8. Evolution of the Proximal Third Phalanx in Oligocene-Miocene Equids, and the Utility of Phalangeal Indices in Phylogeny Reconstruction

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8.1 Introduction

The late Oligocene – early Miocene of Florida contain *Miohippus, Archaeohippus, Anchitherium*, and *Parahippus*, equid genera that possess and define many of the character state transitions that occurred between advanced anchitheriine and primitive equine horses. Although much previous research regarding *Archaeohippus* has emphasized its uniqueness, the genus is equally interesting for those characters that suggest its affinities to other taxa.

The affinities of *Archaeohippus* are obscured in part by a complicated taxonomic history. Specimens of this small, brachydont Miocene horse were first mentioned in publication by Cope (1886) from the early Barstovian Mascall Fauna of Oregon. Cope named the species *ultimus*, and assigned it to *Anchitherium*, a genus of large, tridactyl Miocene horses with brachydont teeth. Osborn (1910) placed both *Anchitherium* and *Archaeohippus* in the grossly paraphyletic subfamily "Anchitheriinae," what I will refer to as "Anchitheriinae" *sensu lato* (ASL). Osborn's (1910) formulation of this subfamily also included *Mesohippus, Miohippus, Parahippus*, and *Hypohippus*, as well as the European palaeothere *Anchilophus*. The inclusion of the palaeothere renders this concept of the subfamily polyphyletic. In a more recent review of Osborn's grouping (MacFadden, 1992), ASL is defined as those horses with fully molarized P2-M3 that lack the dental characters that define the subfamily Equinae (Hulbert, 1989; Hulbert and MacFadden, 1991). This gradistic concept is MacFadden's (1992, 1998) paraphyletic "Anchitheriinae," derived from Osborn's (1910) definition and used by many museum collections today. Thus,

ASL includes the late Eocene-Oligocene genus *Mesohippus*, its Oligocene-Miocene descendent *Miohippus*, and at least eight genera derived from one or more species of *Miohippus* (and perhaps *Mesohippus*). These taxa comprise the Arikareean anchithere radiation (AAR) of the New and Old Worlds, which begins in the late Oligocene (early Arikareean) and ends in the middle Miocene (late Clarendonian). The eight taxa in the AAR are *Archaeohippus, Desmatippus sensu* MacFadden (1998; *Anchippus sensu* Albright, 1998, 1999), and *Parahippus*, as well as the "Anchitheriinae" *sensu stricto* (ASS) of MacFadden (1992): *Anchitherium, Kalobatipus, Sinohippus, Megahippus*, and *Hypohippus*. All members of the AAR are united by possession of a connection between the metaloph and the ectoloph (Evander, 1989). This connection is absent in *Mesohippus* and only occasionally present in *Miohippus* (both members of ASL). All members of ASS are united by "greatly increased tooth crown area and estimated body size, relatively well developed cingula, and loss of ribs between styles on cheek teeth" (MacFadden, 1992, p. 101), as well as a mesentocuneiform facet on MTIII (Osborn, 1918). Generally, they are further distinguished from other members of the AAR by the possession of robust, strongly divergent lateral digits on the manus and pes. Thus, these groups, arranged from most to least inclusive, are ASL > AAR > ASS. Of these, only ASS is possibly holophyletic.

Although the systematics of the AAR is poorly understood, it has a sizeable fossil record. This record indicates an increase in morphological diversity unparalleled in the earlier evolutionary history of horses (Webb et al., 1995). Prior to the AAR, horse evolution in North America was much more conservative. Seminal work on the subject (Osborn, 1918; Matthew, 1924; Stirton, 1940) interprets this horse phylogeny as a series of gradistic genera, each genus distinguished from its ancestor by increased molar complexity and a slight increase in body size. This gradistic reconstruction of the

evolutionary history of early horses may be due in part to very gradual evolution, which produced only subtle morphological differences between different species. However, it may also reflect the perspectives of horse systematists. Much of the systematics of equids from the middle Miocene and younger is based on distinct characters in the complex occlusal surfaces of their molars, characters that are not always present in earlier equids. Another factor that explains the lack of resolution in the early part of the phylogeny of horses is the paucity of species-level cladistic studies on pre-Miocene taxa other than *Hyracotherium*. A recent revision of *Hyracotherium* (Froehlich, 1999) demonstrated that the traditional definition of this taxon includes a variety of primitive equids and other perissodactyls. Modern revisions of such taxa as *Epihippus, Orohippus, Mesohippus*, and *Miohippus* may similarly reveal more complex relationships than previously envisioned. Even considering this possibility, overall known equid morphological diversity was relatively low until the AAR was fully underway in the late Arikareean.

Certain lineages in the AAR demonstrate early phases of the trends in limb and tooth evolution that characterize the later radiation of advanced equids in the middle Miocene. The adaptive radiation of equine horses during the middle Miocene of North America is a well-studied macroevolutionary phenomenon that resulted in at least 11 late Miocene clades (Webb and Hulbert, 1986; MacFadden and Hulbert, 1988; Hulbert and MacFadden, 1991; Hulbert, 1993; for a review, see MacFadden, 1992). Morphological trends characteristic of this radiation include reduction of the side toes, elongation of distal limb elements, and increase in tooth crown height and occlusal complexity. These trends have been interpreted as adaptations to life in open country and a diet that included grasses (Marsh, 1879; Simpson, 1951; Janis, 1976; Behrensmeyer et al., 1992; Janis et al., 1994). These evolutionary trends can be traced back to the AAR in members of the genus *Parahippus*. Primitive members of this genus, sometimes assigned to the genus *Anchippus* (*sensu* Albright, 1998) or *Desmatippus* (*sensu* MacFadden, 1998), are dentally little more derived than advanced species of *Miohippus*. The most derived species of *Parahippus*, such as the Hemingfordian *P. leonensis*, possessed cheek teeth that were incipiently hypsodont and usually covered with cement. Its feet were tridactyl, but the lateral digits were reduced in length and thickness and held close to the middle digit, such that it was probably functionally monodactyl under normal locomotor conditions (Sondaar, 1968). These and other derived characters led Hulbert and MacFadden (1991) to identify *P. leonensis* as the nearest sister group of the middle Miocene adaptive radiation of equines.

The clade of large-bodied horses designated Anchitheriinae *sensu stricto* (ASS) is characterized by a suite of morphological trends that differ fundamentally from those that led to the advanced grazing horses (MacFadden, 1992, Figure 5.15, node 3). These include an increase in body size without an increase in relative crown height or occlusal complexity of

the molars (MacFadden, 1992), and perhaps an even more functionally tridactyl foot than that seen in many species of *Miohippus*. The lateral metapodials and phalanges are very robustly built and the lateral metapodials are not firmly appressed to the medial metapodial (Sondaar, 1968). Whereas the morphology of *P. leonensis* suggests that it may have been an early inhabitant of the first North American savannas (Hulbert and MacFadden, 1991), the morphology of members of the ASS (brachydont teeth and splayed digits) reflects a continuation of the forest-dwelling ecology of earlier equids (Sondaar, 1968).

Archaeohippus is perhaps the most enigmatic genus in the AAR and shows an interesting mosaic of primitive and derived features. Among anchitheres, it possesses a unique facial morphology, including a long pre-orbital region of the skull with a deeply pocketed malar fossa confluent with a deep lacrimal fossa. It possessed primitively brachydont teeth, but with slightly more occlusal complexity than that seen in the ASS. However, its pedal adaptations are as advanced as those of *Parahippus* (Matthew, 1932; Sondaar, 1968), with strongly reduced lateral metapodials entirely attached by ligaments to the medial metapodial. In addition, *Archaeohippus* has been cited as an example of phyletic dwarfism (MacFadden, 1987, 1998). At approximately 20 kg (Janis et al., 1994), the estimated body weight of *Archaeohippus* is about half that of most species of *Miohippus*, the common equid of the late Oligocene. The ecology of *Archaeohippus* must have bridged that of the more ecologically distinct members of the AAR. Its primitively brachydont teeth indicate a diet of browse, like that of *Anchitherium*, whereas its limb morphology suggests an affinity for open country, like *Parahippus*.

As stated above, in the original description of the type species *Archaeohippus ultimus*, Cope (1886) assigned material from Cottonwood Creek, Oregon, to the genus *Anchitherium*. In his description of fossils from the same locality from the Mascall Fauna of Oregon, Gidley (1906) erected a new genus, *Archaeohippus*, to distinguish this small brachydont horse from the anchitheres *sensu stricto*. The next named species, the somewhat larger and younger *Archaeohippus mourningi* (Merriam, 1913), was originally assigned to *Parahippus*. *Archaeohippus penultimus* was described from the Sheep Creek of Nebraska by Matthew (1924). Hay (1924) described both *Miohippus blackbergi* and *Parahippus minutalis* from the Garvin Gully Local Fauna of Texas. Simpson (1932) described *A. nanus* from the Thomas Farm Local Fauna of Florida.

Matthew (1932) recognized the derived nature of the pes and manus shared by *Archaeohippus* and *Parahippus* and the facial fossa shared by *Archaeohippus* and *Parahippus pristinus*, and suggested that *Archaeohippus* was a subgenus of *Parahippus*. In an excellent synthesis, Bode (1933) rediagnosed the species *Archaeohippus ultimus, Archaeohippus penultimus*, and *Archaeohippus mourningi*, and defended the generic status of *Archaeohippus*. Schlaikjer (1935, 1937) considered *Archaeohippus blackbergi* (=*Archaeohippus minutalis*)

to be a dwarf *Parahippus*, as did White (1942). White's (1942) justification was that individuals in the Thomas Farm population of *A. blackbergi* variably possess advanced dental characters such as a crochet, additional plications, and a hypostyle that connects to the ectoloph and metaloph to close the postfossette. White (1942, p. 19) noted that the patterns of variation of the dentitions of other species of *Archaeohippus* do not display these advanced characters, but are "simple and stable." Bode (1933) and Downs (1956) also noted that these characters were rare and weak when present in populations of *A. mourningi, A. penultimus*, and *A. ultimus*. Rather than accept the possibility that reduced variation in later species might involve the loss of advanced dental characters, Schlaikjer (1935, 1937) and White (1942) concluded that the other species of *Archaeohippus* were convergent with *A. blackbergi*. White (1942) considered "*Parahippus*" *blackbergi* to be an intermediate between *Miohippus* and more advanced *Parahippus*. White (1942) also identified several teeth from Thomas Farm lacking a metaloph connected to the ectoloph as belonging to *Miohippus*. However, this character is variable within individual dentitions and cannot be considered diagnostic when found in isolated teeth (Forsten, 1975).

Downs (1956) compared *A. blackbergi* with the western species and returned *A. blackbergi* to *Archaeohippus*. For the next two decades the debate was dropped, to resurface briefly in the work of Forsten (1975), who agreed with Downs (1956) that *A. blackbergi* is the correct name for the species of tiny horse found in both Texas and Florida during the Hemingfordian. More recently, Storer and Bryant (1993) identified *A. stenolophus* (Lambe, 1905) from the early Hemingfordian of Saskatchewan.

8.2   Abbreviations and Conventions Used in this Study

ADP = *Archaeohippus/Desmatippus/Parahippus* clade; ASL = "Anchitheriinae" *sensu lato*; ASS = Anchitheriinae *sensu stricto*; AAR = Arikareean Anchithere Radiation; FAM = Frick American Mammals, American Museum of Natural History; LSUMG = Louisiana State University Museum of Geoscience; Ma = Mega anna (millions of years ago), MCIII = metacarpal III; MTIII = metatarsal III; MCZ = Museum of Comparative Zoology, Harvard University; PPIIIL/MW = Proximal Phalanx III Length vs. Midshaft Width index; UF = University of Florida.

8.3   Specimens Used in this Study

Anchitherium clarencei: UF 175395, UF 58782, UF 47570, Thomas Farm, FL
cf. *Anchitherium*: UF uncatalogued, La Camelia Mine, FL
Anchippus texanus: LSUMG V-2258, LSUMG V-2549
Archaeohippus blackbergi: 101 phalanges, 37 uncatalogued UF, 64 lot catalogued as UF V-6414, Thomas Farm, FL

Archaeohippus mannulus: UF 160784, Curlew Creek, FL
Archaeohippus penultimus: FAM 71650, Thomson Quarry Sheep Creek, NE
Hypohippus wardi: uncatalogued FAM
Mesohippus bairdi: 3 phalanges lot catalogued as MCZ 20475, White River Badlands, SD
Mesohippus sp.: UF 200610, Toadstool Park, NE; UF 191530, Turkey Foot East High, NE; UF 191842, Horse Hill High NE; UF 208155, Suzan's Cat Site, NE; UF 208165, Sagebrush Flats, NE; UF 207944, Horse Hill New, NE; UF 207642, Sagebrush Flats 1, NE; UF 207923, Twin Buttes, NE; UF 207124, Horse Hill Low, NE; UF 201879, Twin Buttes, NE; UF 203240, Sagebrush Flats 1, NE; UF 209585, Twin Buttes, NE; UF 209566, Sand Creek Flats North, NE; UF 209584, Sagebrush Flats 2, NE
Miohippus intermedius: AMNH 1196 (cast), Protoceras Beds, White River, SD
Miohippus sp.: UF 200375, Turkey Foot, NE; UF 16872, I-75, FL; UF 163794, UF 178933, UF 178934, Brooksville 2, FL; UF/FGS V 3442, Franklin Phosphate, FL
Parahippus leonensis: UF 188515, UF 188711, UF 188022, UF 188418, UF 188021, UF 188776, UF 188497, UF 188020, UF 192872, UF 192325, UF 190381, UF 192873, UF 192621, UF 192620, UF 190361, UF 186430, UF 186431, UF 187542, UF 187715, UF 187716, UF 185568, UF 185890, UF 195591, UF 195004, UF 193194, UF 195001, UF 193030, UF 195059, UF 195003, UF 192975, UF 195002, UF 193031, Thomas Farm, FL
Parahippus pawniensis: FAM 71705, Elder Ranch, Dawes County, NE

8.4   Discussion

A phylogenetic analysis (O'Sullivan, 2002; in preparation) of 21 ASL equids and 62 characters in PAUP 4.04b4a for MacIntosh produced 106 shortest trees 190 steps long. A strict consensus tree (Figure 8.1) supports the monophyly of a clade that includes *Archaeohippus* and *Parahippus*, and excludes the ASS. The analysis included the Proximal Phalanx III Length vs. Midshaft Width index (PPIIIL/MW; see Table 8.1). A character analysis performed on MacClade 4.0 demonstrates that this index and several supporting dental characters define a clade including *Archaeohippus, Parahippus*, and primitive parahippines included in the genus *Desmatippus* (the ADP clade). All taxa within this clade possess derived elongate phalanges (Figure 8.2), and have a PPIIIL/MW index of 2.0 or greater.

The elongation of the proximal third phalanx is one of the most significant morphological developments in the complex of character transformations that signify the evolutionary transition among tridactyl equids from the digitigrade "padfoot" to the unguligrade "springfoot", the acknowledged precursor to the monodactyl state found in modern *Equus* (Camp and Smith, 1942; Sondaar, 1968; Hussain, 1975;
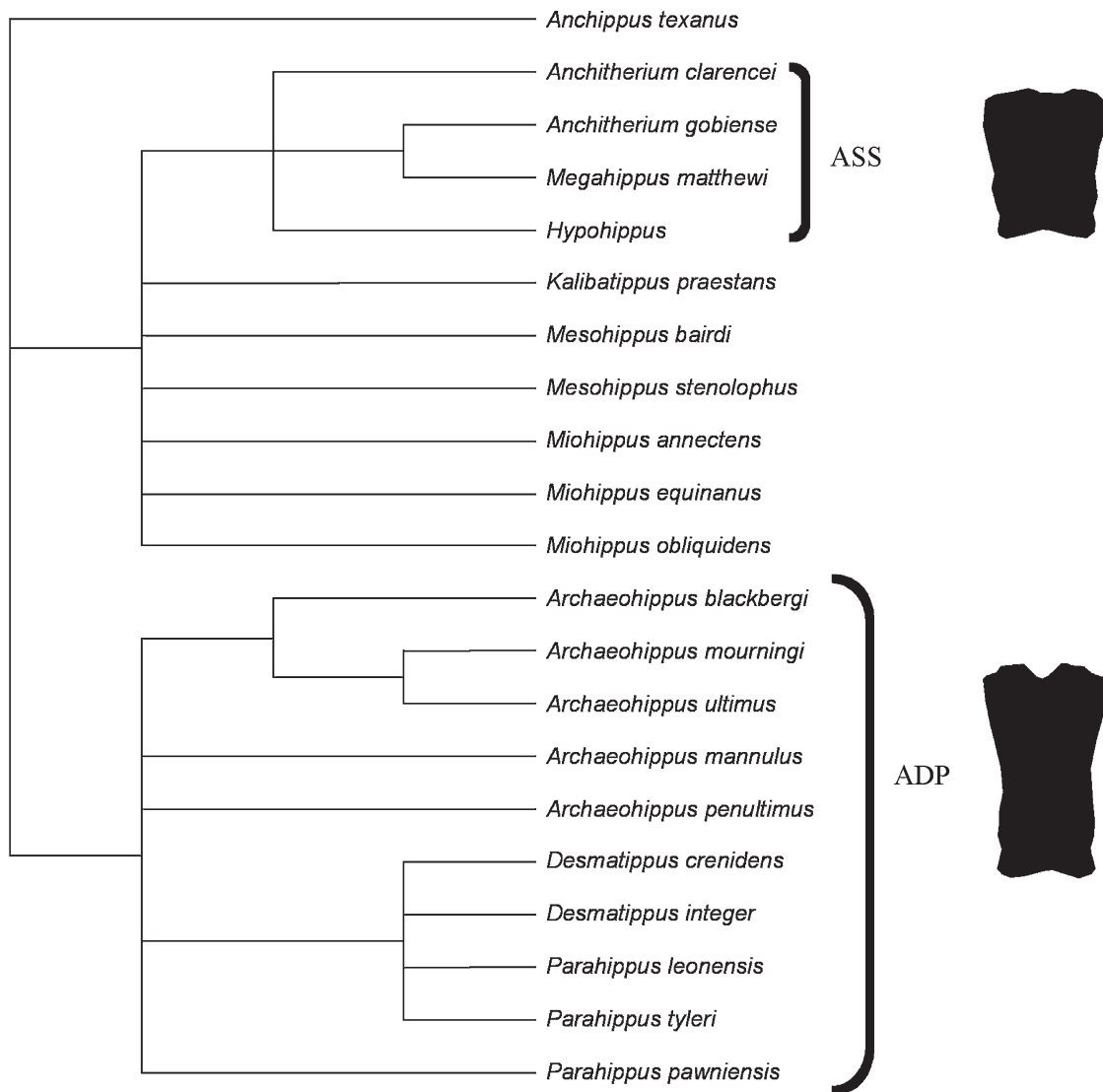
FIGURE 8.1. Strict consensus tree of anchithere *sensu lato* relationships without the constraint of an outgroup. To the right of designated clades are silhouettes depicting proportions of proximal third phalanges of the types of *Mesohippus protoeulophus* (above; AMNH 524a) and *Archaeohippus mannulus* (below; UF 160784). The ASS clade is supported by derived dental character states including: (1) protoconule submerged in protoloph, and (2) metaconule submerged in metaloph. The ADP clade is supported by derived dental character states including (1) hypostyle tall and (2) hypostyle connected to the metaloph.

Thomason, 1986). The shared derived character complexes of the manus and pes of the springfoot equids was recognized by Matthew (1932). While the padfoot equids (in the form of the ASS clade) successfully radiated throughout Europe and Asia during the Miocene, they were less common in North America during this same period. Presumably, their autecology was better suited to the persistent forested biomes of the Old World than to savanna-dominated North America. The padfoot ASS clade equids went extinct during the middle Miocene as the springfoot equids of the ADP clade were experiencing unprecedented taxonomic diversity (see MacFadden, 1992 for an overview).

The dental characters that support the ADP clade pertain to trends in the development of the hypostyle and the protocone, and are rather subtle. The pedal adaptations, on the other hand, are easily evaluated with the PPIIIL/MW index. A phalanx with an index ≥ 2 came from a springfoot ADP equid, while a phalanx with an index <2 came from a padfoot equid, either a member of the ASS clade or a more plesiomorphic equid such as *Mesohippus*. Thus, a simple index of two linear measurements from one of the most common skeletal elements in the equid fossil record is a powerful indicator of one of the most significant ecomorphological transitions in the evolution of the Equidae, and of the evolution of the ancestors of the subfamily Equinae.

TABLE 8.1. Measurements and indices from phalanges of ASL equids included in this study.

| Taxon	Proximal phalanx III		Proximal phalanx III	
	n	Length	Midshaft ML width	PPIIIL/MW
Anchippus texanus	1	24.6	12.1	2.03
Anchitherium clarencei	4	38.5	24.3	1.58
Archaeohippus blackbergi	101	25.1	10.4	2.41
Archaeohippus mannulus	1	16.8	7.5	2.24
Archaeohippus penultimus	1	27.2	12	2.27
Hypohippus wardi	1	40	25	1.60
Miohippus intermedius	1	21.6	12.1	1.79
Parahippus leonensis	32	31.9	14.6	2.18
Parahippus pawniensis	1	35	15.5	2.26
Mesohippus sp.	19	15.9	10.3	1.54
Miohippus sp. *(I-75)*	1	20.9	13	1.61
Brooksville 2	3	21.5	12.7	1.70
Franklin phosphate	1	27	15.7	1.72
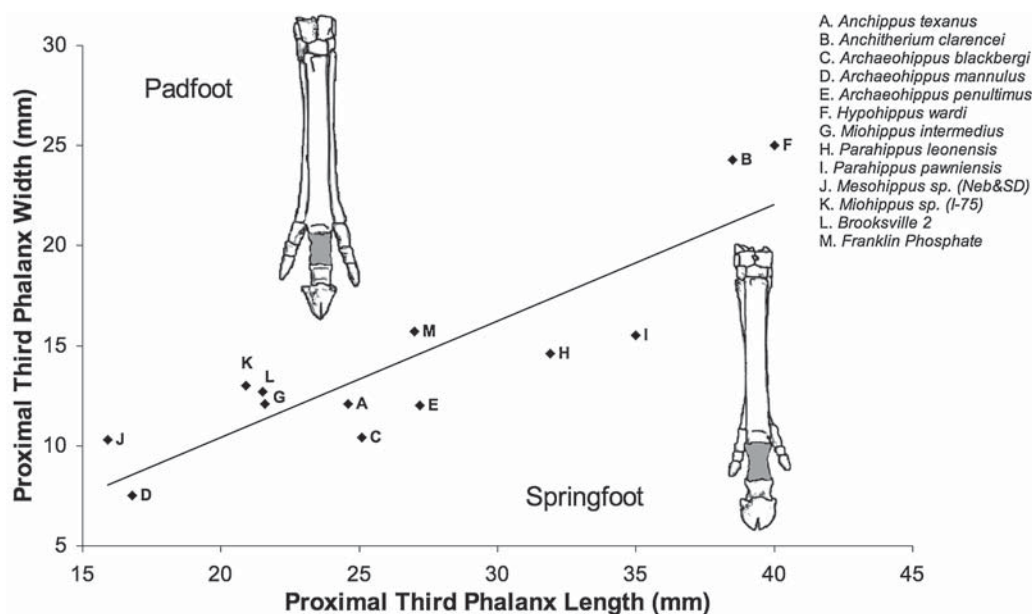
FIGURE 8.2. Plot of PPIIIL/MW index for ASL equids included in this study. The trend line differentiates the broad phalanx of the padfoot equid from the narrow waisted phalanx of the springfoot equid. The *Mesohippus* (padfoot) and *Merychippus* (springfoot) manual skeletons are redrawn from Simpson (1951).

8.4.1 Using Phalangeal Indices As a Diagnostic

The fossil record of Florida indicates that the peninsula has at times been an island, and perhaps at other times an archipelago (White, 1942; Frailey, 1980; Huddleston, 1993). The strong selectional imperatives of island endemism have been cited as influencing body size evolution in Florida equids (Frailey, 1980), possibly resulting in the extreme size reduction seen in the earliest known species of *Archaeohippus*, *A. mannulus* (O'Sullivan, 2003) from the Gulf Coast of Florida. In the phylogenetic analysis cited above, one species of *Parahippus*, *P. pawniensis*, usually nests within the *Archaeohippus* clade, not with the other parahippines. Therefore, *Archaeohippus* likely shares a common ancestor with *P. pawniensis*, a larger, fairly advanced equid, and is therefore a dwarfed parahippine itself.

Several other tiny fossil equids have been recovered from late Oligocene and early Miocene sediments in Florida. As absolute dating techniques are usually not available for these early terrestrial sites in Florida, the exact chronological relationships of these sites are unknown.

These unresolved chronological and geographical relationships could be very complex. For instance, if a small peninsular Florida during the Oligocene was subsequently

subdivided into numerous islands, a single taxon of equids may have diverged simultaneously through this single vicariance event into multiple dwarf taxa. Conversely, minor cycles of sea level increase/decrease could have placed a sequence of different taxa on peninsular Florida, then isolated and dwarfed each. Rising sea levels might drive some of these dwarf taxa to extinction, while decreasing sea levels might permit reattachment to the mainland and emigration of island taxa (as is probably the case with *Archaeohippus*).

The above speculation on sea level change serves but one purpose in this discussion—to establish that there is no *a priori* reason to assume that small equids in Oligocene-Miocene Florida are closely related. While some may be assignable to *Archaeohippus*, instances of convergent body size evolution are also likely. When proximal phalanges are available for analysis, application of the PPIIIL/MW index can be used to assess the ADP affinities of these specimens.

The small equid from Brooksville 2 described by Hayes (2000) is within the size range of *A. blackbergi*. However, it possesses some plesiomorphic character states that exclude it from that genus. Among these is a PPIIIL/MW index of 1.70. Undescribed fossils from the Cowhouse Slough site of Hillsborough County (Albright, 1998) include elements from a small equid that cannot be included in the ADP due to its broad proximal phalanx III and metapodial. The Buda Local Fauna (Frailey, 1979) does not include a proximal third phalanx, but does include a fairly large, primitive proximal lateral phalanx with a *Miohippus* aspect to it. The Franklin Phosphate Local Fauna (Simpson, 1930) has several teeth assigned to *P. leonensis*. However, some plesiomorphic dental characteristics, plus a PPIIIL/MW index of 1.72, make this assignment unlikely. The PPIIIL/MW index in ADP equids is 2.0 or greater; thus, this equid is more likely an advanced *Miohippus*. A phalanx from the I-75 site (Patton, 1969) near Gainesville has an index of 1.6, and is therefore probably correctly identified as *Miohippus* sp., as it is definitely not an ADP equid.

The utility of this index is immediately apparent. Dental indices pertaining to crown height evolution are not reliable for Oligocene-early Miocene taxa. The dietary trends these indices pertain to were not yet established among equids. Except for the ASS equids, most AAR equids were probably mixed feeders (MacFadden, 1997, 2004), with specialist grazers evolving in the middle Miocene. In contrast, the pedal adaptations found in the ADP clade were already evident by the late Oligocene. Thus, the PPIIIL/MW index can distinguish advanced springfoot ADP equids from plesiomorphic padfoot equids among the taxa recovered from some of the earliest terrestrial fossil sites in Florida. Variation in this index in Oligocene-early Miocene equid taxa from the Florida Gulf Coast suggests the possibility that multiple, convergent dwarf taxa inhabited Florida. Thus, a single index, viewed as a proxy for a suite of pedal adaptations that occurred at the base of the equine radiation, provides improved resolution of phylogenetic relationships within the Equidae.

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