

BULLETIN
OF THE
FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 12

Number 5

**PLIO-PLEISTOCENE MEGALONYCHID
SLOTHS OF NORTH AMERICA**

Sue E. Hirschfeld and S. David Webb



UNIVERSITY OF FLORIDA
Gainesville
1968

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

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Published December 16, 1968

Price for this issue \$1.20

PLIO-PLEISTOCENE MEGALONYCHID SLOTHS OF NORTH AMERICA

SUE E. HIRSCHFELD AND S. DAVID WEBB

SYNOPSIS: Although ground sloths appear in South America in Mustersan (late Eocene) time, they are not found in North America until the Hemphillian (middle Pliocene) when three genera appear, two of them megalonychids. It now appears that the genus *Megalonyx* was widely distributed through North America by that time. The most primitive is *M. mathisi*, new species, from the upper Mehrtens formation, Merced Co., California. Additional material of *M. curvidens* Matthew from the Upper Snake Creek channels of Sioux Co., Nebraska, differs in its shorter cheek teeth and narrower caniniforms from later species. Likewise a fine collection of late Blancan (early Pleistocene) *M. leptostomus* Cope from Cita Canyon, Randall Co., Texas, exhibits small cranial, dental and podial differences from typical late Pleistocene species of *Megalonyx*. *M. leptonyx* (Marsh) is a *nomen dubium*. The general features of *Megalonyx* are reviewed and the great variability of its dentition is analyzed.

The earliest megalonychid from North America is a new genus and species, *Pliometanastes protistus*, from early Hemphillian deposits at McGehee Farm, Alachua Co., Florida. Relatively complete material of this new genus is described. Another new species from New Mexico, ?*P. galushai*, and other records from western North America are presented. The genus bears no special relationship to *Megalonyx* nor to any of the West Indian megalonychids, but stems from some Mio-Pliocene stock that gave rise to all of these.

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INTRODUCTION

Ground sloths appear in South America in the Mustersan (late Eocene), but the group is unrecorded in North America until the Hemphillian (middle Pliocene). Fossil records of these earlier North American forms have hitherto been few and fragmentary. For this reason, the discovery of relatively abundant remains of two genera of Hemphillian ground sloths in central Florida adds significantly to our knowledge of the phyletic and zoogeographic relationships between North and South American forms. The genera are *Thinobadistes* Hay, a mylodontid from Mixson's Bone Bed, and a new megalonychid genus from McGehee Farm. This contribution concerns the new megalonychid and a review of other early North American megalonychid sloths. A nearly complete skull from the late Hemphillian of California representing a new structurally primitive species of *Megalonyx*, new material of *M. curvidens* from latest Hemphillian deposits, as well as an excellent collection of *M. leptostomus* from the late Blancan of Texas are described and problems of defining species of *Megalonyx* on the basis of isolated teeth are analyzed.

When the family Megalonychidae (as constituted by Simpson, 1945) first appears in the Deseadan (early Oligocene) of Patagonia, it is represented by fragmentary material. By the Santacrucian (middle Miocene) stage in Patagonia seven megalonychid genera are distin-

guished, most of them represented by abundant material. Within the most completely known genus, *Hapalops*, 22 species have been proposed.

Skipping to the Pleistocene, *Megalonyx*, the best known Pleistocene megalonychid, is well represented by skulls, teeth, and two complete skeletons. Although it is not found in South America, it ranges widely through North America, reaching north to Alaska (Stock, 1942). In the West Indies nine genera of megalonychid sloths have been recognized (Paulo Couto, 1967), all presumably Pleistocene in age.

This substantial knowledge of megalonychid sloths in the Miocene of South America and in the Pleistocene of Nearctica and the West Indies contrasts strikingly with our ignorance of the group in the Pliocene of the entire hemisphere. The new genus from Florida is now the most completely known Pliocene megalonychid. Its description, together with the review of other early North American megalonychids, is intended to fill the Pliocene gap and thereby to provide new insight into the taxonomic and geographic relationships of megalonychid sloths.

ACKNOWLEDGMENTS

The present contribution grew from the analysis of several unpublished collections of early North American megalonychids. We began with the new Hemphillian genus from Florida in the collections of the Florida State Museum, University of Florida (abbreviated UF). The first specimens of this form were discovered by Florida State Museum parties under Clayton E. Ray during preliminary excavation of the McGehee Farm Site in the summer of 1963. Intensive work began in 1964 with support from the Frick Corporation and continued from 1965 through 1967 aided by NSF grant GB 3862. Then Donald E. Savage suggested that we study the megalonychid material from the extensive Cita Canyon fauna that he and others had collected for the Panhandle Plains Museum at West Texas State, Canyon, Texas (hereafter WT). Thirdly, (we investigated the Tertiary megalonychids in the incomparable Frick collection of Cenozoic vertebrates now in the American Museum of Natural History in New York (FAM), and the Blancan material from Hagerman, Idaho in the U.S. National Museum collections (USNM). We studied Pliocene megalonychids in the Museum of Paleontology of the University of California at Berkeley (UCMP) and those in the collections of the University of Oregon (UO). And finally we compared these earlier materials with the fine collection of late Pleistocene *Megalonyx* in the Academy of Natural Science of Philadelphia (ANSP).

We wish to thank the many colleagues who received us graciously and loaned us material from their institutions. We are particularly grateful to Malcolm C. McKenna, Bryan Patterson, Donald E. Savage, R. J. G. Savage, Morris Skinner, Ted Galusha, S. J. Olsen, J. A. Shotwell, Horace Richards, H. K. Brooks, and R. A. Edwards for their advice and assistance.

All measurements in this paper are in millimeters unless otherwise indicated. Statistical methods and abbreviations follow Simpson et al. (1960). Additional abbreviations of collections are AM (American Museum of Natural History), OMP (Oklahoma Museum of Paleontology), and PU (Princeton University). Our dental nomenclature distinguishes the caniniforms from the molariforms, and therefore the abbreviation M_1 indicates the first lower molariform tooth, which some systems label M_2 .

Megalonyx Harlan

Megalonyx Harlan, R. 1825. Fauna Americana, Anthony Finley, Philadelphia: 201. (Type species *M. jeffersoni* Wistar, West Virginia).

Morotherium Marsh, O. C. 1874. Notice of new Tertiary mammals III. Amer. Jour. Sci., 1874: 531. (Type species *M. gigas* Marsh, Central California).

DIAGNOSIS. — (Modified from Stock, 1925.) Skull short, broad, and deep, with anterior end truncated and strong sagittal crest. Mandible deep, without spoutlike premental region. Dentition $\frac{5}{4}, \frac{5}{4}$. First tooth separated by diastema from cheek tooth series; cross-section meniscoid with inner bulge. Last superior tooth subtriangular in cross-section. Appendicular skeleton more robust than in *Nothrotherium*. Winglike process of calcaneum broad; astragalus retaining essentially the structure seen in *Hapalops* and distinctly less modified than in *Nothrotherium*. Astragalus possessing V-shaped notch for reception of the tibia. Shaft of fibula curved dorso-medial to distal end in region of peroneus brevis attachment. Metatarsal IV-short; metatarsal V with relatively slender lateral process.

DENTAL VARIABILITY

It has long been recognized that the dimensions of sloths are among the most variable of any mammals. This is exemplified among fossils by the 22 "species" of *Hapalops* described from the Santa Cruz deposits of Patagonia. Similarly in *Megalonyx* nearly every good specimen has been described as a different species. Whether this variability is inter- or intraspecific is a crucial, but rarely answered, question.

Simpson (1959) shows that while considerable individual variation is manifest within a single collection of *Megalocnus rodens*, this variation is continuous and appears to represent a single population. We present a similar analysis of all the complete adult megalonychid teeth from the Port Kennedy Bone Cave collection in the ANSP (Tables 1 and 2). Measurements were taken just below the occlusal surface of each tooth. Cope (1871) described four species of *Megalonyx* from this collection and, for the sake of objectivity, we have followed his assignments for all teeth used in this analysis.

Table 1. STATISTICAL ANALYSIS OF THE TEETH OF *Megalonyx wheatleyi*

Tooth	N	O R		X		S		V	
		AP ¹	ML ²	AP	ML	AP	ML	AP	ML
C ¹	21	35.9-29.5	19.3-16.0	32.6	17.7	1.99	1.18	6.09	6.66
C ₁	23	36.9-29.1	17.7-13.0	32.5	15.5	2.12	1.29	6.52	8.34
M ¹	6	15.7-14.7	20.0-17.0	15.3	19.0	.33	1.22	2.16	6.43
M ₁	14	15.9-14.4	23.0-20.0	15.4	21.5	.66	.77	4.29	3.57
M ²	9	15.9-14.4	23.8-19.4	15.8	22.2	.63	1.67	4.20	7.53
M ₂	10	16.4-13.7	24.8-20.7	15.3	22.9	.72	1.10	4.72	4.80
M ³	7	16.5-14.6	25.9-21.0	15.5	23.5	.73	1.87	4.71	7.96
M ₃	9	17.9-14.6	23.1-20.3	16.2	21.9	1.09	1.02	6.72	4.66
M ⁴	9	12.3-11.0	19.2-17.0	11.4	18.4	.35	.67	3.06	3.65

¹AP = anteroposterior.
²ML = mediolateral.

Table 2. STATISTICAL ANALYSIS OF THE CANINIFORM TEETH OF *Megalonyx wheatleyi*, *M. tortulus*, AND *M. loxodon*

Tooth	N	O R		X		S		V	
		AP ¹	ML ²	AP	ML	AP	ML	AP	ML
C ¹	24	35.9-29.5	19.3-16.0	32.7	17.7	1.88	1.08	5.75	6.10
C ₁	24	36.9-29.1	17.7-13.0	32.5	15.4	2.08	1.27	6.40	8.25

¹AP = anteroposterior.
²ML = mediolateral.

Two sets of calculations were made on these teeth: The first uses just those teeth Cope designed as *M. wheatleyi*; the second includes all adult sloth teeth from the deposit, among them one lower and two upper caniniforms of *M. tortulus* and one upper caniniform of *M. loxodon* (the specimen of *M. sphenodon* was omitted because it is a juvenile). The second set of calculations yields coefficients of variation that are not unusually high and graph in a homogeneous cluster of points (Fig. 1). This strongly suggests that the Port Kennedy Bone Cave specimens belong to a single population.

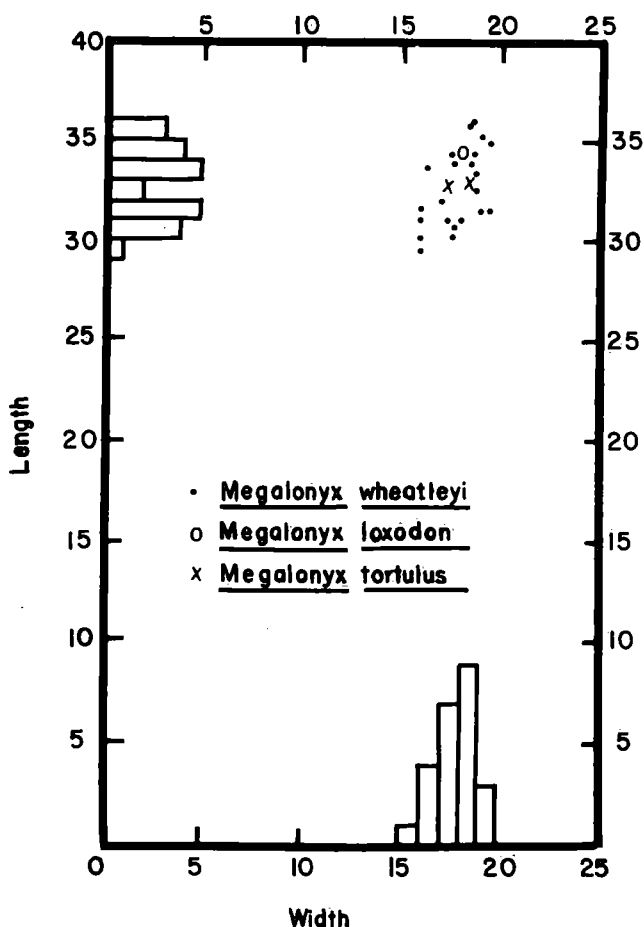


FIGURE 1. Size distribution of upper caniniform teeth of adult *Megalonyx wheatleyi*, *M. loxodon*, and *M. tortulus* from Port Kennedy Bone Cave, Pa. Measurements taken just below occlusal surface.

In study of megalonychid teeth too little attention has been paid to ontogenetic variation. Juvenile specimens of *Megalonyx* and of Recent tree sloths have consistently failed to yield deciduous teeth. Owen (1840-45) describes a newly erupted (permanent) tooth of *Bradypus* as conical and completely covered by cement. As the tooth erupts, the cement wears away and exposes the dentinal layers. We have observed in a series of X-ray plates of a young *Choloepus hoffmani* that in younger stages the teeth taper sharply from root to crown, whereas in more mature stages the sides of the teeth become nearly parallel. The same variations occur in *Megalonyx* teeth.

The length of the inner dentinal layer may also serve as an age indicator. For example, in a tapered lower caniniform of a young *Megalonyx* from Devil's Den, Florida, the inner dentine layer occupies only the lower 10 per cent of the tooth length, but in a parallel-sided mature specimen from Santa Fe I, Florida, this layer occupies 72 per cent of the total tooth length.

We have observed considerable change in the shape of the occlusal surface accompanying these other dimensional changes in living *Choloepus*. Such changes evidently occurred in *Megalonyx* as well. A comprehensive investigation of *Megalonyx* probably will show that several of the proposed species are actually ontogenetic stages of a single natural species.

Megalonyx leptostomus Cope

Megalonyx leptostomus Cope, 1893. A preliminary report on the Vertebrate Paleontology of the Llano Estacado. 4th Ann. Rept. Geol. Surv. Texas: 49.

TYPE. — The type of *M. leptostomus* consists of some skull fragments and an upper molariform tooth from the Blanco Beds near the eastern edge of the Llano Estacado in Crosby Co., Texas. Meade (1945) referred several additional teeth and jaw fragments from the same area to this species. The new materials described below were collected in the lowest stratigraphic unit in the Blancan section in Cita Canyon, 3½ miles south and 13 east of Canyon, Randall Co., Texas (Johnston and Savage, 1955). Thus all of the material known is derived from Blancan age deposits in the Panhandle of Texas. These new materials are the most complete known.

DIAGNOSIS. — Skull smaller than *Megalonyx brachycephalus* (Stovall and McNulty, 1950), narrow at postorbital protuberances; height and breadth of occiput considerably less than in other species, jugals flaring anteriorly, mastoid process rounded and not

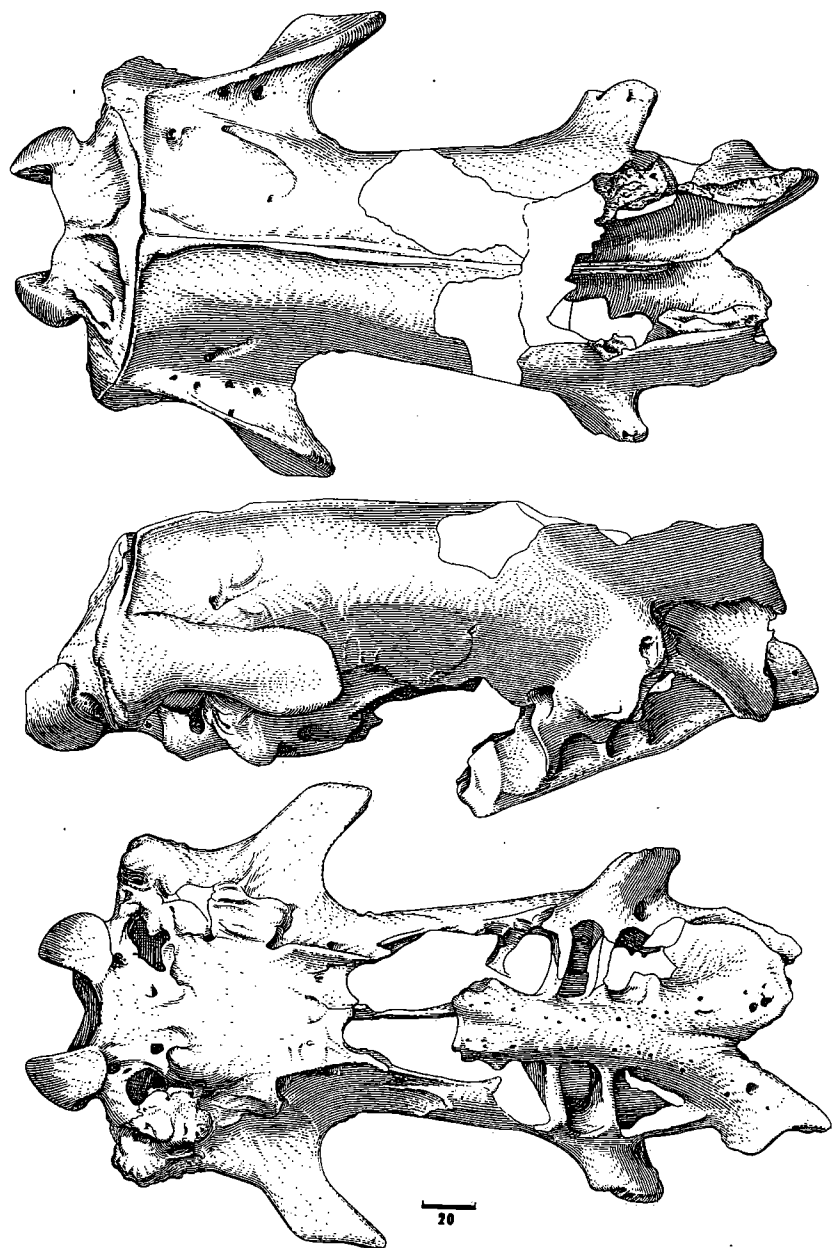


Figure 2. Skull of *Megalonyx leptostomus*, WT 1956, dorsal, lateral, and ventral views.

hooklike, foramen ovale surrounded on the posterior side by a round protuberance, wider posterior divarication of palatines, adult caniniforms with prominent median bulge, and M^2 and M^3 with relatively greater mediolateral diameter than in other species, phalanges 1 and 2 and digit III of pes not co-ossified.

SKULL. — The skull, WT 1956 (Fig. 2) is well preserved but lacks the pterygoids, palatines, nasal region, and most of the zygomatic arch. All teeth are missing. Sutures in the occipital region are not well fused, although those between the frontals and parietals are almost obliterated and the sagittal crest is closed.

The sagittal crest is well developed as in all species of *Megalonyx* and about 112 mm long, as compared with 78.9 in *M. brachycephalus* and 127 in *M. jeffersoni*.

The jugal bones flare anteriorly and laterally, whereas in *M. jeffersoni* they project more ventrally and posteriorly. The postorbital protuberance is poorly defined and extremely narrow. The distance across the postorbital protuberance is 92 mm, compared to 120 in *M. brachycephalus* (Stovall and McAnulty, 1950) and 142 in *M. hogani* (Stovall, 1940).

The Cita Canyon skull presents a flat dorsal profile similar to that in Owen's specimen of *M. jeffersoni* (Leidy, 1885) and in *M. milleri* (Lyon, 1938), unlike the profile in Dickeson's specimen of *M. jeffer-*

Table 3. MEASUREMENTS OF *Megalonyx leptostomus* SKULL,
(WT 1956) IN MM

Length of skull from posterior end of occipital condyles to posterior border of caniniform alveolus	270.0
Width of maxillary at posterior internal angle of caniniform alveolus	65.0
Width of palate anterior to first cheek teeth	42.5
Least width of palate	22.5
Width across anterior end of glenoid fossa	166.0
Minimum orbitotemporal width	72.8
Minimum postzygomatic width	117.0
Transverse diameter of occipital condyles	70.2
Width of basisphenoid anterior to basilar tubercles	48.5
Mediolateral width of process lateral to foramen ovale	16.8
Median length of palate from point of bifurcation to posterior margin	106.3

Table 4. COMPARATIVE MEASUREMENTS OF KNOWN SKULLS OF *Megalonyx* SPECIES

Measurement	<i>M. brachycephalus</i> ¹	<i>M. jeffer-soni</i> (Owen) ¹	<i>M. jeffersoni</i> (Dickeson) ¹	<i>M. leidyi</i> ¹	<i>M. milleri</i> ¹	<i>M. hogani</i> ¹	<i>M. leptostomus</i>	<i>M. mathisi</i>
Length of skull from occipital condyles to anterior margin of first cheek teeth	256	356	334	343	291	245	230	223
Breadth of face at post-orbital protuberance	120	127	138	123	129	142	92	
Breadth of cranium at narrowest part of temporal region	86	90	102	91	75	98	73	
Length of sagittal crest	78	127	127	144	95	95	112	
Height of occiput from dorsal margin of foramen magnum	70				76	70	46	51
Height of occiput from basioccipital		110	110	107			72	75
Breadth of occiput at mastoid process	141	159	165	165	153	175	126	123
Length of diastema	41	50	49	40			50	
Maximum width first cheek tooth alveolus							24	21
Maximum width second cheek tooth alveolus	24	27				28	28	25

¹From Stovall and McAnulty (1950).

soni (Leidy, 1855) or in *M. hogani*, and *M. brachycephalus*, in which the anterior portion of the frontal bones arch above the nasal region. These differences in the dorsal profile may reflect age differences. Dickeson's specimen of *M. jeffersoni* appears to be the oldest, as most of the sutures are obliterated and the sagittal crest is closed and fused. In Owen's specimen the sagittal crest is an open fissure and most of the sutures are fused but still distinguishable. In the Big Bone Cave specimen sutures are fused and the sagittal crest is just forming, thus indicating a juvenile.

Comparison of the Big Bone Cave juvenile and Dickeson's adult suggests that, as the individual becomes older, the vaulting of the frontal region becomes more pronounced and the frontal ridges running from the sagittal crest to the postorbital protuberances diverge more. Thus the flat dorsal profile of the City Canyon skull probably came from a relatively young specimen.

The vertical distance from the dorsal border of the foramen magnum to the supraoccipital crest is extremely short, measuring 45.5 mm, compared to 70.0 for *M. brachycephalus*. Similarly the height from the ventral border of the foramen magnum measures 71.7 mm compared with 107.0 in *M. leidyi* and 110.0 in *M. jeffersoni*. The Cita Canyon specimen is only slightly higher in this area than in the new genus from McGehee where it is 67.8 mm. The breadth of the occiput measured across the mastoid processes is considerably less than in the other species of *Megalonyx*, 126 mm in this specimen, 141 in *M. brachycephalus*, and 175 in *M. hogani*.

The median occipital ridge does not extend to the foramen magnum as in Owen's specimen of *M. jeffersoni* but is lost in a depression about halfway down the occiput. As a whole the occiput is considerably less rugose and lacks the large tuberosities on either side of the median ridge in Owen's *M. jeffersoni*. The juvenile specimen from Big Bone Cave also lacks these prominent tuberosities; the base of its mastoid process is not depressed below the supraoccipital surface nor is it concave posterolaterally as in *M. jeffersoni*. Also, the process is smaller and more rounded than in that species. The occipital condyles of the Cita Canyon skull have shorter mediolateral diameters than the condyle Cope (1893) figured for *M. leptostomus* from the Blanco Fauna.

In the posterior portion of the skull the excavation between the basilar tubercles of the basioccipital is not so deep as in *M. jeffersoni*. The projection of bone medial to the glenoid fossa and surrounding

the posterior border of the foramen ovale is large and rounded, whereas in *M. Jeffersoni* it is short and narrow. The basilar tubercles in the Cita Canyon skull are situated more ventrally in relation to the condyles than in *M. jeffersoni*. The median lacerate foramen is located farther posteriorly in relation to the basilar tubercles than in that species, in which it opens adjacent to the anterior border of the tubercles, and the foramen ovale and foramen rotundum are farther apart. The pterygoids and palatines project at a more obtuse angle from the basisphenoid and the parasphenoid does not project as far ventrally as in *M. jeffersoni*.

The epitympanic ring is complete on the left side of the skull and forms a circular loop of bone which is firmly fused with the mastoid process of the squamosal posteriorly, the entotympanic medially, and the squamosal anteriorly. The external auditory meatus thus formed is directed laterally. The entotympanic is fused with the stylohyal process anteriorly and the epitympanic laterally. The eustachian tube apparently occupied a groove running obliquely anteroventrally from the anterolateral margin of the entotympanic toward the midline of the skull. The stylohyal process appears to be abnormal, either it is exostosed or contains a fused fragment of the stylohyal. At the base of the stylohyal process, posterior to the epitympanic, is the opening of the stylomastoid foramen. The foramen immediately posterior to the stylomastoid (second stylomastoid, Leidy, 1855: 10) opens into a canal that leads into the mastoid process of the squamosal. Posterior to this foramen a groove runs along the posterior side of the mastoid process, fading out just ventral to the supraoccipital crest. In other specimens this groove is roofed over and opens in the mastoid process as the mastoid foramen. Apparently the latter two foramina are for venous drainage from the cranium and exhibit considerable individual variation.

On the right side of the skull the stylohyal process, entotympanic, and ectotympanic are missing, exposing the petrosal quite clearly. The opening of the fenestra ovalis in the dorsolateral portion of the petrosal is directed anterolaterally. The facial foramen is located anterior to the fenestra ovalis. Posteroventral to the fenestra ovalis is the fenestra rotunda, the opening of which is directed posteroventrally. Lateral to the petrosal, the epitympanic recess opens dorsally into the epitympanic sinus, which extends anteriorly within the squamosal to the posterior margin of the glenoid fossa.

In its anterior region the palate resembles that of *M. jeffersoni*, but

more posteriorly the angle of bifurcation between the palatines becomes greater than in *M. jeffersoni*, thus resembling the type specimen of *M. leptostomus* (Cope, 1893). The posterior alveolar border for the caniniform does not display any of the distinct grooves or concavities in the *M. jeffersoni* teeth.

DENTITION. — Isolated megalonychid teeth available from Cita Canyon include four upper caniniforms and one lower caniniform, four M^2 's or M^3 's, one upper or lower M_1 , one M_2 , and two M_3 's. In addition a left mandible, WT 580, with a fragmentary caniniform, M_1 , and M_2 , and a right mandible with a caniniform, M_2 , and M_3 . A fragmentary palate includes the left $M^1 - M^4$, right $M^3 - M^4$ and a partial alveoli of $M^1 - M^2$ (Table 5).

This collection is of interest because it comprises a series of specimens ranging from very young to presumably fully adult. The variations in the teeth are presumed to represent stages in ontogenetic age rather than specific differences. The left mandible, WT 580, is from an

Table 5. MEASUREMENTS OF TEETH OF *Megalonyx leptostomus* IN MM

Tooth	Catalog Number	Estimated Age	Measurement	
			AP ¹	ML ²
C ₁	WT 579	juvenile	26.9	13.4
C ₁	WT 2548	juvenile	22.8	12.0
M ₁	WT 580	very young	7.9	10.6
M ₂	WT 580	very young	8.0	10.0
M ₂	WT 2321	adult	15.5	24.0
M ₂	WT 579	juvenile	12.6	18.5
M ₃	WT 579	juvenile	13.7 ³	13.4
M ₃	WT 2376	juvenile	12.9	18.0
M ₃	WT 2376	juvenile	13.5	18.0
C ¹	WT 1746	adult	30.1	19.6
C ¹	WT 1746	adult	30.0	19.4
C ¹	WT 1746	juvenile	25.8	15.0
C ¹	WT 2376	juvenile	26.9	16.4
M ¹	WT 580	juvenile	10.3 ³	13.5 ³
M ²	WT 580	juvenile	11.9	16.2 ³
M ³	WT 580	juvenile	11.7	15.8
M ⁴	WT 580	juvenile	7.9 ³	12.9
M ² or M ³	WT 1746	adult	15.5	24.6
M ² or M ³	WT 1746	adult	15.0	25.3
M ² or M ³	WT 2548	juvenile	14.2	19.6
M ² or M ³	WT 1789	juvenile	13.0	19.9
M ¹ or M ₁	WT 2548	juvenile	13.4	17.0

¹ AP = anteroposterior

² ML = mediolateral

³ Estimated

extremely young individual, for it is very small, short, and rather rounded anteroposteriorly in comparison with the longer, slimmer adult jaw. The bone of the mandible is rather porous in texture. The distance from the anterior border of M_1 to the posterior border of M_2 is 17 mm. the teeth are embedded in the jaw in such a way that their taper cannot be measured, nor can the amount of internal dentine be determined. Observed differences between the presumed juvenile and adult teeth are larger size and greater relative width in the latter. Only the lateral wall of the caniniform is preserved. It is long-ovate in shape and measures 16.6 mm in length.

The caniniform associated with the adult mandible WT 579 differs from all the other caniniforms from Cita Canyon, as well as from the caniniforms of later species of *Megalonyx*, in lacking the prominent median bulge on the lingual side and in being more convex on the lateral side. In this respect it closely resembles the canine of *M. curvidens*. M_2 and M_3 show no significant differences from the other specimens and M_3 closely resembles one from the Snake Creek beds that Matthew (1924) referred to *M. curvidens*.

Two isolated upper caniniforms, a right and a left, WT 1746, represent adult individuals. The extreme development of the median bulge on the lingual side makes both teeth almost triangular in cross section. This bulge is better developed in these specimens than in the other Cita Canyon caniniforms, as well as in any other species of *Megalonyx*. The anteroposterior dimension is shorter than in most specimens of *M. wheatleyi* and the mediolateral dimension is greater. The occlusal surface is concave, and the median bulge projects above the rest of the occlusal surface.

A third upper caniniform, also numbered WT 1746, is smaller than the two just described and represents a younger individual, as the sides are not quite parallel and the internal dentinal layer is not so deep as in the preceding specimen. Otherwise this tooth has the same characters as the adult specimens.

Another upper caniniform, WT 2376, appears to be an adult but does not have so large a median bulge as the WT 1746 specimens. The occlusal surface is worn evenly and thus lacks the central excavation and projecting lingual bulge characteristic of later *Megalonyx* caniniform teeth. The lower caniniform, WT 2548, is similar to WT 2376 in lacking a prominent median bulge and having an almost flat occlusal surface. These two teeth do not differ in age from those with

the prominent median bulge; the differences may represent extreme individual variation or sexual dimorphism.

Two molariform teeth, a left and a right M^2 or M^3 , both numbered WT 1746, presumably represent fully adult individuals, while two other right upper M^2 or M^3 , WT 2548 and WT 1789 represent younger individuals. The former are considerably longer mediolaterally than in either WT 2548 or WT 1789. The mediolateral widths are comparable to those of *M. jeffersoni*, but the anteroposterior dimensions are considerably less than for that species. The mediolateral widths fall within the upper limits of the observed range of M^3 and near

Table 6. MEASUREMENTS OF *Megalonyx leptostomus* POSTCRANIAL MATERIAL IN MM

<i>Tibia</i> (WT 1716)	
Length at anteroexternal surface	251
Max. breadth of head	132 ¹
Max. breadth of tarsal end	112
Max. anteroposterior diameter of tarsal end	63
<i>Calcaneum</i> (WT 2599)	
Width of neck	25.3
Length of neck	44.9
Distance from inner border of external astragalar facet to inferoexternal prominence of articulating end	72.0
Distance from dorsal border of external astragalar facet to ventral border of cuboid facet	73.0
<i>Metatarsal II</i> (WT Uncatalogued)	
Max. length	54
Breadth of shaft	22
Depth of proximal end	38 ¹
Depth of distal articulation (obliquely)	37 ¹
<i>Metatarsal III</i> (WT 1836)	
Anteroposterior diameter through middle	39.9
Depth of median vertical convexity at distal end	55.0 ¹
Depth of proximal articular face	38.5
Max. width	51.5
<i>Phalanx I of Digit III of Pes</i> (WT 1714)	
Max. anteroposterior length	34.5
Max. width	46.8
Depth of proximal end	55.6
Height of distal condyles	41.7
<i>Phalanx II of Digit III of Pes</i> (WT 1714)	
Max. anteroposterior length	53.0
Width of proximal end	39.5
Depth of proximal end	51.4
Width of distal condyles at middle	27.4
Depth of distal condyles	36.6

¹ Estimated

the upper end of the range for M^2 from the Blanco beds. The tooth of *M. leptostomus* that Cope (1893) thought was a last superior molar is probably an M^2 or M^3 . Its dimensions correspond to two M^2 or M^3 (WT 1746) from Cita Canyon. Cope's tooth measures 14 mm anteroposteriorly and 25 mediolaterally, whereas the Cita specimens measure 15.0 anteroposteriorly and 25.3 mediolaterally for one, and 15.5 anteroposteriorly and 24.6 mediolaterally for the other.

The shapes of these teeth agree with those Cope (1893) described for the Blanco specimens of *M. leptostomus*. In cross section they are subangular trapezoids with one side of the occlusal surface bevelled outward. The posterior side is slightly concave, the anterior side slightly convex.

TIBIA. — The left tibia (Fig. 4G, H), WT 1716, is smaller than that of *M. jeffersoni* described by Leidy (1855) by about one-fifth, but is larger than that described by Stirton (1939) from the Mulholland Fauna in California. The element is essentially complete but lacks the external femoral facet and posterior border of the internal femoral facet. In overall outline, the Cita Canyon tibia does not differ significantly from that of *jeffersoni* figured by Leidy (1855).

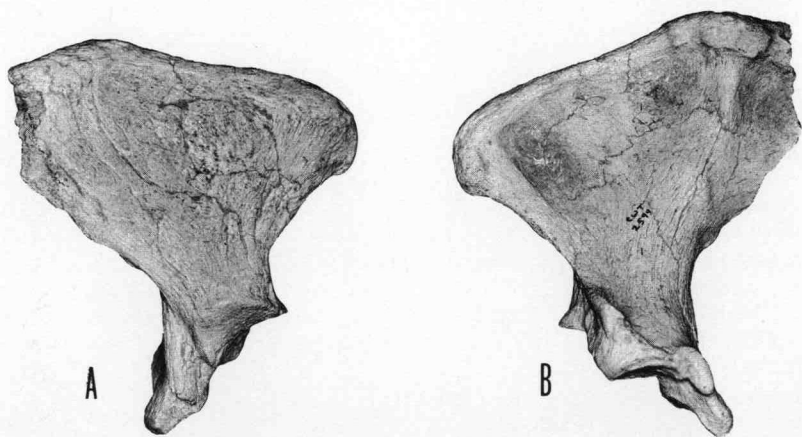


FIGURE 3. Left calcaneum of *Megalonyx leptostomus*, WT 2599. A.—inner view, B.—outer view. $\times \frac{1}{2}$.

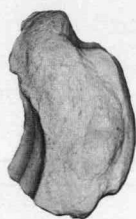
It differs from the megalonychid from Mulholland in the greater ventral projection of the internal malleolus and the smaller and less conspicuous astragalar spine. The facet for the astragalus is not as wide as in that specimen; in this respect it resembles *M. jeffersoni*.

CALCANEUM. — The left calcaneum (Fig. 3), WT 2599, from Cita Canyon lacks only the extreme posterior border of the tuber calcis and the medial edge of the internal astragalar facet. It is slightly smaller and less robust than the calcaneum from Hagerman, Idaho, USNM 23209. The tuber calcis of *M. leptostomus* is similar in shape to that of the new Hemphillian genus (below) in its greater posterior expansion. The proximal articular surfaces lack the distinct grooves between the facet seen in *M. jeffersoni californicus* Stock (1925), and the cuboid facet lacks the inner lip flattened at right angles to the rest of the surface observed in that species. The distance between the internal astragalar facet and the cuboid facet is greater in *M. leptostomus* than in the specimen from Idaho. The area for attachment of the peroneus muscle is not so prominent and does not project laterally as a narrow ridge of bone as in that specimen.

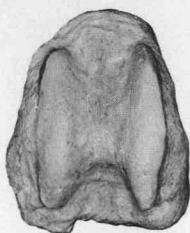
METATARSALS. — A poorly preserved left metatarsal II is available from the Cita Canyon collections. It is smaller than the same element in the Hagerman, Idaho sample, but in overall appearance the two specimens agree.

A third metatarsal in the Cita Canyon collections lacks only the ventral extremity. It has about half the bulk of metatarsal III of *M. jeffersoni*, and differs from that of *Hapalops* and *M. jeffersoni* in having the medial and lateral distal articular facets for phalanx I raised above the surrounding surface and very well defined. However, the carina is less robust than in *M. jeffersoni* and the facet for articulation with metatarsal IV projects farther ventrally. The facet for the ectocuneiform is similar in shape to that of *M. jeffersoni*, except that it is slightly convex at the center of the facet rather than uniformly concave.

PHALANGES. — The Cita Canyon material includes phalanges I and II of the third pedal digit (Fig. 4). The remarkable feature of these specimens is that they are unfused even though they appear to represent a mature individual or individuals. The same is observed in specimens from the Santa Fe I site in Florida and from Hagerman, Idaho, both of Blancan age. This is in sharp contrast to all observed later Pleistocene *Megalonyx* specimens, including



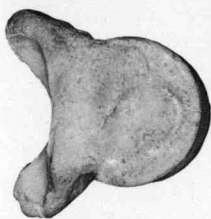
A



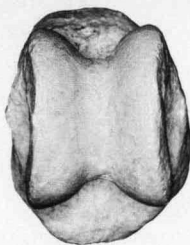
B



C



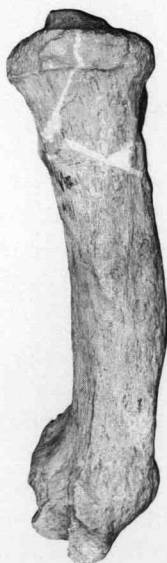
D



E



F



G



H

those of *M. jeffersoni* described by Leidy (1855) and Stock (1925), in which phalanges I and II are completely co-ossified.

Phalanges I and II from Cita Canyon are less robust than those from Idaho, but do not differ significantly in shape. The anterior facets on phalanx I are much more flattened in these early species of *Megalonyx*, than in later Pleistocene specimens.

The posterior surface of the phalanx II is similar to that of *Hapalops*. A facet is located on the dorsal and another on the ventral end of the median ridge between the articular surfaces for phalanx I. These facets contact the dorsal and ventral margins of phalanx I and prevent much movement between the two phalanges. Considerably less movement is possible between these phalanges than in *Hapalops*.

Megalonyx leptonyx (Marsh)

Morotherium leptonyx Marsh 1874, Notice of new Tertiary mammals III, Amer. Jour. Sci., Vol. 7, p. 532.

TYPE. — Marsh (1874) described a small ungual phalanx of the third digit of the manus from the Snake River Basin, Idaho, as the type of *Morotherium leptonyx*. Evidently it represents a small megalonychid, probably *Megalonyx*, but more refined determination is impossible. The only locality data Marsh provided in the original description is "Pliocene beds of Idaho." According to Hay (1927) this claw is the same one that Leidy (1871) mentioned as having come from Castle Creek, Owyhee County. Gazin (1935) tentatively referred two mandibles, some teeth, and a few footbones from the Hagerman beds (early Blancan) to *Megalonyx leptonyx*? (Marsh) on the basis of their small size and the lack of determinable material of other ground sloths from the area. The type of *Morotherium leptonyx* has been misplaced. As the description of type is inadequate for specific diagnosis and the age and locality are uncertain, we consider *Megalonyx leptonyx* a *nomen dubium*.

Other Blancan *Megalonyx*

HAGERMAN, IDAHO. — We doubt Gazin's (1935) tentative reference of the *Megalonyx* sample from Hagerman, Idaho to *M.*

FIGURE 4. Postcranial elements of *Megalonyx leptostomus*. A. Phalanx I of digit III of pes, WT 1714, lateral view, $\times\frac{1}{2}$. B and C, proximal and distal views of same, $\times\frac{1}{2}$. D. Phalanx II of digit III of pes, lateral view, $\times\frac{1}{2}$. E and F, proximal and distal views of same, $\times\frac{1}{2}$. G. Left tibia, WT 1714, anterior view, $\times 0.38$. H. Inner view of same, $\times 0.38$.

leptonyx (Marsh). It seems more probably referable to *M. leptostomus*. In any case we defer specific assignment until the discrimination of species within *Megalonyx* is placed on a more secure and consistent basis.

Gazin (1935) described the following material from the Hagerman beds: imperfect mandible with complete lower dentition, associated with upper caniniform, upper cheek tooth, claw and patella USNM 13477; mandible edentulous except for left caniniform of immature individual, USNM 12669, both from *Plesippus* quarry; last upper molariform tooth, USNM 13568, co-ossified trapezium and first metacarpal, USNM 13570; and two fourth metacarpals, USNM 12675; a claw and several toe bones, from "various localities south of the horse quarry." Two additional lots of associated specimens Elmer Cook and George Pearce collected about 5 miles south of

Table 7. MEASUREMENTS OF ASSOCIATED RIGHT HIND LIMB ELEMENTS OF *Megalonyx* FROM HAGERMAN, IDAHO, (USNM 23209) IN MM

<i>Fibula</i>	
Estimated length	280.0
Anteroposterior diameter at middle of shaft	33.5
Transverse diameter at middle of shaft	26.5
Anteroposterior diameter of distal end	63.3
Max. transverse diameter of distal end	63.8
<i>Calcaneum</i>	
Max. length	178.0
Max. diameter of tuber calcis	171.0
Max. thickness posterior border	30.0
Width of neck	28.3
Thickness of neck	48.0
Distance from inner border of external astragalar facet to inferoexternal prominence of articulating end	71.3
Distance from dorsal border of external astragalar facet to ventral border of cuboid facet	85.4
<i>Astragalus</i>	
Max. anteroposterior diameter parallel to fibular facet	92.0
Max. transverse diameter measured at right angles to fibular facet	66.2
Depth of fibular facet at distal end	44.1
Max. transverse diameter of head	49.9
Anteroposterior length of external calcaneal facet	63.2
<i>Cuboid</i>	
Max. diameter from astragalar to cuneiform surface	43.9
Max. diameter from calcaneal to dorsal surface	32.4
Max. diameter from medial to lateral surface	43.5
<i>Navicular</i>	
Max. diameter across cuneiform facets (width)	60.1
Diameter taken at right angles to greatest (dorsoplantar) diameter	53.0
Max. thickness through convexity articulating with astragalus	27.6

Cuneiform

Max. dorsoplantar diameter	49.9
Max. mediolateral diameter	31.8
Max. thickness through navicular to mtt III surface	18.2

Metatarsal II

Max. length	35.0
Breadth of shaft	37.8
Depth of proximal end	39.9
Depth of distal articulation	29.7

Metatarsal III

Anteroposterior diameter through middle	51.3
Depth of median vertical convexity at distal end	66.6
Depth of proximal articular face	58.8
Max. width	47.6

Metatarsal IV

Anteroposterior diameter through middle	57.9
Depth of median vertical convexity at distal end	50.1
Depth of proximal articular face	51.9
Max. width	41.0

Metatarsal V

Anteroposterior diameter	51.1
Depth of major convexity at distal end	24.1
Depth of proximal end	25.3
Max. width	21.1

Phalanx I of Digit III of Pes

Max. anteroposterior length	58.3
Max. width	49.3
Depth of proximal end	54.6
Height of distal condyles	45.8

Phalanx II of Digit III of Pes

Max. anteroposterior length	45.9
Width of proximal end	45.5
Depth of proximal end	36.7
Width of distal condyles at middle	31.5
Depth of distal condyles	38.3

Phalanx I of Digit IV of Pes

Max. anteroposterior length	28.9
Max. width	38.3
Depth of proximal end	36.7
Height of distal condyles	30.2

Phalanx II of Digit IV of Pes

Max. anteroposterior length	62.3
Width of proximal end	34.0
Depth of proximal end	37.1
Width of distal condyles at middle	23.2
Depth of distal condyles	29.1

Phalanges I and II of Digit II of Pes

Max. anteroposterior length	37.5
Width of proximal end	21.0
Depth of proximal end	28.9
Width of distal condyles	17.9
Depth of distal condyles	17.0

Plesippus Quarry, near Hagerman, Idaho, contain: 10 podial fragments, USNM 23208 and a right fibula, calcaneum, astragalus, cuboid, navicular, cuneiform and four metatarsals, three sesamoids and many of the phalanges of the three lateral digits, USNM 23209. The unfused condition of phalanges I and II in the third pedal digit has been noted above. Phalanges I and II of the second pedal digit are fused. The measurements are presented in Table 7 and the foot is illustrated in figure 5.

PROCTOR PITS, TEXAS. — A *Megalonyx* palate with the right first molariform, left caniniform, and alveoli for the remaining upper teeth, FAM 77811, was collected in Proctor Pit C in the Texas Panhandle. The widest dimension of the palate is 86.6 mm across the

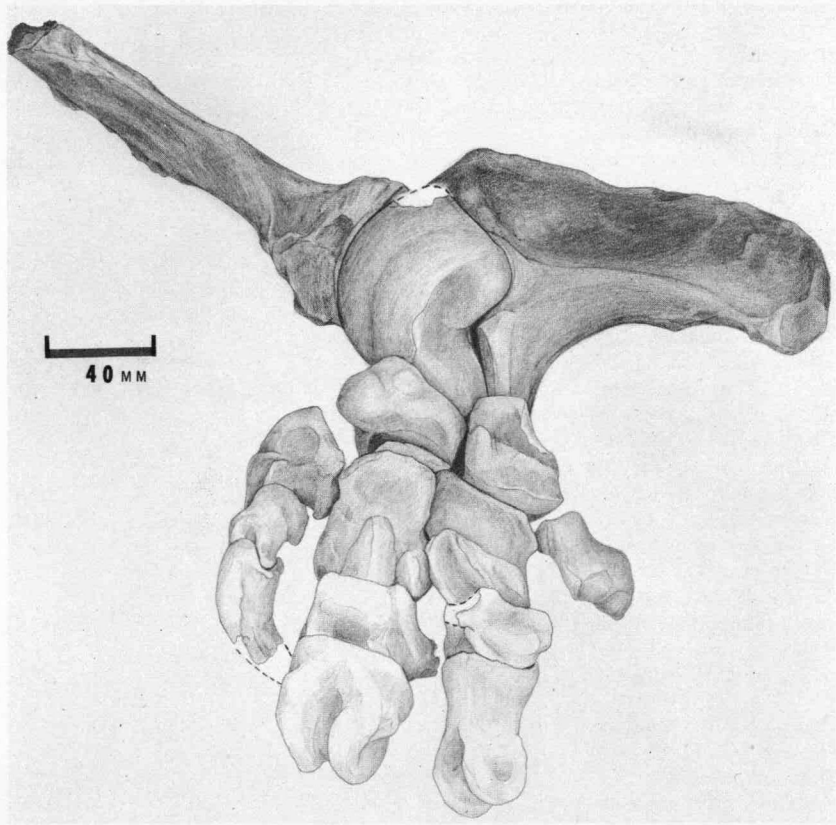


FIGURE 5. Left pes of *Megalonyx* from Hagerman, Idaho, USNM 23209, dorsal view.

caniniforms. The palate is constricted posterior to the caniniforms to a width of 37.2 mm. The width across the posterior molariforms is 58.0 mm; between them it is 16.8. The posterior narial opening lies opposite the last molariforms. The caniniform measures 29.8 mm long by 16.6 wide and has the lingual convexity characteristic of advanced *Megalonyx*. M^1 measures 17.2 by 14.0 mm. The cheek tooth row is 65.5 mm long.

In anterior view the rostrum presents an elliptical narial opening with a maximum width of about 38 just dorsal to the palate and narrowing to about 20 between the lateral edges of the nasal bones. The tips of the nasals stand 8 behind the anterior edges of the canines. The anterior edge of the jugal lies immediately posterior to the caniniform. The jugal plate slopes ventrad, posteriad, and slightly laterad. The posterior edge lies posterolateral to M^2 .

SANTE FE I, FLORIDA. — A medial phalanx of the third pedal digit, UF 10441, was collected by D. Webb, R. Allen, and J. Robertson in June, 1965 from locality I, Sante Fe River, Gilchrist County, Florida. Its length is 64.9 mm, its width 32.1, and its depth at the proximal end 46.5. The significance of this specimen lies in the fact that it is unfused to the proximal phalanx as in other Blancan *Megalonyx*.

JACKASS BUTTE, IDAHO. — An isolated intermediate lower molariform tooth, UO 2404, from locality 6, Grandview Fauna, Jackass Butte, Idaho measures 17.9 by 12.4 mm at the occlusal surface.

Megalonyx curvidens Matthew

Megalonyx curvidens Matthew, W. D. 1924. Third Contribution to the Snake Creek Fauna. American Mus. Nat. Hist. Bull., 50; 149.

TYPE. — Tooth, probably RM_3 , AM 17601, from upper level, Quarry 1. Upper Snake Creek Beds, Sioux Co., Nebraska, collected by Albert Thomson in 1918.

REFERRED MATERIAL. — Left ramus and symphysis with caniniforms and left cheek teeth, FAM 77800, collected by M. F. Skinner in East Pliohippus Draw about 10 feet above the site from which the type of *Pliohippus leidyanus* came along with rhinoceros, mastodon, horse, camel, and peccary material (Skinner field notes, vol. 2, p. 44); two isolated upper cheek teeth, AM 20493 and 21460; humerus, FAM 77801, from East Pliohippus Draw; navicular, PU 12079 (Sinclair, 1915); two proximal phalanges of the third manual digit, AM 81034 and 85970, the latter collected by the late Harold

Cook 6 September 1949 while walking with Glen Evans and Grayson Meade, in high exposures about 100 yards east of the *Plihippus leidyanus* site (Cook's notes); second phalanx of third manual digit FAM 77802; and an ungual phalanx, AM 14051.

DIAGNOSIS. — Caniniforms long ovate with concave lingual sides; symphysis protruding relatively farther and more rounded at anterior tip than in *M. leptostomus*. Alveolar ridge posterior to the caniniform teeth same width as adjacent cheek teeth. Molariform teeth slightly more curved than in later species.

DESCRIPTION. — The mandible, FAM 77800, (Fig. 6) belongs to a young animal as indicated by the tapering teeth. This is most evident in the caniniforms, the occlusal dimensions being 14.8 by 8.0 in contrast to basal dimensions of 21.5 by 11.1.



FIGURE 6. Mandible of *Megalonyx curvidens*, FAM 77800, occlusal and lateral views.

The caniniform teeth present a long subcircular occlusal surface that wears nearly flat, much as in typical *Megalonyx*. The caniniforms differ in having faintly concave lingual sides, whereas caniniforms of *M. jeffersoni* show a pronounced lingual bulge. The absence of this bulge also has been noted above in some *M. leptostomus* specimens.

The symphysis protrudes somewhat more than in late Pleistocene *Megalonyx* specimens, reaching 14.3 anterior to a line between the anterior ends of the caniniforms. But as the canines erupt and reach mature proportions the protrusion presumably decreases accordingly. The keel on the anterior slope of the symphysis is weak and confined to the upper third of the slope. The anterior border of the symphysis rises in a nearly straight profile, in contrast to the sigmoid curve, concave at the base, convex at the top, typical of later species of *Megalonyx*. The mental foramen appears 10 mm posterior to the "chin" and 9 mm below the alveolar border, about as in typical *Megalonyx*. The symphysis attains a depth of about 42 mm below the caniniform teeth. The posterior end of the symphysis lies between the roots of the caniniforms as in other *Megalonyx*.

The alveolar ridge posterior to the caniniform retains the same width as the adjacent cheek tooth. In this respect *M. curvidens* differs from typical late Pleistocene *Megalonyx* specimens and agrees with Meade's (1945) description of a mandible of *M. leptostomus* from Mt. Blanco, Texas.

The cheek teeth closely approximate those of later *Megalonyx* species in shape and the development of wear facets. The principal wear is on the posterior edge of each tooth.

The last molar in the mandible agrees closely with Matthew's type tooth, except that the type is slightly larger and comes from the right side. Measurements of the base of left M_3 are 16.9 by 13.4 mm as compared with 17.8 and 15.0 in the type. These teeth are slightly narrower on the labial than on the lingual side. A concavity passes down the posterior side and a faint one down the labial side. The highest corners are the posterolabial and anterolingual. Each tooth curves gently along its length producing a slight arch posteriorly and a lesser one lingually. This feature of the type tooth inspired the species name and distinguishes it from late Pleistocene *Megalonyx*.

The upper half of the ascending ramus is missing. A large fora-

men through which the mandibular nerve and blood vessels passed, occupies the base of the coronoid process, but somewhat higher than in most *Megalonyx* specimens.

An upper molariform tooth, AM 21460, measures 14.0 mm anteroposteriorly and 19.8 transversely. It is slightly concave on the posterior and convex on the anterior side. Another such tooth, AM 20493, measures 13.7 by 19.0 mm.

The left humerus from the Snake Creek channels is an incomplete distal half of the shaft. The deltoid and pectoral crests are well developed, being especially well defined at their junction near the midpoint of the shaft. Between this point and the distal condylar expansion the narrowest width of the shaft is 44.2.

Sinclair (1915) described a navicular from the Upper Snake Creek channels, P.U. 12079. Measurements taken from the illustration of the Snake Creek specimen show its natural size to be about 52 mm across the cuneiform facets and 46 mm in the dorsopalmar diameter. The Upper Snake Creek navicular is similar to that of *Pliometanastes* in that the mediolateral diameter is greater than the dorsopalmar diameter and unlike *Megalonyx jeffersoni*, *M. sierrensis*, and the Idaho specimen where the opposite occurs. The Snake Creek navicular differs from *Pliometanastes* but is similar to the navicular of *Megalonyx* in having the mesocuneiform facet elevated above the ectocuneiform facet.

Table 8. MEASUREMENTS OF PHALANGES OF *Megalonyx curvidens* IN MM

<i>Proximal Phalanges</i>	(AM 81034)	(85970)
Prox. Length	53.3	53.1
Prox. Width	42.9	46.8
Max. Depth	31.8	34.2
Dist. Length	43.1	43.5
Dist. Width	32.1	30.2
<i>Second Phalanx</i>	(FAM 77802)	
Max. Length	62.2	
Median Length	55.3	
Prox. Width	ca. 39	
Dist. Width	32.4	

The phalanges from the Upper Snake Creek channels closely correspond to specimens of later *Megalonyx*, except for their generally smaller size. Their principal dimensions are presented in Table 8.

Megalonyx mathisi new species

TYPE. — Ventral half of skull, UCMP 80416 (Figs. 7 and 8).

TYPE HORIZON AND LOCALITY. — Black Rascal Creek, V-67223, Upper Mehrten Formation, east of Merced, Merced County, California. Hemphillian, probably late Hemphillian, tentatively correlated with the Pinole Tuff site, Contra Costa County, California, which has a potassium-argon date of approximately 5.2 million years.

ETYMOLOGY. — Patronymic for Glen E. Mathis whose generous assistance made collecting the type specimen possible.

DIAGNOSIS. — A relatively small animal, slightly smaller than *Mega-*

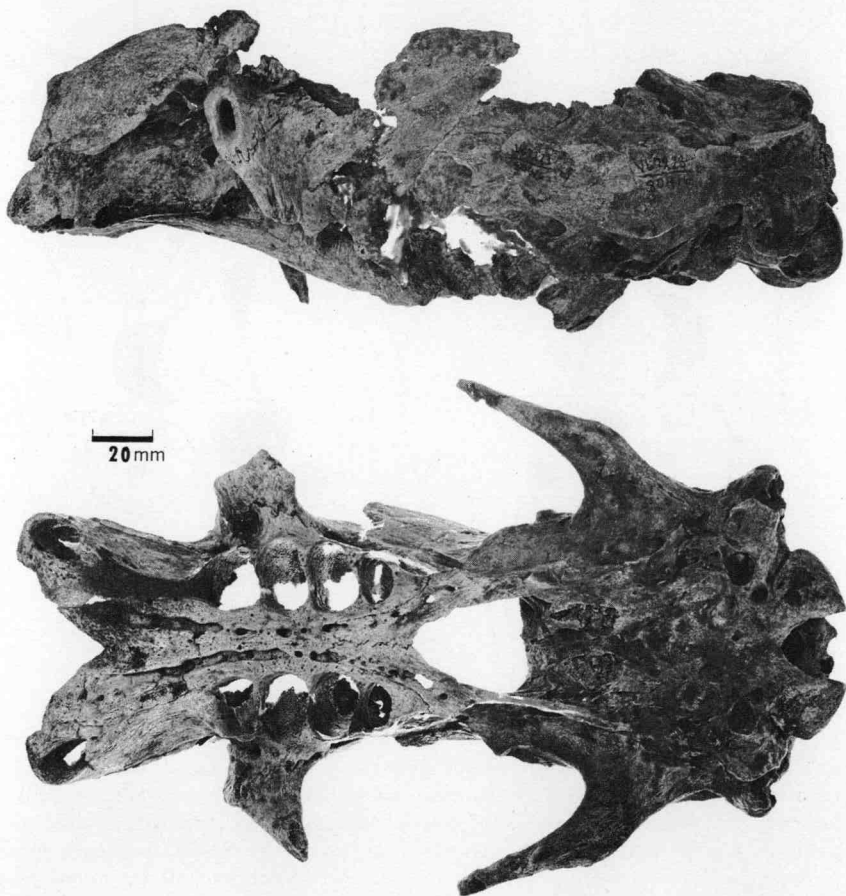


FIGURE 7. Skull of *Megalonyx mathisi*, UC 80416, lateral and palatal views.

lonyx leptostomus but larger than *Pliometanastes protistus*. Caniniform smaller than first molariform, oval in cross section with greatest diameter obliquely anteroexternal to posterointernal, unlike all other species of *Megalonyx* in which the greatest diameter is obliquely anterointernal to posterointernal. Caniniform without median bulge, lingual side of tooth relatively flatter than labial side. Maxillary plate between caniniform teeth wide and very thin. Palate distinctly arched, concave posterior to caniniform teeth, be-

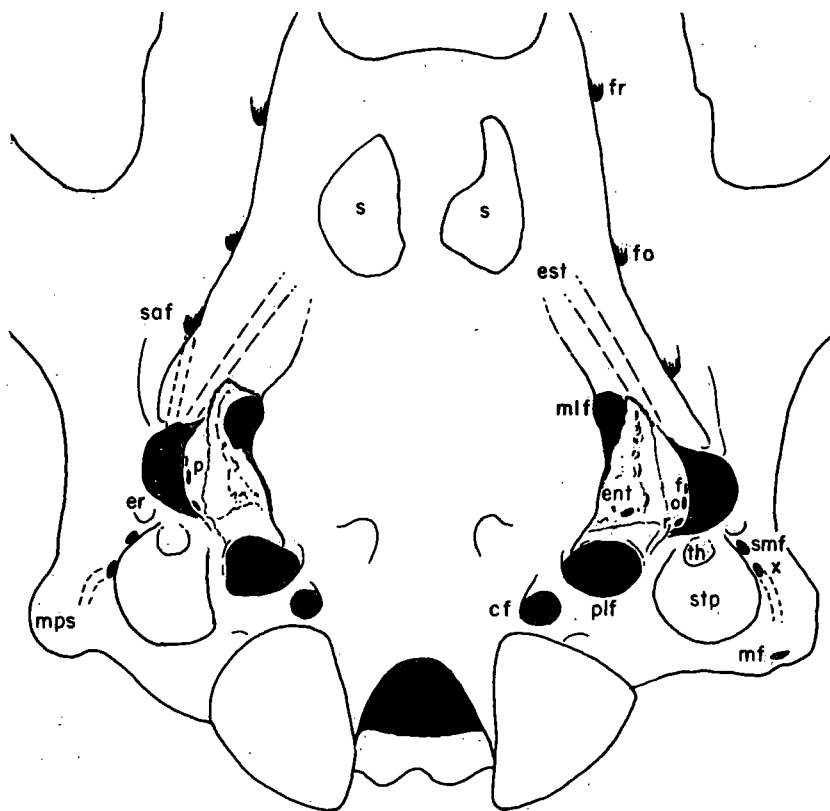


FIGURE 8. Basicranial region of skull of *Megalonyx mathisi*, UC 80416. Abbreviations: cf, condyloid foramen; ent, entotympanic bone; er, depression for epitympanic ring; est, groove for eustachian tube; f, fenestra ovalis; fo, foramen ovale; fr, foramen rotundum; mf, mastoid foramen; mlf, median lacerate foramen; mps, mastoid process of squamosal; o, fenestra ovalis; p, petrosal; plf, posterior lacerate foramen; o, fenestra ovalis; p, petrosal; plf, posterior lacerate foramen; r fenestra rotunda; saf, canal for inferior ramus of stapedial artery; smf, stylomastoid foramen; stp, stylohyal pit; th, tympanohyal; x, unnamed foramen posterior to stylomastoid foramen.

coming convex at level of M^2 . Palate with long narrow canals for nutritive foramina. Nasal region not as highly vaulted as in other species. Sagittal crest present and supraoccipital crest prominent. Rectus capitis ventralis excavations posteromedial to basilar tubercles. Occipital condyles relatively closer together and do not project so far posteriorly as in *M. leptostomus*. Dorsal margin of the condyles nearly confluent with the occiput.

SKULL. — The skull, UCMP 80416, lacks the nasals, dorsal part of the frontals and parietals, expanded portion of the jugal, ventral part of the pterygoids, ectotympanic, and all teeth. All sutures are firmly fused indicating a fully adult individual. The skull is slightly smaller than *Megalonyx leptostomus* but larger than *Pliometanastes protistus*.

The most striking differences between *M. mathisi* and the other

Table 9. MEASUREMENTS OF *Megalonyx Mathisi* SKULL, (UCMP 80416) IN MM

Max. length	286.0	
Length posterior end occipital condyles to posterior border caniniform alveoli	263.0	
Width maxillary at level of caniniforms	92.7	
Width palate anterior to first molariforms	45.8	
Min. width of palate between molariforms	21.3	
Width across zygomatic arches anterior end glenoid fossa	152.0	
Max. width across mastoid processes	122.8	
Min. postzygomatic width across squamosal	104.0	
Transverse diameter inside foramen magnum	23.6	
Dorsoventral diameter foramen magnum	23.2	
Max. width across occipital condyles	66.0	
Max. width across one condyle	22.8	
Max. depth of one condyle	28.0	
Height occiput from dorsal margin foramen magnum	51.0 ¹	
Height maxillary, anterior alveolar border to nasal suture	50.0	
Width between premaxillary sutures	56.5	
alveoli ²	left	right
Max. length caniniform alveolus	18.5	18.5
Max. width caniniform alveolus	12.0	11.3
Max. anteroposterior alveolar diameter M^1	16.5	16.0
Max. mediolateral alveolar diameter M^1	21.0	21.5
Max. anteroposterior alveolar diameter M^2	17.0	17.5
Max. mediolateral alveolar diameter M^2	24.0	24.5
Max. anteroposterior alveolar diameter M^3	17.0	17.5
Max. mediolateral alveolar diameter M^3	24.0	23.0
Max. transverse alveolar diameter M^4	16.5	17.0

¹ Estimated

² Measurements of molariforms taken just below level of palate where alveolar walls are straight. These measurements do not take into account distortion due to preservation and reconstruction and thus may be as much as 1 mm more than true alveolar diameter.

species of *Megalonyx* are found in the anterior region of the skull. The nasal bones are lacking, but from the curvature of the maxillaries apparently the nasal region was not so highly vaulted as in the other species. The maxillary between the caniniform teeth is a thin broad plate in *M. mathisi*, whereas in *M. leptostomus* it is considerably thicker, attaining its greatest thickness in *M. jeffersoni*. This difference in thickness of the maxillary is greater than would be expected if it were due solely to allometric increase in skull size. Medial to the caniniform alveoli, on the antero-internal side, is a pair of depressions for the premaxillary. The distances between these articular surfaces is relatively farther apart in *M. mathisi* than in other species.

The size, shape, and orientation of the caniniform teeth distinguishes *M. mathisi* from all later species of the genus. The caniniform alveoli are smaller than the alveoli of the M¹ and are distinctly oval, the internal margin being straighter and less convex than the external to posterointernal, in marked contrast to other species where the greatest diameter is anterointernal to posteroexternal. The posterior margin of the tooth projects medially in *M. mathisi*, whereas in other species it projects laterally. The size and cross section of the caniniform alveolus are structurally intermediate between the small triangular tooth of *Pliometanastes* and the typical long ovate tooth of *Megalonyx leptostomus*.

The molariform alveoli are subtriangular and do not differ in shape from the later species of the genus.

The palate is distinctly arched, concave immediately posterior to the caniniform teeth, becoming convex at the level of the M². *M. mathisi* resembles *M. jeffersoni* in this character and differs from *M. leptostomus* in which the palate is straight along its length. The palate contains long narrow canals for nutritive foramina. These run the length of the palate as in *Pliometanastes* and they are especially prominent in the anterior part of the palate, just posterior to the caniniform teeth.

There is some distortion and displacement in the dorsal part of the occiput, but not enough to obscure the major characters. The supraoccipital crest is strongly developed, as is the vertical occipital crest. The occiput rises nearly perpendicular to the basi-cranial axis. The occipital condyles do not project so far from the occiput as in other species and are nearly confluent with the occiput along

their dorsal margin. The occiput crest projects outward posteriorly above the condyles.

Compared with *Megalonyx leptostomus*: The mastoid process is not quite so prominent and is somewhat pointed; the area of attachment of the digastric muscles dorsal to the mastoid process is more rugose and more deeply excavated; the occipital condyles are closer together and the foramen magnum more rounded; the bone of the dorsal margin of the foramen magnum is considerably thicker and has a prominent pair of processes projecting posteriorly on either side of the midline and articulating with the atlas; the occipital condyles are more elongate medio-laterally; and the triangular notch so prominent in *M. leptostomus* is barely evident in *M. mathisi*.

The basicranial region is remarkably well preserved; only the ectotympanic ring is lacking. In ventral view the occipital condyles are positioned closer to the skull and are relatively closer together in *M. mathisi* than in *M. leptostomus*. The condyloid foramen opens anterior to the condyles and posteromedially to the posterior lacerate foramen, the largest of the basicranial foramina. The stylohal process borders the lateral edge of the posterior lacerate foramen and appears to be formed by the paroccipital process, tympanohyal, and a process of the mastoid region, which together form an articulating surface for the stylohyal. Anterolateral to the tympanohyal and posterolateral to the epitympanic recess is an oval depression for the epitympanic ring. The entotympanic forms the anterior margin of the posterior lacerate foramen, sutured to the paroccipital process at the anterior margin of the stylohyal process on the lateral side and the basioccipital on the medial side, lying against the lateral margin of the basilar tubercles. It is widest posteriorly, narrowing anteriorly where it meets the pterygoid and lateral margin of the median lacerate foramen. Dorsal to the entotympanic is the petrosal which lies in the epitympanic recess. The fenestra ovalis opens from the dorsal portion of the petrosal, with the opening directed laterally. Posteroventral to the fenestra ovalis is the fenestra rotunda which opens posterolaterally.

Some confusion exists in the literature concerning the designation of the stylomastoid-mastoid foramina. The skull of *Megalonyx mathisi* has two foramina at the lateral base of the stylohyal process and a dorsal foramen in the mastoid process on the posterior side. The anterior foramen lies immediately posterior to the oval depression for the epitympanic ring, lateral to the tympanohyal, and at the

base of the stylohyal process. This foramen, the stylomastoid foramen, communicates via the sulcus facialis with the facial foramen, which is located antero-dorsal to the fenestra ovalis. The canal of the foramen immediately posterior to the stylomastoid bends posterodorsally into the mastoid region. This latter foramen and the mastoid foramen on the occiput probably function as openings for venous drainage leaving the skull. The latter foramina are highly variable, as is demonstrated by the skull of *M. mathisi* in which the mastoid foramen is lacking on the right side of the skull. This variability is further indicative of venous circulation.

In the anterior part of the ear region, the eustachian tube lies in a very shallow and poorly defined groove that begins at anterolateral margin of the entotympanic and continues forward obliquely across the pterygoid towards the midline of the skull. Lateral to this groove are two structures of uncertain function. Anteroventral to the epitympanic recess is a dorsoventrally aligned furrow that may have served to house the anterior portion of the epitympanic ring. Medial to this furrow a canal runs within the squamosal but close to the pterygoid from the anterodorsal base of the petrosal to a foramen opening posterior to the foramen ovale. This prominent foramen may represent an enclosure of the inferior ramus of the stapedia artery. The foramen ovale, foramen rotundum, and orbital fissure are in the same position as in other species.

The basilar tubercles are excavated internally along the posterior and medial sides. Anterior to the basilar tubercles is a pair of deep sinuses in the basisphenoid, ventral to the anterior portion of the brain cavity.

The zygomatic process of the squamosal narrows anterior to the glenoid fossa and is mediolaterally compressed. The glenoid fossa is more concave and its anterior side lies more dorsal than in *M. leptostomus*. No sutural connection is apparent between the zygomatic process of the squamosal and the jugal as in *M. leidyi*. The articular surface for the mandibular condyle in *M. mathisi* appears to be restricted to the lateral margin of the glenoid fossa where the zygomatic process flares laterally, whereas in *M. leptostomus* the articular surface appears to have extended medially almost to the lateral margin of the pterygoid.

Other Hemphillian *Megalonyx*

In addition to the above described material, a number of specimens have been discovered that do not warrant specific taxonomic

assignments. They are arranged below according to geographic origin.

BEAR TOOTH SLIDE, NEBRASKA — A lower caniniform, FAM 77803, M. F. Skinner collected in the same channel at Bear Tooth Slide, middle fork of Deep Creek, in the middle of the Ash Hollow Formation, Brown Co., Nebraska, has a long oval cross section with a flat, slightly convex, lingual border. This border is not concave as in *M. curvidens*, but it is far less convex than typical late Pleistocene *Megalonyx*. This tooth measures 22.0 x 13.8 mm.

COGSWELL QUARRY, KANSAS — FAM 77805 represents an immature stage of development in an upper caniniform of *Megalonyx*. The upper surface is worn flat and measures only 14.1 by 9.3 mm. It expands rapidly toward the root, but is broken off 25 mm above the crown. At that point its dimensions are 15.9 by 10.4 mm. In cross section its shape approaches the long ovate form characteristic of *Megalonyx*. A strong lingual convexity exactly resembles that observed in caniniforms of typical Pleistocene *Megalonyx*.

OPTIMA, OKLAHOMA — Savage (1941) described an upper and a lower caniniform tooth from the Optima Fauna. The lower, OMP 41-26-S1, has an occlusal length of 24.8 mm. This specimen is from a mature individual as the tooth walls are parallel. A faint bulge on the lingual side suggests the more massive bulge of later species of *Megalonyx*. The upper caniniform, OMP 41-BE-S2 is 19 mm long and also from a mature sloth. Its strong lingual bulge is posterolingual rather than mediolingual as in most later *Megalonyx* specimens.

PINOLE, CALIFORNIA — Stirton (1939) described an upper or lower first molariform tooth, UCMP 22110. Its transverse diameter is 17.0 mm and its length 12.3. It agrees closely in size and wear pattern with a tooth of *M. leptostomus* from Cita Canyon, Texas (WT 2548) described above.

WESTEND BLOWOUT, OREGON — Two astragali from Hemphillian sites in Oregon (Shotwell, 1958) pertain to *Megalonyx*. UO 6332 is an incomplete specimen but retains enough of the tibial and navicular surfaces to reveal features characteristic of *Megalonyx*, most conspicuously the deep tibial notch.

KREBS RANCH, OREGON — UO 8080, the second Oregon astragalus, is complete. It differs from astragali of *Pliometanastes* and resembles those of *Megalonyx* in its more nearly equal medial and

lateral sides, less rectangular and more convex internal calcaneal facet, and deeper navicular facet. It also differs from *P. protistus* in its greater size (anteroposterior diameter 75.7 mm, transverse diameter 64.6, transverse diameter of head 44.1, length of external calcaneal facet 61.6).

Pliometanastes new genus

GENOTYPE: — *Pliometanastes protistus*. As only a single species is certainly attributed to this genus, the characterization of the genus is identical to that of the species below.

ETYMOLOGY: — Greek; *Plio* = pliocene, *meta* = change, *nastes* = occupants; thus referring to a Pliocene wanderer.

Pliometanastes protistus new species

TYPE: — UF 9479, a partial skull, including the posterior two-thirds of the cranium (from the postorbital constriction posteriorly) as well as the left lacrimal, jugal, lateral portion of the maxillary containing the alveoli of M^1 - M^3 , the right maxillary containing the alveoli of M^1 - M^2 , the right portion of the palate containing the alveoli of M^2 - M^3 .

ETYMOLOGY: — Greek *protistos* = the first.

REFERRED MATERIAL: — Anterior skull fragments, UF 10337, 10338, and UF 9561; posterior skull fragment, UF 13211; anterior portion of a right mandible, UF 9450; posterior portion of a left mandible, UF 9480; left superior second of third molariform, UF 9449; left superior fourth molariform UF 9613, and UF 10341; thoracic vertebrae, UF 9464 and UF 9468; lumbar vertebrae, UF 9465, UF 9466 and UF 9467; caudal vertebrae, UF 10342; fragmentary left humerus, UF 9445; proximal half of ulna, UF 9447; right metacarpal II, UF 9453; left metacarpal II, UF 9454; associated right metacarpal II, UF 11524; right metacarpal III, UF 11525; right metacarpal IV, UF 11526, and right metacarpal V, UF 11527; patella, UF 9774; right fibula, UF 9446; right navicular, UF 9474; right calcaneum, UF 9437; left astragalus, UF 9440; phalanx I of digit III of the pes, UF 9459; ungual phalanges, UF 9640, UF 9461, UF 9462, and UF 10340.

TYPE HORIZON AND LOCALITY: — McGehee Farm, about 3 miles north of Newberry, Alachua County, Florida. Alachua Formation, Hemphillian (Middle Pliocene).

For many years diverse nonmarine sediments occurring as sinkhole, cave, and fissure fillings, and as isolated accumulations in various depressions in the Ocala Limestone, have been assigned to the Alachua Formation (Simpson, 1930; Cooke, 1945; Pirkle, 1956; and Webb, 1964). The lithologies of the sediments assigned to the Alachua Formation are quite heterogeneous, ranging from sinkhole fillings of reddish sandy clay, blue-gray in unweathered condition, to gray phosphatic sands in larger basins with commercially significant zones of hard-rock phosphate.

The type locality of the Alachua fauna and Alachua Formation is Mixon's Bone Bed northeast of Williston, Levy County. This locality has yielded a vertebrate fauna of Hemphillian age. Vertebrate fossils found in other Alachua sediments range in age from early Miocene through Recent. Typically these fossil collections are not mixed, but occur as discrete faunas in historically distinct sinkhole fillings and solution deposits.

The vertebrate-bearing deposits at McGehee lie unconformably upon an irregular surface of Ocala Limestone of Late Eocene age. Two main strata can be distinguished: a lower clayey sand lying directly upon the limestone, and above this a coarse, poorly sorted and weakly stratified gravelly sand. The greater part of the sloth material has come from the lower clayey sand layer, as has most of the associated vertebrate fauna. The upper gravelly layer contains shark teeth, ray crusher plates, gar and drum scales, turtle shells, large amounts of pebble phosphate, chunks of Ocala Limestone and blackened, waterworn bones and teeth. Much postdepositional solution of the limestone has occurred, and in many places the deposits have dropped 10 feet or more into large solution pipes.

The McGehee Farm deposits accumulated in an estuary in a coastal solution valley when the sea stood approximately 90-100 feet above its present level (Webb, 1964). Vertebrate hard parts accumulated in solution pockets in the estuary.

Of the 14 mammals from McGehee Farm (Table 10 and Fig. 9) that have been identified to genus, 12 (*Mylagaulus*, *Osteoborus*, *Seridentinus*, *Tapiravus*, *Teleoceras*, *Aphelops*, *Calippus*, *Nannippus*, *Neohipparion*, *Pliohippus* or *Dinohippus*, *Prosthennops*, and *Megatylopus*) are known to occur in both the Clarendonian and Hemphillian. *Tanupolama* is known from Hemphillian faunas but is more typical of the Blancan and later. The species of *Neohipparion* from McGehee (near *N. eurystyle*) and the species of *Nannippus* (near

Table 10. MCGEHEE FARM FAUNAL LIST

CHONDRICHTHYES¹

Odontaspis cuspidata (Agassiz)
O. macrota (Agassiz)
Isurus hastalis (Agassiz)
Carcharodon megalodon Agassiz
Hemipristis serra Agassiz
Carcharhinus cf. *leucas* (Muller and Henle)
C. limbatus group
Galeocerdo cuvieri (Peron and Le Sueur)
G. aduncus Agassiz
Rhizoprionodon sp.
Negaprion brevirostris (Poey)
Pristidae
Dasyatidae
Myliobatidae

OSTEICHTHYES

Lepisosteus
Elopidae¹
Ariidae¹
Sciaenidae¹

AMPHIBIA

Siren sp.

REPTILIA

Macroclermys sp.
Trionyx aff. *T. ferox* (Schneider)
Chrysemys williamsi Weaver and Rose¹
C. carri Weaver and Rose¹
Geochelone alleni Auffenberg
Geochelone aff. *G. hayi* (Sellards)
Gopherus sp.
Gavialosuchus americanus
Alligator cf. *A. mississippiensis*
Ophisaurus sp.
Farancia sp.
Crotalidae

AVES

Phalacrocorax wetmorei Brodkorb
Nycticorax fidens Brodkorb
Ereunetes rayi Brodkorb

MAMMALIA

Talpidae
Mylagaulus kinseyi Webb¹
Lagomorpha
Pliometaenastes protistus n. gen. et sp.¹
Osteoborus spp.
Mustelidae¹
Felidae¹
Serridentinus floridanus (Leidy)

Tapiravus sp.
Teleoceras proterus (Leidy)
Aphelops longipes (Leidy)
Calippus sp.
Dinohippus or *Pliohippus*
Nannippus nr. *N. ingenuus* (Leidy)¹
Neohipparion nr. *N. eurystyle* (Cope)¹
Hipparion plicatile Leidy¹
Prosthennops sp.
 Protoceratidae
Tanupolama sp.
Megatylopus sp.
 Antilocapridae

¹ Additions to preliminary list in Webb (1964).

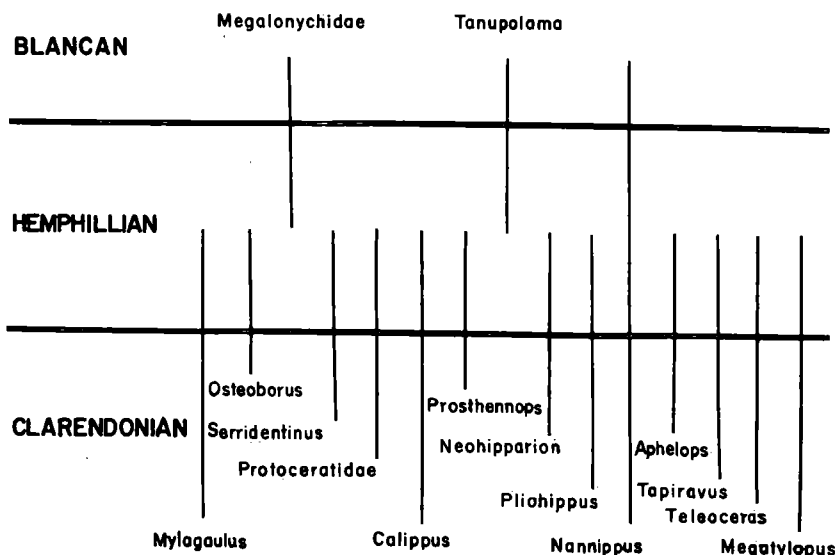


FIGURE 9. Stratigraphic ranges of mammalian genera from McGehee Farm.

N. ingenuus) are both characteristically Hemphillian species. No immigrants from Asia such as *Indarctos* and *Plesiogulo*, valuable criteria for defining many Hemphillian faunas, have been found at McGehee. No sloths, here represented by *Pliometanastes*, have yet been reported from pre-Hemphillian localities in North America. Protoceratidae previously were not known in post-Clarendonian deposits. Taking all of these facts into consideration, the McGehee assemblage is assigned an early Hemphillian age.

DIAGNOSIS: — Dental formula 5/4. A relatively small animal, the next larger North American megalonychid being the Hemphillian

Megalonyx mathisi (new species). Mandible with long, deep, and relatively wide premental spout; posterior end of symphysis below caniniform tooth; caniniform nearly vertical in orientation, nearly circular in cross section, but flattened lingually. Dorsal ridges not united to form a sagittal crest and diverging just anterior to the external occipital protuberance. A pair of depressions present on either side of the median ridge on the occiput at the external occipital protuberance. *M. rectus capitis ventralis* excavations lateral rather than posteromedial to the basilar tubercles. Dorsal border of occipital condyles nearly confluent with the occiput. Mastoid foramen at dorsal margin of mastoid region. Palate with long, narrow canals for nutritive foramina. Shaft of ulna straight on anterior side. Metacarpal II with prominent dorsoexternal process of proximal end. Patella proportionally longer than in *Hapalops* or *Megalonyx*. Fibular shaft not curved dorsomedially to the distal end in the region of attachment of the *peroneus brevis* muscle as in *Megalonyx*. Tuber calcis and its neck intermediate in development between *Megalonyx* and *Hapalops*. Astragalus lacking V-shaped tibial notch. Metatarsals slender with restricted muscle scars.

SKULL. — The skull of *Pliomatanastes* is known from a number of fragments. The most complete specimen, UF 9479, consists of the posterior two-thirds of a cranium (from the postorbital constriction back), as well as the left lacrimal, jugal, and lateral portion of the maxillary containing the alveoli of $M^1 - M^3$, the right maxillary containing the $M^1 - M^2$, the right portion of the palate containing the alveoli of $M^2 - M^3$, and a fragment that may represent the right dorsal projection of the jugal. No teeth are associated with this skull.

Isolated skull fragments include four specimens UF 9561, 10337, 10338, and 13211, two of which appear to belong to the same individual. These specimens contain the lacrimal, the jugal, and the anterior portion of the maxillary with the alveoli of $M^1 - M^2$, and the base of the caniniform alveolus. The other skulls, UF 9479 and 13211 appear to represent adults as all but the squamosal-supraoccipital-exoccipital sutures are obliterated.

The skull of *Pliomatanastes* is about half the size of the skull of *Megalonyx jeffersoni* and is considerably smaller than that of *M. leptostomus* (Figs. 10 through 13).

A prominent ridge running from the dorsal margin of the foramen magnum to the external occipital protuberance has a depression on each side just ventral to the supraoccipital crest similar to the

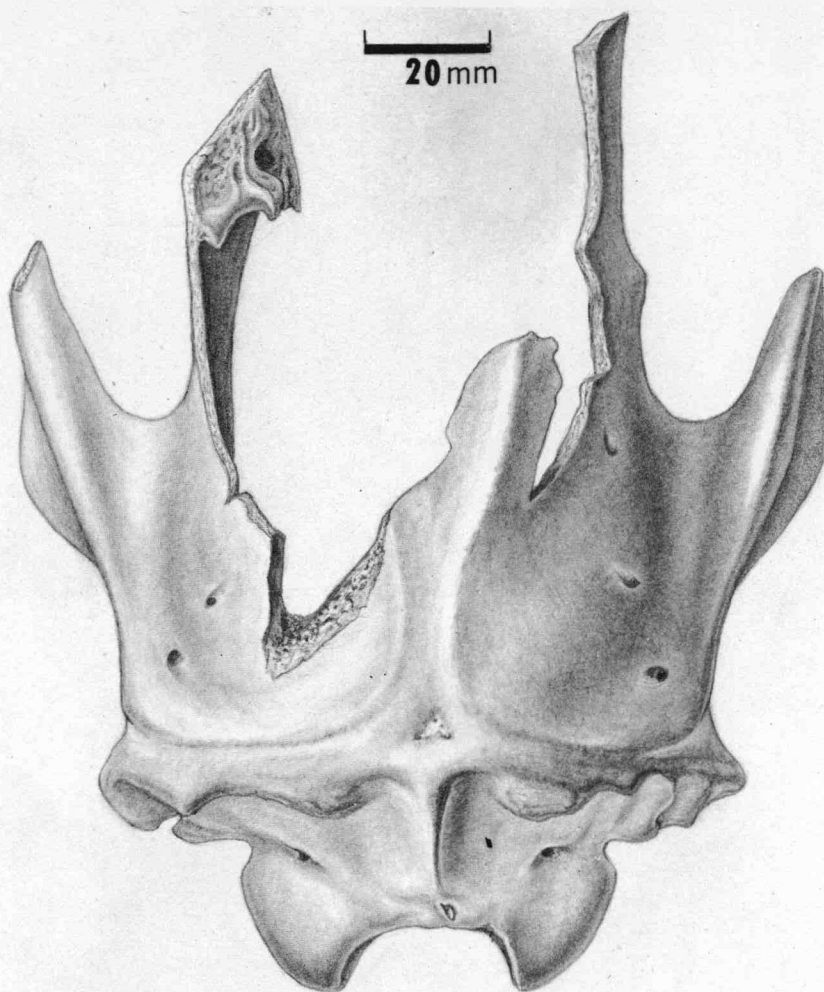


FIGURE 10. Skull of *Pliometanastes protistus*, UF 9479, dorsal view.

condition in *Eucholoeops fronto* (Scott, 1903-1904, pl. 55, fig. 1b). *Megalonyx* lacks these depressions. In *Pliometanastes* the dorsal occipital depressions are bordered laterally by a pair of semicircular tuberosities that merge dorsally with the supraoccipital crest. Lateral to these tuberosities and medial to the suture of the exoccipital bone is a smaller and more pointed pair, each bearing a ventrally projecting ridge of bone. A deep groove lies on the suture between the supraoccipital and squamosal bones.

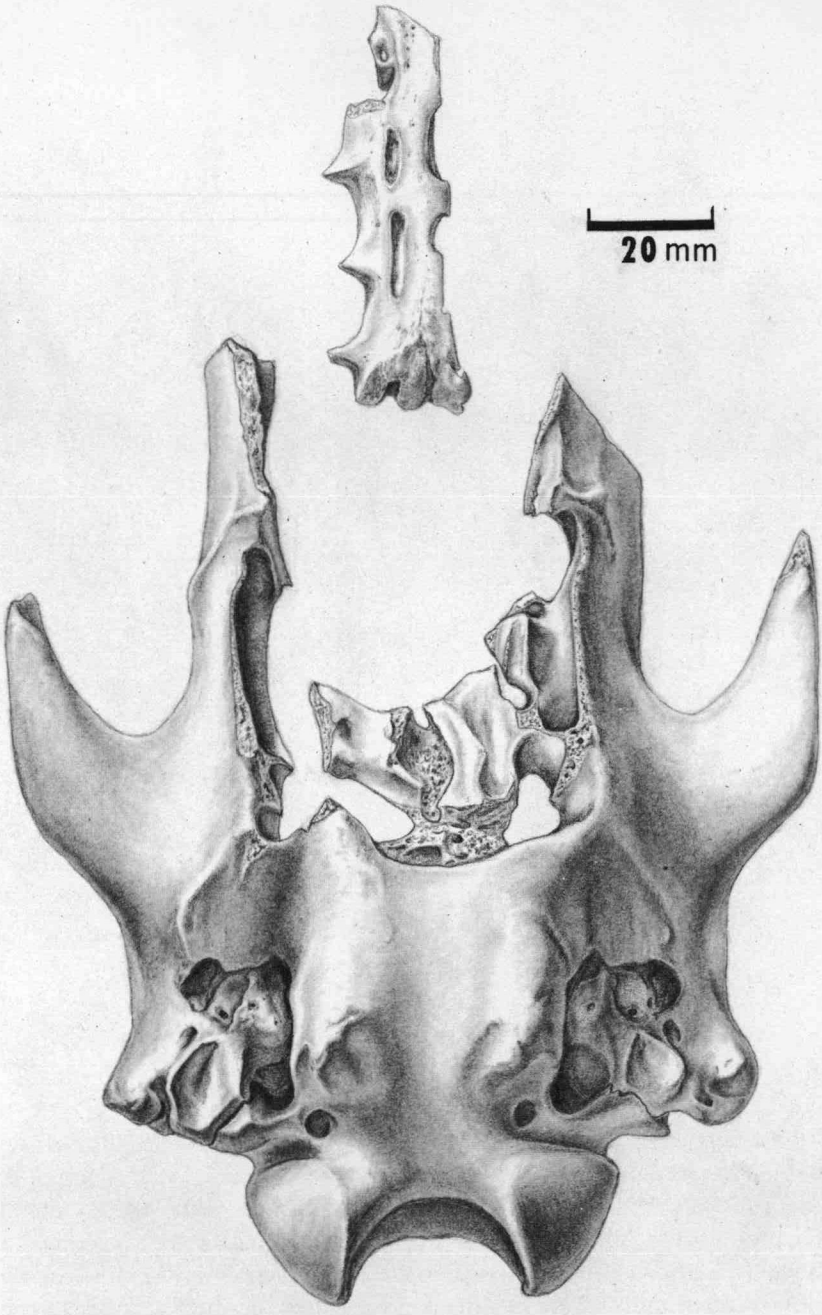


FIGURE 11. Skull of *Plometanastes protistus*, UF 9479, ventral view.

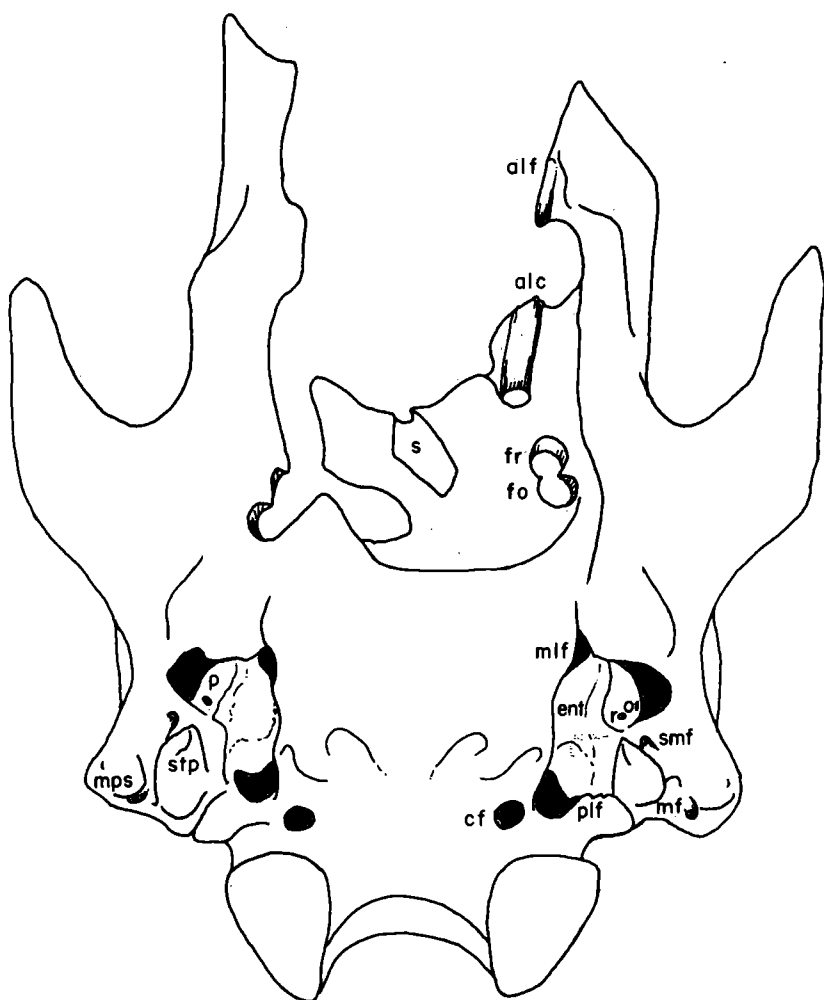


FIGURE 12. Basicranial region of skull of *Pliomatanastes protistus*, UF 9479. Abbreviations as in figure 8, and alc, anterior lacerate canal; alf, anterior lacerate foramen; s, sinus of basisphenoid bone.

Considerable variation in this region of the occiput has been observed in three specimens of *M. jeffersoni*: A cast of Owen's specimen preserved in the Florida collections, Dickeson's specimen and a juvenile from Big Bone Cave, Tennessee, both in the collections at the ANSP. The Owen skull has a depression in the region of the squamosal-supraoccipital suture, the squamosal bone being depressed below the level of the supraoccipital bone; just medial to the suture

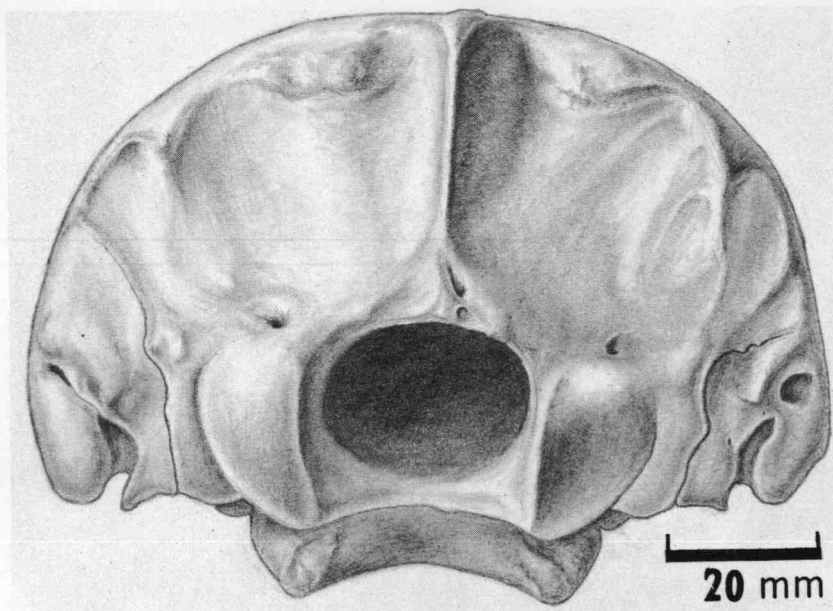


FIGURE 13. Skull of *Pliometanastes protistus*, UF 9479, occipital view.

is a relatively flat space, concave at its dorsal extremity, about 15 wide; medial to this a large tuberosity about 13 wide projects ventrally from the transverse area of muscle attachment on the occiput. An entirely different situation exists in the Dickeson skull: Medial to the squamosal-supraoccipital suture, which is deeply indented, a projection of bone about 18 wide projects laterally over the suture at its dorsal end. Medial to this projection is an excavated area with the rest of the occiput rather smooth. The occiput of the juvenile from Big Bone Cave is quite similar to that of *M. leptostomus* from Cita Canyon, Texas. In the region of the suture the bony protuberances, prominent in the Owen and Dickeson specimens, are lacking.

In overall shape the occipital region in *Pliometanastes* most closely resembles that in *M. leptostomus*. The mastoid process is not hooklike as in *M. jeffersoni*, but is rounded as in *M. leptostomus*. The occipital condyles are nearly confluent with the back of the skull as in *Eucholeops fronto*, whereas in *M. jeffersoni* and *M. leptostomus* a depression separates the condyles from the general posterior surface of the occiput. The condyles are set farther dorsally from the basilar tubercles than in *M. jeffersoni*.

In *Pliometanastes* the excavation of the basioccipital, posterior to the basilar tubercles, is not so deep as in *Megalonyx*. The most

Table 11. MEASUREMENTS OF *Pliometanastes Protistus* SKULL, (UF 9479) IN MM

Height of occiput from dorsal margin of foramen magnum	36.0
Height of occiput from basioccipital	67.8
Max. width of occiput across mastoid process	108.0
Max. width across occipital condyles	60.5 ¹
Max. width of individual condyle	16.0
Max. depth of individual condyle	27.0
Transverse diameter inside foramen magnum	26.8
Dorsoventral diameter of foramen magnum	23.7
Width across the zygomatic arches at the anterior end of the glenoid fossa	132.0
Min. orbitotemporal width	71.0 ¹
Min. postzygomatic width across squamosal	94.0
Width of basisphenoid anterior to basilar tubercles	45.0

¹ Estimated.

prominent basicranial muscle scar, for the rectus capitis muscle, is on the lateral side, whereas in *Megalonyx* it is on the medial side of the basilar tubercle. The area between the tubercles is nearly flat in *Pliometanastes* as in *E. fronto*, whereas it is slightly concave in *M. leptostomus*, and deeply concave in *M. jeffersoni*.

The stylomastoid foramen lies at the base of the stylohyal process on its anterolateral side, as in all the other megalonychids observed. The position of the mastoid foramen varies considerably between individual specimens of *M. jeffersoni*, as well as between that species and the unique skulls of *M. leptostomus* and *Pliometanastes*. In the most complete skull from McGehee, the mastoid canal enters the squamosal bone starting at the base of the stylohyal process on its posterolateral side, ascending through the mastoid process, passing near the posterior surface for about 16, then turning anteriorly and entering the squamosal bone at its dorsal extremity. The location of the mastoid foramen at the dorsal border of the squamosal is similar to that in *E. fronto*, but the canal leading to the foramen is not enclosed in bone as in *Pliometanastes*.

In *Pliometanastes* the stylohyal pit is widest at the posterior margin, whereas in *M. jeffersoni* it is widest anteriorly. The stylohyal pit in *Pliometanastes* is not so deep as in *M. jeffersoni*. *Pliometanastes* lacks the bony protuberances surrounding the posterolateral side of the foramen ovale; these are very prominent and rounded in the skull of *M. leptostomus* from Cita Canyon and are long, narrow, and less prominent in *M. jeffersoni*.

The median lacerate foramen lies farther anteriorly to the basi-

lar tubercles in *Pliometanastes* than in *M. leptostomus* and particularly *M. jeffersoni*, but not so far forward as in *E. fronto*. The foramen ovale opens in the same position in relation to the glenoid fossa in *Pliometanastes* as it does in both *Megalonyx* and *Eucholoeops*. The McGehee skull is broken in the area of the opening of the foramen rotundum, but the canal leading to it is preserved. Although it is not possible to say positively where the foramen is located, it appears from the position of the canal that it lay just anterior to the glenoid fossa, ahead of its position in *Megalonyx* and more nearly in the anterior position observed in *Hapalops ruetimeyeri*.

Pliometanastes lacks the prominent sagittal crest seen in *Megalonyx*, *Eucholoeops*, and *Megalonychotherium*. Instead a pair of low ridges extend anteriorly from the supraoccipital crest a distance of 24 and then diverge. It appears that in some juvenile specimens of *Hapalops*, as illustrated by Scott (1903-1904), a pair of ridges run along the midline of the skull, but these do not diverge in the same manner as in this adult skull of *Pliometanastes*. In *Pliometanastes* the supraoccipital crest is low and relatively flat; in *Megalonyx* it rises well above the parietals and forms a V-shaped ridge. In the McGehee crania a deep triangular depression below the external occipital protuberance marks the insertion of the nuchal ligament. This depression is not observed in *Megalonyx*, *Hapalops*, or *Eucholoeops*.

Large sinuses beneath the frontal and parietal bones extend farther posteriorly beneath the parietal in *Pliometanastes* than in a partial skull of *M. cf. jeffersoni* from Hornsby Springs, Florida (UF 4045). The distance from the posterior margin of the sinus to the supraoccipital crest is about 26 mm in the McGehee cranium, in UF 4045 it is about 63. Furthermore the parietal sinuses in the McGehee cranium have a lateral pair of vertical partitions in addition to a median partition, whereas *Megalonyx* (UF 4045) exhibits only the median one. *Megalonyx* and *Pliometanastes* differ from *Nothrotherium*, which lacks a parietal sinus, and from *Choeloeopus hoffmani* in which the parietal sinus extends all the way posteriorly to the occiput.

The posterior portion of the zygomatic arch arises as a ridge just above the squamosal-supraoccipital suture. The shape of the zygomatic arch dorsal and anterior to the glenoid fossa is similar in the McGehee cranium to that in the *M. leptostomus*, but it does

not project so far laterally as in the Cita Canyon specimen. As this part of the zygomatic arch is not preserved in the specimens of *M. jeffersoni* observed, no comparison with this species can be made. The dorsal border of the zygomatic arch curves laterally as it projects from the skull in *Pliometanastes* but curves more medially in *M. leptostomus* and *M. jeffersoni*.

The sutures of the maxillary, jugal, and lacrimal bones in *Pliometanastes* lie in the same positions as in *Hapalops ruetimeyeri*, the suture between the lacrimal and jugal running just posterior to the lacrimal foramen, that between the lacrimal, jugal, and maxillary running between the anterior opening of the infraorbital canal and the lacrimal foramen and meeting the squamosal bone at the dorsal side of the posterior opening of the infraorbital canal.

The jugal in *Pliometanastes* is directed outward and posteriorly as in *Hapalops*, quite unlike that of *M. leptostomus* in which it projects outward and slightly anteriorly. In *M. jeffersoni* the jugal is directed downward and posteriorly very close to the skull. In UF 9479 the posterior part of the jugal is flattened mediolaterally opposite the third molariform tooth, at which point it twists and widens laterally resembling the jugal in *Hapalops longiceps* (Scott 1903-1904, pl. 31).

A fragment believed to represent the dorsal projection of the right jugal, associated with UF 9479, is more slender anteroposteriorly than in either *Megalonyx* or *Hapalops*. It is flat on the lateral side, rounded on the medial side, and flattened at the dorsal extremity. The overall shape of this fragment resembles the parallel-sided jugal of *Megalonyx* and *Nothrotherium* and not that of *Hapalops*, in which the anterior side of the projection is concave and the posterior side convex.

The base of the alveolus for the upper caniniform tooth is subcircular in each of five specimens. Estimated internal measurements of the two specimens in which the anterior alveolar wall is preserved are: UF 10337, 10.7 mm anteroposteriorly, 7.0 mediolaterally; UF 10338, 10.4 mm anteroposteriorly and 6.7 mediolaterally. The base of the caniniform alveolus is no larger than the base of the alveolus for the first upper molariform tooth. This is in sharp contrast to *Megalonyx* in which the caniniform is considerably larger than the first molariform tooth.

A small fragment of the right posterior side of the palate preserved in UF 9479 differs from *Megalonyx*, *Hapalops*, and *Eucho-*

loeops in the manner in which the nutritive foramina open into the ventral surface. In the McGehee palate long narrow canals run anteroposteriorly on the ventral surface of the palate, whereas in the other genera they run dorsoventrally so that only small round foramina appear on the palatal surface.

MANDIBLE. — The mandible is represented by two specimens, UF 9450 and 9480, from McGehee Farm. A third specimen from the Withlacoochee River, UF 11941, a symphysis, is referred to the same species. UF 9450, the right anterior portion, includes the ventral part of the symphysis, caniniform alveolus, and anterior margin of the alveolus of M_1 , but lacks most of the predental "spout." UF 9480 includes the posterior two-thirds of the left ramus (Figs. 14 and 16).

Table 12. MEASUREMENT OF *Pliometanastes protistus* MANDIBLES IN MM

Measurement	(UF 9450)	(UF 9480)	
		right	left
Depth of horizontal ramus at middle of diastema	42.0		
Length of diastema	20.0	16.5	16.5
Length of symphysis from caniniform alveolus to tip		37.4	37.9
Anteroposterior diameter of caniniform alveolus	10.0	13.2	12.9
Max mediolateral diameter of caniniform alveolus	8.6	10.9	11.1
Height of condyle above ventral border of angular process		53.0	

The two symphyseal specimens of *Pliometanastes* reveal a number of distinctive features. The symphyseal spout is long, extending 34.0 mm anterior of the caniniform alveoli in UF 11941 and evidently about the same in UF 9450. The predental spout is rounded at the tip as in *Paulocnus* and not pointed as in *Acratocnus*. The sides of the spout are parallel, not converging anteriorly as in *Paulocnus*. In side view the spout is flat along the dorsal surface as in *Paulocnus*, not decurved as in *Mesocnus*. The symphysis is deep with a slightly concave outline ventrally. It does not bear a keel as in Pleistocene *Megalonyx*. The posterior edge of the symphysis lies between the roots of the lower caniniform teeth. In this respect *Pliometanastes* agrees with *Megalonyx* and differs

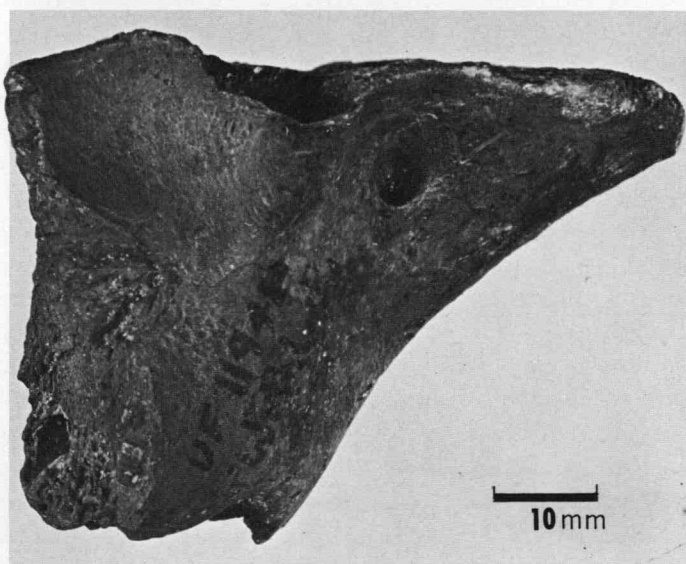


FIGURE 14. Mandibular symphysis of *Plometanastes protistus*, UF 11941, occlusal and lateral views.

from *Paulocnus* and other West Indian megalonychids in which the symphysis extends posteriorly at least as far as the first cheek tooth.

The caniniform alveolus presents a rounded to triangular cross section. The lingual wall is slightly convex, nearly flat. The apex of the triangle faces labially. Although no caniniform has been discovered, we are confident that the tooth wore on a near vertical anterior surface producing a sharp point as in similar teeth of *Choloepus*, *Eucholoeops*, *Pliomorphus*, and *Paulocnus*.

The alveolar ridge between the caniniform and first cheek teeth is considerably thicker in *Pliometanastes* than in typical *Megalonyx* (for example, UF 10348 a small Rancholabrean *Megalonyx* jaw from Sumter Co., Florida), but as noted above, the same broadened ridge is observed in Blancan specimens of *Megalonyx*. The postcaniniform diastema attains a length of 20.1 mm in UF 9450 and a greater but indefinite amount in UF 11941, thus exceeding the diastema in *Paulocnus* and approximating that in *Megalonyx* of similar size.

UF 9450 includes the condyle but lacks the coronoid process and the posterior portion of the angle. The horizontal ramus is preserved as far forward as the alveolus of M_1 and contains the lateral walls of the alveoli of $M_2 - M_3$. The poorly developed muscle scars and porous texture of the bone suggest that this specimen is from a young individual. The angular process does not project ventrally as in *Hapalops*, but is more horizontal as in *Megalonyx*. The angle does not attain the dorsoventral height seen in *M. jeffer-soni* (see Leidy, 1855, pl. 1). The condylar process does not curve dorsally and is set in a more horizontal position than in *Megalonyx*. The dental canal passes through the alveolus of M_3 , whereas in *Megalonyx* it runs outside the alveolus, being enclosed in the side of the wall of the jaw. The foramen lateral to M_3 is situated in the same position in the McGehee mandible as in *Megalonyx* and *Eucholoeops*, not on the ascending ramus as in *Hapalops*.

DENTITION. — Only three isolated teeth have been found at the McGehee Farm: two left M^4 's, UF 10341 and UF 9613, and a left upper M^2 or M^3 , UF 9449. The two M^4 's differ in size, the antero-posterior diameter of UF 10341 being 9.0 mm, while that of UF 9613 is 7.1 mm and the mediolateral diameter of UF 10341 being 12.8 mm, that of UF 9613, 10.7 mm. The fourth upper molariform, UF 10341, probably represents an older individual as the sides are

parallel. In UF 9613 the tooth tapers slightly, the crown measuring 10.7 mm in length and the root 11.2 mm. Both teeth resemble the triangular tooth of *M. wheatleyi* figured by Cope (1871), though within the whole sample of *M. wheatleyi* this tooth varies considerably in shape. As Cope (1899) states, "The last superior molar, however, differs considerably in form. In some individuals it is triangular in section; in others the section is a transverse oval. All intermediate forms occur in *Megalonyx wheatleyi*." The pattern of wear of the fourth upper molariform teeth in *Pliometanastes* is similar to that in *Megalonyx*.

The left M^2 or M^3 of *Pliometanastes* resembles that of *M. leptostomus* in shape and wear of the crown; both have a slight concavity on the posterior side and a slight convexity on the anterior side. Both *Pliometanastes* and *Megalonyx* have irregular triangular-shaped second and third molariform teeth, whereas in *Hapalops* these teeth are squared. In these genera M^4 most nearly resembles that of *Hapalops* in shape, but here too the tooth of *Hapalops* is more squared.

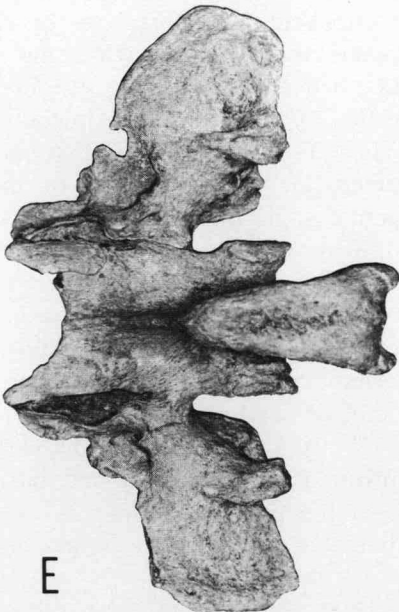
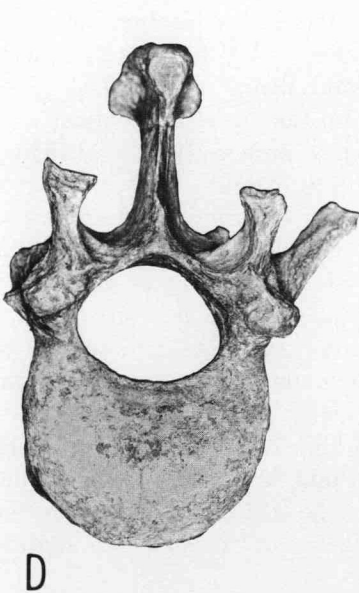
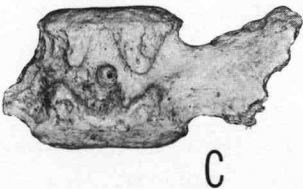
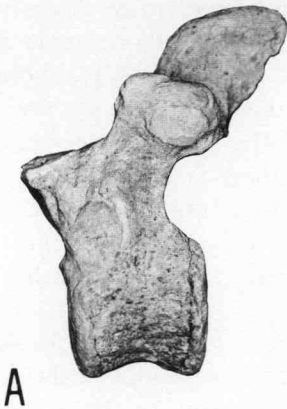
The posterior mandibular fragment, UF 9480 described above, indicates that the lower molariform teeth were of the broad trapezoidal type observed in *Megalonyx*, *Megalocnus*, and *Paulocnus*, with the labial side longer than the lingual.

THORACIC VERTEBRAE. — In the McGehee collection are two thoracic vertebrae, UF 9464 and UF 9468. UF 9464 is complete, while UF 9468 lacks the epiphyses and neural spine. The exact position of these vertebrae in the column cannot be determined.

In UF 9464 the neural spine slopes posteriorly, the articular surface for the tuberculum of the rib is convex, and the dorso-external angle of the posterior face of the centrum is not truncated by an articular facet. The articular surface for the capitulum is ovate and concave. The ventral part of the centrum is pierced by two pairs of nutritive foramina and numerous smaller ones. These larger foramina are considerably smaller than those observed in the lumbar vertebra. A single median foramen opens on the dorsal side of the centrum below the neural canal.

UF 9468 differs from UF 9464 in that the ventral part of the centrum is less rounded and has a slight keel, the concavity between the prezygapophyses is deeper, the articular surface for the tuberculum of the rib is larger, and the neural canal has a slightly greater diameter.

These thoracic vertebrae differ from the vertebrae of *M. jeffer-*



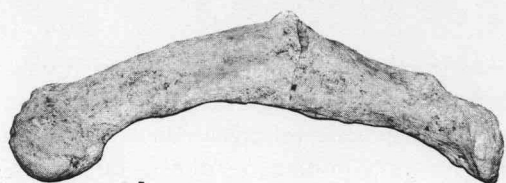
soni californicus figured by Stock (1925, pl. 18) in having relatively shorter neural spines, the dorsal end of the spine longer, less rounded, and more horizontal, the centrum relatively thicker antero-posteriorly, the prezygapophyses not sloping ventrally but more horizontal, and the articular surface for the capitulum of the rib more oval and slanting more anteriorly.

LUMBAR VERTEBRAE. — Three lumbar vertebrae, UF 9465, UF 9466, and UF 9467, are available. UF 9465 lacks the transverse processes, UF 9466 lacks the transverse processes and neural spine, and UF 9467 lacks the centrum. Each of the specimens differs considerably from the others, suggesting that they belong to different parts of the series. In UF 9465, the posterior face of the centrum is deeper and narrower and the fragment of the transverse process is inclined more dorsally than in UF 9466. A small foramen pierces the ventrolateral side of the transverse process in UF 9465, but is lacking in UF 9466. In UF 9467 a large foramen pierces the transverse process posterior and slightly lateral to the prezygapophyses. The medioventral edges of the medial postzygapophyses are closest together in UF 9467, and are farther apart in UF 9465 and 9466, the distance between them being 20.6, 24.2 and 26.4 mm, respectively. The neural spine preserved in two of the vertebrae is broad anteroposteriorly and flattened. At the dorsal end a terminal enlargement bears two prominent posterior projections. The winglike transverse processes in UF 9467 are broad, flattened, and intricate in construction. In dorsal view a concavity is observed on the posterolateral margin of each process, medial to it a prominence that projects posteriorly, and, medioventral to it, the postzygapophysis. The vertebral canal opens anterior and slightly ventral to the postzygapophysis.

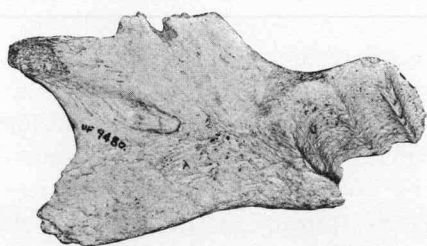
CAUDAL VERTEBRAE. — Two caudal vertebrae are available, UF 10342 and UF 10343. In both the neural arch is missing and the transverse processes are incomplete. Both vertebrae are probably from the middle of the series.

The centrum of UF 10342 is oval shape, the anterior face measuring 40.2 mm in width and 31.3 in height, the posterior face measuring 37.4 and 29.3 mm respectively. A single large foramen pierces

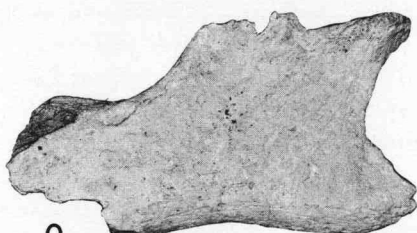
FIGURE 15. Vertebrae of *Pliomastodon protistus*. A.—Anterior thoracic vertebra, UF 9464, lateral view. B.—Anterior view of same. C.—Caudal vertebra, UF 10342, ventral view. D.—Lumbar vertebra, UF 9465, anterior view. E.—Dorsal view of same. Scale $\times \frac{1}{2}$.



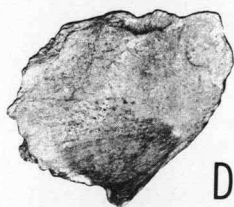
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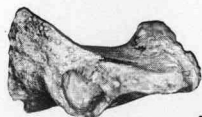
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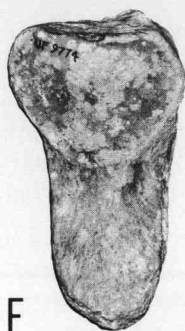
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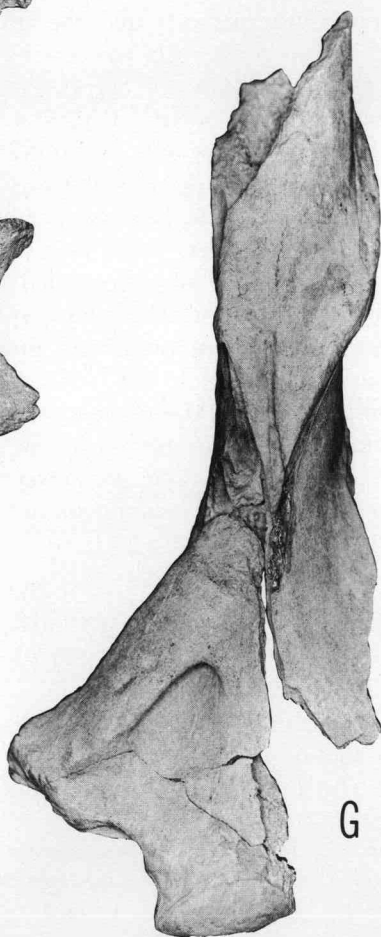
D



E



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the median ventral surface of the centrum. Two pairs of prominences, at the anterior and posterior extremities of the ventral surface of the centrum, are present for articulation with the haemapophyses (Fig. 15 and Table 13).

CLAVICLE. — A right clavicle, UF 10344, is represented in figure 16. The compressed shaft forms a single arc between the extremities, the curvature being more arcuate than in *M. jeffersoni* but lacking the sigmoid curvature in *Nothrotherium*. It is much more slender, especially medial to the articular facet for the scapula, than in *M. jeffersoni*. The most rugose area for muscle attachment extends about halfway up the shaft from a point just lateral to the sternal facet. The shaft attains its greatest depth near the middle at the end of this most prominent muscle scar. It also broadens medially to form the articular facet for the sternum. This surface is not so wide as in *Nothrotherium*, but is relatively wider than in *M. jeffersoni*. The head is convex, almost circular in side view, compressed, and slightly wider and deeper than the shaft.

HUMERUS. — Three incomplete humeri, a left (UF 9445) and two rights (UF 9444 and 9443), are represented. All lack the proximal end, and only in UF 9445 is the lateral portion of the distal end preserved. (Fig. 16).

The humerus appears to be a relatively conservative element compared to the Santa Cruz megalonychids. The major changes appear to be in the size and development of the pectoral, medial, and deltoid crests. In *Hapalops* the junction of the pectoral, medial, and deltoid crests stands prominently above the surrounding shaft. The pectoral crest rises posteriorly and then curves anteriorly, forming a hooklike projection on the medial side. This projection is less prominent in *Pliometanastes*. Along the anterolateral border of the shaft just posterior to the deltoid crest is a prominent ridge in *Pliometanastes* and *Megalonyx*, absent in *Hapalops*. In both *Pliometanastes* and *Megalonyx* the median ridge formed between the pectoral and deltoid crests is more prominent than in *Hapalops*.

In *Megalonyx* dorsal and slightly lateral to the entepicondylar foramen is a convex protuberance that is absent in *Pliometanastes* and *Hapalops*.

FIGURE 16. Limb elements and mandible of *Pliometanastes protistus*. A.—Clavicle, UF 10344. B.—Left mandible, UF 9480, lingual view. C.—Labial view of same. D.—Right mandible, UF 9450, labial view. E.—Occlusal view of same. F.—Patella, UF 9774, femoral view. G.—Left humerus, UF 9445, anterior view. Scale $\times \frac{1}{2}$.

Table 13. MEASUREMENTS OF *Pliometanastes protistus*
POSTCRANIAL MATERIAL IN MM

<i>Thoracic Vertebrae</i>	(UF 9464)	(UF 9468)
Length of centrum	38.4	
Width of centrum measured over anterior face	44.4	42.5 ^a
Depth of centrum measured over anterior face	34.4	32.8 ^a
Max. width across transverse process	84.2	84.0
Length of neural arch along middle at base of neural spine	51.0	51.7
Height measured from middle of ventral border of posterior face of centrum to end of neural spine	102.0	
Dorsoventral diameter of neural canal measured at anterior end	24.9	27.8
Transverse thickness of neural spine at middle	34.0	
Transverse thickness at end of neural spine	18.0	
Transverse width across anterior zygapophyses	47.2	49.0
<i>Lumbar Vertebrae</i>	(UF 9465)	(UF 9466) (UF 9467)
Length of centrum	45.6	42.5
Width of centrum measured across anterior face	60.4	61.0
Depth of centrum measured across anterior face	40.9	39.3
Width across supports for anterior zygapophyses	59.0 ^a	
Width across transverse process		154.0
Max. width across posterior zygapophyses	42.6	44.0 40.3
Length of neural arch along middle and at base of neural spine	53.5	48.0 56.0
Height measured from middle of ventral border of posterior face of centrum to end of neural spine	131.0	
Dorsoventral diameter of neural canal measured at anterior end	31.3	27.2
Transverse thickness of neural spine at middle		52.0
Transverse thickness at end of neural spine	25.8	27.0
<i>Clavicle</i>		(UF 10344)
Max. length		127.0
Min. depth of shaft (medial to scapular facet)		15.7
Max. depth of shaft (about halfway between extremities)		25.4
Long diameter of scapular facet		24.4
<i>Humerus</i>	(UF 9443)	(UF 9444) (UF 9445)
Max. width of shaft at middle	49.2	40.7 44.7
Min. width of shaft	31.0	
Thickness of shaft at end of deltoid crest	43.8	40.5 43.4
Thickness of bridge over entepicondylar foramen		22.4
<i>Ulna</i>		(UF 9447)
Max. mediolateral diameter of olecranon process		37.5

Width of shaft at concavity of sigmoid cavity			40.8
Dorsoventral diameter of radial notch			30.0
<i>Metacarpal III</i>			(UF 11525)
Max. length			66.5
Max. depth of proximal end			32.9
Max. width of proximal end			32.0
Max. depth of distal end			34.9
Max. width of distal end			24.0
Min. depth of shaft			15.3
Min. width of shaft			21.4
<i>Metacarpal IV</i>			(UF 11526)
Max. length			73.5
Max. depth of proximal end			31.0
Max. width of proximal end			19.5
Min. depth of shaft			14.8
Min. width of shaft			12.1
<i>Metacarpal V</i>			(UF 11527)
Max. length			64.3
Max. depth of proximal end			23.7
Max. width of proximal end			25.0
Max. depth of distal end			22.4
Max. width of distal end			17.6
Min. depth of shaft			11.0
Min. width of shaft			14.1
<i>Metacarpal II</i>	(UF 11524)	(UF 9453)	(UF 9454)
Max. length	56.6	54.9	61.1
Max. depth of proximal end	30.7	30.5	34.4
Max. width of proximal end	27.5	23.4	29.2
Max. depth of distal end	32.4	31.7	35.7
Max. width of distal end	22.2	22.0	23.4
Min. depth of shaft	14.0	13.7	15.6
Min. width of shaft	17.3	20.1	20.4
<i>Patella</i>		(UF 10347)	(UF 9774)
Dorsoventral diameter of femoral facet		33.5	32.0
Transverse diameter of femoral facet		41.1	43.0
Thickness through femoral facet		24.0	20.5
Total length			80.0
<i>Fibula</i>		(UF 9448)	(UF 9446)
Length through shaft			224.0
Max. anteroposterior diameter of proximal end		31.0	33.8
Transverse diameter of proximal end (perpendicular to tibial facet)		42.2	37.6
Anteroposterior diameter at middle of shaft			19.0
Transverse diameter at middle of shaft			16.4
Anteroposterior diameter of distal end			44.5
Max. transverse diameter of distal end			47.0
<i>Calcaneum</i>		(UF 9437)	(UF 9442)
Max. anteroposterior diameter		131.0	128.0
Max. diameter of tuber calcis		110.4	
Max. thickness at posterior border		24.4	24.0
Width of neck		24.0	20.7
Thickness of neck		34.4	34.4

Distance from inner border of external astragalar facet to inferoexternal prominence of articulating end	53.0	50.8		
Distance from dorsal border of external astragalar facet to ventral border of cuboid facet	67.2	63.5		
<i>Astragalus</i>	(UF 9440)	(UF 9441)	(UF 10339)	
Max. anteroposterior diameter parallel to fibular facet	67.0		65.4	
Max. transverse diameter measured at right angles to fibular facet	57.2	58.0	57.5	
Depth of fibular facet at distal end	31.2	33.9	34.0	
Max. transverse diameter of head	35.2	39.0	36.5	
Anteroposterior length of external calcaneal facet	43.5	46.0	43.3	
<i>Navicular</i>			(UF 9474)	
Max. diameter across cuneiform facets (width)			42.8	
Diameter taken at right angles to greatest (dorsoplantar) diameter			41.5	
Max. thickness through convexity articulating with astragalus			19.4	
<i>Phalanx II of Digit III</i>			(UF 9459)	
Length through middle			27.5	
Width of proximal end			37.5	
Depth of proximal end			38.3	
Width of distal end			35.6	
Depth of distal condyles			34.4	
<i>Ungual Phalanges</i>	(UF 9460)	(UF 9554)	(UF 9462)	(UF 10340)
Max. length from posterior end of overhanging process to tip of claw process	50.0		49.8	
Max. depth from dorsal surface of hood to discoid area on ventral surface	55.0	22.4	31.0	21.4
Length of subungual base	20.0			
Width of ventral surface of claw process just anterior to hood	23.0	11.0	15.3	10.3

¹Estimated

ULNA. — The proximal half of a right ulna, UF 9447, is illustrated in Fig. 17. The coronoid process and the area for attachment of the *brachialis* muscle are lacking.

The McGehee ulna is intermediate between *Hapalops* and *Megalonyx* in several characters. In *Hapalops* the anterior border of the shaft from the olecranon process to the styloid process forms a single convex arc, whereas in *Megalonyx* this area is concave. In *Pliome-*

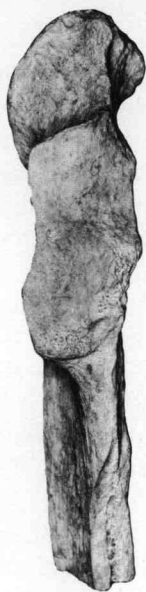
tanastes the anterior border of the shaft is straight dorsoventrally. The lateral projection of the olecranon is considerably greater in *Megalonyx* than in either *Pliometanastes* or *Hapalops*. In *Hapalops* the posterior border of the shaft is slightly convex dorsal to the sigmoid cavity, in *Pliometanastes* it is nearly straight, and in *Megalonyx* it is concave, and slopes less steeply posteriorly than in either *Hapalops* or *Pliometanastes*.

The olecranon process in *Pliometanastes* is relatively wider across the anterior border than in *Hapalops*. The vertical ridge along the posterior border of the olecranon process is sharper and less rounded than in *Hapalops*. The dorsoventral height of the radial notch is much greater in *Pliometanastes* than in *Hapalops* or even in *Megalonyx*. In *Pliometanastes* and *Hapalops* the radial notch is not distinctly separated from the sigmoid cavity by a groove as in *M. jeffersoni californicus* (Stock, 1925). The radial notch faces almost directly anteriorly in *Megalonyx*, considerably to the side in *Hapalops*; in *Pliometanastes* its orientation is intermediate.

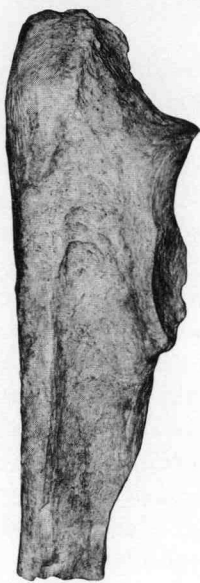
MANUS. — Four right metacarpals, numbers II, III, IV, and V, (UF 11524 - UF 11527), were collected together at McGehee and appear to belong to one individual (Fig. 18). Metacarpal IV is damaged and lacks the anterolateral posteromedial portion of the distal end above the carina. There are also two isolated metacarpal II, a right (UF 9453) (Fig. 19), and a left (UF 9454). The corresponding metacarpal elements of *Pliometanastes*, *Hapalops* and *Megalonyx* are all closely similar, the major differences being functions of the differences in size.

The fourth metacarpal of *Pliometanastes* is the longest, as in *Megalonyx*. The fifth metacarpal is slightly shorter than the third, whereas in *Megalonyx* the fifth is second in length.

The available specimens of metacarpal II of *M. jeffersoni*, ANSP 12507 and ANSP 12475, differ notably in the width of the shaft, length (ANSP 12507 is shorter and more robust than ANSP 12475), and degree of concavity of the facet for metacarpal III. The trapezoid facet of *M. jeffersoni* is almost uniformly concave, whereas in *Pliometanastes* the surface becomes concave near the dorsal extremity of the facet, and convex ventrally as it does in *Hapalops*. The dorso-lateral process of the proximal end is extremely prominent, thus accentuating the sigmoid shape of the facet. This process is not quite so prominent in *Hapalops* and is almost lacking in *M. jeffersoni*. The palmar extremity of the trapezoid facet curves anteriorly in *Pliometanastes*, whereas in *M. jeffersoni* it is flattened in the dorso-



A



B



C



D



E



F



G

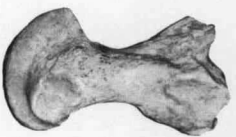
palmer plane. The dorsal end of the facet proximal to the facet for metacarpel III is convex in *Pliometanastes*, concave in *jeffersoni*. The dorsolateral extremity of the trapezoid facet proximal to the facet for mc I does not extend so far dorsally as in *jeffersoni*.

UF 9453 has a ridge from the dorsomedial end of the facet for metacarpal I to the medial projection for the articulation with phalanx I, and on either side of this ridge the shaft is concave. In UF 9454 and 11524 no ridge is apparent and the shaft is concave dorsally and convex ventrally. In both specimens of *jeffersoni* the shafts are completely round. The shape of the lateral side of the shaft in UF 9453 closely resembled that of *Megalonyx*, ANSP 12475, but in UF 9454 the ventrolateral side of the shaft is more deeply excavated. The shape of the distal end of metacarpal II is similar in both *Pliometanastes* and *Megalonyx*. On the dorsomedial side of the distal end proximal to the projection for the articulation with phalanx I, a distinct ridge of bone runs from the dorsal end of the carina ventrally, with a depression below it. This ridge and depression are much more pronounced in *Megalonyx* and *Hapalops* than in the McGehee metacarpal II UF 9453 and 11524, and they are even less distinct in UF 9454.

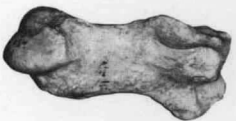
Metacarpal III of *Pliometanastes*, UF 11525, closely resembles that of *Megalonyx* and *Hapalops*. The differences lie in size and in the shape of the facets of the proximal end. In *Pliometanastes*, as in *Hapalops*, the facet for metacarpal IV consists of two parts that are continuous with one another. The dorsal end of the facet is oval with the long axis extending down the shaft. The palmar part is also oval but the long axis runs transversely; the facet is thus shaped like an English saddle in side view. In *Megalonyx* the facet for metacarpal IV consists entirely of the dorsal part with little or no palmar extension.

The facet for metacarpal II is similar in shape in *Pliometanastes*, *Megalonyx*, and *Hapalops*. In *Pliometanastes* the palmar half of the facet turns medially so that it almost faces ventrally; in *Megalonyx* and *Hapalops* the facet curves more gently and does not turn so far ventrally. The shaft in *Pliometanastes* is more slender and rounded than in *Megalonyx*. This appears to be the result of increase in size,

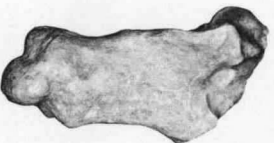
FIGURE 17. Ulna and fibula of *Pliometanastes protistus*. A, B.—Proximal half of right ulna, UF 9447, outer and radial views. C, D.—Right fibula, UF 9446, tibial and outer views. E, F, G.—Left metatarsal IV, UF 11572, left, plantar, and outer views. Scale, A-D $\times \frac{1}{2}$, E-F, natural size.



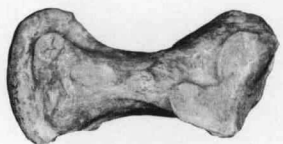
A



B



C



D



E



F



G



H



I



J

as metacarpal III of *Pliometanastes* most closely resembles the smaller, more slender element of *Megalonyx* from the Hagerman beds in Idaho.

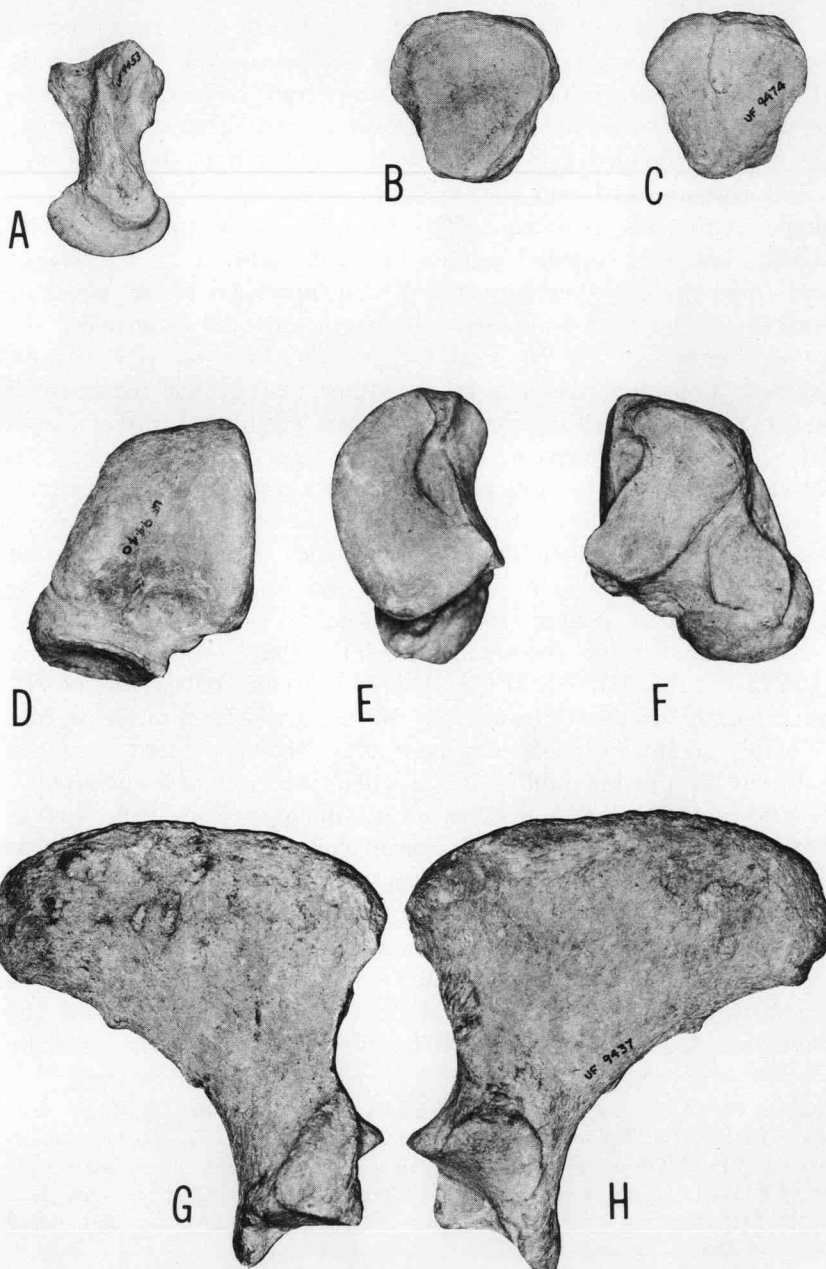
Metacarpal IV of *Pliometanastes*, UF 11526, is a long, slender bone with a dorsopalmar expansion of the proximal and distal ends. It resembles that of *Hapalops*, and differs from both in the extreme mediolateral compression of the proximal end. The shaft is more slender and rounded than in *Megalonyx*, especially at the distal end.

At the proximal end the facet for metacarpal V is similar in shape to that of *Megalonyx*. The facet for metacarpal III is also similar, but it is flattened against the shaft, whereas in *Megalonyx* and *Hapalops* it curves outward. The compression of the proximal end where the facet is flattened for metacarpal III is striking; the palmar portion of the proximal end in *Pliometanastes* is a narrow, pointed projection, whereas in the other two genera this part is wider and somewhat squared. The flattened facet for metacarpal III brings the two metacarpals closer together, especially at the distal end. The facet for articulation with the metacarpal III extends farther ventrally than in *Megalonyx*. The facet for the unciform is similarly shaped in both *Pliometanastes* and *Megalonyx*, except for the extreme narrowing of the palmar end in *Pliometanastes*. The distal end of this element closely resembles that of *Megalonyx*.

Metacarpal V of *Pliometanastes*, UF 11527, is slightly shorter than metacarpal III, UF 11525. This is in sharp contrast to the relative lengths of these elements in *Megalonyx*, where mc V is considerably greater in length than metacarpal III. The shorter distance between the proximal and distal articular processes of metacarpal V of *Pliometanastes* make it more robust in appearance than that of *Megalonyx*. The proximal end is irregularly triangular in shape as in *Megalonyx*. The distal end is considerably shorter in the dorso-palmar direction than in *Megalonyx*.

On the proximal end the surface for articulation with the lateral extension of the cuneiform is almost square in outline and presents a relatively flat surface. Situated on the dorsomedial side of the cuneiform facet is the unciform facet which is confluent medially

FIGURE 18. Associated metacarpus of *Pliometanastes protistus*. A.—Right metacarpal II, UF 11524, inner view. B.—Dorsal view of same. C.—Right metacarpal III, UF 11525, dorsal view. D.—Outer view of same. E.—Right metacarpal IV, UF 11526, outer view. F. and G.—Dorsal and inner views of same. H.—Right metacarpal V, UF 11527, inner view. I. and J.—Outer and dorsal views of same. All natural size.



with the facet for the fourth metacarpal. The unciform facet is semi-circular in outline, and the surface forms a smooth sigmoid curve with the concave portion on the dorsal and the convex portion of the palmar part. A similar sigmoid shape appears in the facet for metacarpal IV but in reverse, the convex portion dorsal and the concave palmar. On the far lateral side of the proximal end is an oval area for ligamentary attachment; the shaft is depressed on either side of it. The median part of the shaft is oval and compressed in the dorso-palmar direction. The facet for the first phalanx at the distal end is broad and only slightly convex, unlike the other metacarpals of the manus which have a large rounded carina. This indicates considerable restriction of movement in this last digit.

Patella. — The articular facet of UF 9774 is kidney-shaped, the medial and lateral sides being almost symmetrical (Fig. 16). In UF 10347 one side of the facet extends farther ventrally than the other. The patella has proportionally longer distal projection below the facet than in either *Hapalops* or *Megalonyx*; the ventral projection does not narrow below the facet as in those genera, but remains relatively wide to the distal extremity.

Fibula. — One complete right fibula, UF 9446 (Fig. 17), a proximal end of a right fibula, UF 9448, and an immature left fibula, UF 9555, lacking the epiphyses, are represented.

In the McGehee fibula the shaft is essentially straight; whereas in *Megalonyx* the shaft is curved posteriorly distal to the region for attachment of the peroneus brevis muscle. The shaft in this region is more enlarged and rugose in *Megalonyx* than in *Pliometanastes*. The scar is considerably less distinct in *Pliometanastes* than in *Megalonyx*. In *Megalonyx* fibulae a ridge running from the tibial facet to the dorsal margin of the muscle scar gives the shaft a triangular slope, whereas in the McGehee fibula this ridge is lacking and the shaft is round.

In *Pliometanastes* the calcaneal facet is distinctly concave with a slight papilla at the junction of the astragalar and calcaneal facets. The astragalar facet is likewise concave, whereas it is flat in *Megalonyx* fibulae, which lack the raised area at the junction of the two facets.

FIGURE 19. Podial elements of *Pliometanastes protistus*. A.—Right metacarpal II, UF 9453, inner view. B.—Right navicular, UF 9474, astragalar surface. C.—Cuneiform surface of same. D.—Left astragalus, UF 9440, tibial view. E. and F.—Fibular and calcaneal views of same. G.—Right calcaneum, UF 9437, outer view. H.—Inner view of same. Scale $\times \frac{1}{2}$.

In *Pliometanastes* and *Megalonyx* the proximal end of the fibula is shorter and broader than in *Hapalops*. A deep depression appears on the anteromedial side of the proximal end in these genera but not in *Hapalops*; a depression in *Hapalops* posteromedial to the tibial facet of the proximal end is absent in the other genera.

Calcaneum. — Four calcanea (Fig. 19) are represented, three right, UF 9437, 9438, and 9442, and one left, UF 9439. Only UF 9437 is complete; UF 9439 from an immature individual lacks the epiphysis. The calcaneum of *Pliometanastes* retains several primitive features associated with *Hapalops* and its allies; the major differences result from an increase in size.

The length of the tuber calcis is intermediate between those of *Hapalops* and *Megalonyx*. An adult calcaneum of a small *Megalonyx* from Sumter County, Florida, is no larger than the McGehee calcaneum yet has considerably longer tuber calcis. The McGehee calcaneum also differs from the Sumter County *Megalonyx* specimen in lacking an anterodorsal projection of the tuber calcis. *Pliometanastes* differs from all species of *Megalonyx* observed including the Sumter County specimen, in having the dorsal region of the tuber calcis proportionally thicker.

Apparently the degree of proximity of the astragalar facets and the depth of the grooves separating them vary considerably within the genus *Megalonyx*. In *Pliometanastes*, as in the Blacan *M. leptostomus*, the grooves do not appear to be so deep as those described by Stock (1925) and Leidy (1855) for *M. jeffersoni*.

In *Pliometanastes* the two astragalar facets are almost confluent, whereas in *Hapalops*, *M. leptostomus* and the Sumter County *Megalonyx* the large external astragalar facet is set ventrally below the level of the smaller internal astragalar facet.

In the McGehee calcaneum the cuboid and internal astragalar facets are closer than in *Hapalops* and almost touch. The distance between them varies in the different species of *Megalonyx* and appears to be greatest in *M. leptostomus*; the distance is greater in all *Megalonyx* than in *Pliometanastes*.

The shape of the external astragalar facet in *Pliometanastes* is identical to that of *Hapalops*, both sides being mirror images of each other. In *Megalonyx* the side of the facet dorsal to the internal astragalar facet is longer than the side dorsal to the cuboid facet.

The shape of the cuboid facet is similarly almost circular and slightly concave in *Hapalops*, *Pliometanastes*, and *Megalonyx*, but *Pliometanastes* does not have the inner lip flattened almost at right

angles to the rest of the surface as Stock (1925) describes for *M. jeffersoni californicus*. This inner lip is also absent in *M. leptostomus* and the Sumter County *Megalonyx*.

The internal astragalar facet in *Pliometanastes* is more ovate than that of *Hapalops*, which is almost round. It differs from that of *Megalonyx* mainly in the dorsal margin, which is convex and curves toward the external astragalar facet as in *Hapalops*. In *Megalonyx* the dorsal margin is concave and forms a distinct separation between the two facets.

The lateral area for attachment of the peroneus muscle posterior to the cuboid facet varies in shape and thickness in *Pliometanastes*, *Hapalops*, and *Megalonyx*. The McGehee calcaneum has a distinct and relatively wide groove immediately lateral to the external astragalar facet. This groove is less well defined in *M. leptonyx*, and is only a slight depression in *M. leptostomus* and *Hapalops*. In *Pliometanastes*, as in *Hapalops*, the projection for attachment of the peroneus is large, relatively long, and wide; in *jeffersoni*, in *M. leptostomus*, and the *Megalonyx* from Hagerman, Idaho, it is considerably smaller, shorter, and narrower. The area for attachment of the peroneus thus decreases with increase of size in *Megalonyx*, but in *Pliometanastes* more closely resembles *Hapalops* than the small species of *Megalonyx*.

Astragalus. — Three left astragali, UF 9440, 9441, and 10339, in the collection from McGehee (Fig. 19) all are complete, well preserved, and appear to represent adult individuals.

The most conspicuous difference between a McGehee astragalus and those of *M. jeffersoni* and *M. wheatleyi* is its more rounded shape. The medial side is shorter than the lateral side in *Pliometanastes* whereas in *M. jeffersoni* and *wheatleyi* the medial and lateral sides are more nearly equal. The McGehee astragalus more closely resembles *Hapalops* in this condition. This increase in the width of the medial side of the stragalus appears to be related to increase in size, as a specimen of *Megalonyx* from the Santa Fe River in Florida, which has an astragalus smaller than the McGehee astragalus, is relatively narrow on the medial end as in *Pliometanastes*.

All specimens of *Megalonyx* examined have a deep, V-shaped notch between the tibial and navicular facets to receive a process of the tibia. UF 10339 and 9440 have only a vague depression, UF 9441 a very shallow notch. Although no tibia is represented in the McGehee collection, the lack of a deep notch in the McGehee astragali implies the lack of a very well developed tibial projection. This is of considerable interest, because the tibia Stirton (1939) described from the

Mulholland Fauna in the San Francisco Bay Region has a well developed and quite prominent astragalar spine on the distal end of the tibia. In *Hapalops*, PU 15913, a relatively deep notch is present.

The internal calcaneal facet is not separated from the external calcaneal facet by a wide, distinct furrow as in all specimens of *Megalonyx* observed. The internal calcaneal facet in UF 9440 is connected to the external calcaneal facet by a low ridge. In the other two specimens there is only shallow depression between the two facets. In *Hapalops*, PU 15913, as in *Megalonyx*, a distinct separation exists.

The internal calcaneal facet varies considerably in shape in the specimens of *Megalonyx* available, but in all cases it is either relatively flat or slightly convex. In *Pliometanastes* it is slightly concave and somewhat diamond-shaped, with apex curving up toward the external calcaneal facet. The shapes of the external calcaneal facet and fibular facet are similar in *Pliometanastes*, *Hapalops* and *Megalonyx*. The navicular facet in the McGehee astragalus is ovate, having almost a tear-drop shape, whereas in *Megalonyx* it is considerably deeper in a dorso-plantar direction.

NAVICULAR. — A right navicular, UF 9474, is shown in Figure 17.

The McGehee navicular exhibits the condition seen in *Hapalops* where the mesocuneiform facet is raised above the ectocuneiform facet, whereas the opposite condition exists in *M. jeffersoni* and the Hagerman *megalonyx* where the mesocuneiform is lower than the ectocuneiform facet.

The two cuneiform facets do not meet each other as a distinct ridge in *Pliometanastes* as they do in *Hapalops*, *M. jeffersoni*, *M. sierrensis* (Sinclair, 1905), the megalonychid from the Snake Creek Beds of Nebraska described by Sinclair (1915), and the *Megalonyx* from Hagerman, Idaho. Instead in the McGehee navicular the mesocuneiform facet slopes gently to merge with the ectocuneiform facet.

In the navicular of *Pliometanastes* and *Hapalops*, the mediolateral diameter (width across the cuneiform facets) is greater than the dorsoplantar diameter. This condition is also found in the navicular, PU 12970, from the Snake Creek Beds (Sinclair, 1915). In *M. jeffersoni*, *M. sierrensis* and the specimen from Hagerman, Idaho the mediolateral diameter across the cuneiform facets is less than the dorsoplantar diameter.

The mammillate surface in the McGehee navicular is less rounded than in *M. jeffersoni*.

The navicular in both *Pliometanastes* and *Hapalops* lacks the deep notch on the median side of the ectocuneiform facet, between the

ectocuneiform and mesocuneiform facets, which is prominent in the later species of *Megalonyx* and in *M. curvidens* from the Snake Creek beds. Instead, in the McGehee navicular, as in *Hapalops*, the medial border of the ectocuneiform facet slopes gently upward to meet the median ridge surrounding the medial border of the mesocuneiform facet.

METATARSAL IV. — A nearly complete left metatarsal IV, UF 11572, is represented in the McGehee collections. The element lacks the dorsal projection of the proximal end, broken slightly ventral to the level of the dorsal part of the facet for articulation with metatarsal III, as well as lacking the exteriorodorsal projection of the distal end above the carina.

Metatarsal IV of *Pliometanastes* is slightly shorter than in *Megalonyx* from Hagerman, Idaho and about the same length as the megalonychid from the Mulholland site II, California, described by Stirton (1939). The greatest length of the McGehee metatarsal measures 82.5 mm while the Hagerman *Megalonyx* element measures 87.3, and the Mulholland metatarsal measures 82.7.

Metatarsal IV of *Pliometanastes* resembles *Hapalops* in retention of a long and slender shaft and thus differs from the Hagerman *Megalonyx* in which the element is short and robust with relatively less distance between the more massive proximal and distal extremities.

The portion of the cuboid facet that is preserved is quadrilateral in shape and extends to the posteroventral margin of the element as in *Hapalops* and the Hagerman *Megalonyx* but differs in the latter aspect from the Mulholland specimen in which the cuboid facet slopes sharply toward the facet for the metatarsal III.

The facet of metatarsal IV for articulation with metatarsal III is elliptical in outline and slightly convex in *Pliometanastes*. In this character it is similar to the Mulholland metatarsal IV and differs from the Hagerman *Metalonyx* and *Hapalops* in which the facet is concave. This character, however, appears to vary considerably within the genus *Megalonyx*.

The facet for articulation with the metatarsal V is parallel to the shaft and is subtriangular in shape as in the Hagerman *Megalonyx* and the Mulholland specimen. The facet of *Pliometanastes* differs from the Mulholland specimen in that the lower portion of the facet of *Pliometanastes* does not flare outward but is flat and very slightly depressed into the shaft.

The region of the proximal end immediately posteroventral to the facet for the metatarsal V is depressed in *Pliometanastes*, unlike

the situation in the Hagerman *Megalonyx* and the Mulholland metatarsal in which this region is level with the facet or in the case of *Megalonyx*, slightly bulging.

Pliometanastes differs from the Hagerman *Megalonyx* and the Mulholland specimen in the posteroventral view of the proximal end. In *Pliometanastes* the dorsal area of muscle attachment is relatively small, somewhat square in shape, and projects outward from the shaft, but not nearly so prominently as a projection in *Hapalops*. Where the shaft curves upward to meet this region of attachment lies a concavity that is more distinctly demarcated in *Pliometanastes* than in the Hagerman *Megalonyx* or the metatarsal from Mulholland. In the Hagerman specimen, the region for muscle attachment covers a much greater area of the proximal end and shaft than in *Pliometanastes* or the Mulholland metatarsal. The Mulholland metatarsal differs from those of *Pliometanastes* and the Hagerman *Megalonyx* in that the cuboid facet does not extend all the way to the ventral margin of the proximal surface, but terminates just ventral to the level of the ventral margin of the facet for metatarsal III. A specimen of *M. cf. wheatleyi* from Florida, discussed by Simpson (1928, Figure 8) exhibits a similar condition with respect to the foreshortened cuboid facet and depression at the extreme ventral side of the proximal end.

The metatarsals of *Pliometanastes* are notable for their slender proportions and for their terminally restricted muscle scars. In the small Blacan *Megalonyx* from Hagerman, Idaho for example, the least depth of the shaft of metatarsal IV is 27.7 mm and the least width is 23.5, whereas in *P. protistus* the corresponding dimensions are 16.4 and 18.5 mm. Although the areas of muscular and tendinous attachment at the extremities of this element are closely comparable in these two taxa, they are smaller and occupy proportionally less of the shaft in *Pliometanastes*. Although the genus *Megalonyx* encompasses considerable variation in these same features—compare the stocky specimen of *M. jeffersoni californicus* Stock (1925, fig. 49) with the slender one of *M. jeffersoni* in Leidy (1855, pl. XIII)—*Pliometanastes* falls well beyond the scope of variation observed in *Megalonyx*.

PHALANX I OF DIGIT III.—A single well preserved right phalanx I of digit III of the pes, UF 9459, is represented. Its distal end differs considerably from the pes of *Hapalops* and *Megalonyx* in the shape of the condyles, the depth of the median groove between the condyles, and the proximity of the condyles to each other.

The distal condyles of the McGehee phalanx I are considerably

more rounded than in *Hapalops* or *Megalonyx*, where they are quite flattened. In these two genera the lateral wall of each condyle is flattened to form a ridge, whereas in *Pliometanastes* the lateral wall is smoothly rounded with no ridge.

The groove between the condyles is relatively deeper and narrower, the condyles being closer together in the McGehee phalanx I than in either *Megalonyx* or *Hapalops*. A ridge around the dorsal margin encloses a pit at the dorsal end of the groove between the condyles in *Pliometanastes*. This ridge is poorly developed in *Hapalops* and is absent in *Megalonyx*.

Both *Pliometanastes* and *Hapalops* lack the dorsal lip above the proximal articular surface for metatarsal III, which is well developed in *Megalonyx*. The proximal articular facets for the metatarsal III in *Pliometanastes* are similar in size to those of *Hapalops* and *Megalonyx*. In all three genera the medial facet is larger than the lateral and the proximoplantar facet on the medial side is about twice as large as on the lateral side.

The proximoplantar facets in the McGehee phalanx I are most similar to those in the same element of *Megalonyx*. In both genera the medial facet is trapezoidal; the lateral facet is triangular in *Megalonyx* and nearly so in *Pliometanastes*. In *Hapalops* these facets project distally, but not so in these two genera.

In both *Pliometanastes* and *Megalonyx* the proximoplantar border is nearly flat, whereas in *Hapalops* it is distinctly concave. The proximal facets for metatarsal III agree with those in *Hapalops* and differ from those in *Megalonyx* in having the broad articular facets meet the facet for the carina abruptly at the right angles, whereas in *Megalonyx* the broad facets turn anteriorly and grade into the carinate facet.

In *Pliometanastes* phalanx I lacks the hook-like projection above the medial facet for mt III in *Megalonyx* and *Hapalops*. The distal articular surface of the first phalanx is relatively well rounded in *Pliometanastes*, indeed even the phalanges of *Hapalops* are more flattened on this surface. This contrasts sharply with the flattened articulation in *Megalonyx* which restricts movement between the first and second phalanges and leads to fusion of these elements in late Pleistocene time.

UNGUAL PHALANGES.—Five ungual phalanges are preserved in the McGehee collection. They are readily recognized as megalonychid claw cores by their strong lateral compression, with a triangular cross-section as in *Megalonyx* and the Santa Cruz megalonychids.

The largest claw in the collection, UF 9460 is believed to represent phalanx 3 of digit III of the pes. The bony sheath is partially preserved on one side, and the very anterior tip is lacking. The base is relatively more robust than in any of the other McGehee claws. On the anterior half of the base is a well-marked discoid area for tendon attachment. Posterior to this area two nutritive foramina, equal in size, open to the distal part of the claw. The dorsal surface of the claw is broadly convex at the proximal end and narrows about halfway to the tip of the phalanx. From this point to the tip it has a narrow dorsal edge and is triangular in cross section. The two articular concavities are symmetrical, of equal width and depth. At the dorsal and plantar extremities of the median ridge between them the ridge is squared instead of pointed as in the other claws. The posterior dorsal surface above the median ridge is deeply indented.

The smallest claws, UF 10340 and UF 9554, are complete and lack only the bony sheath. The area for tendon attachment on the base is a small, raised area anterior to the two nutritive foramina, but it is not a well-marked discoid area as in phalanx 3 of digit II of the pes. The dorsal surface is not so broadly convex at the proximal end as in the large claw of the pes. The dorsal surface does not narrow as in that element to form a sharp ridge, but remains more nearly convex to the anterior tip. The two articular concavities are not divided by a distinct median ridge as in the phalanx 3 of digit III. A slight rise between the two concavities fades out completely at the dorsal half of the inner surface. In UF 9554 the dorsal and plantar extremities of the proximal end are more pointed than in UF 10340, and the dorsal border of the proximal end is not indented as in phalanx 3 of digit III of the pes.

The claw UF 9462 is intermediate in size between the claws discussed above and lacks the bony sheath and anterior tip. It differs from the others in that the articular concavities are not so symmetrical, and one concavity extends farther proximally than the other. The median ridge between the two concavities is well defined. This median ridge is pointed, at both dorsal and plantar proximal extremities, unlike the squared condition in the phalanx 3 digit III. On the dorsal border, above the articular surface for phalanx II, is an indentation, but it is not so deep and well defined as in phalanx 3.

A claw from the small Sumter County, Florida *Megalonyx* is slightly larger than the McGehee claw UF 9462. The base of the Sumter County claw is more robust and the dorsal projection at the proximal end is longer with a greater dorsoplantar height than in

Pliometanastes. Along the entire dorsal length of the phalanx the claw core of the Sumter County specimen is less compressed than in *Pliometanastes*. However, these may not represent the same digital elements.

?Pliometanastes galushai, new species

TYPE.—FAM 77811, right half of mandibular symphysis with caniniform root and part of right ramus containing two anterior molari-form teeth.

ETYMOLOGY.—Patronymic for Ted Galusha of the American Museum of Natural History, in recognition of his extensive contributions to vertebrate paleontology in general, and to North American gravi-grade collections in particular.

DIAGNOSIS.—A small megalonychid with long, relatively deep symphyseal spout, posterior end of symphysis below caniniforms, triangular caniniforms, and transversely broadened, subrectangular molari-forms.

AGE AND LOCALITY.—Hemphillian, from horizon stratigraphically between Round Mountain and San Juan Quarry. Collected by Ted Galusha in 1947 below lower Tuffaceous Zone, San Juan locality, north of Espanola, Lyden Quadrangle, New Mexico.

DESCRIPTION.—The type and only specimen is from a subadult, as indicated by the slight taper along the teeth and by the porous nature of the bone. (Fig. 20).

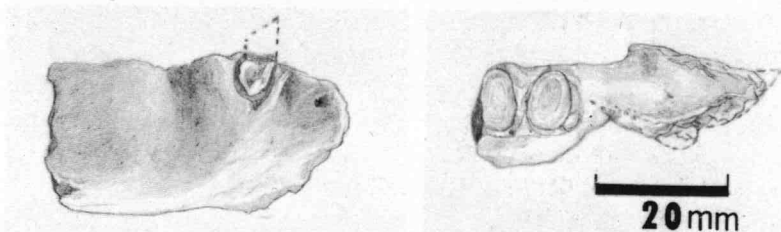


FIGURE 20. Mandible of *Pliometanastes galushai*, FAM 77811, lateral and occlusal views.

The symphyseal region produces a long spout that reaches at least 14 mm anterior to the caniniform. Whether the spout was pointed or parabolic at the tip is not determinable. The anteroventral border presents a convex to flat profile. As in *Pliometanastes* the symphysis terminates posteriorly between the caniniform roots, not farther posterior as in *Acratocnus* and most West Indian megalonychids. The symphyseal depth at this point is 24.5 mm.

As in *Pliometanastes* and several West Indian megalonychids, the caniniform tooth presents a subtriangular cross section. The lingual wall is slightly convex; the apex of the triangle is labial.

The post caniniform diastema is 13.1 mm long; it is longer than in *Paulocnus* and approximates that of *Pliometanastes protistus*.

The two molariforms are wider than long (10.0 x 5.3 mm). Unlike cheek teeth of *Pliometanastes* and *Megalonyx*, they are subrectangular rather than subtrapezoidal in cross section. The first and second cheek teeth closely resemble one another. In their shape and small size, they present a strong resemblance to those of *Acratocnus* or *Hapalops*.

The unique combination of features in the type clearly separates this species from other North American and West Indian megalonychids, but the limited material makes it difficult to decide to which described genus it has closest affinities. If comparable juvenile specimens of *P. protistus* were known, the two species might be seen to be closely related. The structure of the symphysis and caniniform both agree more closely with those in *P. protistus* than with those in other known megalonychids, but the geometry of the cheek teeth suggests fundamentally different and more primitive relationships. The post-caniniform constriction may be a less important, possibly ontogenetic difference. Further interpretations must await better material of these taxa.

Other Hemphillian *Pliometanastes*

DUNNELLON PLANT 6, FLORIDA. — A well preserved black second left metacarpal (V-2877, Florida Geological Survey), collected from Plant 6, Dunnellon Phosphate Company near Dunnellon, Marion Co., Florida, is almost identical in size and features to that described from McGehee Farm. On that basis and because of its geographical proximity it is assigned to *Pliometanastes protistus*.

BOX-T, HIGGINS, OKLAHOMA. — M. F. Skinner collected three isolated megalonychid teeth in 1939 from Pit 1 of the Box T quarries. A pair of lower caniniforms, FAM 77809, and a lower right first molariform, FAM 77808, probably belong to a single individual. The caniniforms clearly would fit the alveoli in *P. protistus*. They are subtriangular in cross section, with the presumed lingual side slightly convex, the apex of the triangle labial. At the occlusal surface the tooth measures 11.7 mm anteroposteriorly and 10.4 transversely. The shearworn surface slopes anteriorly, but the angle is only about 20 degrees below the horizontal, as compared with an angle of over 50

degrees in *Choloepus*. *Pliometanastes* caniniforms do not change shape in any important way with age, as the cross sectional shape remains unchanged through a length of over 48 mm in these specimens. A faint ovate wear facet occupies the posterior vertical wall of the caniniform. The first molariform is slightly longer on the labial than on the lingual side. It measures 12.6 long by 15.0 wide. Faint grooves occupy the lingual and anterior faces.

NORTH SANTA CLARA CANYON, NEW MEXICO. — The posterior portion of a braincase, FAM 77810, was collected in 1946 by Ted Galusha from the third promontory in Santa Clara Canyon north of Pueblo San Juan. Its stratigraphic position lies between those of the San Juan and Leyden quarries. The specimen agrees in size and detailed morphology with the cranial material of *Pliometanastes* from McGehee Farm. In particular this specimen exhibits the low occiput, absence of sagittal crest, protrusive occipital condyles and nuchal depressions characteristic of *Pliometanastes*.

KLIPSTEIN RANCH, CALIFORNIA. — From the Klipstein Ranch 3, Upper Caliente formation of the Caliente Range of California, UCMP V-5684, are several fragments of an upper dentition plus M¹ - M³ of the right side and M¹ - M² of the left side (Table 14). The teeth of the right side are all broken below the occlusal surface, except the caniniform which has a sharp-pointed wear surface.

Table 14. MEASUREMENTS OF UPPER TEETH OF *Pliometanastes* FROM KLIPSTEIN RANCH, CALIFORNIA IN MM

	Right		Left	
	Anteroposterior	Mediolateral	Anteroposterior	Mediolateral
C ¹	13.4	9.0	13.5	9.3
M ¹	12.2	16.4	12.6 ¹	17.8 ¹
M ²	13.2	19.5	14.4	19.8 ¹
M ³	11.3	19.5		

¹Measured at the occlusal surfaces; all others measured at uppermost margin.

The caniniform is subtriangular approaching trihedral as in *Pliometanastes*. It measures 13.4 mm anteroposteriorly and 9.0 mm mediolaterally and is smaller than any of the molariform teeth, unlike the situation in *Megalonyx* where the caniniform is larger than the molariform teeth. The narrowest part of the caniniform is anterior, opposite that of the caniniform alveolus of the mandible from McGehee Farm. The medial side is slightly convex forming an acute angle at the posteromedial side. On the posterolateral side the tooth bulges outward completing the triangle. The shape

of the caniniform is the only feature that distinguishes this specimen from *Megalonyx*. The molariform teeth are smaller than those of *Megalonyx leptostomus* but do not differ significantly in shape.

Other Hemphillian Megalonychidae

JIM SWAYZE QUARRY, KANSAS. — A left intermediate upper molariform tooth, FAM 77804, was collected by M. F. Skinner from the Jim Swayze Quarry of Hemphillian age. It has a heavily worn anterior slope, is narrower labially than lingually, and has a shallow concavity on the labial side. Its dimensions are 19.7 by 12.5 mm. It cannot be determined with certainty whether this tooth pertains to *Megalonyx* or to a large individual of *Pliometanastes*.

GUYMON, OKLAHOMA. — A mature left intermediate upper molar, FAM 77806, is from the Guymon Quarry. Its dimensions are 14.0 by 9.8 mm. It is heavily worn anteriorly. In occlusal view the posterior side is slightly convex. The lingual side of the tooth is considerably wider than the labial side.

HEMME HILLS, CALIFORNIA. — An essentially complete left fibula was collected from the Hemphillian Hemme Hills Site, UCMP V-5053, Contra Costa County, California. This fibula is small, the greatest length measuring 235.7. The shaft is distinctly curved distally and has a prominent area for attachment for the peroneus brevis muscle, as in *Megalonyx*.

MT. EDEN, CALIFORNIA. — Frick (1921) described a mature intermediate upper molariform tooth from the Mt. Eden fauna. Its dimensions are 18.8 by 12.3 mm. It is slightly larger than the corresponding tooth of *Pliometanastes protistus*, but is an inadequate basis for a generic assignment to *Megalonyx*.

MULHOLLAND, CALIFORNIA. — Four postcranial elements are described by Stirton (1939) from Mulholland, site 2, of California. They include a left tibia, a third and a fourth metatarsal and a median phalanx. The tibia from Mulholland has a prominent astragalar spine and it must be assumed that the astragalus possessed a deep notch to receive it. The astragalus of *Pliometanastes* lacks a prominent V-shaped notch and presumably a prominent spine on the tibia as well, but until the variability of this character can be assessed, a generic assignment on this basis is unwarranted.

RATTLESNAKE CREEK, OREGON. — Sinclair (1906) described a megalonychid claw core for which Ameghino (1912) proposed the name *Sinclairia oregoniana*. The claw cannot be distinguished from those of *Megalonyx* or *Pliometanastes*, so that the name is a *nomen dubium*.

Sinclair's supposition that this specimen was from Miocene Mascall deposits seems unlikely; a more probable interpretation is that it came from the Pliocene Rattlesnake beds of the same area.

OTIS BASIN, OREGON. — A very small proximal phalanx, UO 23275, measuring only 24.7 mm wide, 30.1 long and 22.1 deep, was collected from the Hemphillian fauna of Otis Basin (Shotwell, 1963).

KREBS RANCH, OREGON. — A proximal third manual phalanx, UO 8074, and two large, and a small second phalanx, UO 8057, 8058 and 8060 cannot be identified generically but further attest to the ubiquity of megalonychids in the Hemphillian of North America.

WESTEND BLOWOUT, OREGON. — Three elements of a moderate sized megalonychid, a third metacarpal, UO 9812, a proximal third manual phalanx, UO 9814, and a partial second phalanx, 9813, occur in this late Hemphillian site. This material and that from the previous locality were alluded to by Shotwell (1958).

RELATIONSHIPS

The fundamental subdivisions of sloth phylogeny become evident by Santacrucian time in South America. Among megalonychoids the megatheriids (including nothrotheres) reduce and then lose their anterior sets of caniniform teeth, at the same time expanding their symphyseal regions into great predental scoops. The true megalonychids, by contrast, develop a secant, self-sharpening pair of caniniforms, in front of which only a modest predental "spout" is retained. Other major differences, such as the twisted astragalus, subsequently develop between the megatheriids and the megalonychids. Many such differences are still reflected in the contrasts between *Bradypus* and *Choloepus*, the two genera of living tree sloths.

Eucholoeps represents the Santacrucian megalonychid stock (Scott, 1903-04). Its arrangement of shearing caniniforms and moderate symphyseal spout have been retained by most later megalonychids: by *Pliomorphus* and *Ortotherium* in South America, by *Acratocnus*, *Miocnus*, *Synocnus*, *Paulocnus* and most genera in the West Indies, and by *Pliometanastes* in North America. The exceptional genera in which this system has been considerably modified are *Megalocnus* in the West Indies, and *Megalonyx* in North America.

Another primitive feature observed in *Eucholoeps* is the nearly rectangular shape of its molariform teeth. This pattern is retained in *Miocnus*, *Synocnus* and *Acratocnus* of the West Indies and in *Pliometanastes galushai* of North America. Most of the late genera develop subtrapezoidal molariform teeth.

Important transitional genera from *Eucholeops* to later forms are *Pliomorphus* Ameghino and *Ortotherium* Ameghino from the late Miocene of South America. In both genera the caniniform teeth remain subtriangular, the symphyseal spout is moderately shortened, and the molariforms subrectangular. The West Indian and North American megalonychid radiations stemmed from some Miocene South American sloths closely allied to *Pliomorphus*. *Paulocnus* and *Pliometanastes* also lie very near that common stock.

Although the West Indian sloths are known only from Pleistocene deposits, their evident diversity implies a much longer occupation of the region, possibly from late Miocene time. It is not yet clear whether this diversity represents one, two or even more independent invasions by South American pioneer stocks. In the most recent study of the group de Paulo Couto (1967) avoids explicit discussion of this question; however, his classificatory headings, separating the megalocninae from the ortotheriinae, might imply a double invasion. The simplest interpretation, pending further evidence, remains a single late Miocene invasion of the West Indies followed by an insular radiation.

We have compared the various West Indian genera with *Pliometanastes* in search of some common ancestral pattern. As indicated below, however, the comparisons are relatively remote.

Megalocnus is the most specialized of the West Indian genera. Some of the major differences from *Pliometanastes* are as follows: rodent-like specialization of the anterior teeth, palate greatly depressed in relation to the basicranial axis, mandible lacking a pre-dental spout and being considerably more robust posterior to the diastema, pectoral and deltoid crests of the humerus wholly separate, and tuber calcis of the calcaneum lacking the degree of posterior expansion observed in calcanea of *Pliometanastes*.

Mesocnus differs from *Pliometanastes* in its meniscoid caniniform, relatively shallower and more slender mandibular symphysis, and the absence of an entepicondylar foramen on the humerus. *Megalocnus* and *Mesocnus*, however, resemble *Pliometanastes* and *Megalonyx* in their obliquely set, subtrapezoidal cheek teeth.

Microcnus has a shorter, even smoother cranial roof than *Pliometanastes*. And it has a shorter narrower symphyseal spout. Its most remarkable specializations are its very small size and the arboreal modifications of its skeleton, particularly evident in the distinct neck of the astragalus. These bradypodid-like features distinguish *Microcnus* from all other megalonychid ground sloths.

The genera *Acratocnus*, *Miocnus* and *Synocnus* have subtriangular caniniform teeth that seem at first to ally them with *Pliometanastes* (de Paulo Couto, 1967) but the symphysis in each of these genera is fundamentally different from the Florida genus: the symphyseal spout is shallower, narrower and it is abruptly inflected anterior to the caniniform; the caniniform teeth are set well anterior to the posterior edge of the symphysis, are separated laterally from the symphyseal groove by a distinct ridge, and are inclined strongly anteriorly, whereas in *Pliometanastes* they are nearly vertical. These genera also have more rectangular, transversely implanted teeth than *Pliometanastes*, *Megalonyx*, *Megalocnus* and *Mesocnus* in which the teeth are set obliquely and are subtrapezoidal in shape. Postcranial differences separating *Acratocnus* from *Pliometanastes* include the long neck of the calcaneum (Anthony, 1916), the relatively small tuber calcis with little posterior expansion, and the long slender proportions of the limb elements.

Perhaps the closest comparison to *Pliometanastes* may be made with *Paulocnus petrifactus* from eastern Curacao (Hooijer, 1962, 1964). It is about the same size as the Florida genus and similarly lacks a sagittal crest. The lower caniniform tooth approaches the nearly vertical orientation of that tooth in *Pliometanastes*, and the symphyseal spout is relatively broader than in the other West Indian forms. Also the distance between the caniniform and the next tooth is relatively short in *Paulocnus* as in *Pliometanastes*. However in *Paulocnus*, the lower caniniforms are not flattened lingually, the symphyseal spout is shorter, and the symphysis extends farther posteriorly, underlying M_1 . Comparison of limb elements is rendered exceedingly difficult by the poor preservation of the Curacao material. However, it is clear that the neck of the calcaneum is more constricted in *Paulocnus* than in *Pliometanastes*.

From these comparisons we conclude that of all the West Indian genera *Paulocnus* most resembles *Pliometanastes*. These two genera probably resemble the ancestral Mio-Pliocene stock that lived in northern South America. Curacao lies so close to the mainland of South America that *Paulocnus* is unlikely to bear any immediate relationship to the radiation(s) that occurred in the Greater Antilles. These other West Indian forms appear to be divided into two broad groups: (1) *Mesocnus* and *Megalocnus*, both with subtrapezoidal molariform teeth; and (2), the remaining genera with more rectangular molariform teeth. Possibly these stem from two separate inva-

sions; more probably they represent a complex radiation from a single stock allied to *Paulocnus* and *Pliometanastes*.

Pliometanastes is clearly the more primitive of the North American megalonychids, but it does not follow that this genus is directly ancestral to *Megalonyx*. Evidently, *Megalonyx* already existed along with *Pliometanastes* in the Hemphillian. By late Hemphillian time the genus had attained its essential progressive features. Although *M. mathisi* presumably represents a primitive stage within the evolution of *Megalonyx*, it occurs too late in the Hemphillian to be part of the original transition. The common ancestor of the North American genera must have been pre-Hemphillian. It presumably ranged south of the United States at that time.

The course of development of the caniniform of *Megalonyx* has an important bearing on this phylogenetic reconstruction. Scott (1903-04) attempted to recognize an early phylogenetic line with *Megalonyx*-like canines in his *Megalonychotherium* from the Santa Cruz beds. However, its teeth are in fact no different from those of *Eucholeops*; we, therefore, support Kraglievich's (1925) view that these two genera are synonymous. Moreover the new records of *Megalonyx* suggest that it developed the characteristic canines during or just prior to the Hemphillian in North America. *Pliomorphus* shows some striking similarities to *Megalonyx* in the configuration of the skull, particularly the basicranial region. The major differences are found in the low dorsoventrally constricted nasal region of *Pliomorphus* and its triangular caniniform teeth.

In order to understand the significance of the long, ovate, blunt-worn caniniforms of *Megalonyx*, it is necessary to analyze their masticatory function. In his excellent study of mastication in tree sloths, Sicher (1944) emphasized the pattern of dental attrition facets as the key to a functional analysis. In *Bradypus* the flat glossy facets occupy the posterior slopes of the lower molariforms and the anterior slopes of the uppers, indicating that the principal masticatory stroke has an anterior component. In *Choloepus* the opposite occurs: the principal stroke has a posterior component, even though a lesser protractive closing phase also occurs when the caniniforms are used for cutting. This different emphasis in the two Recent sloth genera is reflected in the zygomatic and mandibular construction (Sicher, 1944).

In *Megalonyx*, *Pliometanastes*, and *Paulocnus* the heavy attrition facets occupy the posterior edges of the lower and the anterior edges of the upper molariform teeth. The opposite edges of the teeth are

more or less flat. The principal masticatory stroke presumably had an anterior component as in *Bradypus*. The same muscular complex could also have served to engage the self-sharpening triangular caniniform teeth in *Pliomastanastes* and *Pseudocnus* (Fig. 21).

The transition from a sharp triangular to a blunt ovate caniniform in *Megalonyx* is represented by *M. mathisi*. Placement of the caniniforms more directly above one another would produce blunt horizontal occlusion rather than sharp vertical occlusion, with no major change in jaw movements. The adaptive value of this change may be associated with a shift from tropical to more temperate forests where the more sclerophyllous leaves were more readily stripped off by the broad blunt caniniform teeth. After this pattern became established, the caniniforms broadened considerably as evidenced by the change from *Megalonyx curvidens* to *M. leptostomus* to later species. As this trend continued, the vertical shearing surface of the anterior caniniforms lost its effectiveness. A longer more horizontal occlusal surface between the canines, however, came to function as an additional grinding mill.

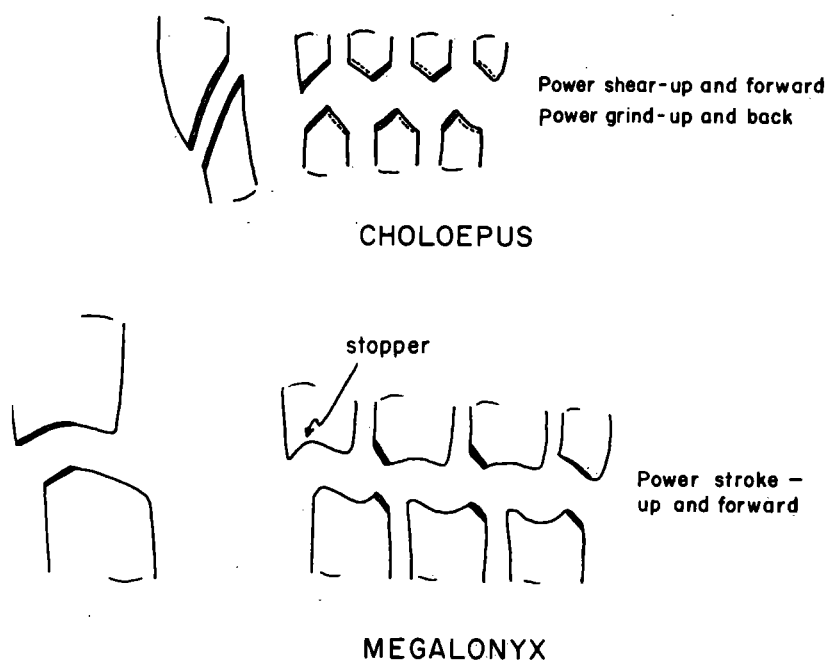


FIGURE 21. Diagram of dental wear surfaces in *Choloepus* and *Megalonyx*. Shear surfaces solid, grinding surfaces dashed.

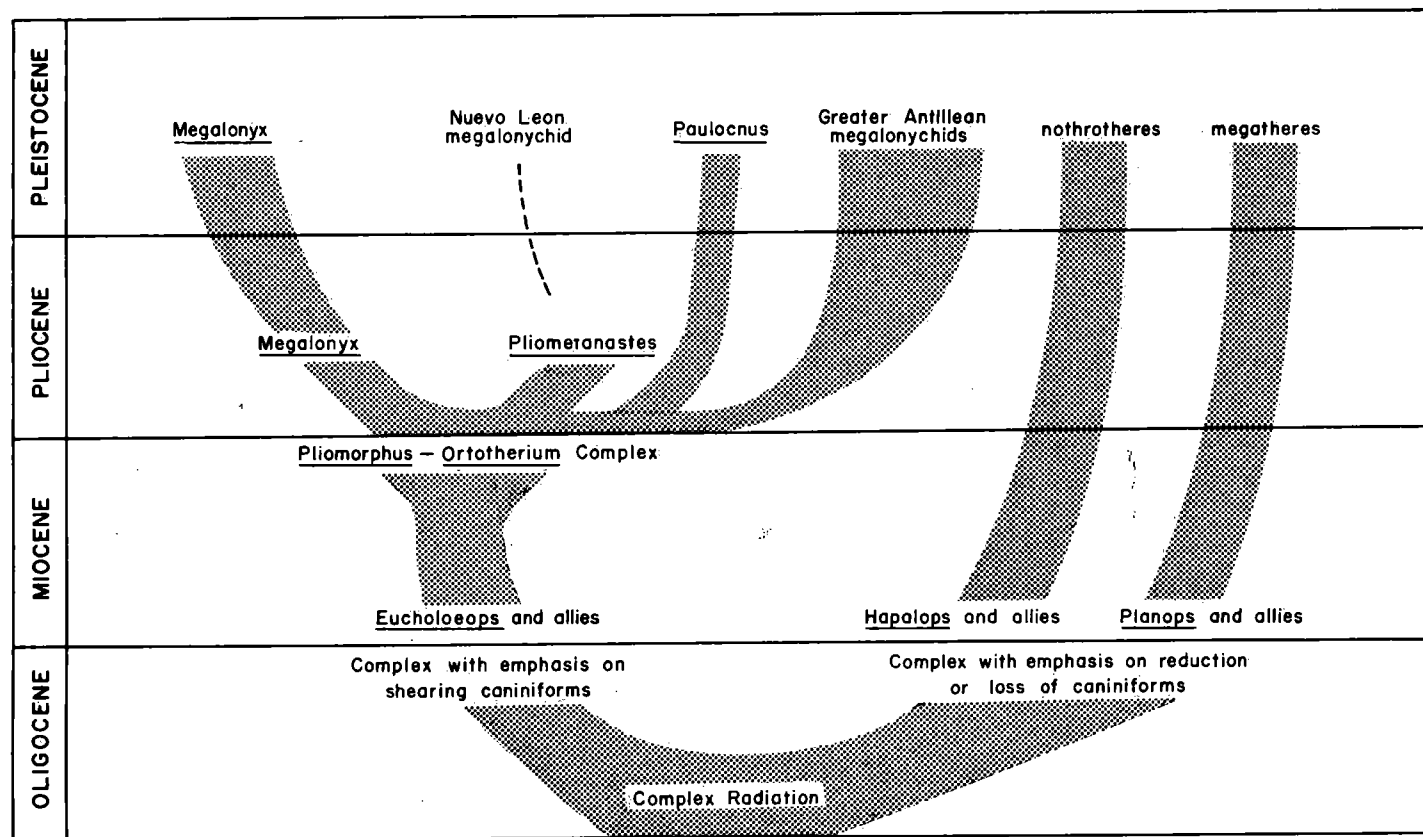


FIGURE 22. Phylogenetic diagram of the relationships of megalonychid sloths.

Accompanying enlargement of the caniniforms in *Megalonyx*, the symphyseal spout was greatly reduced and the bone between and behind the upper and lower caniniforms considerably thickened. *M. mathisi* represents a primitive stage in this respect as in the little enlarged caniniform teeth. Analogous modifications evidently occurred in *Megalocnus*. No other changes in the jaw of *Megalonyx* have been observed. The articulation and musculature of the jaw and the occlusion of the molariform teeth appear to remain the same in *Pliometanastes* and *Megalonyx*.

Reduction of the symphyseal spout and buttressing of the alveolar bone behind the caniniforms probably represent structural changes to support heavier wear on the caniniforms. Moreover, the grasping function of the spout may have been supplanted in part by the modified caniniforms. Furthermore the caniniforms of *Megalonyx* project little above the level of the cheek teeth and thus allow the tongue greater freedom of movement.

Suggested relationships between known megalonychids are illustrated in figure 22.

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Manuscripts and all editorial matters should be addressed to:

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