MIRACINONYX TRUMANI (CARNIVORA; FELIDAE) FROM THE RANCHOLABREAN OF THE GRAND CANYON, ARIZONA AND ITS IMPLICATIONS FOR THE ECOLOGY OF THE "AMERICAN CHEETAH"

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Abstract— A new record of *Miracinonyx trumani* has been recognized from the Grand Canyon of northern Arizona. Three sites along the length of the canyon contain fossils of *M. trumani*; Rampart Cave, Next Door Cave, and Stanton's Cave. Rampart Cave contains partial skeletons of a juvenile and a sub-adult cat. Cranial materials from Rampart Cave are distinct from *Puma* in the presence of a heavy dentition, a reduced protocone of the P4, short robust canine, and a reduced diastema between the c1 and p3. Next Door Cave has a single record of an adult calcaneum of *M. trumani* that is morphologically distinct from *Puma* by its large size and presence of a well-developed navicular facet. Stanton's Cave contains phalanges that are similar to *Puma* but are proportionately gracile in comparison to the modern *Puma*.

The presence of *Miracinonyx* within the Grand Canyon raises questions about the ecology of this large cat. Previously, *Miracinonyx* was proposed as a cheetah (*Acinonyx jubatus*) ancestor or an unrelated felid which co-evolved a cheetah-like ecology hunting prey in open savanna-like habitats. The rarity of ungulates adapted to a savanna-like habitat during the Rancholabrean within the Grand Canyon and the occurrence of the fossils of *Miracinonyx* within the canyon suggest that *Miracinonyx* was not confined to the cheetah-like model. The extinct mountain goat *Oreamos harringtoni* was the most common ungulate within the Rancholabrean of the Grand Canyon and occurs at Rampart Cave and Stanton's Cave and was perhaps the preferred prey for the *Miracinonyx* population at the Grand Canyon. We propose that the ecology of the Grand Canyon *Miracinonyx* was similar to the living Asiatic cheetah (*Acinonyx jubatus venaticus*) and snow leopard (*Uncia uncia*), large felids adapted for pursuit of mountain and canyon ungulates over near vertical rocky and mountainous terrain.

INTRODUCTION

Puma concolor (mountain lion or puma; Felidae), is one of the most familiar of the large cats of the Americas. In Arizona, *Puma* has an extensive range that includes the desert woodlands of southern part of the state to the ponderosa pine forest of the Grand Canyon. For the late Pleistocene of Arizona, *Puma concolor* is the most commonly cited felid for the Rancholabrean (250,000 to 11,000 BP) North American Land Mammal Age (NALMA) (Mead et al., 2005). The first record of fossil *Puma* from Arizona was reported by Wilson (1942) based on a partial skull and skeleton from Rampart Cave in the far western end of the Grand Canyon. Wilson (1942) questionably referred these materials to "*Puma concolor*". Olsen and Olsen (1984) identified large felid phalanges from Stanton's Cave, in the east end of the Grand Canyon, as *Puma concolor*. Mead et al. (1984) described a record of *Puma concolor* from Deadman Cave in Southern Arizona. Harris (1985) identified, though did not describe, *Puma concolor* fossils from Pyeatt Cave in southern Arizona. Czaplewski et al. (this volume) identified a partial radius as *Miracinonyx trumani* from Pyeatt Cave, which is probably based on the same specimen as Harris' (1985) *Puma* record. The most recent description of late Pleistocene *Puma concolor* from Arizona is by Mead et al. (2003) from Next Door Cave in the eastern Grand Canyon, based on a well preserved calcaneum.

The fossil record of *Puma concolor* for the Grand Canyon, particularly the Rampart Cave fossils, has long been cited in work on the Rancholabrean NALMA of the Grand Canyon (Harington, 1972; Mead, 1981) and work on the evolutionary history of pumas (Kurtén, 1976). However, our recent review of the Grand Canyon *P. concolor* remains suggests that the designation of a Rancholabrean *P. concolor* at the Grand Canyon is incorrect. We contend that there is no late Pleistocene record of *P. concolor* for the Grand Canyon. Here we present our qualitative and quantitative analysis and conclude the large Grand Canyon felid materials of Rancholabrean age belong to the extinct, cheetah-like felid *Miracinonyx trumani*. These records of *Miracinonyx trumani* from the Grand Canyon are the first for the Grand Canyonand the Colorado Plateau.

Miracinonyx was a large North American gracile cat with skull and body proportions similar to the modern African cheetah, *Acinonyx jubatus* (Adams, 1979; VanValkenburgh et al., 1990; Turner and Antón, 1997). At present two species of *Miracinonyx* are recognized: *M. inexpectatus* and *M. trumani*. *Miracinonyx inexpectatus* occurred during the Blancan to Irvingtonian NALMA (Pliocene and early Pleistocene) and is characterized as being a more robust species of *Miracinonyx* (Van Valkenburgh et al., 1990). *M. trumani* is known only during the Rancholabrean and is more gracile than *M. inexpectatus* (Adams, 1977). *Miracinonyx* is generally considered to have an extant African cheetah-like ecology and as a long-limbed pursuit-predator specializing in ungulates such as antilocaprids that lived in open savanna-like habitats (Adams, 1977; 1979; Martin et. al, 1977; Van Valkenburgh et. al, 1990; Turner and Anton, 1997). This prompted some to consider *Miracinonyx* ancestral to *Acinonyx* (Adams, 1977, 1979). Other researchers felt that *Miracinonyx* was convergent with *Acinonyx* and had a

A Pleistocene scene from Rampart Cave in the western portion of the Grand Canyon, Arizona. The painting by artist Julius Csotonyi features a cheetah-like cat (*Miracinonyx trumani*) mother and cubs feeding on a Harrington's mountain goat (*Oreamnos harringtoni*), while a Shasta ground sloth (*Nothrotheriops shastensis*) and woodrat (*Neotoma*) watch from near the cave entrance. Two Stock's vampire bats (*Desmodus stocki*) hang from the cave ceiling and a California condor (*Gymnogyps californianus*) flies past. Dung of the Shasta ground sloth covers the cave floor. Fossils of these Pleistocene animals have been found in Rampart Cave.

FIGURE 1. Distribution of *Miracinonyx trumani* in the Rancholabrean of North America. Numbers refer to sites listed in Table 1.

closer evolutionary relationship to *Puma* (Kurtén, 1976; Martin et al., 1977; Van Valkenburgh et al., 1990). Recent work has shown the latter relationship scheme to be the most likely based on genetic analysis of the Natural Trap Cave sample of *M. trumani* (Barnett et al., 2005). Recent genetic analysis of extant Felidae has shown that *Puma* and *Acinonyx*, along with the jaguarundi *Herpailurus*, are part of the same clade that diverged from a common ancestor roughly 6.7 mya in North America (Johnson et. al., 2006).

MATERIALS AND METHODS

All Grand Canyon *Miracinonyx trumani* materials used in this study are currently housed at the Grand Canyon National Park Collections and the Paleobiology Collections at the Smithsonian National Museum of Natural History. Measurements were taken in millimeters with digital calipers. Dental nomenclature follows Van Valen (1966). Cranial and post-cranial nomenclature follows (Reighard and Jennings, 1925). Comparative data of extant felids were obtained from the Richard S. White Collection (then at the International Wildlife Museum, Tucson AZ; now at Eastern Tennessee State University, Johnson City, TN) and the Mammalogy Collections in the Department of Vertebrate Zoology at the National Museum of Natural History.

Institutional Abbreviations—**GRCA**, Grand Canyon National Park Collections, Grand Canyon AZ; KU, University of Kansas Museum of Natural History, Lawrence KS; **LACM HC/LACMRLB**, Los Angeles County Museum Rancho La Brea, Los Angeles CA; **NAUQSP**, Northern Arizona University Quaternary Sciences Program, Flagstaff AZ (collection is now at Eastern Tennessee State University, Johnson City TN); **RSW**, Richard S. White Collection, International Wildlife Museum, Tucson AZ (collection is now at Eastern Tennessee State University, Johnson City TN); **USNM**, National Museum of Natural History, Washington D.C.; **WT**, West Texas A&M University Panhandle Plains Museum, Canyon TX; **YPM**, Yale Peabody Museum, New Haven CT.

Dentition abbreviations— **Upper dentition**; **I1**- upper first incisor, **I2**- upper second incisor, **I3**- upper third incisor, **C1**- upper canine, **P2**- upper second premolar, **P3**- upper third premolar, **dP3**- upper deciduous third premolar, **P4**- upper fourth premolar, **M1**- upper first molar. **Lower dentition**; **i1**- lower first incisor, **i2**- lower second incisor, **i3**- lower third incisor, **c1**- lower canine, **dp3**- lower deciduous third premolar, **p3**- lower third premolar, **p4**- lower fourth premolar, **m1**- lower first molar.

AGE AND LOCALITIES FOR THE GRAND CANYON *MIRACINONYX*.

Miracinonyx is now known from three late Pleistocene localities within the Grand Canyon: Next Door Cave, Rampart Cave, and Stanton's Cave. All occurrences were previously thought to represent *Puma concolor* (see below).

Next Door Cave—the locality (CB: 8:1) represents a small overhang adjacent to and most likely connected to Kaetan Cave (Mead, 1981). The cave in the Redwall Limestone is in the more open central region of the Grand Canyon at 1,431 m elevation and well above the Inner Gorge with the Colorado River (Mead et al., 2003). The region is steep, with many cliffs and talus slopes reaching up to the South Rim. The entrance to the cave system is a talus slope with a 10 m cliff below connecting to a talus slope that grade onto the upper portions of the Tonto Platform. The location provides steep access to the rim and to the flat platform below, with ultimate entry to the river corridor.

The floor deposit in the cave has not been excavated but surface remains indicated that subsurface remains are likely present (Mead, 1981). A single element was removed from the cave during the 1980s excavations of Kaetan Cave. The fossil is preserved in the same manner that late Pleistocene remains from the deposits in other caves in the region (see Mead et al. 2003: fig 4.1).

Stanton's Cave—Stanton's Cave is a solution cavern in the Redwall Limestone in the Inner Gorge and 45 m above the Colorado River in the Marble Canyon portion of the Eastern Grand Canyon. The deposits were extensively excavated in the late 1960s and early 1970s, with late Holocene-age archaeological artifacts and late Pleistocene-age faunal remains being recovered (Euler, 1984). The predominant large animal recovered from the cave was the extinct *Oreamnos harringtoni* (Harrington's mountain goat; Mead and Lawler, 1994). Felid remains reported here come from sedimentary layers and association with directly-dated extinct fauna with multiple radiocarbon dates indicating a Rancholabrean time (between 17, 300 BP to 10870 BP) for deposition (Mead et al. 1986; Mead and Agenbroad 1992).

Rampart Cave—Rampart Cave is a well-known cave located in the Muav Limestone at the western limit of the Colorado River as it exits the Grand Canyon and the Colorado Plateau. Excavations in the 1930s produced clear evidence of the cave being used by the extinct *Nothrotheriops shastensis* (Shasta ground sloth) and *Oreamnos harringtoni*, among other species (Mead, 1981 and review of all history and references in Carpenter 2003). Felid remains were first reported from the deposit by Wilson (1942). Much of the felid material, both bone and fecal specimens, was collected from "pit B" during the 1930's excavations and along the northwest wall by R. Kellogg's 1942 Smithsonian excavations. These elements were approximately mapped on Kellogg's cave plan, in Kellogg's 1942 field notes, and notes in the GRCA archives (Figure 2). According to Kellogg's field notes, nearly all the felid specimens were collected between 30 to 36 inches, (76.2 cm to 91.4 cm), which accumulated during a phase of little to no sloth inhabitation (Long and Martin, 1974; Carpenter, 2003). Long and Martin (1974) created a fine-grade stratigraphic and radiocarbon dated profile of the Rampart Cave and divided this profile into three units, "A", "B", and "C". The notes with the Smithsonian 1942 field collection shows these specimens were collected within the "B" unit and are approximately dated between 19,000 B.P. and 24, 000 B.P. Correlation of the remains to field notes and depth within the extensive sloth dung deposit indicates a

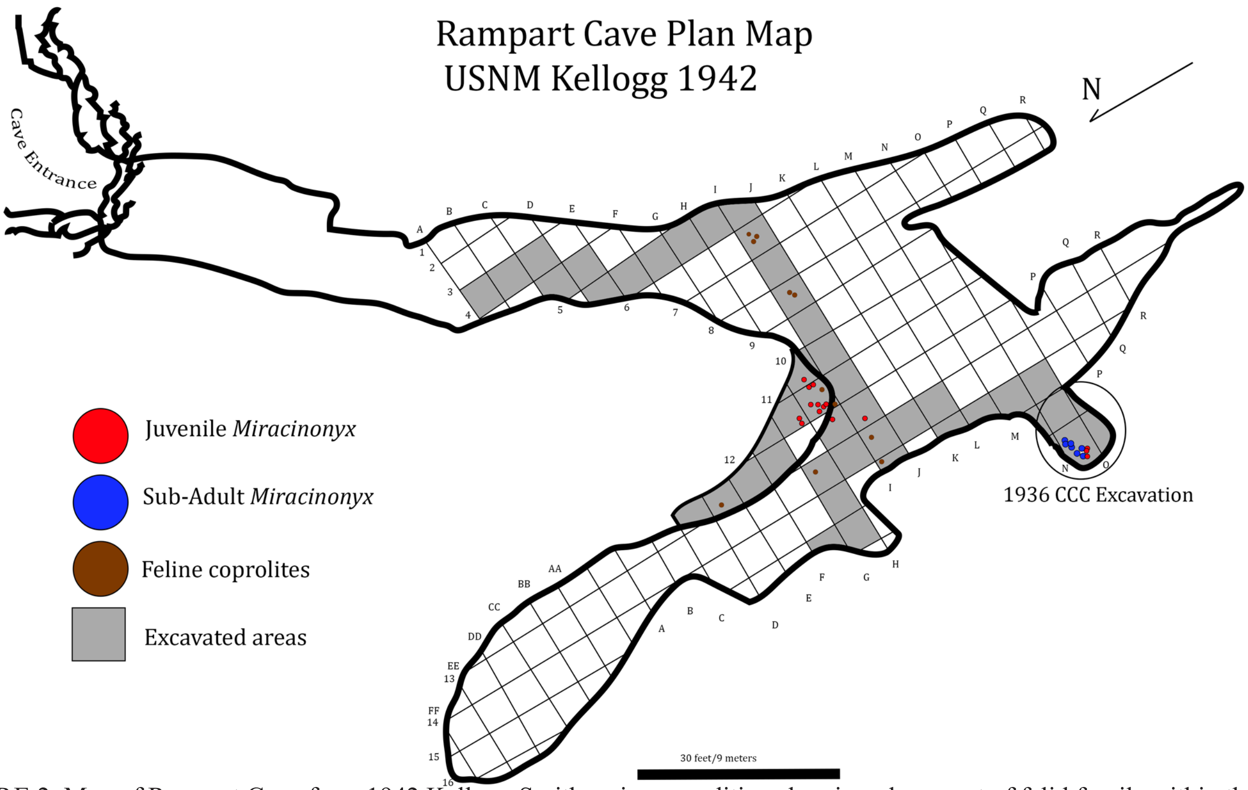


FIGURE 2. Map of Rampart Cave from 1942 Kellogg Smithsonian expedition showing placement of felid fossils within the cave; brown- felid feces, red- juvenile cat, blue- sub-adult cat. Placement of materials taken from R. Kellogg's field notes and GRCA records.

Rancholabrean age assignment for the felid specimens during the Last Glacial Maximum (~25,000 to 15,000 BP) (Carpenter 2003; Mead et al., 2003).

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family FELIDAE Fischer de Waldheim 1817
Subfamily FELINAE Fischer de Waldheim 1817
Genus MIRACINONYX Adams, 1979
Miracinonyx trumani (Orr, 1969)

Materials and Descriptions
Tsé an (Next Door) Cave

Referred Material—GRCA 55756, a right adult calcaneum.

Description—the calcaneum (Figure 3) was first described by Mead et al. (2003) as pertaining to a large *Puma concolor*. The calcaneum is larger than *Puma concolor*, but smaller than the Pleistocene felid *Panthera atrox* (Figure 4). The calcaneum is complete with no signs of animal gnawing and has little signs of erosion or abrasion. The shaft of the calcaneum is long and mediolaterally compressed, more so than in *Panthera* but less so than in *P. concolor* or *Acinonyx jubatus*. The attachment for the calcaneal tendon is broad mediolaterally and has a shallow groove, whereas *P. concolor* has a deep groove, and the groove in *A. jubatus* is deeper still. The susentaculum tali has a broad rounded shelf above the astragular facet, similar to that in *A. jubatus* whereas *P. concolor* has a more squared shaped shelf. *Panthera atrox* has a less pronounced shelf above the minor astragular facet. The depth of the calcaneum from the major astragular facet to the plantar border is greater in absolute measurement in the Grand Canyon specimen, *Miracinonyx trumani* and *M. inexpectatus* than in *Puma concolor* or *A. jubatus*. The peroneal tubercle is relatively long, longer than in *Panthera onca* or *Smilodon*, and is similar to that seen in *Puma concolor*, *A. jubatus*, and *Panthera atrox*. The groove for the peroneal tubercle is less developed than *P. concolor* and *P. atrox*. A facet for the navicular is present. This facet is broad and rectangular like that seen in *Miracinonyx* and *Acinonyx*. In *Puma concolor* the facet is usually absent. However, when present, this facet is small and narrow. In *Panthera atrox*, the navicular facet is absent. The facet for the cuboid of the Grand Canyon felid is broad and rounded, similar to that seen in *Panthera atrox*. In *Puma*, the cuboid facet is less broad and rounded. The broad facet for the calcaneal tendon, long and slender shaft of the calcaneum, the depth of the calcaneum, and the length of the peroneal tubercle, the less development of the groove for the peroneal tubercle, broad navicular facet, and rounded cuboid facet all are characters seen in *Miracinonyx*. Size is the only difference between the calcaneum of *M. trumani* and *M. inexpectata*. Both species are identical in morphological characters but *M. inexpectatus* is notably longer than *M. trumani* (Figure 4B).

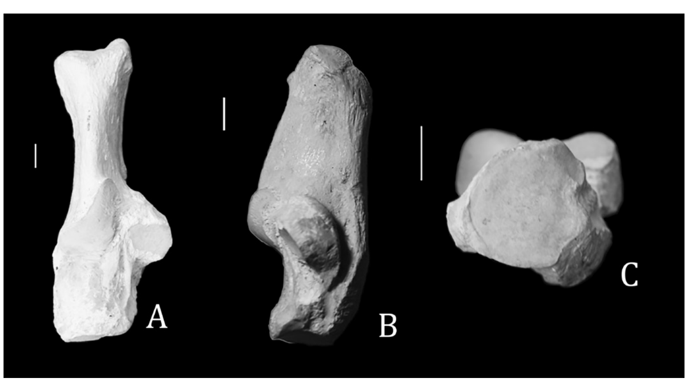


FIGURE 3. GRCA 55756. Right Calcaneum of *Miracinonyx trumani* from Next Door Cave, Grand Canyon. **A**) Proximal view. **B**) Medial view. C) Distal view showing cuboid and navicular facets. Scale 1cm.

Rampart Cave

Wilson (1942) referred the Rampart Cave material to a single individual of *Puma concolor*. We have examined the material from the GRCA and USNM collections and conclude that there are at least two individuals present in the collection; one sub-adult, and one juvenile based on duplication and size variation of cranial (Figure 5A-B), post-cranial remains (Figure 5C-D), and the tooth eruption sequence within the preserved dentition. Possible association between the two individuals is discussed below.

Sub-Adult

Referred Material—GRCA 21734, partial skull rostrum with premaxilla, maxilla, left and right I1-I3, right P2, left and right P3-M1; GRCA 21743, temporal fragment; GRCA 21739, frontal and parietal fragment; GRCA 21736/21738, right lower jaw with i1-i3, alveolus for c1, p3-p4, fragmentary m1; GRCA 21725/21726, thoracic vertebrae 6-13 and lumbar vertebra 1; GRCA 21579/21580, lumbar vertebrae 3 and 4; GRCA 21729,

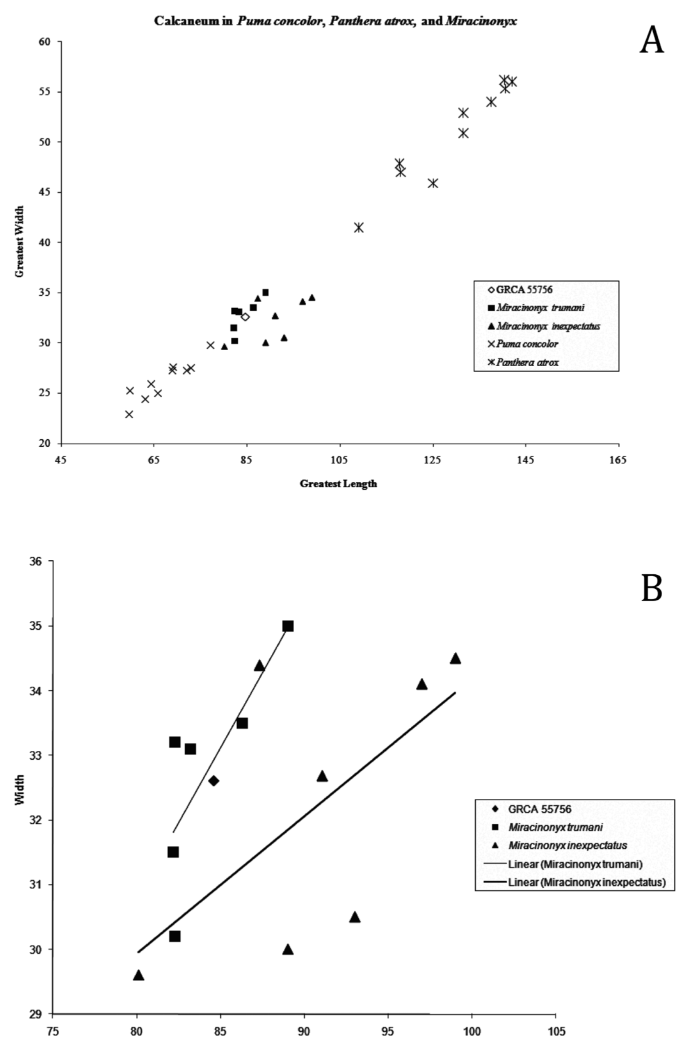


FIGURE 4. Comparative measurements of large Pleistocene felid calcanei. **A**) bi-variate plot of GRCA 55756 with *Miracinonyx trumani, M. inexpectatus*, *Puma concolor*, and *Panthera atrox*. **B**) Comparison bi-variate plot of *Miracinonyx trumani* and *M. inexpectatus*, note GRCA 55756 placing within range of *Miracinonyx trumani*.

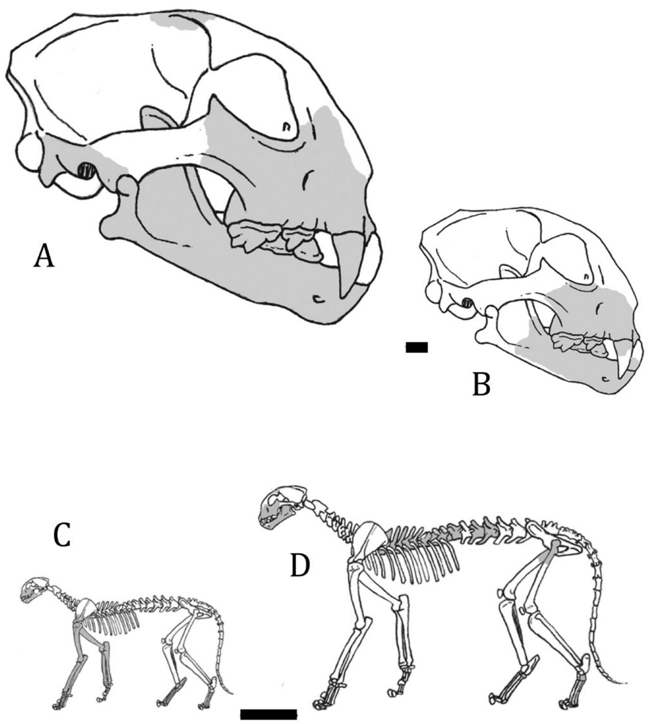


FIGURE 5. Relative size comparison of the skulls and skeletons of *Miracinonyx trumani* from Rampart Cave, preserved portions in gray; **A, D**) sub-adult, **B, C**) juvenile (drawn and modified from Van Valkenburgh et al., 1990 and Turner and Antón, 1997). **A-B**, Scale 1cm; **C-D**, scale approximately 240 cm.

right proximal femur fragment; GRCA 21733, left proximal femur fragment; GRCA 21729, right articulated rear foot with navicular, cuboid, mesocunneiform, ectocuneiform, mt2-mt4; USNM 509143, left navicular.

Description— the sub-adult specimens represent a partial skeleton of a single individual at near full size with its dentition nearly fully erupted. This individual was slightly larger than a large adult male *Puma*.

Skull—The premaxilla, maxilla, a fragment of the right temporal, a fragment of the left frontal and parietal and the right ramus represent the skull (Figure 6); many elements have mummified flesh still attached. The nasal opening is broader than *P. concolor*. The premaxillary bones are partially fused with remnant flesh of the gum around the dentition. The premaxilla does not extend as far out as seen in *P. concolor* and it has a broader dental battery. The diastema between the premaxillary and the maxillary dentition is shorter than in *P. concolor*. The infraorbital foramen is ovate where it is more rounded in *P. concolor*. The palate has part of the flesh of the hard palate still in place (Figure 6). The temporal fragment has the mandibular fossa and postmandibular process and part of the auditory bulla. The postmandibular process does not project quite as ventrally as it does in *P. concolor*.

Upper dentition—all upper teeth are present. The incisors are fully erupted. The I1 and I2 are similar to *P. concolor* but are broader mediolaterally and have more pronounced posterior cusps. The I3 is broader than the I3 of *P. concolor* and has two pronounced medial cusps whereas *P. concolor* has a single medial cusp. The C1 is fully erupted and broad but has a shorter crown height from the gum line than *P. concolor*. There is no diastema between the C1 and P2 as in *P. concolor*. The P2 is fully erupted and is a short robust tooth with a cusp running mediolaterally on the dorsal surface. The P2 of the Grand Canyon felid is larger than the average P2 of *P. concolor*. There is no diastema between the P2 and P3. The P3 is nearly fully erupted and is more robust than in *P. concolor*. The posterior cuspid is not as enlarged as in *P. concolor*. The P4 is nearly fully erupted and is more robust than in *P. concolor*. The Grand Canyon felid has a very prominent parastyle, while the parastyle is more reduced in *P. concolor*. The protocone in the Grand Canyon felid is less developed and broad anteroposteriorly with a more rounded border whereas in *P. concolor* the protocone is narrower, ending in a dull rounded point. The paracone is more robust than in *P. concolor*. There is a deep lateral trench between the paracone and metacone, which is shallower in *P. concolor*. The metacone is more robust than in *P. concolor*. There is some overlap of the P4 of the sub-adult with the largest *P. concolor*, and the smallest adult *Miracinonyx trumani* (Figure 7). The M1 is elongate mediolaterally with two distinct cusps. The M1 of *P. concolor* is a small button-like tooth with a single slight cusp.

Mandible—the horizontal ramus is complete on the right side (Figure 6F-G), while a small portion of the left ramus at the symphysis remains. The symphysis is inclined at a greater angle than in *P. concolor*, giving the anterior jaw a somewhat squared shape like that seen in *Miracinonyx* (Orr 1969). The diastema between the c1 and p3 is reduced whereas it is longer in *P. concolor*. The mental foramen cannot be seen due to the presence of adhering sediment and dried tissue. The coronoid process is gracile and ascends closer to the m1, where it is broader in *P. concolor* and ascends more posteriorly from the m1. The coronoid fossa is not as deep as in *P. concolor*. The condyloid process does not extend out from the coronoid process as far as in *P. concolor*. The angular process is reduced and projects at a downward angle.

Lower dentition—the lower dentition is mostly complete with only the c1 missing. The i1-i2 are fully erupted and similar in size and morphology to those seen in *P. concolor*. The i3 differs from *P. concolor* in being slightly longer anteroposteriorly. The p3 is fully erupted and has a prominent anterior accessory cuspid, with a pronounced and robust primary cusp, and prominent posterior accessory cusp with the posterior medial margin of the tooth broad. In *P. concolor* the p3 has a less pronounced anterior accessory cuspid, a less robust primary cusp, and a less pronounced posterior accessory cupid with the posterior medial margin not as broad as in the Grand Canyon felid. The p4 is nearly fully erupted but is erupting with its anterior margin just under the posterior edge of the p3. The anterior accessory cuspid is very pronounced. The primary cusp is missing the proximal tip and portions of the medial side; however, the tooth is robust with the primary cusp very prominent. The posterior accessory cuspid is pronounced with a broad medial margin with a slight posterior cingulum. In *P. concolor* the anterior accessory cuspid is less pronounced, the primary cusp not as prominent, and the posterior accessory cuspid is not as pronounced with a less pronounced medial margin. The posterior cingulum on the p4 of *P. concolor* is slightly more prominent than in the Grand Canyon felid. The m1 is present in the Grand Canyon felid but is not complete. The m1 is fully erupted and mediolaterally broader than in *P. concolor*. The size of the m1 for *Miracinonyx trumani* and *Puma concolor* overlap considerably, therefore this is not a good character to use to differentiate the two species (Figure 7).

The ontogenetic age at death can be estimated based on the tooth eruption sequence, assuming the eruption sequence is similar to that of *Puma* and *Acinonyx*.

The incisors, canines, P2, and molars fully erupted and the premolars nearly full erupted, giving the approximate age between nine or ten months to a year based on the timing of the tooth eruption sequence in *Puma concolor* (Slaughter et al. 1974) and in *Acinonyx jubatus* (Broom 1949).

Axial skeleton—the vertebral column is represented by an

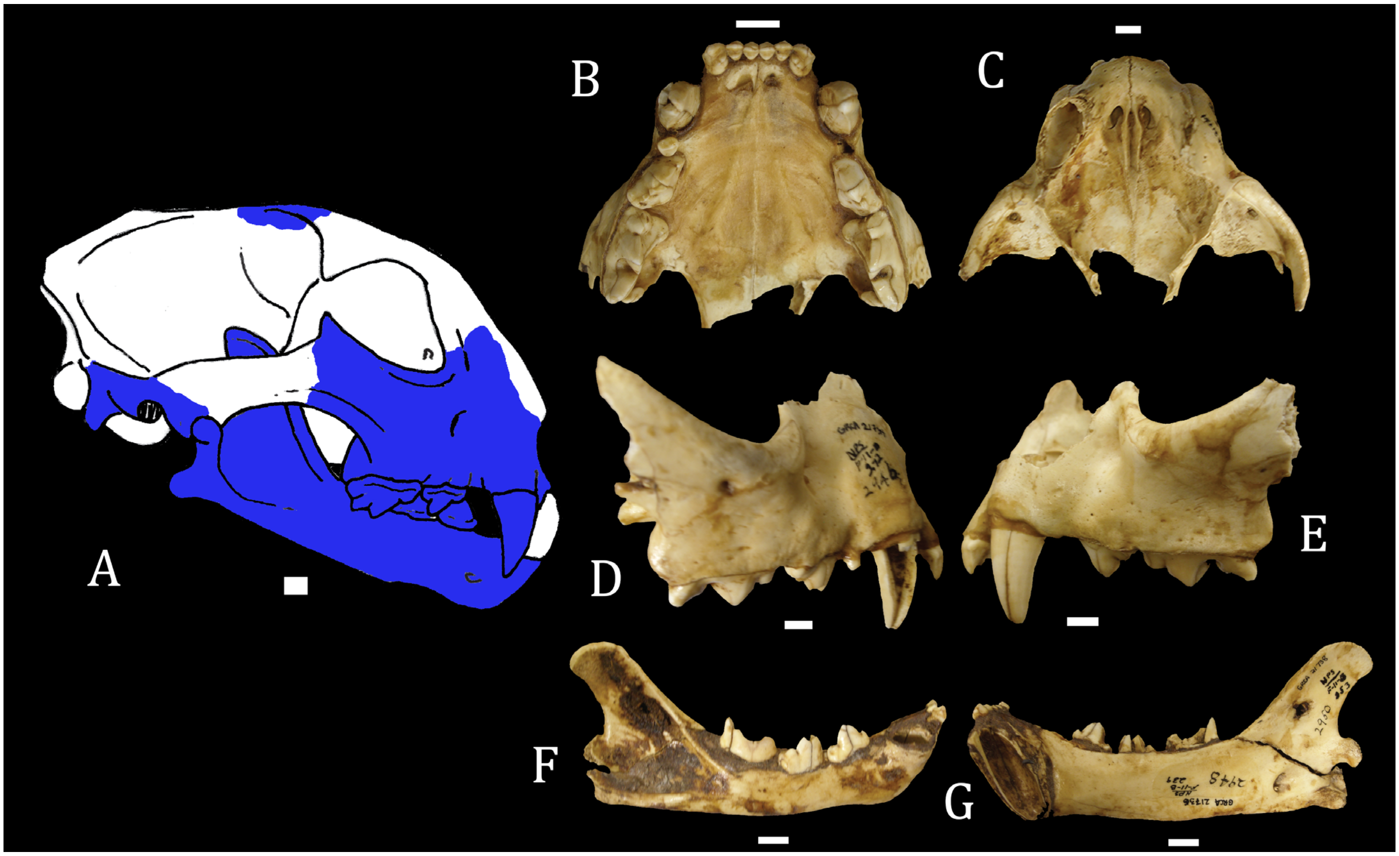


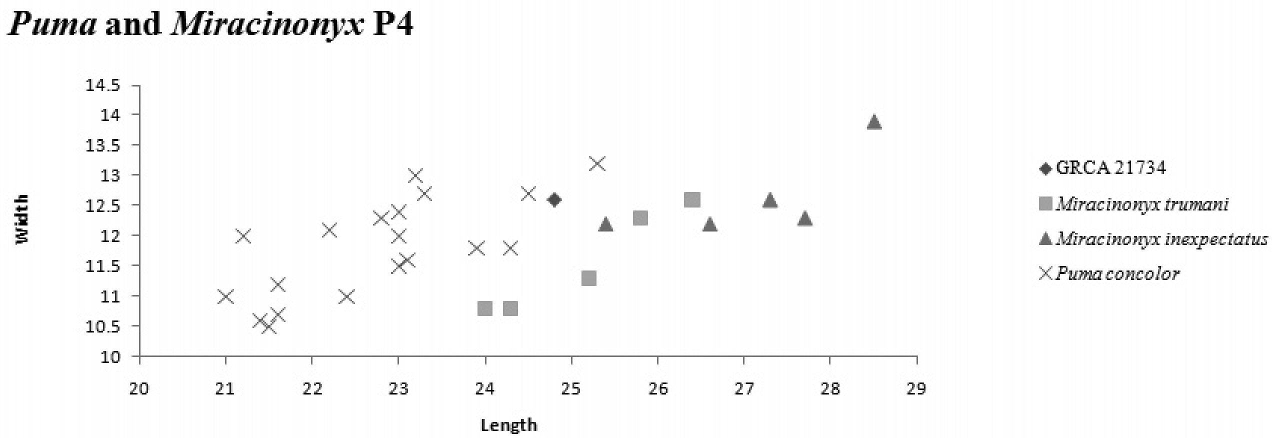
FIGURE 6. Cranial elements and mandible of the sub-adult *Miracinonyx trumani* from Rampart Cave. **A**) Cranial reconstruction of *Miracinonyx trumani* with preserved areas indicated in blue. **B-E**) GRCA 21734, rostrum and palate with dentition. **B**) Oral view, note the close association of the P2 between the C1 and the P3 and preserved hard palate tissues. **C**) Dorsal view. **D**), Right lateral. **E**) Left lateral view. **F-G**) GRCA 21736/21738, right ramus. **F**) Right lateral view. **G**) Medial view. Scale 1 cm.

articulated section of thoracic vertebrae 6 through 13, lumbar vertebra 1 and articulated lumbar vertebrae 3 and 4. There is also an isolated section of lumbar spinal process that may represent lumbar 2. The articulation is due to the presence of dried ligaments and cartilage. Allocation to the sub-adult individual is based on the vertebral column having been collected in close association with the sub adult skull; and the pedicle or radix of the vertebrae being completely fused with only the epiphyses of the centra remaining unfused. In a juvenile individual, the pedicles would not be completely fused to the centra. Lastly, there are a series of pathologies present on the vertebrae that match similar pathologies found on the skull as discussed below.

Pelvic skeleton—the pelvic skeleton is represented by left and right proximal femora, an articulated partial right hind foot, and an isolated left navicular. The right femur fragment is the more complete of the two femur specimens. As compared to *P. concolor* the femoral head is larger and lacks a defined 'hook' that leads into the femoral neck as in *P. concolor*. The trochanteric fossa is shallower in the Grand Canyon cat than in *P. concolor*. The greater trochanter is not as robust as in *P. concolor*. The lesser trochanter is less developed than in *P. concolor*. The mid-shaft of the femur in the Grand Canyon cat shows a slight narrowing compared to that in *P. concolor* which is more or less straight. The articulated right foot (Figure 8) consists of the cuboid, navicular, ectocuneiform, mesocuneiform, and metatarsals II-IV. The bones are partially eroded and gnawed on the posterior surface. The tarsals of the Grand Canyon felid tend to be more elongate compared to the tarsals of *P. concolor*. The proximal ends of the metatarsals are broader mediolaterally compared to those in *P. concolor* and although missing the distal ends, the shafts of the metatarsals are more gracile, elongate, and relatively straighter than seen in *P. concolor*. The isolated left navicular differs from *P. concolor* in having a broader articular surface for the cuboid, a broader articular surface with the mesocuneiform, a more elongate articulation with the ectocuneiform and is overall more elongated proximodistally.

Juvenile

Referred Specimens—USNM 509134, right premaxilla, right maxilla with I2-I3, C1, P2, erupting P3, dP3, fragments of erupting P4; USNM 509132/509133, right lower jaw with portion of left lower jaw with R i1-i3, L i1-i3, fragmentary R c1, R dp3, erupting Rp3, fragmentary Rdp4, fragmentary erupting Rp4, fragmentary Rm1; USNM 509198, distal caudal vertebra; USNM 509264, distal caudal vertebra; USNM 509218, left? clavicle; GRCA 21727, fragment of left scapula; USNM 509184, left humerus, USNM 509216, fragmentary right mid-shaft and distal humerus; USNM 509215, right radius and ulna; GRCA 21723, left radius and ulna; USNM 509202, right articulated metacarpals II-IV; USNM 509270, left metacarpal I; USNM 509265, left metacarpal II; USNM, 509271 left metacarpal III; USNM 509268, left metacarpal IV; USNM 509179, proximal phalanx of manus; USNM 509200, proximal phalanx of manus; USNM 509267, medial phalanx of manus; GRCA 21730, proximal phalanges of manus; USNM 509201, right rear foot with navicular, cuboid, mesocunneiform, ectocunneiform, metatarsals II-V; GRCA 21732, left astragulus and calcaneum; USNM 508998, left navicular; USNM 509000, left cuboid; USNM 508999, left ectocunneiform; USNM 508996, metatarsal III; USNM 508994, metatarsal IV; USNM 508997, metatarsal V; USNM 509269, two proximal phalanges of pes; USNM 509199,



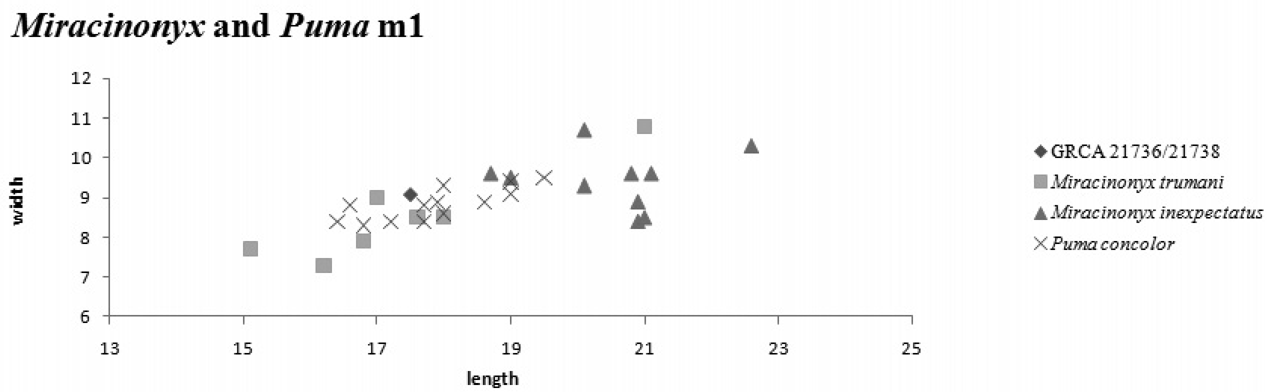


FIGURE 7. Bi-variate plot of the P4 and m1 in *Miracinonyx trumani*, *Miracinonyx inexpectatus,* and *Puma concolor* (data from this study; Kurtén, 1976; Adams, 1977; Van Valkenburgh et al., 1990).

proximal phalanx of pes; USNM 509266, proximal phalanx of pes; USNM 509080, medial phalanx and ungual phalanx with dried flesh.

Description—the juvenile material belongs to one individual and is roughly the size of an average adult *Puma concolor*. Based on the tooth eruption sequence in *Acinonyx* (Broom, 1949) and *Puma* (Kitchener, 1991), the juvenile *Miracinonyx* is estimated to have been 6 months old at the time of death.

Skull—the skull (Figure 9) consists of the right anterior portion of skull including the premaxilla, maxilla, and malar bones. The bone is very delicate and fragile. There is a short diastema between the I3 and the C1. The maxilla has two infraorbital foramina with the lower foramen slightly larger than the upper foramen. There is no diastema between the C1 and P2.

Upper dentition—most of the teeth are broken, with the exception of I3 and P2, which are complete. The I2 is only represented by a fragmentary crown and root. The I3 is as large as in an adult puma, more robust mediolaterally and has a very prominent medial cusp. The C1 is fragmentary, missing much of the crown. The P2 is very robust and larger than in an adult puma. P3 is just starting to erupt under the dP4 (Figure 9C). Its position suggests that it will be very close to the P2 when fully erupted. The dP4 is fragmentary. The protocone of the dP3 is centered medially on the tooth. The protocone narrows anteroposteriorly, with the P3 and P4 erupting just on either side of the protocone. The P4 is erupting and is represented only by a section of the anterior crown with a complete protocone (Figure 9C-D). The protocone of the P4 is broad anteroposteriorly and rounded, much like that seen in the sub-adult from Rampart Cave, the holotype of *M. trumani* from Crypt Cave, Nevada (Orr, 1969), and the *M. trumani* skull from the McKittrick local fauna, California (Shultz, 1938).

Lower jaw—the lower jaw (Figure 9E-F) consists of the symphysis with part of both horizontal rami with left and right i1- i3, fragmentary right and left c1, right fragmentary dp3 and a fragmentary section of the right horizontal ramus with fragmentary dp4, erupting p3-p4, and fragmentary m1. The angle of the mandibular symphysis is relatively steep, more so than that seen in *Puma concolor* and is similar to the sub-adult from Rampart Cave. The diastema between the c1 and dp3 is very short (8.11 mm). The ramus is proportionately deeper than in an adult puma. There are four mental foramina on the lateral anterior portion of the ramus.

Lower dentition—the incisor battery is fully erupted, differing from *P. concolor* in that the i3 is slightly more robust. The c1 is partially erupted and is missing most of the crown. The lower canine is robust as compared to an adult puma. The dp3 is missing the anterior portion of the crown, but two posterior accessory cuspids are intact. The p3 is just starting to erupt under the dp3 and fragments of the roots in the alveoli represent the p4. The m1 is fragmentary but fairly broad and is about the same size as an adult puma and the sub-adult from Rampart Cave.

Axial skeleton—there are two distal caudal vertebrae, with the epiphyses beginning to fuse to the centrum.

Appendicular skeleton—front limb; the front limb is represented by a clavicle, fragment of the left scapula, a complete left humerus (Figure 10 B-C), a fragmentary right humerus, right and left radius and ulna (Figure 10 D-E), right metacarpal II-IV,

FIGURE 8. Right rear foot with navicular, cuboid, mesocuneiform, ectocuneiform, and mtII-IV, GRCA 21729, of the *Miracinonyx trumani* sub-adult from Rampart Cave. Scale 1cm.

left metacarpal I and III-IV. The clavicle is typical of most felids in being long, gracile, and lacking articular facets for the scapula or sternum. The scapula consists of the glenoid and part of the blade. The glenoid fossa is more elongate anteroposteriorly than in *P. concolor*, which is more ovate and wider mediolaterally. The supraglenoid tubercle projects more anteriorly whereas in *P. concolor,* the supraglenoid tubercle angles steeply. The coracoid process is absent in the juvenile Grand Canyon felid, although it is present in *P. concolor*. Both right and left humeri are present; the left humerus being the more complete of the two. The humerus is smaller than an adult puma. The proximal and distal epiphyses are partially fused. The head of the humerus does not project as far posteriorly as in *P. concolor*, nor is it as robust. The greater tuberosity is less prominent than in *P. concolor*. The lesser tuberosity is not as well developed as in *P. concolor*. The bicipital groove is shallower than in *P. concolor*. The deltoid ridge is less developed than in *P. concolor*. The shaft of the humerus is gracile. The medial border for the entepicondylar foramen runs proximodistally center of the shaft whereas in *P. concolor*, this border is inclined more anterior on the shaft. The medial epicondyle is less developed than in *P. concolor*. Both right and left radii and ulnae are present and articulated, held together by dried remnants of the interosseous ligament. The proximal and distal epiphyses on all elements were unfused and are missing. The anterior border of the olecranon is at a sloping angle whereas in *P. concolor* the anterior border is straight. The shafts of both the ulna and radius are more gracile than in *P. concolor*. The manus is represented by right and left metacarpals. The left metacarpal I is more elongate than and not as broad as that in *P. concolor*. The shafts of metacarpal II-IV are straight and gracile whereas in *P. concolor* the shafts are more robust and curved. There is a distinct notch in the medial border of the proximal end of metacarpal III, which is not present in *P. concolor*. The proximal phalanges of the manus are shorter than the proximal phalanges of the pes. The shafts of the phalanges are dorsal-ventrally flattened when compared to the phalanges of *P. concolor*.

The hind limb is represented by the left calcaneum and astragalus (Figure 10F-H), and isolated elements of the left foot which include the navicular, cuboid, ectocuneiform, metatarsals III-V, and articulated right foot (Figure 10I) with navicular, cuboid, ectocuneiform mesocuneiform and metatarsals II-V. The tarsals overall are more elongate proximodistally in than in *P. concolor*. The calcaneum and astragalus are articulated, held together with dried tissue. The calcaneum is roughly the size of an adult puma but differs in having a rounded shelf for the sustentaculum tali like that seen in the Next Door cave felid. Other characters for the calcaneum are obscured by flesh, weathering, and gnawing on the bone. The astragalus is roughly the same size as an adult puma, however much of the bone is heavily weathered and gnawed. The navicular has a broad astragular facet, which is narrower in *P. concolor*. The proximal ends of the metatarsals of the Grand Canyon kitten are broader as compared to *P. concolor*. The shafts of the metatarsals are straight and gracile compared to those in *P. concolor*. The shafts of the proximal phalanges (Figure 10J-K) of the pes are more dorso-ventrally flattened than those in *P. concolor*. A single pedal ungual phalanx is articulated with a medial phalanx (Figure 10L-M). This ungual retains the keratin claw sheath with the fleshy hood still in place. The claw is in the retracted position. The claw is rather long, narrow, and dorso-ventrally slender. In *P. concolor* the claw is more robust, broad, and dorso-ventrally deep. The bony hood of the distal phalanx has been eroded although it was obviously present. Typical of all cats (Bryant et al. 1996) the claws of the pes are less recurved than the claws of the manus, suggesting that this claw is from the pes.

Feline Coprolites

Referred Specimens—USNM 509317, 509323, 509325, 509327, 509328

Multiple feline-like fecal droppings (Figure 11) were collected by the 1942 excavation at a depth between 76.2 cm to 91.4 cm near the entrance of the main chamber and near the juvenile. Droppings are chalky white to light gray, sausage shaped, and tightly packed with some small fragments of hair. Coprolites sampled ranged between 6.4 cm 4.5 cm in length and to 3.5 cm to 2.6 cm in width. The largest and most complete dropping is approximately 7.5 cm long and 3.2 cm wide.

Taphonomic considerations of the Rampart Cave Materials

The *Miracinonyx trumani* body fossils were collected in the western portion of Rampart Cave in two main concentrations (Figure 2). The sub-adult was collected during the 1936 Civilian Conservation Corps excavations of Pit B (Kellogg 1942 "F-11-B") located in a small alcove along the western wall of the cave. Records of this excavation are relatively poor so the placement of the sub-adult is approximate though deep below

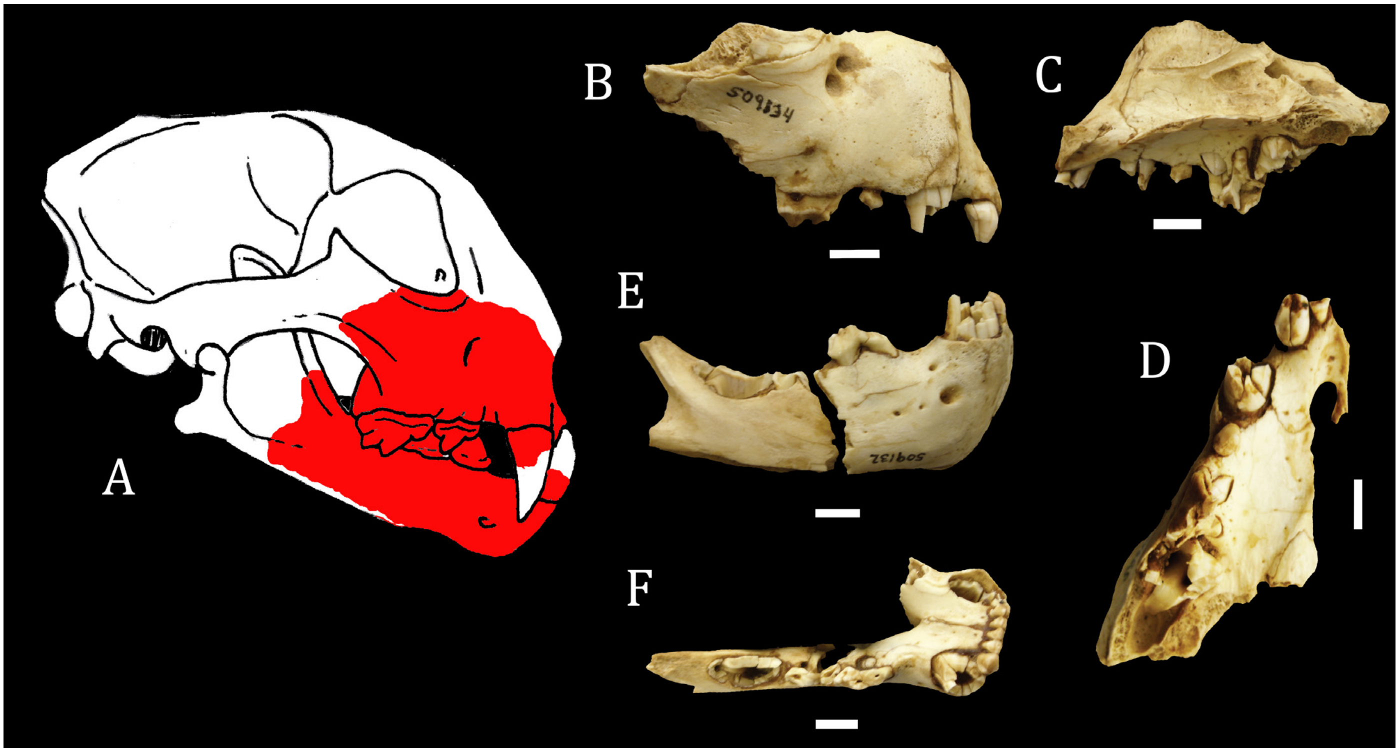


FIGURE 9. Cranial and mandibular elements to the Rampart Cave juvenile *Miracinonyx trumani*. **A**) Cranial reconstruction of *Miracinonyx trumani* with preserved areas indicated in red. **B-D**) USNM 509134. Right rostral and maxillary cheek fragment. **B**) Lateral view. **C**) Medial view showing the erupting P3 and fragment of P4. **D**) Oral view showing broad rounded reduced protocone on P4 fragment. **E-F**) USNM 509132, right lower fragmentary ramus. **E**) Lateral view. **F**) Oral view. Scale 1cm.

the surface dung layer. The 1942 Smithsonian excavations are more precisely documented thanks in part to Kellogg's field-notes and map of the cave. The bulk of the juvenile materials were collected from the 1942 Smithsonian excavation and are concentrated near the north-central wall near the entrance to the northwestern room (figure 2). These materials were collected from the same average depth of "12 to 30 inches" (Kellogg's field notes, 1942) below the surface dung layer. Evidence of association between these two individual felids comes from pit B. In the collection of felid materials made by the 1936 CCC the articulated left calcaneum and astragalus (GRCA 21732) were in amongst the sub-adult materials. The calcaneum and astragalus are too small to fit the articulated foot of the sub-adult and do fit for the juvenile left tarsals collected by the Smithsonian in 1942. Rodents may have been responsible for the postmortem scattering of the juvenile materials. The juvenile calcaneum and astragalus have heavy gnaw marks that were identified as rodent by their sharply defined lateral edges, rather than the rounded gnaw marks left by carnivores.

Examination of the skeletal elements of the sub-adult reveals rounded un-healed punctures roughly 6.75 mm to 3.80 mm in width on the right malar bone (Figure 12A) just above the suture for the maxilla, on the right coronoid process (Figure 12B), the right side of the 12th thoracic spinous process, the left side of 13th thoratic spinous process, the left side of the 1st lumbar vertebra spinous process (Figure 12C), and the right side of the proposed 2nd lumbar spinous process fragment. This series of punctures are all roughly 30 mm apart and rounded. The rounded shape and regular spacing of the punctures on the bone suggests these marks were made by canine teeth. The small round shape and spacing of the punctures suggests that another individual *Miracinonyx* is the most likely candidate to inflict these wounds. Other Pleistocene carnivores such as bears, saber-tooth cats, American lion, wolves, and even *Puma* have too wide of spacing for the canines and most likely would have left larger punctures. Such injuries could have been sustained in mating activities or in conflict over territory or food for *Miracinonyx*, similar to that seen in the behavior of extant pumas (Logan and Sweanor, 2001).

Stanton's Cave

Referred Specimens—GRCA 76271, articulated left medial and distal phalanges; GRCA 76035, left medial phalanx.

Description—The materials of the large felid from Stanton's Cave represent three left medial phalanges and two distal phalanges of the pes (Figure 13), one with a keratin claw sheath in place. The size of the medial phalanges is larger than the medial phalanges of *P. concolor* that were available to us. The shaft of the phalanges is broader than in *P. concolor*. The distal phalanges differ from *P. concolor* in that the dorsal border of the hood is rounder and the plantar process is mediolaterally more compressed than in *P. concolor*. The shape of the keratin claw sheath resembles that of the Rampart Cave kitten but is larger and is more gracile and dorso-ventrally narrower than *P. concolor*. The keratin claws of the distal phalanges of the pes in *Puma* have a greater degree of curvature than the Stanton's Cave felid. The shape of the claw and the characters of the medial and distal phalanges suggest identification as *Miracinonyx trumani*, rather than *P. concolor*.

DISCUSSION AND CONCLUSIONS

The record of *Miracinonyx trumani* within the Grand Canyon is surprising given the usual interpretation of the feeding ecology of this cat. *Miracinonyx* has long been considered a cheetah-like cat, implying a need for open woodlands to savanna-like conditions. The occurrence of the fossil remains of *M. trumani* within the canyon itself raises the possibility that this felid was adapted for a habitat that was composed of closed woodlands and rocky steep surfaces with prey that were adapted to those conditions.

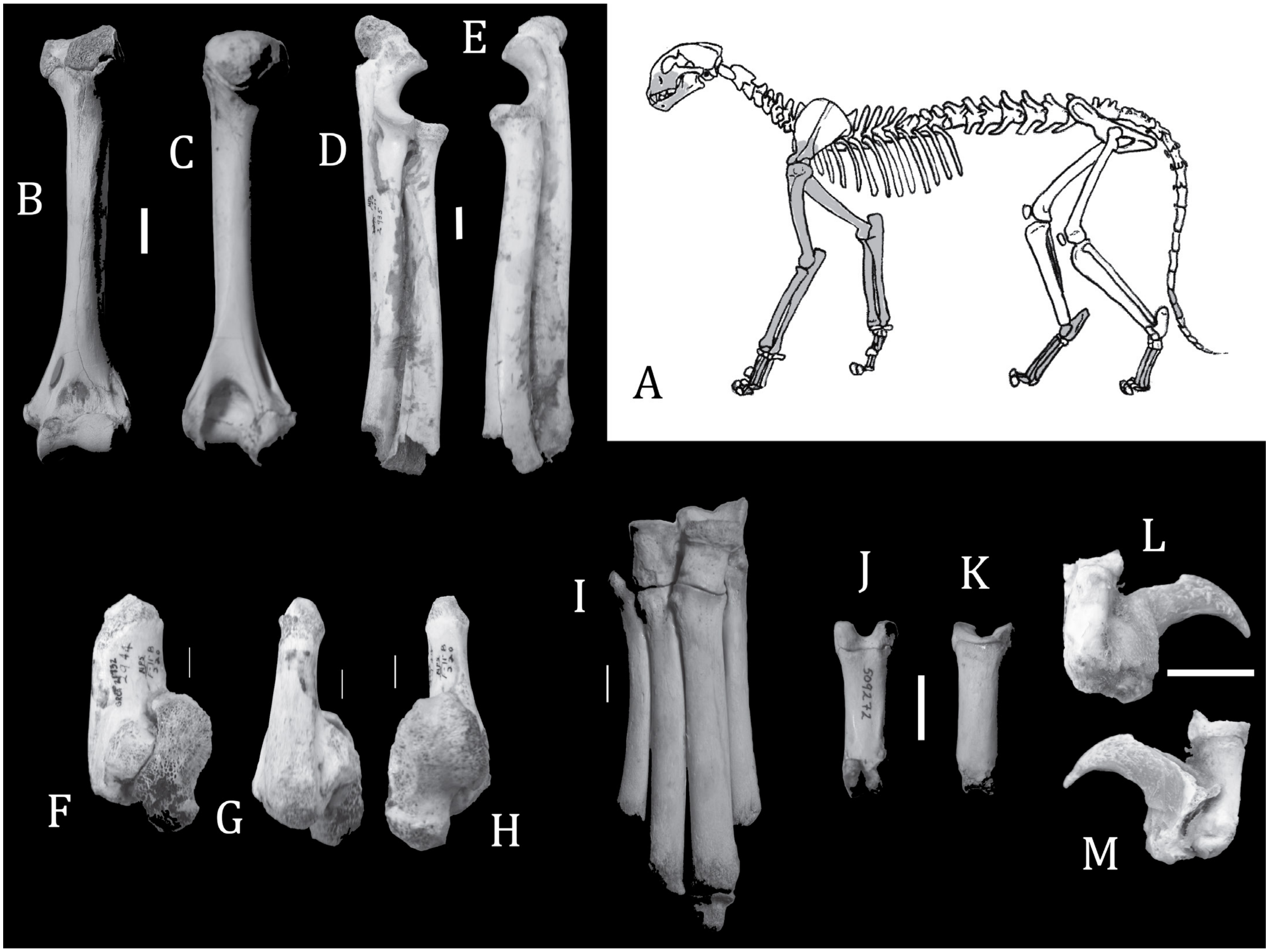


FIGURE 10. Selected postcranial elements of the Rampart Cave juvenile *Miracinonyx trumani*. **A**) Skeleton reconstruction showing the preserved elements in gray. **B-C**) USNM 509184, left complete humerus. **B**) Anterior view. **C**) Posterior view. **D-E**) GRCA 21723, Left radius and ulna. **D**) Medial view. **E**) Lateral view. **F-H**) GRCA 21732, Left calcaneum and astragalus. **F**) Medial view. **G**) Posterior view. **H**) Anterior view. **I**) USNM 509201, right articulated hind foot with navicular, cuboid, ectocuneiform, mesocuneiform, and mt II-V. **J-K**) USNM 509272, proximal pes phalange. **J**) Ventral view. **K**) Dorsal view. **L-M**) USNM 509080, articulated medial and distal phalanx with preserved claw. **L**) Lateral view. **M**) Medial view. Scale 1 cm.

Accumulation

The remains from Stanton's Cave, Next Door Cave, and Rampart Cave all represent occurrence of *Miracinonyx trumani* within the gorge of the Grand Canyon. The occurrence of isolated phalanges at Stanton's Cave is suggestive of two possible scenarios: either the phalanges were brought in as food bones by California condors (*Gymnogyps californianus*) (Emslie, 1987); or the phalanges were brought in by rodents. Though California condors are well known for bringing small bones to nesting sites (Emslie, 1987) and the remains of condors have been found in the cave, Stanton's Cave was easily accessible by predators and would not have been ideal as a condor roost or feeding site. This leaves the latter scenario. Pack rats (*Neotoma*) and ringtails (*Bassariscus astutus*) currently occupy the cave as they did during the last glacial period within the canyon and certainly would have brought in small bones, such as the felid phalanges. Unlike condors, which can have a 150-mile foraging radius, pack rats (Stones and Hayworth, 1968) and ringtails (Trapp, 1978; Mead and Van Devender, 1981) have a shorter and limited foraging radius (100 m for pack rats and 140 ha for ringtails). This suggests the felid phalanges may have been picked up within a close proximity to Stanton's Cave.

The Next Door Cave calcaneum was collected on the surface of a cave which has not been excavated. Though it is possible the calcaneum was brought in by a condor or pack rat, the lack of rodent gnaw marks or erosion from stomach acids from condor regurgitate suggests this bone was collected in situ and more of this individual cat could be in the cave.

Rampart Cave has the largest sample of *Miracinonyx trumani* materials from the Grand Canyon. The occurrence of large felid feces does strongly suggest occupation of Rampart Cave by *Miracinonyx trumani* for at least a short period of time. Stratigraphically, the occurrence of *M. trumani* at Rampart was in "unit B" of Long and Martin (1974) during the deposition of which there was little to no occupation of by the ground sloth *Nothrotheriops shastensis*. The lack of *Nothrotheriops* in "unit B" was suggested to have been due to the full Glacial environment that would not been favorable for the Shasta ground sloth. Alternatively, if *Miracinonyx* moved into the cave, the presence of a large carnivore might have kept *Nothrotheriops* out of the cave during the deposition of Unit B. The use of Rampart Cave as a denning site for *Miracinonyx* may also explain the large number of bovid (*Oreamnos* and *Ovis*) remains within this unit.

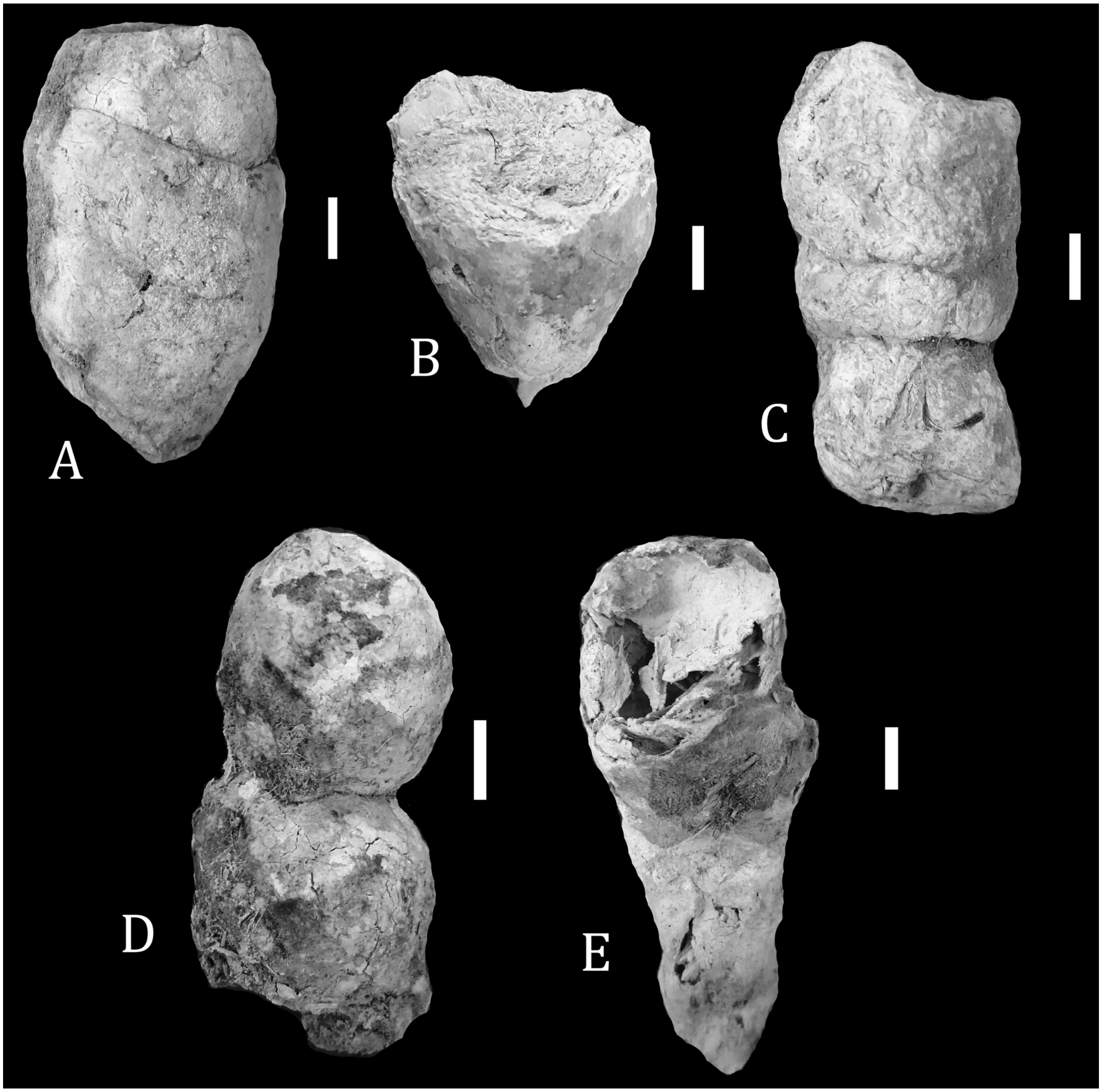


FIGURE 11. Large felid feces pertaining here to *Miracinonyx trumani* from Rampart Cave. **A**) USNM 509312. **B**) USNM 509323. **C**) 509325. **D**) 509327. **E**) 509328. Scale 1cm.

The possible association of the two individual cats in Rampart Cave remains problematic. The calcaneum and astragalus of the juvenile were found during the excavation of "pit B" along with the remains of the sub-adult. Though the juvenile skeleton was scattered, most of it was found along the northern wall of Rampart Cave. The sub-adult skeleton was concentrated in the area of "pit B" along the southern end of the western wall of the cave. The presence of rodent gnaw marks on the calcaneum and astragalus of the juvenile suggests that rodents may have moved those elements. Since both felids were collected at roughly the same stratigraphic interval and there is some mixing of elements it is assumed that both individuals died within a short period of time. Rodents, such as *Neotoma*, could have dragged the astragalus and calcaneum of the juvenile in amongst the sub-adult remains, which also show gnawing on some of the elements (metatarsals and femur).

The cause of death of the juvenile is difficult to determine. The scattering of the remains by rodents could have taken place any time after the death of the animal. There is no sign of wounds on the bones to suggest a violent struggle or lesions which might suggest a crippling disease.

The cause of death for the sub-adult may be easier to assess. As noted above, the sub-adult has puncture marks on the skull, the lower jaw, and along the vertebral column roughly 6.75 mm to 3.80 mm in width and 30 mm apart were most likely made by another adult or subadult *Miracinonyx*. Violent attacks for intraspecific competition are not uncommon in large felids (Sunquist and Sunquist, 2002), and are well documented in *Puma concolor* of the North American southwest (Logan and Sweanor, 2001). In *Acinonyx jubatus*, violent interactions between cheetah individuals are reported to be rare (Caro, 1994; Sunquist and Sunquist, 2002).

Revised Feeding Ecology of *Miracinonyx*

With *Miracinonyx trumani* now established to have been present in the Rancholabrean of the Grand Canyon, the

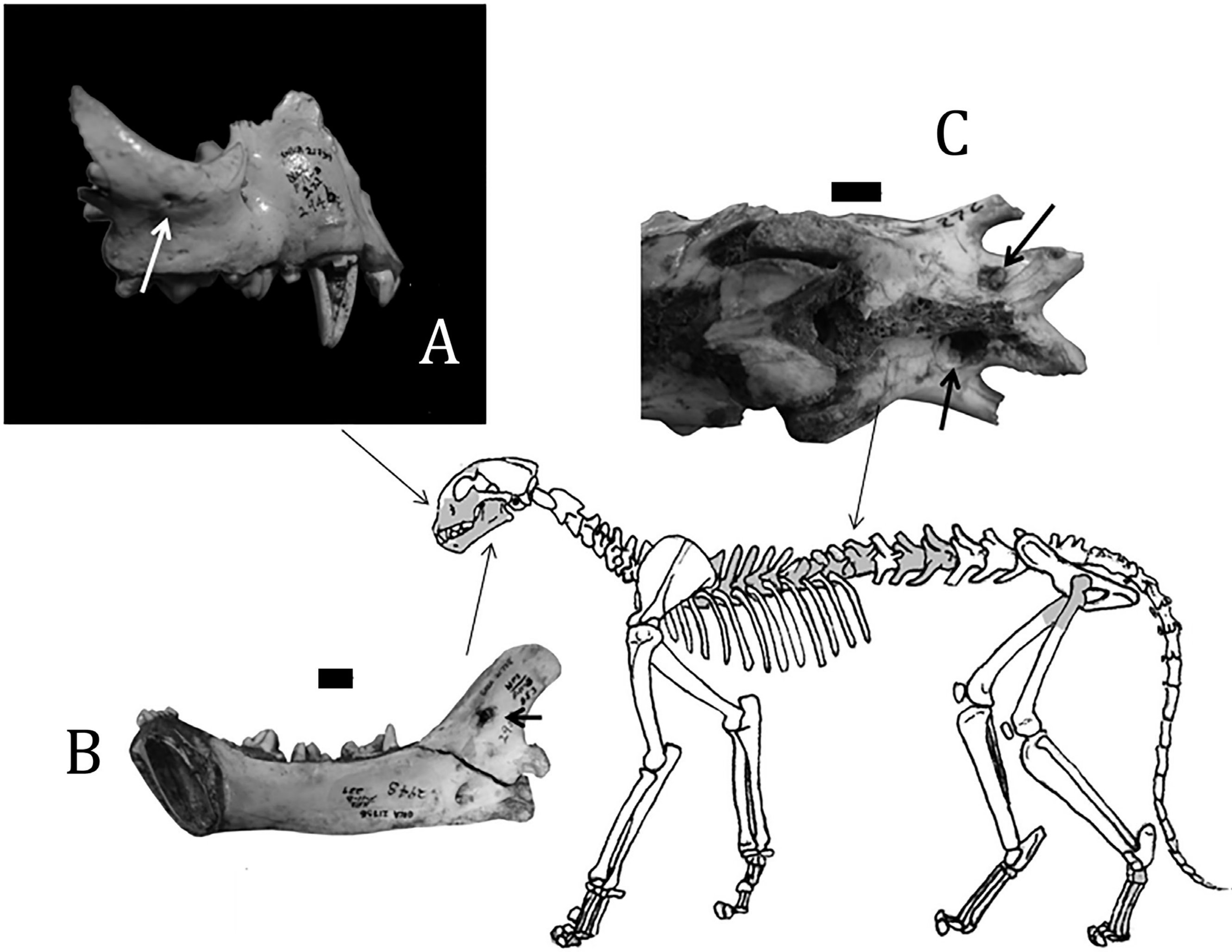


FIGURE 12. Elements showing tooth puncture marks on the sub-adult *Miracinonyx trumani* from Rampart Cave and their relative position on the skeleton. **A**) Puncture on the right malar bone of the skull. **B**) Medial view of right lower jaw with puncture in the coronoid process. **C**) Two punctures on the dorsal surface on the first lumbar vertebra. Scale 1cm.

feeding ecology of this animal is open to question. Previously, researchers have considered *Miracinonyx* analogous to the extant cheetah *Acinonyx jubatus*; a swift moving pursuit predator with a preference for small antelope-like ungulates (Martin et al., 1977; Adams, 1979; Turner and Antón, 1997). It has even been considered that *Miracinonyx* may have influenced the evolution of the American pronghorn, *Antilocapra americana*, which is one of the fastest ungulates on the planet (Byers, 1997), although these facile "evolutionary arms race" scenarios have been questioned (Janis and Wilhem, 1993). To determine the nature of the feeding ecology for the Grand Canyon population of *Miracinonyx trumani,* we review felids with a similar morphology and their feeding ecologies below.

Acinonyx jubatus—the living cheetah (*Acinonyx jubatus)* occurs in savannas, open woodlands, and desert grasslands of sub-Saharan and southern Africa and in small populations in the uplands of the Middle East (Sunquist and Sunquist, 2002; Krausman and Morales, 2005; Nowak, 2005; Farhadinia and Hemami, 2010).The cheetah is small headed and has long limbs, a deep chest, a gracile body build with a long tail, and semi-retractile claws (Caro, 1994). In much of its modern range the African cheetah prefers open habitats rather than higher rocky habitats (Sunquist and Sunquist, 2002; Krausman and Morales, 2005). However, the African *A. jubatus* is not restricted as a savanna specialist and can range into thick woodlands as well (Bissett and Bernard, 2007). Prey of the African *A. jubatus* is primarily ungulates weighing from 20 to50 kg, averaging around 40 kg (Sunquist and Sunquist, 2002). Species include impala, gazelle, and other small to medium sized bovids known to inhabit open habitats (Caro, 1994; Sunquist and Sunquist, 2002). New research on the feeding ecology of the Asiatic cheetah (*Acinonyx jubatus venaticus*) from Iran shows a different picture compared to the African species habits. Farhadinia and Hemami (2010) have shown that the Asiatic subspecies of cheetah from the Dare-Anjir Wildlife Refuge in Iran prey rarely on Jeebers gazelle (*Gazella bennettii*) while wild sheep (*Ovis orientalis*) and Persian ibex (*Capra aegagrus*) are the most commonly taken. This prey difference is seen in the occurrence of the Iranian population living in mountainous terrain and foothill areas and other Asiatic cheetahs living in dry steppe habitats with cold winters (Farhadinia and Hemami, 2010; Hemami et al., 2018).

Puma concolor—the puma occupies a greater diversity of habitats than any other modern felid; it has the largest north-south range of any mammal (Nowak, 2005) This small headed, long tailed, robustly built felid with retractable claws is known

FIGURE 13. Pes phalanges of *Miracinonyx trumani* from Stanton's Cave. **A-D**) GRCA 7627, two articulated medial and distal phalanges. **A-B**) phalanges in extended position. **A**) Lateral view. **B**) Medial view. **C-D**) Medial and distal phalanges in retracted position, **C**) medial, **D**) lateral. **E-F**) GRCA 76035, left medial phalanx, **E**) ventral, **F**) dorsal. Scale 1cm.

to occur in high uplands and mountains of North America and South America, conifer forests and temperate woodlands of North America, desert woodlands of the American Southwest, and dry and wet tropical forests of Central and South America (Currier, 1983; Sunquist and Sunquist, 2002; Nowak, 2005). In the American Southwest, the puma inhabits the desert uplands and mountain "islands" of deciduous woodlands and conifer forests (Logan and Sweanor, 2001). Prey preferences for populations of puma vary based on its geographic location and latitude (Sunquist and Sunquist, 2002). In Central and South America, for example, prey includes large marsh deer, medium sized deer, rodents, armadillos, peccaries, capybaras, domestic horses and cattle and some marsupial species (Kitchener, 1991; Sunquist and Sunquist, 2002). In the most southern part of its range of Argentina, *P. concolor* regularly takes guanacos and hares (Sunquist and Sunquist, 2002). Deer tend to be the preferred prey for North American *P. concolor,* where cervids (deer, elk, and moose) make up roughly eighty percent of their diet (Kitchener, 1991; Logan and Sweanor, 2001; Sunquist and Sunquist, 2002). Other ungulates such as big horn sheep (*Ovis canadensis*) and mountain goat (*Oreamos americana*) are rare in the diet (Logan and Sweanor, 2001; Sunquist and Sunquist, 2002). Pronghorns are occasionally taken by *Puma* only if the terrain is suitable for stealthy attack (Ockenfels, 1994).

Uncia uncia— the snow leopard is an enigmatic pantherine felid from the highlands and mountainous regions of central and eastern Asia. The snow leopard appears externally as a stocky large cat that creeps low to the ground (Sunquist and Sunquist, 2002). Structurally, however, the snow leopard has a skeletal morphology similar to *Acinonyx* (Turner and Antón, 1997), having a smaller short faced domed skull (relative to other *Panthera* species that have larger longer skulls), long gracile limbs, gracile body form, and a longer tail in proportion to the body length than seen in other *Panthera* species (Turner and Antón, 1997; Sunquist and Sunquist, 2002). *Uncia uncia* lives in high altitude mountainous and rocky canyon habitats that can have vertical slopes of 40° or more (Sunquist and Sunquist, 2002). Favored prey species for the snow leopard tend to be wild sheep and goats, particularly the blue sheep (*Pseudois nayaur*), Himalayan tahr (*Hemitragus jemlahicus*), and ibex (*Capra* sp.) (Kitchener, 1991; Sunquist and Sunquist, 2002). Other prey includes musk deer, wild pigs, gazelles, and small game such as marmots, pikas, hares, rabbits, and ground nesting birds (Sunquist and Sunquist, 2002). Snow leopards are observed stalking prey within rocky slopes until within striking distance and then chasing prey 100 yards or more over steep slopes and rocky terrain (Sunquist and Sunquist, 2002).

New Feeding Model?

Taking into consideration the Grand Canyon sample of *Miracinonyx trumani*, we question the notion that the Rancholabrean *Miracinonyx* was strictly African cheetah-like in its habits. The locations of the fossils from the Grand Canyon, as discussed above, are from relatively steep rocky sloped areas with little access to open habitats. Next Door Cave is located above the Tonto Platform with access to the Inner Gorge river corridor of the Colorado River and had a steep talus and cliff access to the rims above. An exception to this habitat type is the Rampart Cave fauna. The Rampart Cave fauna is located near the western end of the canyon and would have had access to a relatively wide river valley at the opening of the canyon where the present Lake Mead is located today (Carpenter, 2003). Access to Rampart Cave was not as steep as is the case in the other two caves. Much of the upper rim of the Grand Canyon during the last full glacial event (25,000 BP to 12,000 BP) was covered by a mixed conifer forest and an open mixed juniper-conifer-single-leaf-ash woodland for the Inner Gorge (Cole, 1982). These habitats on the upper rim and lower gorge are not the open savanna-woodland where one would expect a cheetah-like cat to occur. Instead these are the kind of habitats for a felid like *Puma* and are similar to, though warmer and drier than, the broken vegetation and scrubby woodlands where snow leopards occur.

Miracinonyx of the Rancholabrean

All known occurrences of *Miracinonyx* from the Rancholabrean pertain to *M. trumani*. *Miracinonyx trumani* has been reported from 9 localities outside of Arizona (Figure 1, Table 1). Two localities in Florida have produced *M. trumani*, Lecanto 2A in Citrus County and the underwater Cardinale site 24 km west of St. Petersburg, Pinellas County (Morgan and Seymour 1997). A right metacarpal II, metacarpal III, and metacarpal V from Lecanto were allocated by Morgan and Seymour (1997) to '*Miracinonyx cf. M. inexpectatus*'. The morphological similarity of the metacarpals of *M. inexpectatus* and *M. trumani* makes it difficult to distinguish between the two species. However, the Rancholabrean age of the site would strongly suggest allocation to *M. trumani*. A partial right radius collected at the Cardinale site was given a Rancholabrean age and assigned to '*Miracinonyx* sp.' (Morgan and Seymour 1997).

Slaughter (1966) described a third right metatarsal that he assigned to '*Felis* cf. *F. inexpectata'* from the Rancholabrean Moore Pit Local fauna from outside near Dallas, Texas. His identification was based largely on the size of the specimen, which is intermediate between *Puma concolor* and *Panthera atrox*. He compared it to a *Miracinonyx inexpectatus* metatarsal from Cumberland Cave (Gidley and Gazin 1938) as described by Simpson (1941). The Rancholabrean age of the Moore Pit Local Fauna and the size of the specimen would suggest the Texas *Miracinonyx* be assigned to *M. trumani.*

In Wyoming, two localities are known with the remains of *M. trumani*. The most prolific collection of *M. trumani* was obtained from the Natural Trap Cave local fauna in Little Big Horn County (Martin et al. 1977; Adams, 1977, 1979). The Natural Trap Cave is a karst sinkhole breeched cave chamber that acted as a natural trap resulting in an accumulation of large number of Rancholabrean vertebrates (Martin and Gilbert 1978). Of these vertebrates, multiple partial skeletons of *M. trumani*, including a juvenile cat, were collected and this sample allowed for a more detailed description of the Rancholabrean *Miracinonyx* (Adams 1977 and 1979). Additionally, a fragmentary pelvis of *M. trumani* was collected from Little Canyon Creek Cave in Washakie County (Walker, 1987).

Colorado has a single record of *Miracinonyx* from the Rancholabrean Haystack Cave in Gunnison County (Emslie 1986). This single record is based on a right medial phalanx which Emslie (1986) assigned to '*cf. Acinonyx* (*Miracinonyx*) *trumani*' due to its larger size as compared to *Puma concolor* and similarity in size to phalanges of *M. trumani* from Natural Trap Cave. As discussed below, size is an appropriate character to use in distinguishing between *M. trumani* and *P. concolor* though there may be some overlap between the two species. However, further characters of the medial phalanx should be determined for distinguishing between these two felids (see description of Stanton's Cave materials).

Logan (1981) briefly mentions without identifying the skeletal elements, the occurrence of *M. trumani* (as '*Acinonyx trumani*') from Muskox Cave local fauna in Eddy County New Mexico. Muskox Cave is located in the Guadalupe Mountains and was once a spruce-fir forest with grassy glades and meadows (Logan, 1981). The holotype for *M. trumani*, originally described as *Felis trumani*, was collected from Crypt Cave in Pershing County, Nevada (Orr 1969). The holotype consists of a complete skull and mandible and a partial post-cranial skeleton consisting of portions of the axial skeleton and a scapula (Orr 1969).

The records from California are based on re-examining published photos and descriptions of Rancholabrean felids referred to as *Puma concolor*. In examining the published descriptions and illustrations we found that *Miracinonyx trumani* occurred at two Rancholabrean sites, the McKittrick tar seeps and Rancho La Brea. The specimen from McKittrick was mentioned by Merriam and Stock (1932) and described in further detail with figures by Schultz (1938) as the skull of "*Felis daggetti*". The specimen consists of a partial skull, UCMP 29524, with complete dentition. Though described as being distorted, the photo for the skull (Schultz 1938, plate 4, figure 1) shows the skull is more dorsally domed than *Puma concolor* and with a shorter sagittal crest, whereas in *P. concolor* the sagittal crest is longer. When compared to the holotype of *M. trumani* from Crypt Cave, the cranial characters and proportions of the McKittrick skull are identical to the *M. trumani* holotype (figure). Schultz (1938), citing Merriam and Stock (1932), that the dentition "is exceptionally heavy, nearly all tooth dimensions being in excess of those of the type of *Felis bituminosa* (*Puma concolor*)". The heavy proportions of the dentition are a strong character for *Miracinonyx*. Additionally, the incisor battery is broader than *P. concolor*, the canines are broad but have a shorter length from the gum line, there is no diastema between C1 and P2, the P2 is proportionally larger than *P. concolor*, and the P4 has a reduced rounded protocone; all characters seen in *Miracinonyx* and not *Puma*. The holotype of *Felis daggetti* from Rancho La Brea was described by Merriam (1918) as a puma-like felid with "unusual massiveness of the cheek-teeth and of the jaw, by unusual width of the angle of the mandible, and by the unusual backward curve or sweep of the coronoid process as compared to recent pumas". In addition, the ramus has a short diastema between the c1 and the p3 that is shorter than *Puma concolor*, as well as a steep angle for the mandibular symphysis. Merriam and Stock (1932) described a partial humerus and complete femur that they assigned to *Felis daggetti*. The left humerus was described but not figured and is lacking the proximal epiphysis. Merriam and Stock (1932) noted the humerus is more similar to *P. concolor* than to *Panthera onca*. A complete right femur was described as belonging to *Felis daggetti* and differing from *Puma concolor* (described as "*Felis bituminosa*") in its larger and more robust size, shallower trochantric fossa, narrowing of the lateral wall formed by the greater trochanter, heavier and wider shaft, and broader patellar surface (Merriam and Stock, 1932, Adams, 1977). Jefferson (1983) has argued that the femur (LACM HC X-8848) is that of *Panthera onca*, based on size alone. Adams (1977) noted that the La Brea femur shares with *Miracinonyx trumani* the shallow trochanteric fossa, the narrowing of the lateral wall of the greater trochanter, and less developed lesser trochanter but does differ from typical *M. trumani* specimens in its heavier and wider shaft and broader patellar surface.

The relatively steep angle of the mandibular symphysis, the short diastema between the c1 and p3, the heavy dentition with a short robust canine, and the backward sweep of the coronoid process strongly suggest that the holotype mandible for *Felis daggetti* is *Miracinonyx* and not an individual variation of *Puma concolor* as suggested by Simpson (1941) and Kurtén (1976). The femur from Rancho La Brea has a shallow trochantric fossa and the narrowing of the lateral wall formed by the greater trochanter are both strong characters for *Miracinonyx.* The size of the ramus and femur are more comparable to the Blancan and Irvingtonian *M. inexpectatus* than to the average

Rancholabrean *M. trumani*. However, the robust nature of the shaft of the femur and the distal femur characters need further investigation before it can be firmly placed in *Miracinonyx* or *Panthera onca*. The unusually large size of the ramus can only be argued as an individual character trait and we suggest the *Felis daggetti* holotype mandible be assigned to *M. trumani*. A humerus (LACMRLP R11704) and radius (LACMRLP R54033) referred to by O'Keefe et al. (2009) may belong to *Miracinonyx trumani* (see discussion). A more intensive review of the post-cranial remains of the puma and jaguar materials at Rancho La Brea is needed to positively identify them.

Comparison of Grand Canyon fauna with Natural Trap Cave fauna, Wyoming

The Natural Trap Cave sample of *Miracinonyx trumani* is found in a plateau-like location in the Bighorn Mountains of northern Wyoming at an elevation of 4,560 feet (Martin and Gilbert, 1978). The ancient environment in the vicinity of Natural Trap Cave is interpreted as alpine meadow parkland with surrounding conifer forests based on the occurrence of alpine rodents and lagomorphs (Martin and Gilbert, 1978). The mammalian fauna for Natural Trap Cave has long been interpreted as being dominated by cursorial mammals such as horse, bighorn sheep, pronghorn, wolf, and the cheetah-like cat (Martin and Gilbert, 1978; Wang and Martin, 1993). *Ovis* (bighorn sheep) and *Bootherium* (extinct woodland muskox) are ungulates that are known from upland habitats, and the extant *Antilocapra* is known to occur in open uplands. Of the ungulates from Natural Trap Cave, *Equus* is the most common representing 36.6% of the fauna (Wang and Martin, 1993). Of the three species of equine recognized from Natural Trap Cave, the most common belonged to *Haringtonhippus francisci*, a wild ass-like equine with a distinct lineage (Martin and Gilbert, 1978; Heintzman et al., 2017). If *Haringtonhippus* was similar to extant hemionine horses like the kiang, African wild ass, and the onager, it may have preferred dry upland habitats that would have been present at Natural Trap Cave and the Grand Canyon during the Rancholabrean. Fossils of an ass-like horse have been recovered from along the length of the Grand Canyon (Mead, 1981; Carpenter, 2003). The sample of big horn sheep (*Ovis canadensis catclawensis*) from Natural Trap Cave shows that this extinct subspecies was notably heavier than the modern living subspecies (Wang, 1988) and probably occurred in the uplands of the Bighorn Mountains. Fossils of bighorn sheep are the second most common ungulate (after the mountain goat) at the Grand Canyon and the second most common ungulate at Natural Trap Cave (20.7%; Wang and Martin, 1993). The strong presence of *Miracinonyx* at Natural Trap Cave and the large number of ungulates with preference for upland habitats suggest that upland and canyon lands were perhaps the preferred habitat for *Miracinonyx trumani* for the Rancholabrean of North America. Dunn et al. (2019) recently demonstrated that the scapholunar of the *M. trumani* from Natural Trap Cave had a morphology less like those seen in extant African cheetahs, which is more canid-like for cursorial running, and more of a pantherine-like morphology that allowed for grappling of prey.

Notes on the Rancholabrean *Puma* record

The lack of *Puma* fossils during the latest Pleistocene of the Grand Canyon does correspond to recent ideas of the distribution of ancient *Puma* into North America. Analysis of the genomic history of both North and South American pumas by Culver et al. (2000) shows that the modern populations of *Puma concolor* did not arrive in North America until 10,000 to 12,000 BP. O'Keefe et al. (2009) dated two elements (a radius and humerus) identified as *Puma concolor* from Rancho La Brea Pit 91 between 26,150 BP and 28,650 BP. We examined these specimens based on photographs (Chris Shaw and Aisling Farrell, Pers. Com., 2010). The humerus (LACMRLP R11704) is from an adult large felid and has less defined muscle scarring than seen in adult *Puma concolor*, the distal end of the humerus is mediolaterally compressed, and the medial and lateral epicondyles is less developed as seen modern *P. concolor* which has the heavy rugosities for the insertion of the muscles of the manus lacking in the Rancho La Brea humerus. These traits strongly suggest that LACMRLP R11704 is *Miracinonyx trumani*. The radius (LACMRLP R54033) has a shaft that is also as expanded mediolaterally as seen in *Puma concolor* and there is less development of the muscle scarring typically seen in *Puma*. This suggests that this radius is *Miracinonyx trumani*. *Puma* does occur at Rancho La Brea based on cranial materials described by Merriam and Stock (1932). The skulls and mandibles of the reported *Puma* have not been directly dated so it is difficult to say if they fit within the parameters of Culver et al. (2000). There is the possibility that another extinct species of *Puma* occurring at Rancho La Brea and elsewhere in North America before the entry of the modern *Puma concolor* at the end of the Pleistocene. However, more work would be needed to determine the age and correct species designation for the Rancho La Brea *Puma* cranium.

Simpson (1941) was the first to review the known materials of fossil pumas of North America. Before the recognition of *Miracinonyx* (Adams, 1979), Simpson (1941) included "*Felis*" *inexpectatus* within *Puma* and included many other non-*Panthera* Pleistocene large cats into "*Felis*" *inexpectatus* or "*Felis*" (*Puma*) *concolor*. Kurtén (1976) followed Simpson's (1941) classification and considered "*Felis*" *inexpectatus* to be a species of *Puma*. Kurtén (1976) regarded the Rampart Cave large cat materials as *Puma concolor* but gave no indication that he ever viewed these materials. Also, it seems that Kurtén in his review of fossil *Puma* (1976) was unaware of Orr's (1969) description of *Felis trumani* (Kurtén and Anderson, 1980; Van Valkenburgh, et al., 1990). In light of this review of the Grand Canyon materials it is necessary to review the known fossils of *Puma* and puma-like cats to gain a better understanding of the diversity of the large non-*Panthera* felids of the Pleistocene of North America. It is possible that both Simpson and Kurtén overlooked the significance of some of the gracile traits in their "*Puma concolor*" samples. Kurtén (1976) stated the San Josecito Cave (Mexico) sample of *Puma* is one of the largest in North America but discussed how the sample varied in having longer limb proportions than modern *Puma*. It is possible that some of the *Puma* fossils from San Josecito Cave are *Miracinonyx*. Other *Puma* fossils from the North American Rancholabrean could be *Miracinonyx* as well.

The fossil evidence from the Grand Canyon shows that *Miracinonyx trumani* occurred in unexpected habitats and was not restricted to savanna-like conditions that are usually suggested for this taxon. The Grand Canyon fossils (and perhaps those from Natural Trap Cave) show that this felid was adapted to dry uplands and rocky canyons. To survive in these kinds of conditions *M. trumani* must have been able to traverse the steep canyon slopes to hunt fleet footed canyon-adapted ungulates and other canyon prey. The modern felids most closely fitting this kind of present-day ecology are the snow leopard (*Uncia uncia*) and the Asiatic Cheetah (*Acinonyx jubatus venaticus*). The snow leopard has additional adaptations for colder snow covered climates (Sunquist and Sunquist, 2002), but is a gracile, long limbed and tailed, small-headed large felid that hunts canyon and mountainous ungulates (Sunquist and Sunquist, 2002). The Asiatic cheetah occurs in mountainous habitats and feeds on upland ungulates (Farhadinia and Hemami, 2010). Ungulates like *Oreamos harringtoni* and *Ovis canadenensis* were the most common prey species in the Grand Canyon area during the Rancholabrean. *M. trumani* likely exploited these potential prey species.

The Rancholabrean *Miracinonyx trumani* occurred from the Gulf Coast of Florida (Morgan and Seymour, 1997) to near the Pacific coast of southern California at Rancho La Brea (this study). *M. trumani* lived in upland Alpine parklands of Wyoming (Martin and Gilbert, 1978) to the arid southwest canyon lands of northern Arizona and southern New Mexico. We suggest that *M. trumani* was better adapted at upland habitats (where fossils of *M. trumani* are more common) but would have traversed habitats in the lower valleys which could explain why, though rare, *M. trumani* fossils do occur in valley deposits and tar seeps. *Miracinonyx trumani* was perhaps one of the most multi-habitat adapted felids to have occurred during the Rancholabrean of North America, capable of preying on upland ungulates and swift footed open grassland specialists like the American pronghorn.

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APPENDIX

TABLE 1. Rancholabrean localities for *Miracinonyx trumani* (see Figure 1)

Florida

1) Lecanto 2A Citrus County (Morgan and Seymour, 1997)
2) Cardinale 2A, Gulf of Mexico, Pinellas County (Morgan and Seymour, 1997)

Texas

3) Moore Pit Local Fauna, Dallas County (Slaughter, 1966)

Wyoming

4) Natural Trap Cave, Big Horn County (Adams, 1979)
5) Little Canyon Creek Cave, Washakie County (Walker, 1987)

Colorado

6) Haystack Cave, Gunnison County (Emslie 1986)

New Mexico

7) Muskox Cave, Eddy County (Logan, 1981)

Arizona

8) Stanton's Cave, Grand Canyon, Cocconino County (This report)
9) Tse an Cave, Grand Canyon, Cocconino County (This report)
10) Rampart Cave, Grand Canyon, Mohave County (This report)

Nevada

11) Crypt Cave, Pershing County (Orr, 1969)

California

12) McKittrick Local Fauna, Kern County (Schultz 1938, This report)
13) Rancho La Brea, Los Angeles County (Merriam 1918, Merriam and Stock 1932, This report)

TABLE 2. Measurements of *Miracinonyx trumani* right calcaneum, GRCA 55756, from Next Door Cave, measurements in mm.

Greatest length	84.6
Greatest width across astragular facets	32.6
Greatest Depth	35.1
Widith across cuboid facet	22.8
Height of cuboid facet	18.2

TABLE 3. Comparative measurements for the calcaneum of *Miracinonyx*, *Puma concolor*, and *Panthera atrox*. Measurements in mm.

GRCA 55756										
Greatest Length	84.6									
Greatest Width	32.6									
Miracinonyx trumani										
Natural Trap Cave WY	KU 35731	KU 33076	KU 41274	KU 33491	KU 36538					
Greatest Length	89	82.3	83.2	82.2	86.3					
Greatest Width	35	33.2	33.1	31.5	33.5					
Miracinonyx inexpectatus										
Cita Canyon TX	WT 608	WT 1940	WT 1757	WT 1321						
Greatest Length	99	97	93	89						
Greatest Width	34.5	34.1	30.5	30						
Rex Rodgers Ranch TX	YPM 51665									
Greatest Length	82.3									
Greatest Width	30.2									
Curtis Ranch AZ	USNM 12866									
Greatest Length	87.31									
Greatest Width	34.39									
Dry Mountain AZ	USNM 521081									
Greatest Length	80.1									
Greatest Width	29.6									
Hamilton Cave WV	USNM 401092									
Greatest Length	91.05									
Greatest Width	32.68									
Puma concolor										
Puma concolor recent	NAUQSP 12846	RSW PCV	RSW PCVI	RSW 0121	RSW PCI	RSW PCII	RSW PCIII	RSWIV		
Greatest Length	64.29	63.08	68.98	65.77	77.08	59.91	59.72	69.04		
Greatest Width	25.92	24.39	27.23	24.97	29.78	25.23	22.89	27.58		
Puma concolor fossil latest Rancholabrean (Kurten, 1976)										
Hawver Cave CA	72									
Greatest Length	27.3									
Greatest Width										
Little Box Elder Cave WY	73									
Greatest Length	27.5									
Greatest Width										
Panthera atrox										
Rancho La Brea CA LACM	R-1	R-2	R-3	R-4	R-5	R-6	R-7	R-8	R-9	R-10
Greatest Length	142	140.3	140.5	137.5	131.5	131.5	125	118	117.8	109
Greatest Width	56	56.2	55.3	54	50.9	52.9	45.9	47	47.9	41.5

TABLE 4. Measurements and listing of specimens for the sub-adult *Miracinonyx trumani* from Rampart Cave. Measurements in mm.

GRCA 21734- rostrum and palatal material with I1-M1

Rostrum	
premaxillary Width	25.53
Maxillary Width	55.25
Depth of cheek from orbit to P4	26.11
Width between both P4	44.11
Dentition	
I1	
length	4.31
width	3.05
I2	
length	4.71
Width	3.98
I3	
Length	
Width	
C1	
Length	12.81
Width	9.05
Depth	25.54
P2	
Length	4.47
Width	4.92
P3	
Length	16.34
Width	9.91
P4	
Length	24.4
Width	12.6
M1	
Length	4.29
Width	7.25

GRCA 21943- basal cranial fragment

GRCA 21739- frontal/parietal fragment

GRCA 21736/21738- Right lower jaw with i1-i3, alveolis for c1, p3-m1

Ramus	
Greatest Length	111.38
Depth of articular process	9.14
Depth of Coronoid process	53.21
Depth of ramal symphysis	34.28
Depth of ramus at p4	16.45
Width of ramus at p4	12.08

Dentition	
i1	
length	3.53
width	2.5
i2	
length	4.18
width	3.3
i3	
length	4.99
width	4.29
c1*	
length	15.32
width	12.52
p3	
length*	14.4
width	7.8
p4	
length	15.16
width	7.92
m1	
length	17.53
width	9.08

USNM 509143- left navicular

greatest length	25.36
transverse diameter	21.98

GRCA 21729- right articulated foot with navicular, cuboid, mesocuneiform, ectocuneiform, mtII-mtIV

mtIII	
Proximal width*	19.1
Shaft width	11.65

GRCA 21733- left proximal femur

GRCA 21728- right proximal femur

width of proximal end	49.61
anteroproximal breadth	25.47
depth of articulation	24.96
shaft length	18.54
shaft width	18.45

GRCA 21726- thoratic articulated colume 6-13 and lumbar 1

GRCA 21579- lumbar section 3-4

GRCA 21735- lumbar fragment 2

TABLE 5. Measurements and list of the juvenile specimens of *Miracinonyx trumani* from Rampart Cave, measurements in mm, (*) Asterisk= estimated.

USNM 509134- right premaxilla, Maxilla with I2-I3, C1, P2, dP4, Frag P4 erupting, erupting P3

I2	
Length	4.22
Width	3.15
I3	
Length	6.91
Width	5.62
C1	
Length	8.88
Width	6.85
P2	
Length	5.04
Width	3.89
dP4	
Length	X
Width	8.07
P4*	
Length	21.27
Width	11.09

USNM 509132/509133- fragmentary right lower jaw and fragment of left lower jaw with left and right i1-i3 and c1, right dp3, erupting p3, dp4 fragments, p4 erupting, and fragmentary m1

i1	
Length	3.11
Width	2.69
i2	
Length	3.7
Width	2.71
i3	
Length	5.26
Width	4.66
c1	
Length	10.84
Width	8.5
dp3	
Length	11.9
Width	5.05
dp4*	
Length	13.17
Width	4.55
m1*	
Length	16.66
Width	7.87
Mandible	
Diastema between c1-dp3	8.11

Height of mandibular symphysis	30.15
Depth at dp3	23.31
Width at dp3	10.77

USNM 509184- left humerus

Greatest Length	180.62
Proximal Width	35.32
Proximal Length	50.55
Midshaft Width	16.4
Midshaft Length	22.65
Distal Width	48.31
Distal Length	32.25
Width of Condyles	33.25
Depth of Medial Condyles	23.49
Width of Olecranon Process	21.78
Length of Entepicondylare foramen	14.95
Width of Entepicondylare foramen	3.94

USNM 509216- Right fragmentary humerus

Greatest Distal Width	41.53
Epicondyle foramen length	14.3
Epicondyle foramen width	4.14

USNM 509215- Right Radius

Greatest Length *	138.16
(minus epiphyseal caps)	
Width of proximal end	12.84
Length of proximal end	18.71
Midshaft width	10.38
Midshaft length	14.98
Distal Length	25.54
Distal Width	18.64

USNM 509215- Right Ulna

Inner Diameter of Sigmoid Notch	18.91
Depth of lower sigmoid notch	
Posterior Border	16.13
Anteroposterior Diameter	23.37

USNM 509202- Articulated manus, MCII-MCIV

MCII	
Greatest Length	70.1
Proximal Width	10.75
Proximal Length	14.8
Midshaft Width	8.24
Midshaft Length	8.96
Distal Width	10.84
Distal Length	10.22

MCIII	
Greatest Length	78.96
Proximal Width	12.75
Proximal Length	11.58
Midshaft Width	8.87
Midshaft Length	7.9
Distal Width	13.81
Distal Length	10.66

MCIV	
Greatest Length	74.67
Proximal Width	10.82
Proximal Length	10.2
Midshaft Width	8.23
Midshaft Length	8.05
Distal Width	11.47
Distal Length	10.55

USNM 509265- Left MCII

Greatest Length	70.19
Proximal Width	9.27
Proximal Length	13.87
Midshaft Width	8.54
Midshaft Length	8.95
Distal Width	12.53
Distal Length	9.06

USNM 509199- Proximal phalanx (pes?)

Greatest Length	39.97
Proximal Width	14.6
Proximal Length	9.05
Shaft Width	9.38
Shaft Length	6.43

USNM 509200- Proximal phalanx (manus?)

Greatest Length	34.56
Proximal Width	11.49
Proximal Length	7.56
Shaft Width	8.75
Shaft Length	6.16

USNM 509266- Proximal phalanx (pes?)

Greatest Length	34.67
Proximal Width	12.42
Proximal Length	8.99
Shaft Width	9.27
Shaft Length	7.22

USNM 509267- medial phalanx

Greatest Length	22.41

USNM 509080- medial phalanx and ungual claw with flesh

Greatest Length of medial phalanx	22

USNM 509218- clavicle

Greatest Length	61.97
Width of shaft	5.71
Length of Shaft	7.3

USNM 509264- Caudal Vertebra

Greatest Length	35.83

USNM 509198- Caudal Vertebra

Greatest Length	36.32

USNM 509201- articulated right rear foot with navicular, cuboid, ectocuneiform, mesocuneiforn, mtII-mtV

MtIII	
Greatest Length	95.27
width of shaft	11.33

USNM 508998- left Navicular

Greatest Length	25.07
Transverse Diameter	18.79

USNM 509000- left cuboid

Greatest Length	17.61
Transverse Diameter	15.59
Dorsoplantar	13.82

USNM 508996- mtIII

Width of proximal end	15.01
Length of proximal end	18.55
width of shaft	12.04
length of shaft	9.08

USNM 508994- mtIV

Width of proximal end	9.17
Length of proximal end	15.99
Width of shaft	9.59
Length of Shaft	9.41

USNM 508997- mtV

Width of proximal end	11.59
Length of proximal end	10.63
Width of shaft	6.58
Length of shaft	6.22

USNM 509270- mcI

Greatest Length	25.19
Proximal width	9.49
Proximal Length	10.25
Shaft width	9.77
Shaft length	9.09
Distal Width	11.13
Distal Length	8.89

USNM 509371- mcIII

Greatest Length	78.89
Proximal Width	12.31
Proximal Length	12.77
Shaft Width	8.84
Shaft Length	7.71
Distal Width	13.57
Distal Length	11.26

USNM 509268- mcIV

Greatest Length	74.8
Proximal width	10.54
Proximal Length	11.51
Shaft Width	8.01
Shaft Length	7.71
Distal Width	12.44
Distal Length	10.41

USNM 509170- proximal phalanx (manus?)

Greatest Length	32.88

USNM 509269- proximal phalanx(pes?)

Greatest Length	40.52

USNM 509269- proximal phalanx (pes?)

GRCA 21727- left scapula fragment

length of glenoid	38.6
width of glenoid	23.57

GRCA 21732- articulated astragalus and calcaneum

astragalus	
length	39.01
width	26.32
calcaneum	
length*	62.98
width	26.11

GRCA 21723- articulated radius and ulna

radius	
proximal width	19.48
proximal length	18.03
shaft width	15.27
shaft length	9.32
Ulna	
depth of sigmoid	17.9
width of sigmoid	19.7
anteroposterior diameter	28.25

GRCA 21730- 2 phalanges (manus?)

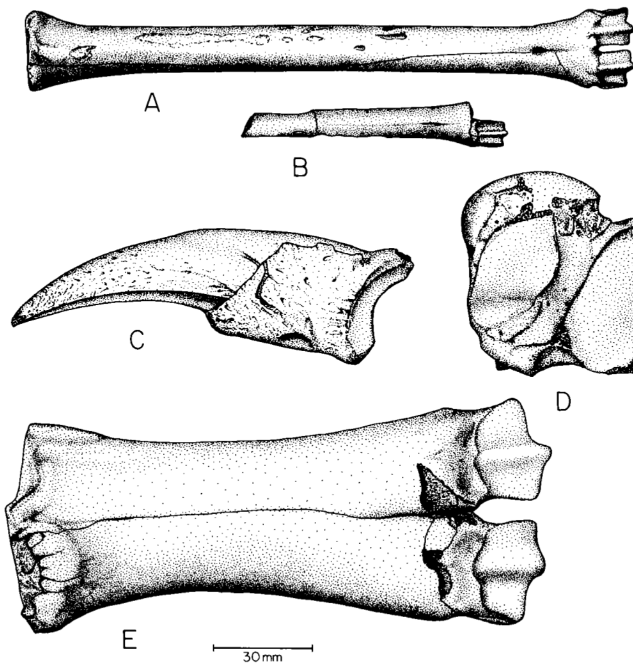

FIGURE 2—**A**, Museum of New Mexico (MNM) 5689–59–1, *Stockoceros onusrosagris*, dorsal view right metacarpal; **B**, MNM 5689–67–10, *Capromeryx* sp., dorsal view, partial metapodial; **C**, MNM 5689–1–61, *Nothrotheriops shastensis*, lateral view, phalanx III, digit II, manis; **D**, MNM 5689–1–4, *Arctodus simus*, distal surface left astragalus; **E**, MNM 5689–2–3, *Euceratherium collinum*, dorsal view, left metacarpal.

Late Pleistocene mammals from U-Bar Cave, Hidalgo County, New Mexico. (From Harris, 1985b; Reference in Morgan, this volume).