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LARGE FELID TRACKS AND BONES FROM CHILLY BOWL CAVE, ARKANSAS

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Abstract

Multiple large cat tracks were found within Chilly Bowl Cave, Arkansas, representing at least two individuals of the genus *Panthera*. Large felid bone fragments were also found in a passageway near the tracks. These poorly preserved skeletal remains primarily consist of metapodials and phalanges and represent the North American Pleistocene jaguar, *Panthera onca*. Fusion of metapodial epiphyses indicate adult foot size had been reached for this large jaguar. One set of tracks is also consistent with the size and morphology of *P. onca.* The other tracks are much larger than is known for extant or prehistoric jaguars, and are here attributed to *Panthera atrox*, the American lion. An alternate hypothesis for the smaller tracks is that they could represent a younger *P. atrox* instead of *P. onca*. Regardless of the inability to identify the smaller feline prints to species, these remains and tracks from Chilly Bowl Cave record cave utilization by two separate Pleistocene felids, interpreted here as jaguar and American lion.

INTRODUCTION

There are few published reports of fossil trackways that have been attributed to *Panthera* from North America. Before now, these have entirely been known from Missouri and Tennessee and are mostly attributed to jaguars (*Panthera onca*) (Fig. 1). Extant jaguars are known to use caves as dens, and an association between jaguar fossil remains and

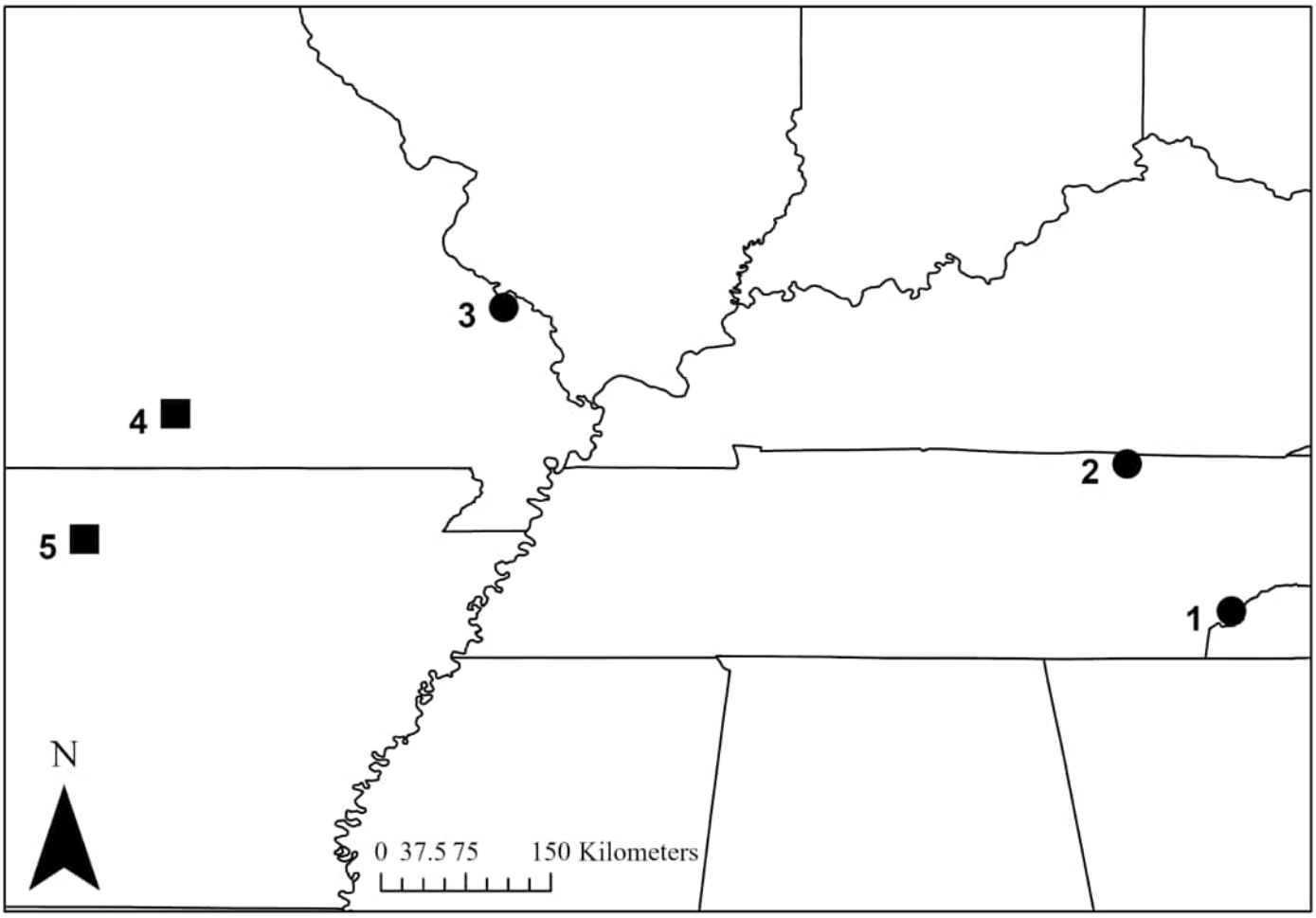

Figure 1. Map of published *Panthera* trackways of North America, including *Panthera onca* (circles) and *Panthera atrox* (squares). Locations are Craighead Caverns, Tennessee (1) (Simpson, 1941); Wolf River Cave, Tennssee (2) (Robbins et al., 1981); Berome Moore Cave, Missouri (3) (Hawksley, 1986); Cat Track Cave, Missouri (4) (Graham et al., 1996); and Chilly Bowl Cave, Arkansas (5) (this study).

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caves has been noted (Guilday and McGinnis, 1972; Seymour, 1989). These trackways can extend for well over a kilometer in some cases (Robbins et al., 1981; Hawksley, 1986). The other member of *Panthera* in North America, the American lion (*Panthera atrox*), has a weaker connection to caves than the jaguar. While skeletal remains are known from several cave localities in the western US, only one set of tracks attributed to *P. atrox* has been reported. A set of felid tracks from Cat Track Cave, Missouri, was reported by Graham et al. (1996) and was assigned to *P. atrox* based on morphology and the immense size of the prints, which exceeded the size of modern lions and tigers. This follows with the immense size of the American lion that could be as much as 25 percent larger than the living lion (Merriam and Stock, 1932).

While exploring and mapping Chilly Bowl Cave in northern Arkansas, the Middle Ozark Lower Earth Society (MOLES), a chapter of the National Speleological Society, discovered large cat tracks and some animal bones. By invitation of Jim Terry of MOLES, one of the authors (BWS) visited the cave on three occasions to assess paleontological resources (twice in 2002 and once in 2004) and identified multiple areas with fossils that appeared to be Pleistocene (Schubert, 2004). These include gray fox (*Urocyon cinereoargenteus*), proboscidean, large ungulate, and felid. The cat tracks are in close proximity to each other and are near the fox skeleton, which is in a shallow pit. The felid bone fragments were discovered in a passage near the cat tracks on a follow-up trip. Like the tracks, the degraded bones were on the current surface of the cave floor. A sample of the bones was collected from a small area, roughly 1 m square. The remains, molds, and casts are now housed in the East Tennessee State University Museum of Natural History collection at the Gray Fossil Site & Museum in Gray, Tennessee.

In this study we present the fossil remains and trackways of felids from Chilly Bowl Cave. The skeletal remains are assigned to *P. onca*, and the largest set of tracks are referred to *P. atrox.* Both the skeletal specimens and the tracks are described and compared with other records. A review of the few other large Pleistocene felid trackways is also presented, and measurements for known trackways are provided.

BACKGROUND

The first major report of large, Pleistocene cat tracks in North America was by Simpson (1941), who describes a partial skeleton of a jaguar and tracks that he attributed to the cat from Craighead Caverns, Tennessee. Some of the Craighead Caverns tracks have been cast with plaster to preserve them. The tracks are not well defined, only clearly showing digits two to four with digit five only leaving a brief mark in the ground. Additionally, the claws are visible in the tracks, an unusual occurrence for cat prints, but as described by Simpson (1941), possibly due to the movement of the animal and the sediment in which it was walking.

Oesch (1969) reported extensive felid trackways and a partial mandible identified as *Panthera onca augusta* from Berome Moore Cave, Missouri. The trackways appeared to extend for over a kilometer in the cave and some have been mapped in detail (e.g., Hawksley, 1986). The tracks from Berome Moore Cave were the first to be reported from the Ozark region. Measurements for one of the tracks were reported by Graham et al. (1996), where the size of this track was roughly as large as extant lion (*P. leo*) and tiger (*P. tigris*) tracks collected from the Indianapolis Zoo. The Berome Moore tracks were also larger in size than the Craighead Cavern tracks reported by Simpson (1941) (Graham et al., 1996). Hawksley (1986) discusses five primary track samples from Berome Moore Cave, one of which is in flowstone and the other four of which are plaster casts. These tracks vary in size based on the likelihood of multiple individuals, variation in movement, and retreading steps. In addition, Hawksley gives general estimates of the size of these tracks where most of these casts are slightly smaller than the Berome Moore track reported by Graham et al. (1996). Based on size, Hawksley (1986) identified the tracks from Berome Moore Cave as either *Panthera onca* or *Smilodon* due to the presence of both taxa in the local fossil record. Graham et al. (1996) deemed that the tracks are those of a fossil jaguar. Hawksley (1986) also mentions the possibility of a smaller felid trackway in Berome Moore Cave, hypothesized as potentially a younger individual. Further investigation of the Berome Moore Cave trackways is necessary to better understand which and how many cats made those tracks.

In the late 1970s, tracks and faunal remains were discovered in Wolf River Cave (Jaguar Cave) in Tennessee. A large assemblage of vertebrate species is reported from this cave including mastodon, dire wolf, and camel. Additionally, human trackways were discovered in a separate portion of the cave and considered to be mid-Holocene in age. Of primary interest for this study is the presence of two jaguar skeletons, extensive tracks, as well as a fecal specimen. Full descriptions and measurements of this material are yet to be published, but Robbins et al. (1981) describe the material as articulated and in poor condition. A significant portion of the cave (2 km) is said to have jaguar prints or claw marks (Robbins et al., 1981). These prints are similar in size to those from Craighead Caverns and Berome Moore Cave as reported by Simpson (1941) and Oesch (1969), respectively (Robbins et al., 1981).

Another Missouri cave site, Cat Track Cave, contains extremely large felid tracks. The tracks were originally found by members of the Missouri Department of Natural Resources in 1982. These tracks do not form any complete trackways

but do extend into the cave and down several clay banks. Two plaster casts were made of these tracks. Compared to the tracks from the other cave sites noted here, the Cat Track Cave prints are extremely large, measuring around 140 mm long and 170 mm wide (Graham et al., 1996). Graham et al. interpreted these prints as being from the American lion, *Panthera atrox*. No fossil remains of any animal were found in Cat Track Cave at the time of discovery, nor have any been reported since. Additionally, no remains of *P. atrox* have yet been reported from the Ozarks, though it is known from Kansas and Nebraska (Kurtén and Anderson, 1980).

Bustos et al. (2018) report the presence of felid tracks in the Pleistocene deposits of White Sands National Monument, New Mexico. This locality is known for its preservation of trackways of late Pleistocene megafauna, as well as potentially the earliest footprints of humans in North America (Bennett et al., 2021). Most of the work done on these Pleistocene trackways focused on proboscidean, ground sloth, and human tracks (Bustos et al., 2018; Urban et al., 2018; Bennett et al., 2021). However, as of this study, the felid tracks have not been described and measurements have not been published. Further study into these tracks would add another data set for comparison among Pleistocene felid trackways or potentially identify the first trackways on the continent to be referred to *Smilodon*, *Homotherium*, or *Miracinonyx*.

METHODS

Plaster casts were made of two tracks in Chilly Bowl Cave and fossil remains collected. Silicone molds were made of the tracks at the Illinois State Museum, and replicas were produced and painted by Mona Colburn. For osteological comparisons, the skeletons of a modern lion (East Tennessee State University Museum of Natural History zoology collection (ETMNH-Z) catalog number 7114) and jaguar (ETMNH-Z 2997) were initially used. Further comparisons were made with jaguar (American Museum of Natural History collection (AMNH) catalog numbers 135928, 135929, 139959, 209135, 209136, and 214738) and lion postcranial material (AMNH 52078, 54995, 54996, 8140, 85141, 85142, 85143, 85144, 85145, 85147, 85149, and 13531). Physical specimens were supplemented with descriptions and measurements from Merriam and Stock (1932), Kurtén (1965, 1973), and Seymour (1983). Measurements of fossil material and track casts were performed by the authors with digital calipers.

Locality

Chilly Bowl Cave is located in Newton County, Arkansas, within the Boston Mountains of the southern Ozarks (Fig. 1). Caves in this region formed within the Boone Formation of Mississippian age (359–323 MYA) limestones (Tennyson et al., 2017). The only known entrance of Chilly Bowl Cave is a surface pit that requires a 25 m rappel. The cave has at least 9 km of passageways, and the shortest route to the cat tracks from the current entrance is about 0.8 km (Jim Terry, personal communication). Though the cave has been surveyed, a map is not currently available. Some geologic aspects of the cave have been reported, including examples of hypogene speleogenesis and faults (Tennyson et al., 2017).

RESULTS

Bones

Skeletal remains from Chilly Bowl Cave, East Tennessee State University Museum of Natural History paleontology collection (ETMNH) catalog number 31379, (Fig. 2) comprise almost entirely distal limb elements, the majority of which are phalanges and partial metapodials. Identifiable elements include proximal second left metacarpal, third distal metacarpal, fourth distal metacarpal, fifth proximal left metacarpal, fifth distal left metatarsal, left unciform, and right unciform. Some tooth fragments are also present but unidentifiable. The condition of this material is very poor with extreme degradation of the bone. Much of the material has major cracks throughout. There is no duplication of any elements, so the material likely comes from one individual. Measurements of the second proximal left metacarpal and fifth proximal left metacarpal are in Table 1.

Tracks

There are two sets of felid trackways in Chilly Bowl Cave, and each is a different size. They were found in a flat, mud floor within the same passage as the skeletal material. Both tracks occur in the same area of the cave, indicate a steady walking pace, and preserve similar morphological characteristics. These characters include four rounded digital pads with no claw imprints, as is typical with felids. They also share a similar round or sub-triangular interdigital pad. A cast was made of a print from each trackway (Fig. 3). The smaller trackway is represented by the cast ETMNH 31741 (Fig. 3A) and cast ETMNH 31740 is from the larger trackway (Fig. 3B). Measurements for ETMNH 31741 and 31740 are presented in Table 2. Additional trips are needed to further assess the extent of the trackways and obtain photographs for photogrammetric models. This information could lead to a better understanding of stride patterns and pace of the cats.

Figure 2. Fossil and modern *Panthera* second metacarpals (Metacarpal 2) in lateral view, showing exaggerated curvature in jaguar. A: Modern *Panthera leo* R Metacarpal 2 (view flipped) (AMNH 85141). B: Fossil *Panthera onca* from Chilly Bowl Cave, L Metacarpal 2 (ETMNH 31379). C: Modern *Panthera onca* L Metacarpal 2 (ETMNH-Z 2797). Scale bar is 2 cm.

DISCUSSION

Bones

While most of the felid skeletal material from Chilly Bowl Cave is either undiagnostic or in very poor condition, some of the metapodials are preserved well enough to assist with identification. Though there is overlap in measurement ranges, especially of the metapodials between fossil jaguars and *Smilodon fatalis*, and the metapodials exhibit characters to distinguish the identity of these remains as *Panthera*. The proximal, left second metacarpal of ETMNH 31379 has a shallow groove for the radial artery. This groove is deeper in *Smilodon* than in *Panthera* (Merriam and Stock, 1932). The proximal left fifth metacarpal of *Panthera* has a more convex outer surface as well, with a large articular surface for the fourth metacarpal when compared to *Smilodon* (Merriam and Stock, 1932). ETMNH 31739 also differs from *Homotherium*, the other late Pleistocene machairodont of North America. The proximal articular surfaces of *Homotherium* metacarpals are larger in relation to the shaft width compared to that of ETMNH 31739 based on measurements by Rawn-Schatzinger (1992). In addition, Rawn-Schatzinger notes the elongate and thin nature of *Homotherium* metacarpals that contrasts with the shorter, robust appearance of ETMNH 31739. Compared with *Miracinonyx* and *Puma* metacarpals described and measured by Van Valkenburgh et al. (1990), ETMNH 31739 is considerably more robust.

Merriam and Stock (1932) report that *P. onca* metapodials are more longitudinally bowed than those of *P. atrox.* Like the American lion, the African lion has relatively straight metapodial shafts compared to jaguars (Fig. 2). The size of the Chilly Bowl Cave metapodials is similar to that of a female African lion and are within the range known for fossil jaguars presented by Seymour (1983). Very rarely does any measurement of the Chilly Bowl Cave material reach the minimum size of adult *P. atrox* reported by Merriam and Stock (1932) (Table 1), and there is no indication these bones would have grown any larger if the individual had continued living (i.e., the metapodial epiphyses are fused). Based on these characters and measurements, the remains are identified as *P. onca.* However, it should be noted that the measurements for the metapodials put this jaguar as one of the larger known when compared with measurements from Kurtén (1965, 1973) and Seymour (1983). North American Pleistocene jaguars had relatively long metapodials compared to modern *P. onca* (Seymour 1993), so the large Chilly Bowl Cave specimens are not surprising.

Tracks

The two Chilly Bowl Cave trackways, represented by ETMNH 31740 and 31741, have similar morphologies and are consistent with other feline trackways. Tracks attributed directly to late Pleistocene machairodonts in North America have yet to be described. Agnolin et al. (2019) report a felid trackway from Argentina that they refer to the machairodont *Smilodon populator.* These tracks are larger in size than ETMNH 31740, ETMNH 31741, and the trackway referred to *Panthera atrox* by Graham et al. (1996). The *S. populator* tracks from Argentina have an unusual kidney-shaped interdigital pad as opposed to the more ovular/subtriangular interdigital pad seen with the tracks attributed to *Panthera*

Table 1. Measurements of recent and fossil *Panthera onca* and fossil *Panthera atrox* metacarpals. PW= proximal width; PD = proximal depth.

Specimen	No. of Specimens	Length, mm		PW, mm		PD, mm		Shaft Width, mm		Source
		Max	Min	Max	Min	Max	Min	Max	Min	
Second Metacarpal										
Fossil *P. onca* from Chilly Bowl Cave (ETMNH 31739)	1	>72.41	...	18.48	...	26.87	...	13.57	...	This Study
Recent *P. onca*	11	67.90	52.00	19.90	12.00	15.70	25.30	6.90	15.00	Seymour (1983)
Fossil *P. onca*	21	88.80	69.90	19.30	14.70	25.30	20.80	15.00	11.00	Seymour (1983)
Fossil *P. atrox*	63	124.40	100.40	29.00	22.90	38.50	32.00	19.80	16.40	Merriam and Stock (1932)
Fifth Metacarpal										
Fossil *P. onca* from Chilly Bowl Cave (ETMNH 31739)	1	>46.41	...	18.82	...	18.29	...	11.50	...	This Study
Recent *P. onca*	11	60.70	46.00	16.20	12.00	17.50	12.20	10.60	7.20	Seymour (1983)
Fossil *P. onca*	22	76.50	61.50	21.40	16.40	22.70	17.50	13.60	10.40	Seymour (1983)
Fossil *P. atrox*	6	115.30	90.60	30.00	24.90	33.20	27.00	15.80	12.20	Merriam and Stock (1932)

Figure 3. Casts of felid tracks from Chilly Bowl Cave. A: Small individual referred to *Panthera onca* or a juvenile *P. atrox* (ETMNH 31741). B: Large individual referred to *Panthera atrox* (ETMNH 31740). Scale bar is 2 cm.

and other felines (Agnolin et al., 2019). This kidney shape of the interdigital pad has also been seen in felid tracks from the Pliocene of Mexico that have tentatively been assigned to *Homotherium* (Rodriguez-de la Rosa et al., 2007). While the interdigital pad of these tracks retains the kidney shape, it is asymmetrical, whereas the *S. populator* tracks are symmetrical. Rawn-Schatzinger (1992) also suggests that *Homotherium* could have been semi-plantigrade instead of the standard digitigrade of cats. As suggested by Agnolin et al. (2019) and Rodriguez-de la Rosa et al. (2007), these differences in morphology have the potential to be used to identify machairodontine tracks from feline tracks. Additionally, the podial elements for *S. fatalis* are a fair bit smaller than that of *P. atrox* and *S. populator* as seen in Merriam and Stock (1932) and Kurtén and Werdelin (1990), which further suggests it is not the creator of the larger set of tracks from Chilly Bowl Cave. Based on the morphology and size of the Mexican and Argentine machairodontine tracks, we infer that the Chilly Bowl Cave tracks were not made by a machairodont.

ETMNH 31740 is the larger of the two track casts from Chilly Bowl Cave. It is only as long as the prints from Berome Moore Cave but exceeds them in width by over 30 mm (Table 2). ETMNH 31740 is massive in comparison to most cat tracks. Its great width makes it larger than the modern lion and tiger print measurements from Graham et al. (1996). It is also morphologically similar to the Cat Track Cave prints. As this track is larger than even modern pantherines and is morphologically distinct from tracks referred to machairodonts, we refer this track to *Panthera atrox*. The prints from the larger Chilly Bowl Cave trackway are some of the biggest felid tracks in North America, second only in size to the Cat Track Cave prints. Tracks from both Chilly Bowl Cave and Cat Track Cave are larger in width than measurements of trackways attributed to *Panthera spelaea* from Bottrop-Wehlheim, Germany (Diedrich, 2011; Table 2). The *P. spelaea* tracks have a similar wide pad (Diedrich 2011) but are not as wide as the North American tracks from both Cat Track Cave and ETNMH 31740.

From the smaller trackway (seen in Fig. 3 and in situ in the cave in Fig. 4), the cast ETMNH 31741 is that of a large cat, but clearly smaller than the larger tracks from Chilly Bowl Cave including ETMNH 31740. Because it also does not share the kidney-shaped

Table 2. Measurements of fossil and modern Panthera tracks. DPW= digital pads width, IPW= interdigital pad width.

Specimen	Locality	Track Dimensions, mm			Source
		Length	DPW	IPW	
Panthera atrox (ETMNH 31740)	Chilly Bowl Cave	120.91	156.48	97.75	This study
Panthera onca or juvenile *P. atrox* (ETMNH 31741)	Chilly Bowl Cave	98.03	100.47	76.19	This study
Panthera atrox	Cat Track Cave	138	175	113	Graham et al. (1996)
Panthera atrox	Cat Track Cave	140	173	118	Graham et al. (1996)
Panthera onca	Berome Moore Cave	127	120	85	Graham et al. (1996)
Panthera onca	Berome Moore Cave	115	110	…	Hawksley (1986)
Panthera onca	Berome Moore Cave	115	115	…	Hawksley (1986)
Panthera onca	Berome Moore Cave	125	110	…	Hawksley (1986)
Panthera spelaea Maximum Manus	Bottrop	165	150	…	Diedrich (2011)
Panthera spelaea Maximum Manus	Bottrop	125	125	…	Diedrich (2011)
Panthera spelaea Maximum Pes	Bottrop	180	155	…	Diedrich (2011)
Panthera spelaea Maximum Pes	Bottrop	120	130	…	Diedrich (2011)
Panthera leo	Indianapolis Zoo	131	99	87	Graham et al. (1996)
Panthera leo	Indianapolis Zoo	125	100	96	Graham et al. (1996)
Panthera leo	Indianapolis Zoo	133	127	84	Graham et al. (1996)

interdigital pad with the machairodont tracks, it is unlike *Smilodon* or *Homotherium*. Due to the smaller size of ETMNH 31741, other felids such as *Puma concolor* or the closely related *Miracinoynx* also must be considered. De Angelo et al. (2010) provide some potential characters in separating *Puma concolor* tracks from that of *Panthera onca*. The one most applicable to ETMNH 31741 is that jaguars tend to have more rounded digital pads while the puma has more elongated ones (De Angelo et al., 2010). ETMNH 31741 has very rounded digital pads that are almost circular in shape (Fig. 3A). Tracks attributed to jaguars from Craighead Caverns are smaller but incomplete and some tracks from Berome Moore Cave as described by Hawksley (1986) are only slightly larger (Table 2). Additionally, the presence of *P. onca* in Chilly Bowl Cave is already identified by the skeletal remains described in this study and that species could have made the smaller series of tracks. It is also possible that this track is that of a juvenile or female *P. atrox*.

Wheeler and Jefferson (2009) determined that there is a significant difference in size between male and female *P. atrox.* The smallest female individual in Wheeler and Jefferson (2009) was estimated to be 89 kg. This is the mass of a large modern jaguar and nearly the same mass as the Rancholabrean average of *P. onca* (88.0 kg) presented by Seymour (1993) using the same mass estimation regressions of the lower first molar of Van Valkenburgh (1990). The average female mass presented by Wheeler and Jefferson (2009) was 178 kg, roughly the size of a modern male African lion. Christiansen and Harris (2009) estimated body mass using allometric comparisons of condylobasal skull lengths in pantherines. The smallest mass of *P. atrox* by this method was 125 kg (Christiansen and Harris 2009) using a similar sample of specimens as Wheeler and Jefferson (2009). Unfortunately, these studies primarily focus on cranial and dental measurements (Wheeler and Jefferson (2009) include femoral measurements) and do not include measurements of podial elements such as phalanges and metapodials, elements that are relevant to size and shape of the prints the cats make.

Based on this, the smaller trackway including ETMNH 31741 represents an individual of *Panthera,* either a small- to mid-size *P. onca* or potentially a juvenile or small female *P. atrox*. Without further investigation of how these bones contribute directly to the morphology of prints through anatomical studies or practical experimentation with living cats, attributing the intermediately sized *Panthera* tracks to species is problematic.

CONCLUSIONS

The skeletal remains and trackways from Chilly Bowl Cave add additional records of *Panthera* from the Ozarks. The skeletal material, while in poor condition, is identifiable as a large adult *Panthera onca*. Composed of mostly metapodials and phalanges, the material is large for a jaguar but does not reach the size of *Panthera atrox*. There

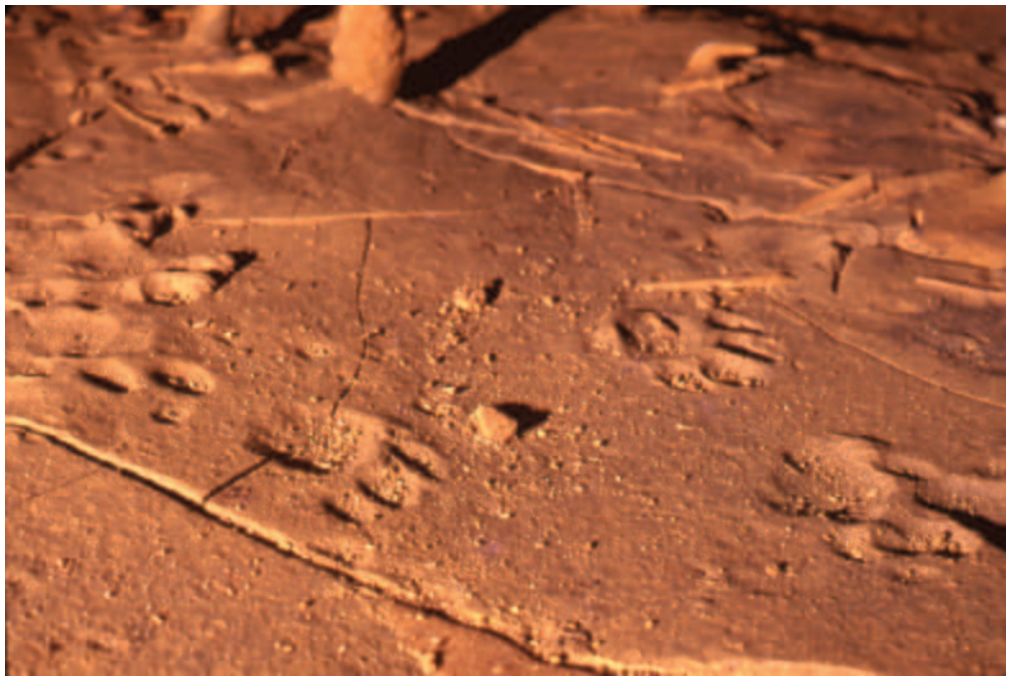

Figure 4. Photo of the smaller *Panthera onca* or juvenile *Panthera atrox* tracks from Chilly Bowl Cave.

are two cat trackways in the cave, both within 50 m of the skeletal remains. The larger trackway is similar in size and morphology to the trackway from Cat Track Cave, Missouri, that was assigned to *P. atrox*. We concur with that identification and assign the large Chilly Bowl Cave track to that taxon as well. The smaller trackway from Chilly Bowl Cave is closer in size to fossil jaguar trackways from Tennessee and Missouri. However, the presence of large tracks referred to *Panthera atrox* raises the possibility that these tracks were made by a juvenile or female *P. atrox* instead of an adult jaguar. If our identifications are correct, these tracks and bones indicate that at least one *P. atrox* traveled through this part of the cave, and one *P. onca* died in the same general area. Other tracks indicate that a smaller *P. atrox* or a *P. onca* also traveled through this section. *Panthera atrox* is only known south of Alaska from the last interglacial period (125,000 YBP) until the end of the Pleistocene (Kurtén and Anderson, 1980). Based on the identification of *Panthera atrox* tracks, this site is considered to be late Pleistocene in age. Since this area of the cave is a considerable distance from the current entrance, which is vertical, these large cats probably used an entrance that no longer exists.

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Photo Figure 4 courtesy of Jim Terry.

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