

MEGANTEREON HESPERUS FROM THE LATE HEMPHILLIAN OF FLORIDA WITH REMARKS ON THE PHYLOGENETIC RELATIONSHIPS OF MACHAIRODONTS (MAMMALIA, FELIDAE, MACHAIRODONTINAE)

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ABSTRACT—The smilodontine felid *Megantereon hesperus* is described from the latest Hemphillian (early Pliocene) Upper Bone Valley Formation of central Florida. The Florida record marks the earliest known occurrence of *Megantereon* and adds to our poorly known record of this genus in North America. Old World records suggest immigration of *Megantereon* to Eurasia and Africa in the early Villafranchian (middle Pliocene). The genus is not known in North America after the middle Blancan (middle Pliocene).

Within a cladistic framework, *Megantereon hesperus* is more primitive than the Old World species as judged by its larger lower canine and P₃. Diagnostic characters of *M. hesperus* include: development of a prominent groove on the medial surface of the mandible and a stronger dorsoventral ridge marking the anterolateral rim of the mandibular flange. *Megantereon* and *Smilodon* are sister taxa and form the tribe Smilodontini Kurtén, 1963.

INTRODUCTION

THE SMILODONTINE genus *Megantereon* is well known from the Villafranchian (middle Pliocene-early Pleistocene) of Europe, Asia and Africa. Following Ficarelli's (1978) review of the literature, European representatives of *Megantereon* can be referred to a single species, *M. cultridens* Cuvier, 1824. This species is well represented by cranial, dental, and postcranial material from such classic Villafranchian localities as Les Etouaires (Perrier), Senèze (Haute-Loire), Saint-Vallier (Puy-de-Dôme) in France (Viret, 1954; Schaub, 1925), Olivola (Val di Magra), and Upper Valdarno in Italy (Ficarelli, 1978), and La Puebla de Valverde (Teruel) in Spain (Kurtén and Crusafont Pairó, 1977).

In Asia, skulls and dentaries referred to *Megantereon "nihowanensis"* have been reported from Nihowan, Shansi Province, People's Republic of China (Teilhard de Chardin and Piveteau, 1930). Viret (1954) and Ficarelli (1978) have suggested that this species may represent an Asian population of *M. cultridens*. *Megantereon falconeri* Pomel, 1853 [= *M. sivalensis* (Falconer and Cautley, 1868 in Falconer, 1868)] and *M. palaeindicus* Bose, 1880 have been reported by Matthew (1929),

Pilgrim (1932) and Colbert (1935) from the Upper Siwaliks (Pinjor Zone) and *M. praecox* Pilgrim 1932 has been reported from the Middle Siwaliks (Nagri Zone) in Pakistan and adjacent India (Colbert, 1935). Bonis (1976) and Ficarelli (1978) have questioned assignment of these species to *Megantereon* and they have suggested that *M. falconeri* and *M. palaeindicus* may represent *Homotherium* whereas *M. praecox* is probably related to Chinese Pontian forms of *Machairodus*.

Petter and Howell (1982), in a review of the Siwalik *Megantereon* problem, have referred specimens from the Upper Siwaliks (Pinjor Zone) to *M. falconeri* and they have suggested that this species may represent a chronocline of *M. cultridens*. A very late Biharian (latest middle Pleistocene) occurrence of *Megantereon*, *M. inexpectatus* (Teilhard de Chardin, 1939) is reported from locality 1 of Choukoutien, Shansi Province, People's Republic of China.

In South Africa, considerable material remains to be described. However, *M. gracilis* Broom and Schepers, 1946 from Sterkfontein; *M. whitei* Broom, 1937 from Schurberg; and *M. eurynodon* Ewer, 1955 from Kromdraai A can definitely be referred to *Megantereon*. "*Megantereon*" *problematicus* Collings, 1972 from Makapansgat appears to have been incorrectly assigned to this genus

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and may also represent *Homotherium*. Hendey (1973, 1974) has suggested that only one *Megantereon* lineage was present in South Africa and that specimens from these different localities can be regarded as temporal variants of *M. gracilis*.

In North America *Megantereon* has previously been recorded from three Blancan localities: the Hagerman Local Fauna of Idaho (Gazin, 1933; Bjork, 1970), the Rexroad Local Fauna of Kansas (Hibbard, 1937), and the Broadwater Local Fauna of Nebraska (Schultz and Martin, 1970). Gazin (1933) provided the first description of the smilodontine felid from North America that he named *Machairodus* (?) *hesperus*, based on a right ramal fragment bearing M_1 from the Hagerman Local Fauna (early Blancan) of Idaho. Schultz and Martin (1970) referred a fragmentary but diagnostic mandible from the Lisco Member of the Broadwater Formation (middle Blancan), Nebraska to *Megantereon hesperus*, emending Gazin's doubtful placement of *M. hesperus* in *Machairodus*. A left P_4 from Rexroad Formation (early Blancan), Kansas assigned by Hibbard (1937) to *Machairodus* sp. was identified by Schultz and Martin (1970) as representing *Megantereon*. We provisionally refer this specimen to *M. hesperus*. In central Florida, the late Hemphillian Upper Bone Valley Formation records the earliest known *Megantereon*. The purpose of this report is to describe *M. hesperus* from Florida and to discuss the phylogenetic and biostratigraphic significance of this occurrence.

The following institutional abbreviations are used in the text: IGF, Geological and Paleontological Museum, Florence University, Florence, Italy; TRO, Timberlake Research Organization, Lake Wales, Florida (private collection); UF, Vertebrate Paleontology Collection, Florida State Museum, University of Florida, Gainesville, Florida; UKMNH, University of Kansas Museum of Natural History, Lawrence, Kansas; UNSM, University of Nebraska State Museum, Lincoln, Nebraska; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY
Order CARNIVORA Bowdich, 1821

Suborder FELIFORMIA Kretzoi, 1945
Superfamily FELOIDEA Simpson, 1945
Family FELIDAE Gray, 1821
Subfamily MACHAIRODONTINAE Gill, 1872
Tribe SMILODONTINI Kurtén, 1963
Genus MEGANTEREON
Croizet and Jobert, 1828

Type species.—*Ursus cultridens* Cuvier, 1824 (senior synonym of *Megantereon megantereon* Croizet and Jobert, 1828).

Included species.—Type species and *M. nihowanensis* Teilhard de Chardin and Piveteau, 1930; *M. inexpectatus* Teilhard de Chardin, 1939; *M. whitei* Broom, 1937; *M. gracilis* Broom and Schepers, 1946; *M. euryrnodon* Ewer, 1955; *M. falconeri* Pomel, 1853; and *M. hesperus* Gazin, 1933.

Revised generic diagnosis.—Differs from all other machairodont genera but shares with *Smilodon* the following derived characters: glenoid process enlarged; prominent postorbital process; well developed supraoccipital crest; upper canines elongate, compressed and recurved; upper and lower incisors enlarged; P_2^2 lost; long postcanine diastema; P_3^3 reduced; P^4 protocone reduced; mandibular flange; coronoid process reduced; lower canines reduced; and limbs and feet short and stocky. More primitive than *Smilodon* in having: upper and lower incisors proportionately less enlarged and not as procumbent; upper canines relatively shorter and less robust; P^4 ectoparastyle less developed; and enlarged mandibular flange. Differs from *Smilodon gracilis* in possessing a large P_3 relative to P_4 with a well developed posterior cusp on P_3 . Differs from *Smilodon populator* in its smaller size; lack of serrations on canines and cheek teeth; less inflation of maxillary at sides of canines; and less reduction of nasals.

Known distribution.—Latest Hemphillian–Middle Blancan, North America; Early–Late Villafranchian, Europe; Villafranchian–Biharian, Asia; and Villafranchian, Africa.

MEGANTEREON HESPERUS (Gazin, 1933)
Figures 1A, B

Machairodus (?) *hesperus* GAZIN, 1933.

Machairodus sp. HIBBARD, 1937.

Megantereon hesperus SCHULTZ AND MARTIN, 1970.

Holotype.—USNM 12614, partial right ramus with M_1 .

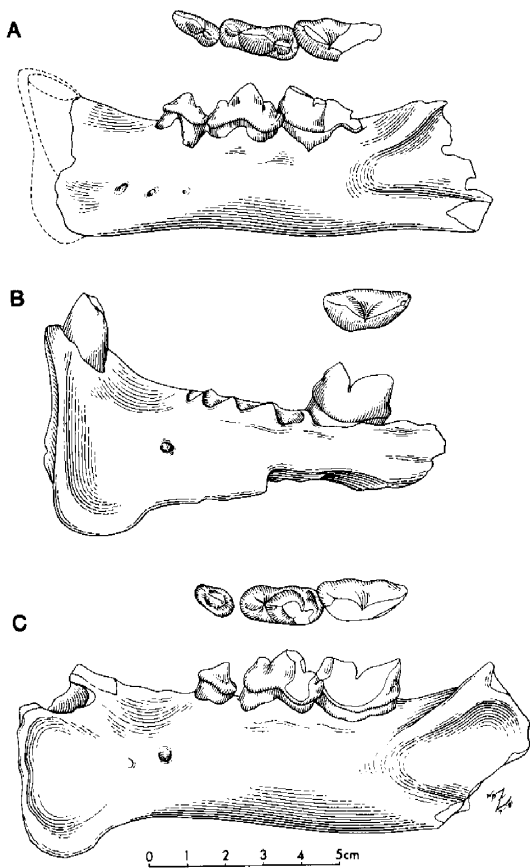


FIGURE 1—Lateral and occlusal views of right rami of *Megantereon* and *Smilodon*. (A) *Megantereon hesperus*, UF 22890 from Bone Valley Formation, Florida, (B) *Megantereon hesperus*, UNSM 25494 from Broadwater Formation, Nebraska, and (C) *Smilodon gracilis*, TRO 1665 from Inglis 1A, Florida.

Type locality.—Hagerman Local Fauna, Glens Ferry Formation, Twin Falls County, Idaho (Bjork, 1970).

Known distribution.—Latest Hemphillian, Florida; Early Blancan, Idaho and Kansas; Middle Blancan, Nebraska.

Hypodigm.—Holotype; UNSM 25494, partial left ramus with I_{2-3} alveoli, C broken near crown, P_{3-4} alveoli, and M_1 , partial right ramus with P_{3-4} alveoli, M_1 root from Lisco Member, Broadwater Formation, Morrill Co., Nebraska; UF 22890, partial left ramus with C alveolus, P_{3-4} , anterior one-half of M_1 from the Palmetto Mine, Upper Bone Valley Formation, Polk Co., Florida; UKMNH 3917,

left P_4 , from Rexroad Formation, Meade Co., Kansas.

Diagnosis.—*Megantereon hesperus* can be distinguished from all other species of *Megantereon* in possessing primitively a larger lower canine and P_3 , and by the development of a prominent groove on the medial surface of the mandible and a stronger dorsoventral ridge marking the anterolateral rim of the mandibular flange.

Description of Florida specimen.—The Bone Valley ramus, UF 22890 (Figure 1A) was collected by Mr. Bill MacDonald of Tampa, Florida in 1970 and generously donated to the FSM. The jaw occurred in coarse phosphatic gravels presumably the Upper Bone Valley Formation, although it was not collected in situ. It represents a young adult as indicated by the slight wear on the cheek teeth. The ramus, exclusive of teeth, has suffered some post mortem abrasion and breakage suggesting transportation before deposition. The anterior portion of the symphysis is missing leaving no indication of incisor alveoli or the anterior wall of the canine alveolus. However, the posterior wall of this alveolus clearly shows that the canine root was laterally compressed suggesting a similar condition of the tooth, as in other *Megantereon* species. In UF 22890, the greater difference in depth of the ventral insertion of the canine root indicates that the crown may not have projected as high above the toothrow as in the Broadwater mandible, UNSM 25494 (Figure 1B). Although the anterolabial portion of the mandibular flange is missing, it clearly deepens at its anterior end and extends below the ventral border of the symphysis (Figure 1A). The mandibular flange is also enlarged in *Smilodon gracilis* (Figure 1C) although it is thinner and lacks the strong dorsoventral ridge marking the anterolateral rim of the flange, a diagnostic character of *Megantereon hesperus* (Figure 1B). The masseteric fossa extends to the anterior root of M_1 .

The diastema between the canine alveolus and P_3 is marked by a dorsal ridge which runs along the medial side of the jaw. This ridge is better developed in the Broadwater specimen and other *Megantereon* species. Three mental foramina are positioned in a straight row slightly ventral to the midline of the ra-

mus. The posteriormost foramen, the smallest, is placed below the posterior root of P₃ and is separated from the anteriormost foramen by a distance of 15 mm. The anterior and medial foramina are slightly larger and positioned below the postcanine diastema and anterior root of P₃ respectively. In the Broadwater ramus, only one large mental foramen is present (possibly homologous with the anteriormost foramen in the Bone Valley specimen) which is positioned relatively higher on the ramus below the alveolus for the anterior root of P₃. The greatest depth of the Bone Valley mandible is below the middle of M₁ (Table 1).

In medial view, the anterior face of the symphyseal region is pitted by numerous foramina. The posterior face of the symphysis slopes backward. A shallow groove passes horizontally just below the midline of the ramus. A large mandibular foramen is present behind M₁.

The cheek teeth (Figure 1A) are crowded, the posterolingual margins of P₃ and P₄ overlapping the anterolabial margins of P₄ and M₁. The primary cusps of the cheek teeth are obliquely oriented relative to the anteroposterior axis of the horizontal ramus. The P₃ of UF 22890 is relatively large. It has two distinct roots which are widely separated, more so than in the Broadwater mandible. In the other *Megantereon* species, for example, *M. eurynodon* from South Africa, the roots are weak and positioned close to one another. P₃ displays an elliptical occlusal outline with a broadly rounded posterior end. A midline ridge extends the length of this tooth and P₄ giving the crown a strongly trenchant aspect. A small conical cusp lies behind the principal cusp of P₃. The tooth terminates in an upturned cingular heel. P₄ is tricuspid, displaying strong subequal anterior and posterior cusps. Both anterior and posterior ends of the tooth are broadly rounded. P₄ is longer than M₁ owing to the relative size of the accessory cusps and the expanded posterolingual portion of the tooth. *Megantereon hesperus* differs from *Smilodon gracilis* (Figure 1C) in having a larger P₃ relative to P₄ with widely separated double roots and a well developed posterior cusp on P₃. The structure and proportion of P₃₋₄ are most similar to those of *M. cultridens* from Saint-Vallier, France (Vi-

TABLE 1—Mandible and lower tooth measurements (mm) and statistics of *Megantereon hesperus* and related taxa. Abbreviations: a, alveolus only; e, estimated measurement; 'measurements following Ficcarelli, 1978; N, number of specimens; \bar{x} , mean; O.R., observed range.

Measurement	<i>M. cultridens</i> ¹						<i>M. hesperus</i>						<i>Smilodon gracilis</i>						
	Italy (Upper Valdarno)			(Olivola)			Nebraska		Idaho		Kansas		Florida		Florida		Pennsylvania		
	IGF	IGF	IGF	IGF	IGF	IGF	UNSM	USNM	USNM	UKMNH	UF	UF	UF	UF	\bar{x}	O.R.			
Depth of flange, posterior C alveolus to ventral border of flange	827	826	829	18485	4711	4709	25494	12614	3917	22890	22890								
Depth of ramus below M ₁							48.1	25.0		28.9				52.3	47.8-55.7				
Length of tooththrow, P ₃ -M ₁							50.1e			48.5				30.1	27.5-32.4				
Canine, anteroposterior length							11.2							54.2	48.6-59.3				
Canine, transverse width							8.1							9.8	7.0-11.3				
P ₃ , anteroposterior length							10.7a			12.0				7.5	7.1-8.3				
P ₃ , transverse width							5.6a			5.6				10.8	10.1-12.0				
P ₄ , anteroposterior length	19.6			18.8	19.2	19.0e	18.3a		18.6	19.1	10			5.2	4.0-6.0				
P ₄ , transverse width	9.2			8.0	8.5	8.0e	7.2a		9.0	8.0	10			20.1	18.2-22.0				
M ₁ , anteroposterior length	23.1	23.0	18.4	22.1	20.0	20.0e	19.7	19.8		21.0e	10			8.5	7.8-9.5				
M ₁ , transverse width	11.0	10.4	9.3	10.0	9.5e	9.5e	9.3	8.5		9.5	10			22.3	20.8-25.2				
														9.7	7.7-10.5				

ret, 1954). No serrations are developed on P_{3-4} , a diagnostic character of all *Megantereon* species.

Unfortunately, M_1 is badly damaged posterior to the carnassial notch, leaving no trace of the protoconid. The size of the paraconid and the transverse area of the notch indicate that although the paraconid is worn, it seems to have been tall relative to the height of P_4 . As indicated by the fragmentary M_1 and its alveolus, the carnassial of the Bone Valley specimen was longer than that of the type of *M. hesperus* (Table 1), moreover, the transverse width across the notch is also greater. The M_1 of both the holotype, USNM 12614, and the Broadwater specimen, UNSM 25494, has a relatively narrow notch as in the Old World species of *Megantereon*.

The Florida specimen is assigned to *M. hesperus* based on its similarity to the Broadwater mandible; the Hagerman and Rexroad specimens being less complete. M_1 in UF 22890 differs from both the Broadwater and Hagerman specimens in its larger size (both absolute and relative to P_4) and greater transverse width (Table 1). This difference, as well as the possible deeper canine insertion and more numerous mental foramina in the Bone Valley specimen are judged of minor taxonomic significance. Due to the incomplete nature of the jaw, the authors prefer to take a taxonomically conservative approach, understanding that better material may show the Bone Valley form to be distinct.

DISCUSSION

Relationships.—The Machairodontinae including the tribes Machairodontini (*Nimravides*, *Miomachairodus*, *Machairodus*, *Homotherium*, and *Dinobastis* (= *Ischyrosmilus* in part)); Metailurini (*Adelphailurus*, *Stenailurus*, *Metailurus*, *Therailurus*, *Dinofelis* and *Pontosmilus*); and the Smilodontini (*Megantereon* and *Smilodon*) form the sister group to the Felinae. Recognition of the tribe Machairodontini proposed by Beaumont (1964) is followed here with addition of *Ischyrosmilus ischyryus* Merriam, 1905, the genoholotype which we synonymize with *Dinobastis*. Other species referred to *Ischyrosmilus*, *I. johnstoni* Mawby, 1965, *I. crusafonti* Schultz and Martin, 1970 and *I. idahoensis* Merriam, 1918 are reassigned to *Homotherium*.

At the tribal level for the Metailurini we

follow the group distinction recognized by Crusafont Pairó and Aguirre, 1972. *Adelphailurus* Hibbard, 1934 and *Pontosmilus* Kretzoi, 1929 (= "*Paramachairodus*" *orientalis* Kittl, 1887) are included for the first time in the Metailurini. The generic names *Pontosmilus* Kretzoi, 1929 and *Paramachairodus* Pilgrim, 1913 have been confused in the literature. *Pontosmilus* is the proper generic name for "*Machairodus*" *orientalis* Kittl, 1887. Pilgrim (1913, 1915) failed to designate a type species for *Paramachairodus*, which is therefore a *nomen dubium*. Kretzoi (1929) properly reestablished *Paramachairodus* for the species *P. pilgrim* Kretzoi, 1929 and assigned a new genus *Pontosmilus* for "*M.*" *orientalis*. According to Kretzoi (1929) *Pontosmilus* includes the species *P. ogygius* Kaup (1833), *P. hungaricus* Kormos (1911), *P. schlosseri* Weithofer (1888), and *P. indicus* Kretzoi (1929). *Adelphailurus* and *Pontosmilus* are very similar to *Metailurus* Zdansky, 1924 and their generic validity may prove doubtful in a thorough review. In comparison with *Metailurus major* Zdansky, 1924, *Adelphailurus* is primitively smaller with P^2 still present and with no development of an anterior cusp on P^3 . *Pontosmilus* differs only slightly from *M. major* in its lack of an anterior cusp on P^3 . The close relationship between *Megantereon* and *Smilodon* was recognized by Schaub (1925), Thenius (1967), Kurtén (1963, 1968), Repenning (1967), Schultz and Martin (1970), Beaumont (1978), and Martin (1980). Kurtén's (1963) referral of *Megantereon* and *Smilodon* to the tribe Smilodontini is followed here. The taxonomic position of *Megantereon* can be most clearly discussed in a cladistic framework (Figure 2).

The Machairodontini, Metailurini, and Smilodontini share primitively the following derived characters (Figure 2, point 1): (a) upper canines elongate and laterally compressed; (b) upper incisors enlarged; (c) P^4 parastyle enlarged; (d) P_{3-4}^3 with strong anterior and posterior accessory cusps; (e) robust, rectangular symphysis; and (f) coronoid process reduced. The Smilodontini include the two closely related genera *Megantereon* and *Smilodon* and they share the following characters (Figure 2, point 2): (a) prominent postorbital process; (b) postglenoid process enlarged; (c) well developed supraoccipital crest; (d) upper canines further elongated, lat-

erally compressed, and recurved, (e) P_2^2 lost; (f) P_3^3 reduced; (g) P^4 protocone reduced, ectoparastyle enlarged, and anteriorly directed; (h) lower canines reduced; (i) long post-canine diastema; (j) mandibular flange; (k) coronoid process further reduced; (l) limbs and feet short and stocky; (m) shortened tail.

Smilodon differs from *Megantereon* in the following derived characters (Figure 2, point 3): (a) postglenoid process greatly enlarged; (b) mastoid process enlarged; (c) incisors enlarged and procumbent; (d) upper canines further elongated and robust; (e) P^4 ectoparastyle further enlarged; and (f) mandibular flange reduced. *Smilodon populator* is more derived than *S. gracilis* in the following characters (Figure 2, point 4): (a) larger size; (b) broadened muzzle; (c) upper canines and cheek teeth with serrated margins; (d) P^4 protocone very reduced; (e) P_3 usually lost; (f) mandibular flange greatly reduced; and (g) mandible with single large mental foramen. *Megantereon* species are united in possessing an enlarged mandibular flange (Figure 2, point 5). *M. hesperus* can be distinguished from all other species of *Megantereon* by (Figure 2, point 6): the development of a prominent groove on the medial surface of the mandible and a stronger dorsoventral ridge marking the anterolateral rim of the mandibular flange. The more advanced Asian, African, and European species of *Megantereon* share (Figure 2, point 7): reduction of the lower canine and P_3^3 .

Beaumont (1978) proposed that the genus *Pontosmilus* (=“*Paramachaerodus*” *orientalis* Kittl, 1887) is the primitive sister taxon of *Megantereon* and *Smilodon*. Our study does not support this conclusion. Comparisons show that loss of dental serrations has not occurred in felids. It seems unlikely therefore, that the non-serrated upper canines in *Megantereon* were derived from a form with serrations such as *Pontosmilus*. We have interpreted the absence of serrations in *Megantereon* as retention of the primitive condition.

Biochronology.—The earliest known occurrence of *Megantereon* is *M. hesperus* here recorded from the Upper Bone Valley of Florida. The Upper Bone Valley Formation and its vertebrate fauna have been considered late Hemphillian in age (Webb, 1973). MacFadden and Galiano (1981) suggest that this assemblage is of very latest Hemphillian

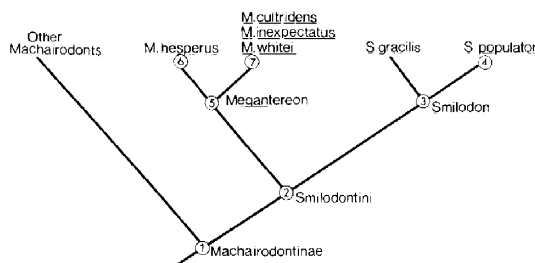


FIGURE 2—Cladogram expressing relationships among the Smilodontini.

age or perhaps approximates the Hemphillian–Blancan boundary (within the early Pliocene, about 4.5 MYBP). The Hagerman and Rexroad faunas are both younger, early Blancan in age. According to Lindsay, Johnson and Opdyke (1975) and Neville, Opdyke, Lindsay and Johnson (1979), both the Rexroad Formation of Kansas and the upper part of the Glenns Ferry Formation (Hagerman Horse Quarry) of Idaho are normally magnetized sections that probably correlate with the Gauss Chron (2.5–3.4 MYBP). The Broadwater Formation of middle Blancan age (Skinner and Hibbard, 1972) represents the latest occurrence of this taxon in North America.

Old World records of *Megantereon* indicate that the genus appeared in Eurasia and Africa during the early Villafranchian (middle Pliocene). Of these occurrences only the Les Etouaires fauna of France has been dated at 3.5–3.0 MYBP (Savage and Curtis, 1970). *Megantereon* apparently became extinct in the Old World during the latest middle Pleistocene. The latest recorded occurrence is that of *Megantereon inexpectatus* from Choukoutien. Fission track and Uranium series dating of locality 1 at Choukoutien provide an average date of 0.4–0.5 MYBP (Zhao and others, 1980; Shilun and others, 1980) which suggests a very late Biharian age. According to Berggren and Van Couvering (1974) the Biharian is equivalent to the latter part of the Matuyama and early part of the Brunhes Chron (1.9–0.5 MYBP).

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ADDENDUM

Since this paper was accepted for publication, re-study of the Bone Valley collection at the Florida State Museum and the acquisition of new material indicates that several additional specimens can be provisionally referred to *Megantereon hesperus*. These specimens were collected from the Upper Bone Valley Formation from Fort Green Mine, Hardee County and from the Payne Creek Mine (TRO Quarry), Polk County, Florida.