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NEW RECORDS OF *PSEUDHIPPARION SIMPSONI* (MAMMALIA, EQUIDAE) FROM THE LATE HEMPHILLIAN OF OKLAHOMA AND FLORIDA

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Webb and Hulbert (1986) described the diminutive horse *Pseudhipparion simpsoni* from the latest Hemphillian Palmetto Fauna (very early Pliocene, ca. 4.5 Ma) of central Florida. They also referred two lower molars from the late Hemphillian Delmore Formation of central Kansas to *P. simpsoni*. This species is the youngest of its genus and unique among the Equidae in the development of its cheek teeth and incisors. As the permanent cheek teeth erupted and began to wear, the base of the crown remained open and the onset of root formation was extensively postponed, more so than in any other equid. Enamel and dentine were added to the base of the crown for a significant period of time, although eventually roots formed and the teeth wore down in a manner typical of equids. Webb and Hulbert (1986) termed this pattern incipient hypselodonty and estimated that at a minimum it effectively doubled the crown height of the cheek teeth of *P. simpsoni*. Webb and Hulbert (1986) referred two equid incisors from the Palmetto Fauna to *P. simpsoni* because of their small size and lack of root formation. Neither specimen was collected in direct association with cheek teeth of *P. simpsoni*, so the referral, although logical, was not conclusive.

Since 1986, many additional specimens of *P. simpsoni*, all isolated teeth or postcranial skeletal elements (Appendix), have been collected from the central Florida phosphate mines that produce the Palmetto Fauna (Morgan, 1994; Webb et al., in press). Most notable has been the increase in number of incisors, with a current total of 12. The records of *P. simpsoni* outside of the type region in Florida have also increased. Of these, the most significant addition is Buis Ranch, Beaver County, Oklahoma (Hibbard, 1954, 1963; Stevens, 1966). One of the two Buis Ranch specimens is a relatively complete dentary that for the first time allows direct association between the incisors and cheek teeth of *P. simpsoni*. This specimen also documents the first known canine of the species. The purposes of this note are to describe the new specimens of *P. simpsoni*, emphasizing previously unknown or poorly known features, and to review its geographic distribution and paleoecology.

Methods and Abbreviations—Terminology for equid cheek teeth is that of MacFadden (1984) and Hulbert (1988). Radius of curvature of incisors was measured along the labial (external) surface (Skinner and Taylor, 1967). All linear measurements were taken with digital calipers and are reported in millimeters. Abbreviations: **OMNH**, Oklahoma Museum of Natural History, Norman; **TMM**, Texas Memorial Museum, Austin; **UF**, Florida Museum of Natural History, Gainesville; **UG**, University of Georgia, Athens; **UM**, University of Michigan Museum of Paleontology, Ann Arbor; and **USNM**, National Museum of Natural History, Smithsonian Institution, Washington D. C.

DESCRIPTION OF NEW SPECIMENS

Buis Ranch Specimens—Both Buis Ranch specimens are left dentaries. UM 38409 (listed as *Nannippus minor* by Stevens, 1966:6) is less complete, consisting of the p4-m2 and portions of the lateral wall and ventral base of bone surrounding these teeth. The teeth are cracked and chipped, and small sections of their occlusal surfaces are missing (Fig. 1C). OMNH 8296 preserves the entire left dentition (i1-i3, c, p2-m3), much of the left half of the symphysis, and all of the horizontal ramus to a point about 1 cm posterior to the m3 (Fig. 1A, B). A “window” was cut into the bone on the lateral side to expose the bases of the crowns of p2-m3.

The depth of the rami in both specimens is similar: about 45 mm in UM

38409 and 44 mm in OMNH 8296 (measured between the p4 and m1). Dentary depth remains relatively constant below p3-m2. Lower tooth row length (p2-m3) on OMNH 8296 is 84.5 mm; p2-p4 length, 39.4 mm; and m1-m3 length, 45.6 mm. Muzzle width across the i3s is estimated to have been about 50 mm (Fig. 1A). The canine-p2 diastema length is 34.3 mm; the i3-p2 diastema length, 44.8 mm. A small, circular mental foramen is located midway between the canine and p2. The symphysis is relatively short and broad.

The i2 and i3 on OMNH 8296 are complete, but the base of the i1 crown is missing (Figs. 1A, 2A). The i1 is bilaterally symmetrical, with flattened medial and distal sides. Its occlusal surface is 8.1 mm wide and 6.5 mm long. Crown width and length on the i1 decrease slightly basally; about 15 mm below the occlusal surface, crown width is 7.9 mm. The radius of curvature of the i1 is about 33 mm. The i2 is nearly symmetrical, with a flat medial side and a slightly more rounded, shorter distal side; its occlusal dimensions are 9.0 mm wide, 6.6 mm long. The crown of the i2 narrows slightly more rapidly than that of the i1; 15 mm below the base of the occlusal surface its width is 8.7 mm. Total length of the i2 is about 44 mm and its radius of curvature is 33 mm. The i3 is the smallest incisor, with a rounded triangular occlusal surface. Its total length is about 38 mm. On both the i2 and i3 the base of the crown is open and no root has formed. The incisors are very procumbent (Fig. 1B) and lack infundibula and dentine tracts.

The alveolus of the canine is separated from that of the i3 by a short diastema of about 4.5 mm. The basal half of the i3 occupies the space in the symphysis normally occupied by the root of the canine in equids. Therefore the shape and orientation of the canine is unusual (Fig. 2A). The morphology of the crown of the canine is like that of most equines, but it projects more laterally. Dimensions of the crown are 6.8 by 5.5 mm. The root of the canine lies dorsal to the i3 and i2. Unlike the other teeth, the canine had formed a root in the fashion typical of equids. The end of the root is twisted laterally with respect to the rest of the tooth, so that it ends directly posterior to the base of the i3.

UM 38409 is from an ontogenetically younger individual than OMNH 8296, judging by the deeper metaflexid on the m1. The base of the crown is observable for the p4-m2 of UM 38409 and the p2-m3 of OMNH 8296. Only the p2 of the latter had closed off the base of the crown and initiated root formation. Almost the entire lingual sides of the teeth are visible in UM 38409. The measurable crown height of all three teeth is about the same, ca. 47 mm. All three teeth curve posteriorly (in medial view); the p4 is the straightest. In OMNH 8296, all three molars as well as p3-p4 are strongly curved posteriorly (Fig. 1B). The crown height of the m1 (ca. 42 mm) is shorter than that of the m2 (ca. 46 mm).

The occlusal enamel pattern of the p2 of OMNH 8296 appears heavily worn, much more so than the others in this specimen (Fig. 1A). All of the flexids are shallow and reduced, especially the metaflexid and lingua-flexid. UF 18316 is a Palmetto Fauna p2 at a similar stage of wear (Fig. 1D), yet it has a minimum remaining crown height of 28 mm (its total crown height can not be measured due to breakage). UF 18316, UF 17113, and OMNH 8296 indicate that the p2 of *P. simpsoni* reduces and then loses its flexids and initiates root formation earlier in ontogeny than the other cheek teeth.

The p3 of OMNH 8296 has shallower flexids than the p4, and this results in a much broader isthmus and greater confluence of the metaconid and metastylid. The p3 and p4 have shallow ectoflexids, broad but

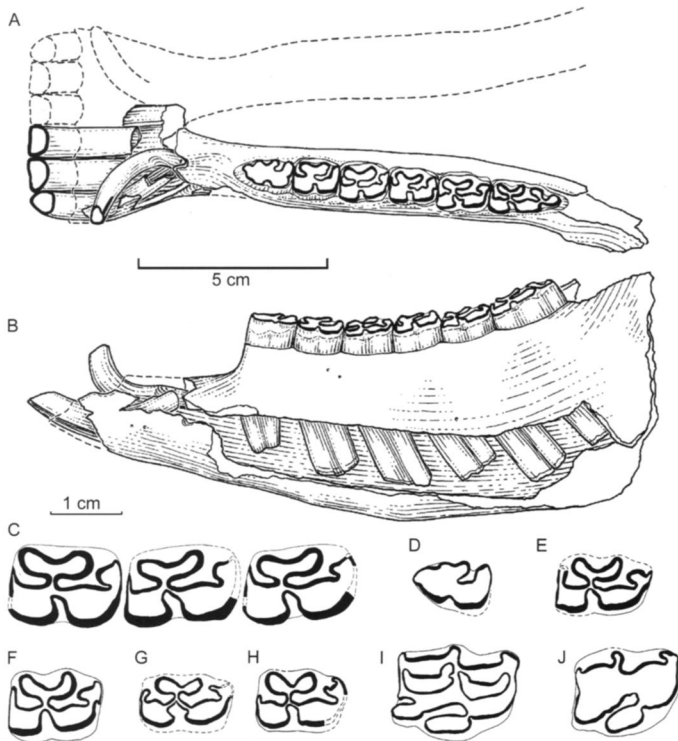


FIGURE 1. *Pseudhipparion simpsoni* from the very late Hemphillian of Oklahoma and Florida. **A**, dorsal, and **B**, lateral views of OMNH 8296, left dentary with i1-i3, c, p2-m3 from Buis Ranch, Beaver County, Oklahoma. **C**, occlusal view of UM 38409, left p4-m2 from Buis Ranch. **D-J** are all occlusal views of isolated teeth from the Palmetto Fauna, Polk County, Florida. **D**, UF 18316, left p2. **E**, UF 53574, left m1 or m2. **F**, UF 58313, right m1 or m2 (reversed). **G**, UF 119803, right m1 or m2 (reversed). **H**, UF 69654, left m1 or m2. **I**, UF 58310, right DP3 or DP4. **J**, UF 101963, right DP3 or DP4. Upper scale bar for A–B; lower scale bar for C–J.

shallow U-shaped linguaflexids, and metastylids equal in size to metaconids. Occlusal enamel patterns of the molars are similar to those of the premolars, differing in slightly deeper ectoflexids and linguaflexids and in metastylids that are narrower than the metaconids. The enamel is simple and lacking plications or folds such as pli caballinids or protostylids on all of the lower cheek teeth of OMNH 8296 and UM 38409. Their morphology can be duplicated in the topotypic sample of *P. simpsoni* from Florida (Fig. 1E, F).

New Palmetto Fauna Specimens—Additions and changes to the original Palmetto Fauna hypodigm of *Pseudhipparion simpsoni* are listed in the Appendix. The newly collected permanent cheek teeth do not substantially change any of the descriptions or conclusions of Webb and Hulbert (1986).

The four upper deciduous premolars in the original hypodigm of *P. simpsoni*, while very hypsodont for deciduous teeth, did not display any of the unusual developmental features of the permanent teeth. UF 58310 (Fig. 1I) and 68999, the most complete specimens, had closed the base of the crown and begun to form roots, apparently in the same manner as observed in other equid teeth (Stirton, 1941). UF 101963, a right DP3 or DP4 (Fig. 1J), is the first known, heavily worn deciduous premolar of *P. simpsoni*. It lacks fossettes, the hypoconal groove is closed, and the parastyle and mesostyle are exaggerated, all features found on well-worn permanent teeth of this species (Webb and Hulbert, 1986:fig. 15).

The initial sample of *P. simpsoni* included only two incisors. Currently 12 are known from the Palmetto Fauna, and OMNH 8296 contains three more. This increased sample, plus knowledge from OMNH 8296 regarding known lower incisor morphology, indicates that some of the initial interpretations regarding the incisors were incorrect. Webb and Hulbert (1986:260) stated that both incisors "...have open infundibula from wear surface to broken base." An infundibulum in an equid incisor is a cement-filled depression composed of enamel. It is likely that slightly worn incisors of *P. simpsoni* had true infundibula, because they are present in

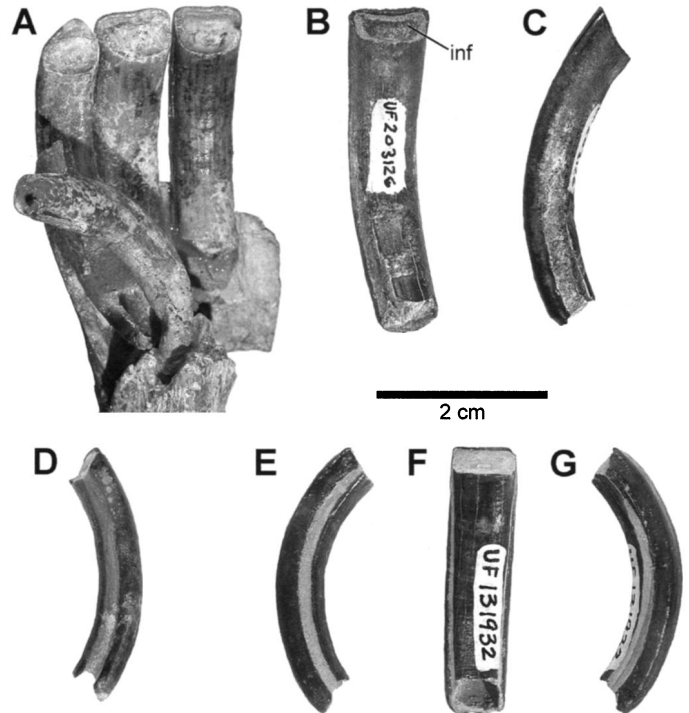


FIGURE 2. Incisors and canine of *Pseudhipparion simpsoni* from the very late Hemphillian of Oklahoma and Florida. **A**, dorsal view of symphyseal region of OMNH 8296 with left i1-c, from Buis Ranch, Beaver County, Oklahoma. **B–G**, incisors from the Palmetto Fauna, Polk County, Florida. **B**, lingual, and **C**, medial views of UF 203126, left I2; **D**, medial view of UF 95774, I2; **E**, medial, **F**, lingual, and **G**, distal views of UF 131932, left I1. Complete dentine tracts (extending from occlusal surface to base of crown) are present in **D** and **E**. In **G**, the dentine tract extends to within a few millimeters of the occlusal surface. In **C**, a dentine tract is present only on the basal half of the tooth, but is less visible than those in **D–G** because of less contrast between the color of enamel and dentine. An infundibulum (**inf**) occupies most of the occlusal surface area in UF 203126 (**B**), but is not observed in ontogenetically older specimens such as UF 131932 (**F**).

the incisors of other species of *Pseudhipparion*. But, like the fossettes of the upper cheek teeth in *P. simpsoni*, they are lost with wear. The oval feature in the center of the occlusal surface interpreted by Webb and Hulbert (1986) as an infundibulum is instead repair dentine that is filling the original pulp cavity. In many Palmetto Fauna specimens, repair dentine preserves as a different color than regular dentine; this difference can be dramatic (as in UF 69920 and 220005) or more subtle (e.g., UF 95774). That these are not true infundibula is evidenced by the absence of an internal surrounding band of enamel. This is especially obvious in specimens where the enamel and dentine are preserved in very different colors, e.g., UF 95774, 100274, 124515, and 131932. Of the Palmetto Fauna incisors, only UF 203126 preserves the base of an infundibulum (Fig. 2B); the structure is definitely absent in the other 11 specimens.

Webb and Hulbert (1986) described both UF 57315 and 69920 as having dentine tracts along their medial surfaces. This is true only for UF 57315. The enamel thins along the medial and distal walls of UF 69920, producing a shallow trough that is filled with cement. However, the enamel passes uninterrupted around the entire crown of UF 69920, so it lacks true dentine tracts. With the increased sample size of *P. simpsoni*, it is now apparent that while some of its incisors had dentine tracts, others lacked them (Table 1; Fig. 2B–G).

One cause for some of the variation in development of dentine tracts in this species is ontogenetic differences between the specimens. Dentine tracts were apparently not present on newly erupted teeth, but were acquired as enamel was added to the base of the crown following a certain period of wear. For example, UF 131932 has a dentine tract (a narrow strip where no enamel covers the dentine) along its entire medial side, extending all the way to the occlusal surface (Fig. 2E). But the

enamel tract on the distal side of UF 131932 ends about 5 mm from its occlusal surface (Fig. 2G). Thus the absence of dentine tracts on unworn or slightly worn incisors could simply mean that the tracts did not have sufficient time to form before death. However, an additional factor must play a role in the distribution of dentine tracts on *P. simpsoni* incisors, because some relatively small specimens lack them completely (Table 1; size can be used as a proxy for ontogenetic age, as incisor occlusal dimensions progressively decrease with wear). Tooth position does not seem to be a factor, as some first, second, and third incisors have dentine tracts and others lack them.

Our current hypothesis is that dentine tracts were formed primarily, perhaps exclusively, on upper incisors and were typically not present on lower incisors. The lower incisors instead have medial and distal grooves (medial only on i3) where the enamel is thin and the cement is thick. This is the condition observed on OMNH 8296, and about half of the Palmetto Fauna sample of *P. simpsoni* incisors. If this hypothesis is correct, then UF 69920 is actually a lower incisor, probably an i2, instead of an upper incisor as identified by Webb and Hulbert (1986). UF 57315 is an upper incisor, as listed by Webb and Hulbert (1986), but is an I2, not an I3.

None of the Palmetto Fauna incisors referred to *P. simpsoni* has formed a root. All have an open pulp cavity. Thus the hypothesis of Webb and Hulbert (1986:260) that the incisors of *P. simpsoni* were truly hypselodont (ever-growing) has not been falsified. This means that very small specimens, such as UF 57315 and 100273, represent very old individuals, and not those of exceptionally small body size.

COMPARISONS BETWEEN FLORIDA AND OKLAHOMA SPECIMENS

OMNH 8296 and UM 38409 resemble *Pseudhipparion simpsoni* from the Palmetto Fauna of Florida more than they do any other species (Figs. 1, 2). The most important point of resemblance is the rootless condition of the teeth. Among equids, only molars of *P. simpsoni* are rootless at a point in ontogeny after the p4 has replaced its deciduous predecessor. The morphology of the incisors of OMNH 8296 is completely matched by Palmetto Fauna incisors such as UF 69920, 100274, and 100275. The enamel pattern of the cheek teeth of the two Buis Ranch specimens falls within the range of variation of the Palmetto Fauna sample of lower cheek teeth of *P. simpsoni*.

The primary difference between the Oklahoma and Florida samples of *Pseudhipparion simpsoni* is size. The depth of the ramus between p2 and p3 is about 40 mm on OMNH 8296 and about 30 mm in UF 24791, although this is one of the most extreme differences. The teeth of the Oklahoma specimens are between 10 and 20 percent larger than average-sized Palmetto Fauna individuals. This degree of size difference between Florida and Great Plains populations is also observed in teeth of the late Miocene *Pseudhipparion skinneri*, the sister taxon of *P. simpsoni* (Webb and Hulbert, 1986). The Palmetto Fauna does contain individual specimens of similar size to those from Buis Ranch, e.g., UF 60830, 69657, 93217, and 100268.

GEOGRAPHIC DISTRIBUTION

During the latest Hemphillian, *Pseudhipparion simpsoni* occurred in the southern Atlantic and Gulf Coastal Plains and the southern Great

Plains of North America. Its presence is regarded as secure in four different faunas and is likely in two others. The four definite records are: Palmetto Fauna, Florida; Buis Ranch Fauna, Oklahoma; Delmore Formation (Moundridge and Kinerman's sand pits), McPherson County, Kansas; and Wright Materials Incorporated gravel pit, Neuces County, Texas. The Florida, Kansas, and Oklahoma specimens were described by Webb and Hulbert (1986) and in this study.

Baskin (1991) described a sample of latest Hemphillian equid fossils found reworked into late Pleistocene alluvium on the southern Texas Coastal Plain. Most of the specimens belong to either *Neohipparion eurystyle*, *Nannippus* spp., or *Astrohippus stockii* (= *A. albidens* of Baskin, 1991). One small lower molar, TMM 43064-1, represents a fourth genus. Baskin (1991) questionably referred it to either *Calippus* or *Pseudhipparion*. It is here referred to *Pseudhipparion simpsoni*. All of the morphological features of TMM 43064-1 that Baskin (1991) regarded as distinctive can be matched with lower molars of *P. simpsoni* from the Palmetto Fauna. These include its very small size (length = 13.1 mm), lack of a protostylid, reduced entoconid and parolophid, and configuration of the metaconid and metastylid.

TMM 43064-1 displays an unusual pattern in its isthmus (Baskin, 1991:fig. 2.10). The angular ectoflexid partially penetrates the isthmus, forming a narrow antisthmus and postisthmus that meet at a 120° angle in the middle of the tooth. A short isthmus begins at the juncture of the antisthmus and postisthmus, and is directed lingually. All three have approximately the same length, so the general appearance is that of an inverted 'Y.' Most of the lower molars of *P. simpsoni* from the Palmetto Fauna that retain deep metaflexids and entoflexids like TMM 43064-1 have shallower ectoflexids that do not penetrate the isthmus. This results in a strikingly different isthmus morphology than is observed in TMM 43064-1 (although otherwise the enamel patterns are the same). However, a small number of Palmetto Fauna lower molars have the inverted 'Y' isthmus pattern of TMM 43064-1, including UF 69654, 69655, and 119803 (Fig. 1G, H). Baskin (1991) was unaware of this rare variant in *P. simpsoni* lower molar morphology because it was neither discussed nor illustrated by Webb and Hulbert (1986).

The presence of *Pseudhipparion simpsoni* at two eastern localities is problematic because of the quality of the specimens. Eshelman and Whitmore (in press) tentatively refer a small sample of isolated postcranial elements from the Lee Creek Mine local fauna, eastern North Carolina, to *P. simpsoni*. The most definitive specimen is the proximal end of a metacarpal 3 (USNM 421962), which is smaller than metacarpals of *Nannippus aztecus* and similar in size to metapodials referred to *P. simpsoni*. Its presence in the Lee Creek Mine local fauna would not be surprising, as it shares a number of species with the Palmetto Fauna of Florida (Eshelman and Whitmore, in press).

The second tentative record of *P. simpsoni* is UG V-56, a poorly preserved upper molar from terrace gravel beds near Reynolds, Taylor County, Georgia. Voorhies (1974) referred this and a second upper cheek tooth in better condition, UG V-55, to *Nannippus minor* (now *N. aztecus* for the reasons discussed by Hulbert, 1990). UG V-55 does represent *N. aztecus*, although it is a molar and not a premolar as identified by Voorhies (1974). UG V-56, on the other hand, is smaller than *N. aztecus* and its protocone and fossette morphology are more like those of

TABLE 1. Incisors of *Pseudhipparion simpsoni* from the Palmetto Fauna, central Florida. Measurements in mm. Width is measured at the occlusal surface mesiodistally; length, labiolingually. An 'a' before a value indicates an approximation due to breakage at the occlusal surface. **ROC**, radius of curvature of labial side. For dentine tracts (**DT**), three states are recognized: present (P), absent (A), or incomplete (I). In the latter, a dentine tract is present at the base of the crown, but has not reached the occlusal surface.

		WIDTH	LENGTH	ROC	MESIAL DT	DISTAL DT
UF 131932	I1	7.75	5.40	23	P	I
UF 220005	I1	8.50	5.87	33	I	I
UF 17572	I1	a9.6	a6.0	27	P	I
UF 203126	I2	9.74	6.65	37	I	I
UF 57315	I2	7.05	4.74	23	P	P
UF 95774	I2	7.47	5.51	25	P	P
UF 95773	I3	7.90	a6.4	30	P	I
UF 100274	i1	8.55	5.08	25	A	A
UF 100275	i2	a8.5	5.29	28	A	A
UF 124515	i2	9.88	5.21	25	A	A
UF 69920	i2	7.88	5.64	30	A	A
UF 100273	i3	5.10	4.73	27	A	A

P. simpsoni. Unfortunately, the condition of the specimen prevents definitive identification.

PALEOECOLOGY

A significant correlation between diet and muzzle shape in ungulates is well established in the ecological and paleoecological literature (e.g., Gordon and Illius, 1988; Janis and Ehrhardt, 1988; Solounias and Moelleken, 1993; Spencer, 1995; Eisenmann, 1998). A short, broad muzzle with a straight-line incisor arcade as observed in *Pseudhipparion simpsoni* is characteristic of a grazer. Other species of *Pseudhipparion*, including its sister taxon *P. skinneri*, have slender muzzles with rounded incisor arcades (Webb and Hulbert, 1986). The worn occlusal surfaces of upper molars of *P. simpsoni* have very low occlusal relief and predominantly blunt or rounded buccal cusps, mesowear features characteristic of grazers (Fortelius and Solounias, 2000). Enamel microwear analysis (MacFadden et al., 1999) also suggests that *P. simpsoni* was a grazer, as do its incipiently hypselodont cheek teeth.

Two hypotheses have been put forward to explain the evolution of incipiently hypselodont cheek teeth in this species. Webb and Hulbert (1986) suggested a shift to a much coarser diet as the primary factor, while MacFadden (1992) proposed instead that it was increased individual longevity. The dramatically different incisor and muzzle morphologies between *P. simpsoni* and all other species of *Pseudhipparion* indicate that an adaptation to a pure grazing diet (or an otherwise much more abrasive diet) was associated with the speciation event responsible for this species. Although other equid clades made this transition without resorting to incipient hypselodonty, nearly all were of substantially larger body size than *P. simpsoni*, which had an estimated mass of about 40 kg (Hulbert, 1993). Fossil samples necessary to document increased individual longevity in this species as yet do not exist.

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LITERATURE CITED

- Baskin, J. 1991. Early Pliocene horses from late Pleistocene fluvial deposits, Gulf Coastal Plain, South Texas. *Journal of Paleontology* 65:995–1006.
- Eisenmann, V. 1998. Folivores et tondeurs d'herbe: forme de la symphyse mandibulaire des équidés et des tapiridés (Perissodactyla, Mammalia). *Geobios* 31:113–123.
- Eshelman, R. E., and F. C. Whitmore. In press. Terrestrial mammals of Lee Creek Mine, North Carolina. *Smithsonian Contributions to Paleobiology*.
- Fortelius, M., and N. Solounias. 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing diets. *American Museum Novitates* 3301: 1–36.
- Gordon, I. J., and A. W. Illius. 1988. Incisor arcade structure and diet selection in ruminants. *Functional Ecology* 2:15–22.
- Hibbard, C. W. 1954. A new Pliocene vertebrate fauna from Oklahoma. *Papers of the Michigan Academy of Science, Arts, and Letters* 39: 339–359.
- Hibbard, C. W. 1963. *Tanupolama vera* (Matthew) from the late Hemphillian of Beaver County, Oklahoma. *Transactions of the Kansas Academy of Sciences* 66:267–269.
- Hulbert, R. C., Jr. 1988. *Cormohipparion* and *Hipparion* (Mammalia, Perissodactyla, Equidae) from the Late Neogene of Florida. *Bulletin of the Florida State Museum* 33:229–338.
- Hulbert, R. C., Jr. 1990. The taxonomic status of *Hipparion minus* Sellards, 1916 (Mammalia, Equidae). *Journal of Paleontology* 64: 855–856.
- Hulbert, R. C., Jr. 1993. Late Miocene *Nannippus* (Mammalia: Perissodactyla) from Florida, with description of the smallest hipparionine horse. *Journal of Vertebrate Paleontology* 13:350–366.
- Janis, C. M., and D. Ehrhardt. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society* 92:267–284.
- MacFadden, B. J. 1984. Systematics and phylogeny of *Hipparion*, *Neohipparion*, *Nannippus*, and *Cormohipparion* (Mammalia, Equidae) from the Miocene and Pliocene of the New World. *Bulletin of the American Museum of Natural History* 179:1–196.
- MacFadden, B. J. 1992. Fossil Horses; Systematics, Paleobiology, and Evolution of the Family Equidae. Cambridge University Press, Cambridge, 369 pp.
- MacFadden, B. J., N. Solounias, and T. E. Cerling. 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. *Science* 283:824–827.
- Morgan, G. S. 1994. Miocene and Pliocene marine mammal faunas from the Bone Valley Formation of Central Florida; pp. 239–268 in A. Berta and T. A. Deméré (eds.), *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.* San Diego Natural History Society, San Diego, California.
- Skinner, M. F., and B. E. Taylor. 1967. A revision of the geology and paleontology of the Bijou Hills, South Dakota. *American Museum Novitates* 2300:1–53.
- Solounias, N., and S. M. C. Moelleken. 1993. Dietary adaptation of some extinct ruminants determined by premaxillary shape. *Journal of Mammalogy* 74:1059–1074.
- Spencer, L. M. 1995. Morphological correlates of dietary resource partitioning in the African Bovidae. *Journal of Mammalogy* 76:448–471.
- Stevens, M. S. 1966. The osteology and relationships of the Pliocene ground squirrel, *Citellus dotti* Hibbard, from the Ogallala Formation of Beaver County, Oklahoma. *Pearce-Sellards Series* 4:1–24.
- Stirton, R. A. 1941. Development of characters in horse teeth and the dental nomenclature. *Journal of Mammalogy* 22:339–410.
- Voorhies, M. 1974. The Pliocene horse *Nannippus minor* in Georgia: geological implications. *Tulane Studies in Geology and Paleontology* 11:109–113.
- Webb, S. D., and R. C. Hulbert, Jr. 1986. Systematics and evolution of *Pseudhipparion* (Mammalia, Equidae) from the Late Neogene of the Gulf Coastal Plain and the Great Plains; pp. 237–272 in K. M. Flanagan and J. A. Lillegraven (eds.), *Vertebrates, Phylogeny, and Philosophy*. University of Wyoming Contributions to Geology, Special Paper 3.
- Webb, S. D., R. C. Hulbert, Jr., G. S. Morgan, and H. F. Evans. In press. Terrestrial mammals of the Palmetto Fauna (early Pliocene, latest Hemphillian) from the central Florida Phosphate Mining District. *Natural History Museum of Los Angeles County, Contributions in Science*.

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APPENDIX

Additions and corrections to the original hypodigm of *Pseudhipparion simpsoni* Webb and Hulbert, 1986. All specimens except UF 136489 are from the Palmetto Fauna (sensu Webb et al., in press), upper Bone Valley Formation, central Florida (Polk, southeastern Hillsborough, northeastern Manatee, and northwestern Hardee counties). More detailed locality information for specimens can be obtained using the online UF vertebrate paleontology collection catalogue at <http://www.flmnh.ufl.edu/scripts/DBs/VP_UF_pub.asp>. UF 136489 is from De Soto Shell Pit 5, De Soto County, Florida, about 40 km south of the Bone Valley phosphate mining district. Although most vertebrate fossils from the De Soto shell pits are latest Pliocene and derive from the Caloosahatchee Formation, UF 136489 was collected from a clay bed at the bottom of the pit that represents the Tamiami Formation, an older unit that, in part, is a correlative of the upper Bone Valley Formation (Morgan, 1994).

Upper Teeth—UF 17572, 131932, 220005 I1; UF 57315, 95774, 203126 I2; UF 95773 I3; UF 101963, 102596, 208280, 217051 DP3 or DP4; UF 100257 P2; UF 68981, 102594, 102595, 119824, 131933, 155037, 162914, 162915, 203179, 208039, 208397, 212205, 217116 P3 or P4; UF 68985, 100258–100261, 123819, 136489, 155035, 162916, 203175, 211776, 217112, 217117 M1 or M2; UF 100262–100266, 115665, 155036, 208398, 211777 M3.

Lower Teeth—UF 100274 i1; UF 69920, 100275, 124515 i2; UF 100273 i3; UF 162917 p2; UF 17112, 93217, 100267–100270, 119764, 131934, 208040, 208396, 211778, 212206, 216997 p3 or p4; UF 93631, 95775, 100271, 100272, 119803, 208041, 217014, 220021 m1 or m2.

Postcranial Elements—UF 53962 distal radius; UF 93259 proximal metacarpal 3; UF 115662, 123790, 124219 distal metacarpal 3; UF 95705 proximal metatarsal 3; UF 212680 distal metatarsal 3; UF 49006, 53961, and 58297 proximal phalanx of digit 3.