Palaeogeography, Palaeoclimatology, Palaeoecology 267 (2008) 175–184

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

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

Paleobiogeography of Miocene Equinae of North America: A phylogenetic biogeographic analysis of the relative roles of climate, vicariance, and dispersal

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ARTICLE INFO

Article history:
Received 16 November 2007
Received in revised form 19 May 2008
Accepted 18 June 2008

Keywords:
Radiation
Geodispersal
Great Plains Grassland
Neogene
Climate Change

ABSTRACT

The horse subfamily Equinae underwent a major radiation during the Miocene in North America, diversifying from one species, *Parahippus leonensis*, to 70 species. This radiation has been linked to climatic and vegetation changes that occurred in North America during this time. However, the relationship between climate change and speciation has not previously been studied quantitatively using phylogenetic biogeography. Distribution and age-range data were collected for all North American species within eighteen equine genera through a literature review and use of the Paleobiology Database. Fitch parsimony analysis of the taxon-area cladogram indicate that speciation by dispersal (Allopatry model II) was more common in the evolution of the clade than speciation by vicariance (Allopatry model I). Distribution data were analyzed using the Lieberman-modified Brooks Parsimony Analysis (LBPA) to determine patterns of vicariance and geodispersal, using four constrained biogeographic regions within North America in the analysis: the Great Plains, the Southwest, the Gulf Coast and the Southeast. Resulting general area cladograms are congruent with geological events, such as uplift of the Rocky Mountains, and climatic conditions, such as the change from a warm and moist to cool and arid climate during the Miocene. Well supported vicariance and geodispersal trees derived from the LBPA analysis are largely congruent with each other, indicating that cyclical events, in particular, climate change during the Miocene influenced the radiation of the clade.

1. Introduction

The coevolution of the Earth and its biota has long been studied to investigate speciation and the process of evolution (Wallace, 1855; Valentine and Moores, 1970; Mayr, 1982; Tiffney and Niklas, 1990; Lieberman, 2000). Depending on where and when an organism lived, large scale Earth history events (orogenesis, continental fragmentation) or climatic change may have resulted in environmental changes which led to the divergence of populations and ultimately speciation. By analyzing the distribution of the species within a phylogenetic framework, it is possible to elucidate the roles of climatic change and/or Earth history events influencing speciation (Lieberman, 2000). Deciphering the influences of speciation and subsequent evolution within a lineage provides insight into how these taxa interacted with their environment in the past, and potentially, may predict how similar taxa may react to present and future environmental change.

This study quantitatively assesses paleobiogeographic patterns within North American members of the subfamily Equinae during their Miocene radiation using phylogenetic biogeography. The subfamily Equinae is an excellent candidate for phylogenetic biogeographic study because evolutionary relationships between the species within the clade are well constrained (MacFadden, 1998; Hulbert, pers. communication 2007) (Fig. 1) and the fossil record of horses is densely sampled in North America during this interval (MacFadden, 1992) (Fig. 2). These two factors combine to create a strong evolutionary and taphonomic framework in which to examine biogeographic response to climate change. In particular, we evaluate (1) the dominant style of speciation apparent in the clade, (2) the relationship among biogeographic areas inhabited, and (3) the relative roles of climatic versus tectonic events during the evolution of the group.

Analyzing species ranges and distributions within a phylogenetic framework will provide additional insight into the radiation of the subfamily Equinae during climate change and the subsequent extinction of the clade. The dramatic radiation of the horse subfamily, Equinae, is often cited as a classic example of an adaptive radiation, reflecting rapid speciation in response to environmental change (e.g., MacFadden and Hulbert, 1988; Hulbert, 1993). During the Early Miocene, this clade consisted of a single species, *Parahippus leonensis*, but by the Late Miocene had diversified into 70 named species belonging to 18 named genera (Fig. 1) (MacFadden, 1992). This diversification occurred contemporaneously with environmental

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doi:10.1016/j.palaeo.2008.06.014

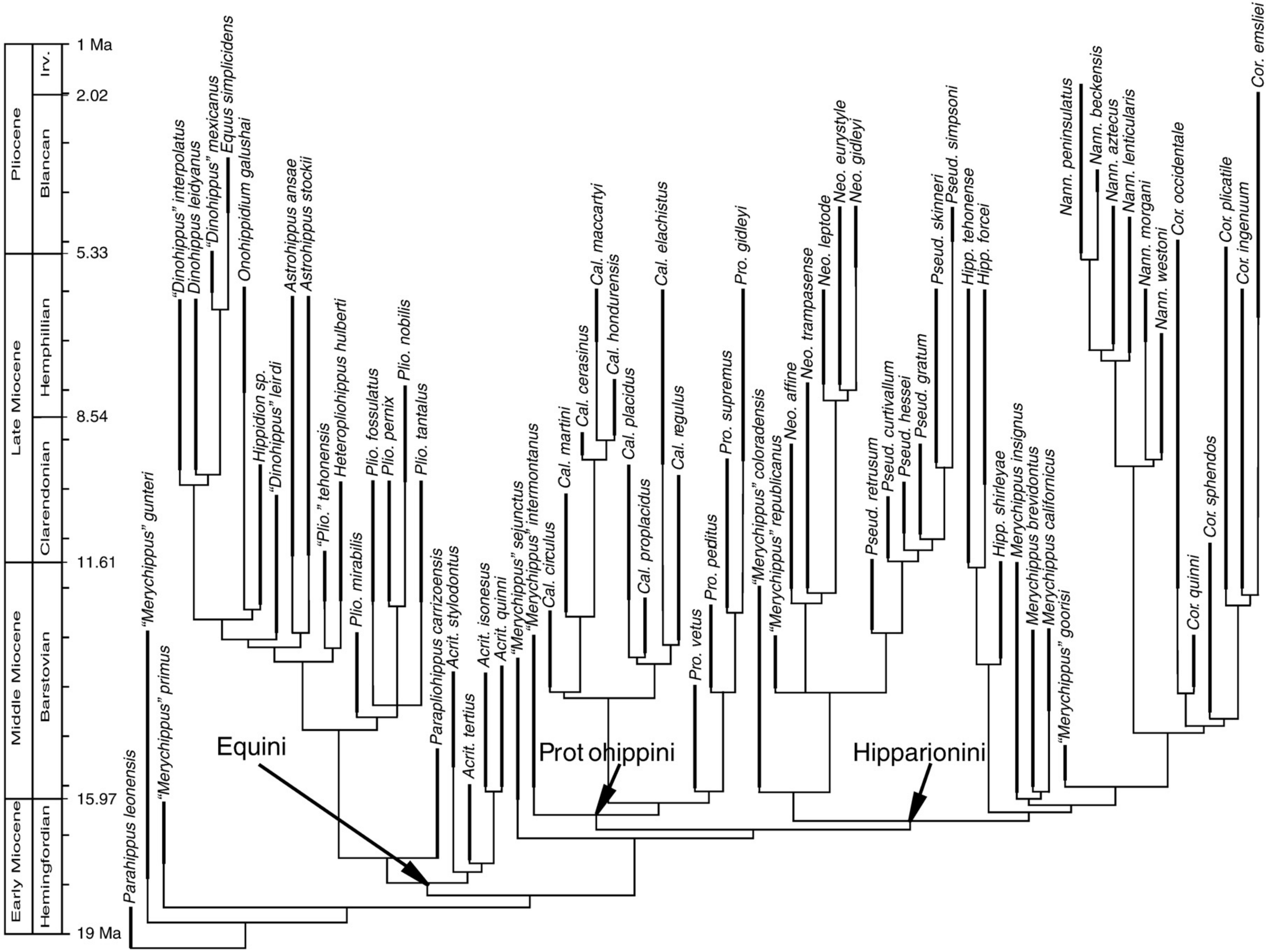

Fig. 1. Temporally calibrated cladogram of the Equinae. Phylogenetic relationships adapted from Hulbert (1993) and modified using Kelly (1995, 1998), Prado and Alberdi (1996), and Woodburne (1996). ICS temporal scale from Gradstein et al. (2004) and North American Land Mammal Ages (NALMA) from Alroy (2003). Narrow vertical lines indicate ghost lineages, whereas bold vertical lines indicate the recorded range. Stratigraphic distribution of data derived from sources in Supplementary Data. Taxa abbreviations: *Plio* = *Pliohippus*, *Acrit* = *Acritohippus*, *Cal.* = *Calippus*, *Pro.* = *Protohippus*, *Neo.* = *Neohipparion*, *Pseud.* = *Pseudhipparion*, *Hipp.* = *Hipparion*, *Nann.* =*Nannippus*, *Cor.* = *Cormohipparion*.

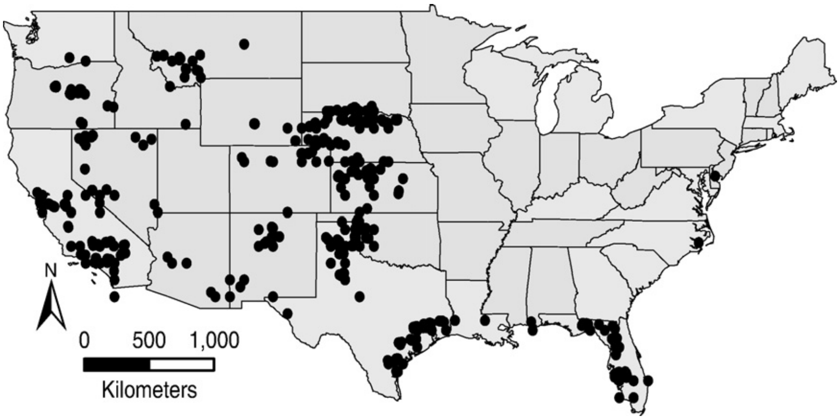

Fig. 2. Geographic distribution of species occurrence data included within the study. Grey circles represent occurrence points for all species in Fig. 1 in North America during the Miocene and Pliocene. References for species occurrences are in Supplementary Data.

changes resulting from climatic cooling and the spread of grasslands across North America. Whereas the overall patterns, including phylogenetic relationships, associated with the Equinae diversification are well understood, prior analyses have not utilized quantitative paleobiogeographic methods to examine the relationship between biogeographic and cladogenetic patterns in the group.

This study employs phylogenetic biogeography, the analysis of biogeographic distributions of species in concert with a well support phylogenetic hypothesis to assess general patterns of vicariance and dispersal within the clade, to analyze the evolutionary history of the Equinae. Used here, "phylogenetic biogeography" is synonymous with Brooks et al. (2001), also defined as phylogenetic biogeography II in Lomolino et al. (2006). Lieberman-modified Brook Parsimony analysis includes two phases biogeographic analysis. In the initial phase, the internal nodes of the taxon area cladogram are optimized using Fitch Parsimony (Lieberman, 2000). This provides a means to assess speciation mode at individual cladogenetic events. In particular, two speciation styles can be ascertained: speciation by vicariance or speciation by dispersal. Speciation by vicariance, also known as allopatry style I of Wiley (1981), occurs when a parent population is passively broken into two or more populations due to the introduction of a physical barrier such as orogenic uplift or tectonic rifting zones. Fragmentation of the population leads to reproductive isolation and eventually the populations evolve into separate species (Mayr, 1942; Lieberman, 1997). Speciation by dispersal, also known as allopatry style II of Wiley (1981), occurs when a population actively crosses a barrier and differentiates into a new species (Wiley and Mayden, 1985). The second phase of LBPA uses the optimized taxon-area cladogram to search for congruent general patterns of vicariance and geo-dispersal within the clade overall. General patterns of vicariance within the clade indicate that specific tectonic or climatic factors promoted vicariance in numerous lineages simultaneously, while general patterns of geodispersal occur when multiple species expand their ranges as barriers fall and then become fragmented when the same or new barriers rise again, leading to reproductive isolation and speciation (Lieberman and Eldredge, 1996). Geodispersal, therefore, indicates cyclical processes, with the rising and falling of barriers. It is an active mode of biogeographic differentiation in which the organisms have migrated, whereas vicariance is passive. During the Miocene, terrestrial clades may have experienced vicariance due to processes such as mountain uplift, introduction of new waterways, or habitat fragmentation following climate change. Since there were no cyclical tectonic events in North America during the Neogene, continental clades may have speciated by geodispersal from the fragmentation, rejoining and shifting of habitats due to climate change.

Phylogenetic biogeographic analysis, and in particular Lieberman-modified Brooks Parsimony Analysis (LBPA), the methodology used herein, is effective in interpreting the underlying factors, such as tectonic events and climate change, driving the speciation of a clade (Lieberman, 1997). Moreover, the impact of climate change on speciation can also be analyzed by comparing the geographic ranges of species with changes in the climate (Stigall and Lieberman, 2006). Whereas this method has previously been applied to marine invertebrates (Lieberman and Eldredge, 1996; Lieberman, 1997; 2000; Stigall Rode and Lieberman, 2005) and fossorial reptiles (Hembree, 2006), this represents the first application of the method to mammals.

2. Geologic and paleoclimatic framework

The position of the North American plate during the Miocene was similar to its present geographic position. Significant tectonic activity occurred along the western margin of the continent including upwarping in the Rocky Mountains, creation of the Basin and Range province, and volcanic eruptions in the Northwest (Cole and Armentrout, 1979; Prothero, 1998) (Fig. 3). Although the eastern portion of the continent was tectonically quiescent, this region was heavily influenced by fluctuating sea levels. For example, early in the Miocene, sea level was approximately 20 m higher than present (Kominz et al., 1998). Low-lying parts of the continent, like Florida and the Gulf Coast were repeatedly inundated by transgressive events (Scotese, 1998). Overall, sea level dropped by the Late Miocene, exposing Florida and parts of the Gulf Coast (Kominz et al., 1998).

From the Miocene into the Pliocene climate fluctuated with an overall trend changing from warm and humid toward cool and dry (Barron, 1973; Partridge et al., 1995; Zachos et al., 2001). Temperatures increased from the cooler Oligocene into the Miocene and peaked at 17 Ma (Woodruff et al., 1981; Prothero, 1998). About 15 Ma, during the Middle Miocene, ice sheets formed permanently on Antarctica, causing cooling in North America (Zachos et al., 2001; Rocchi et al., 2006; Lewis et al., 2007). In addition, a large rain shadow effect developed in the Great Plains and southwestern regions of North America due to the uplift of the Cordilleran region including the Cascade and Sierra Nevada Ranges (Leopold and Denton, 1987; Hulbert, 1993). Moisture levels decreased in North America due to both the rain shadow effect (Woodruff et al., 1981; Zubakov and Borzenkova, 1990) and global cooling (Leopold and Denton, 1987). Around 8 Ma, North America experienced a brief warming trend and then cooled again during the Messinian (Hemingfordian) glaciation (Prothero, 1998).

The fluctuating and changing climate created a mixture of vegetative habitats across North America. Axelrod (1985) and Leopold and Denton (1987) suggest a subtropical mesic climate and vegetation in North America during the Early Miocene. Savanna and grassland

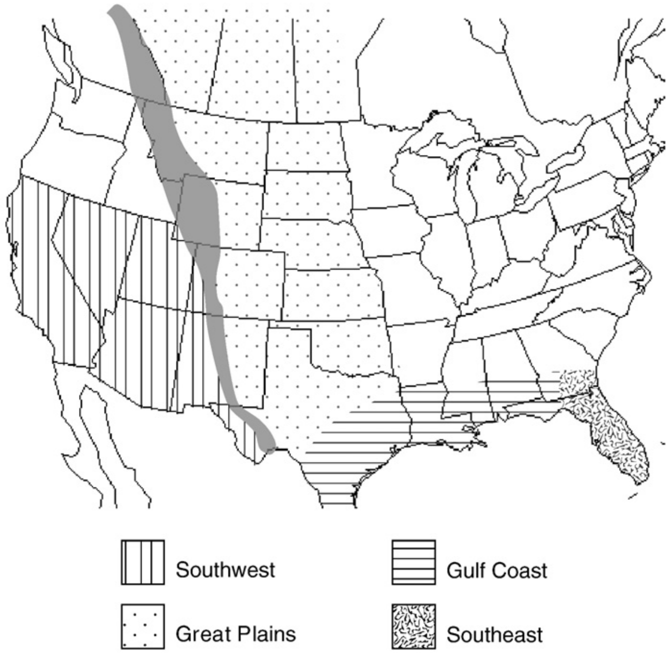

Fig. 3. Endemic geographic areas of the subfamily Equinae in North America analyzed in this study. The Southeast area includes sites in Florida. The Gulf Coast area stretches along the coast from Florida to the Mexican border. The Great Plains area begins approximately 400 km north of the Gulf Coast and stretches on the eastern side of the Rocky Mountains (indicated in gray) through Texas, New Mexico, Oklahoma, Kansas, Nebraska, Colorado, Wyoming, North and South Dakota and Montana. The Southwest region includes locations west of the Rocky Mountains in New Mexico, Arizona, California, Nevada and Utah.

habitats increased throughout the Miocene due to cooling and the rain shadow effect. This transition included an increase in grasslands with lower productivity. Isotopic evidence from mammalian tooth enamel reveals a shift from C3-based savannas to C4-based grasslands during the Miocene (Cerling, 1992; Cerling, et al., 1993; Wang et al., 1994). By the Pliocene, central North America was covered in a mostly treeless prairie (Webb et al., 1995). A variety of habitats, therefore, existed in North America during the Miocene from grasslands in the Great Plains and swamps along the Gulf Coast to arid regions in the Southwest. Changing climate led to fragmentation and shifting of habitats, resulting in a diverse assemblage of vegetative regimes in each region. In each of the regions, a range of vegetative habitats existed that shifted laterally as the climate changed. These habitats supported a diverse group of browsers, grazers and mixed-feeders (Webb, 1983).

The climate change from warm and humid to cold and dry was initiated by both tectonic events, such as uplift in the Cordilleran region, and the onset of continental glaciations over the South Pole. On the timescale of this study (approximately 15 million years), however, the only mechanism fluctuating was climate and not tectonic processes. To clarify, geological conditions of the Miocene refer to those described in this section (i.e., uplift in the Rocky Mountains and Cordilleran regions, sea level). Climatic conditions refer to what is described above with the changing climate that resulted in changing vegetations throughout North America during the Miocene.

3. Evolutionary framework

The evolution of taxa in response to climate during the Miocene has been well documented for equines (e.g., Shotwell, 1961; Webb, 1977, 1983; Stebbins, 1981; Janis, 1984, 1989; Thomasson and Voorhies, 1990). Horses have been cited as a classic example of evolution in the fossil record (ex., Marsh, 1879; Matthew, 1926; Stirton, 1940; MacFadden, 1992) and these studies demonstrate a clear link between climate change and evolution (e.g., Simpson, 1951). Previous biogeographic studies of horses have ranged from analyses of local patterns, such as in the Great Basin (e.g., Shotwell, 1961), to global surveys, hypothesizing that horses originated in North America and later dispersed to Europe and Asia (e.g., Lindsay et al., 1979; Lindsay et al., 1984; MacFadden, 1992; Opdyke, 1995). Whereas these studies provide an excellent framework for examining the correlation between the diversification of the Equinae and environmental change, none have analyzed spatial distributions in a phylogenetic framework or applied quantitative biogeographic methods.

The Miocene radiation of the subfamily Equinae was associated with significant changes in both the dentition and aspects of the locomotory apparatus (MacFadden, 1992). The basal genus *Merychippus*, a taxon with mesodont dentition, radiated between 18 and 15 Ma (Hemingfordian), the warmest period of the Miocene (Hulbert, 1993). Vegetation during this time consisted primarily of riparian forests, deciduous open forests, and wooded, semi-open savanna (Axelrod, 1985) that supported browsing species with mesodont dentition. During a second radiation, between 15 and 12 Ma, hypsodonty evolved and became dominant within the tribes Hipparionini, Protohippini and Equini. Hypsodont species richness became greater than that of mesodont species (Hulbert, 1993), and eventually mesodont taxa became extinct by ~11 Ma. This taxonomic shift corresponds with the first two cooling events of the Miocene at 15.3-13.5 and 12.8-12.3 Ma (Hulbert, 1993) that led to a decrease in rainfall and a shift from woodland to grassland habitats (Axelrod, 1985). Hulbert (1993) attributed the turnover from mesodonty to hypsodonty to the climate and vegetation changes. The subfamily's diversity reached a peak of 13 genera during the Clarendonian (11.5-9 Ma.) with a mixture of mesodont and hypsodont forms (Hulbert, 1993). By the middle of the Pliocene, however, only three equine genera remained, all exhibiting extreme hypsodonty. By the end of the Pleistocene all genera except the modern *Equus* had become extinct (Webb, 1984).

The major radiation of the subfamily Equinae during the Miocene has been attributed to the spread of grasslands. The classic story, however, has been augmented in recent years. For example, original hypotheses of orthogenetic evolution of the clade (e.g., Simpson, 1951), have been dismissed with the discovery of the tridactyl *Nannipus*, *Neohipparion* and *Cormohipparion* living in the Late Miocene with the “advanced” monodactlys (MacFadden, 1984, 1998). In addition, while the level of hypsodonty is often considered a proxy for browsing vs. grazing lifestyles (Kowalevsky, 1874; Matthew, 1926; Simpson, 1951, Stebbins; 1981), other studies have demonstrated that the dentition of a horse species is not always conclusive evidence for the type of vegetation in their diet (Stirton, 1947; Fortelius, 1985; Janis, 1988) and, therefore, cannot be used as the sole proxy for vegetation types. Stromberg (2006) advised against using tooth morphology alone to reconstruct habitat change due to inconclusive evidence regarding whether hypsodonty was an adaptive characteristic. The adaptation and speciation of this clade is more complex than originally thought. It is accepted, however, that environmental changes due to climate fluctuations and vegetation shifts influenced the radiation of the clade (e.g., Hulbert, 1993; Webb et al., 1995). Here we assess this claim and elucidate the details of the pattern by examining and statistically analyzing distributional data to better understand environmental influences on equine speciation.

4. Materials and methods

4.1. Analytical biogeographic method

Lieberman-modified Brooks Parsimony Analysis (LBPA) as described in Lieberman and Eldredge (1996) and Lieberman (2000) is the phylogenetic biogeographic method employed in this study. This method was selected because it is designed to resolve both vicariance and geodispersal patterns as well as assess the relative impact of cyclic versus singular events on the biogeographic history of a clade. Whereas other analytical methods for phylogenetic biogeography exist, they either cannot detect geodispersal or require simultaneous analysis of multiple clades (see discussion in Stigall, 2008). LPBA has been successfully used to resolve biogeographic patterns in the fossil record during intervals in which the primary driver of biogeographic patterns included both climatic oscillations (e.g., Lieberman and Eldredge, 1996; Stigall Rode and Lieberman, 2005) and tectonic events (Lieberman, 1997; Hembree, 2006).

The methodology of this analysis is explained in detail in Lieberman (2000) but a brief discussion is presented here. The first step in the analysis is to convert the phylogenetic tree of Equinae into an area cladogram by replacing taxon names with the areas of endemism in which each species occurred. Biogeographic states for the internal nodes are optimized using Fitch Parsimony (Fitch, 1971). The cladogram based on Hulbert (1993), Kelly (1995, 1998) and Woodburne (1996) is shown as a taxon-area cladogram with optimized nodes in Fig. 4. Speciation mode at individual cladogenetic nodes can be inferred from the optimized taxon-area cladogram following Lieberman (2000). Cladogenetic events where the descendant species occupies only a subset of a larger ancestral range are interpreted as vicariant speciation events. Conversely, when descendant species colonize areas additional to or distinct from the ancestral species, speciation is interpreted to result from dispersal. For analysis of the general biogeographic pattern, two matrices, a vicariance matrix and a geodispersal matrix, are coded for parsimony analysis from the taxon-area cladogram. In both matrices, areas of endemism are treated as taxa, whereas individual nodes and branches of the area cladogram are coded as characters (see Supplementary Data). The two matrices are then evaluated separately using parsimony analysis to determine relationships between the areas of endemism.

The vicariance matrix is used to ascertain vicariance patterns within the area cladogram. In coding the matrix, an ancestral area is added for character polarization and is coded 0 for all character states. The biogeographic state of each node or terminus is coded as 0 when it is absent from an area and 1 if present. If a node represents a derived speciation event due to range contraction (vicariance) it is coded 2, which is treated as an ordered character state. Similarily to the matrix for vicariance, a matrix was coded with geodispersal events to examine geodispersal events across the clade. In the geodispersal matrix, descendant taxa that occupy novel or additional areas of endemism are coded as a derived presence (2). The resulting matrices were analyzed with PAUP 4.0b10 (Swofford, 2002) under an exhaustive search to determine the most parsimonious tree. The vicariance tree indicates the relative timing of separation for the four areas. Areas that group most closely on the tree were separated most recently by a barrier, such as orogenic uplift or habitat fragmentation. In contrast, areas more distally related on the tree were separated by a barrier more ancestrally. The geodispersal tree indicates the relative timing that dispersal occurred between areas. It demonstrates which areas were most recently connected, thereby allowing dispersal between them, and which ones were connected more ancestrally.

Comparison of the two tree topologies indicates whether deterministic events, such as tectonic events, are driving the evolution of a clade or whether cyclical events, such as oscillatory climate change, more strongly influenced biogeographic patterns. Congruent tree topologies illustrate that the order in which barriers arose is the same order in which they fell. Consequently, if the vicariance and geodispersal trees exhibit congruent topologies, then cyclical events have influenced the resulting biogeographic patterns. Cyclical patterns may include fluctuating climate conditions. Conversely, if the trees are incongruent, then geodispersal and vicariance events did not occur between regions in a cyclical pattern (or at least are not cyclical on a timescale effecting speciation). Instead, singular events such as tectonic rifting, mountain uplifting, new river formation, or flooding influenced the evolution of the clade (Lieberman and Eldredge, 1996; Lieberman, 1997).

4.2. Taxa and geographic regions

The phylogenetic hypothesis of equine relationships used in this study is adopted primarily from Hulbert (1993) and amended with relationships presented in Kelly (1995, 1998), Prado and Alberdi (1996), and Woodburne (1996) (Fig. 1).

Distribution data for included taxa were compiled from the primary literature, the Paleobiology Database (www.paleodb.org), and the National Museum of Natural History (NMNH). Tentative species identifications (e.g., cf.) were excluded from this study. Only confirmed identifications were included to ensure taxonomic accuracy and establish a threshold for of acceptable preservation quality to account for taphonomic concerns. A complete list of referenced studies is included in Supplementary Data.

To assess biogeographic patterns North America was divided into four areas of endemism (Fig. 3): the Southeast, the Gulf Coast, the Great Plains, and the Southwest. Areas of endemism were defined based on previous biogeographic divisions of the clade (Webb and Hulbert, 1986; Hulbert, 1987; Hulbert and MacFadden, 1991; Webb et al., 1995) and the presence of natural barriers (either climatic or geographic) on the North American plate during the Miocene. Previous biogeographic divisions are based on provinciality within equine fossil assemblages. Natural barriers separating these areas of endemism include the Gulf Trough between Florida and the mainland continent, the Rocky Mountains between the Southwest and the Great Plains, and a climatic barrier between the Great Plains and the Gulf Coast regions. Additional areas of endemism may have existed, but the fossil record of those regions is too sparse to include in this analysis. Fossil Equinae are known from the Northwestern region of North America (e.g. Oregon, Idaho) and the Northeastern region (North Carolina and Delaware). The remains of only four species were located in the Northwest and only two species in the Northeast. When areas of endemism with only a few species are incorporated into phylogenetic biogeographic analyses, insufficient character data are present in the data matrix for these areas, and the optimization procedure cannot assess correctly their placement in the parsimony analysis. These areas will simply place out at the base of the reconstructed area cladograms, thereby providing no information (Lieberman, 2000;

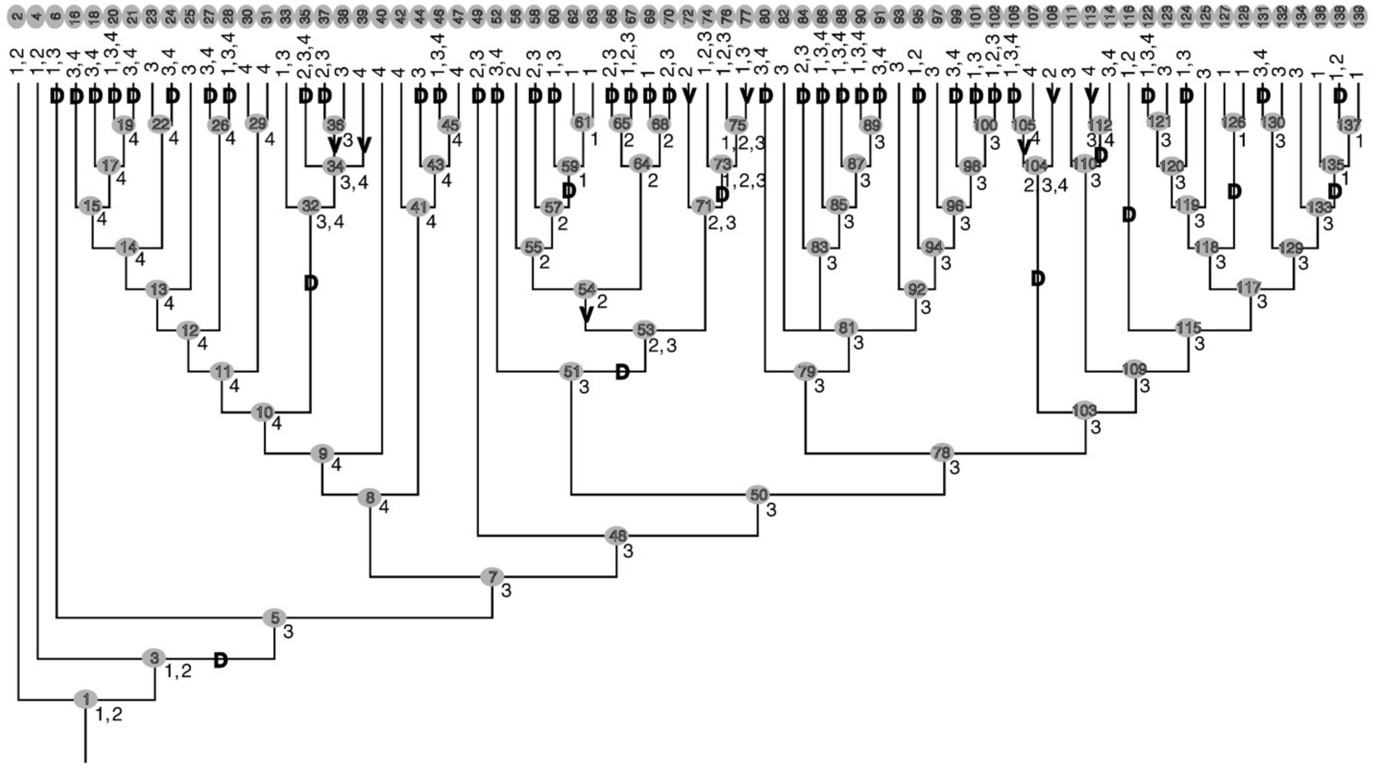

Fig. 4. Area cladogram of the subfamily Equinae based on phylogenetic topology in Fig. 1. Areas of endemism from Fig. 3 labeled as: 1 — Southeast, 2 — Gulf Coast, 3 — Great Plains, 4 — Southwest. Circles indicate character number in the data matrix (Appendix A). Speciation at nodes identified as: V — vicariant event, or D — dispersal event.

Stigall Rode and Lieberman, 2005). Consequently, we excluded these areas from this analysis due to methodological limitations.

5. Results

5.1. Speciation patterns

Analysis of the biogeographic optimization from Fitch Parsimony provides the opportunity to assess mode of speciation. Speciation by dispersal is the more common mode of speciation across this clade (Fig. 4). Of cladogenetic events where speciation mode could be assessed, there were 47 speciation events by dispersal and only 9 speciation events by vicariance.

The overall progression of biogeographic evolution in this clade can also be assessed from the taxon-area cladogram (Fig. 4). *Parahippus leonensis* and *"Merychippus" gunteri*, the ancestral species, lived primarily along the Gulf Coast and Southeast. However, the Equinae clade began its radiation further inland in the Great Plains. The three tribes of the Equinae clade (Equini, Protohippini and Hipparionini) diversified in three different areas of North America. The tribe Equini separated from the other two tribes first and diversified in the Southwest. Then the tribe Protohippini divided from the tribe Hipparionini. Ancestors of the tribe Protohippini continued to diversify in the Great Plains as well as along the Gulf Coast. The tribe Hipparionini continued to speciate in the Great Plains (Fig. 4). Later, however, species in each tribe dispersed from their ancestral regions into other areas.

5.2. Biogeographic area analysis

The vicariance analysis produced a single most parsimonious tree (Fig. 5.1). The consistency index (0.821), a measure of homoplasy, is statistically significant ($p<0.05$) and indicates strong tree support (Sanderson and Donoghue, 1989; Klassen et al., 1991). The g_1 statistic ($g_1=-0.214$) indicates the tree length distribution is skewed to the left, and shows a significant phylogenetic signal at the level of $p<0.05$ (Hillis and Huelsenbeck, 1992). The Great Plains and Southwest are most closely related indicating that a vicariance event created a

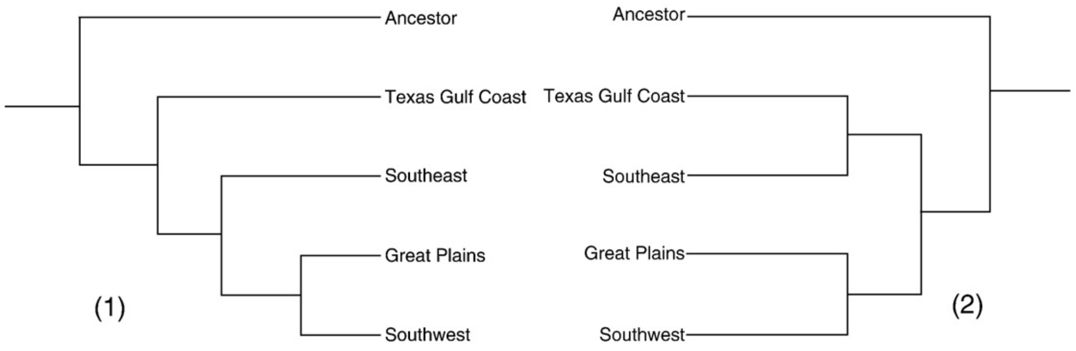

Fig. 5. Vicariance and geodispersal area cladograms derived from Lieberman-modified Brooks Parsimony Analysis. (1) Vicariance tree; length is 181 steps, consistency index is 0.821, and g_1 statistic is −0.214. (2) Geodispersal tree; length is 231 steps, consistency index is 0.805, and the g_1 statistic is 0.148.

barrier between them most recently. Ancestral to this event, the Southeast was separated from the Great Plains and Southwest by a vicariant event. The Gulf Coast was separated from all three of the areas ancestrally.

The geodispersal analysis also produced a single most parsimonious tree (Fig. 5.2). The consistency index (0.805) and g_1 (g_1=0.148) are statistically different from random ($p<0.05$) (Sanderson and Donoghue, 1989; Klassen et al., 1991; Hillis and Huelsenbeck, 1992), indicating strong tree support. The Gulf Coast and Southeast are closely related as well as the Great Plains and Southwest. Dispersal between these subregions occurred ancestrally.

The topologies of the vicariance and geodispersal trees are largely congruent (Fig. 5). The primary difference between them is the relative relationship of the Southeast. In the geodispersal tree the Southeast is most closely related to the Gulf Coast; whereas in the vicariance tree the Southeast is more closely related to the Great Plains/Southwest than to the Gulf Coast. The geodispersal tree represents a clear division between the Great Plains/Southwest and the Gulf Coast/Southeast whereas the vicariance tree represents a relative progression of separation between all four regions. The Great Plains and Southwest, however, have a sister relationship on both trees.

6. Discussion

6.1. Distributional patterns

In this analysis, speciation by dispersal was more common within the Equinae than vicariant speciation (Fig. 4) This is consistent with the migratory life habits of horses. The ancestral *Parahippus leonensis* did not breed seasonally or migrate, most likely because its habitat was consistent year round (Hulbert, 1984). Hyposodont horses, however, did migrate to exploit food resources and did breed in a seasonal environment (Van Valen, 1964; Voorhies, 1969). Studies of the global biogeographic distribution of the clade apply the mode of dispersal to explain their migration from North America to Europe and Asia through the Neartic (Lindsay et al., 1984; Opdyke, 1995). The few vicariant events in Fig. 4 are either related to the isolation of the Southwest region or the climatic deviation between the Gulf Coast and Great Plains areas. These events likely resulted from tectonic uplift in the west and differences in vegetation types in the east, respectively.

The area cladogram and distribution of the subfamily Equinae is consistent with Miocene tectonics in North America. For example, species are distributed in areas of the Florida Platform that were above sea level during the Miocene (Supplementary Data). Species are also distributed in areas of central New Mexico where the Rocky Mountain range had a narrower expanse during the Neogene compared to northern parts of its range (Trimble, 1980). The narrower expanse provided an area of passage between the Southwest and Great Plains regions in New Mexico during the Miocene. Conversely, no taxa were recorded from areas in the northern Rocky Mountains where the mountains had a wider expanse (Supplementary Data).

The ancestral biogeographic states and the topology of the area cladogram show patterns of speciation that are consistent with the climate and distribution of vegetation during the Miocene. Ancestral taxa, *Parahippus leonensis* and *Merychippus gunteri*, inhabited the Gulf Coast regions (Fig. 4). However, none of the basal equid nodes diversified there. The consistently moist conditions of the Gulf Coast provided a stable habitat that may have reduced opportunities for allopatric differentiation and inhibited the speciation of equid ancestors in the area. The Protohippini was the only tribe to diversify in the Gulf Coast area whereas the tribes Hipparionini and Equini speciated in the changing and fragmented habitats of other regions in North America (Fig. 4).

Changing climatic conditions led to altered vegetation regimes in North America, but this change affected the areas of endemism considered herein differently. The Gulf Coast and Southeast areas continued to include browsing habitats after the Great Plains and Southwest regions transitioned into arid grasslands (Wolfe, 1985). The Gulf Coast region became a refuge for taxa that became extinct in the Great Plains (Webb et al., 1995). Species such as *Cormohipparion emsliei*, *Pseudhipparion simpsoni* and *Nannippus aztecus*, tridactyls belonging to the tribe Hipparionini and adapted for browsing and selective grazing, survived in the Gulf Coastal regions long after becoming extinct in the Great Plains and Southwest (Webb and Hulbert, 1986; Webb et al., 1995). Ancestral members of the tribe Hipparionini were distributed in the Great Plains (Fig. 4). Several of the terminal taxa, however, occupied the Gulf Coast and Southeast areas indicating a movement to the warmer areas. The area cladogram (Fig. 4) expresses the refuge characteristic of the moist coastal regions.

The general distribution of taxa throughout North America expressed in the area cladogram is closely related to the morphology of the Equinae species (Fig. 4). Although it has been demonstrated that monodactyl and tridactyl species were sympatric in North America (MacFadden, 1992), limb morphology was found to vary between different areas and, consequently, vegetation types (Fig. 4). The tribe Equini that contains the dominantly monodactyl genera *Astrohippus*, *Dinohippus*, and *Equus* diversified in the Great Plains area (Fig. 4). Tridactyl genera of the tribe Hipparionini (e.g. *Cormohipparion* and *Nannipus*) diversified in the Great Plains but were the more common taxa in the Southeast. The tribe Protohippini contained tridactyl genera that diversified along the Gulf Coast. According to Renders (1984), tridactyl limb morphology provided more traction in muddy substrates. Muddy substrates were more abundant in warm humid areas of the Gulf Coast regions as opposed to the arid conditions of the Great Plains (Retallack, 2007). Although monodactyl and tridactyl species lived in the same endemic areas, they did occupy different ecological niches within those regions (MacFadden, 1992). Shotwell (1961) determined that the tridactyl horses preferred a mosaic of savanna and forest habitats of the northern Great Basin. As the grasslands became more widespread in the Great Basin, monodactyl horses became dominant (Shotwell, 1961).

6.2. Vicariance patterns

The vicariance tree indicates the relative order in which areas of endemism were separated by vicariance events. The relative order presented in Fig. 5.1 is congruent with the interpreted geologic and climatic conditions of the Miocene in North America. The Southwest and Great Plains were separated most recently by a barrier (Fig. 5.1). This separation is related to the final phase of uplift in the Rocky Mountains, which began in the Miocene following a tectonic quiescent period from the Cretaceous through the Oligocene (Effinger, 1934; Frazier and Schwimmer, 1987). This slow and gradual upwarp during the late Cenozoic persisted into the Pliocene. During the Miocene, the Southwest and Great Plains had different vegetations due to the uplift (Leopold and Denton, 1987). A rain shadow resulted in drier conditions east of the Rocky Mountains, thereby creating a vegetative difference between the two regions. East of the Rocky Mountains, vegetation consisted of deciduous open forests and prairie. To the west of the mountain range, deciduous hardwood forests and swamps dominated the vegetation (Leopold and Denton, 1987). Although grasses were present west of the Rocky Mountains in the Early Miocene, their abundance was not significant. Leopold and Denton (1987) attribute the difference in abundance to the inability of grasslands to spread across the mountainous barrier and the montane conifer forest that occupied the mountainous terrain. Grasslands became sporadically abundant west of the Rocky Mountains during the Blancan (Pliocene) when they spread from the northern Great Plains as they adapted to a summer-dry climate from a summer-wet climate.

The Southeast branches from the tree next (Fig. 5.1). Its position here on the vicariance tree is probably a result of pre-Miocene sea level fluctuations. As the amount of exposed land of the Florida

Platform varied, populations were divided. Leading into the Miocene, the Gulf Trough separated Florida from the continent (Randazzo and Jones, 1997). Through the Neogene, sediment shed from the North America continent filled in the trough until Florida was contiguous with the North American continent, thereby allowing dispersal of the ancestral species. The early vicariant events, however, are represented by the ancestral location of the Southeast on the vicariance tree.

The Gulf Coast region branches off ancestrally on the vicariance tree because there were no tectonic barriers between it and the Great Plains/Southwest areas (Fig. 5.1). It acted as a passage way between the Southwest and Great Plains, and the Southeast (Fig. 5.1). There were no physical barriers in the Gulf Coast region restricting dispersal - the Mississippi River had not developed to its current size yet (Scotese, 1998).

During the Early Miocene vegetation supported by a warm and humid climate was present in all four areas of endemism (Axelrod, 1985; Wolfe, 1985). A relatively quiescent tectonic setting combined with a stable flora allowed dispersal between the northern (Great Plains) and coastal areas (Gulf Coast and Southeast) by early members of the clade. These areas do not form a polytomy, however, because a climatic and vegetative difference developed between the northern and coastal areas during the mid-late Miocene. Although Axelrod (1985) describes the environment of the entire Great Plains region during the Miocene as wooded grasslands with semi-open grassy forests and patchy grasslands, Retallack (2007) discusses a moisture gradient in the Great Plains from Montana to Nebraska and Kansas. Paleosols from Montana during the Miocene have weak pedogenic structure, low clay content, limited chemical weathering, and shallow calcic horizons indicating an arid environment (Retallack, 2007). Such paleosols represent aridic conditions from the rain shadow caused by the uplift in the Cordilleran region. Paleosols developed in Nebraska and Kansas during the Miocene exhibit fewer calcareous nodules and a higher clay content indicative of higher levels of precipitation (Retallack, 1983, 1997). Paleosols in Oregon from the Miocene also have greater clay content and fewer calcareous nodules. Retallack (2007) interpreted that the difference in paleosols among these regions is due to the proximity of Nebraska, Kansas and Oregon to the maritime air masses from the Gulf and Pacific Coasts early in the Cenozoic.

The relative separation of the endemic areas is consistent with the tectonic and climatic history of the North American continent during the Miocene. Vicariance events such as uplift in the western United States, isolation of Florida, and vegetational gradients influenced the evolution of the Equinae clade.

6.3. Geodispersal patterns

The geodispersal tree indicates the relative time in which dispersal occurred between the endemic areas. Relationships within the geodispersal tree are congruent with the tectonic and climatic events of the Miocene as well. The close association between the Great Plains and Southwest on the geodispersal tree indicates that species dispersed several times between these two regions (Fig. 5.2). As discussed previously, a corridor existed through the Rocky Mountains during the Miocene that allowed dispersal across the southern part of the mountain range (Trimble, 1980). Forty-three percent of the species in the Great Plains also lived in the Southwest compared to the 24% that also lived in the Gulf Coast area. Although both the Southwest and Gulf Coast are proximal to the Great Plains region, dispersal occurred more frequently between the Great Plains and Southwest than with the Gulf Coast. A physical barrier (i.e., Rocky Mountains) separated the Great Plains and Southwest (Cole and Armentrout, 1979; Trimble, 1980), whereas a climatic barrier separated the Great Plains and Gulf Coast (Retallack, 2007). Based on the available data, the climatic barrier appears to be more influential than the physical barrier.

The close relationship between the Gulf Coast and Southeast is intuitive (Fig. 5.2). These two areas were not divided by physical barriers and shared similar climates and vegetation (Wolfe, 1985) allowing migration and dispersal between them. Florida connected to the mainland continent during the Miocene when the Gulf Trough filled in with sediment shed from the Appalachian Mountains, allowing dispersal to and from the Gulf Coast (Randazzo and Jones, 1997).

Consistent vegetation in the Gulf Coast and Southeast regions may have inhibited allopatric speciation. Ancestral species that occupied the coastal regions did not speciate as frequently as species that migrated to the fragmented habitats of the cooler and drier Great Plains and Southwest regions.

The Gulf Coast and Southeast areas are separated from the Great Plains and Southwest by a climatic gradient (sensu Retallack, 2007) as discussed above. Dispersal between all four regions most likely occurred before the global climate began to cool and vegetation shifted from woodland to grassland in the Great Plains. During the Middle Miocene, when distinct climatic regimes were in place (Wolfe, 1985), separating the four regions, dispersal was rare, occurring only for species tracking a browsing habitat and seeking refuge from the Great Plains in the moist, woodland coastal regions. The divergence of the four regions located ancestrally on the geodispersal tree supports the early dispersal among the areas and restricted dispersal later (Fig. 5B).

6.4. Comparison and synthesis

The vicariance and geodispersal trees are largely congruent with one another. The primary difference between the two trees is the location of the Southeast region. On the geodispersal tree, the Southeast is more closely related to the Gulf Coast than it is in the vicariance tree (Fig. 5). The Gulf Coast and Southeast had similar climatic regimes and woodland vegetation allowing almost continuous dispersal between them whereas the western areas (Great Plains and Southwest) had more arid climates (Axelrod, 1985; Wolfe, 1985; Thomasson et al., 1990; Retallack, 2007) restricting dispersal to and from the coastal areas (Webb et al., 1995). The location of the Southeast on the vicariance tree separates it from the Gulf Coast (Fig. 5). This separation may be a result of pre-Miocene fluctuations in sea level and the presence of the Gulf Trough potentially mediating vicariant speciation between the Southeast and other regions before the Miocene. Dispersal occurred during the Miocene when the Gulf Trough was filled in with sediment and Florida was continuous with the mainland. This is represented by the location of the Southeast on the geodispersal tree. The location of the Southeast on both trees is consistent with geological data and together they give an accurate representation of Southeast's relationship with the other three areas.

The congruency between the trees indicates cyclical events (i.e., rise and fall of barriers) were the most significant factors driving the speciation and biogeographic evolution of the Equinae during the Miocene. The only type of cyclical events that can influence speciation on the time scale of this study on a continental scale is climate change. Fluctuating climatic conditions resulting from global cooling and a rain shadow effect from the Cordilleran region created a mixture of habitats in North America during the Miocene (Hulbert, 1993; Webb et al., 1995). A variety of habitats that resulted from these climatic changes, supported a large diversity of Equinae species that were grazers, mixed feeders, and browsers (Webb et al., 1995).

7. Conclusions

Speciation in the subfamily Equinae occurred primarily via dispersal (allopatry style II) with a few episodes of vicariance (allopatry style I). Speciation by dispersal was a facilitated by biogeographic shifts in response to environmental alteration following climate change. In North America during the Neogene, the fluctuating climate resulted in a variety of fragmented habitats as woodlands slowly shifted to open grasslands. The variety of available habitats likely promoted taxonomic differentiation and the resulting high diversity of the clade. Although this has been documented in previous studies (Hulbert, 1993; Webb et al., 1995), it is quantitatively presented here for the first time. The general area cladograms recovered from LBPA analysis are congruent with geological events, such as uplift of the Rocky Mountains, and climatic conditions, such as the change from a warm and moist to cool and arid climate during the Miocene. Well supported vicariance and geodispersal trees derived from the LBPA analysis are largely congruent with each other, indicating that cyclical events, in particular, climate change during the Miocene influenced the radiation of the clade. The decline in diversity of the clade during the Pliocene has been attributed to climate change as well (Hulbert, 1993). Loss of woodland habitat from climate change may have resulted in the demise of several browsing species during early stages of global cooling (Webb et al., 1995). The first major extinction interval within the clade, effecting hypsodont horses, occurred during the driest time of the Neogene and the second occurred during a return to moist conditions similar to those seen in the Clarendonian (Axelrod, 1985; Leopold and Denton, 1987, Hulbert, 1993). During the second extinction interval, species exhibiting extreme hypsodonty were affected (Hulbert, 1993). A drop in diversity has also been attributed to increasing grasslands with lower productivity (MacFadden, 1998) due to a shift from C3-based savannas to C4-based grasslands (Cerling, 1992; Cerling, et al., 1993; Wang et al., 1994). In addition, as grasslands spread, vegetation became more consistent and may have led to a decline in opportunities for allopatric speciation.

The LPBA analysis presented here on a mammalian fauna from the Neogene is consistent with previous studies of Equinae evolution and North American geology. Phylogenetic biogeographic studies can be used on continental taxa that have a well constrained phylogeny and abundant fossil record. Such studies may provide additional insight into the mechanisms driving the evolution of clades with respect to the climate and geology of the distributional area. Dispersal and migration patterns can be more accurately reconstructed with such statistical methods as LBPA than with qualitative analysis.

Acknowledgements

We thank Daniel Hembree, Patrick O'Connor, and two anonymous reviewers for constructive and helpful reviews. We also thank R.C. Hulbert and J. Alroy for clarification with the phylogenetic relationships in the clade and R. Purdy for assistance with and access to the collections at the NMNH. Chris Dobel assisted with geographic locality data collection. This project was funded by an Ohio University Geological Sciences Graduate Alumni Research Grant and a GSA Grants-in-Aid Award to KCM and an Ohio University Research Challenge Award to ALS. This is Paleobiology Database publication number 83.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2008.06.014.

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