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LATE PLEISTOCENE MYLODONT SLOTH *PARAMYLODON HARLANI* (MAMMALIA: XENARTHRA) FROM ARIZONA

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ABSTRACT—The late Pleistocene ground sloth *Paramylodon harlani* was widely distributed across North America, but it is represented in Arizona by only 2 records. These include a nearly complete skeleton from the Richville Gravels near Springerville, Apache County, and a second partial skeleton from Shonto, Navajo County. Both specimens are from reportedly lacustrine deposits and suggest that the species was not adapted to xeric conditions. Thus, its distribution in the Southwest and potential for dispersal might have been determined by the presence of permanent water sources.

RESUMEN—El perezoso terrestre *Paramylodon harlani* del Pleistoceno tardío tenía una distribución amplia en América del Norte, pero su presencia en Arizona está documentada con sólo dos registros. Estos incluyen un esqueleto casi completo de los Richville Gravels cerca de Springerville, condado de Apache, y un esqueleto parcial de Shonto, condado de Navajo. Ambos especimenes, según se dice son de depósitos lacustres e indican que la especie no estaba adaptada a condiciones secas. Entonces, su distribución en el sudoeste de USA y su potencial para diseminar podía haber sido determinado por la presencia de fuentes permanentes de agua.

Currently, 3 types of ground sloth are known from the late Pleistocene of Arizona. The best known is *Nothrotheriops shastensis,* represented by numerous specimens, primarily from cave sites, such as Rampart Cave in the Grand Canyon (Martin et al., 1961). The other 2 species, *Megalonyx jeffersonii* and *Paramylodon harlani,* have not been as well documented for Arizona (Lindsay and Tessman, 1974) or for the southwestern United States in general. Herein we provide descriptions of records of *P. harlani* based on partial skeletons from near Shonto, Navajo County, and Springerville, Apache County, Arizona. These records expand our knowledge of the distribution of this species in the Pleistocene, and the context from which they were recovered provides insights into the paleoecology of Harlan's ground sloth.

LOCALITY DESCRIPTIONS AND GEOLOGY—Gregory (1917) first described the geology of the Shonto area (listed by him as Shato Springs), providing a faunal list based on identifications made by R. S. Lull that included *Megalonyx, Elephas, Bison*?, and *Equus*. Alan Townsend, of Inscription House, Arizona, discovered the humerus of the Shonto *Paramylodon* reported here in 1982. A visit to the site in 1982 by crews from the Geology Department of Northern Arizona University resulted in the recovery of additional parts of the skeleton. The Shonto *Paramylodon* and associated fauna were recovered from the side of a stabilized sand dune in Shonto Creek Canyon (36°34′N, 110°39′W), Navajo County, Arizona, at an elevation of 1,905 m (Museum of Northern Arizona [MNA] Locality 186–1). The dune formed on the leeward side of a bedrock island near the center of the canyon. The deposit containing the sloth is a remnant of a deltaic deposit inundated by a perennial lake formed by an impoundment within the canyon during the late Pleistocene. The sloth was found in situ in a clay-rich horizon of the dune, which might indicate a former shoreline of the lake. The age of the Shonto fauna is 30,800 ± 1,700 yr BP (GX-10493) based on a conventional carbon-14 date on a sample of bone from the sloth (Agenbroad and Downs, 1984).

The Springerville fauna comes from sections 2, 11, and 12, T10N, R28E, Lyman Lake Quadrangle, 34°16′N and 109°20′W, Apache County, Arizona (MNA Locality 184–1). The almost complete skeleton of *Paramylodon harlani* reported herein was recovered from gravels in the southwestern portion of section 12 at an elevation of about 1,906 m. The Richville gravels were deposited behind lava basalts, which impounded the Richville reach of the Little Colorado River. These basalts have been dated using K/Ar at 1.67 ± 0.09 mya (Laughlin et al., 1980).

Descriptions of Specimens—The sloth from Springerville was reported briefly by Brady (1933), and the skeleton was mounted and displayed at the Museum of Northern Arizona for many years. Its dismantling made it possible to obtain measurements provided in this paper. This paper expands upon the previous report by McDonald et al. (1994) and provides more details.

The Springerville sloth consists of a reasonably complete skeleton. Parts of the skeleton were collected on separate occasions, resulting in separate catalog numbers. It is assumed that only a single adult is represented because there is no duplication of skeletal elements, all of the recovered material is from a similar stage of ontogenetic development, and all specimens were collected in the same area. The catalog number MNA V1374 was assigned to the skull and jaw (Figs. 1, 3), atlas, right scapula, right humerus, right ulna, left radius, pelvis, right femur, left tibia, left astragalus, left calcaneum, left third metatarsal, right fourth metatarsal, vertebrae, and ribs. Other cataloged elements of skeleton at the Museum of Northern Arizona include left third metacarpal P1.1231, sesamoid P1.1235, stylohyal P1.1242, proximal phalanx from manus P1.1238 and P1.1232, left cuboid P1.1233, left lunar P1.1240, right clavicle P1.1241, right fourth metatarsal with phalanges, P1.1243, left fourth metacarpal P1.1236, and unguals from digit 1 of manus P1.1228 and P1.1230.

The Shonto sloth, cataloged by the Northern Arizona University Quaternary Science Program (NAUQSP 12523), consists of the skull (Fig. 2) and lower jaw (Fig. 3), the cervical series, both humeri, and the left astragalus (MNA P1.1291, G2.6898).

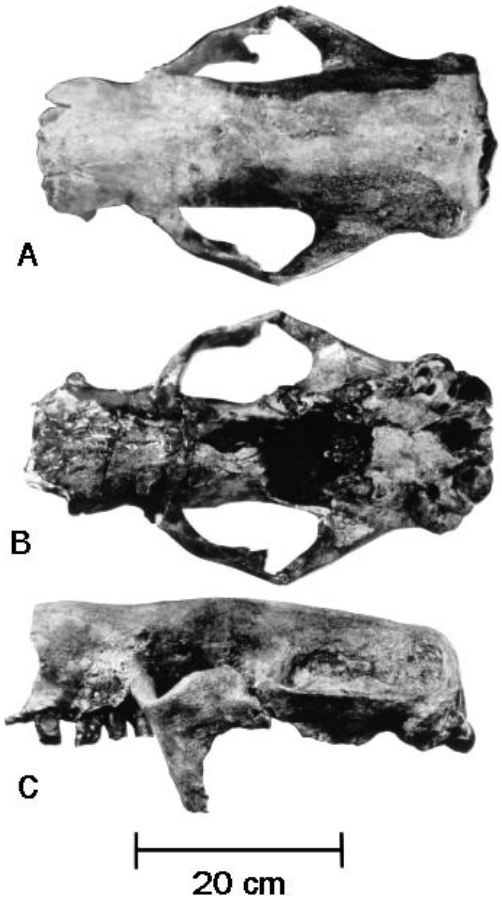

Fig. 1—Skull of *Paramylodon harlani* from Springerville (MNA V1374). A) dorsal view; B) ventral view; C) left lateral view.

Descriptions of individual bones of the skeleton of *P. harlani* (Stock, 1925) were based on a large sample from Rancho La Brea, Los Angeles County, California. Both specimens from Arizona compare well with the Rancho La Brea material and can be assigned readily to *P. harlani*. Because the measurements provided by Stock (1925) were from isolated bones, and because associated skeletons of *P. harlani* are uncommon, we provide measurements of individual bones in Appendix 1.

Stock (1925) noted the variability in the presence of the caniniform in skulls of *P. harlani*. Based on the sample of 50 skulls from Rancho La Brea, he reported that 21 individuals retained the caniniform on both sides, 14 lacked the caniniform on both sides, 5 had only a right caniniform, 7 possessed only the

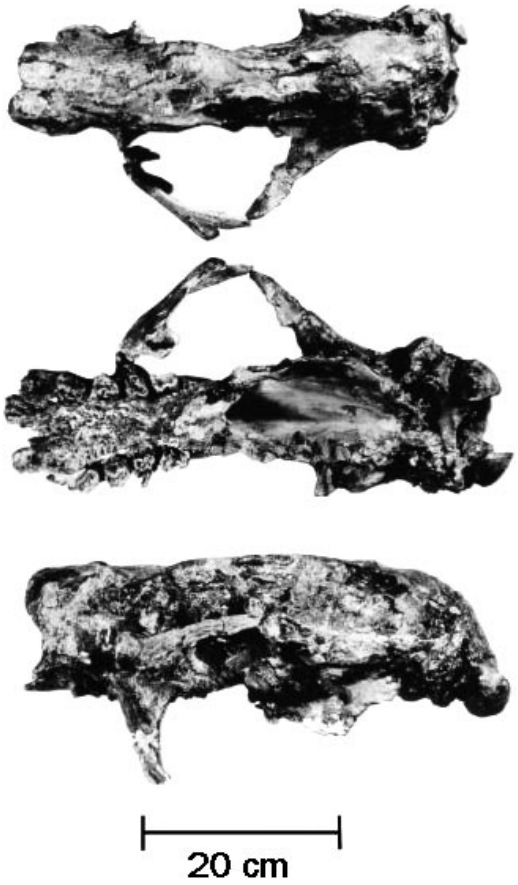

FIG. 2—Skull of *Paramylodon harlani* from Shonto (NAUQSP 12523). A) dorsal view; B) ventral view; C) left lateral view.

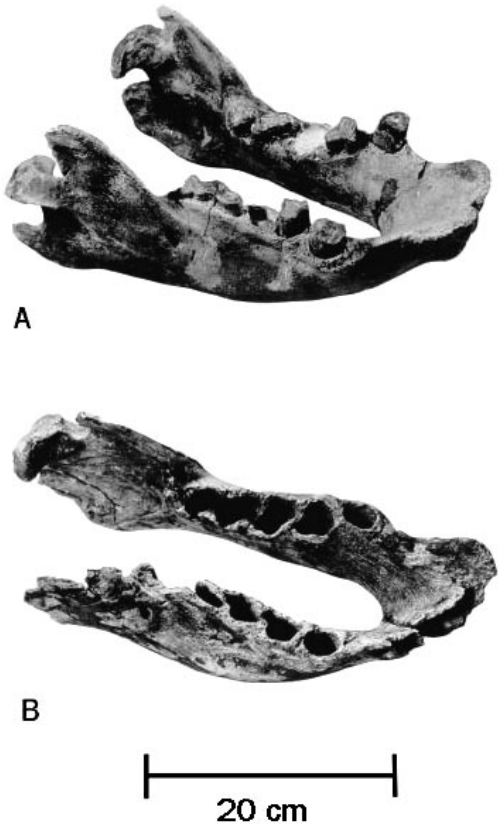

FIG. 3—Oblique view of mandibles of *Paramylodon harlani*. A) MNA V1374 from the Richville Gravels, Springerville, Apache County, Arizona. B) NAUQSP 12523 from Shonto, Navajo County, Arizona.

left caniniform, and 3 specimens were indeterminate. This variability in the presence of the caniniform also is expressed in the Arizona specimens, with both caniniforms present in the Springerville skull and both absent in the skull from Shonto.

Stock (1917) described *Mylodon harlani tenuiceps* from Rancho La Brea. Pleistocene mylodonts from North America formerly referred to either *Mylodon* or *Glossotherium* now are considered a separate genus, *Paramylodon* (McDonald, 1995). Stock distinguished *M. h. tenuiceps* based on the greater constriction of the skull behind the postorbital processes and the relative narrowness of the cranium compared to other crania from Rancho La Brea. Stock (1925:plate 42) illustrated 4 skulls referred to this subspecies. The only other mention of this subspecies in the literature since the monograph by Stock (1925) was by Lundelius (1972), who noted that some of the skulls of *P. harlani* from Ingleside, Texas, had narrower proportions and a narrower postorbital constriction than some of the other skulls in the sample. These 2 types of cranial morphology, a more robust and wider skull and a more gracile and narrower skull, also are present in the sample from American Falls, Idaho. The 2 skulls from Arizona show the presence of the 2 morphologies, with the specimen from Springerville having relatively wider dimensions for its length, or a robust morphology (Fig. 1), and the Shonto specimen having relatively narrower dimensions for its length, or a gracile morphology (Fig. 2).

McDonald (1995) documented the presence of 2 morphologies in the form of the occlusal

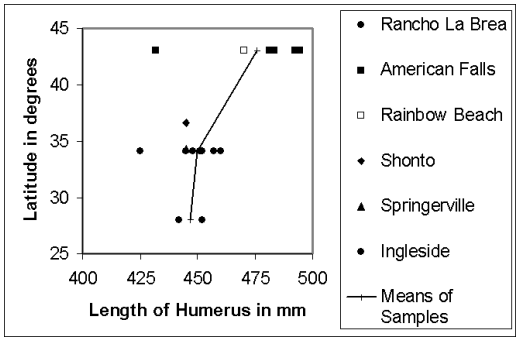

FIG. 4—Scatter diagram for humeri of *Paramylodon harlani* showing relationship between maximum length and latitude.

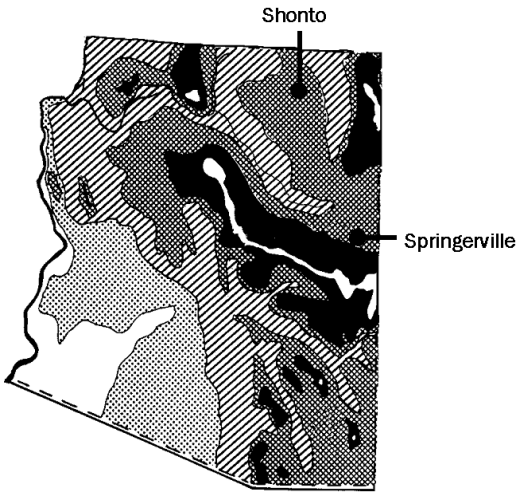

FIG. 5—Map showing a reconstruction of full-glacial vegetation in Arizona 17,000 to 23,000 years ago from Martin and Mehringer (1965). White is desert, stippled is sagebrush/chaparral, hatched is piñon-juniper woodland, cross-hatched is yellow pine parkland, solid black is spruce, fir, pine forest, and the white area within the black is subalpine to alpine habitat. Shonto and Springerville localities are associated with areas interpreted as parkland habitat.

surface of the caniniform in *P. harlani* from Leisey 1A, Florida, and suggested that these indicated sexual dimorphism in the species. These 2 occlusal morphologies also are present in samples from Rancho La Brea and American Falls, and in other samples of *P. harlani* represented by multiple specimens of the caniniform from a single locality. Based on the samples mentioned above, and because the 2 cranial and caniniform morphologies are found together in faunas with multiple skulls, it is unlikely that they represent 2 subspecies that completely overlap in range. In contrast to Stock (1925), McDonald interpreted the presence of the 2 morphologies to be indicative of sexual dimorphism in the species rather than subspecific variation. At this time, it is not possible to equate a particular morphology with a specific sex. Additional study and an independent means of determining the gender of ground sloths are needed.

Utilizing the humerus as an indicator of size, the lengths of the 2 Arizona specimens are similar to those of individuals from Rancho La Brea (Fig. 4), and both are smaller than individuals from farther north in Idaho. Remains of another sloth, *Megalonyx jeffersonii,* might be demonstrating a Bergmann's response, with the average size of the animal changing with latitude (McDonald et al., 2000). While the present sample for *P. harlani* is not robust, it does show a trend, with the average size of individuals larger in northern populations.

DISCUSSION—Previous studies of the Shonto fauna included those by Hay (1927), Saunders (1970), and Agenbroad and Mead (1989) on *Mammuthus,* that of Agenbroad and Downs (1984) on *Tapirus* cf. *T. merriami,* and the faunal list by Lindsay and Tessman (1974). The Shonto fauna also contained *Lepus, Peromyscus, Thomomys,* a sciurid, *Urocyon, Felis, Equus, Cervus,* and *Ovis.* The fauna associated with the Springerville *Paramylodon* in the Museum of Northern Arizona included *Equus, Camelops,* an antilocaprid, a cervid, *Mammuthus,* and *Megalonyx jeffersonii.*

Since the work of Stock (1925), *P. harlani* has been considered a grazer in open country. Naples (1989) suggested that *Paramylodon* was capable of using foods of lower nutritional value than other grazers and might better be considered a browser-grazer rather than a grazer only. Many of the taxa found with *Paramylodon* in Arizona and in other faunas included species of mammoth, horse, and camel, species commonly associated with open habitat. Each of these groups also seems to have been labile in its food habits, including browse as well as graze in the diet (Akersten et al., 1988; Dompierre and Churcher, 1996).

There are many physical and biological factors that determine the distribution of a spe-

cies. The identification of these limiting factors is often difficult for extant species and might be nearly impossible for extinct ones. However, it is possible to make some reasonable inferences about the paleoecology of an extinct species based on a critical examination of its distributional patterns.

Paramylodon is distributed widely across the United States, with numerous records west of the continental divide, except for the Colorado Plateau, where it is relatively rare. Besides the specimens from Arizona, the only other records of the taxon from or immediately adjacent to the Colorado Plateau are from Silver Creek, Summit County, Utah, based on skeletal material (Miller, 1976) and hair recovered from Bechan Cave (Davis et al., 1984; Mead et al., 1986). Elevation does not seem to have been a limiting factor. *Paramylodon* has been found at higher elevations, such as the Silver Creek fauna in Utah (1,952 m) and at the Magna Site in Saguache County, Colorado, (2,330 m) east of the continental divide (McDonald, unpubl. data).

Remains of *Paramylodon* west of the continental divide show that it was absent in areas now considered deserts, although numerous records of another sloth, *Nothrotheriops,* are known from these regions. McDonald (1993) listed 62 Rancholabrean localities in California for *P. harlani,* noting that its distribution was biased towards the coastal lowlands and that it was absent from the inland deserts, areas with numerous faunas that include *Nothrotheriops. Paramylodon* and *Nothrotheriops* rarely are found in the same fauna (McDonald, 1996), but their distributions were not totally exclusive. However, in the few faunas that included both genera and a record of vegetation, such as Rancho La Brea, the plants differed markedly from those preserved in the dung of *Nothrotheriops* in caves in the arid Southwest. These plant remains suggest a significant difference in the types of vegetation preferred by the 2 species of sloth, and that their co-occurrence was possible only in a few areas with vegetation suitable for both.

The Shonto and Springerville localities are in areas mapped (Fig. 5) as parkland with yellow pine (*Pinus ponderosa*) during the full glacial (Martin and Mehrenger, 1965). Whereas the vegetation map was extrapolated from a number of widely distributed records, the area of inferred vegetation for that part of Arizona coincides with both localities with *Paramylodon.* This coincidence provides some support for our interpretation that the ecology of *P. harlani* included a preference for open grassland or parkland habitat.

Paramylodon harlani is virtually absent from all 4 of the current biologically-defined North American deserts (Spaulding et al., 1983). The only exceptions are a few records along the periphery of the Great Basin, including Carson City at the western edge of the basin near the foothills of the Sierra Nevada Mountains, and a small area on the Snake River Plain (9 localities). The Carson City record is based primarily on tracks preserved in sediments associated with the shoreline of a pluvial lake, and the Idaho records are in close proximity to the Snake River. As suggested by the records from Arizona, the availability of a permanent water source in southern Idaho and western Nevada provided the appropriate local environment for the species. Riparian vegetation associated with rivers and lakes would not only have been important habitat, but also might have served as corridors that permitted dispersal. Records of the lineage of *P. harlani* in Idaho begin in the Blancan, about 2.5 mya, from sites associated with Lake Idaho, which drained into California at that time (Taylor, 1985). The river system that connected Lake Idaho with California was undoubtedly a dispersal route for aquatic species and also could have provided suitable riparian habitat for terrestrial species.

Agenbroad and Downs (1984) argued that riparian forests formed an interconnected network traversing the Pleistocene grasslands and deserts of the Southwest. This network of riparian habitat would have provided links between faunas of the Basin and Range Province to those of the Colorado Plateau, California, and elsewhere. Such a network might explain the distribution of anomalous species, such as the extinct tapir (*Tapirus* cf. *T. merriami*), in current semiarid and desert regions. McDonald (1996) used a similar argument to explain the distribution of another browsing ground sloth, *Megalonyx jeffersonii,* in the Southwest, as did Gillette et al. (1999) to infer the mode of dispersal of *Megalonyx* into the Bonneville Basin. *Megalonyx* is part of the Springerville fauna with *Paramylodon.*

The presence of tapir (*Tapirus* cf. *T. merria-*

mi) in the Shonto fauna (Agenbroad and Downs, 1984) indicates riparian habitat. As noted by Agenbroad and Downs (1984), the pollen-based environmental reconstruction for the Southwest during the late Pleistocene suggests a broad expanse of grasslands with associated xeric oak-conifer woodlands in what are now deserts (Martin and Mehringer, 1965). These woodlands would have been densest along perennial streams and permanent water. The Springerville sloth was preserved in gravels associated with the Little Colorado River and with a lake formed by an impoundment resulting from lava flows. The Shonto specimen also was associated with permanent water. Based on records from Arizona and elsewhere, it seems that the distribution of the species in xeric areas was controlled by the presence of permanent water. Although water seems to be one factor controlling the distribution of the animal, it probably was not the single primary limiting factor, because types of vegetation seem to have been equally critical. The Great Basin contained numerous permanent pluvial lakes during the Pleistocene (Morrison, 1965), yet *Paramylodon* was absent from the entire basin except for the 2 areas on the periphery noted above. Its absence indicates that multiple factors were needed to permit its survival in an area. The distribution and potential dispersal of Harlan's ground sloth in Arizona and Idaho seem to follow similar patterns, and these areas both seem to have provided the necessary combination of water and appropriate vegetation.

We recognize that the size, extent, and types of vegetation in these deserts have been dynamic, changing throughout the Pleistocene (Spaulding et al., 1983; Van Devender, 1986), and that the present aridity in these areas might have been less severe during the Pleistocene. Evidence indicates that during the late Pleistocene the 4 present North American deserts had less extreme temperatures, a greater variety of vegetation, and more effective moisture. Yet, despite these less desert-like conditions, *P. harlani* is absent from these deserts, although its distribution west of the continental divide extends all around them. In the future *P. harlani* might be recovered from within these deserts, but such records most likely will reflect specific restricted or localized conditions, similar to those just discussed, with both a dispersal corridor and an area suitable for supporting a local population.

Both Arizona records, along with the pattern of distribution elsewhere, support the interpretation that *P. harlani* was not adapted to xeric conditions. If *Paramylodon* was restricted to a particular set of environmental conditions including specific types of vegetation, then its distribution might have been discontinuous, composed of numerous, small, isolated populations in geographically restricted habitat. These habitats, particularly in the western United States, might have been connected via a tenuous network of narrow corridors along waterways. If our interpretation is correct, then these small, localized populations would have been particularly vulnerable to any changes in the local habitat. Any explanation of the extinction of Harlan's ground sloth at the end of the Pleistocene needs to take into account these and other details of the ecology of the species.

Swetnam et al. (1999) documented the decline in the extent of grasslands in Arizona from 12,000 B.P. to present, and this decline was paralleled by an increase in deserts. The decline of grassland, the presumed preferred habitat of *Paramylodon,* and fluctuations in vegetation no doubt influenced the distribution of Harlan's ground sloth and other fauna. Likewise, any possibility of dispersal to appropriate habitat could have been disrupted easily if Harlan's ground sloth depended on narrow corridors of vegetation along permanent waterways. Although it is always dangerous to argue from negative evidence, there are sufficient records for the species that the gaps in its distribution in the western United States apparently are real and not merely a sampling artifact. As such, the distributional records reflect specific attributes of the ecology of the species, with any exceptions to the general pattern reflecting suitable local conditions. As is often the case, it might be these exceptions that prove the rule.

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APPENDIX 1—Measurements (mm) of the skeletons of *Paramylodon harlani* from Springerville, Apache County, and Shonto, Navajo County, Arizona. Numbers in parentheses are approximate. Measurements marked with an ''a'' are taken from the alveoli.

Measurement	Springerville MNA V1374	Shonto NAUQSP 12523
Skull and upper dentition		
Skull length anterior process of maxilla to occipital condyles	469.7	513.7
Length of skull from anterior edge of caniniform to occipital condyles	440.0	500.0
Distance from posterior edge of last molariform to occipital condyle	286.0	333.2
Alveolar length from front of caniniform to back of last molariform	157.5	—
Alveolar length from front of first molariform to back of last molariform	115.7	129.8
Width of skull between lachrymal foramina	128.2	(93)
Width of occiput across mastoid processes	191.8	(169)
Width across the occipital condyles	134.2	(136)
Length of occipital condyles	52.3	57.2
Height of occiput	119.5	129.4
Length of temporal fossa from post-orbital process to anterior edge occipital crest	251.6	253.9
Anteroposterior length of caniniform	22.1	—
Mediolateral width of caniniform	21.6	—
Anteroposterior lenght of first molariform	26.3	—
Mediolateral width of first molariform	18.2	—
Anteroposterior length of second molariform along medial side	26.0	—
Mediolateral width of second molariform along anterior edge	26.6	—
Mediolateral width of second molariform along posterior edge	34.5	—
Anteroposterior length of third molariform along medial side	21.6	—
Mediolateral width of third molariform along anterior edge	29.5	—
Mediolateral width of third molariform along posterior edge	32.3	—
Anteroposterior length of fourth molariform	30.7	—
Mediolateral width of anterior lobe of fourth molariform	25.4	—
Mediolateral width of posterior lobe of fourth molariform	16.6	—
Mandible and lower dentition		
Mandible length anterior edge of symphysis to posterior edge of angular process	399	(421)
Mandible length anterior edge of symphysis to posterior edge of condyle	378.4	(396)
Length from anterior edge of symphysis to anterior edge of first cheek tooth	107.4	107.4
Length from anterior edge of symphysis to posterior edge of last cheek tooth	240.3	257.2
Alveolar length of tooth row	117.2	(115)
Depth of mandible below the last molariform	95.3	103.4
Mediolateral width of mandibular spout	91.2	—

APPENDIX 1—Continued

Measurement	Springerville MNA V1374	Shonto NAUQSP 12523
Anteroposterior length of first cheek tooth	25.3	26.9a
Mediolateral width of first caniniform	19.7	18.7a
Anteroposterior length of second molariform tooth along medial side	26.6	27.8a
Mediolateral width of second molariform along anterior side	23.3	26.7a
Mediolateral width of second molariform along posterior side	28.9	28.6a
Anteroposterior length of third molariform along medial side	15.6	17.8a
Anteroposterior length of third molariform along lateral side	15.9	21.0a
Mediolateral width of third molariform along anterior side	29.6	30.5a
Mediolateral width of third molariform along posterior side	30.9	29.3a
Anteroposterior length of fourth molariform	57.8	59.5a
Mediolateral width of anterior lobe of fourth molariform	35.9	34.9a
Mediolateral width of posterior lobe of fourth molariform	24.9	27.6a
Width of isthmus between anterior and posterior lobes of fourth molariform	9.4	7.3a
Atlas		
Width across transverse processes	224.1	
Dorsoventral height	83.7	
Mediolateral width of anterior articulations	135.9	
Mediolateral width of posterior articulations	109.7	
Anteroposterior width of transverse process	86.9	
Scapula		
Greatest length along scapular spine	320.1	
Anteroposterior length of glenoid	125.4	
Mediolateral width of glenoid	75.1	
Greatest width of blade of scapula	427.6	
Humerus		
Length from middle of head to middle of medial condyle	444.8	(445)
Mediolateral width of proximal end	167.5	189
Anteroposterior length of proximal end	—	154.1
Width of shaft across deltoid crest	114.4	131.8
Mediolateral width of distal end	247.9	—
Mediolateral width of distal condyles	133.7	133.8
Anteroposterior depth of lateral distal condyle	75.7	82.7
Anteroposterior depth of medial distal condyle	—	78.5
Ulna		
Greatest length	381.2	
Length of olecranon process	92.7	
Length of shaft from anterior edge of radial articular facet to distal end	(255)	
Depth of ulna at coronoid process	157.7	
Mediolateral width across humeral articulation	121.8	
Anteroposterior dimension of distal articulation	56.5	
Mediolateral dimension of distal articulation	55.8	
Radius		
Length from middle of proximal to middle of distal articular surface	229.9	
Length from middle to proximal articular surface to tip of	282.0	
Anteroposterior dimension of proximal end	78.6	
Mediolateral dimension of proximal end	(59.5)	
Anteroposterior dimension of distal end	112.9	
Mediolateral dimension of distal end	89.9	

APPENDIX 1—Continued

Measurement	Springerville MNA V1374	Shonto NAUQSP 12523
Femur		
Length from head to distal condyles	514.3	
Anteroposterior diameter of head	119.0	
Mediolateral diameter of head	126.4	
Mediolateral width of proximal end	263.8	
Mediolateral width of distal end of epicondyles	227.8	
Mediolateral width of condyles	193.5	
Mediolateral width of lateral condyle	64.4	
Mediolateral width of medial condyle	76.1	
Patella		
Length	119.2	
Mediolateral width of proximal end	121.1	
Thickness through femoral articular surface	63.5	
Tibia		
Length	219.4	
Mediolateral width of proximal end	179.1	
Anteroposterior width of proximal end	107.8	
Mediolateral width of distal end	140.2	
Anteroposterior width of distal end	101.5	
Astragalus		
Greatest anteroposterior length	132.4	146.4
Height of fibular facet	73.5	76.7
Anteroposterior length of lateral articular surface for tibia	117.9	123.7
Mediolateral width of articular surface for tibia	91.9	97.4
Calcaneum		
Greatest length	194.9	
Mediolateral width of tuber calcis	113.4	
Greatest dorsoventral height	118.0	
Length of tuber calcis along ventral side	137.7	
Length of confluent cuboid-astragalar facet	120.0	
Mediolateral width of astragalar facet	90.7	
Third metatarsal		
Greatest length from lateral edge to distal articular surface	75.5	
Length along medial side from proximal articular surface to middle of distal articular surface	55.2	
Mediolateral width of proximal end	57.8	
Anteroposterior length of distal end	58.0	
Mediolateral width of distal end	37.5	

Measurement	MNA P1.1243
Fourth metatarsal	
Greatest length	122.8
Mediolateral width of proximal end	56.8
Anteroposterior width of proximal end	65.2
Anteroposterior length of distal end	58.9
Mediolateral width of distal end	39.0