Kevin L. Seymour. The Oregon Caves National Monument fossil jaguar and the paucity of fossil jaguars from the western USA.. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 202-215. DOI:10.4311/2024PA0105

THE OREGON CAVES NATIONAL MONUMENT FOSSIL JAGUAR AND THE PAUCITY OF FOSSIL JAGUARS FROM THE WESTERN USA.

Kevin L. Seymour[1]

ABSTRACT

The most northerly excavated partial skeleton of a fossil jaguar (*Panthera onca /augusta*) from the USA (Oregon Caves National Monument, or ORCA) is described, illustrated and identified. Most of the individual bones preserved as fossils are compared with those found in living puma (*Puma concolor*) and jaguar (*Panthera onca*) skeletons to demonstrate the identification characters for each element and to establish their identification as those of a fossil jaguar. The carbon date on this specimen dates to 38,620 +/- 440 years BP, making it the oldest dated jaguar specimen to date, and within the Rancholabrean land mammal age. Its dentition is about average in size for a Rancholabrean jaguar, but its canine teeth are larger, suggesting a male. Eight localities (including ORCA) containing specimens of fossil jaguar are identified from the western USA., whereas six others containing felid specimens purported to be jaguar are identified as other felids. Given that there was no apparent bias against the preservation of felids in the fossil record in the western USA, it is suggested that there was a relative lack of the preferred prey species in the west (peccaries, armadillos or species associated with water such as turtles, caimans, capybaras or tapirs) compared to the southeast USA, where fossil jaguars are more frequently found.

INTRODUCTION

The jaguar (*Panthera onca*), the largest living new world cat, was once part of the native fauna of the USA, with historical records from Arizona, New Mexico, California, Texas, and possibly a few other states (Brown, 1983; Hall and Kelson, 1969; Merriam, 1919). This species has a tenuous foothold in the USA with only a handful of recent records (Brown and López-González, 2001; McCain and Childs, 2008), consequently it is still on the USA Endangered Species list (Rogers, 1997). Pleistocene fossil material documents this species as being present throughout much of the southern and central USA, from West Virginia and Pennsylvania to Florida in the east, through Nebraska, Nevada and California in the west (Kurtén, 1973). In the fossil record, it is much more common in the east, especially from Florida where there are 37 known localities (Morgan and Seymour, 1997), with many fewer records from the west. The most northerly specimens recorded so far are a few scraps from Oregon (Lake Co. and Malheur Co.) with inexact locations, which are barely enough to document the presence of this species there. The Oregon Caves specimen, although located slightly further south than these previous Oregon records, is still the most northerly-known fossil jaguar skeleton in North America.

This paper documents the new specimen of fossil jaguar from the Oregon Caves National Monument (ORCA 2021), that was only briefly discussed by Roth (1996) and Seymour (2003). It is important to document this specimen, as fossil jaguar skeletons are exceedingly rare. As of 1993, only five localities have so far produced partial skeletons (Seymour, 1993), and all are from eastern USA or Texas and from caves. No complete fossil jaguar specimen has been recovered anywhere in North America.

A note about jaguar taxonomy is relevant here. As discussed by Seymour (1993), the larger Pleistocene form of the living jaguar has received various names. Some workers have considered this larger form to be a different subspecies from the living forms (naming it *Panthera onca augusta*), for example Simpson (1941) and Kurtén (1973), while others have considered it to be a different species (naming it *Panthera augusta*), for example McCrady et al. (1951), even while all acknowledge that there was probably genetic continuity between the fossil and living forms. Neither naming option is ideal. Naming it a different species would imply an extinction whereas naming it a different subspecies risks confusing geographic subspecies (variation at one time) with temporal subspecies (variation through time). For this reason, I prefer to use the informal lineage segment naming system as proposed by Martin (1993), resulting in the name *Panthera onca /augusta* for this form.

ABBREVIATIONS:

Institutional: AMNH: American Museum of Natural History, New York, New York
LABE: Lava Beds National Monument, Tulelake, California
LACM HC: Los Angeles County Museum, Hancock Collection (at the George Page Museum), Los Angeles, California
ORCA: Oregon Caves National Monument, Cave Junction, Oregon
NSM: Nevada State Museum, Carson City, Nevada
ROM: Royal Ontario Museum, Toronto, Ontario, Canada

[1]Department of Natural History, Royal Ontario Museum, 100 Queen’s Park, Toronto, Ontario, Canada M5S 2C6. kevins@rom.on.ca

TMM: Texas Memorial Museum, Austin, Texas
UALP: University of Arizona Lab of Paleontology, Tucson, Arizona
UCMP: University of California, Museum of Paleontology, Berkeley, California
USNM: United States National Museum (Smithsonian), Washington, D.C.
UTEP: University of Texas at El Paso, El Paso, Texas.
MC: metacarpal; MT: metatarsal; MNI: minimum number of individuals.

LOCATION AND OCCURRENCE

Oregon Caves National Monument is located in southeastern Josephine County, within the northern Siskiyou mountains of south-west Oregon, Lat 42 05’ 53” N, Long 123 24’ 26’’ W. The monument itself is fairly small (about 488 acres or 1.97 sq km) consisting mostly of old-growth coniferous forest, dominated by Douglas Fir (*Pseudotsuga menziesii*). The entrance to the cave system is at about 1200 m elevation. The marble cave itself is about 5.6 km long, and harbors one of the largest assemblages of endemic cave-dwelling insects in the USA.

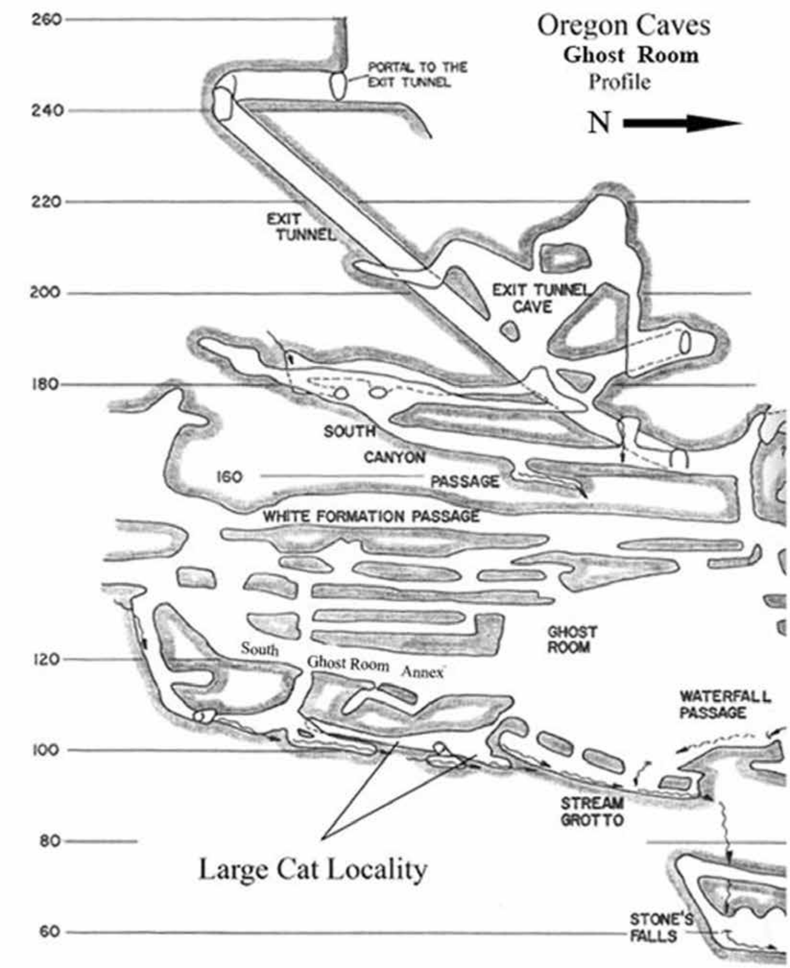

Figure 1. Cross section of a portion of the cave system at Oregon Caves National Monument. The numbers at the left measure depth in meters above the lowest point in the cave system. The jaguar specimen was recovered near the bottom of this diagram, below the Ghost room, labelled as “Large cat locality”. Diagram provided by Blaine Schubert.

The new fossil jaguar specimen (ORCA 2021) was found by Steve Knutson in August 1995 in a tight tunnel just down from a part of the cave called the Ghost Room (Fig. 1). The difficult access to the specimen made it hard to see for a positive identification and initially it was thought to be a bear, because of its large size and the fact that bear bones commonly have been found in other parts of this cave system. John Roth contacted Greg McDonald, then at Hagerman Fossil Beds National Monument in Idaho and requested that he work with the park to determine what animal the partial skeleton represented. Steve and Greg McDonald recovered the skull, jaws and a few long bones in 1997. The recovery of the skull and jaws allowed for an immediate identification as a large cat. The remainder of the skeleton was recovered on March 9, 1998 by Larry Coats, Blaine Schubert, and Jim Mead. Although most material was on the surface, some was coated with flowstone and was not possible to remove, some material was under water, and some was scattered in the crawl tunnel above the creek. Judging by the positioning of the bones, it is likely that the animal died in the crawl tunnel and that the material scattered slightly downhill from there (Blaine Schubert, pers. comm.).

GEOLOGICAL SETTING

A total of fourteen U-series dates on three different sample series were used as the basis for developing a speleothem growth chronology for the Oregon Caves flowstone (Turgeon and Lundberg, 2004). The Neptune’s Grotto flowstone series range between 359 and 122.9 ka, the Exit Tunnel Cave flowstone series range between 119.3 and 116.7 ka, and then another series ranges from 14.3 to 12.0 ka, and finally the White Formation Passage stalagmite dates between 3.9 ka and 2.3 ka (Turgeon and Lundberg, 2004). These dates represent when the cave formations were growing, mostly during mid to late Pleistocene interglacials, when excess moisture allowed the flowstones to grow.

Although the cave formations seem to have formed primarily earlier in the Pleistocene, the jaguar could have entered the cave at any time. It probably would have preferred to enter a drier rather than a wetter cave, judging from the evidence of jaguars in dry caves (Guilday and McGinnis, 1972). The carbon date indicates that the jaguar died in the cave during a time when the cave formations were not actively growing.

CARBON DATES ON JAGUAR SPECIMENS

Usually, the age of fossil jaguars is judged by the associated fossils preserved with them. No North American jaguar specimen appears to be older than about 1.6 million years old (Seymour, 1993) and all North American fossil jaguars are from the Pleistocene.

Previously only two accelerator mass spectrometry (AMS) carbon dates have been published for fossil jaguars, both published on Tennessee specimens (Corgan and Breitburg, 1996), although I attempted to obtain AMS carbon dates on two jaguar specimens from the Talara tar seeps, Peru (TO-B3649 and TO-B3650), but the impregnated tar prevented this. These dated Tennessee specimens are the two collected by Edward McCrady that were discussed by McCrady et al. (1951). The first (USNM 18262) was found in Little Salt River Cave, Franklin Co., Tennessee, and dates to 13,455 +/- 100 years BP (C-13 corrected; done on bone apatite; GX-20705-AMS). The second specimen, mentioned by McCrady et al. (1951) as being stored at the University of the South in Sewanee, Tennessee (where I examined the specimen in 1998), has since been transferred to USNM, and is now USNM 521280. This specimen, found in Johnson Cave, near Sparta, Putnam Co., Tennessee, dates to 28,855 +/- 300 years BP (C-13 corrected; done on bone gelatin; GX-20143-G).

An AMS carbon date on the L pelvis fragment of ORCA 2021 yielded a date of 38,620 **+/-** 440 years (C-13 corrected; done on bone apatite; TO-11167). This date should be considered a minimum age, as further research would be required to answer the question if the specimen is in fact older than this result. Regardless, ORCA 2021 is the oldest directly dated North American fossil jaguar specimen to date.

Description of the Oregon Caves specimen, ORCA 2021

The Oregon Caves jaguar skeleton is incomplete, although the individual bones are well preserved. Most elements are fragmented in some way, but 14 are complete, as follows: thoracic vertebra X, an anterior caudal vertebra (about caudal IX), right ulna, radius, calcaneum, MT II, and proximal phalanx of the same digit and the following elements from the left side: scapholunar, magnum, MC II, MC IV, MC V, navicular and MT III. This partial skeleton will be discussed below bone by bone.

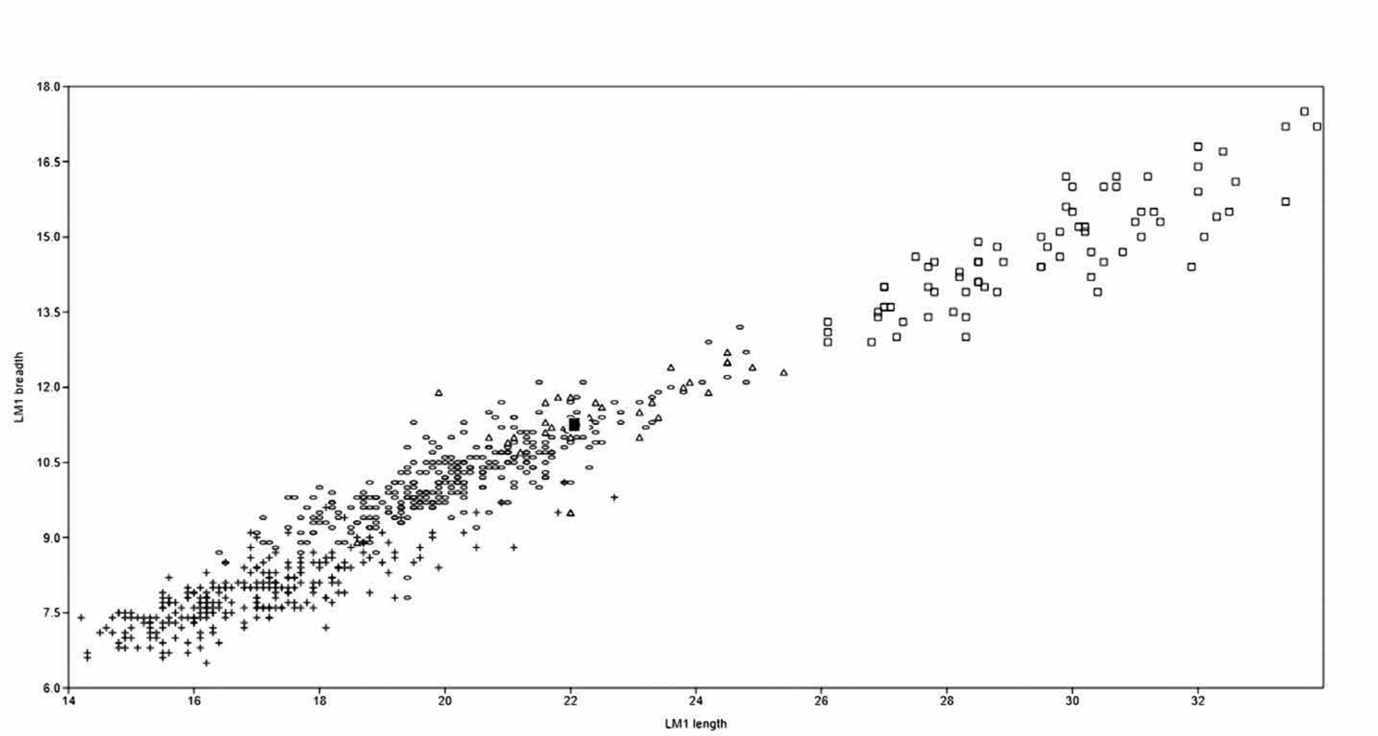

Figure 2. Bivaraiate graph plotting lower first molar length against lower first molar breadth for a selection of cats. Open squares represent Pa. atrox from North America, open ovals represent recent Pa. onca from both North and South America, open triangles represent fossil Pa. onca /augusta from North America, solid square represents ORCA 2021 and plus signs represent recent Pu. concolor from North and South America. Data from Seymour (1993) or Seymour (1999). Graph constructed using PAST (Hammer et al., 2001).

IDENTIFICATION

Identification of fragmentary fossil felid remains can be difficult (Schultz et al, 1985). Fortunately, ORCA 2021 is a partial, associated skeleton, with several complete elements available for comparison. These elements were compared directly with skeletal material of Recent *Puma concolor* (ROMVP R1510, ROMM 34.5.10.1), Recent *Panthera onca* (ROMVP R5703, ANSP 19349, FMNH 57199), fossil *Homotherium serum* (casts of TMM material) and fossil *Smilodon fatalis*, consisting of a series from Talara, Peru discussed by Kurtén and Werdelin (1990) and Seymour et al. (2018). The identification criteria discussed by Seymour (1983) were applied to confirm the identification. These criteria will be discussed below for each element. This specimen can be identified as *Panthera onca laugusta* using the system of informal lineage segments recommended by Martin (1993) and Seymour (1993).

Table 1 Comparison of the lengths of four teeth for a selection of fossil cats

Element length	ORCA	Rlb avg	Rlb N	Irv avg	Irv N
Upper carnassial (P4)	30.5	30.3	19	31.6	9
Lower carnassial (m1)	22.0	21.6	23	23.5	9
Upper canine (C)	21.2	20.6	16	21.5	10
Lower canine (c)	21.0	20.0	18	20.5	8

Abbreviations for Table: avg, average; C, upper canine; c. lower canine; Irv, Irvingtonian land mammal age; m, lower molar; N, samples size; ORCA, Oregon Cave National Monument; P, upper premolar; p, lower premolar; Rlb, Rancholabrean land mammal age. Specimen data from Seymour (1993).

DENTITION

The dentition clearly identifies this specimen as a non-machairodont cat. The canines are conical and the post-canine teeth do not angle posteriad as in the machairodonts. Almost the full dentition of ORCA 2021 has been preserved. The only teeth lacking from this specimen are left I1, right I1-2, right M1 and all lower incisors except right i3. Most publications on fossil cats discuss the dentition because the dental-bearing elements are taphonomically the most often preserved, however, individual felid teeth look very similar between species. The large size of the ORCA specimen and its robust teeth suggest a pantherine, but both *Puma* and *Miracinonyx* during the Pleistocene were larger than present-day *Pu. concolor*, and fossil lion, *Pa. atrox*, was also present in the area, so size alone is not necessarily a safe criterion for identification. Compared to *Pu. concolor*, p4 of *Pa. onca* is longer relative to m1, m1 is relatively broad (Hoffstetter, 1949), and Ic is relatively large whereas p3 is relatively small (Werdelin, 1983). Compared to *Pa. atrox*, size alone seems to be the major criterion for identification. For instance, in Fig 2, the lower first molar length is plotted against the lower first molar breath. There is no overlap between *Pa. onca* and *Pa. atrox*, but there is significant overlap between *Pu. concolor* and *Pa. onca* in both the length and width of the m1. However, for any given length, the breath of the m1 is relatively wider in *Pa. onca* and so this can be used to secure an identification. ORCA 2021 fits very nicely in the plot with the fossil and recent jaguar specimens found in North America.

Table 1 shows the measurements of selected teeth of ORCA 2021 compared to a sample of Rancholabrean jaguars and older Invingtonian jaguars (specimen list in Seymour, 1993). The carnassial teeth (P4 and m1) are the first to erupt in the adult dentition, and hence, these teeth are used when predicting body mass (Van Valkenburgh, 1990). The ORCA carnassials are very close to the Rancholabrean average, and smaller than the Irvingtonian average, as expected. However, the canines are larger than the Rancholabrean average, and closer to the average for the Irvingtonian jaguars. Since jaguars are particularly dimorphic in their canine size (Seymour, 1989; 1993), this indicates an animal with above average canine size for a Rancholabrean animal, which suggests a male.

Simpson (1941) stated that some North American fossil jaguar specimens had a relatively larger P2 compared to the largest living jaguar subspecies. Using a larger sample size of all living subspecies (N= 53) than was measured by Simpson (who used N= 8) gives the following P2 length data: average 6.9 mm, range 4.9 to 8.7 (Simpson's data were average 7.3, maximum of 7.7). ORCA 2021 has a P2 length of 7.7, which places it above average, but not out of the range of the living jaguar. This tooth might be considered vestigial in the living species, and so its slightly larger size on average in fossil jaguar is not unexpected but of dubious taxonomic significance.

SKULL

The skull is fragmented into several pieces, consisting of the two maxillae, the glenoid/mastoid/occipital region, several pieces of frontal and parietal and a number of smaller fragments.

Three portions of the posterior part of the skull are useful for the separation of *Pu. concolor* from *Pa. onca* (Seymour, 1999). The petrosal bones are exposed and easily visible due to the breakage of the skull. The disconfigured subarcuate fossa on the petrosal bone, as described and illustrated by Salles (1992: Fig 26) and Seymour (1999: Fig. 2-6), is an indication of a pantherine rather than *Puma*. The mastoid and paramastoid are well developed and well separated from each other, another jaguar character (Fig. 3; also Hoffstetter, 1949: #34, 35; Seymour, 1999: Fig. 2-4). Finally, the anterior entotympanic is extended into a narrow, finger-like projection (best seen on the left side of ORCA 2021), and the anterior ectotympanic is well developed anteriorly, contrasting the *Puma* condition (Fig. 3; also Hoffstetter, 1949: #39, 40; Seymour, 1999: Fig. 2-4). As discussed by Seymour (1999), all these characters show some variation but the character states present in ORCA 2021 are usually only present in *Pa. onca* rather than in *Pu. concolor.* In addition, pumas show a well-developed bregmatic process (finger-like extensions of the parietal growing anteriad on top of the frontal), a feature that is absent in ORCA 2021.

The differentiation of *Pa. atrox* from *Pa. onca* on skull morphology is more problematic. For instance, of the 57 characters utilized by Salles (1992) in his study of the skull morphology of the cat family, he listed only three characters that differentiate *Pa. leo* (a presumed close relative of *Pa. atrox,* although see Christiansen and Harris 2009) from *Pa. onca*. One is an internal sinus feature present only in *Pa. leo* (which does not appear to be present in the frontal fragment of ORCA 2021), another is the presence of a processus brevis on the malleus ear ossicle (which does appear to be present in ORCA 2021 as in *Pa. onca*; both the left malleus and an incomplete right malleus were preserved) and the third is the relative loss of the internal grooves on the upper canine in *Pa. onca*, which are present in all other pantherines. ORCA upper canines do not have grooves, as in *Pa. onca*.

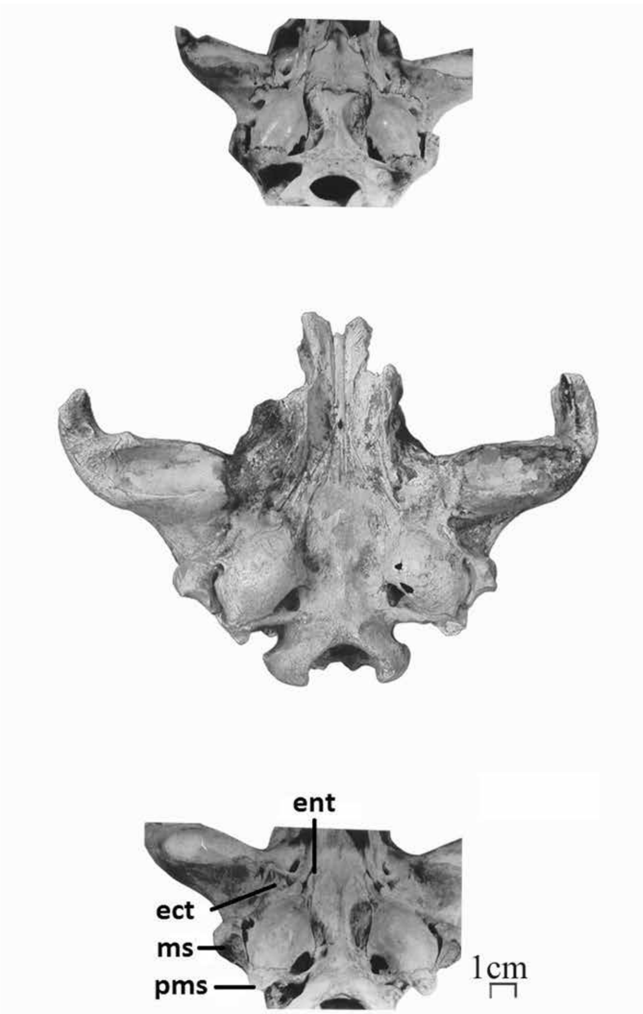

Figure 3. Ventral view of the skull to show the basicranium, anterior is at top. At top is Pu. concolor (ROMM 46326), in the middle is the fossil (ORCA 2921), at bottom is Pa. onca (FMNH 57199). Abbreviations: ect, anterior ectotympanic; ent, anterior entotympanic; ms, mastoid process; pms, paramastoid process.

Seymour (1983) suggested several other characters for the separation of *Pa. atrox* and *Pa. onca*, and all of them can be seen on ORCA 2021. However, it must be emphasized that these characters have not been examined yet on a series of skulls, and hence, the intraspecific variability is as yet unknown. Characters 4 through 7 are well-illustrated in Merriam and Stock (1932, Fig. 145). These include:

1. Lachrymal tubercle well developed in *Pa. onca*, weak or absent in *Pa. atrox*. ORCA 2021 is well developed, hence more like *Pa. onca*.
2. Mesopterygoid fossa strongly developed in *Pa. onca*, weakly developed in *Pa. atrox*. ORCA 2021 is weakly developed. I have seen a number of *Pa. onca* skulls with weakly developed fossae, so I do not put much trust in this character.
3. Infraorbital foramen relatively small in *Pa. onca*, large in *Pa. atrox*. In ORCA 2021, it is relatively large. I have seen wide variability in this character as well and tend not to trust it, until it has been quantified.
4. Auditory bulla more dome shaped in *Pa. onca*, more elongate in *Pa. atrox*. This character is rather difficult to quantify, but ORCA 2021 does appear to be more similar to *Pa. onca* than *Pa. atrox*.
5. Entotympanic process less developed in *Pa. onca*, more pronounced in *Pa. atrox*. ORCA 2021 is more like *Pa. onca*.
6. Bridge of bone anterior to the tympanohyal pit and stylomastoid foramen is flattened in *Pa. onca*, thicker in *Pa. atrox* (see Merriam and Stock 1932:197). ORCA 2021 is more like *Pa. onca*.

An additional character not discussed by Seymour (1983) is:

Postero-lateral palatal foramen is larger and placed more laterally in *Pa. atrox* than in *Pa. onca*. ORCA 2021 is more like *Pa. onca*.

In summary, 5 of the 7 characters demonstrate that ORCA 2021 is more similar to *Pa. onca* than to *Pa. atrox*. Although this confirms the identification as a fossil jaguar, it also indicates that characters 2 and 3 may be too variable to be used for the purpose of identification.

MANDIBLE

Other than the dentition, the mandible is a conservative element in felines. Although both halves are somewhat incomplete in ORCA 2021, the left is complete enough that the length can be measured, whereas the articular for the right half is separate from the main body and cannot be re-attached due to some missing bone.

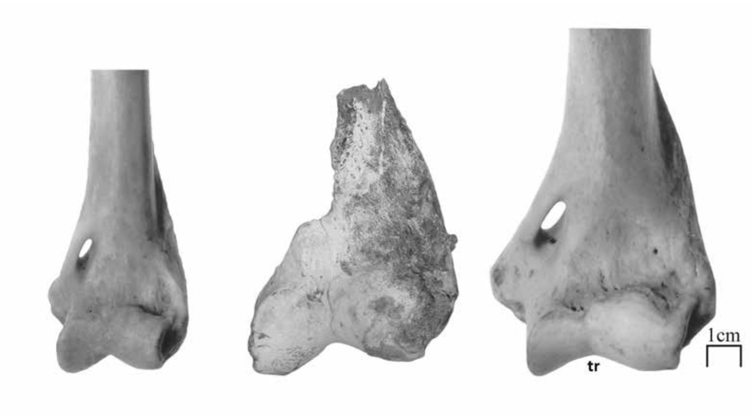

Figure 4. Anterior view of the distal part of the left hunerus. At left is *Pu. concolor* (ROMM 34.5.10.1), in the middle is the fossil (ORCA 2021) and at right is Pa. onca (FMNH 57199). Abbreviation: tr, trochlea.

Figure 5. Top row is the anterior view of the proximal part of the left ulna, middle row is the lateral view of the proximal part of the left ulna and the bottom row is the lateral view of the distal part of the left ulna. Specimen numbers as in Figure 4. Abbreviations: b, bridge of bone; ol, olecranon process; sp, styloid process.

The mental foramina are quite variable, but there are trends. Generally, they are relatively small in *Pa*. *onca*, and relatively large in *Pa*. *atrox*. The mental foramina of ORCA are relatively small as in *Pa*. *onca*.

LIMB AND FOOT BONES

The limb and foot bones of *Pa*. *atrox* are larger than those of *Pa*. *onca*, and so there should be little confusion between these two species, unless the material in question is fragmentary. However, the limb and foot bones of *Pu*. *concolor* and *Pa*. *onca* need to be carefully differentiated, as they can be similar in size. The morphological differences between the postcranial bones of these two species has not been discussed in any detail in the literature, other than in a thesis (Seymour, 1983). Here comparative descriptions of the elements preserved in ORCA 2021 are provided for the purposes of separating these two species, and identifying ORCA 2021. The source for these descriptions is Seymour (1983).

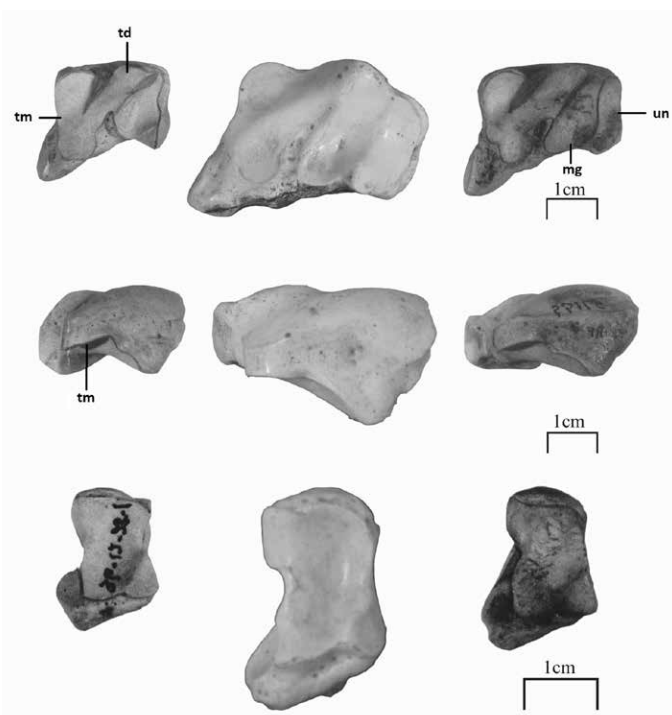

Figure 6. Top row is the distal view of the right scapholunar (flipped to appear left), middle row is the anterior view of the right scapholunar (flipped to appear left) and bottom row is the distal view of the right magnum (flipped to appear left), therefore lateral side is on the left. Specimen numbers as in Figure 4. Abbreviations: mg, articular surface for the magnum; td, articular surface for the trapezoid; tm, articular surface for the trapezium; un, articular surface for the unciform.

FORELIMB

The left humerus is broken into two pieces that cannot be re-attached, so the length of this element needs to be estimated, whereas the right humerus was not recovered. The trochlear notch on the distal end of the humerus is shallower in *Pa. onca* than in *Pu*. *concolor* (Fig. 4), and in this respect ORCA 2021 matches *Pa. onca*.

The left ulna is missing only a small portion of the distal end, whereas the right ulna is complete. Three characters that separate the ulna of *Pa*. *onca* from *Pu*. *concolor*: 1. The bridge of bone on the anterior face between the proximal extremity and the proximal end of the articulation for the humerus is broad, not narrow (Fig. 5, top row) 2. The posterior part of the olecranon process is squarish (not rounded) in outline, in lateral view (Fig. 5, middle row) 3. In lateral view, the notch between the styloid process and the articular surface for the radius is deeper than in the puma (Fig. 5, bottom row). All three characters of ORCA 2021 align with *Pa*. *onca*.

The left radius is represented by the proximal portion of the bone only, whereas the right radius is complete. The radius is one of the most conservative elements in felids,

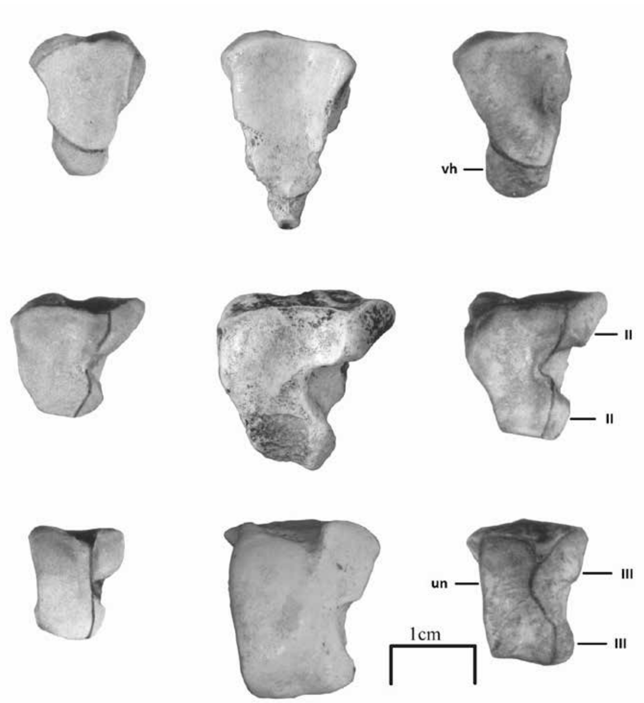

Figure 7. Top row is the proximal articular surface of the right metacarpal II (flipped to appear left, dorsal is at top and lateral is at left), middle row is the proximal articular surface of the right metacarpal III (flipped to appear left), bottom row is the proximal articular surface of the right metacarpal IV (flipped to appear left). Specimen numbers as in Figure 4. Abbreviations: II, articular surfaces for the articulation of metacarpal II; III, articular surfaces for the articulation of metacarpal III; un, articular surfaces for the unciform; vh, ventral hook.

often containing few or no characters, but three are listed here. The three characters that separate the radius of *Pa. onca* from *Pu. concolor* are: 1. The head is relatively larger, so that there is often a lip formed around the edge 2. the tubercle is elongate and aligned with the long axis of the bone and 3. the distal articular facet is larger and less elevated than in the puma. All three characters of ORCA 2021 align with *Pa. onca*, but are not illustrated here.

MANUS

From the manus, there is a complete left scapholunar and left magnum, as well as complete left MC II, IV and V, and an incomplete left MC III that is lacking the distal part. Since carpals and metacarpals are relatively diagnostic, each bone will be described separately.

The following characters separate the scapholunar of *Pa. onca* from that of *Pu. concolor*: 1. the unciform articular facet is angled less dorsad (almost vertical in puma; Fig. 6, top row) 2. the trapezoid and trapezium articular facets, although still angled dorsad as in the puma, are angled more laterad (Fig. 6 top row) 3. the most ventral end of the articular facet for the trapezium is broad (not narrow; Fig. 6, top row) 4. the articular facet for the magnum is not as deep as in puma (Fig. 6, top row) 5. the ventral end of the articular facet for the magnum is wider medio-laterally than in the puma (Fig. 6, top row) 6. the roughly rectangular protrusion of bone proximal to the articular facet for the trapezium is medio-laterally elongate (not dorso-ventrally thickened as in puma; Fig 6, middle row).

The following characters separate the magnum of *Pa. onca* from *Pu. concolor* (Fig 6, bottom row): 1. the lateral side has little or no indentation (well indented in puma) 2. the bone is more elongate in the dorso-ventral direction (less elongate in the puma).

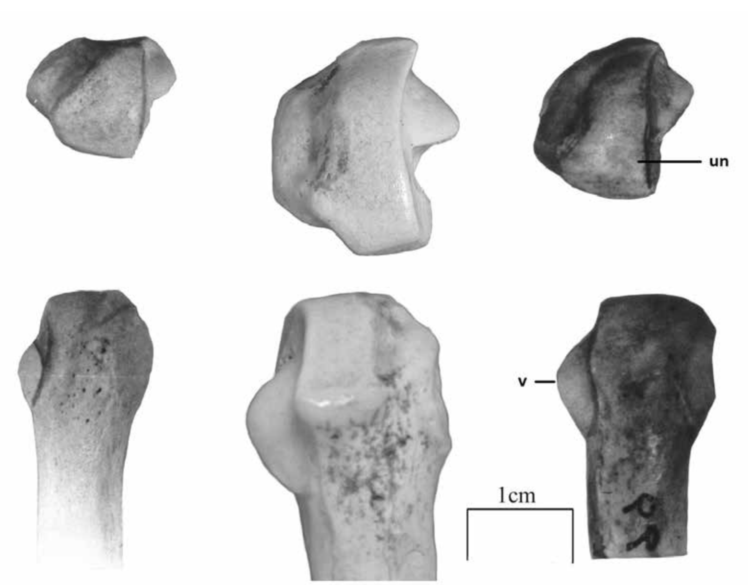

Figure 8. Top row is the proximal articular surface of the right metacarpal V (flipped to appear left, dorsal is at top and lateral is at left) and bottom row is the anterior view of the right metacarpal V (flipped to appear left). Specimen numbers as in Figure 4. Abbreviations: IV, articular facet for metacarpal IV; un, articular surface for the unciform.

The following character on the head of MC II separates *Pa. onca* from *Pu. concolor* (Fig. 7, top row): 1. the ventral hook on the proximal end is well developed, lengthening the head in a dorso-ventral direction.

The following characters on the head of MC III separate *Pa. onca* from *Pu. concolor* (Fig. 7, middle row): the head is more elongate in a dorso-ventral direction 2. the indentation between the two articular facets for MC II is relatively large.

The following characters on the head of MC IV separate *Pa. onca* from *Pu. concolor* (Fig. 7, bottom row): 1. the articular facets for MC III and unciform are not distinctly separated 2.the dorsal part of the articular facet for MC III is more elongate than in the puma 3. the indentation separating the two articular facets for MC III is dorso-ventrally shallow and wider than in puma 4. the outline of the ventral end is indented (rounded in puma).

The following characters on the head of MC V separate *Pa. onca* from *Pu. concolor* 1. the articular facet for the unciform is slightly elongated dorso-ventrally

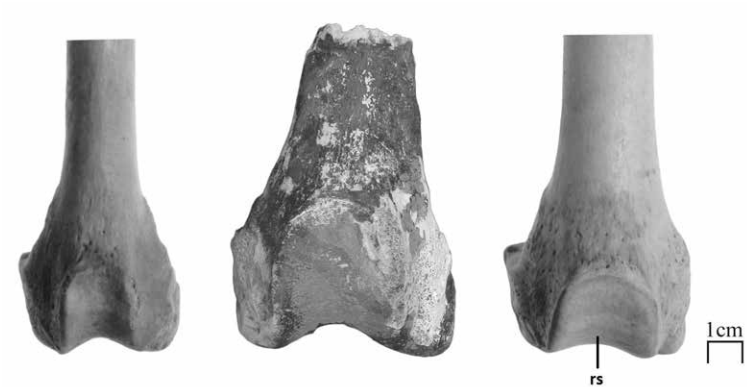

Figure. 9. Anterior view of the distal part of the left femur (flipped to appear right). Specimen numbers as in Figure 4. Abbreviation: rs, rotular surface.

(Fig. 8, top row) 2. in dorsal view, the ventral outline is rounded (straight in puma; Fig. 8, top row) 3. in anterior view, the articular facet for MC IV is larger and it extends further distally than in the puma (Fig. 8, bottom row).

HIND LIMB

The right femur is represented by the distal end only, whereas the left femur is represented by the head and a separate piece of shaft. The most diagnostic character on the femur for the identification of *Pa. onca* is the shape of the patellar trochlea. In the jaguar (and in ORCA 2021), it is relatively wider and less deeply notched than in the puma (Fig. 9).

The left tibia is represented by the distal end only whereas the right tibia is represented by the proximal head only. In addition, there is only a piece of the shaft of the left fibula. Proportionally, the tibia of the jaguar is one of its most diagnostic elements, as it is relatively short and broad compared to the puma. However, all the good morphological features for separating jaguar from puma are on the unpreserved shaft, so the tibia is not illustrated here.

PES

There are two complete elements from the tarsus, the right calcaneum and left navicular.

The following characters separate the calcaneum of *Pa. onca* from *Pu. concolor*: 1. the neck is relatively short and stout (Fig. 10, top row) 2. the distal portion between the astragalar and cuboid articulations is shorter than in the puma (Fig. 10, top row) 3. the minor astragalar facet is laterally elongate and the protrusion of bone proximal to it is less well developed in a proximo-distal direction than in the puma (Fig. 10, middle row) 4. the groove for the peroneal tubercle is absent or not distinct (Fig. 10, middle row).

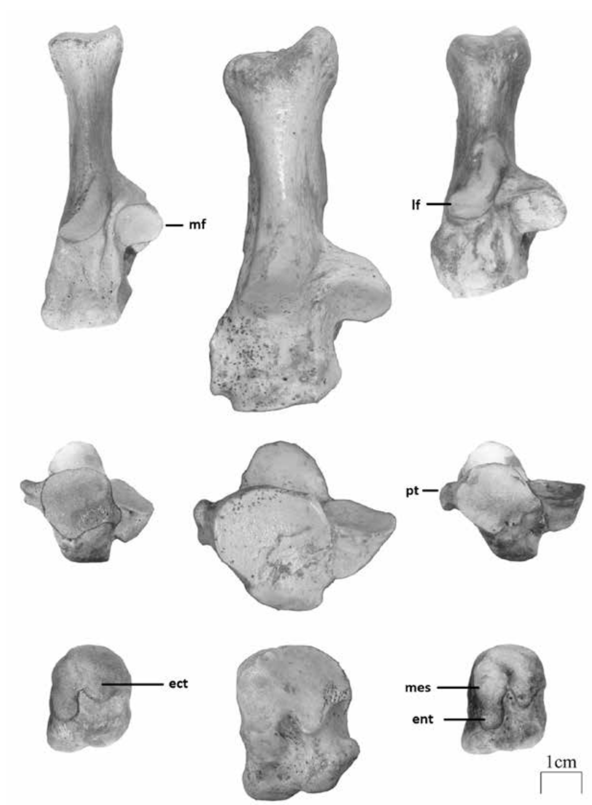

Figure 10. Top row is the dorsal view of the left calcaneum (flipped to appear right), middle row is the distal view of the left calcaneum (flipped to appear right) and the bottom row is the distal view of the left navicular. Specimen numbers as in Figure 4. Abbreviations: ect, articular surface for the ectocuneiform, ent, articular surface for the entocuneiform; lf, lateral facet; mes, articular surface for the mesocuneiform; mf, medial facet.

The following characters separate the navicular of *Pa. onca* from *Pu. concolor* (Fig. 10, bottom row): 1. the cuboid articular facet is not distinct and is flattened 2. the entocuneiforma and mesocuneiform articular facets are broadly joined (separated by a groove in puma) 3. the ventral extension of the ectocuneiform articular facet is well defined and raised.

From the metatarsus there are three complete elements, the right MT II and associated proximal phalanx, a left MT III, and an incomplete right MT IV.

The following characters separate the MT II of *Pa. onca* from *Pu. concolor* (Fig. 11, top row): 1. the articular facet for the mesocuneiform is only slightly indented on the lateral side (more clearly indented in puma) 2. the ventral portion of the proximal end is more elongated and curved to the lateral side than in the puma.

For the MT III, the following characters separate *Pa. onca* from *Pu. concolor*: 1. the lateral indentation on the proximal end is formed more dorsally (the lateral and medial indentations are opposite each other in puma; Fig. 11, second row) 2. On the lateral face, the plantar articulation for MT IV is only slightly raised (if at all) and not separated from the proximal articular surface (the ventral articulation in puma is raised and separated from the proximal articulation by a small bridge of bone; Fig. 11; third row) 3. On the lateral face, the two articular facets for MT IV are more widely separated than in puma (Fig. 11, third row).

For the MT IV, the following characters separate *Pa. onca* from *Pu. concolor*: 1. The ventral end of the proximal articular surface bears a strong groove, slanting laterally. This groove is also visible in lateral view, but it is lacking in puma 2. In medial view, the dorsal articular facet for MT III is placed more distally than in the puma (Fig. 11, bottom row) 3. In medial view, the ventral articular facet for MT III is placed more ventrally than in the puma (Fig. 11, bottom row).

Table 2 Comparison of the lengths of four bones for a selection of fossil cats

Element	ORCA	Rlb avg	N	Irv avg	N
Ulna L	270	266	2	293	1
Radius L	213	226	6	240	3
MT II L	91.0	86.7	6	99.5	5
MT IV L	103	101	12	112	5

Abbreviations for Table: avg, average; Irv, Irvingtonian land mammal age; L. length; N, samples size; ORCA, Oregon Cave National Monument; Rlb, Rancholabrean land mammal age). Specimen data from Seymour, 1993.

LIMB BONE SIZE

Using the limb bones, the overall size of this animal is average compared to other USA specimens of similar Rancholabrean age (Table 2), but smaller than older specimens of Irvingtonian age. There is no complete humerus, femur, tibia or fibula, so limb proportions cannot be calculated for ORCA 2021.

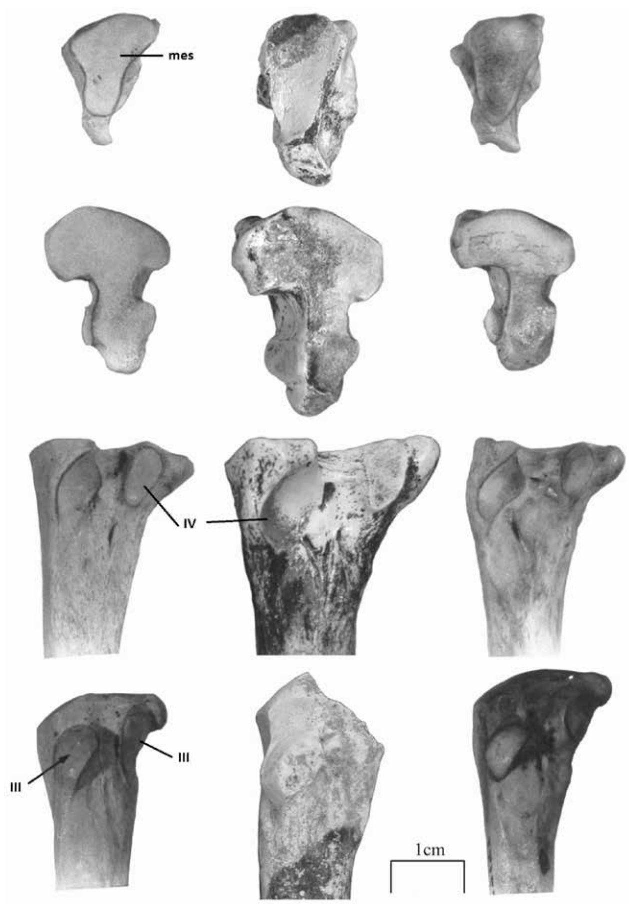

Figure 11. Top row is the proximal articular surface of the left metatarsal II (flipped to appear right, dorsal is at top, lateral is at right), second row is the proximal articular surface of the left metatarsal III (lateral is at left), third row is the lateral view of the left metatarsal III and bottom row is the medial view of the left metatarsal IV (flipped to appear right). Specimen numbers as in Figure 4. Abbreviations: III, facet for the articulation with metatarsal III; IV, facet for the articulation with metatarsal IV; mes, articular surface for the mesocuneiform.

VERTEBRAE AND GIRDLE ELEMENTS

Two vertebrae were recovered, a thoracic X and a caudal vertebra, about caudal IX.

Portions of both the right and left pelvis were collected, and a small sample from the left side was used for carbon dating.

MORPHOLOGICAL SUMMARY

In summary, this fossil specimen is average in overall size for a Rancholabrean fossil jaguar (*Panthera onca laugusta*), but the teeth are above average for a specimen of this age, suggesting that this partial skeleton probably represents a male.

REVIEW OF WESTERN JAGUARS

A summary of fossil jaguars in the USA was provided by Kurtén (1973) and updated by Seymour (1983; 1993); a summary of Seymour (1983) was presented in Arroyo-Cabrales (2002). The Florida records were briefly discussed by Morgan and Seymour (1997). None of these papers focused particularly on western USA jaguars. Here I provide an annotated list of the known fossil record of jaguars, or specimens purported to be jaguars, from the western USA (west of Texas). They are sorted into two groups, valid records and invalid records. All material was examined by the author unless noted otherwise. To date, the Oregon specimens are the most northerly jaguar specimens known in North America.

Valid *Panthera onca laugusta* records

Fossil Lake, Lake Co. Oregon

Material: UCMP 2979 distal portion of left radius, UCMP 26914 right metacarpal IV, UCMP 26966 right metatarsal IV.

Minimum number of individuals represented = 1

As summarized by Seymour (1993:348), this material was once thought to be Irvingtonian by Kurtén (1973:8) probably due to its large size. It is now considered to be younger, or Rancholabrean in age (Kurtén and Anderson, 1980:76). This locality was discussed by Elftman (1931) and Allison (1966). Two additional felid specimens from this locality are UCMP 26957 distal part of left tibia and UCMP 2980 an anterior thoracic vertebra, perhaps thoracic III. I cannot assign these latter two specimens to genus due to their incomplete nature, although the former appears closest to *Homotherium* sp.

“Oregon desert”, Oregon

Material: AMNH 8680 proximal part of ulna

Minimum number of individuals represented = 1

No more specific locality data is available for this specimen. It may derive from Lake Co. or Malheur Co. or another unknown locality.

Holden Cave, Shasta Co., California

Material: UCMP 130468 left metatarsal IV.

Minimum number of individuals represented = 1

This specimen is suspected to be Rancholabrean due to its associated fauna (H. Hutchison pers. comm.). It was originally part of UCMP 27308, a collection of *Ursus americanus* bones. Overall proportions plus all three jaguar characters identified by Seymour (1983) as diagnostic for MT IV confirm this identification.

Rancho La Brea tar pits, Los Angeles Co., California.

Material: All LACM HC material. 15 specimens found from five different pits, details were given by Jefferson (1983).

Minimum number of individuals represented = 5

Given the volume of carnivore material extracted from the Rancho La Brea tar pits, the few jaguar bones recovered speak to its rarity in the habitats represented by these deposits, or its ability to avoid being trapped in the sticky tar deposits. Bone collagen dates from the levels in the Hancock Park excavations that have yielded this jaguar material range in age from about 28.0 K to 11.6 K years BP (Jefferson, 1983; Marcus and Berger, 1984)

Irvington site 2, Alameda Co., California

Material: UCMP 71237, right dentary fragment with m1, a loose p4, and a p3 in a separate fragment.

Minimum number of individuals represented = 1

This specimen was discussed Kurtén (1973:6). The site was described by Savage (1951:219), and Lindsay et al. (1975) discussed the age of this site. Kurtén and Anderson (1980:27) note that a large *Smilodon* and an advanced *Mammuthus* occur at this site suggesting it might be younger than originally supposed. Schultz et al. (1985) state their suspicion that this site is late Irvingtonian in age. The tooth measurements fit very well with the Irvingtonian-aged jaguar from Hamilton Cave, West Virginia (USNM 299767) and the Rancholabrean-aged jaguar from Talara, Peru (ROM 2115), and the tooth morphology matches a cast of the Little Airplane Cave, Tennessee jaguar very well (ROM 4849). The dentary depth (dorso-ventrally) is small for a jaguar of this tooth size, due primarily to the fact that a subadult specimen is represented: p3 is still in the crypt and p4 was incompletely erupted when this individual died.

Smith Creek Canyon, White Pine Co., Nevada

Material: NSM 26WP46-1-09, left m1 lacking posterior root.

Minimum number of individuals represented = 1

According to Miller (1979:294), the presence of jaguar from this site is established by measurements (not given) on an isolated left m1. Other jaguar material apparently consists of a femur head, the distal end of a left femur, proximal end of an ulna, metatarsals, metacarpals, and first and third phalanges (Miller, 1979). I have been able to examine and confirm the identity only of the m1, whose length is 24.6 mm and width is 11.9 mm. The only other material located was the distal end of a metapodial (NSM 26WP46-2-09) that probably represents a left metatarsal IV fragment. This fragment is probably unidentifiable, but seems to match better with Pa. onca than Pu. concolor.

Dry Cave, Eddy Co., New Mexico

Material: All UTEP material. 7-1: left P3-4 in a maxillary fragment, right P4, left MC III, distal part of left MC II and distal part of right femur; 27-24 distal part of left MT II; 27-35 left MC III, right MT III and left MT IV; 27-42 left MC II; 27-43 phalanx one of right pes, digit III; 27-44 left MC I; 27-47 right MC III; 27-48 left maxilla with P3 and P4, right P4 in fragment of maxilla, right P3, 3 isolated incisors, phalanx one of right pes digit IV, and proximal part of right calcaneum.

Minimum number of individuals represented = 2

Both *Pu. concolor* and *Pa. onca* have been found in Dry Cave. So far the jaguar material is restricted to two sub-localities, South Chimney (UTEP 7), and Above Room of the Vanishing Floor (UTEP 27); MNI is one for each sub-locality.

Invalid records of *Panthera onca /augusta*

Delight (=Washtuckna Lake), Adams Co., Washington

Material: AMNH 8651, distal portion of left humerus, here identified as *Homotherium* sp.

Minimum number of individuals represented =1

Simpson (1941:22) identified this material as from Whitman Co. and considered this specimen to be large enough to be *Pa. atrox*, although he admitted it might be *Pa. onca*. Kurtén (1973:8) listed this specimen as a jaguar, and this assignment was followed by Kurtén and Anderson (1980:35) and Seymour (1983). The age of this locality is stated to be Irvingtonian or younger (Kurtén and Anderson, 1980). The locality was discussed by Matthew (1902) and Fry and Gustafson (1974). This is the most northerly record of purported jaguar. A re-examination of the single specimen reveals that it more correctly can be referred to *Homotherium* sp. for the following reasons: the lateral portion is greatly expanded, the medial portion projects in a bulbous way, the ectepicondylar foramen is placed more proximally on the shaft and the area just proximal to the lateral portion of the distal condyle is more indented. All but the second of these four characters can be seen illustrated in Figure 16 of Rawn-Schatzinger (1992).

In all these respects, this specimen is more similar to a cast of the Friesenhahn Cave, Texas, *Homotherium serum* (ROM 22631, cast of TMM 933-2206), than it is to available *Panthera* or *Smilodon* specimens.

Rome beds, Malheur Co., Oregon

Material: CIT VP 647 (now in LACM collection) right dentary fragment with roots of p3 and p4 and alveolus for lower canine, here identified as cf. *Panthera atrox*.

Minimum number of individuals represented = 1

The age of this specimen is unknown (Kurtén and Anderson, 1980:192); Kurtén (1973:5-6) guessed it might be Irvingtonian due to its size and northerly location, but these are hardly valid criteria. It was first discussed and illustrated by Merriam and Stock (1932:226-227; figure 152). Assessment of this specimen is difficult due to the lack of dentition, although overall conformation confirms the pantherine identification. By estimating the size of the teeth from the alveoli, and comparing these estimates with the tooth measurements presented in Seymour (1983), I conclude the following: the antero-posterior length of the lower canine (estimated at 25mm, but not estimated by Kurtén [1973]) is larger than any known specimen of *Pa. onca*, fossil or recent and about average for *Pa. atrox*; the p3 length (estimated at between 17.5 and 18.2 mm; Kurtén [1973] estimated an even larger 19 mm) is near the upper limit in size for *Pa. onca /augusta* and slightly below average for *Pa. atrox*; the p4 length (estimated at between 22.5 and 23.0 mm; Kurtén [1973] estimated an even larger 25 mm) is above average for *Pa. onca /augusta* and at the lower limit for *Pa. atrox*. In addition, the dentary depth at the diastema (45.8 mm; Kurtén [1973] estimated 45 mm) is at the upper limit for *Pa. onca /augusta* but average for *Pa. atrox*. We can conclude that this specimen represents either a *Pa. atrox* with a small p4, a *Pa. onca /augusta* with a record-sized canine, or another unknown pantherine; at this point I prefer the first of these possibilities. Kurtén (1973) made a case for the second of these possibilities, but also thought that this specimen aligned with the Curtis Ranch tooth which I suggest below represents cf. *Homotherium* sp.

Fossil Cave, Lava Beds National Monument, Siskiyou County, California

Material: LABE 2922 fragment of right P4

Minimum number of individuals represented =1

This single incomplete tooth was collected sometime in the 1930's and was said to be a jaguar left lower molar fragment. The symmetry of the cusp fragments indicates that it is actually a portion of the right upper carnassial, P4. The only parts of this tooth preserved are the anterior part of the metacone and posterior part of the paracone, hence no standard measurements can be collected from it. However, this tooth appears to be larger than living *Pa. onca*, and therefore, may represent *Pa. atrox*, but is probably too incomplete to be certain.

Curtis Ranch, Cochise Co., Arizona

Material: USNM 12865 right p4

Minimum number of individuals represented =1

This specimen was identified as jaguar by Kurtén (1973) and Kurtén and Anderson, (1980), but Seymour (1993) identified it as non-*Panthera*. Here I suggest it can be identified as cf. *Homotherium* sp. There are three other felid specimens from this locality, the first two of these were mentioned by Seymour (1993) as non-*Panthera*: USNM 12866 right calcaneum, USNM 12867 proximal part of left metatarsal III, and UALP 2479 fragment of left dentary. All three are here identified as *Miracinonyx* sp.

The age of this locality is now thought to be latest Blancan, or about 2.0 to 2.2 million years old (Morgan and White, 2005).

Algerita Blossom Cave, Eddy Co., New Mexico

Material: fragmentary metapodial UTEP

Minimum number of individuals represented =1

This specimen was reported by Harris (1993) as "*Panthera*?" but this identification has recently been rescinded by Harris and he now considers the specimen to represent *Puma*.

Pit N+W Animal Fair, Dry Cave, Eddy Co, New Mexico

Material: UTEP 122-665 Left upper P3

This specimen was reported by Harris (1993) as "*Panthera* cf. *onca*". I had examined this specimen in 1984 and had thought it was jaguar, but Harris' website now makes a case for this tooth to be *Pa. atrox* and I am inclined now to agree with him. It sits almost on the border between the two species but fits better as a very small *Pa. atrox* rather than a record-sized *Pa. onca /augusta*.

DISCUSSION

Fossil jaguars (*Pa. onca* /*augusta*) in North America tend to be larger than most living jaguars although there is overlap with the largest living subspecies from southern Brazil (Seymour, 1993). Geologically speaking, the older specimens tend to be larger than the younger ones (Seymour, 1993). This demonstrates a size change through time for this species. However, the whole animal did not change at the same rate. The limb bones shrunk proportionately more than did the teeth or skull, leaving the living species larger headed and shorter limbed than its oldest Pleistocene ancestors (Seymour, 1983; 1993). The taxonomic identification of these larger fossil jaguars is problematic as already noted. An increased sample size of North American fossil jaguar skeletons in the future might enable a re-consideration of these taxonomic issues.

On average in the living species, male jaguars are larger than females. Depending on the particular measurement, males average between 6% and 17% larger, a pattern called sexual dimorphism (Kurtén, 1973; Seymour, 1993). Jaguars are most dimorphic in their canines. Also, the largest living jaguars exist in the most southerly portions of the present range of this species, in southern Brazil and northern Argentina (subspecies *P. o. paraguensis*; Seymour, 1989).

The Oregon Caves individual appears to fit with the youngest fossil *Pa. onca* /*augusta* material, in that its limb and foot bones are relatively short, although its teeth are not that small. This suggests it might have been a male. Although there are some older faunal elements found in this cave, the proportions of this skeleton suggest that it may not belong with these. In other words, this animal came into the cave and died there at a later time than the rest of the material preserved in this cave.

GEOGRAPHICAL AND ECOLOGICAL CONSIDERATIONS

The earliest jaguars in North America may have been conspecific with the middle Pleistocene Eurasian *Pa. gombaszoegensis* (Hemmer, 1971; Kurtén, 1986) that apparently dispersed over the Bering land bridge to reach North America at that time or earlier (Johnson et al., 2006). More recent papers by European authors have taken to labelling this species *Pa. onca gombaszoegensis* to recognize this idea, but without morphological justification (for example Hemmer et al., 2003; Mol et al. 2011). The living species therefore can be considered a relict population of a once more widely distributed Holarctic form (Kurtén and Anderson, 1980; Kurtén, 1986). Obviously, these early jaguars would have survived on prey found in these regions, and so, even though we tend to think of the jaguar today as a more tropical-living form, their ancestors clearly were not.

Although living jaguars are reported from all habitat types within their range, including deserts, they live predominantly in areas with considerable plant cover, a water supply, and sufficient prey (Seymour, 1989). More than 85 prey species have been reported (Seymour, 1989), with a preference for diurnal terrestrial mammals with a body mass of > 1kg, although other kinds of prey are certainly taken (Emmons, 1987). Today, jaguars prefer peccaries, capybaras, pacas, agoutis, armadillos, caimans, and turtles (see references in Seymour, 1989). Most prey is taken in about the ratio of occurrence in an ecosystem, although jaguars in Peru were found to prey on peccaries more frequently than expected (Emmons, 1987). Indeed, this preference for peccaries is well-known and was used by Schultz et al. (1985) to suggest that the northerly distribution of the jaguar in the North American Pleistocene was limited by the occurrence of peccaries and perhaps also tapirs.

Where puma and jaguar ranges overlap, pumas tend to be more abundant in the drier areas and jaguars select wetter areas (Emmons, 1987; Schaller and Crawshaw, 1980). In contrast to puma, jaguars rarely take deer, although they may take brocket deer or marsh deer (Schaller and Vasconcelos, 1978; Watt, 1987). When beyond the range of these deer species, e.g. in Mexico, the White-tailed deer *Odocoileus virginianus* can be taken by both cats (Nuñez et al, 2000). There is broad overlap between the diet of jaguar and puma (Novack et al, 2005; Nuñez et al, 2000; Scognamillo et al., 2003). These two species can co-exist when the habitat is sufficiently heterogeneous or there is sufficient medium-sized prey for both species (Scognamillo et al., 2003). Also, pumas tend to have a broader food niche than jaguars, consuming smaller prey items more than the jaguar (Nuñez et al, 2000).

These two cat species co-occur in 10 out of the 15 Late Pleistocene fossil sites in Florida in which *Pu. concolor* is known [jaguar is much more common with 37 sites known in the Pleistocene of Florida; Morgan and Seymour (1997)]. This gives evidence that the broad overlap of habitat and prey use was probably present in the Pleistocene as well.

With these ecological parameters, it seems strange that the jaguar has been rarely recovered in the fossil record of the western USA, while it is much more common in the eastern USA. For the 11 western-most states [WA, OR, CA, ID, MT, WY, NV, UT, CO, AZ, NM] (and excluding Holocene localities), there are only 3 fossil jaguar records in the Faunmap database (although 8 are recorded here), while there are 19 *Pa. atrox* localities listed (5 considered questionable), 19 *Pu. concolor* localities (3 considered questionable), 20 *Lynx rufus* localities (3 questionable) and 13 *Smilodon* sp. localities (Graham and Lundelius, 1994). Therefore, it is apparent that the jaguar occurs in less than half as many fossil sites compared to most other fossil felids. Since jaguars exhibit a preference for entering caves in Appalachia (Guilday and McGinnis, 1972), then we would expect this species to be recovered in more western cave faunas.

Given that generally there was food and cover in the western USA, and not necessarily a bias against preserving felid specimens in the fossil record, we can conclude that Schultz et al. (1985) were most likely correct: that fossil jaguars are only rarely found north of the range of their preferred prey, peccaries, even though it is established that they will consume a wide variety of prey items. Schultz et al. (1985) provided a map showing the overall co-occurrence of fossil jaguar and fossil peccary ranges in North America. Even where the jaguar's range overlaps with peccary, though, such as Rancho la Brea, CA (where tens of thousands of bones of *Smilodon fatalis* and *Pa. atrox* also have been recovered) it is still relatively rare, with an MNI of only five for jaguar (Jefferson, 1983). All other locations in the western USA record an MNI of one, with the exception of Dry Cave, NM where there is evidence for two individuals in different parts of the cave system.

The importance of caves for the study of fossil cats

All five partial skeletons from Texas or eastern North America mentioned above were found in caves. In fact ,it is highly unusual for cat fossils found in regular deposits (fluvial, lacustrine, deltaic etc.) to consist of more than one tooth or bone. Six of 14 western sites discussed above were also found in caves including the ORCA site that produced ORCA 2021, the best western fossil jaguar skeleton known to date. More of this individual is still in the cave covered in flowstone. Associated bones or partial skeletons are the most useful when studying cat fossils, as individual teeth, for instance, can be tricky to identify because the teeth of different cats species are relatively simple and similar to each other. More jaguar material derived from caves is needed if we are to understand the full process of the size change that occurred in this lineage during the Pleistocene.

ACKNOWLEDGEMENTS

Thanks go to the collectors of ORCA 2021: Steve Knutson, Larry Coats, Blaine Schubert, Jim Mead and Greg McDonald. Greg McDonald got me involved with this project and Blaine Schubert gave me access to his field notes and provided Figure 1. John Roth (of ORCA) generously funded the carbon date. The following people either lent specimens or provided access to specimens, and I am grateful to all of them: Pat Holroyd (UCMP), Mary Merryman (LABE), Rachel Malloy (NSM), Art Harris (UTEP), Jeffrey Saunders (UALVP), Bob Purdy (USNM), Larry Barnes (LACM), John Alexander (AMNH), Chris Shaw (LACM HC). Sue Hobson assembled and manipulated the figures for which I am very grateful.

REFERENCES

Allison, I.S., 1966, Fossil Lake, Oregon: its geology and fossil faunas: Oregon State University Studies in Geology, v. 9, p. 1-48.

Arroyo-Cabrales, J., 2002, Registro fósil del jaguar: *in* Medellín, R.A. and others (compilers), El jaguar en el Nuevo milenio: Universidad Nacional Autónoma de México, p. 343-354.

Brown, D.E., and López-González, C.A., 2001, Borderland Jaguars: Tigres de la Frontera: Salt Lake City, University of Utah Press, 170 p.

Brown, D.F., 1983, On the status of the jaguar in the Southwest: Southwestern Naturalist, v. 28, p. 459-460.

Christiansen, P., and J.M. Harris, J.M., 2009, Craniomandibular morphology and phylogenetic affinities of *Panthera atrox*: implications for the evolution and paleobiology of the lion lineage: Journal of Vertebrate Paleontology, v. 29, p. 934-945.

Corgan, J., and Breitburg, E., eds., 1996, Tennessee's Prehistoric Vertebrates: Tennessee Division of Geology Bulletin, v. 84, p. 1-170.

Elftman, H.O., 1931, Pleistocene mammals of Fossil Lake, Oregon: American Museum Novitates, v. 481, p. 1-21.

Emmons, L.H., 1987, Comparative feeding ecology of felids in a Neotropical rainforest: Behavioral Ecology and Sociobiology, v. 20, p. 271-283.

Fry, W.E., and Gustafson, E.P., 1974, Cervids from the Pliocene of central Washington: Journal of Paleontology, v. 48, p. 375-386.

Graham, R.W., and Lundelius, E.L. Jr., 1994, Faunmap: a database documenting Late Quaternary distribution of mammal species in the United States: Illinois State Museum Scientific Papers, v. 25, pt. 2, p. 1-690.

Guilday, J.E., and McGinnis, H., 1972, Jaguar (*Panthera onca*) remains from Big Bone Cave Tennessee and east central North America: The National Speleological Society Bulletin, v. 34, p. 1-14.

Hall, E.R., and Kelson, K.R., 1969, The Mammals of North America: New York, Ronald Press Co., 1083 p.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001, PAST: Paleontological statistics software package for education and data analysis: Palaeontologia Electronica, v. 4, pt. 1, p. 1-9. Online at: http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Harris, A. H., 1993, Quaternary vertebrates of New Mexico, *in* Vertebrate Paleontology in New Mexico: New Mexico Museum of Natural History Bulletin, v. 2, p. 179-197.

Hemmer, H., 1971, Zur Charakterisierung und stratigrahischen Bedeutung von *Panthera gombaszoegensis* (Kretzoi, 1938): Neues Jahrbuch für Geologie und Paläontologie Monatschefte, v. 1971, p. 701-711.

Hemmer, H., Kahlke, R.-D., and Keller, T., 2003. *Panthera onca gombaszoegensis* (Kretzoi, 1938) from the Early Middle Pleistocene Mosbach Sands (Wiesbaden, Hessen, Germany) – a contribution to the knowledge of the variability and history of the dispersal of the jaguar: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 229, p. 31-60.

Hoffstetter, R.,1949, Les félins du Pléistocène de l'Équateur. I. Faune actuelle et methods de comparison: Travaux de l'Institut Français d'Études Andines, v. 1, p. 1-52.

Jefferson, G.T., 1983, First record of jaguar from the Late Pleistocene of California: Bulletin of the Southern California Academy of Sciences, v. 82, p. 95-98.

Johnson, W.E., Eizirik, E., Pecon Slattery, J., Murphy, W.J., Antunes, A., Teeling, E., and O'Brien, S.J., 2006, The late Miocene radiation of modern Felidae: a genetic assessment: Science, v. 311, p. 73-77.

Kurtén, B., 1973, Pleistocene jaguars in North America: Societas Scientiarum Fennica, Commentationes Biologicae, v. 62, p. 1-23.

Kurtén, B., 1986, Trans-Beringian carnivore populations in the Pleistocene, *in* Kontrimavichus, V.L., ed., Beringia in the Cenozoic Era: Rotterdam, A.A. Balkema, p. 349-355.

Kurtén, B., and Anderson, E., 1980, Pleistocene mammals of North America: New York, Columbia University Press, 442 p.

Kurtén, B., and Werdelin, L., 1990, Relationships between North and South American *Smilodon*: Journal of Vertebrate Paleontology, v. 10, p. 158-169.

Lindsay, E.H., Johnson, N.M., and Opdyke, N.D., 1975, Preliminary correlation of North American land mammal ages and geomagnetic chronology: University of Michigan Papers in Paleontology, v. 12, p. 111-119.

McCain, E.B., and Childs, J.L., 2008, Evidence of resident jaguars (*Panthera onca*) in the southwestern United States and the implications for conservation: Journal of Mammalogy, v. 89, p. 1-10.

McCrady, E., Kirby-Smith, H.T., and Templeton, H., 1951, New finds of Pleistocene jaguar skeletons from Tennessee caves: Proceedings of the United States National Museum, v. 101, p. 497-511.

Marcus, L.F., and Berger, R., 1984, The significance of radiocarbon dates for Rancho La Brea, *in* Martin, P.S., and Klein, R.G., eds., Quaternary Extinctions, a prehistoric revolution: Tucson, University of Arizona Press, p. 159-183.

Martin, R.A., 1993, Patterns of variation and speciation in Quaternary rodents, *in* Martin, R.A., and Barnosky, A.D., eds., Morphological Change in Quaternary Mammals of North America: New York, Cambridge University Press, p. 226-280.

Matthew, W.D., 1902, List of the Pleistocene fauna from Hay Springs, Nebraska: Bulletin of the American Museum of Natural History, v. 16, p. 317-322.

Merriam, J.C., 1919, Is the jaguar entitled to a place in the California fauna?: Journal of Mammalogy, v. 1, p. 38-40.

Merriam, J.C., and Stock, C., 1932, The Felidae of Rancho La Brea: Carnegie Institute of Washington Publication v. 422, p. 1-231.

Miller, S.J., 1979, The archaeological fauna of four sites in Smith Creek Canyon, *in* Tuohy, D.R., and Rendall, D.L., eds., The archaeology of Smith Creek Canyon, eastern Nevada: Nevada State Museum Anthropological Papers, v. 17, p. 271-329.

Mol, D., van Logchem, W., and de Vos, J., 2011, New record of the European jaguar, Panthera onca gombaszoegensis (Kretzoi, 1938), from the Plio-Pleistocene of Langenboom (The Netherlands): Cainozoic Research, v. 8, p. 35-40.

Morgan, G.S., and Seymour, K.L., 1997, Fossil history of the panther (*Puma concolor*) and the cheetah-like cat (*Miracinonyx inexpectatus*) in Florida: Bulletin of the Florida Museum of Natural History, v. 40, p. 177-219.

Morgan, G.S., and White, R.S. Jr., 2005, Miocene and Pliocene vertebrates from Arizona, *in* Heckert, A.B., and S.G. Lucas, S.G., eds., Vertebrate paleontology in Arizona: New Mexico Museum of Natural History and Science Bulletin, v. 29, p. 115-136.

Novack, A.J., Main, M.B., Sunquist, M.E., and Labisky, R.L., 2005, Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala: Journal of Zoology, London, v. 267, p. 167-178.

Nuñez, R., Miller, B., and Lindzey, F., 2000, Food habits of jaguars and pumas in Jalisco, Mexico: Journal of Zoology, London, v. 252, p. 373-379.

Rawn-Schatzinger, V., 1992, The scimitar cat *Homotherium serum* Cope: osteology, functional morphology and predatory behaviour: Illinois State Museum Reports of Investigations, v. 47, p. 1-80.

Rogers, J.G., 1997, Final Rule to Extend Endangered Status for the Jaguar in the United States, Document 97-19208, Federal Register 62(140), p. 39147-39157. Online at: http://endangered.fws.gov/r/fr97622.html

Roth, J., 1996, Fossil finds and the age of Oregon Caves: Crater Lake National Park Nature Notes, v. 27, p. 1-4. Online at: http:// www.nps.gov/crla/notes/vol27i.htm

Salles, L.O., 1992, Felid phylogenetics: extant taxa and skull morphology (Felidae, Aeluroidea): American Museum Novitates, v. 3047, p. 1-59.

Savage, D.E., 1951, Late Cenozoic vertebrates of the San Francisco Bay region: University of California Bulletin of the Department of Geological Sciences, v. 28, p. 215-314.

Schaller, G.B., and Crawshaw, P.G. Jr., 1980, Movement patterns of jaguar: Biotropica v. 12, p. 161-168.

Schaller, G.B., and Vasconcelos, J.M.C., 1978, Jaguar predation on capybara, Zeitschrift für Säugetierkunde, v. 43, p. 296-301.

Schultz, C.B., Martin, L.D., and Schultz, M.R., 1985, A Pleistocene jaguar from north-central Nebraska: Transactions of the Nebraska Academy of Sciences, v. 13, p. 93-98.

Scognamillo, D., Maxit, I.E., Sunquist, M., and Polisar, J., 2003, Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos: Journal of Zoology, London, v. 259, p. 269-279.

Seymour, K.L., 1983, The Felinae (Mammalia, Felidae) from the Late Pleistocene tar seeps at Talara, Peru, with a critical examination of the fossil and recent felines of North and South America [M.Sc. thesis]: Toronto, University of Toronto, 240 p.

Seymour, K.L., 1989, *Panthera onca*: Mammalian Species v. 340, p. 1-9.

Seymour, K.L., 1993, Size change in North American Quaternary jaguars, *in* Martin, R.A., and Barnosky, A.D., eds., Morphological Change in Quaternary Mammals of North America: New York, Cambridge University Press, p. 343-372.

Seymour, K.L., 1999, Taxonomy, morphology, palaeontology and phylogeny of the South American small cats (Mammalia: Felidae) [Ph.D. thesis], Toronto, University of Toronto, p. 929.

Seymour, K.L., 2003, The Oregon Caves fossil jaguar: National Park Service, Park Paleontology, v. 7, pt. 2, p. 3-4.

Seymour, K.L., Reynolds, A.R., and Churcher, C.S., 2018, *Smilodon fatalis* from Talara, Peru: Sex, Age, Mass, and Histology, *in* McDonald, H.G., Shaw, C., and Werdelin, L., eds., *Smilodon*: the Iconic Sabertooth: Baltimore, John's Hopkins University Press, p. 30-52.

Simpson, G.G., 1941, Large Pleistocene felines of North America: American Museum Novitates, v. 1136, p. 1-27.

Turgeon, S.C., and Lundberg, J., 2004, Establishing a speleothem chronology for southwestern Oregon: climatic controls and growth modeling, *in* Sasowsky, I.D., and Mylroie, J.E., eds., Studies of cave sediments: physical and chemical records: New York, Kluwer Academic/Plenum Publishers, p. 273-302.

Van Valkenburgh, B., 1990, Skeletal and dental predictors of body mass in carnivores, *in* Damuth, J. and MacFadden, B.J., eds., Body Size in Mammalian Paleobiology: New York, Cambridge University Press, p. 181-205.

Watt. E.M., 1987, A scatological analysis of parasites and food habits of jaguar (*Panthera onca*) in the Cockscomb Basin of Belize [M.Sc. thesis]: Toronto, University of Toronto, 90 p.

Werdelin, L., 1983, Morphological patterns in the skulls of cats: Biological Journal of the Linnean Society, v. 19, p. 375-391.