a proxy for body size evolution. The linear regression of all data analyzed, $R^2=0.73$. If one excludes the three extant tapirs (*T. bairdii*, *T. pinchaque*, and *T. terrestris*) and the fossil *Tapirus polkensis*, which demonstrate recent declines in body size since the late Miocene, $R^2=0.94$. Data were measured from specimens at the AMNH, YPM, FLMNH, and compiled from the Paleobiology Database (<http://paleodb.org>). The following taxa were included: *Colodon* (including *C. occidentalis*), *Helaletes*, *Heptodon*, *Miotapirus*, *Nexuotapirus* (including *N. marslandensis*, *N. robustus*), *Plesiocolopirus* (including *P. hancocki*), *Protapirus* (including *P. obliquidens*, *P. simplex*), *Tapiravus* (including *T. validus*), and *Tapirus* (including *T. bairdii*, *T. haysii*, *T. indicus*, *T. johnsoni*, *T. pinchaque*, *T. simpsoni*, *T. terrestris*, *T. veroensis*).



fossil tapirs and other extinct mammalian herbivores, we can document dietary changes through time.

Stable carbon isotopes of fossil tapir enamel have been analyzed from several North American sites spanning the past ~10 million years (MACFADDEN & CERLING 1996, KOCH et al. 1998, KOHN et al. 2005, FERANEC & MACFADDEN 2006, fig. 5). The localities included in our analysis are, from oldest to youngest (Ma): Love Bone Bed (~9.5); McGehee and Mixons (~7.5); Withlacoochee (~7); Palmetto (~4.5); Haile 15A, Macasphalt, Port Charlotte, Punta Gorda and Santa Fe 1 (~2.5); Leisey 1A (~1.5); Harleyville (~0.4); Cutler, Hornsby Springs, Ichetucknee, Page-Ladson, Rock Springs, and Santa Fe (~0.1–0.01) (MACFADDEN & CERLING 1996, KOCH et al. 1998, KOHN et al. 2005, FERANEC & MACFADDEN 2006, fig. 5). Fossil tapirs consistently demonstrate diets composed of predominantly C_3 vegetation, with enamel $\delta^{13}C$ values ranging from -10.1 to -14.3 ‰ (fig. 5). Additionally, fossil tapirs likely maintain their presence in denser canopied forests because their $\delta^{13}C$ values consistently are among the most depleted isotopic values as compared to other co-occurring mammalian herbivores (fig. 5). For example, fossil horses from these sites demonstrate a pattern different from tapirs, instead consuming more isotopically enriched vegetation (fig. 5).

Since their first appearance approximately 2.5–1.5 Ma during the Great American Biotic Interchange (STEHLI

& WEBB 1985), fossil and extant South American tapirs inhabit dense canopied environments, as inferred from stable isotopes (MACFADDEN & SHOCKEY 1997, DESANTIS 2005). MACFADDEN & SHOCKEY (1997) interpreted *Tapirus tarijensis* as a browser (based on morphological characters), along with peccaries (*Tayassu* sp.), deer (*Hippocamelus* sp.), and llamas (*Palaeolama weddelli*) at the Tarija Pleistocene (0.5 to 1.0 Ma) site in Bolivia. As is also seen in ancient North American ecosystems, the isotopic values of *T. tarijensis* of -13.4 to -10.5 ‰ are among the most depleted of all herbivores sampled within the Tarija fauna (total whole faunal range of -13.4 to -3.4 ‰; MACFADDEN & SHOCKEY 1997). Similarly, the modern tapir *Tapirus bairdii* (from specimens collected between 1873–74 in Acapulco, Mexico) demonstrates mean $\delta^{13}C$ values of -14.6 ‰ (DESANTIS 2005), consistent with their classification as forest occupying browsers. Because tapirs consume fruits that have isotopic values more enriched than corresponding sub-canopy foliage (due to vertical stratification of $\delta^{13}C$ values; VAN DER MERWE & MEDINA 1989, CERLING et al. 2004) their dietary $\delta^{13}C$ values are likely more enriched than the foliage in these environments. Therefore, tapirs likely reside in even more densely forested environments than indicated isotopically. In conjunction with their conservative morphology, the depleted $\delta^{13}C$ values justify tapirs as robust indicators of forested environments in Deep Time.

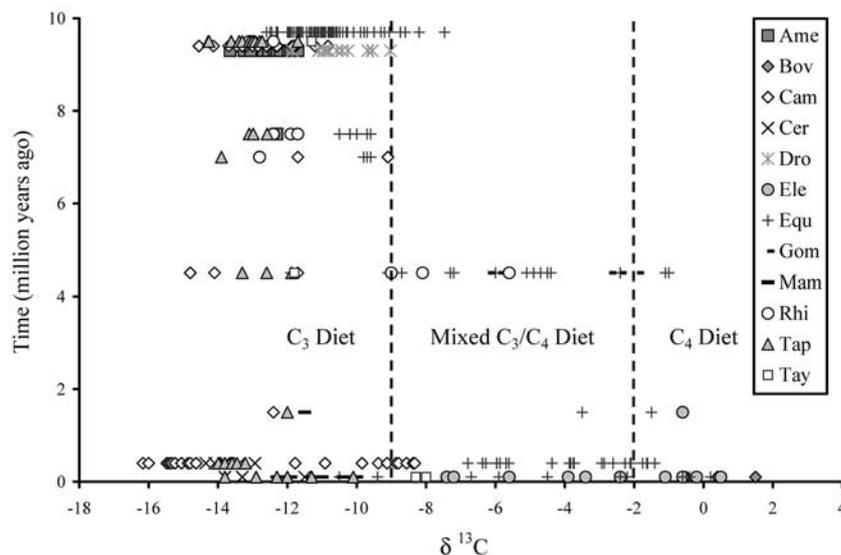


Fig. 5: Carbon isotope data for tooth enamel of fossil tapirs and their associated faunas for the past 10 million years in North America (compiled from MACFADDEN & CERLING 1996, KOCH et al. 1998, KOHN et al. 2005, FERANEC & MACFADDEN 2006). Additional new isotope data sampled from the McGehee and the Palmetto Fauna localities in Florida are also included. Family abbreviations are, as follows (number of samples noted in parentheses): Ame=Amebelodontidae (N=12), Bov=Bovidae (N=3), Cam=Camelidae (N=51), Cer=Cervidae (N=9), Dro=Dromomerycidae (N=11), Ele=Elephantidae (N=11), Equ=Equidae (N=141), Gom=Gomphotheriidae (N=5), Mam=Mammutidae (N=14), Rhi=Rhinocerotidae (N=12), Tap=Tapiridae (N=33), and Tay=Tayassuidae (N=4). Each data point represents a single specimen. Additionally, all data points between 9–10 Ma are from the Love Bone Bed Local Fauna ~9.5 Ma; however, they are slightly offset to improve visual clarity.

Distributions

From the Paleocene-Eocene Thermal Maximum to the Miocene-Pliocene expansion of C_4 grasslands, North America underwent great environmental change throughout the Cenozoic. Paleobotanical studies document dramatic vegetation shifts in mesothermal (i.e. moderate moisture and heat with mean temperatures between 15–20 °C, *sensu* WOLFE 1975 modified from DE CANDOLLE 1874) broad-leaved evergreen forests, contracting from Eocene distributions of 60° latitude from the equator, to only 35° during the sharp cooling of the early Oligocene (POTTS & BEHRENSMEYER 1992, WING 1998). Megathermal (i.e. humid and warm with mean temperatures ≥ 20 °C, *sensu* DE CANDOLLE 1874) vegetation also became restricted to within 15° from the equator during the Oligocene, compared to early Eocene latitudinal distributions of 60–65° and modern ranges of 20–25° (POTTS & BEHRENSMEYER 1992). Corresponding to these shifts in vegetation, cooling occurred from the late Eocene to early Miocene, with periodic warming events that consistently declined in temperature from preceding warming events (WOLFE 1994). While these changes in forest distributions are inferred from paleobotanical evidence including pollen, plant macrofossils, and subsequent Climate-Leaf Analy-

sis Multivariate Program (CLAMP) analyses, tapirs can provide an independent line of evidence for the presence of ancient forests in Deep Time. As COLBERT and SCHOCH (1998) suggested, the lack of significant tapiroid remains in the Oligocene and Miocene may be a result of declines in the mesothermal forests they likely inhabited.

The Paleobiology Database (2006) is a valuable tool for analyzing the distribution of ancient faunas both temporally and spatially. Using the Paleobiology Database (2006), we generated maps of tapiroid distributions in North and Central America from the Eocene to the present (tab. 2, fig. 6). During the Eocene, tapiroid distributions are most wide-ranging, extending from central Mexico to Arctic Canada (tab. 2, fig. 6). The widespread distribution of Tapiroidea during the Eocene correlates with paleobotanical evidence that suggests extensive mesothermal and megathermal vegetation ranges with boreotropical flora extending to at least 65° N in North America (WOLFE 1975, WING & SUES 1992, WING 1998). However, based on the presence of tapiroids at latitudes up to 78.5° N during the Eocene, boreotropical flora may have extended farther north than previously anticipated. This is in agreement with the presence of semi-tropical fossil forests found at Axel Heiberg Island of ~80° N latitude (CHRISTIE & McMILLAN 1991). Additionally, the

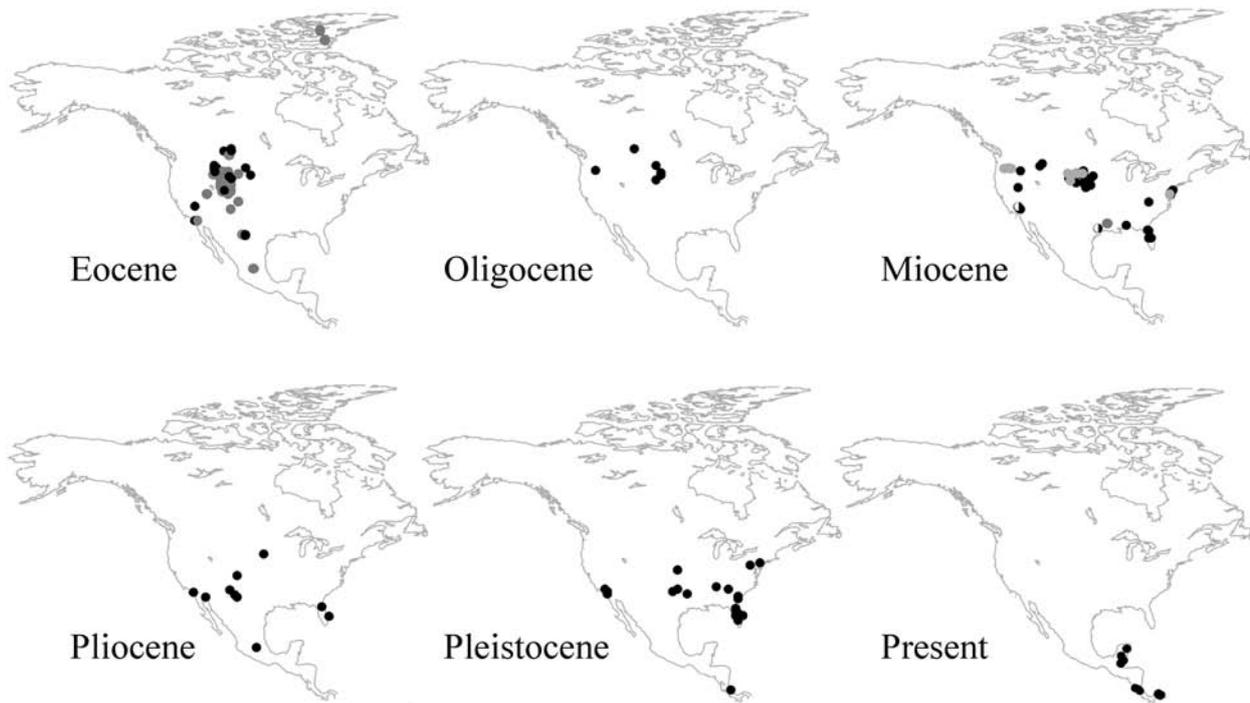


Fig. 6: Maps of tapiroid localities on continental North America from the Eocene through the present. The maps were created from the Paleobiology Database (<http://paleodb.org>). For the Eocene, gray circles (●) indicate early Eocene (Wasatchian, Bridgerian; ~55–46 Ma) localities and black circles (●) represent late Eocene (Uintan, Chadronian; ~46–34 Ma) sites. The Miocene is also sub-divided, with gray circles (●) signifying early Miocene (late Arikarean, Hemingfordian, Barstovian; ~24–11 Ma) ages, black circles (●) representing the late Miocene (Clarendonian, Hemphillian; ~11–5 Ma), and black and white circles (●) indicating undifferentiated Miocene localities. Additionally, present tapir distributions as summarized from the IUCN Tapir Status Survey and Conservation Action Plan (Brooks et al. 1997) were added to the present maps.

dramatic decline in tapiroid latitudinal ranges during the Oligocene (tab. 2, fig. 6) is likely a result of sharp global cooling that decreased their mesothermal habitats (COLBERT & SCHOCH 1998, WING 1998). After the Oligocene, tapiroid ranges expand through the Pleistocene (tab. 2, fig. 6) concurrently with fluctuating warming and cooling events (including the Miocene Thermal Maximum at ~16 Ma; WING 1998). These tapiroid range expansions oc-

Table 2: Summary of Paleodatabase (2006) results of tapiroid localities in North and Central America. Additionally, Holocene collections include present localities taken from the IUCN Tapir Status Survey and Conservation Action Plan (Brooks et al. 1997).

Geological Epoch	Age Range (million years ago)	Latitudinal Range	Total Latitudinal Range
Eocene	54.8–33.7	21° N to 79° N	58
Oligocene	33.7–23.8	42° N to 50° N	8
Miocene	23.8–5.3	28° N to 46° N	18
Pliocene	5.3–1.8	20° N to 42° N	22
Pleistocene	1.8–0.01	9° N to 40° N	31
Holocene	0.01–present	9° N to 21° N	12

cur from northern to southern regions with relatively consistent upper latitudinal range limits of between 40–46° N, from the Miocene to the Pleistocene (tab. 2, fig. 6). Subsequently, the upper range limits of *Tapirus* contracted from 40° to 21° N during the last ~2 million years (tab. 2, fig. 6). This recent contraction likely resulted from the inability of *Tapirus* to live in the seasonally cool and/or glacially inundated higher latitudes. Overall, tapiroid distributions correlate well with paleobotanically derived climatic inferences. Along with tapiroid morphology and isotopic data, these distribution maps provide reconstructions of ancient forested environments with both temporal and spatial resolution.

Concluding Remarks

Cenozoic tapirs have been under appreciated, mostly because as LEN RADINSKY noted in the 1970's, the most interesting phases of their evolution occurred during the Eocene. Thereafter, despite significant global change in terrestrial ecosystems, tapirs are prime examples of SIMPSON's (1953)

concept of bradytely, i.e., a group demonstrating slow, or arrested evolution. This mostly resulted from Tapiroids being well adapted to their respective adaptive zone (niche complex in modern parlance) in ancient forests. Tapirs may not be a good group to investigate evolution “in the fast lane”, but they are model taxa for paleoecological reconstructions. Our morphologic, isotopic, and biogeographic analyses presented above indicate that tapiroids are excellent indicators of ancient forested environments, and adds to our knowledge of these ancient habitat types based on other fossil evidence, e.g., as derived from paleobotany. As additional localities are discovered and analyzed in the future, we are bound to find more evidence of herbivore-plant interactions such as those exemplified by extinct forest-dwelling tapirs.

Acknowledgements

We are grateful for the opportunity to have participated in the Dilcher-Wolfe Symposium and for the invitation to develop this paper as part of the Festschrift. We thank the following persons for access to, and help with, the relevant collections of tapirs under their care; J. FLYNN, Vertebrate Paleontology, AMNH; E. WESTWIG, Mammals, AMNH; K. ZYSKOWSKI and G. WATKINS-COLWELL, Vertebrate Zoology, YPM; and W. JOYCE, Vertebrate Paleontology, YPM. Additionally, we would like to thank our reviewers and R. HULBERT for comments on this manuscript. Our study benefited from the data compiled and mapping algorithms in the Paleobiology Database project (<http://paleodb.org>). This study was supported by the Lucy Dickinson Scholarship and the Vertebrate Paleontology funds at the Florida Museum of Natural History, UF. This paper is University of Florida Contribution to Paleobiology number 593 and Paleobiology Database publication number 57.

References

- BODMER, R. E. (1990): Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). — *Journal of Zoology*, **222**: 121–128.
- BODMER, R. E. (1991): Influence of digestive morphology on resource partitioning in Amazonian ungulates. — *Oecologia*, **85**: 361–365.
- BROOKS, D. M., BODMER, R. E. & MATOLA, S. (1997): Tapirs – status survey and conservation action plan. — I–VIII, 1–164; Gland (IUCN/SSC Tapir Specialist Group).
- CERLING, T. E. & HARRIS, J. M. (1999): Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. — *Oecologia*, **120**: 247–363.
- CERLING, T. E., HARRIS, J. M. & LEAKEY, M. G. (1999): Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. — *Oecologia*, **120**: 364–374.
- CERLING, T. E., HART, J. A. & HART, T. B. (2004): Stable isotope ecology in the Ituri forest. — *Oecologia*, **138**: 5–12.
- CERLING, T. E., WANG, Y. & QUADE, J. (1993): Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene. — *Nature*, **361**: 344–345.
- CERLING, T. E., HARRIS, J. M., MACFADDEN, B. J., LEAKEY, M. G., QUADE, J., EISENMANN, V. & EHLERINGER, J. R. (1997): Global vegetation on change through the Miocene/Pliocene boundary. — *Nature*, **389**: 153–158.
- CHRISTIE, R. L. & McMILLAN, N. J. (Eds.) (1991): Tertiary Fossil Forests of the geodetic hills, Axel Heiberg Island, Arctic Archipelago. Geological Survey of Canada, Bulletin, **403**: 1–227.
- COLBERT, M. W. (2005): The facial skeleton of the Early Oligocene *Colodon* (Perissodactyla, Tapiroidea). — *Palaeontologia Electronica*, **8**: 12 A, 1–27.
- COLBERT, M. W. & SCHOCH, R. M. (1998): Tapiroidea and other morphomorphs. — In: JANIS, C. M., SCOTT, K. M. & JACOBS, L. L. (Eds.): Evolution of Tertiary Mammals of North America, **1**. — 569–582; Cambridge (Cambridge University Press).
- COPLEN, T. B. (1994): Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. — *Pure and Applied Chemistry*, **66**: 273–276.
- DAMUTH, J. & MACFADDEN, B. J. (Eds.) (1990): Body size in mammalian paleobiology: estimation and biological implications. — I–XII, 1–397; New York (Cambridge University Press).
- DE CANDOLLE, A. P. A. (1874): Constitution dans le règne végétal de groupes physiologiques applicables à la géographie botanique ancienne et moderne. — *Archives des Science Physiques et Naturelles*, **50**: 5–42.
- DE NIRO, M. J. & EPSTEIN, S. (1978): Influence of diet on the distribution of carbon isotopes in animals. — *Geochimica et Cosmochimica Acta*, **42**: 495–506.
- DE SANTIS, L. R. G. (2005): Straight from the tapir’s mouth: applying stable isotope analyses of extant tapirs to constrain paleoecological hypotheses. — In: KELLNER, A. W. A., HENRIQUES, D. R. H. & RODRIGUES, T. (Eds.): Congresso Latino-Americano de paleontologia de vertebrados: boletim de resumos, **2**: 94–95; Rio de Janeiro (Museu Nacional).
- DOWNER, C. C. (1996): The mountain tapir, endangered ‘flagship’ of the high Andes. — *Oryx*, **30**: 4458.
- DOWNER, C. C. (2001): Observations on the diet and habitat of the mountain tapir (*Tapirus pinchaque*). — *Journal of Zoology*, **254**: 279–291.
- EBERLE, J. J. (2005): A new ‘tapir’ from Ellesmere Island, Arctic Canada – Implications for northern high latitude paleobiogeography and tapir palaeobiology. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **227**: 311–322.
- EHLERINGER, J. R. & MONSON, R. K. (1993): Evolutionary and ecological aspects of photosynthetic pathway variation. — *Annual Review of Ecology and Systematics*, **24**: 411–439.
- EISENBERG, J. F. (1981): The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. — 1–610; Chicago (University of Chicago Press).
- FERANEC, R. S. (2003): Stable isotopes, hypsodonty, and the paleodiet of *Hemiauchenia* (Mammalia: Camelidae): a morphological specialization creating ecological generalization. — *Paleobiology*, **29**: 230–242.
- FERANEC, R. S. & MACFADDEN, B. J. (2006): Isotopic discrimination of resource partitioning among ungulates in C3-dominated communities from the Miocene of California and Florida. — *Paleobiology*, **32**: 191–205.
- FOERSTER, C. R. & VAUGHAN, C. (2002): Home range, habitat use, and activity of Baird’s tapir in Costa Rica. — *Biotropica*, **34**: 423–437.
- GALETTI, M., KEUROGHILIAN, A., HANADA, L. & MORATO, M. I. (2001): Frugivory and seed dispersal by the lowland tapir (*Tapirus terrestris*) in southeast Brazil. — *Biotropica*, **33**: 723–726.
- HENRY, O., FEER, F. & SABATIER, D. (2000): Diet of the lowland tapir (*Tapirus terrestris* L.) in French Guiana. — *Biotropica*, **32**: 364–368.
- HOLDEN, J., YANUAR, A. & MARTY, D. J. (2003): The asian tapir in Kerinci Seblat National Park, Sumatra: evidence collected through photo-trapping. — *Oryx*, **37**: 34–40.
- JANIS, C. M., DAMUTH, J. & THEODOR, J. M. (2000): Miocene ungulates and terrestrial primary productivity: Where have all of the browsers gone? — *Proceedings of the National Academy of Sciences*, **97**: 7899–7904.
- KAPOS, V., GANADE, G., MATSUI, E. & VICTORIA, R. L. (1993): $\delta^{13}\text{C}$ as an indicator of edge effects in tropical rainforest reserves. — *Journal of Ecology*, **81**: 425–432.

- KOCH, P. L., DIFFENBAUGH, N. S. & HOPPE, K. A. (2004): The effects of the late quaternary climate and $p\text{CO}_2$ change on C_4 plant abundance in the south-central United States. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **207**: 331–357.
- KOCH, P. L., HOPPE, K. A. & WEBB, S. D. (1998): The isotopic ecology of late Pleistocene mammals in North America – Part 1. Florida. — *Chemical Geology*, **152**: 119–138.
- KOCH, P. L., TUROSS, N. & FOGEL, M. L. (1997): The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. — *Journal of Archaeological Science*, **24**: 417–429.
- KOHN, M. J., MCKAY, M. P. & KNIGHT, J. L. (2005): Dining in the Pleistocene – Who's on the menu? — *Geology*, **33**: 649–652.
- KRUEGER, H. W. (1991): Exchange of carbon with biological apatite. — *Journal of Archaeological Science*, **18**: 355–361.
- LEE-THORP, J. A. & VAN DER MERWE, N. J. (1991): Aspects of the chemistry of modern and fossil biological apatites. — *Journal of Archaeological Science*, **18**: 343–354.
- LIZCANO, D. J. & CAVELIER, J. (2004): Características químicas de salados y hábitos alimenticios de la danta de montaña (*Tapirus pinchaque* Roulin, 1829) en los Andes Centrales de Colombia. — *Mastozoología Neotropical*, **11**: 193–201.
- MACFADDEN, B. J. (1986): Fossil horses from “Eohippus” (*Hyracotherium*) to *Equus*: scaling, Cope's law, and the evolution of body size. — *Paleobiology*, **12**: 355–369.
- MACFADDEN, B. J. (1992): Fossil horses – systematics, paleobiology, and evolution of the Family Equidae. — I–X, 1–369; New York (Cambridge University Press).
- MACFADDEN, B. J. (2005): Diet and habitat of toxodont megaherbivores (Mammalia, Notoungulata) from the late Quaternary of South and Central America. — *Quaternary Research*, **64**: 113–124.
- MACFADDEN, B. J. & CERLING, T. E. (1996): Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: A 10 million-year sequence from the Neogene of Florida. — *Journal of Vertebrate Paleontology*, **16**: 103–115.
- MACFADDEN, B. J. & HIGGINS, P. (2004): Ancient ecology of 15-million-year-old browsing mammals within C_3 plant communities from Panama. — *Oecologia*, **140**: 169–182.
- MACFADDEN, B. J. & SHOCKEY, B. J. (1997): Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. — *Paleobiology*, **23**: 77–100.
- MACFADDEN, B. J., CERLING, T. E. & PRADO, J. (1996): Cenozoic terrestrial ecosystem evolution in Argentina: evidence from carbon isotopes of fossil mammal teeth. — *Palaios*, **11**: 319–327.
- MACFADDEN, B. J., SOLOUNIAS, N. & CERLING, T. E. (1999): Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. — *Science*, **283**: 824–827.
- MCKENNA, M. C. & BELL, S. K. (1997): Classification of mammals above the species level. — I–XII, 1–631; New York (Columbia University Press).
- MENDOZA, M., JANIS, C. M. & PALMQUIST, P. (2002): Characterizing complex craniodental patterns related to feeding behavior in ungulates: a multivariate approach. — *Journal of Zoology*, **258**: 223–246.
- PALEOBIOLOGY DATABASE (2006): Tapiroidea. — *Paleobiology Database Online Archives* (<http://paleodb.org>).
- PASSEY, B. H., CERLING, T. E., PERKINS, M. E., VOORHIES, M. R., HARRIS, J. M. & TUCKER, S. T. (2002): Environmental change in the Great Plains: an isotopic record from fossil horses. — *Journal of Geology*, **110**: 123–140.
- POTTS, R. & BEHRENSMEYER, A. K. (1992): Late Cenozoic Terrestrial Ecosystems. — In: BEHRENSMEYER, A. K., DAMUTH, J. D., DiMICHELE, W. A., POTTS, R., SUES, H.-D. & WING, S. L. (Eds.): *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. — 419–541; Chicago (University of Chicago Press).
- QUADE, J., CERLING, T. E., BARRY, J. C., MORGAN, M. E., PILBEAM, D. R., CHIVAS, A. R., LEE-THORP, J. A. & VAN DER MERWE, M. J. (1992): A 16-Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. — *Chemical Geology*, **94**: 183–192.
- RADINSKY, L. R. (1984): Ontogeny and phylogeny in horse skull evolution. — *Evolution*, **38**: 1–15.
- RESTALLACK, G. J. (2001): Cenozoic expansion of grasslands and climatic cooling. — *Journal of Geology*, **109**: 407–426.
- SALAS, L. A. (1996): Habitat use by lowland tapirs (*Tapirus terrestris* L.) in the Tabaro River Valley, southern Venezuela. — *Canadian Journal of Zoology*, **74**: 1452–1458.
- SIMPSON, G. G. (1953): *The major features of evolution*. — 1–434; New York (Columbia University Press).
- SOLOUNIAS, N. & MOELLEKEN, S. M. C. (1993): Dietary adaptation of some extinct ruminants determined by premaxillary shape. — *Journal of Mammalogy*, **74**: 1059–1071.
- STEHLE, F. G. & WEBB, S. D. (Eds.) (1985): *The great American biotic interchange*. — I–XVII, 1–532; New York (Plenum Press).
- STROMBERG, C. A. E. (2005): Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. — *Proceedings of the National Academy of Sciences*, **102**: 11980–11984.
- TOBLER, M. W. (2002): Habitat use and diet of Baird's tapirs (*Tapirus bairdii*) in a montane cloud forest of the Cordillera de Talamanca, Costa Rica. — *Biotropica*, **34**: 468–474.
- VAN DER MERWE, N. J. & MEDINA, E. (1989): Photosynthesis and $^{13}\text{C}/^{12}\text{C}$ ratios in Amazonian rain forests. — *Geochimica et Cosmochimica Acta*, **53**: 1091–1094.
- VAN DER MERWE, N. J. & MEDINA, E. (1991): The canopy effect, carbon isotope ratios and foodwebs in Amazonia. — *Journal of Archaeological Science*, **18**: 249–259.
- WANG, Y., CERLING, T. E. & MACFADDEN, B. J. (1994): Fossil horses and carbon isotopes: new evidence for Cenozoic dietary, habitat, and ecosystem changes in North America. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **107**: 269–279.
- WEST, A. G., MIDGLEY, J. J. & BOND, W. J. (2001): The evaluation of $\delta^{13}\text{C}$ isotopes of trees to determine past regeneration environments. — *Forest Ecology and Management*, **147**: 139–149.
- WING, S. L. (1998): Tertiary vegetation of North America as a context for mammalian evolution. — In: JANIS, C. M., SCOTT, K. M. & JACOBS, L. L. (Eds.): *Evolution of Tertiary Mammals of North America*, **1**: 37–65; Cambridge (Cambridge University Press).
- WING, S. L. & SUES, H.-D. (1992): Mesozoic and Early Cenozoic Terrestrial Ecosystems. — In: BEHRENSMEYER, A. K., DAMUTH, J. D., DiMICHELE, W. A., POTTS, R., SUES, H.-D. & WING, S. L. (Eds.): *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. — 327–416; Chicago (University of Chicago Press).
- WING, S. L., HARRINGTON, G. J., SMITH, F. A., BLOCH, J. I., BOYER, D. M. & FREEMAN, K. H. (2005): Transient floral change and rapid global warming at the Paleocene-Eocene boundary. — *Science*, **310**: 993–996.
- WOLFE, J. A. (1975): Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary. — *Annals of the Missouri Botanical Garden*, **62**: 264–279.
- WOLFE, J. A. (1994): Tertiary climatic changes at middle latitudes of western North America. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **108**: 195–205.
- ZAZZO, A., BOCHERENS, H., BRUNET, M., BEAUVILAIN, A., BILLIQU, D., TAISSO MACKAYE, H., VIGNAUD, P. & MARIOTTI, A. (2000): Herbivore paleodiet and paleoenvironmental changes in Chad during the Pliocene using stable isotope ratios of tooth enamel carbonate. — *Paleobiology*, **26**: 294–309.

