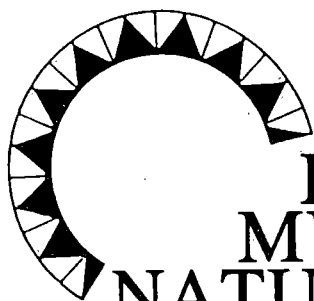


# BULLETIN

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**FOSSIL HISTORY OF THE PANTHER (*PUMA*  
*CONCOLOR*) AND THE CHEETAH-LIKE CAT  
(*MIRACINONYX INEXPECTATUS*)  
IN FLORIDA**

**Gary S. Morgan and Kevin L. Seymour**

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# FOSSIL HISTORY OF THE PANTHER (*PUMA CONCOLOR*) AND THE CHEETAH-LIKE CAT (*MIRACINONYX* *INEXPECTATUS*) IN FLORIDA

Gary S. Morgan<sup>1</sup> and Kevin L. Seymour<sup>2</sup>

## ABSTRACT

Fossils of the Florida panther or puma (*Puma concolor*) are reported from 15 late Pleistocene (Rancholabrean) sites and one Holocene archaeological site on the Florida peninsula (11 of these are unpublished records). This large cat was widely distributed in Florida during the late Pleistocene, from as far north as Columbia County near the Georgia state line, throughout the northern and central portions of the state, along both the Atlantic and Gulf coasts, and as far south as Dade County at the southernmost tip of the peninsula. *P. concolor* is unknown from late Pleistocene faunas in the Florida panhandle. The living Florida panther, *P. concolor coryi*, is now restricted to southernmost peninsular Florida in Glades, Hendry, Collier, and Dade counties, although it was fairly common farther north along the central Atlantic coast until the late nineteenth century. All of the *P. concolor* fossils reported here compare closely in size and morphology to Recent skulls and postcranial skeletons of *P. concolor* from southern Florida. The associated mammalian faunas from the Florida sites containing *P. concolor* indicate that this species is restricted to the late Rancholabrean and Recent (between 130 ka and the present).

The cheetah-like cat, or puma-like cat, *Miracinonyx* is identified from eight late Pliocene and Pleistocene sites in Florida, only two of which were published previously. *M. inexpectatus* occurs in four Florida late Pliocene and early Pleistocene sites, including the late Blancan Santa Fe River 2A and Northport faunas and the early Irvingtonian Inglis 1A and Leisey Shell Pit local faunas. Three associated metacarpals from the Rancholabrean Lecanto 2A local fauna are tentatively identified as *M. inexpectatus*, representing one of the youngest records of this species. Fossils identifiable only as *Miracinonyx* sp. are recorded from the late Irvingtonian Coleman 2A local fauna, from a Plio-Pleistocene locality in Port Charlotte and from the Pleistocene Cardinale site, an underwater fossil site in the Gulf of Mexico located 25 km offshore. *Miracinonyx* appears to be closely related to the genus *Puma* and is distinguished from *P. concolor* by its somewhat larger size and conspicuous elongation of the limbs and metapodials.

## RESUMEN

Los fósiles de la pantera o puma de la Florida (*Puma concolor*) son reportados de 15 sitios del Pleistoceno tardío (Rancholabreano) y de un sitio arqueológico del Holoceno en la península de la Florida. Este gato de gran tamaño estaba ampliamente distribuido en la Florida durante el Pleistoceno tardío, desde tan al norte como el condado de Columbia próximo a la línea estatal de Georgia, a través de las porciones norteañas y centrales del estado, a lo largo de ambas costas la atlántica y la del Golfo, y tan al sur como en el condado de Dade en la punta más sureña de la península. *P. concolor* es desconocido de la fauna del

<sup>1</sup> New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104.

<sup>2</sup> Department of Palaeobiology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Pleistoceno tardío en la región noroeste de la Florida. La pantera de la Florida que actualmente existe, *P. concolor coryi*, esta ahora restringida a la parte más sureña de la península de la Florida en los condados de Glades, Hendry, Collier, y Dade, aunque ésta era regularmente común más al norte a lo largo de la costa central atlántica hasta finales del siglo diecinueve. Todos los fósiles de *P. concolor* reportados aquí se asemejan bastante en tamaño y morfología a los cráneos y esqueletos postcraneales de *P. concolor* del Reciente en el sur de la Florida. Las faunas de mamíferos asociadas a los sitios de la Florida que contienen *P. concolor* indican que ésta especie esta restringida al Rancholabreano tardío y al Reciente (entre 130 kilo años y el presente).

El gato semejante al cheetah, o semejante al puma, *Miracinonyx* es identificado en ocho sitios del Plioceno tardío y del Pleistoceno en la Florida, solo dos de estos sitios fueron reportados previamente. *M. inexpectatus* ocurre en cuatro sitios del Plioceno tardío y del Pleistoceno temprano en la Florida, incluyendo las faunas locales del Santa Fe River 2A y Northport del Blancan tardío y del Inglis 1A y Leisey Shell Pit del Irvingtoniano temprano. Los tres huesos asociados del metacarpo de la fauna local del Lecanto 2A del Rancholabreano son tentativamente identificados como *M. inexpectatus*, representando uno de los más recientes registros de ésta especie. Los fósiles identificados únicamente como *Miracinonyx* sp. son registrados en la fauna local de Coleman 2A del Irvingtoniano tardío, en una localidad en Port Charlotte del Plio-Pleistoceno y en el sitio Cardinale del Pleistoceno, que es un sitio de fósiles bajo el agua en el Golfo de México localizado a 25 Km mar afuera. *Miracinonyx* aparenta estar cercanamente relacionado con el género *Puma* y se distingue de *P. concolor* por su aproximado gran tamaño y su conspicua elongación de las extremidades y de los metapodios.

## ACKNOWLEDGMENTS

Many individuals have collected fossils of *Puma concolor* and *Miracinonyx* from sites throughout Florida and generously donated their finds to the Florida Museum of Natural History (FLMNH). The largest fossil sample of *P. concolor* from Florida is from the Cutler Hammock site, which was excavated by archaeologists from the Metro-Dade Archaeology Division and the Dade County Archaeological Conservancy under the direction of Robert Carr. Access to the Cutler Hammock site was granted by the Deering family, who donated the entire Cutler collection of vertebrate fossils to the FLMNH. Lewis D. Ober, William G. Weaver, and several of their students from Miami-Dade Community College excavated the Monkey Jungle Hammock Site and deposited the fossils in the FLMNH. Frank Dumond, general manager of Monkey Jungle, kindly permitted access to the property. Erika Simons and Laurie Wilkins helped collect panther fossils from the Wekiva River. Arthur Poyer collected a maxilla of *P. concolor* from Orange Lake 2A. Robin Brown donated a panther mandible from the Peace River to the FLMNH collection. Thomas Cardinale brought the underwater site in the Gulf of Mexico west of St. Petersburg (now named the Cardinale Site in his honor) to the attention of FLMNH paleontologists and donated the fossils from this site, including a *Miracinonyx* radius. Steven Beck contributed a large collection of vertebrate fossils from the Lecanto 2A site to the FLMNH, including the metacarpals of *Miracinonyx inexpectatus* described here. Ralph (Tony) Estevez donated a metatarsal of *M. inexpectatus* from the Leisey Shell Pit to the FLMNH. We are grateful to Erika Simons who took the photographs in Figures 5-7 and helped produce all the photographic plates. Marc Frank provided information on fossil felid specimens in the FLMNH Vertebrate Paleontology Collection. We thank Laurie Wilkins and Charles Woods of the FLMNH Mammalogy Collection for allowing us to examine their excellent collection of Recent skulls and postcranial skeletons of *P. concolor coryi*. John Eisenberg, Richard Franz, and two anonymous reviewers made numerous helpful comments on the manuscript. We are particularly grateful to John Eisenberg for providing funds from the Ordway endowment for the publication of this paper.

## INTRODUCTION

*Puma* (= *Felis*) *concolor*, the puma or Florida panther, previously was identified from six Pleistocene fossil sites in Florida (Webb, 1974a; Kurtén, 1976; McDonald, 1990). This meager record is surprising considering the large number of Pleistocene vertebrate faunas known from Florida (Webb, 1974a; Kurtén and

Anderson, 1980), and the fact that southern peninsular Florida is the only region east of the Mississippi River where *P. concolor* still survives. Fossils of *P. concolor* reported here add 11 new localities from the state. The number of Florida sites known to contain *P. concolor* is now 16, which also takes into account one previous record that is shown below to be erroneous. Of these sites, 15 are late Pleistocene (late Rancholabrean) in age and one is a Holocene archaeological site. We also identify the cheetah-like or puma-like cat, *Miracinonyx*, a probable fossil relative of *P. concolor*, from eight Florida sites ranging in age from late Pliocene (late Blancan and earliest Irvingtonian) to Rancholabrean.

Simpson (1929) first reported a puma-like cat from the Pleistocene of Florida. He referred an upper carnassial from Seminole Field in Pinellas County to *Felis* cf. *F. inexpectata* (Cope). It should be noted here that the generic names for the large cats have changed significantly over the years. We repeat the generic names as they were used by the original authors to avoid confusion in this brief historical review. Discussion under the Systematic Paleontology section clarifies our opinion on the generic designations of the Florida fossil cat species reviewed here. Ray (1958) identified a radius, astragalus, six phalanges, and two fragmentary metapodials from Melbourne in Brevard County as *Felis* cf. *F. (Puma) inexpectata*. Ray noted that the Melbourne fossils could not be clearly separated from comparable elements of extant *Felis concolor*. The next mention of fossil panther from Florida was by Kurtén (1965, fig. 9) who referred a single astragalus from Reddick 1A in Marion County to *Felis concolor*. Kurtén regarded the Reddick astragalus as indistinguishable in size and morphological characters from the living puma.

Webb (1974a) listed *Felis concolor* from the Santa Fe 2A locality, a mixed late Blancan and Rancholabrean assemblage. This record apparently was based on a metacarpal that is here re-identified as a Blancan specimen of *Miracinonyx inexpectatus* (see discussion below), as no other fossils of *F. concolor* are present in the Florida Museum of Natural History collections from Santa Fe 2A. Kurtén (1976) reviewed the fossil history of pumas (*Felis concolor*) and puma-like cats (*F. inexpectata*) in North America. He referred specimens from Blancan and Irvingtonian sites to *F. inexpectata* and Rancholabrean fossils to the living species *F. concolor*. Kurtén distinguished *F. inexpectata* from *F. concolor* by its larger size and more elongated postcranial elements. Kurtén (1976) reported fossils of *F. concolor* from four Florida Rancholabrean sites, three listed above, including Seminole Field, Melbourne, and Reddick 1A, and one that represented a new record, a maxillary fragment with P3-P4 from Devil's Den in Levy County. The fossils from Seminole Field and Melbourne, identified as *F. concolor* by Kurtén (1976), were the same specimens earlier referred to *Felis* cf. *F. inexpectata* by Simpson (1929) and Ray (1958), respectively.

Van Valkenburgh et al. (1990) transferred *F. inexpectata* to the genus *Miracinonyx*, along with the closely related species *M. trumani*, and also suggested

that *M. inexpectatus* might be near the ancestry of the puma. They referred several specimens from the earliest Irvingtonian (latest Pliocene) Inglis 1A site in Citrus County, Florida, to *M. inexpectatus*. McDonald (1990) listed *F. concolor* from the Rancholabrean Warm Mineral Springs site located in Sarasota County in the southwestern portion of the peninsula. Berta (1995) identified a metatarsal of *M. inexpectatus* from the early Irvingtonian (early Pleistocene) Leisey Shell Pit located along the eastern shore of Tampa Bay in Hillsborough County.

Prior to 1980 there were few Recent specimens of the Florida panther, *Puma concolor coryi*, in museum collections. The comparatively large sample of Florida panther specimens now available in the Mammalogy Collection of the Florida Museum of Natural History permits a considerably more detailed analysis of individual, sexual, and geographical variation in this subspecies than was previously possible. Unfortunately, this large sample of museum specimens has come at great cost to the dwindling population of the Florida panther, since the majority of these endangered cats were killed by vehicles as they attempted to cross busy South Florida highways. Wilkins et al. (1997) provides a detailed analysis of individual and geographical variation in the pelage and crania of extant *P. concolor coryi*.

## METHODS AND ABBREVIATIONS

We have examined and confirmed the identification of all *Puma concolor* fossils known from Florida, with one exception. *P. concolor* fossils from eleven of these sites were previously unreported. The single panther fossil we were not able to examine was an astragalus (UF 8895) from the late Rancholabrean Reddick 1A site, identified and figured by Kurtén (1965, fig. 9B). Several specimens from Reddick 1A in the James Gut Collection, including this *P. concolor* astragalus, were catalogued into the UF Vertebrate Paleontology Collection but were never received by the museum. Sometime prior to Gut's death, Kurtén obviously had the opportunity to examine fossils in Gut's private collection.

Dental terminology is standard: incisors (I/i), canines (C/c), premolars (P/p) and molars (M/m). Upper teeth are indicated by upper case letters (e.g. P4 is the upper fourth premolar) and lower teeth are indicated lower case letters (e.g. m1 is the lower first molar). For comparative purposes, we examined and measured 20 skulls (12 males, 8 females) and 18 postcranial skeletons (10 males, 8 females) of Recent adult *Puma concolor coryi* from southern peninsular Florida, primarily Collier and Dade counties.

Detailed map data, field notes, and other information on most Florida sites containing fossils of *Puma concolor* and *Miracinonyx* are on file in the Vertebrate Paleontology Collection of the Florida Museum of Natural History. *P. concolor* and *Miracinonyx* fossils from Florida are housed in the following museums (with acronyms): Field Museum of Natural History, Chicago (FMNH), Florida Museum of Natural History, University of Florida, Gainesville (UF), American Museum of

Natural History, New York (AMNH), Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), and Royal Ontario Museum, Toronto (ROM).

### SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Felidae Gray, 1821

*Puma concolor* (Linnaeus, 1771)

### Material Examined

All fossils of *Puma concolor* identified from Florida are listed below. The fossils are listed separately for each site with their catalogue numbers and a brief description of the element. Each specimen was directly compared with the large Recent sample of *P. concolor* skulls, teeth, and postcranial bones from Florida to confirm its identification. The features illustrated in Seymour (1983) and other publications listed below were used where possible.

#### Late Pleistocene (late Rancholabrean)

Ichetucknee River, Columbia County: UF 45420, left metacarpal III.

Santa Fe River 1, Columbia/Gilchrist County line: UF 124614, right mandible with m1.

Devil's Den, Levy County: UF 9256, partial left maxilla with P3-P4; UF 133802, left m1.

Wekiva River, Levy County: UF 124387, right metacarpal III; UF 124388, right metacarpal IV; UF 124389, left metacarpal V; UF 124386, left proximal femur; UF 124390, right metatarsal III; UF 124391, left proximal metatarsal IV.

Orange Lake 2A, Marion County: UF 134300, partial right maxilla with P3-M1.

Reddick 1A, Marion County (from Kurtén, 1965: fig. 9): UF 8895, left astragalus.

Silver Springs, Marion County: UF 51221, left ulna.

Rock Springs, Orange County: UF 8954, phalanx.

Melbourne, Brevard County: MCZ 17791, right radius, right astragalus, right distal metatarsal II, and at least two phalanges.

Seminole Field, Pinellas County: AMNH 23540, incomplete left P3; AMNH 23541, right P4.

Leisey Shell Pit 2, Hillsborough County: UF 125192, juvenile left metacarpal IV.

Peace River, Hardee County: UF 45949, left mandible with broken canine and worn p3-p4; UF 93415, left p4.

Warm Mineral Springs, Sarasota County: UF 23870, left distal femur.

Cutler Hammock, Dade County: UF 172944, right P4; UF 124376, left mandible with p3-m1; UF 93415, left p4; UF 124377, left humerus; UF 124378, right distal humerus; UF 124379, left metacarpal II; UF 124380, left proximal metacarpal III; UF 124382, right proximal metacarpal V; UF 124381, left proximal metacarpal V; UF 128051, proximal phalanx of right manus, digit V; UF 124384, left astragalus; UF 124382, right proximal metatarsal V; UF 124383, left proximal metatarsal V.

Monkey Jungle Hammock, Dade County: UF 45393, right P4; UF 45392, left m1; UF 24520, partial right p3; UF 124385, left metacarpal V.

### Holocene

Granada Site, Dade County: UF zooarchaeology collection (uncatalogued), distal epiphysis of metapodial and phalanx.

### Distribution

All of the fossil sites in Florida that have produced specimens of *Puma concolor* are indicated on the map in Figure 1. The 15 late Pleistocene sites and one Holocene archaeological site are distributed throughout peninsular Florida, from Columbia County in the northern part of the state not far from the Georgia line to Dade County at the extreme southeastern tip of the peninsula. Seven sites are located in Columbia, Levy, and Marion counties in northern Florida, two are in the central part of the state (one in Orange County and one near the central Atlantic Coast in Brevard County), three are in southwestern Florida along the Gulf Coast (one each in Pinellas, Hillsborough, and Sarasota counties), one is in south-central Florida in Hardee County, and three sites are located in southernmost Florida in Dade County. Fossils of *P. concolor* currently are unknown from the Florida panhandle. Fewer late Pleistocene fossil sites are known from the panhandle than from the peninsula, but at least five late Rancholabrean river-bottom/spring deposits in this region have diverse mammalian faunas, including the Aucilla River in Jefferson and Taylor counties, Wacissa River in Jefferson County, Wakulla Springs and Wakulla River in Wakulla County, St. Marks River in Leon and Wakulla counties, and Chipola River in Jackson County (Webb, 1974a).

There are three major types of Rancholabrean fossil deposits in Florida that have produced fossils of *Puma concolor*. River or spring deposits comprise eight of the fossil sites from which panthers are known, sinkhole/cave/fissure deposits account for four panther records, and sites deposited in coastal rivers or lagoons constitute the remaining three sites. Three of the underwater sites, Devil's Den, Rock Springs, and Warm Mineral Springs, probably were dry caves or sinkholes in the late Pleistocene, and thus could be classified in either of the first two locality types. Most of the late Pleistocene sites known from Florida fall into one of these



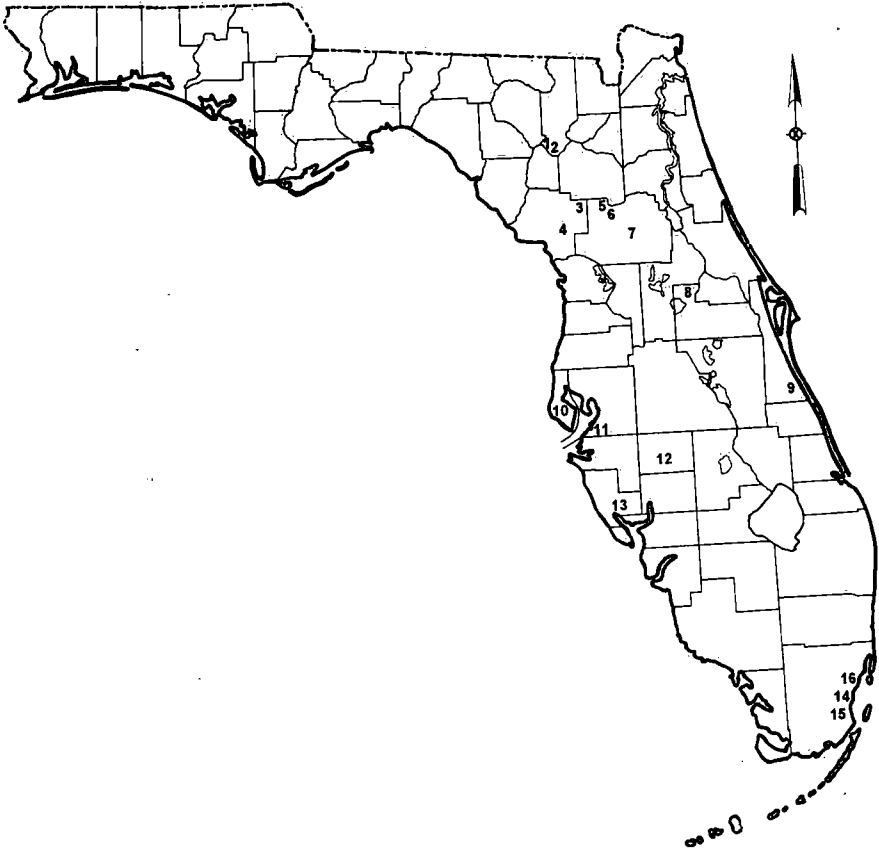


Figure 1. Late Pleistocene (Rancholabrean ) and Holocene sites from Florida containing *Puma concolor*. Rancholabrean: 1. Ichetucknee River, Columbia County; 2. Santa Fe River 1, Columbia/Gilchrist County line; 3. Devil's Den, Levy County; 4. Wekiva River, Levy County; 5. Orange Lake 2A, Marion County; 6. Reddick 1A, Marion County; 7. Silver Springs, Marion County; 8. Rock Springs, Orange County; 9. Melbourne, Brevard County; 10. Seminole Field, Pinellas County; 11. Leisey Shell Pit 2, Hillsborough County; 12. Peace River, Hardee County; 13. Warm Mineral Springs, Sarasota County; 14. Cutler Hammock, Dade County; 15. Monkey Jungle Hammock, Dade County. Holocene: 16. Granada Site, Dade County.

three categories (Webb, 1974a), and thus the type of site probably has little effect on the presence or absence of *P. concolor* fossils. This is not unexpected considering that living Florida panthers and western pumas/mountain lions have very large home ranges and, as a consequence, regularly travel through a number of habitats over a wide geographical area.

Wilkins et al. (1997) map the distribution of Recent specimens of *Puma concolor coryi* collected in the Florida peninsula over the past century. Florida panthers are now restricted to the southern third of the peninsula in Glades, Hendry, Collier, and Dade counties; however, in the late 19th century a number of specimens were collected along the central Atlantic coast in Volusia, Brevard, and Indian River counties. *P. concolor* probably was found throughout the Florida peninsula prior to the arrival of Europeans. The fossil record clearly establishes that *P. concolor* was widely distributed in the Florida peninsula in the late Pleistocene.

### Taxonomy

Until recently most members of the family Felidae were placed in the genus *Felis*. Mammalogists generally have used the binomen *Felis concolor* for the puma/mountain lion/cougar and the subspecies name *F. concolor coryi* for the Florida panther. Over the past decade or so felids have been split into a number of genera on the basis of their phylogenetic relationships. As a consequence, felid systematists now prefer to use the genus *Puma* for the puma or Florida panther (Glass and Martin, 1978; Kral and Zima, 1980; Collier and O'Brien, 1985; Herrington, 1986; Wayne et al., 1989; Van Valkenburgh et al., 1990; Salles, 1992; Janczewski et al., 1995), and we follow this convention in the present paper. We do note, however, as did Salles (1992:4), that at this point in the understanding of felid phylogenetics, the choice of generic rank for felids is still largely arbitrary.

### Diagnosis

The puma is different from all other living cats because of its combination of large size, unicolor coat as an adult, relatively long tail, and small head. These external features are, however, little help to the paleontological diagnosis of this species or its relatives. Werdelin (1983) used a correspondence analysis to show that the puma has the cranial proportions of a small cat, while attaining the large body size of a pantherine cat. He also pointed out that the puma differs from other cat species in its short, broad teeth, especially the p4 and m1, and relatively small canines compared with the pantherines. When compared to the jaguar, in particular, the puma has a relatively small canine, larger p3, and longer m1 (Werdelin 1983:385). Comparisons with small cats, such as the jaguarundi (*Herpailurus yagouaroundi*), show the puma to have relatively round canines and a long P3 (Glass and Martin, 1978). These two authors also found that living pumas have a relatively smaller p4, larger m1, larger canines, smaller P3, and less reduced protocone on P4, when compared to a possible fossil relative, such as *Miracinonyx trumani*. Other osteological features that can be used to help differentiate puma skulls from jaguar skulls were described by Hoffstetter (1949), whereas postcranial features differentiating puma bones from jaguar bones were

elucidated by Seymour (1983). We utilized these two works for the identification of isolated feline fossils.

In summary, there are few if any unique osteological features within this group of cats. Identification of fossil material is difficult, with direct comparison preferred in all cases. Furthermore, there were several other large felids present in the Pleistocene of Florida whose bones might be confused with puma fossils. Van Valkenburgh et al. (1990) and Seymour (1993) noted that several of these felids, in particular *Smilodon gracilis*/*S. fatalis*, *Miracinonyx inexpectatus*, and *Panthera onca* often occur together in sites, so that the problem of identification of isolated remains is not imaginary. Papers illustrating many bones of these species are as follows: Berta (1987) for *Smilodon gracilis*; Rawn-Schatzinger (1992) for *Homotherium serum*, Merriam and Stock (1932) for *Panthera atrox* and *Smilodon fatalis*, Van Valkenburgh et al. (1990) for *Miracinonyx inexpectatus* and *M. trumani*, and Seymour (1983) for *Panthera onca*. Although these publications are excellent resources, they tend to illustrate the bones of one or two species and generally lack differential diagnoses which might be used to identify isolated feline fossils.

### Descriptions and Comparisons

The fossils listed above under Material Examined are very similar in size and morphology to bones and teeth of living *Puma concolor* from Florida and are confidently referred to that species. Some confusion existed in the past concerning the few previously published fossil records of *P. concolor* from Florida. Kurtén (1965, 1976) rectified this situation by demonstrating that some of the large felid fossils from Melbourne and Seminole Field were conspecific with *P. concolor*. We found the *P. concolor* samples from both Melbourne and Seminole Field to be a mixture of species. Included within the Melbourne material (MCZ 17791) is a right radius and right astragalus of *P. concolor*. One distal metapodial (a right radius and right astragalus of *P. concolor*, but the other (a left metatarsal V) represents a canid. Of the six phalanges, two are middle phalanges and four are proximal phalanges. The middle phalanges are diagnostically felid-shaped, but we were unable to identify them to species. The smallest and one of the largest of the four proximal phalanges most likely represent *P. concolor*, but the other two large phalanges are heavier and probably belong to *Panthera onca*, the jaguar. The Seminole Field material as identified above differs somewhat from Kurtén (1965, 1976). We agree that AMNH 23541 represents a right P4 of *P. concolor*. However, there are five isolated teeth catalogued under AMNH 23540, only one of which represents *P. concolor* (an incomplete left P3); the other teeth represent primarily jaguar. Kurtén (1965, 1976) identified an astragalus of *Puma concolor* from Reddick. The Reddick astragalus was not available for study (see more detailed discussion above in Methods section), but its identification has not been questioned.

Table 1. Measurements of the upper dentition of Pleistocene and Recent *Puma concolor* from Florida. The mean (x) and observed range (O.R.) are provided for the Recent sample, which consists of 20 individuals (12 males, 8 females) from Collier and Dade counties in southern Florida.

	P3		P4	
	L	W	L	W
Recent				
x	14.2	8.7	21.7	11.6
O.R.	12.5-15.3	8.0-10.1	19.2-23.3	10.4-12.8
Devils Den				
UF 9256	14.3	8.7	23.1	11.6
Orange Lake 2A				
UF 134300	15.1	8.2	23.9	11.8
Cutler Hammock				
UF 172944	—	—	21.5	10.5
Monkey Jungle Hammock				
UF 45393	—	—	22.4	11.0
Seminole Field				
AMNH 23540	—	8.5	—	—
AMNH 23541	—	—	21.4	10.6

Measurements of the upper dentition (P3 and P4) of *Puma concolor* fossils from Florida are provided in Table 1. This table also includes comparative dental measurements for 20 adult skulls (12 males, 8 females) of extant *P. concolor* from southern Florida. Kurtén (1973a) presented comparative measurements of the P4 and m1 of Recent *P. concolor* from throughout the species' wide geographical range (from western Canada to southern Argentina). Although several of the measurements for fossils of *P. concolor* from Florida are slightly outside the size range of Recent Florida panthers, these measurements fit well within the size range of the species as a whole.

The fossil sample of *Puma concolor* from Florida includes two maxillary fragments with P3-P4, one is the specimen from Devil's Den (UF 9256) reported by Kurtén (1976) and the second is a recently collected fossil from Orange Lake 2A (UF 134300). Both of these maxillae are illustrated in Figure 2. There are also three isolated P4s, one each from Monkey Jungle Hammock (UF 45393; see Figs. 2E, F), Cutler Hammock (UF 172944), and Seminole Field (AMNH 23541), as well as a partial P3 from Seminole Field (AMNH 23540). The measurements in Table 1 reveal that, with one minor exception, all of the fossils are within the size range of the modern sample of *P. concolor* from southern Florida. The P4 from

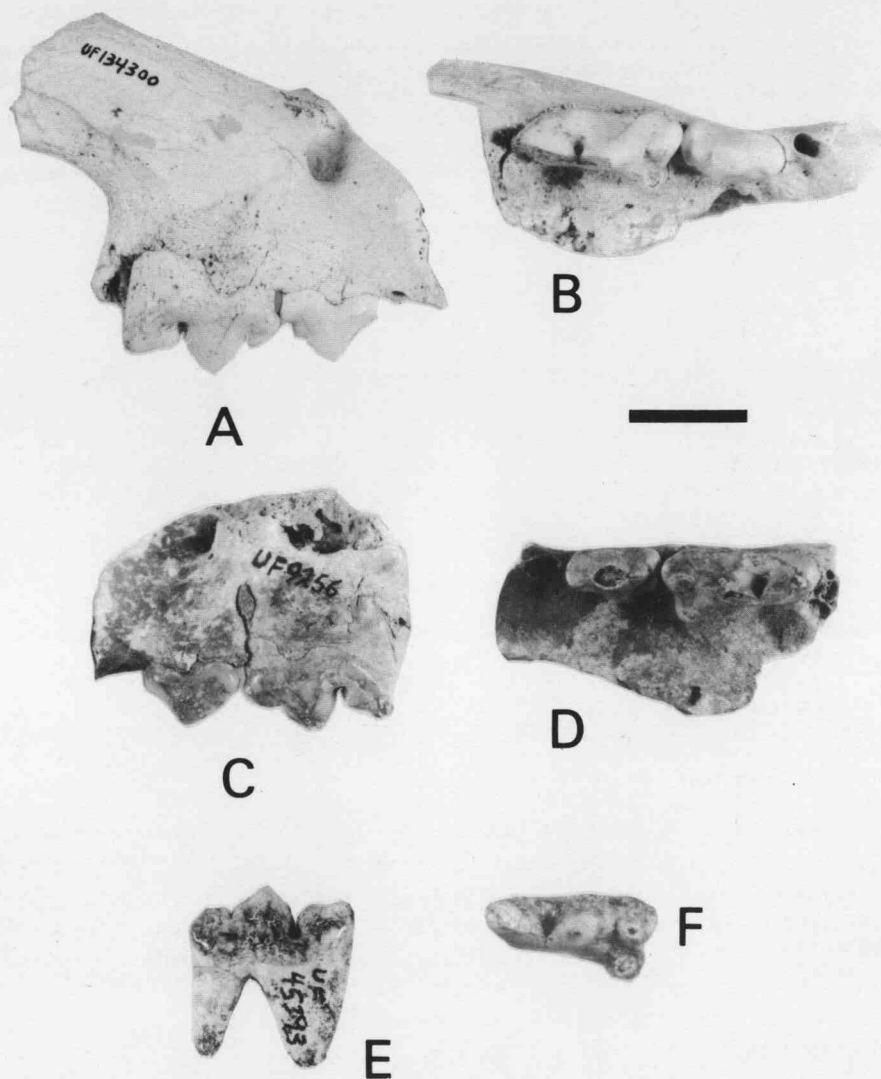


Figure 2. Maxillae and upper dentition of Rancholabrean (late Pleistocene) *Puma concolor* from Florida. A. lateral view and B. occlusal view, partial right maxilla with P3-M1, UF 134300, Orange Lake 2A, Marion County; C. lateral view and D. occlusal view, partial left maxilla with P3-P4, UF 9256, Devil's Den, Levy County; E. lateral view and F. occlusal view, right P4, UF 45393, Monkey Jungle Hammock, Dade County. Scale bar equals 2 cm.

Table 2. Measurements of the lower dentition of Pleistocene and Recent *Puma concolor* and Plio-Pleistocene *Miracinonyx* from Florida. Comparative measurements are also provided for *Miracinonyx inexpectatus* from Hamilton Cave, West Virginia and *M. trumani* from Natural Trap Cave, Wyoming (from Van Valkenburgh et al., 1990). The mean (x) and observed range (O.R.) are provided for the Recent *P. concolor* sample, which consists of 20 individuals (12 males, 8 females) from Collier and Dade counties in southern Florida. The measurements for *M. trumani* are also mean values, but have different sample sizes for individual teeth (see footnotes).

	L	p3	W	L	p4	W	L	m1	W
<i>Puma concolor</i> (Recent)									
x	11.9		6.4	15.2		7.9	16.4		8.3
O.R.	10.7- 12.8		5.5- 6.9	13.2- 16.2		6.9- 8.5	14.3- 18.4		7.6- 8.9
<i>Puma concolor</i> (fossil)									
Cutler									
UF 124376	11.1		7.1	14.9		8.2	18.6		8.4
Devil's Den									
UF 133802	-		-	-		-	18.1		8.9
Monkey Jungle									
UF 45392	-		-	-		-	17.7		7.9
<i>Miracinonyx inexpectatus</i>									
Inglis 1A									
UF 21604	12.6		7.2	17.1		9.0	19.0		9.6
Northport									
ROM 29000	14.9		8.6	19.2		9.5	-		-
ROM 32286	-		-	±17		8.5	-		-
Hamilton Cave									
USNM 401092	14.6		7.0	18.3		8.2	20.1		8.4
<i>Miracinonyx trumani</i>									
Natural Trap Cave									
x	12.6		6.7 <sup>1</sup>	16.0		7.7 <sup>2</sup>	16.1		7.9 <sup>2</sup>

<sup>1</sup> Mean of 9 individuals (from Van Valkenburgh et al., 1990, table 2).

<sup>2</sup> Mean of 10 individuals (from Van Valkenburgh et al., 1990, table 2).

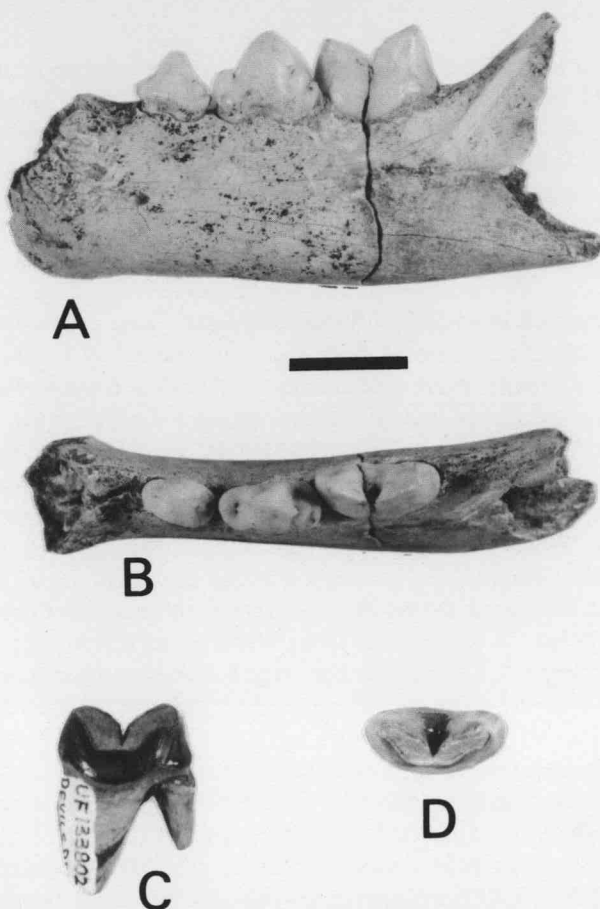


Figure 3. Mandible and lower dentition of Rancholabrean (late Pleistocene) *Puma concolor* from Florida. A. lateral view and B. occlusal view, left mandible with p3-m1, UF 124376, Cutler Hammock, Dade County; C. lateral view and D. occlusal view, left m1, UF 133802, Devil's Den, Levy County. Scale bar equals 2 cm.

Orange Lake 2A is slightly longer anteroposteriorly (23.9 mm) than the largest Florida *P. concolor* measured (23.3), but the Orange Lake fossil is otherwise very similar to the Recent sample. No differences in dental morphology were observed between the Pleistocene and Recent samples of *P. concolor*.

Table 2 compares measurements of the lower dentition and mandible of fossil and living *Puma concolor* from Florida. Measurements are given for only three fossils, a well-preserved left mandible with p3-m1 from Cutler Hammock (UF 124376) and isolated left m1s from Devil's Den (UF 133802) and Monkey Jungle (UF 45392). The Cutler mandible and Devil's Den m1 are illustrated in Figure 3. Mandibles from Santa Fe River 1 and Peace River are either damaged or the teeth

are too worn to provide accurate measurements. As with the upper dentition, the measurements of the fossils closely match those of the Recent sample. The p3 from the Cutler mandible is slightly broader (7.1 mm) than the largest p3 (6.9 mm) in the extant *P. concolor* sample, and the m1 from the same Cutler specimen is slightly longer in the anteroposterior dimension (18.6 mm) than the m1 in any Recent Florida panther mandible measured (18.4 mm). The overall morphology of the fossil mandibles and lower dentition closely matches the Recent sample of *P. concolor*.

Measurements of limb bones of Recent and fossil *Puma concolor* are included in Table 3. A complete humerus from Cutler Hammock (UF 124377) is well within the Recent sample in all measurements. A radius from Melbourne (MCZ 17791) is slightly smaller in several dimensions, including proximal breadth and depth, than the Recent *P. concolor* sample but is otherwise very similar to the radius of a small female Florida panther. An ulna from Silver Springs (UF 51221) is within the range of extant *P. concolor* ulnae in all measurements except for having a slightly broader shaft. A proximal femur from the Wekiva River (UF 124386) is at the small end of the observed range of measurements of Recent *P. concolor* femora, mirroring the situation in several metacarpals from the Wekiva River discussed below. A distal femur from Warm Mineral Springs (UF 23870) is very slightly broader (52.3 mm) than the largest extant panther femur measured (UF 52.2 mm), but the fossil shows no other significant differences from the Recent sample.

Table 4 provides comparative measurements of metacarpals and metatarsals of Recent and Pleistocene *Puma concolor* from Florida. With the exception of two specimens from the Wekiva River, the measurements of the fossil metapodials are within the range of variation in the extant sample. The Wekiva sample includes a metacarpal III (UF 124387), metacarpal IV (UF 124388), and metacarpal V (UF 124389). These specimens were given separate catalogue numbers because they were not directly associated in the field, but the metacarpal III and IV probably belong to the same individual, as they are smaller than the smallest Recent specimens measured in total length and in several other dimensions (Table 4). Except for their somewhat smaller size, these specimens are similar in morphology to *P. concolor* and probably represent a small female individual of that species.

### Biochronology

All Florida fossil sites that have produced *Puma concolor* fossils are Rancholabrean in age. The first appearance of the genus *Bison* in North America generally is used to define the beginning of the Rancholabrean Land Mammal Age (Savage, 1951; Lundelius et al., 1987). Surprisingly, the age of the earliest North American arrival of *Bison*, and thus the lower boundary of the Rancholabrean, is not well established, with dates ranging from about 300 to 500 ka. We follow



Table 3. Measurements of limb bones of Pleistocene and Recent *Puma concolor* and Plio-Pleistocene *Miracinonyx* from Florida. Comparative measurements also are provided for *Miracinonyx inexpectatus* from Hamilton Cave, West Virginia and *M. trumani* from Natural Trap Cave, Wyoming (from Van Valkenburgh et al., 1990). The mean (x), observed range (O.R.), and sample size (N) are provided for measurements of the Recent sample of *P. concolor*, which consists of between 15 and 18 individuals from Collier and Dade counties in southern Florida. The measurements for *M. trumani* are also mean values, but have different sample sizes for each limb element (see footnotes).

	total length	proximal width	proximal depth <sup>1</sup>	shaft width <sup>2</sup>	distal width	distal depth
<b>Humerus</b>						
<i>Puma concolor</i> (Recent)						
x	225.1	43.4	56.7	19.0	50.9	34.1
O.R.	204-245	38.1-47.8	50.5-63.2	15.9-22.2	45.7-57.5	30.2-37.9
N	16	16	16	16	16	16
<i>Puma concolor</i> (fossil)						
Cutler						
UF 124377	227	43.2	57.5	18.9	47.5	32.7
UF 124378	—	—	—	—	49.8	33.0
<i>Miracinonyx inexpectatus</i>						
Inglis						
UF 95766	264	53.5	71.6	22.2	62.1	41.3
Hamilton Cave						
USNM 401092	269	—	—	21.5	59.5	42.8
<i>Miracinonyx trumani</i>						
Natural Trap Cave <sup>3</sup>	236.9	—	—	18.1	52.7	36.3
<b>Radius</b>						
<i>Puma concolor</i> (Recent)						
x	194.1	23.1	17.0	17.4	37.3	21.0
O.R.	181-210	20.5-25.3	15.2-18.9	15.1-19.7	32.9-41.7	17.9-23.5
N	18	18	18	18	16	16
<i>Puma concolor</i> (fossil)						
Melbourne						
MCZ 17791	186	20.2	14.2	18.1	31.6	18.3
<i>Miracinonyx inexpectatus</i>						
Inglis						
UF 45346	232	27.4	19.4	23.2	42.5	23.7
Hamilton Cave						
USNM 401092	245	—	—	—	42.7	—
<i>Miracinonyx trumani</i>						
Natural Trap Cave <sup>4</sup>	232.9	—	—	—	36.4	—
<b>Ulna</b>						
<i>Puma concolor</i> (Recent)						
x	233.9	14.7	27.3	20.8	—	—
O.R.	215-255	12.9-17.1	23.4-31.2	17.0-25.6	—	—
N	15	15	15	15	—	—

Table 3 Continued

	total length	proximal width	proximal depth	shaft width	distal width	distal depth
<i>Puma concolor</i> (fossil)						
Silver Springs						
UF 51221	241	17.0	28.1	26.8	—	—
<b>Femur</b>						
<i>Puma concolor</i> (Recent)						
x	269.3	51.1	25.3	19.3	47.9	48.3
O.R.	252- 290	45.5- 56.3	22.8- 27.7	16.1- 21.7	43.3- 52.2	42.6- 52.7
N	18	17	17	17	16	16
<i>Puma concolor</i> (fossil)						
Wekiva River						
UF 124386	—	46.1	22.0	—	—	—
Warm Mineral Springs						
UF 23870	—	—	—	—	52.3	49.4
<i>Miracinonyx inexpectatus</i>						
Inglis						
UF 45353	293	57.9	28.0	21.1	54.5	52.5
Hamilton Cave						
USNM 401092	334	—	—	27.3	59.8	—
<i>Miracinonyx trumani</i>						
Natural Trap Cave <sup>5</sup>	291.7	—	—	22.2	55.1	—
<b>Tibia</b>						
<i>Puma concolor</i> (Recent)						
x	249.9	50.0	51.7	18.1	36.5	21.5
O.R.	234- 265	44.9- 55.2	45.7- 56.9	15.5- 20.5	33.3- 39.8	19.3- 24.0
N	18	18	18	18	18	18
<i>Miracinonyx inexpectatus</i>						
Inglis						
UF 45350	—	58.4	64.5	26.3	—	—
UF 45351	—	61.9	63.9	27.6	—	—
UF 45354	—	—	—	—	42.0	23.8
Hamilton Cave						
USNM 401092	±311	68.0	—	—	41.9	29.8
<i>Miracinonyx trumani</i>						
Natural Trap Cave <sup>6</sup>	289.2	58.8	—	—	42.6	26.9

<sup>1</sup> Proximal depth of ulna is anteroposterior depth of olecranon process. Proximal depth of femur is anteroposterior depth of femoral head.<sup>2</sup> Shaft width of ulna is maximum anteroposterior depth of shaft.<sup>3</sup> Mean of 8 individuals (from Van Valkenburgh et al. 1990, table 3).<sup>4</sup> Mean of 10-11 individuals (from Van Valkenburgh et al. 1990, table 3).<sup>5</sup> Mean of 6 individuals (from Van Valkenburgh et al. 1990, table 3).<sup>6</sup> Mean of 5 individuals (from Van Valkenburgh et al. 1990, table 3).

Table 4. Measurements of metacarpals and metatarsals of Pleistocene and Recent *Puma concolor* and Plio-Pleistocene *Miracinonyx* from Florida. Comparative measurements are also provided for *Miracinonyx inexpectatus* from Hamilton Cave, West Virginia and *M. trumani* from Natural Trap Cave, Wyoming (from Van Valkenburgh et al., 1990). The mean (x) and observed range (O.R.) are provided for measurements on the Recent sample of *P. concolor*, which consists of 18 individuals (10 males, 8 females) from Collier and Dade counties in southern Florida. The measurements for *M. trumani* are also mean values, but have different sample sizes for each metapodial (see footnotes).

	total length	proximal width	proximal depth	shaft width	distal width
<b>Metacarpal II</b>					
<i>Puma concolor</i> (Recent)					
x	75.6	12.2	16.8	8.5	15.0
O.R.	68.3- 81.4	10.6- 13.4	14.1- 19.2	7.2- 9.5	13.0- 16.7
<i>Puma concolor</i> (fossil)					
Cutler					
UF 124379	70.3	12.5	17.1	7.7	14.2
<i>Miracinonyx inexpectatus</i>					
Ingles 1A					
UF 45464	87.7	15.0	19.8	8.9	16.0
Hamilton Cave					
USNM 401092	92.5	15.0	20.6	10.4	15.8
<i>Miracinonyx</i> cf. <i>M. inexpectatus</i>					
Lecanto 2A					
UF 128349	89.3	14.4	19.0	9.2	14.9
<i>Miracinonyx trumani</i>					
Natural Trap Cave <sup>1</sup>	83.1	13.1	19.4	8.5	14.6
<b>Metacarpal III</b>					
<i>Puma concolor</i> (Recent)					
x	85.3	15.9	14.0	9.2	15.4
O.R.	77.3- 91.6	13.9- 18.0	12.4- 15.6	7.6- 10.4	13.4- 16.8
<i>Puma concolor</i> (fossil)					
Cutler					
UF 124380	—	15.3	15.4	9.6	—
Ichetucknee					
UF 45420	80.5	16.8	16.6	10.4	16.3
Wekiva River					
UF 124387	75.4	13.4	12.8	7.9	12.4
<i>Miracinonyx inexpectatus</i>					
Hamilton Cave					
USNM 401092	105.3	19.1	15.8	12.4	17.4
<i>Miracinonyx</i> cf. <i>M. inexpectatus</i>					
Lecanto 2A					
UF 128350	105.3	16.5	16.3	11.7	17.2
<i>Miracinonyx trumani</i>					
Natural Trap Cave <sup>2</sup>	95.3	—	16.1	10.1	16.2

Table 4 Continued

	total length	proximal width	proximal depth	shaft width	distal width
<b>Metacarpal IV</b>					
<i>Puma concolor</i> (Recent)					
x	80.2	12.2	13.8	8.1	13.8
O.R.	73.1-	10.9-	12.2-	6.9-	11.8-
	86.3	13.3	15.6	9.3	15.4
<i>Puma concolor</i> (fossil)					
Wekiva River					
UF 124388	72.2	10.1	12.0	7.4	11.3
<i>Miracinonyx inexpectatus</i>					
Santa Fe 2A					
UF 45382	96.9	13.4	14.9	10.6	14.5
Hamilton Cave					
USNM 401092	100.4	13.3	15.5	10.8	15.6
<i>Miracinonyx trumani</i>					
Natural Trap Cave <sup>3</sup>	93.2	13.1	15.6	8.8	14.6
<b>Metacarpal V</b>					
<i>Puma concolor</i> (Recent)					
x	63.1	14.4	12.4	8.1	13.7
O.R.	56.8-	12.6-	11.1-	7.2-	11.7-
	67.7	15.7	13.6	9.1	15.1
<i>Puma concolor</i> (fossil)					
Cutler					
UF 124381	—	12.8	12.2	7.6	—
Monkey Jungle					
UF 124385	54.5	12.7	11.4	7.4	11.8
Wekiva River					
UF 124389	58.7	13.9	12.4	8.3	13.2
<i>Miracinonyx inexpectatus</i>					
Hamilton Cave					
USNM 401092	84.0	14.3	15.7	9.7	16.1
<i>Miracinonyx cf. M. inexpectatus</i>					
Lecanto 2A					
UF 128351	80.4	15.8	14.4	10.4	15.6
<i>Miracinonyx trumani</i>					
Natural Trap Cave <sup>4</sup>	75.6	15.9	14.2	9.2	13.9
<b>Metatarsal II</b>					
<i>Puma concolor</i> (Recent)					
x	93.0	13.5	17.1	9.5	15.0
O.R.	85.6-	11.4-	14.0-	8.3-	13.3-
	100.2	15.0	18.8	10.9	16.1
<i>Miracinonyx inexpectatus</i>					
Inglis 1A					
UF 45471	112.0	14.8	22.8	11.7	17.6
Leisey Shell Pit					
UF 124172	120.6	15.7	23.0	11.8	17.8
Hamilton Cave					
USNM 401092	120.1	12.5	22.3	10.5	18.4
<i>Miracinonyx trumani</i>					
Natural Trap Cave <sup>5</sup>	106.0	—	20.6	11.2	16.2

Table 4 Continued

	total length	proximal width	proximal depth	shaft width	distal width
<b>Metatarsal III</b>					
<i>Puma concolor</i> (Recent)					
x	104.3	16.4	21.4	12.0	16.3
O.R.	97.6-	14.0-	18.2-	10.1-	14.1-
	111.9	18.2	23.5	13.4	17.8
<i>Puma concolor</i> (fossil)					
Wekiva River					
UF 124390	94.9	15.6	17.5	10.4	13.9
<b>Metatarsal IV</b>					
<i>Puma concolor</i> (Recent)					
x	102.8	15.2	19.7	10.0	14.9
O.R.	96.1-	13.2-	17.6-	8.7-	13.3-
	110.0	17.0	21.8	11.3	16.4
<i>Puma concolor</i> (fossil)					
Wekiva					
UF 124391	-	12.2	14.4	-	-
<i>Miracinonyx inexpectatus</i>					
Inglis 1A					
UF 45470	129.5	18.7	20.5	11.7	17.4
Hamilton Cave					
USNM 401092	129.5	14.1	20.9	13.3	17.7
<i>Miracinonyx trumani</i>					
Natural Trap Cave <sup>6</sup>	121.3	-	-	12.0	17.1
<b>Metatarsal V</b>					
<i>Puma concolor</i> (Recent)					
x	-	14.2	11.3	7.5	-
O.R.	-	12.4-	9.8-	6.5-	-
	-	16.2	13.1	8.2	-
<i>Puma concolor</i> (fossil)					
Cutler					
UF 124382	-	17.1	12.3	8.2	-
UF 124383	-	15.4	12.1	8.5	-
<i>Miracinonyx inexpectatus</i>					
Hamilton Cave					
USNM 401092	117.3	16.7	12.6	9.8	17.1
<i>Miracinonyx trumani</i>					
Natural Trap Cave <sup>7</sup>	110.7	-	-	9.8	14.9
<i>Miracinonyx</i> sp.					
Port Charlotte					
FMNH PM 39892	108.3	15.0	14.8	7.9	14.9

<sup>1</sup> Mean of 8 individuals (from Van Valkenburgh et al. 1990, table 5).<sup>2</sup> Mean of 12 individuals (from Van Valkenburgh et al. 1990, table 5).<sup>3</sup> Mean of 10-12 individuals (from Van Valkenburgh et al. 1990, table 5).<sup>4</sup> Mean of 10 individuals (from Van Valkenburgh et al. 1990, table 5).<sup>5</sup> Mean of 10 individuals (from Van Valkenburgh et al. 1990, table 5).<sup>6</sup> Mean of 7 individuals (from Van Valkenburgh et al. 1990, table 5).<sup>7</sup> Mean of 6 individuals (from Van Valkenburgh et al. 1990, table 5).

Lundelius et al. (1987) and Morgan and Hulbert (1995) who placed this boundary at about 300 ka.

The presence of *Bison* is convenient for determining that a particular fauna is Rancholabrean in age; however, this genus is often absent in Florida faunas known to be Rancholabrean based on other criteria. Morgan and Hulbert (1995) identified additional species of mammals that are restricted to Florida Rancholabrean faunas. Several of these species (e.g. *Tremarctos floridanus* and *Smilodon fatalis*) are known from older pre-Rancholabrean faunas elsewhere in North America. Among xenarthrans, a glyptodont (*Glyptotherium floridanum*) and Jefferson's ground sloth (*Megalonyx jeffersonii*) occur in Florida only during the Rancholabrean (Kurtén and Anderson, 1980; Gillette and Ray, 1981). Large carnivores restricted to Florida Rancholabrean faunas (Kurtén and Anderson, 1980) include dire wolf (*Canis dirus*), Florida cave bear (*Tremarctos floridanus*), American lion (*Panthera atrox*=*P. leo atrox* of Kurtén and Anderson, 1980), and sabertooth cat (*Smilodon fatalis*). The living black bear (*Ursus americanus*) does not appear in Florida until the Rancholabrean. Three extinct species of rodents, giant beaver (*Castoroides ohioensis*), giant capybara (*Neochoerus pinckneyi*), and a large bog lemming (*Synaptomys australis*), are found in Florida only in Rancholabrean faunas. At least six living species of rodents make their first appearance in the state during the Rancholabrean (Morgan and Hulbert, 1995), including fox squirrel (*Sciurus niger*), rice rat (*Oryzomys palustris*), cotton rat (*Sigmodon hispidus*), meadow vole (*Microtus pennsylvanicus*), pine vole (*Pitymys pinetorum*), and muskrat (*Ondatra zibethicus*). The extinct tapir, *Tapirus veroensis*, is typical of Florida Rancholabrean faunas, although this species does occur in two Florida latest Irvingtonian faunas, Coleman 2A in Sumter County and Sebastian Canal in Brevard County (Hulbert, 1995; Morgan and Portell, 1996).

The Rancholabrean Land Mammal Age is further subdivided into the early Rancholabrean (300 to 130 ka) and late Rancholabrean (130 to 11 ka), with the boundary between the two subages corresponding to the beginning of the last or Sangamonian interglacial at about 130 ka (see more detailed discussion in Morgan and Hulbert, 1995). The beginning of the last interglacial (130 ka) is also the boundary between the middle and late Pleistocene. Fewer than 10 Florida faunas are definitely early Rancholabrean in age, whereas several hundred late Rancholabrean faunas are known from throughout the state. However, some early Rancholabrean faunas probably have gone unrecognized because only two species of mammals are known to be restricted to faunas of this age in Florida (Morgan and Hulbert, 1995), the giant bison (*Bison latifrons*) and an extinct pine vole (*Pitymys hibbardi*). One other large mammal, Cuvier's gomphothere (*Cuvieronius tropicus*), had its last occurrence in Florida during the early Rancholabrean.

Late Rancholabrean faunas are considerably more numerous in Florida than are early Rancholabrean faunas, probably because the younger Rancholabrean faunas are closer in time to the present (and are thus more likely to have been preserved) and are more easily dated, both biochronologically and by the

radiocarbon ( $^{14}\text{C}$ ) method. Faunas from the last half of the late Rancholabrean (i.e. faunas younger than 50,000 years BP) can be radiocarbon dated. Surprisingly few Florida late Rancholabrean sites have been radiocarbon dated, primarily because of the rarity of wood and charcoal in these sites. We hope that the absolute ages of more Florida late Rancholabrean sites will be determined in the near future through direct radiocarbon dating of bone collagen of extinct Pleistocene megafauna using accelerator mass spectrometry (AMS) (Stafford et al., 1991).

For the great majority of Florida late Rancholabrean sites that have not been radiocarbon dated, biochronology remains the most reliable method for estimating their age. At least 10 species of mammals are restricted to late Rancholabrean faunas in Florida. Three of these are extinct species and seven are living species that make their first appearance in the state during the late Rancholabrean. Two members of the extinct Pleistocene megafauna, *Panthera atrox* and the extinct bison, *Bison antiquus*, are found in Florida only during the late Rancholabrean. The large extinct vampire bat, *Desmodus stocki* (*D. magnus*, originally described from Reddick, is a synonym) is rare in Florida, but the few sites in the state from which it is known are late Rancholabrean in age (Morgan, 1991). Five living species of rodents, *Sciurus niger*, *Sigmodon hispidus*, *Pitymys pinetorum*, *Microtus pennsylvanicus*, and *Ondatra zibethicus*, first appear in Florida during the late Rancholabrean, although the latter two species occur in somewhat older faunas elsewhere (Kurtén and Anderson, 1980). The black bear (*Ursus americanus*) is unknown in Florida faunas prior to the late Rancholabrean, despite its nearly statewide distribution at present.

*Puma concolor* first appeared in Florida during the Rancholabrean and still survives in the southernmost part of the peninsula, albeit in ever-decreasing numbers. Furthermore, all of the 15 Rancholabrean sites from which *P. concolor* is known can be shown to be late Rancholabrean in age, based on either radiocarbon dates or the presence of one or more of the species of mammals discussed in the previous paragraph. The Florida panther is not known to occur in any undoubted early Rancholabrean faunas in Florida, and therefore appears to be a good biochronological indicator for late Rancholabrean faunas in the state.

### Florida Fossil Sites Containing *Puma concolor*

The map of Florida in Figure 1 shows the locations of the 15 Pleistocene fossil sites and one Holocene archaeological site in the state from which *Puma concolor* is known. Each site has been assigned a number that corresponds to the numbers in Figure 1. The general location and a brief description are given for each locality, as well as information on the age and associated mammalian fauna.

#### 1. Ichetucknee River

The Ichetucknee River is a well known late Rancholabrean vertebrate fauna collected from the bottom of a spring-fed river located 8 km northwest

of Fort White, Columbia County, northern Florida (Webb, 1974a; Kurtén and Anderson, 1980). No radiocarbon dates are available for the Ichetucknee River fauna, but a late Rancholabrean age is indicated by the presence of *Panthera atrox* and *Bison antiquus*, as well as the extant rodents *Sigmodon hispidus*, *Ondatra zibethicus*, and *Pitymys pinetorum*. Other mammals from the Ichetucknee River that are characteristic of Florida Rancholabrean faunas include *Canis dirus*, *Tremarctos floridanus*, *Smilodon fatalis*, *Oryzomys palustris*, *Synaptomys australis*, and *Tapirus veroensis*.

## 2. Santa Fe River 1

The Santa Fe River 1 fauna was recovered from the bottom of the Santa Fe River in the vicinity of Ginnie Spring and Devil's Ear Spring in northern Florida. In this region the Santa Fe River forms the boundary between Columbia County on the north bank and Gilchrist County on the south bank. This site produces a mixed fauna of Blancan and Rancholabrean vertebrates. The mammals from these two ages are very different at the species level, and consequently the two faunas are not difficult to separate. There is also a difference in preservation between the Blancan and Rancholabrean fossils. The panther mandible reported here is most similar in preservation to the Rancholabrean fossils from the Santa Fe 1 fauna. Morgan and Ridgway (1987) discussed the Santa Fe 1 Blancan fauna, and Morgan and Hulbert (1995) provided a current faunal list. Rancholabrean mammals from Santa Fe 1 include *Canis dirus*, *Castoroides ohioensis*, *Ondatra zibethicus*, *Tapirus veroensis*, and *Bison* sp.

## 3. Devil's Den

Devil's Den is a water-filled sinkhole over 20 m in depth located 3 km northwest of Williston in Levy County. This sinkhole presumably was dry or nearly so during the late Wisconsinan low sea level stand, at which time regional water tables were very low as well. The Devil's Den mammalian fauna was reviewed by Martin and Webb (1974), and Kurtén (1966) discussed the large sample of Florida cave bear (*Tremarctos floridanus*) known from this site. A radiocarbon date suggesting an early Holocene age of 7000 to 8000 yBP for the Devil's Den fauna (Martin and Webb, 1974) is probably spurious, as this site is almost certainly late Pleistocene (late Rancholabrean) in age. Rancholabrean indicators from Devil's Den include *Megalonyx jeffersonii*, *Canis dirus*, *Tremarctos floridanus*, *Smilodon fatalis*, *Oryzomys palustris*, and *Synaptomys australis*. Six mammals from Devil's Den, *Ursus americanus*, *Sciurus niger*, *Sigmodon hispidus*, *Microtus pennsylvanicus*, *Ondatra zibethicus*, and *Pitymys pinetorum*, are extant species that make their first appearance in Florida during the late Rancholabrean.



#### 4. Wekiva River

The Wekiva River fauna was collected from the bottom of the Wekiva River, 7 km northeast of Gulf Hammock in Levy County, north-central Florida. This fauna, which includes the extinct giant land tortoise *Geochelone crassiscutata* and 17 species of mammals, has not been published upon previously. A Rancholabrean age is indicated by the presence of *Canis dirus* and *Bison* sp.

#### 5. Orange Lake 2A

The Orange Lake 2A site was discovered in an abandoned limestone quarry near the town of Orange Lake, Marion County, north-central Florida. The vertebrate fossils are derived from clays and sands deposited in a narrow vertical fissure formed in Eocene marine limestone. This unpublished fauna is dominated by microvertebrates, but there are enough large mammals present to establish its late Pleistocene age. Diagnostic Rancholabrean mammals from Orange Lake 2A include *Megalonyx jeffersonii*, *Canis dirus*, *Tremarctos floridanus*, *Sigmodon hispidus*, *Pitymys pinetorum*, and *Synaptomys australis*.

#### 6. Reddick 1A

The Reddick 1A local fauna is located in an abandoned limestone quarry about 1 km southeast of Reddick, Marion County, north-central Florida. The vertebrate fossils are derived from fissure and cave fillings formed in Eocene marine limestone. Reddick is one of the best known and richest Rancholabrean vertebrate assemblages from Florida, with more than 50 species of mammals reported (Gut and Ray, 1963; Webb, 1974a; Kurtén and Anderson, 1980). The age of the Reddick fauna is Rancholabrean based on the presence of *Megalonyx jeffersonii*, *Glyptotherium floridanum*, *Desmodus stocki*, *Canis dirus*, *Tremarctos floridanus*, *Oryzomys palustris*, *Sigmodon hispidus*, *Pitymys pinetorum*, *Synaptomys australis*, *Tapirus veroensis*, and *Bison* sp. Among these species, the extinct vampire, *Desmodus stocki* and the rodents *Sigmodon hispidus* and *Pitymys pinetorum* further indicate a late Rancholabrean age.

#### 7. Silver Springs

Silver Springs, located 10 km northeast of Ocala, Marion County, north-central peninsular Florida, is one of the largest freshwater springs in North America. Fossil vertebrates have been known from Silver Springs and the Silver Springs Run for some time, but the fauna has not been reviewed. Hoffman (1983) described a mammoth kill site in the Silver Springs Run, several kilometers east and downstream from the main spring. Hoffman did not provide a faunal list for this site, but he did mention the presence of *Bison* and a "large cat," in addition to *Mammuthus columbi*. He did not give the

scientific name or identify the skeletal element of the "large cat," but apparently it is not the same specimen as the *Puma concolor* ulna reported here (UF 51221). Hoffman (1983) obtained a radiocarbon date of 9840 yBP on collagen from a mammoth bone from this site. Despite the early Holocene radiocarbon date from Silver Springs, a late Rancholabrean age seems more likely as recent compilations of radiocarbon dates strongly indicate that no member of the North American Pleistocene megafauna survived after 11,000 yBP (Meltzer and Mead, 1983). The presence of *Megalonyx jeffersonii*, *Nechoerus pinckneyi*, *Tapirus veroensis*, and *Bison* sp. confirms a Rancholabrean age for the Silver Springs fauna.

#### 8. Rock Springs

Rock Springs is located 10 km north of Apopka, Orange County, central Florida. The vertebrate fauna was collected from Rock Springs, an underwater artesian spring, and from Rock Springs Run, a small stream that flows from the spring. Rock Springs has a rich bat fauna (Morgan, 1991) suggesting that the site was not completely underwater in the late Pleistocene. Wilkins (1983) reviewed the mammalian fauna from Rock Springs, including *Canis dirus*, *Tremarctos floridanus*, *Ursus americanus*, *Tapirus veroensis*, and *Bison* sp., all of which are indicative of Florida Rancholabrean faunas.

#### 9. Melbourne

The Melbourne local fauna was collected in the first half of this century, primarily from a golf course 5 km west of Melbourne, Brevard County, on Florida's central Atlantic Coast. The rich mammalian fauna from Melbourne, consisting of 49 species, has been reviewed by several authors (Gazin, 1950; Ray, 1958; Kurtén and Anderson, 1980). The vertebrate fossils from Melbourne occur above the marine late Pleistocene Anastasia Formation, which was deposited during the last (Sangamonian) interglacial, thus indicating a late Rancholabrean age (younger than 120 ka). A Rancholabrean age for the Melbourne fauna is supported by the presence of *Megalonyx jeffersonii*, *Glyptotherium floridanum*, *Canis dirus*, *Tremarctos floridanus*, *Smilodon fatalis*, *Castoroides ohioensis*, *Nechoerus pinckneyi*, *Sigmodon hispidus*, *Oryzomys palustris*, *Synaptomys australis*, *Tapirus veroensis*, and *Bison* sp.

#### 10. Seminole Field

The Seminole Field site is located in the town of Seminole, west of St. Petersburg, Pinellas County, on the central Gulf Coast of Florida. Seminole Field has a rich mammalian fauna consisting of 46 species (Simpson, 1929). The vertebrate fossils from Seminole Field were found above a marine shell bed of the Fort Thompson Formation that was deposited during the last interglacial, thus suggesting a late Rancholabrean age for the Seminole Field

local fauna. The mammalian fauna from Seminole Field is similar to those from Melbourne and Vero and, like those two faunas, is late-Rancholabrean in age (Simpson, 1929; Webb, 1974a; Kurtén and Anderson, 1980). Rancholabrean indicators in the Seminole Field fauna include *Megalonyx jeffersonii*, *Glyptotherium floridanum*, *Canis dirus*, *Tremarctos floridanus*, *Smilodon fatalis*, *Sigmodon hispidus*, *Oryzomys palustris*, *Synaptomys australis*, *Tapirus veroensis*, and *Bison* sp.

#### 11. Leisey Shell Pit 2

The Leisey Shell Pits are a series of commercial shell pits located 7 km southwest of Ruskin along the eastern shore of Tampa Bay, Hillsborough County, west-central Florida. The classic Leisey Shell Pit localities are mostly early Irvingtonian in age; however, Rancholabrean mammal fossils were recovered from spoil piles in Leisey Pit 2 (Morgan and Hulbert, 1995). In addition to the single *Puma concolor* fossil, other Rancholabrean mammals from Leisey Shell Pit 2 include *Sigmodon hispidus*, *Tapirus veroensis*, and *Bison* sp.

#### 12. Peace River

Although fossils from the Peace River in south-central Florida were among the first Pleistocene mammals reported from the state (Leidy, 1889a), little has been written about this important fauna since and no current faunal list is available. The Peace River is over 100 km long and vertebrate fossils are known from about half its length, particularly in Hardee and De Soto counties. Both of the *Puma concolor* fossils from the Peace River reported here are from Hardee County; one was found near Zolfo Springs and the second came from near Gardner, about 10 km farther south. Rancholabrean species found in the Peace River in the general vicinity of the two *P. concolor* fossils include *Glyptotherium floridanum*, *Tapirus veroensis*, and *Bison antiquus*.

#### 13. Warm Mineral Springs

Warm Mineral Springs is a deep, water-filled sinkhole located near Northport, Sarasota County, southwestern Florida, about 20 km inland from the Gulf of Mexico. The sinkhole reaches about 70 m in depth, but the vertebrate fossils were recovered from a ledge about 13 m deep. This ledge was subaerially exposed during the late Pleistocene when sea levels and water tables were considerably lower than at present. Remains of extinct Pleistocene mammals were recovered from the 13 m ledge beneath a layer of organic material, which was radiocarbon dated at 9 to 11 ka (Clausen et al., 1975; McDonald, 1990). McDonald (1990) reported 20 species of mammals from Warm Mineral Springs, including *Puma concolor*. Only two of these species are extinct, *Megalonyx jeffersonii* and *Smilodon fatalis*, both of which

are restricted to Rancholabrean faunas in Florida. Two species of extant rodents identified from Warm Mineral Springs, *Sigmodon hispidus* and *Pitymys pinetorum*, are unknown in the state prior to the late Rancholabrean.

#### 14. Cutler Hammock

The Cutler Hammock site is located in a sinkhole in a tropical hardwood hammock 4 km east of Perrine, Dade County, in southernmost peninsular Florida. This site is less than 5 m above sea level and only about 0.3 km inland from the Atlantic Ocean. The Cutler Hammock sinkhole formed in the oolitic facies of the marine late Pleistocene Miami Limestone, which was deposited during the last interglacial high sea level stand and has been dated between 140 and 110 ka by the uranium series method (Osmond et al., 1965). The Cutler Hammock fauna is therefore younger than the last interglacial and is probably very late Pleistocene (late Rancholabrean) in age, between 20 and 11 ka. Unfortunately, the bones from this site are too highly leached to provide accurate radiocarbon dates (T. W. Stafford, pers. comm.). To date, 47 species of mammals have been identified from the Cutler Hammock local fauna, including 16 species of extinct Pleistocene megafauna (Emslie and Morgan, 1995; Morgan, in press). A taphonomic study of the Cutler Hammock fauna indicates that many of the bones in the site, particularly those of *Mylohyus nasutus* and juvenile *Equus*, were accumulated at a carnivore den, probably by the dire wolf, *Canis dirus* (Emslie and Morgan, 1995). A Rancholabrean age for Cutler Hammock is supported by the presence of *Canis dirus*, *Tremarctos floridanus*, *Smilodon fatalis*, *Oryzomys palustris*, and *Bison* sp. The presence of *Panthera atrox*, *Sciurus niger*, *Sigmodon hispidus*, and *Pitymys pinetorum* at Cutler Hammock restricts the age of this site to late Rancholabrean.

#### 15. Monkey Jungle Hammock

Monkey Jungle Hammock is located on the property of the Monkey Jungle tourist attraction, 5 km west of Goulds and 12 km southwest of Cutler Hammock in Dade County. The Monkey Jungle Hammock and Cutler Hammock sites are the two southernmost Rancholabrean vertebrate faunas in the continental United States. These two sites formed under similar depositional conditions, are close in age, and have a large number of species in common. The fossils at Monkey Jungle also were found in a sinkhole in a tropical hardwood hammock developed in the marine late Pleistocene Miami Limestone. Both the Monkey Jungle and Cutler sites formed during periods of much lower sea level and correspondingly lower water tables. A very late Pleistocene (late Rancholabrean) age for these two sites is most likely, despite the lack of radiocarbon dates. The Monkey Jungle Hammock local fauna has been discussed several times (Martin, 1977; Ober, 1978; Morgan, 1985; Morgan 1991). Morgan (in press) provides a current mammalian faunal list

numbering 41 species, including nine members of the extinct Pleistocene megafauna. Like Cutler Hammock, the presence of *Panthera atrox*, *Sciurus niger*, *Sigmodon hispidus*, and *Pitymys pinetorum* in the Monkey Jungle Hammock fauna indicates a late Rancholabrean age. Other Rancholabrean species from Monkey Jungle are *Canis dirus*, *Tremarctos floridanus*, and *Oryzomys palustris*.

## 16. Granada Site

The Granada Site (archaeology site number 8Da11) from Miami in Dade County along the Atlantic Coast of southeastern peninsular Florida is the only archaeological site in the state from which *Puma concolor* has been identified (Wing and Reitz, 1982; Wing, pers. comm.). The Granada Site is within the historical geographic range of *P. concolor coryi*.

*Miracinonyx inexpectatus* (Cope, 1895)

### Material Examined

#### Late Pliocene (late Blancan)

Santa Fe River 2A, Columbia/Gilchrist County line: UF 45382, right metacarpal IV.

Northport, Sarasota County: ROM 29000, left mandible fragment with p3 and p4; ROM 32286, incomplete p4.

#### Latest Pliocene/early Pleistocene (early Irvingtonian)

Inglis 1A, Citrus County: UF 21604, left mandible with p3-m1; UF 95766, right humerus; UF 45347, right humerus missing proximal end; UF 45346, right radius; UF 45344, left proximal ulna; UF 45464, left metacarpal II; UF 45462, right metacarpal V; UF 45465, 45467, two scapholunars; UF 45353, left femur; UF 45352, left distal femur; UF 45350, right proximal tibia; UF 45354, right distal tibia; UF 45351, left proximal tibia; UF 45471, left metatarsal II; UF 45470, left metatarsal IV; UF 18114, 45463, 45469 three left astragali; UF 45451 left navicular; UF 45452, right cuboid; UF 45468, left cuboid; UF 45466, right ectocuneiform.

Leisey Shell Pit, Hillsborough County: UF 124172, right metatarsal II.

### Taxonomy

Schultz et al. (1985) noted that fragmentary felid specimens are notoriously difficult to identify to species, and we would add that even relatively complete but

isolated specimens should be identified with caution. Van Valkenburgh et al. (1990) also warned against using functional characters in an analysis of relationships between carnivores that have evolved in similar directions. This is particularly true for two closely related genera such as *Miracinonyx* and *Puma*. Although Van Valkenburgh et al. (1990) comparatively illustrated many elements of *Puma* with both species of *Miracinonyx*, their paper was primarily a phylogenetic analysis and did not provide much data on the differential identification of individual skeletal elements of these two genera. Taking into account the problems in identifying isolated felid fossils discussed above, we tentatively identify new specimens of *Miracinonyx* here using the limited material available for direct comparison. In general, postcranial elements of *Miracinonyx*, which constitute the majority of the sample described below, are noticeably elongated compared to the same elements in *Puma concolor*.

Several fossils of *Puma concolor* from Florida originally were identified as *Felis inexpectata*, specifically specimens from the Rancholabrean Seminole Field (Simpson, 1929) and Melbourne (Ray, 1958) sites. In his review of North American fossil pumas, Kurtén (1976) referred the specimens from these two sites to *P. concolor*, and we concur with his identifications. Kurtén recognized *F. inexpectata* as a larger, longer-limbed, puma-like cat that was restricted to Blancan and Irvingtonian faunas. Adams (1979) named *Miracinonyx* as a North American subgenus of the Old World cheetah *Acinonyx*, including the Blancan and Irvingtonian species *Acinonyx (Miracinonyx) studei* (= *F. inexpectata*) and the Rancholabrean species *A. (M.) trumani*. Van Valkenburgh et al. (1990) reviewed the systematics of the North American cheetah-like cats. They elevated *Miracinonyx* to the generic level, including the species *M. inexpectatus* and *M. trumani*. These authors also established that *Felis inexpectata* (Cope, 1895) is the senior synonym of *F. studei* Savage, 1960, in agreement with the conclusion of Kurtén (1976). The Florida fossil record of cheetah-like cats now referred to the genus *Miracinonyx* is briefly reviewed here because of the possible ancestral relationship of *M. inexpectatus* to *Puma concolor* (see Van Valkenburgh et al. 1990).

### Descriptions and Comparisons

Fossils from four Florida sites are here referred to *Miracinonyx inexpectatus* (see map in Figure 4). A right metacarpal IV from the Santa Fe River 2A locality, a mixed late Blancan and Rancholabrean assemblage, probably was the basis for the listing of *Puma concolor* from this site by Webb (1974a). This specimen is much larger and more elongated than any metacarpal IV of *P. concolor* from Florida (see Table 4) and is re-identified as *M. inexpectatus*. The metacarpal of *Miracinonyx* from Santa Fe 2A is almost certainly late Blancan in age. Van Valkenburgh et al. (1990) referred a mandible and a metatarsal IV from the early Irvingtonian Inglis 1A local fauna, Citrus County, Florida, to *M. inexpectatus*.

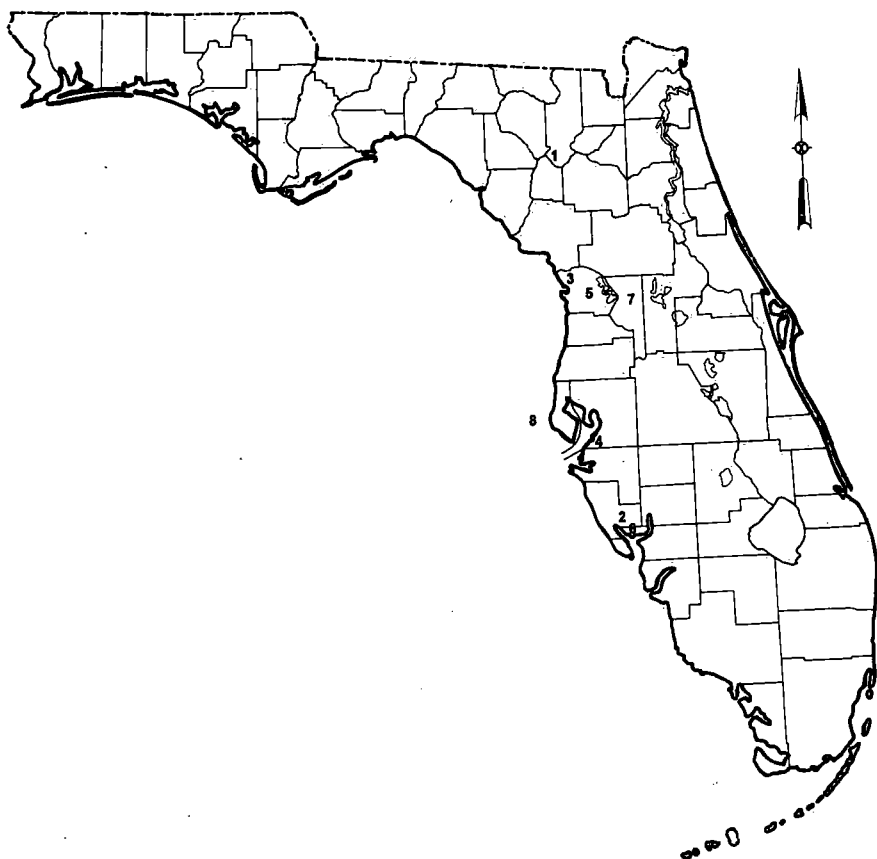


Figure 4. Late Pliocene and Pleistocene sites from Florida containing fossils of *Miracinonyx*. *Miracinonyx inexpectatus*: 1. Santa Fe River 2A, Columbia/Gilchrist County line, late Blancan; 2. Northport, Sarasota County, late Blancan; 3. Inglis 1A, Citrus County, early Irvingtonian; 4. Leisey Shell Pit 3, Hillsborough County, early Irvingtonian. *Miracinonyx* cf. *M. inexpectatus*: 5. Lecanto 2A, Citrus County, Rancholabrean; *Miracinonyx* sp.: 6. Port Charlotte, Charlotte County, Blancan?; 7. Coleman 2A, Sumter County, late Irvingtonian; 8. Cardinale Site, Gulf of Mexico, 25 km west of Pinellas County, Rancholabrean?.

Webb and Wilkins (1984) had previously listed *Felis* cf. *F. inexpectata* from Inglis 1A. We have identified a number of additional elements of *M. inexpectatus* from Inglis (see list under Material Examined). A more thorough examination of the substantial felid sample from Inglis 1A, which includes *Miracinonyx*, *Smilodon*, *Homotherium*, and at least one other smaller cat, would almost surely reveal additional specimens of *M. inexpectatus*, particularly carpals, tarsals, and phalanges. Berta (1995) recently identified a right metatarsal II from the early

Irvingtonian Leisey Shell Pit local fauna in Hillsborough County as *M. inexpectatus*.

Measurements of the lower teeth from the Inglis 1A mandible (UF 21604; Fig. 5) referred to *Miracinonyx inexpectatus* are presented in Table 2. Comparative dental measurements of *M. inexpectatus* from the middle Irvingtonian Hamilton Cave in West Virginia and *M. trumani* from the late Rancholabrean Natural Trap Cave in Wyoming are also provided in Table 2 (from Van Valkenburgh et al., 1990). The Inglis teeth are somewhat smaller than the teeth from Hamilton Cave but are otherwise very similar. Measurements of the Inglis teeth fit within the range of variation of the larger sample of Blancan and Irvingtonian *M. inexpectatus* reported by Kurtén (1976, table IV).

Two specimens from Northport, Sarasota County, may be referred to *Miracinonyx*, probably *M. inexpectatus*. A left mandible fragment with p3 and p4 (ROM 29000) shows the very short diastema of a large short-faced feline (see measurements in Table 2). The p4 looks like a large puma, but we cannot match

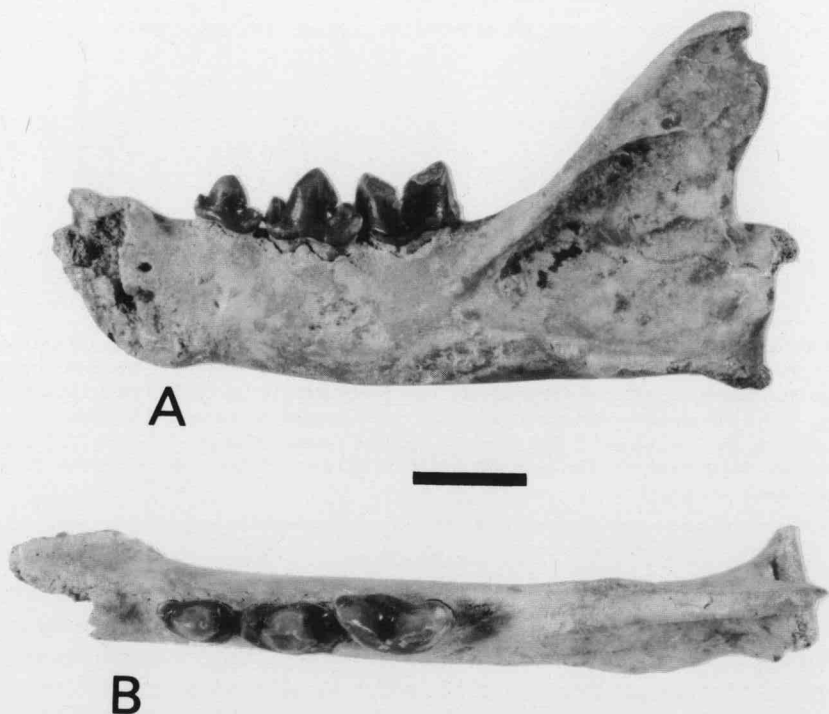


Figure 5. Left mandible with p3-m1, UF 21604, of *Miracinonyx inexpectatus* from Inglis 1A, Citrus County, Florida, earliest Irvingtonian: A, Lateral view; B, occlusal view. Scale bar equals 2 cm.



the morphology of the p3 with any particular species because of an expanded posterior portion. Nevertheless, at this point we do not think it can represent any other feline. An incomplete p4 (ROM 32286) appears to be too large to represent *P. concolor* and so probably also represents *Miracinonyx*. The teeth of the larger Northport specimen (ROM 29000) are slightly larger than those of the Hamilton Cave *M. inexpectatus*, whereas the smaller Northport specimen (ROM 32286) is more similar in size to the comparable tooth (p4) from Inglis. The age of the Northport faunas is not well known, but they appear to have a mixture of late Blancan and Rancholabrean elements. The two Northport *Miracinonyx* specimens are probably late Blancan. Morgan and Ridgway (1987) reported a maxillary fragment with P4 of the Blancan canid *Borophagus diversidens* from Northport.

The sample of postcranial elements referred to *Miracinonyx inexpectatus* from Inglis 1A includes three complete limb bones (humerus, radius, and femur) and several partial limbs, as well as four complete metapodials. Measurements of limb bones of *M. inexpectatus* from Inglis 1A are presented in Table 3, along with comparative measurements of *Miracinonyx* from Hamilton Cave and Natural Trap Cave (from Van Valkenburgh et al., 1990). The Inglis humerus (UF 95766) compares closely in length with the humerus of the Hamilton Cave *M. inexpectatus*; however, both the radius (UF 45346) and femur (UF 45353) of *Miracinonyx* from Inglis are close to the mean size of specimens of *M. trumani* from Natural Trap Cave and are shorter than comparable elements from Hamilton Cave. Despite their similarity in size to limb elements of *M. trumani* from Natural Trap Cave, the radius and femur from Inglis are here referred to *M. inexpectatus*, as are the complete humerus and several partial tibiae. The Inglis limb bones are within the known range of variation of *M. inexpectatus* limbs based on measurements of that species from various Blancan and Irvingtonian sites elsewhere in North America (Kurtén, 1976, tables V, VI, VIII, and IX).

Measurements of metacarpals and metatarsals of *Miracinonyx inexpectatus* from Inglis 1A, Santa Fe 2A, and Leisey Shell Pit are compared to measurements of *M. inexpectatus* from Hamilton Cave and *M. trumani* from Natural Trap Cave in Table 4 (from Van Valkenburgh et al., 1990). Table 4 includes measurements of five metapodials of *M. inexpectatus* from Florida: a right metacarpal IV (UF 45382) from Santa Fe 2A; a left metacarpal II (UF 45464), left metatarsal II (UF 45471), and left metatarsal IV (UF 45470) from Inglis 1A; and a right metatarsal II (UF 124172) from Leisey Shell Pit. Overall, the Inglis and Santa Fe metapodials are somewhat shorter than the comparable elements from Hamilton Cave, whereas the Leisey metatarsal II is slightly longer than the metatarsal II from Hamilton Cave. These measurements may reflect an increase in size through time as Santa Fe 2A (late Blancan) and Inglis 1A (earliest Irvingtonian) are 0.5-1.0 Ma older than Leisey Shell Pit (late early Irvingtonian) and Hamilton Cave (middle Irvingtonian) (Morgan and Hulbert, 1995). The Florida Blancan and Irvingtonian metapodials here referred to *M. inexpectatus* are all considerably longer than the

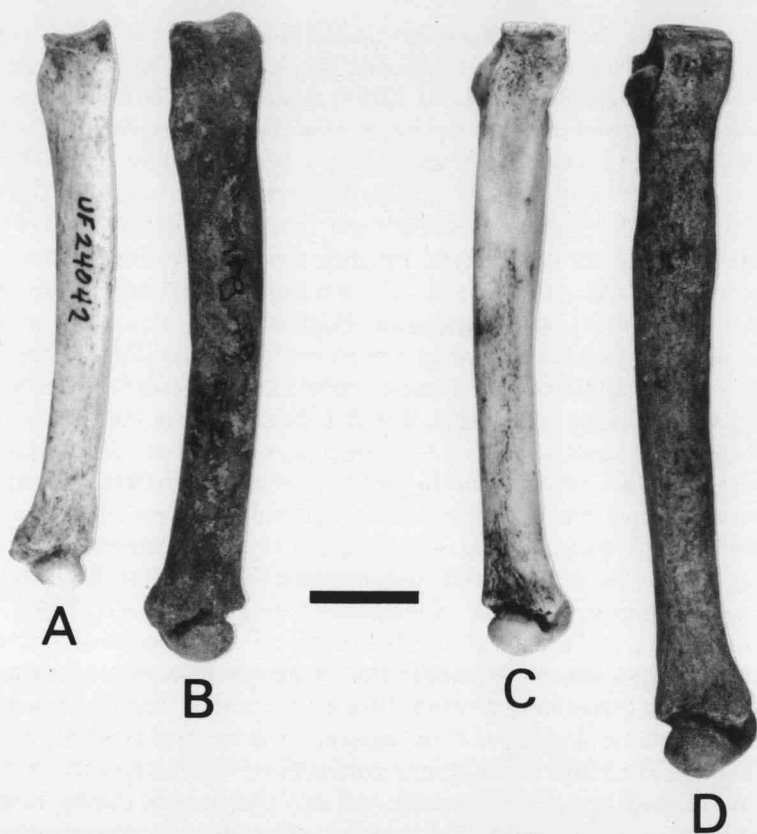


Figure 6. Metatarsals in anterior view of a Recent male *Puma concolor* (A, C) from Volusia County, Florida, and the extinct cheetah-like cat *Miracinonyx inexpectatus* (B, D) from Inglis 1A, Citrus County, Florida, earliest Irvingtonian. A. Left metatarsal II, Recent *P. concolor*, UF 24042, Volusia County; B. Left metatarsal II, *M. inexpectatus*, UF 45471, Inglis 1A; C. Left metatarsal IV, Recent *P. concolor*, UF 24042, Volusia County; D. Left metatarsal IV, *M. inexpectatus*, UF 45470, Inglis 1A. Scale bar equals 2 cm.

comparable elements in Recent *Puma concolor* (see Fig. 6; also see comparative measurements of *P. concolor* in Table 4).

*Miracinonyx* cf. *M. inexpectatus***Material Examined****middle to late Pleistocene (Rancholabrean)**

Lecanto 2A, Citrus County: UF 128349, right metacarpal II; UF 128350, right metacarpal III; UF 128351, right metacarpal V.

**Descriptions and Comparisons**

Several possibly associated metacarpals, including metacarpal II, III, and V (UF 128349, 128350, 128351, respectively) from the Rancholabrean Lecanto 2A local fauna in Citrus County, Florida, are tentatively referred to *Miracinonyx inexpectatus* (see Fig. 7). Measurements of the three metacarpals of *Miracinonyx* from Lecanto 2A are compared to measurements of metacarpals of *M. inexpectatus* from the middle Irvingtonian Hamilton Cave, West Virginia, and metacarpals of *M. trumani* from the late Rancholabrean Natural Trap Cave, Wyoming, in Table 4 (from Van Valkenburgh et al., 1990). The metacarpal II and metacarpal V from Lecanto are intermediate in size between the comparable metacarpals from Hamilton Cave and Natural Trap Cave, although they are both closer in size to the Hamilton Cave *M. inexpectatus*. The metacarpal III from Lecanto is exactly the same length (105.3 mm) as the metacarpal III from Hamilton Cave, and is considerably longer than the sample of metacarpal IIIs from Natural Trap Cave. The Lecanto metacarpals are tentatively referred to *M. inexpectatus* based on their similarity in size and morphology to that species. There are other unstudied fossils of *Miracinonyx* from Lecanto 2A, but these specimens consist of rather undiagnostic carpals, tarsals, and phalanges.

**Biochronology**

The age of the Lecanto 2A local fauna is of interest because almost all previously reported specimens of *Miracinonyx inexpectatus* are from late Blancan and Irvingtonian sites. Morgan (1991) briefly reviewed the mammalian fauna from Lecanto 2A, which is Rancholabrean in age based on the presence of *Canis dirus*, *Tremarctos floridanus*, *Oryzomys palustris*, and *Sigmodon hispidus*. More detailed study of the small mammal fauna from Lecanto 2A is required to determine if the site is early or late Rancholabrean.

The only other possible Rancholabrean record of *Miracinonyx inexpectatus* is an isolated P4 from Cavetown, Maryland. Kurtén (1976) originally identified this specimen as *Felis* (= *Puma*) *concolor*, although he noted that the tooth was actually in the size range of *M. inexpectatus*. Van Valkenburgh et al. (1990) referred the Cavetown P4 to *M. inexpectatus*. Kurtén (1976) regarded the Cavetown site to be

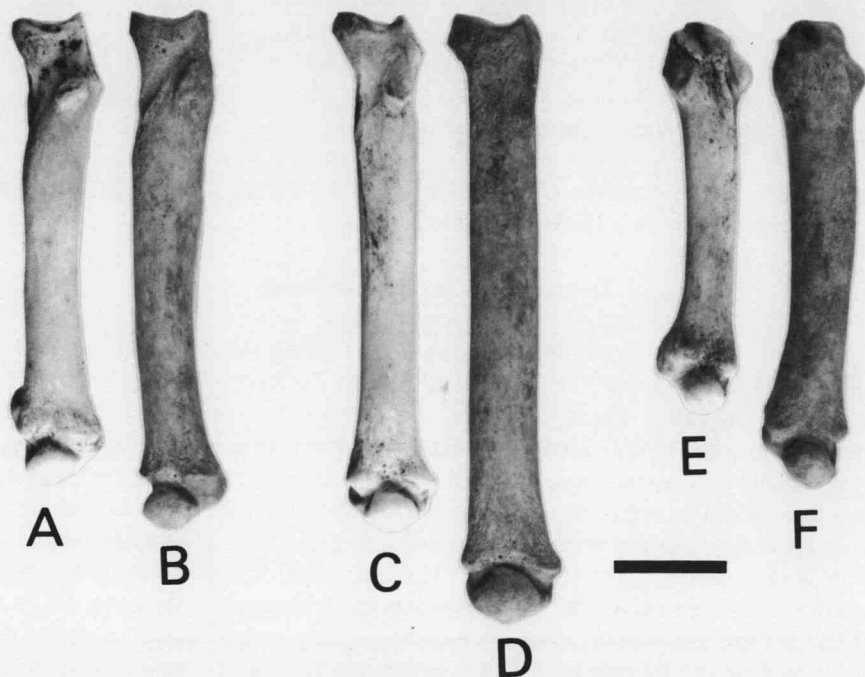


Figure 7. Metacarpals in anterior view of Recent male *Puma concolor* (A, C, E) from Volusia County, Florida, and the extinct cheetah-like cat *Miracinonyx inexpectatus* (B, D, F) from Lecanto 2A, Citrus County, Florida, Rancholabrean. A. Right metacarpal II, Recent *P. concolor*, UF 24042, Volusia County; B. Right metacarpal II, *Miracinonyx* cf. *M. inexpectatus*, UF 128349, Lecanto 2A; C. Right metacarpal III, Recent *P. concolor*, UF 24042, Volusia County; D. Right metacarpal III, *Miracinonyx* cf. *M. inexpectatus*, UF 128350, Lecanto 2A; E. right metacarpal V, Recent *P. concolor*, UF 24042, Volusia County; F. Right metacarpal V, *Miracinonyx* cf. *M. inexpectatus*, UF 128351, Lecanto 2A. UF 128349-128351 are probably from a single individual but were catalogued separately, because their association in the field could not be confirmed. Scale bar equals 2 cm.

of uncertain age, but probably Rancholabrean, whereas Kurtén and Anderson (1980) considered this same fauna to be Wisconsinan (=late Rancholabrean).

There is a substantial gap in time, spanning the late Irvingtonian and much of the Rancholabrean, between the youngest well-dated specimens of *Miracinonyx inexpectatus* from the middle Irvingtonian (Conard Fissure, Arkansas; Cumberland Cave, Maryland; Port Kennedy Cave, Pennsylvania; and Hamilton Cave, West Virginia) and the earliest definite specimens of *M. trumani* from the very late Rancholabrean (Crypt Cave, Nevada, and Natural Trap Cave, Wyoming). *Miracinonyx* underwent significant morphological change during the approximately 0.5 Ma time period when there is a very poor record of this genus in

North America (Van Valkenburgh et al., 1990). Therefore, specimens of *Miracinonyx* from sites of intermediate age, such as the late Irvingtonian Coleman 2A (see below) and the Rancholabrean Lecanto 2A local faunas, are very important to understanding the evolutionary history of the genus. Unfortunately, there is no possibility of collecting additional material of *Miracinonyx* from Coleman 2A or Lecanto 2A, as both fossil sites have been destroyed by limestone mining operations.

### *Miracinonyx* sp.

### Material Examined

#### Blancan?

Courtland Waterway, Port Charlotte, Charlotte County: FMNH PM 39892, left metatarsal V.

#### middle Pleistocene (late Irvingtonian)

Coleman 2A, Sumter County: UF 45363, incomplete left scapholunar.

#### Rancholabrean?

Cardinale Site, Gulf of Mexico, 25 km west of St. Petersburg, Pinellas County: UF 69800, partial right radius lacking proximal and distal ends.

### Descriptions and Comparisons

Overall, the Coleman 2A scapholunar (UF 45363) compares closely with *Puma concolor* (and not *Panthera onca* or *Smilodon gracilis*); however, the facet for the articulation of the unciform is angled more ventrally. Both species of *Miracinonyx* have this facet angled more ventrally (Van Valkenburgh et al., 1990, fig. 9), whereas this facet in *Puma concolor* is almost vertical. Therefore, we tentatively identify the Coleman scapholunar as *Miracinonyx* sp. The diverse mammalian fauna from Coleman 2A is late Irvingtonian in age (Martin, 1974; Morgan and Hulbert, 1995).

A partial right radius lacking both the proximal and distal ends (UF 69800) from the underwater Cardinale Site off the west coast of Florida in the Gulf of Mexico is tentatively referred to *Miracinonyx*. The shaft of this specimen is considerably more elongated than in any radius of Recent *Puma concolor* from Florida examined, but is similar to a complete radius of *M. inexpectatus* from Inglis 1A (UF 45346). Because UF 69800 is incomplete and the site from which it was recovered lacks age-diagnostic mammals, we are only able to identify this

specimen as *Miracinonyx* sp. The fossils from the Cardinale Site were collected from the bottom of the Gulf of Mexico at a depth of about 20 m approximately 25 km west of St. Petersburg in Pinellas County. The fauna represents a mixture of Pliocene marine vertebrates and Pleistocene terrestrial mammals. Fossils of these two different ages presumably were derived from superposed strata that became mixed on the ocean floor. The Pliocene taxa include the extinct great white shark *Carcharodon megalodon*, the marlin *Istiophorus* sp., a mysticete whale, and the monachine phocid *Callophoca obscura*. The partial *Miracinonyx* radius, four *Equus* cheekteeth, and a fragment of proboscidean tusk constitute the Pleistocene fauna. Although the *Equus* teeth belong to an advanced species of the genus typical of the Irvingtonian and Rancholabrean, they do not provide a more specific age refinement for this fauna. The presence of terrestrial mammals on the continental shelf in water 20 m deep obviously indicates that these animals inhabited this region during a period of much lower sea level. It is tempting to suggest that this fauna lived on the continental shelf during the last glacial interval (Wisconsinan, between 120 and 10 ka) when sea levels were as much as 100 m lower than present; however, as many as 20 glacial/interglacial cycles may be represented in Florida during the late Pliocene and Pleistocene (Morgan and Hulbert, 1995).

A left metatarsal V (FMNH PM 39892) from Port Charlotte in Charlotte County, referred to *Puma concolor* by Seymour (1983), is much larger and more elongate than the living Florida panther. The measurements of this specimen compare most closely to those of *Miracinonyx trumani* from Natural Trap Cave (Table 4). We hesitate to refer this single metatarsal to *M. trumani* because this species currently is known only from several very late Rancholabrean sites in the western United States (Crypt Cave, Nevada, and Natural Trap Cave, Wyoming), and we have not had the opportunity to directly compare the Florida specimen with material from these two localities. Furthermore, several Florida specimens referred to *M. inexpectatus* from the late Blancan and early Irvingtonian (including both limb bones and metapodials, see Tables 3 and 4) are smaller than comparable fossils of *M. inexpectatus* from middle Irvingtonian sites, such as Hamilton Cave, and are actually closer in size to specimens of *M. trumani*. The Port Charlotte fossil is of unknown stratigraphic provenience, although vertebrate faunas from this vicinity range in age from late Blancan to Rancholabrean.

## DISCUSSION

*Puma concolor* is now known from 15 late Pleistocene localities in Florida (previously there were only five valid fossil records of the Florida panther from the state), whereas the *Miracinonyx* records from Florida have quadrupled from two to eight. This dramatic increase in the number of fossil sites for *Puma concolor* and *Miracinonyx* reflects a trend in recent studies of Florida's rich late Pliocene and Pleistocene mammalian faunas in which the published fossil record of a particular

species is not necessarily an accurate reflection of its actual distribution or abundance. Perhaps the most obvious reason for this trend has been a very active field program over the past 15 years by vertebrate paleontologists from the Florida Museum of Natural History (FLMNH), concentrating on Florida late Pliocene and Pleistocene faunas. Furthermore, over this same time period there also has been a comprehensive curatorial effort to identify and catalog fossils in the FLMNH vertebrate paleontology collection (e.g. more than 150,000 specimens have been catalogued since 1980, including both recently collected fossils and uncatalogued material that had resided in the collection for as much as 30 or 40 years). Through these combined efforts a vast new wealth of fossils from Florida Plio-Pleistocene sites has accumulated over the past two decades; however, research and publication of these fossils has not kept pace with field and curatorial activities.

The most recent comprehensive review of Florida Pleistocene mammals (Webb, 1974a) is now more than 20 years out of date. Webb (1974a, table 2.1) listed the mammalian species from most of the late Pliocene and Pleistocene faunas known from Florida up until the early 1970s, including two Blancan sites, four Irvingtonian sites, and 35 Rancholabrean sites. Hulbert's (1992) list of the fossil vertebrates of Florida updated the overall fauna and taxonomy of Plio-Pleistocene mammals from the state. Several papers have provided current mammalian faunal lists for Florida late Blancan and Irvingtonian sites (Morgan and Ridgway, 1987; Morgan and Hulbert, 1995), but very few Rancholabrean faunas from the state have been studied recently. Based on data from the FLMNH vertebrate paleontology collection and locality files, as well as information summarized in several recent publications (e.g., Morgan and Hulbert, 1995), there are now 22 Blancan sites, 19 Irvingtonian sites, and well over 100 Rancholabrean sites (a very conservative estimate) known from Florida.

The fossil record of large felids provides a good example of the gap between the published record of Florida Pleistocene mammals and the actual fossil record as preserved in museum collections, particularly the vertebrate paleontology collection at the Florida Museum of Natural History. Kurtén's (1965) review of the Pleistocene Felidae of Florida summarized nearly 80 years of research on Florida's rich fauna of large fossil cats, beginning with Joseph Leidy's (1889b) description of a skull of *Machairodus floridanus* (= *Smilodon fatalis*) from a Rancholabrean fissure fill near Ocala in Marion County. Kurtén identified four species of large felids from Florida Pleistocene faunas (number of sites he reported for each species in parentheses): American lion, *Panthera atrox* (2); jaguar, *Panthera onca* (11); puma, *Puma concolor* (3); and sabertooth cat, *Smilodon fatalis* (10). All of the fossils studied by Kurtén (1965) were Rancholabrean in age. In a review of North American Pleistocene jaguars, Kurtén (1973b) reported *P. onca* from the late Irvingtonian Coleman 2A site in Sumter County and added one new Rancholabrean record of the jaguar from the Waccasassa River in Levy County. Webb (1974a) added one new site record for *Panthera onca*, and Webb (1974b) provided four new site records for *Smilodon floridanus* (= *S. fatalis*), bringing to 14

the total number of Florida Pleistocene sites from which each of these large cats had been identified. Webb (1974a, b) also reported the gracile sabertooth, *Smilodon gracilis*, from two late Blancan sites and one early Irvingtonian site from Florida, and the scimitar cat, *Homotherium*, from the early Irvingtonian Inglis 1A site. Waldrop (1974) reported the only valid Florida record of the scimitar cat, *Homotherium serum*, from the late Rancholabrean Reddick 1A local fauna in Marion County.

Over the past two decades most contributions on Florida fossil felids have concentrated on late Blancan and Irvingtonian species. Churcher (1984) reported *Ischyrosmilus gracilis* (= *Smilodon gracilis*) from the late Blancan Bass Point Waterway 1 and El Jobean sites in southwestern Florida. Berta (1987, 1995) described samples of *Smilodon gracilis* from the early Irvingtonian Inglis 1A in Citrus County and Leisey Shell Pit in Hillsborough County and the middle Irvingtonian McLeod Limerock Mine in Levy County. Samples from three Florida early Irvingtonian sites (Haile 16A, Haile 21A, and Leisey Shell Pit) suggest that a large, undescribed species of *Homotherium* inhabited Florida during the Irvingtonian (Berta, 1995). Van Valkenburgh et al. (1990) reported *Miracinonyx inexpectatus* from the early Irvingtonian Inglis 1A fauna, the first record of a cheetah-like cat from Florida. Berta (1995) later added a second record of *M. inexpectatus* from the Leisey Shell Pit. Seymour (1993) described a skeleton of *Panthera onca* from the middle Irvingtonian McLeod Limerock Mine, the oldest record of jaguar from Florida, and also reported a large sample of *P. onca* from the late Irvingtonian Coleman 2A site.

Morgan and Hulbert (1995) listed the mammal species from five late Blancan and 11 Irvingtonian sites from Florida, including four species of large felids (number of Florida sites from which each species has been identified in parentheses): *Smilodon gracilis* (11); undescribed species of *Homotherium* (7); *Miracinonyx inexpectatus* (6), and *Panthera onca* (2). Combining published data (in particular, Kurtén, 1965, and Webb, 1974a) and unpublished specimens in the FLMNH vertebrate paleontology collection, there are six species of large felids known from Florida Rancholabrean sites (number of Florida sites from which each species has been identified in parentheses—previously published records listed first, followed by total number of records including unpublished specimens): *Miracinonyx inexpectatus* (0, 1), *Panthera atrox* (2, 12), *Panthera onca* (13, 37), *Puma concolor* (5, 15), *Homotherium serum* (1, 1), and *Smilodon fatalis* (14, 26). Excluding the two Rancholabrean felids that are extremely rare in Florida (*Miracinonyx inexpectatus* and *Homotherium serum*), the number of sites from which the four remaining species have been identified has increased dramatically over the past 20 years, ranging from nearly doubling in the sabertooth cat to an increase by a factor of three in the jaguar and puma to a sixfold increase in the American lion. These new data present a considerably more accurate picture of the Pleistocene distribution and abundance of Florida's large cat fauna than can be obtained from the published literature.



The preceding brief summary of large felids from Florida late Pliocene and Pleistocene vertebrate faunas establishes their current status (number of species present, number of Florida sites for each species, and updated taxonomy), and allows for a preliminary analysis of their biochronology, biogeography, and possible ecological interrelationships. During the late Blancan and Irvingtonian there were four species of large felids in Florida. No more than three species occur in a single site, in part resulting from the differing biochronologic ranges of the species. *Miracinonyx inexpectatus* is the only one of these four cats that occurs from the late Blancan through the late Irvingtonian. *Smilodon gracilis* ranges from the late Blancan to the middle Irvingtonian. The large undescribed *Homotherium* is well represented only in the early Irvingtonian, although it is tentatively identified from two late Blancan faunas as well. *Panthera onca* first appears in the middle Irvingtonian and still survives in Middle and South America, although it disappeared from Florida at the end of the Rancholabrean.

The late Blancan Santa Fe River fauna and the early Irvingtonian Inglis 1A and Leisey Shell Pit local faunas all record the association of *Smilodon gracilis*, *Homotherium*, and *Miracinonyx inexpectatus*. If the fossil record for the late Blancan and early Irvingtonian (late Pliocene through early Pleistocene, from about 2.5 to 1.0 Ma) in Florida is considered to be fairly complete, and the presence of more than 40 faunas of this age would indicate that it is, then these three species could be considered the typical large felid fauna during this time period. This fauna, consisting of a very large sabertooth cat, a smaller gracile sabertooth cat, and a cheetah-like cat, compares reasonably well in body size to a typical fauna of large African felids that includes lion, leopard, and cheetah. The similarity to the Recent African large carnivore fauna is reinforced by the presence in two of the three Florida faunas (Santa Fe and Inglis) of the hyaena *Chasmaporthetes ossifragus* (see Berta, 1981). Van Valkenburgh et al. (1990) discussed a fairly widespread association of large felids from North American middle Irvingtonian faunas (Conard Fissure, Hamilton Cave, Port Kennedy Cave) that, like the Florida faunas, includes *M. inexpectatus* and *S. gracilis*, but substitutes *Panthera onca* for *Homotherium*. *P. onca* also replaces *Homotherium* in Florida middle Irvingtonian (McLeod) and late Irvingtonian (Coleman 2A) faunas.

The Florida Rancholabrean large felid fauna is composed of six species, of which only four, *Panthera atrox*, *Panthera onca*, *Puma concolor*, and *Smilodon fatalis*, are widespread in fossil sites in the state. The two rare species, *Homotherium serum* and *Miracinonyx inexpectatus*, each have been identified from only one Rancholabrean fauna in Florida. The cheetah-like cat is also known from several localities of uncertain age that may be late Pleistocene. Of the four common large cats, *S. fatalis* and *P. onca* occur in both early and late Rancholabrean faunas, whereas *P. atrox* and *P. concolor* are restricted to the late Rancholabrean. Two of the Rancholabrean felids, the jaguar and puma, are still extant. The remaining four species are extinct, although some workers (e.g.

Kurtén and Anderson, 1980) consider *P. atrox* to be an extinct subspecies of the lion, *P. leo*.

Four species of large felids are present in four Florida Rancholabrean sites: Ichetucknee River, Santa Fe River, and Reddick 1 in the northern part of the state, and Cutler Hammock at the extreme southern tip of the peninsula. Ichetucknee River, Santa Fe River, and Cutler Hammock all have a large cat fauna composed of *Panthera atrox*, *Panthera onca*, *Puma concolor*, and *Smilodon fatalis*, whereas Reddick has *P. onca*, *P. concolor*, and *S. fatalis*, as well as the very rare scimitar cat, *Homotherium serum*. Four additional Florida sites contain three large felids. The most common association, including *P. onca*, *P. concolor*, and *S. fatalis*, occurs at Devil's Den, Melbourne, and Seminole Field. The large felid fauna from Monkey Jungle Hammock is composed of *P. atrox*, *P. onca*, and *P. concolor*. Three of the four common large cats in Florida Rancholabrean faunas, American lion, jaguar, and puma, compare reasonably well in body size with a typical African felid fauna composed of lion, leopard, and cheetah, respectively. There is no ecological counterpart of the sabertooth cat in living African faunas, although its large body size and saber-like canines have led most paleontologists to propose that they preyed upon large, thick-skinned mammals, such as mammoths, mastodonts, and ground sloths (Kurtén and Anderson, 1980).

One of the most interesting associations of large carnivores in Florida Rancholabrean faunas is that of *Puma concolor* and *Panthera onca*, the only two surviving members of the North American late Pleistocene large cat fauna. The puma and jaguar occur together in 10 of the 15 Florida Rancholabrean sites from which *P. concolor* is known. Although only the puma or Florida panther is still found in Florida, the jaguar is far more common in the fossil record having been identified from 2 Irvingtonian and 37 Rancholabrean sites in the state. *P. concolor* is the only large cat that inhabited much of temperate North America prior to the arrival of Europeans about 500 years ago. The puma has been extirpated from large areas of its former range, particularly in eastern North America, and now occurs only in southernmost peninsular Florida, the western United States and western Canada, and it is also widespread in the Neotropical Region from Mexico to the southern tip of South America. Throughout the tropical portion of its range in Middle and South America, *P. concolor* coexists with *P. onca*; however, pumas generally favor drier, more upland habitats, whereas jaguars more commonly occur in wetter areas, such as in forests and along rivers (Schaller and Crawhaw, 1980; Seymour, 1989).

Jaguars now are found primarily in tropical forests from Mexico south to Brazil, although their historical range extended northward into the deserts of southern Arizona, New Mexico, and Texas (Seymour, 1989). Moreover, *Panthera onca* was widely distributed across the south temperate region of North America (south of 40° North latitude) in the late Rancholabrean (Seymour, 1989). The reason for the extinction, or more properly extirpation, of the jaguar from Florida and elsewhere in temperate North America is not known. It is generally assumed

that most of the large carnivores that went extinct at the end of the Pleistocene (e.g., *Canis dirus*, *Tremarctos floridanus*, *Smilodon fatalis*, and *Panthera atrox*, among others) disappeared because of the extinction of the large herbivores upon which they depended for food (Kurtén and Anderson, 1980). The considerable reduction in the jaguar's range after the end of the Pleistocene is likely related to the extinction of many of the species it preyed upon, probably including peccaries (*Mylohyus nasutus* and *Platygonus compressus*), capybaras (*Hydrochaeris holmesi* and *Neochoerus pinckneyi*), armadillos (*Dasypus bellus*), and tapirs (*Tapirus veroensis*). These North American species are all now extinct, although living species of peccaries, capybaras, armadillos, and tapirs still inhabit the Neotropics in Middle and South America where they comprise some of the favored prey of jaguars (Emmons, 1987; Seymour, 1989).

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Managing Editor of the BULLETIN  
Florida Museum of Natural History  
University of Florida  
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