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NEW FINDS OF PLEISTOCENE JAGUAR SKELETONS FROM TENNESSEE CAVES

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Only very recently has Pleistocene jaguar material been recognized in North America, and thus far extremely few parts have been described in the literature. Aside from *Panthera atrox*, which is now considered a closely related species, only about 12 or possibly 14 fragments that can be assigned to very close relatives of the modern *Panthera onca* have been mentioned in print. Probably the most important feature of the two finds here recorded is the fact that together they include nearly every bone in the body. Accordingly, it should now be possible for the first time to determine fairly definitely the relationships of the extinct form.

We are indebted to the Carnegie Foundation and to the University of the South for grants that made this study possible.

OCCURRENCE OF THE NEW MATERIAL

This paper is concerned with two skeletons found in caves in the St. Louis limestone of the Cumberland Plateau in Tennessee. The first was discovered by the three of us in 1944 in Little Salt River Cave in Franklin County, near the Tennessee–Alabama border. This is an active cave with a stream running through the main passage and issuing on the valley floor. The skeleton was found approximately one-half mile from the entrance in an upper passage accessible only by means of a short vertical climb of some 15 feet. The passage is low (about 30 inches high) and broad (15 to 30 feet), and is richly ornamented with very remarkable helictites. At what originally appeared to be its end, the passage is crossed by a screen of stalactite

columns, so closely spaced that only a near approach discloses the presence of a room beyond. Breaking through, we discovered the cat bones on the inner, or blind side of the rock columns. The animal had lain down on its left side on a wet clay floor to die, and the bones had sunk partly into the clay before drippings from a crack in the roof started the slow process of sealing up everything under a layer of calcium carbonate. The rock had accumulated to a thickness of 1 to 3 inches on top of the clay, leaving only a few parts projecting above, and these exposed portions were themselves encrusted with a thin spatter deposit about an eighth of an inch or less in thickness. We found that by using hammers and chisels we could remove the rock in plates from the surface of the clay, which was still wet and soft beneath, and that the ends of the bones that projected into the clay were cleaned effectively with just a little washing. The other portions, however, were very much more difficult to free from their matrix. On the suggestion of Dr. C. S. Piggot, who at that time was executive director of the Committee on Geophysical Sciences of the Research and Development Board of the National Military Establishment, Dr. C. L. Gazin, curator of the division of vertebrate paleontology of the United States National Museum, came to our assistance and very kindly arranged to have the skeleton cleaned by some of the members of his staff.

The second discovery was made by us in Saltpeter Cave, just north of Sparta, in White County, Tenn., in the fall of 1947. About half a mile back in the cave, in a large room at least 40 feet high and having a dry, loose, sandy earth floor, we uncovered the second skeleton, about as extensive as the first and in many details conveniently complementary. Since it was not encased in rock, it was easily cleaned, but was very fragile.

Each individual was intact when originally deposited in the cave, and the situation of each virtually precludes the possibility of the carcass having been washed in from the outside. The first was found in a high upper passage with no entrance large enough for such a body except the one by which we came, and water definitely did not flow that way. The second was found in a dry cave, located several hundred feet above the present valley floor, that must have been dry at the time the cat died and probably long before that. (All the caves in the Sparta area have their entrances high up on the sides of the mountains and seem to have been formed at a time when the valley floor was several hundred feet higher than it is today.) Both locations are at least half a mile from the entrances of the caves, too far back for casual migrants, so there is every reason to believe that both cats reached the spots in which we found them under their own power. Very few kinds of animals penetrate caves beyond the twilight area near the mouth. It is possible, of course, that sick or injured animals wander farther back to die, but it seems much more

probable, in view of the distances involved and the difficulty of access in one case, that these cats, like cave bears, cave rats, and racoons, frequented the inner recesses of caves, a habit not previously attributed to any members of the cat family in America so far as we know, although *Felis leo spelaea* in Europe was a lion that seems to have frequented caves.

EXTENT OF THE NEW DISCOVERIES

The specimen from Salt River Cave has been deposited in the permanent collections of the United States National Museum. The specimen from Saltpeter Cave will remain in the University of the South, at Sewanee, Tenn. In each case the bones belong to an associated skeleton. We have found two individuals, and we know exactly which bones belong to each, so ratios between different parts of the body can be studied with significance.

Specimen No. 1 (*U. S. N. M. No. 18262*), *from Salt River Cave.*—The skull and axial skeleton are less well represented than the appendages. There is a left half of the calvarium plus the left zygomatic arch. The right side of the specimen does not extend much beyond the saggital crest, but includes most of the lambdoidal ridge. The ossicles are still in place in the left middle ear, though the arm of the malleus is broken off. Of the upper teeth only the right P^4 is present and in good condition. There is a separate fragment of the left malar. Both lower canines and a tip of an upper are present, but the rest of the lower jaw, except for the left coronoid process, is missing. (See plate 16.)

There are very few good vertebrae. These include the third, fourth, and fifth lumbars, the sacrum, and 5 anterior caudals. In the pectoral appendage all bones are present on either the right side or the left, and for the most part they are in excellent condition. The scapula lacks about two-thirds of its glenoid or inferior border. The pelvic appendage is similarly complete, all parts being present on either the left or the right.

Specimen No. 2, from Saltpeter Cave.—In many respects this specimen is complementary to No. 1. The skull had been broken into some 70 pieces, but when reassembled it was much more extensive than the other. The rostral region in particular, which is totally missing in No. 1, is complete in No. 2 except for teeth. The only tooth of the upper jaw in good shape is P^3. The upper canines are present only in splinters, and the incisors are represented only by their roots. Particularly noteworthy is the absence of any indication of P^2 on either side. Part of the paracone and the metacone of P^4 are preserved on the right side, and the left M^1 is complete. The lower jaw is in fairly good condition, though it, too, had to be reassembled from several

fragments. P_3 is present on the right, M_1 on the left, and the left lower canine is perfect. The incisors have all been broken off. The sagittal crest of the skull had been chewed away by rodents and had to be restored according to its dimensions in No. 1. Both occipital condyles and petrosal bones are present, and the left tympanic bulla and zygomatic arch are complete. As finally reconstructed the skull is sufficiently complete to allow all measurements referred to in this paper to be taken from the authentic parts without having to trust any "restorations."

All vertebrae are represented in No. 2 except the seventh lumbar, the sacrum, and the caudals. As for the pectoral appendage, only the humerus and the glenoid border of the left scapula are preserved. The pelvic appendage is complete on the left down to the middle of the ankle. There are no cuneiforms, metatarsals, or phalanges. Ribs exist only in numerous fragments.

Together these two finds include all parts of the skeleton except the intermediate and distal caudal vertebrae, the seventh lumbar vertebrae, the clavicles, the hyoid apparatus, the sternum, the crowns of the incisor teeth, the upper canines (present in No. 2, but splintered), and the second premolars of the upper jaw.

EXTENT OF PREVIOUS DISCOVERIES

In 1872 and 1873 Professor Leidy announced the discovery of a supposed new species of great Pleistocene cat, which he named *Felis augustus*. The type specimen was a left P^4, which had been collected by Hayden on the Niobrara River in Nebraska, and which Leidy declared to be "too large to have belonged either to the panther or the jaguar" and "too small to have belonged to the extinct American Lion, or *Felis atrox*." There was another tooth in this collection not figured or described by Leidy but since then attached by someone else to the fragment of maxilla in the type specimen where it obviously belongs, and these are now cataloged as specimen No. 125 in the United States National Museum.

Leidy also mentions and figures the distal end of a humerus collected by Hayden at the same time and place (though not definitely associated with the teeth) and assigns it tentatively to the same new species. (The humerus fragment is now U.S.N.M. No. 147.) This assignment is definitely a mistake. We have examined it carefully and are certain that it cannot have belonged to the same individual or species from which the teeth came. Now that we have associated skeletons of cats with teeth of approximately the same size, it is easy to see that the humerus fragment is altogether too large. Unfortunately it does not

include the parts that would make possible an easy and certain identification of species, but it can be only from one of two—*Smilodon californicus* or *Panthera atrox*, most likely the latter.

Another error in Leidy's paper, and one that has misled later authors, is his assignment of this material to the Pliocene (not Miocene as Simpson says), thus allowing them to overlook comparisons with Pleistocene cats. This is what happened in the next pertinent paper, in which O. P. Hay (1919) described and figured an upper left carnassial from the No. 2 bed at Vero, Fla. This he named *Felis veronis*, dismissing the possibility of its belonging to *Felis augustus* with the statement, "*Felis augustus*, besides belonging to the Arikaree of the Tertiary, differs in various ways from the Vero specimen." We have compared the two and are confident that Hay must have been convinced primarily by the supposed difference in stratigraphic horizons. The structural differences between the specimens are in features too variable in other cats to warrant serious consideration.

G. G. Simpson described (1929) several isolated teeth from Seminole Field, Fla., as belonging to *Felis veronis*. And in 1928 or 1929, while collecting at Melbourne, Fla., Dr. J. W. Gidley discovered a right lower jaw with canine and P_3–M_1, two carnassials from different individuals, and one lower molar, all from cats of this same general range of dimension. He did not publish these finds, and only the lower jaw has ever been mentioned in the literature. This lower jaw (U.S.N.M. No. 11470) was described and figured by G. G. Simpson (1941b).

Drs. J. W. Gidley and C. L. Gazin (1938) described from Cumberland Cave, Md., a scapholunar, two calcanea, an astragalus, a second metacarpal, and third and fifth metatarsals, which they assigned to "*Felis* near *atrox*." Simpson examined them and concluded (1941b) that they belonged to some group distinct from jaguar, puma, or *atrox*, but that, "supposing all to represent a single species," they were more like puma than anything else.

It does not seem legitimate to lump these bones together as Simpson does in his figure 7.[1] The P^4 included there was assigned by the original authors to the fossil puma *Felis inexpectata* and was never considered to belong to the same individual, or species, as the tarsal bones, for instance. It was separately cataloged as U.S.N.M. No. 11890 instead of U.S.N.M. No. 12840. Furthermore, even those cataloged together as U.S.N.M. No. 12840 clearly include at least two individuals, probably three, and probably two different species. The metatarsal III, scapholunar, two calcanea, and astragalus, are all distinctively jaguaroid and we would accept them as *Panthera augusta*, or, as the original authors said, "near *atrox*." But the two calcanea

[1] See footnote 3, last paragraph (p. 507).

are both lefts and therefore cannot possibly have belonged to one individual. The remaining two bones (metatarsal V and metacarpal II) we consider unquestionably puma.

In 1939 and 1940 J. Kyker and C. Hicks, employees in Craighead Caverns, near Sweetwater, Monroe County, Tenn., discovered footprints and several bones which G. G. Simpson (1941a) identified as jaguar. These bones, now in the American Museum of Natural History, include the right ramus of the lower jaw (A.M.N.H. No. 32633), lacking the incisors and the coronoid process and the medial portion of the articular condyle; the right side of the muzzle and cheek (A. M. N. H. No. 32635) with I^1–I^3, C, and P^2–P^3; the glenoid angle of the right scapula (A.M.N.H. No. 32638); and a left second metatarsal (A.M.N.H. No. 32637).

DISCUSSION

Among fossil cats heretofore described and probably specifically distinct, the closest relationship to the new material is found in what Leidy (1852) originally defined as *Felis atrox*. He based this species upon a lower jaw fragment containing the canine, two premolars, and the molar. The type specimen belonged to the American Philosophical Society (now Academy of Natural Sciences of Philadelphia No. 12546), and it was unlabeled when Leidy studied it. He inferred that it probably came from Natchez, Miss., as it was kept with some fossils sent from that locality by William Henry Huntington. Its origin is thus not certainly known, and it is interesting that no other fossils definitely identified as belonging to the same species have since been found in the eastern part of North America.

A large number of disassociated bones of this species, now called *Panthera atrox*, came out of the famous asphalt pits at Rancho La Brea, Calif., and were elaborately studied by Merriam and Stock (1932) and compared with other species, ancient and modern. These authors concluded that *P. atrox* resembles the jaguar (*Panthera onca*) more closely than any other species and differs primarily in size, being the largest of all cats. They also decided that another species named by Leidy, *Felis imperialis*, which Freudenberg (1910) had called a giant jaguar, is synonymous with *P. atrox* and is based upon smaller individuals.

Simpson (1941) reaffirmed these affinities of *P. atrox* and *P. onca* and suggested a subgenus, *Jaguarius*, to indicate this relationship. He also decided that *Felis augustus* Leidy and *Felis veronis* Hay cannot be separated from each other or from *P. onca* by any reliable criteria of more than subspecific value. He therefore ascribed Leidy's material from Nebraska, Hay's from Florida, and his own from Tennessee to *Panthera* (*Jaguarius*) *onca augusta*.

It is to this material that ours is certainly most closely related. We began by calling our first specimen *P. atrox* because of the striking similarity of shape of all the parts. We recognized that it was small and, at first, thought it was possibly young and immature at the time of death. However, the removal of the rock from the surface of the bones, which permitted a clear view of the epiphyseal regions and sutures, and the discovery of a second individual settled the question of maturity. The epiphyses are completely united to the diaphyses, the sutures in the skull are in most regions wholly overgrown, and the tips of the canines and cusps of the premolars show wear. Both of these, then, were old and fully grown individuals and as such are definitely too small to be *P. atrox* unless there exists a small race of that species, a condition that has not thus far been proved.

In deciding whether they belong to any previously described form it is necessary to compare them with the parts that have been available, and from which the other types have been defined. Unfortunately, *P. augusta* and *P. veronis* were based solely upon upper carnassials, and so the investigation must begin there. Comparison of the type specimens with each other and with our material reveals minor morphological differences among the three in the proportion of width across the protocone to the greatest length of the tooth, in the shape of the cranial border, and in the development of the anteroexternal cuspule; but except for size the features of the type specimens can all be matched among contemporary jaguar teeth. The species *veronis* is invalid, then, as it cannot be separated from the previously described *augusta;* and if *augusta* is defined in terms of the upper carnassial alone, there is nothing to keep our material out of that category (species or subspecies as the case may be).

It is true that Leidy included in his description of the type of *P. augusta* a piece of humerus that did not belong there, but if we eliminate that, the definition of *P. augusta* is: a true cat having a P^4 too large for panther or jaguar and too small for *P. atrox*. To the question, "Is this a valid type?" the answer must depend upon measurements and statistical analysis of the length of the P^4 in the three fossils (*P. augusta*, *P. veronis*, and our specimen from Salt River Cave), and in *P. onca* and *P. atrox*, since the panther can be eliminated at once as altogether too small in that feature. The data are as follows:

The greatest length of the crown in the upper carnassial in our fossil is 31.2 mm. In the types of *P. augusta* and *P. veronis* this dimension, as we measure it, is 33.3 mm. (The measurements given by Simpson for these two types are slightly different, but their average is about the same as our figure.) The data for *Panthera onca* are

taken from table 1 of Nelson and Goldman [2] (1933) and table 102 of Merriam and Stock (1932). They are based upon 30 specimens, including adult males and females of all subspecies, located in the United States National Museum, the American Museum of Natural History, the Chicago Natural History Museum, and the Museum of Comparative Zoology. The combination of all these data shows a range of 23.4 mm. to 29.2 mm. with a mean of 26.6 mm. and a standard deviation of ± 1.64 mm.

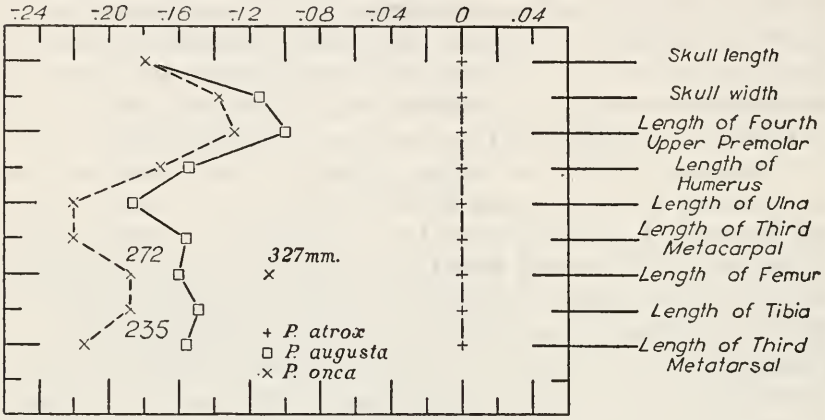

FIGURE 97.—Logarithmic-difference graph for the structures listed on the right, using *Panthera atrox* as the standard of reference and comparing it with *P. onca* and *P. augusta*. The numbers given refer to the actual dimensions in millimeters. The point marked 327 *mm.*, which is not on any of the three curves, is discussed in footnote 4.

The deviation of our fossils is 2.8σ, so that the odds against their belonging to any one of the contemporary subspecies of *P. onca* are 195 to 1. The odds against the types of *P. augusta* and *P. veronis* being simply exceptionally large jaguars of any subspecies still existing are more than 15,000 to 1. And finally, if no subspecies or species of cat other than the jaguars now surviving existed in Nebraska, Florida, and Tennessee in Pleistocene times, the chance of finding three with the dimensions of these fossils would be 2×10^{-11} percent. That is, the odds against it would be 5 trillion to 1! We are not,

[2] In the paper by Nelson and Goldman appears one anomalous measurement that we have tried to verify, but could not. An adult female of *"Felis onca paraguensis,"* U.S.N.M. No. 4361, from Argentina (San José, Entre Ríos) is recorded as having an upper carnassial of 30.8 mm. length. This is strange for several reasons. It is more than 4 per cent bigger than the next largest record. It is from a female, which would be expected to be smaller than the largest males. And most important of all, it is from an animal not at all large in other dimensions. The skull, for instance, is recorded as measuring only 261 mm., in contrast to those from males of *P. paraguensis, P. milleri,* and *P. onca,* which run from 295 mm. to 302 mm. That a relatively small animal should have so disproportionately large a tooth seems too improbable to be accepted without careful confirmation. Unfortunately the specimen seems to have disappeared, and so we were not able to measure it. Of course, it is not certain that the measurement was inaccurate, but the odds against so large a departure from the mean are about 100 to 1; and for such a departure to occur in a relatively small animal seems almost incredible. We therefore suspect an error in the record.

therefore, justified in putting these three fossils into any of the contemporary subspecies of jaguar.

The chances of their belonging to *Panthera atrox*, while not quite so improbable, are also remote. The crown length of P^4 in *P. atrox* averages 39.4 mm. with a minimum of 35.0 mm., a maximum of 45.0 mm., and a standard deviation of ±2.43 mm. The deviation of our fossils is 3.37σ, which means that there is about one chance in 1,400

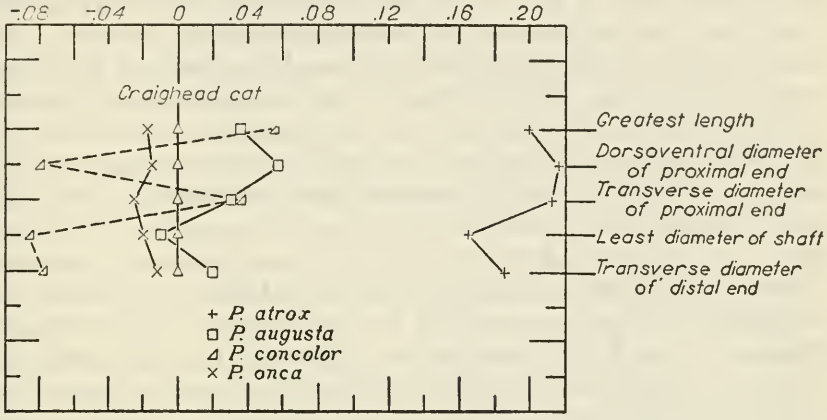

FIGURE 98.—Ratio graph for the second metatarsal, based upon Simpson's (1941b) figure 3, to which has been added the line for *Panthera augusta*.

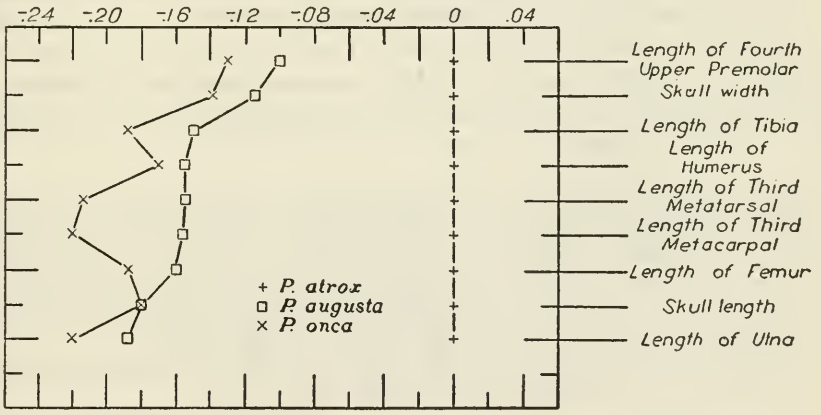

FIGURE 99.—Ratio graph based upon the same data as figure 97, but with the order of structures changed to make comparison of *Panthera atrox* and *P. augusta* clearer, with *P. atrox* still used as standard.

that they could be *P. atrox*. The other two (*P. augusta* and *P. veronis*) might occur as normal variations of *atrox* in about 1.23 percent of all cases, or against odds of 80 to 1. That three premolars of these dimensions would be found if *P. atrox* were the only form involved has an improbability of 10 million to 1.

It seems clear, then, that we are dealing with a different strain of cats, one that was intermediate between *P. atrox* and *P. onca*, and one that, for reasons of priority, should be called *P. augusta.*

It cannot be determined by a study of P^4 alone whether our *P. augusta* was an independent species, or a subspecies of *P. onca* or of *P. atrox.* Even if good fortune should provide us with a large number of these intermediate cats, and the size of their premolars should overlap the range of *P. atrox* on the one side and of *P. onca* on the other (the above statistics are not concerned with this possibility and do not make it at all improbable), this would not indicate that they were all one species. The species *P. atrox* is characterized by many other consistent peculiarities of form, and enough specimens showing such features have already been assembled to make it clear that the species possessing this particular constellation of morphological characters was restricted in range of size of premolars within fairly clear limits. No specimen of *P. atrox* thus far found possesses premolars of the dimension of the one we have found, and the implication of the mathematics is that none existed that did possess such premolars. The same is true for all known races of *P. onca.* In other words, the probability is that a cat having a carnassial measuring from 31 to 34 mm. will be found to differ in other morphological features from *atrox* and *onca.*

To explore further this possibility we have constructed the graphs shown in figures 97 and 98, using Simpson's (1941b) convenient method of plotting logarithmic differences. The characteristics chosen for reference are those used both by Merriam and Stock in their table 98 for comparison of *P. atrox* and *P. spelaea* and by Simpson (1941b, fig. 10) for *P. atrox* and *P. onca.*[3]

[3] The virtue of this kind of graph is that it facilitates the comparison of relative proportions of different parts of the body in different animals. If the proportions of *P. atrox* be taken as the standard for comparison, as in figure 97, the base or zero line represents these, and is straight. Another animal with the same relative proportions would appear on the graph as another straight line, to the left if smaller in all parts, to the right if larger in all parts. A crooked line represents an animal with different proportions, irrespective of the actual dimension of any of the parts. These dimensions may, of course, be calculated if such data as those in the next paragraph are provided.

The base line in figure 97 represents the average values for all the measurements listed on the right. As given in Merriam and Stock they are:

Structure	*Millimeters*
Condylobasal length of skull	353.0
Bizygomatic breadth of skull	250.4
Length of P^4	39.4
Length of humerus	368.5
Length of ulna	416.0
Length of third metacarpal	126.6
Length of femur	421.3
Length of tibia	361.7
Length of third metatarsal	146.1

Such dimensions, which determine the zero line, should always be recorded in connection with any such graph, as they enable the reader both to compute any other dimensions indicated, and to add to the graph additional lines representing other material for comparison.

Examination of figure 97 shows that our fossils, while smaller, resemble *P. atrox* in the proportions of the humerus, third metacarpal, femur, tibia, and third metatarsal—in other words, in most of the limb proportions. The skull is relatively broader and the P^4 proportionately much larger. The length of the skull and the length of the ulna are reduced in about the same degree, having approximately the same relation to each other as in *atrox*, but being smaller in proportion to the other parts of the body.

The Recent jaguar skeleton used for comparison in these figures (U.S.N.M. No. 49393) was chosen for its large size and is therefore not typical in total dimension, but it is presumably normal in the relative proportions of interest here. It has a skull as long as that of our Saltpeter Cave fossil (our specimen No. 2), but all other parts of the skeleton are smaller. The reduction is most conspicuous in the metapodials, which are proportionately shorter than in either of the fossil forms.[4]

The metapodials of these cats are equally distinctive in features other than length. Figure 98 shows Simpson's original ratio diagram comparing the second metatarsal in *P. concolor*, *P. onca*, *P. atrox*, and the fossil jaguar from Sweetwater, Tenn. (see Simpson, 1941b, p. 6, fig. 3), with one line added to represent our new material. It will be seen that although Simpson's jaguar fossil was quite similar to the Recent jaguar, ours differs from it in relative proportions as much as does *P. atrox*, and in a rather similar way; so that ours resembles

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Regarding the interpretation of the graph, it should be noted that relative proportions within the body of any one species (any one line on the graph) are not directly indicated, but only how these relative proportions compare with those of the standard of reference. Thus, if the maximum width of the head is shown displaced to the right and the length of the ulnar to the left, this does not mean that the diameter of the head is greater than the length of the forearm. It means that the head is broader in proportion to other parts of the body in *P. onca* than it is in *P. atrox*. Similarly, if the length of P^4 is displaced farther to the right than is the skull width, it does not mean that the length of this tooth is greater than the width of the skull, but that it is proportionately more enlarged in *P. onca* than is the width of the skull, when both of these are compared with the corresponding proportions in *P. atrox*. This is a tremendously valuable kind of information and it is better exhibited by this means than by any other we know.

It should be noted also that the usefulness of ratio diagrams is completely destroyed when isolated bones from different individuals are mixed together. To have any significance at all, each curve in the graph must represent parts of a single individual, or of two or more individuals definitely known to be of the same species and size, or well established averages for parts of a single species.

[4] One measurement indicated in Simpson's figure 10 is surprising. Though no actual dimensions are given in the figure, the base line is said to be taken from Merriam and Stock. The average length of the femur in *P. atrox* as given by these authors (1932, p. 190) is 421.3 mm. On this scale the femur length indicated for *P. onca* would have to be about 327 mm. We have not seen a jaguar femur anywhere near that size. The largest we have measured is 272 mm. This was from a very large but not maximal specimen. If the same proportions exist in the largest, the femur should not exceed about 282 mm. If we had used Simpson's figure we should have had to claim another distinction between *P. onca* on the one hand and *P. atrox* and *P. augusta* on the other, but the curve was left as found from our own measurements.

P. atrox more than it does *P. onca.* None of these is at all similar to the puma, so we have not included *concolor* in other figures.[5]

One of the features in which *P. augusta* is most dissimilar to modern jaguars is the ratio of width of muzzle to condylobasal length of skull.

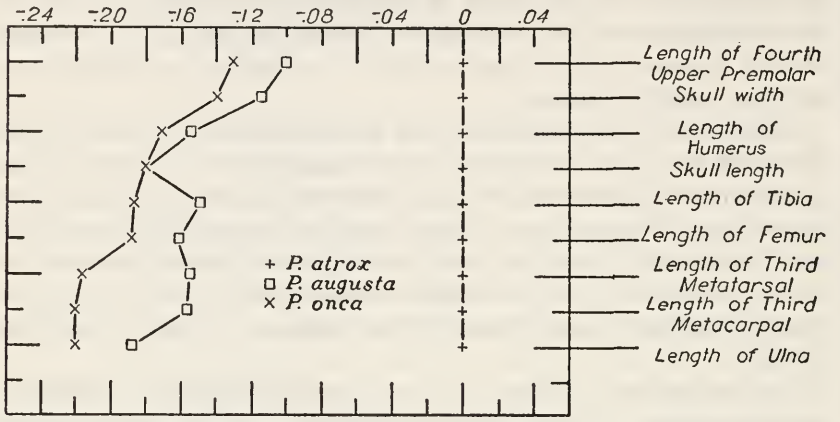

FIGURE 100.—Ratio graph with the order of structures changed to facilitate comparison of *Panthera atrox* and *P. onca.*

In our Saltpeter Cave fossil this ratio has the value 0.347. In a series of jaguars in the United States National Museum it varies from 0.297 to 0.324 with an average value of 0.309 and a standard deviation of ± 0.008. The departure of the ratio in the fossil from the mean for the modern jaguar is 4.75σ. The odds against such a variation occurring in any known subspecies of jaguar are considerably greater than 15,000 to 1. On the other hand, *P. augusta* and *P. atrox* resemble each other sufficiently closely in this ratio to be inseparable by reference to it. *P. atrox* averages only 0.328 ± 0.0129. The *P. augusta* specimen shows a deviation of 0.019, which is only about 1.46 times the standard error and cannot be taken seriously.

Furthermore, *P. augusta* is sharply distinct from *P. onca* in several other features not previously mentioned, and in these it resembles *P. atrox* so closely as to be inseparable with reference to them. Thus, the inflation of the frontal region in *P. augusta* and *P. atrox* is quite

[5] The Sweetwater material, however, is not all from one individual. The teeth will not occlude properly. The lower jaw is decidedly too big for the upper jaw. So at least two individuals are involved, and possibly more. Presumably the mandible belongs to the same species as do our fossils, but we are not at all sure about the second metatarsal. Since the Sweetwater bones are quite definitely not from one individual, there is no compelling *a priori* reason for accepting them as one species. We shall not pursue this puzzle any further in the absence of more material, but the possibility should be borne in mind that there may have existed in Pleistocene times both a true jaguar with the shortened and characteristic metapodials, and another cat, *P. augusta,* which was more like *P. atrox* in these and several other parts, but only slightly larger than *P. onca.* More associated skeletons will be needed to settle this point.

conspicuous in contrast to that of *onca*. This shows up in the interorbital distance, in the maximal width of the frontals at their zygomatic (or postorbital) processes, and in the minimal diameter of the frontal region. In *P. augusta* and *P. atrox* all these dimensions are

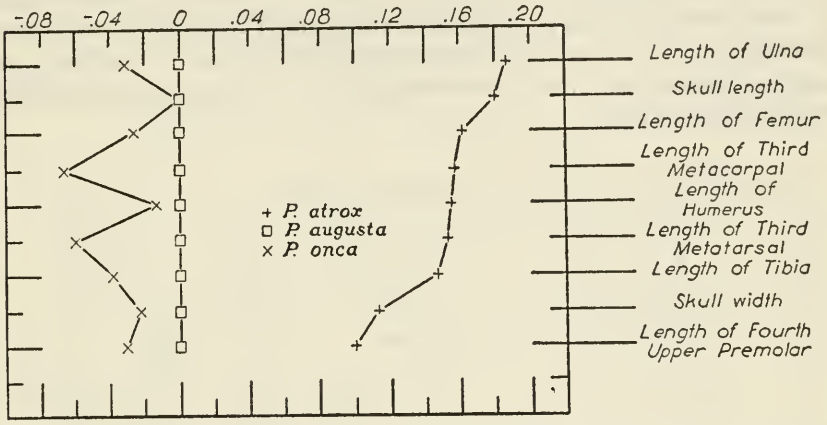

FIGURE 101.—Ratio graph with *Panthera augusta* as standard and structures listed so as to emphasize resemblances between *P. augusta* and *P. atrox*. The dimensions for the zero line are:

Structure	*Millimeters*
Length of ulna	270.0
Condylobasal length of skull	233.0
Length of femur	291.0
Length of third metacarpal	88.0
Length of humerus	257.5
Length of third metatarsal	102.2
Length of tibia	257.0
Bizygomatic breadth of skull	191.6
Crown length of P^4	31.2

much greater in proportion to the condylobasal length of skull than they are in *P. onca*. For instance, the condylobasal length in *P. augusta* is only about 4.07 times the interorbital distance—in contrast to about 5.05 times for *P. onca*. Similarly, the proportions of the calcaneum are just about identical in *P. augusta* and *P. atrox*, and quite different in *P. onca*, where this bone is not only proportionately shorter but has a much elongated medial astragalar facet.

We thus find our *P. augusta* intermediate in many respects between its contemporary, *P. atrox*, and the modern jaguar, *P. onca*. It is nearer *P. onca* in size, in breadth of skull at the zygomatic region, and in shortness of the ulna; but it is nearer *P. atrox* in the proportionate length of the metacarpals and metatarsals, in the relative lengths of all the limb bones except the ulna, in the relative breadth of the muzzle and frontal region, and in the proportions of the calcaneum.

It is distinct from each in having proportionately the shortest skull and the largest P^4. All three are certainly related cats within the subgenus *Jaguarius*.

Clearly *P. onca* and *P. atrox* are considerably different creatures, and while it is difficult to decide whether *P. augusta* is closer kin to *P. onca* or to *P. atrox*, it is likewise clear that *P. augusta* is an intermediate form with more or less equivalent degrees of similarity to each in different ways, as is demonstrated by the ratio graphs in figures 99, 100, 101, and 102.

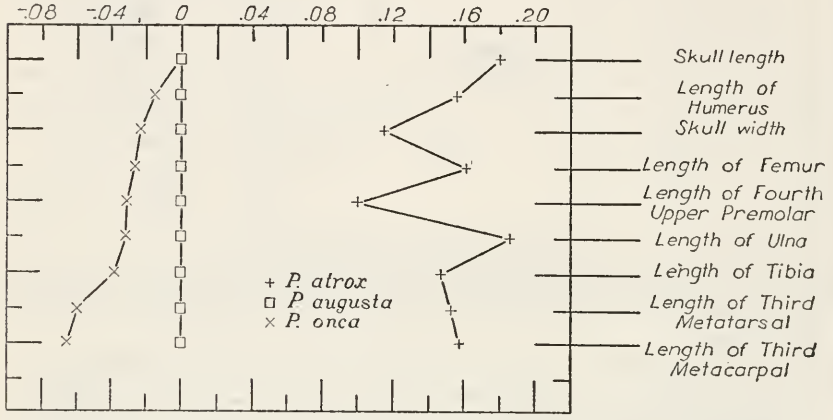

FIGURE 102.—Ratio graph with *Panthera augusta* as standard and structures listed so as to emphasize resemblances between *P. augusta* and *P. onca*.

Historically the concept of species was first applied to organisms at one chronological horizon, and in that context its implications are fairly clear. *P. atrox* and *P. augusta* were contemporary, and statistical data for *P. atrox* are sufficient to show that the species did not include the variations exhibited by *P. augusta*. These two, then, are separate species. They did not intergrade during the late Pleistocene. And if, as seems to be the case, the modern jaguars are at least as different from the fossil *P. augusta* as the latter was from *P. atrox*, then the only practical usage seems to be to recognize all three as separate and valid species.

We have decided, therefore, to call our specimens from Little Salt River and Saltpeter Caves *Panthera* (*Jaguarius*) *augusta*, and to include in this classification Leidy's "*Felis augustus*," Hay's "*Felis veronis*," Simpson's "*Panthera* (*Jaguarius*) *onca augusta*" (with the possible exception of the second metacarpal), and probably some of the Cumberland Cave specimens (with the reservations noted on pages 501 and 502).

LITERATURE CITED

FREUDENBERG, W.
1910. Die Säugetierfauna des Pliocäns und Postpliocäns von Mexico. I. Carnivoren. Geol. Paleont. Abh., new ser., vol. 9, pp. 195–231.

GIDLEY, J. W., and GAZIN, C. L.
1938. The Pleistocene vertebrate fauna from Cumberland Cave, Md. U. S. Nat. Mus. Bull. 171, 99 pp., 50 figs., 10 pls.

HAY, O. P.
1919. Description of some mammalian and fish remains from Florida, of probably Pleistocene age. Proc. U. S. Nat. Mus., vol 56, pp. 103–112, 3 pls.

LEIDY, JOSEPH.
1852. Description of an extinct species of American lion: *Felis atrox*. Trans. Amer. Philos. Soc., new ser., vol. 10, pp. 319–321.
1872. Remarks on some extinct vertebrates. Proc. Acad. Nat. Sci. Philadelphia, vol. 24, pp. 38–40.
1873. Contributions to the extinct vertebrate fauna of the western territories. *In* Hayden, Rep. U. S. Geol. Surv. Territories, vol. 1, pp. 14–358.

MERRIAM, J. C., and STOCK, CHESTER.
1932. The Felidae of Rancho La Brea. Carnegie Inst. Washington Publ. No. 422.

NELSON, E. W., and GOLDMAN, E. A.
1933. Revision of the jaguars. Journ. Mamm., vol. 14, pp. 221–240.

SIMPSON, GEORGE GAYLORD.
1929. Pleistocene mammalian fauna of the Seminole Field, Pinellas County, Fla. Bull. Amer. Mus. Nat. Hist., vol 56, pp. 561–599, 22 figs.
1941a. Discovery of jaguar bones and footprints in a cave in Tennessee. Amer Mus. Nov., No. 1131.
1941b. Large Pleistocene felines of North America. Amer. Mus. Nov., No. 1136.

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