

BULLETIN

of the



**THE FLORIDA PANTHER *Puma concolor coryi*: A
MORPHOLOGICAL INVESTIGATION OF THE
SUBSPECIES WITH A COMPARISON TO OTHER
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THE FLORIDA PANTHER *Puma concolor coryi*: A MORPHOLOGICAL INVESTIGATION OF THE SUBSPECIES WITH A COMPARISON TO OTHER NORTH AND SOUTH AMERICAN COUGARS

**Laurie Wilkins¹, Julio M. Arias-Reveron², Bradley M. Stith³,
Melody E. Roelke⁴, and Robert C. Belden⁵**

ABSTRACT

The endangered Florida panther, *Puma concolor coryi*, has been the subject of ecological and biomedical research, but little work has been done on the morphology of the subspecies. Interest in the morphologic characters that describe the Florida population has increased with the discovery of panthers outside their known range of southwestern Florida, the acquisition of many more specimens than were available to earlier researchers, and the first adult specimens and live captures from the Everglades. The necessity to define morphologic features of Florida panthers also had law enforcement implications.

Characters previously used to describe *Puma concolor coryi* were quantified and re-evaluated using statistical methods. All historic and recent specimens from the southeastern U.S. (n=79) were examined for pelage color, cranial profile and proportions, and other morphological traits. These specimens were compared to a sample of North American and South American specimens. The characters measured provide a basis on which to describe the Florida population and discriminate between it and other subspecies.

Specimens of panthers inhabiting the Everglades region differ from the balance of the Florida population in cranial morphology and other features, a result that is consistent with recent genetic research. There is no evidence to support a permanent geographic or ecological separation of Florida panthers into two populations. The best explanation for the observed morphological differences, consistent with historical information, is that the Everglades panthers are descendants of captive-released animals and may be hybrids. The extent to which other Florida panthers may have been affected by this possible hybridization cannot be detected with the current analytical methods. Most specimens recovered in the last 20 years from southwest Florida exhibit the classic *P. concolor coryi* morphologic features.

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RESUMEN

La pantera de Florida, *Puma concolor coryi*, amenazada de extinción, ha sido objeto de estudios ecológicos y biomédicos, pero poco se ha hecho acerca de la morfología de sus subespecies. El interés en los caracteres morfológicos que describen la población de Florida se ha incrementado con el descubrimiento de panteras fuera de su rango conocido en el sudoeste de Florida, la adquisición de más especímenes (que antes no estaban disponibles a previos investigadores) y los primeros especímenes y capturas vivas provenientes de los Everglades. La necesidad de definir características subespecíficas de las panteras de Florida tiene también implicancias legales.

Los caracteres previamente utilizados para describir *Puma concolor coryi* fueron cuantificados y re-evaluados usando métodos estadísticos. En todos los especímenes históricos y recientes del sudeste de los E.E.U.U. (n=79) se examinaron el color de pelo, perfil cranial, proporciones y otros rasgos morfológicos. Estos especímenes, fueron comparados con una muestra representativa de Norte y Sudamérica. Los caracteres medidos proporcionaron la base para la descripción de la población de Florida y para su discriminación dentro y entre otras subespecies.

Los especímenes de pantera que viven en la región de los Everglades difieren del resto de la población de Florida en su morfología cranial y otras características, hallazgo consistente con recientes investigaciones genéticas. No existen evidencias que soporten una separación geográfica o ecológica de la pantera de Florida en dos poblaciones. La mejor explicación de las diferencias morfológicas observadas, consistente con la información histórica, es que las panteras de los Everglades son descendientes de animales de cautiverio liberados y que por lo tanto serían híbridos. Con este método analítico no se puede detectar hasta que punto otras panteras de Florida podrían haber sido afectados por esta hibridación. La mayoría de los especímenes provenientes del sudoeste de Florida recuperados en los últimos veinte años, exhiben los clásicos rasgos morfológicos de *P. concolor coryi*.

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INTRODUCTION

The puma (*Puma concolor*) has the most extensive distribution of all American carnivores (Cabrera and Yepes 1960). At one time, the range of species covered almost the entire North and South American continents from northern British Columbia to Patagonia, and it was found in virtually every habitat from high mountains to tropical swamps (Young 1946). Consistent with this broad distribution, the species exhibits considerable geographic variation, and 30 subspecies have been recognized (Goldman 1946). The Florida panther (*P. c. coryi*) once ranged the southeastern states from Louisiana throughout the lower Mississippi River Valley east through the southeastern states. Historically, its distribution was continuous and intergraded with other populations to the north and west (Goldman 1946). It has been isolated for at least the past 100 years in the wild lands of south Florida (Bangs 1899) as human settlement patterns caused the decimation of adjacent cougar populations. Current population estimates vary between 30 and 80 individuals in the Big Cypress and Everglades ecosystems (Belden 1986a, Maehr 1997).

This study reviews the morphological characters of the Florida panther (*Puma concolor coryi*). It examines color, cranial morphology and pelage features of the subspecies in the context of the geographic variation expressed by the species throughout its range. The Florida panther was discovered and named a subspecies by Charles Cory (1896). Since that time, there have been only a few published accounts that provide descriptive information (Bangs 1898, 1899, Nelson and Goldman 1929, Goldman 1946, Layne and McCauley 1977, Lazell 1981, Belden 1986b). Specimens of cougars from the southeast have always been rare. At the time of Goldman's comprehensive taxonomic review (1946), only 17 *P. c. coryi* museum specimens were available, including three from Louisiana and 14 from Florida. Layne and McCauley (1977) published weights and measurements for an additional 15 individuals from Louisiana, Arkansas, and Florida; however, only five had been preserved as museum specimens. The need to describe the panther in Florida with a suitable suite of morphological characters has become more important in the last 15 years with (1) the recovery of panthers from areas outside their known range in Florida, (2) the probability of escaped or released captive cats of other subspecies into Florida environment, and (3) problems of verification in law enforcement issues.

In 1986, cats in the Everglades were captured for the first time with the initiation of a radio-telemetry study (Smith and Bass 1994). It was noted that the Everglades cats differed from the panthers in the Big Cypress in size and overall appearance and in the absence of the two physical traits that had been documented in the Big Cypress population; namely, the kinked tail and a mid-dorsal cowlick, or whorl (Belden 1986a, Roelke 1990, Wilkins and Belden, unpubl. data). Genetic studies revealed that free-ranging panthers in Florida consist of two genetically distinct stocks that had evolved separately (O'Brien et al. 1990, Roelke et al. 1993).

Further, the two genotypes are strongly partitioned geographically into the southeastern (Everglades) and southwestern (Big Cypress) populations. The presence or absence of the kinked tail followed a similar pattern, being present in most Big Cypress cats and absent in the Everglades population. O'Brien and his colleagues (1990) suggested the source of the Everglades genotype may have been from seven captive cats released into the Everglades National Park between 1957 and 1967 (archives, National Park Service, Washington DC), from the Piper collection of Everglades Wonder Gardens (Vanas 1976).

A total of 45 panther deaths were documented in Florida between 1972 and 1990, most the result of road mortality, illegal kills, and intraspecific aggression (Roelke 1990). This new material, preserved as specimens in the collections of the Florida Museum of Natural History (FLMNH), provided an opportunity to review physical traits described by earlier investigators. The objectives were to (1) identify and quantify the traits that best describe the Florida population; (2) compare the recent specimens to historic museum specimens (pre-1950) to determine what changes, if any, have occurred over time as a result of isolation or small population numbers; and (3) discern what morphological differences exist within the Florida population that might correspond to the reported genetic differences. In addition to the main objectives, we hoped to resolve some troublesome identifications associated with cats killed outside the current known range of the panther, which were thought to be captive released individuals.

ACKNOWLEDGEMENTS

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We are grateful to the many museum curators and collection staff who allowed one of us (lw) to examine specimens under their care, especially, C. Smart and T. Daeschler (Academy of Natural Sciences, Philadelphia), G. Musser (American Museum of Natural History), D. Holmes (Arkansas Museum of Science and History, Little Rock), P. Jenkins (British Museum of Natural History), Collier County (Florida) Historical Society; J. Bayless (Everglades Regional Collection Center, National Park Service, Homestead FL), B. Patterson and R. Izor (Field Museum of Natural History), M. Hafner (Museum of Zoology, Louisiana State University, Baton Rouge), M. Rutzmoser, J. Chupasko, and M. Massaro (Museum of Comparative Zoology, Harvard University), M. Douglas (Oklahoma State University), M. Carleton and L. Gordon (National Museum of Natural History, Washington), P. Landers (Zoological Museum, University Wisconsin), and numerous others who provided courteous assistance with loans, correspondence and telephone inquiries. Access to skin collections was made more difficult because of the need to also accommodate a 100 lb spectrophotometer. We thank all those who facilitated this arduous task, especially Linda Gordan (National Museum of Natural History) and Timothy McCarthy (then of the American Museum of Natural History). Francisco Bisbal of Venezuela and Andrés Novaro of Chile, students at University of Florida, examined specimens in South American Museums while conducting their own research. Jay Sylvester of the Milton Roy Corporation made the pelage color study possible by his generous loan of the color spectrophotometer.

Henry Setzer originally thought of the contour gauge as a measuring tool for the profile measurement; he also assisted by examining specimens for me while on museum tours of his own. Linda Chandler, Laurie Walz, and Wendy Zonnlefer, produced the graphics. Oron L. Bass, Jr. (National Park Service) provided

information concerning the panthers in the Everglades region. Technical advice was provided by Clarence Abercrombie, Richard Hulbert, Stephen Linda, Rodrigo Medellín and Timothy O'Brien, all previously or currently at the University of Florida. Reviews by Jacqueline Belwood, Michael Kennedy, and Melvin Sunquist greatly improved the manuscript. Constructive comments were also provided by Oron Bass, Deborah Jansen, Thomas Logan, and William Robertson. Rhoda J. Bryant and Dianna Carver (Florida Museum of Natural History) assisted in manuscript preparation. Ideas, insight, and encouragement were offered by John F. Eisenberg.

ABBREVIATIONS

Class designations for populations of southeastern U.S. cougars (*P. concolor coryi*), see methods for explanation:

HIST	historic museum specimens from Florida, including type specimens (pre-1950)
RECENT	recent museum specimens and living animals from southwestern Florida (non-Everglades cats), since 1950
GLADES	Everglades individuals (southeast Florida)
PIPER	captive specimens from the Piper collection (Everglades Wonder Gardens)
TEST	Test animals with no data or of uncertain identity
ARUND	historic museum specimens from Louisiana (formerly <i>P. c. arundivaga</i>)
ARK/LA	Louisiana and Arkansas specimens acquired within the last 30 years, identification to be confirmed.

TAXONOMIC SYNONYMY OF *PUMA CONCOLOR CORYI* (BANGS)

Felis concolor floridana Cory, 1896. Hunting and Fishing in Florida, p. 109. (name preoccupied by *Felis floridana* Desmarest, 1820 (= *Lynx floridanus* Rafinesque, 1817). Type from Alapata Flats, north of Lake Okeechobee, Florida, FMNH 9255, skin only, M adult, Field Museum of Natural History, Chicago. NOTE: Bangs (1898, p. 234) reported the type locality to be north of Lake Okeechobee and east of Kissimee River based on conversation with Mr. Cory.

Felis coryi Bangs, 1899. Proc. Biol. Soc. Wash. 13:15, Jan. 31 (renaming of *F. c. floridana* Cory). Type from "wilderness back of Sebastian, Florida, MCZ 7742, skin and skull, old M adult, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Collected by F. R. Hunter January 1, 1898.

Felis arundivaga Hollister, 1911. Proc. Biol. Soc. Washington. 24:176, June 16. Type from 12 miles southwest of Vidalia, Concordia Parish, Louisiana, USNM 137122, skin and skull, M adult, United States National Museum

(Biological Surveys Collection), Washington, D.C. Collected by B. V. Lilly, June 17, 1905.

Felis concolor coryi (Bangs 1899) Nelson and Goldman, 1929. J. Mamm., 10(4):347. Same as *Felis coryi* Bangs 1899 (see above).

Systematists prefer the use of *Puma* instead of *Felis* Jardine (1834). We follow this convention according to Wilson and Reeder 1993.

Nelson and Goldman (1929) synonymized *Felis arundivaga* Hollister 1911, the canebrake puma, with *Felis concolor coryi*, the Florida puma. According to them, the Louisiana pumas did not appear to be satisfactorily separable from the Florida race, although the skull of type specimen and one other slightly exceed those from Florida in length.

HISTORICAL AND RECENT DISTRIBUTION

The former range of *P. c. coryi* was thought to be the austroriparian zones in eastern Texas or western Louisiana and the lower Mississippi River Valley east through the southeastern states in general, intergrading to the north with *P. c. cougar*, and to the west and northwest with *P. c. stanleyana* and *P. c. hipolestes* (Goldman 1946). Archeological and early records of pumas exist for Alabama (1880), Arkansas (1821-1920), Georgia (1773-1920), Louisiana (1819-1943), and Mississippi (1758-1880) (Young 1946, pp. 12, 14, 19, 23, and 26). In recent years there have been panther reports over much of the historical range (reviewed in Layne and McCauley 1976) and include sightings or specimens from Alabama, Arkansas, Louisiana, Mississippi, and Tennessee (Goertz and Abegg 1966, Eaton 1971, Jenkins 1971, Noble 1971, Wolfe 1971, Sealander and Gipson 1973, Lowery 1974, Lowman 1975, Morine 1976). Only seven specimens outside of Florida could be located: Louisiana (4)—the type specimen (USNM 137122, 1905) from Concordia Parish, two specimens from Prairie mer Rouge (1800s), and one from Caddo Parish (1965); Arkansas (2)—Ashley County (1969) and Logan County (1975); South Carolina (1)—with conflicting data suggesting it was either from Oregon or South Carolina (records of ANSP) (Appendix 3).

Archeological and paleontological evidence exists for pumas in the southeastern United States outside of Florida (Parmalee 1960, Kurtén 1965, Reitz and Roe, Univ. Georgia, pers. comm.). Within Florida, Pleistocene fossil have been recovered throughout the peninsula from Dade County in the south to Columbia County near the Georgia border (Webb 1974, Kurtén 1976, Morgan 1997).

The Florida panther was believed to be extinct in north Florida by the turn of the century (Bangs 1898) although northern sightings and actual shootings have been reported since that time (Tinsley 1970, Layne and McCauley 1976, Belden 1986a, and Konecny and Eisenberg 1984). Historic and recent specimens from Florida (Fig. 1) are restricted to the southern part of the state. The northern-most

localities represented in Florida are those of the type specimen locality "wilderness west of Sebastian" (Bangs 1898), in the vicinity of the current boundary between Indian River and Brevard counties, New Smyrna in 1859, and the recent find of a skeleton in Farnton Wildlife Management Area, Volusia Co. (Belden et al. 1988).

In 1983 an illegal kill was made in Palm Beach County, an area not known to be inhabited by panthers. Eventually, the skull and partial skeleton of that animal was recovered, but the identity of the cat as a true Florida panther could not be resolved (Abercrombie 1984, Belden 1986b). A second puma, also of questionable identity, was killed in Palm Beach County in 1984. In 1988, a young puma was hit by a car in Jefferson County in North Florida, well outside the current range of panthers (Roelke 1988). It was later learned that the animal was captive bred, not of Florida stock, and intentionally released by the owner. There are over 1000 cougars in captivity in the State of Florida (B. Cook, Law Enforcement Division, Florida Game and Fresh Water Fish Commission, pers. comm.). The need to develop a means to identify the Florida panther, particularly in law enforcement issues, was the genesis of this study.

METHODS

Museum specimens of *P. concolor coryi* were examined and compared to specimens of puma throughout its range in North and South America. The sample from the southeastern United States consisted of 72 specimens from Florida dating back to the mid-1800s and the only seven specimens known from outside of Florida (Fig. 1, Appen. 2), including one from South Carolina with mixed data. The data set from Florida contains all specimens, including those of uncertain identity.

In addition to traditional skull measurements, techniques were developed to quantify non-linear characters of color and cranial profile. The latter was intended to measure the distinctive nasal contour seen in Florida panthers, the "roman nose," noted by Goldman (1946). Color was measured in museum skins using a color spectrophotometer, and they were examined for the presence of a mid-dorsal cowlick.

Multivariate techniques were employed to evaluate the possible morphological boundaries of populations (subspecies) and variation within the Florida population. Principal component analysis (PCA) and Canonical discriminant analysis (CDA) are multivariate techniques of data reduction that aid in detecting patterns in the data (measurements of characters) and relationships between and within classes or groups of individuals (other taxonomic units, OTUs). With PCA, the sample is not subdivided *a priori* into discrete groups, and the characters are unweighted. The principal components (axes) are representations of the variables (measures), each of which vary in their relative contribution ("factor loading") to each PC axis. PCA is not designed to discriminate between groups, merely to aid in distinguishing trends in the data.

SOUTHEASTERN SPECIMEN LOCALITIES

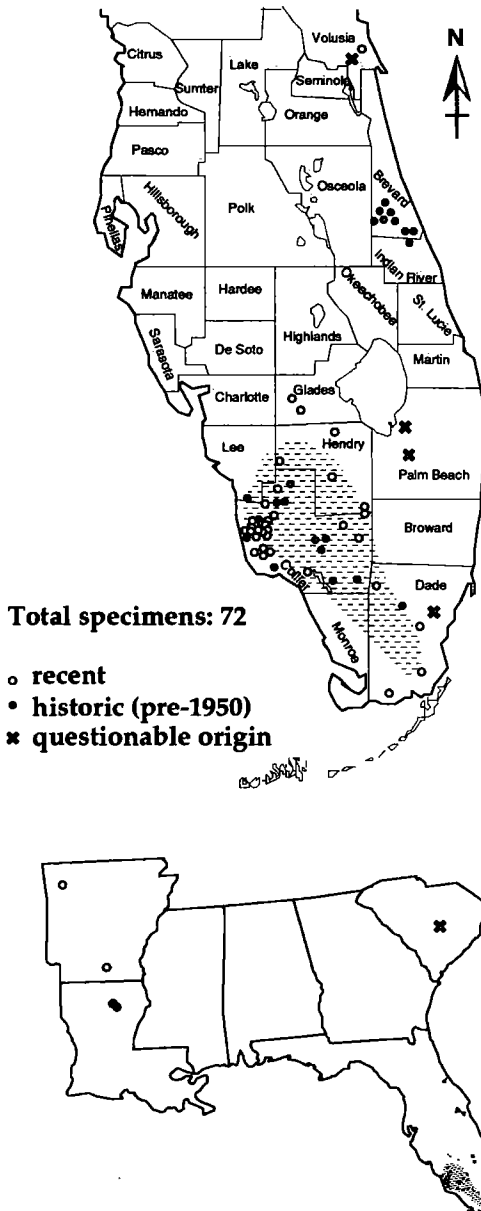


Figure 1. Geographic distribution of *Puma concolor coryi* specimens examined (dots) from the southeastern United States. Three groups of specimens are represented: recent specimens since 1950; historical specimens, including those collected by Charles Cory and Outram Bangs in the late 1800s; and recent specimens whose identity was uncertain. The most northern records include a single specimen from 1859, locality listed only as New Smyrna, and the skeleton of a cougar discovered in 1987 in the Farmington Wildlife Management Area, Volusia County.

CDA is a powerful procedure that maximizes intergroup differences to portray the relationships of the groups more clearly. CDA utilizes OTUs that have been divided into groups on the basis of an *a priori* classification. It may be used to assign group membership to new specimens, or to describe group differences and relationships. MANOVA emphasizes the testing of similarity/difference among centroids of the *a priori* groups and, in that respect is closely related to discriminant analysis. MANOVA tests the hypothesis that all *a priori* groups have the same multi-dimensional mean (centroid) for the variables measured.

In order to examine the morphometric relationships within the Florida population, where *a priori* classification was required, the Florida and southeast specimens were assigned to the following classes: Florida historic (=HIST, pre-1950 Florida specimens); Florida recent (=RECENT, non-Everglades Florida cats since 1950); historic Louisiana specimens (=ARUND); Everglades cats (=GLADES); animals from Florida of questionable identity, or specimens with no data (=TEST), Piper captive cats from Everglades Wonder Gardens (=PIPER); and the southeastern cats from Arkansas and Louisiana (=ARK/LA) that were collected between 1965 and 1975 long after cougars were thought to survive in Louisiana (Goertz and Abegg 1966, Sealander and Gipson 1973). The TEST animals are two females shot in Palm Beach County outside the known range of the Florida population, a specimen in the Everglades Regional Collection Center with no data, the skull of a male cougar found in Volusia County, a male from South Carolina with mixed data, and a specimen from a private collection recently donated to the Florida Museum of Natural History with no data. These labels are used throughout the following discussion. At one time, the canebrake puma from Louisiana was considered a separate subspecies *P. c. arundivaga* (Hollister 1911), but Nelson and Goldman (1929) synonymized it with *P. c. coryi* since they were unable to find any distinctive characters to separate it.

Only adults were included in the study. Cougars are sexually dimorphic, with males being larger than females (Goldman 1946, Kurtén 1973, Anderson 1983, Maehr and Moore 1992, Gay and Best 1995). This sexual variation dictates separate analyses by sex, at least for variables associated with skull measures, thereby reducing the effective sample size for each subspecies. Skins of juveniles and those that were notably faded as a result of continuous exposure to light were eliminated from the color analysis. All data sets were tested for normality prior to analyses using the Shapiro-Wilk statistic (W). With one exception (cranial profile), multivariate analyses were done with the Statistical Analysis System (SAS Institute Inc. 1985). Group sample sizes varied with each statistical procedure, depending upon the availability and condition of specimens. Many skulls were damaged or did not have skins, so it was impossible to combine variables, since complete specimens (skins, or undamaged skulls) were often unavailable. Also, some characters were qualitative and others quantitative. Therefore, each character analysis was conducted independently. Because sample sizes and

analyses varied, methods and results are combined for each of the four characters discussed: pelage color, pelage traits, cranial profile, and cranial variation.

PELAGE COLOR

Methods

Cory (1896) reported the pelage of the Florida panther as being "more rufous or reddish brown" than more northern cats. Goldman (1946), using color standards developed by Ridgeway (1912), described them as 'tawny' heavily mixed with black in the mid-line becoming cinnamon-buffy or dull 'clay color' on the sides of the neck. Florida cats are considered dark, but no melanistic cougars have ever been authenticated. Goldman (1946, p. 235) described a distinct facial pattern as: face in general greyish-brown, the blackish areas at the base of vibrissae prominent, ears black externally. There are subtle color differences between populations in facial patterns and in color shifts along the flanks, inside of the legs, and the underside of the neck and chest; however, these were not incorporated as variables in the quantitative analyses.

A spectrophotometer (Color Scan by Milton Roy Company, Analytical Products Division, Rochester, New York) was used to measure the color of 282 museum pelts representing 13 subspecies from North and South America. The instrument measures spectral variables that correspond to dominant wavelength (or hue), saturation (or chroma), and lightness. In addition, it evaluates each sample (reading) with respect to its position on a red-green scale and a yellow-blue scale (from 1 to 100), with low values toward green and blue and high values toward red and yellow, respectively. Measurements for dominant wavelength and saturation can be expressed in several ways, but those used in this study are trichromatic coefficients for x (=dominant wavelength) and y (=saturation). Each is calculated from the percentage of the three primary colors required to match the sample being measured. Lightness (luminous reflection) is expressed as a number on a relative scale from 1 to 100.

Seven readings were taken on each skin: three mid-dorsal, three lateral, and one belly (Fig. 2). Dorsal values represent the darker midline exhibited by many individuals. Lateral color measurements were taken at the hip, ribs and shoulder. These represent the predominant color of each pelt. The mid-ventral belly measurement was eventually discarded because of the tremendous variability shown by the values as a result of dark basal underfur showing through the lighter guard hairs of the belly fur. High correlation coefficients (>0.9) for each of the two back measurements and each of the three lateral measurements allowed reduction of the dorsal and lateral color variables to one value for each. The final data set consisted of eight variables: three values each (hue, saturation, lightness) for a

FLORIDA PANTHER COLOR MEASURES

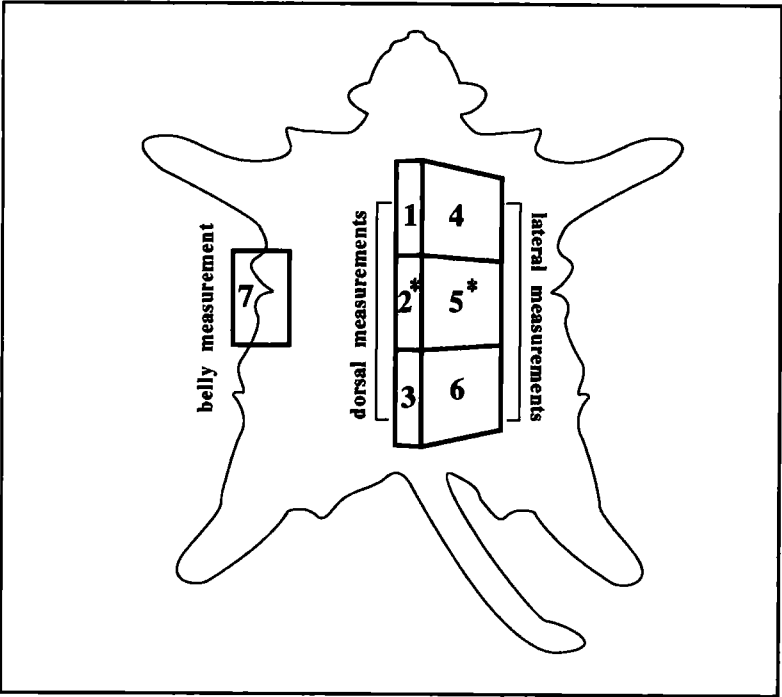


Figure 2. Spectrophotometer readings taken for seven regions of the pelt: three dorsal, three lateral, and a single belly measure. Dorsal values represent the darker midline; lateral measures were taken randomly within the defined regions and represent the predominant color exhibited by each animal. Only the mid-dorsal and mid-lateral measurements (*) were used in the subsequent analyses.

single mid-back and a single mid-lateral measure plus a value for degree of red and one for the degree of yellow for the mid-lateral measure. These eight remaining variables were subjected to PCA as an exploratory method to determine if the considerable within- and between-subspecies variation observed formed a pattern that would warrant further analysis. MANOVA tested the hypothesis that no overall subspecies differences existed between the means of the Florida population and those of other North and South American populations.

Results

Color variables were normally distributed ($p < 0.05$ test for normality) in those subspecies groups represented by large sample sizes, and approached normality in less well represented groups. No observable color differences could be detected between males and females, or between historic and recent *coryi* so these classes were combined in subsequent procedures.

PCA and MANOVA produced similar results. There was considerable overlap among both North and South American subspecies as would be expected given the variation present in the species overall (not shown). However, examination of the principal components when *P. c. coryi* is compared to selected North American and South American subspecies separately reveals patterns that correspond to the qualitative descriptions given by Goldman (1946). *P. c. coryi* is darker than western and northern inland populations from North America (Fig. 3a). There is virtually no difference in color measures between *P. c. coryi* and coastal populations from Oregon and Washington (*P. c. oregonensis* and *P. c. olympus*) (Fig. 3b). This also was noted by Goldman (1946, p. 237): "In dark general color tones *coryi* approaches the geographically distinct *olympus*...." *P. c. coryi* is less red than tropical subspecies from Guatemala, Costa Rica, Panama, Venezuela, and Brazil (*P. c. mayensis*, *P. c. costaricensis*, *P. c. concolor*) (Fig. 3c), although the latter cannot themselves be separated from one another. MANOVA showed significant differences between *coryi* and most other North American subspecies, including *P. c. hipposlestes* ($p = 0.002$) and *P. c. stanleyana* ($p = 0.0001$), two subspecies with which it presumably intergraded in the past (Table 1), but it could not be distinguished from northwest coastal populations of *P. c. californica*, *P. c. oregonensis* or *P. c. olympus* based on color variables ($p > 0.1$). Among the South American subspecies, the differences in the means of color variables for *P. c. coryi* are significant for all subspecies tested except *P. c. araucanus* from Chile ($p = 0.62$) and *P. c. bangsi* from Colombia ($p = 0.3$) (Table 2).

The two GLADES cats, the female cougar from Corbett Management Area (TEST), and one PIPER clustered within the spread of *P. c. coryi* values in PCA; one PIPER is outside the range of variation expressed by *P. c. coryi* (Figs. 3a, b). As with the PCA, no significant differences were detected between the means of *P. c. coryi* and the Everglades cats or the Corbett female with MANOVA, but *P. c. coryi* was shown to be significantly different than the PIPER ($p = 0.02$) (Table 1.) With the exception of one captive, the PIPER and GLADES cats and test animals clustered within the range of variation of *P. c. coryi* (Fig. 3a, b; Table 1). However, the colors of these test animals differed in ways that were not measured with the spectrophotometer.

Table 1. Probability (≤ 0.05) of difference between the means of color variables for selected North American *Puma concolor* subspecies, including *coryi* and Everglades cats. Variables include measures of hue, saturation, lightness degree of redness, and degree of yellowness for mid-dorsal and mid-lateral region of skin (probability of no overall species effect 0.0001 - MANOVA). Not all subspecies were tested.

	<i>coryi</i> (n=24)	<i>ever</i> (n=2)	<i>captive</i> (n=2)	<i>test</i> ¹ (n=1)	<i>azteca</i> (n=36)	<i>calif</i> (n=23)	<i>hippo</i> (n=11)	<i>kaibab</i> (n=22)	<i>mayen</i> (n=4)	<i>missoul</i> (n=16)	<i>olymp</i> (n=12)	<i>oregon</i> (n=18)	<i>stanley</i> (n=23)
<i>coryi</i>		.580	.019*	.426	.0001*	.422	.002*	.0001*	.003*	.0008*	.384	.152	.0001*
<i>everglades</i>			.624	.326	.032*	.424	.196	.125	.185	.322	.917	.870	.045*
<i>captive</i>							.000*1	.0001*	.0008*	.0002*	.018*	.012*	.002*
<i>hippolestes</i>								.560	.0077*	.127	.0005*	.0003*	—
<i>kaibabensis</i>									.003*	.021*	.0001*	.0001*	—
<i>mayensis</i>										.238	.0016*	.034*	—
<i>missoulensis</i>											.0007*	.029*	—
<i>olympus</i>												.271	—
<i>azteca</i>													.275
<i>californica</i>													.0001*

¹ UF 23985 female shot by hunter, Corbett Management Area.

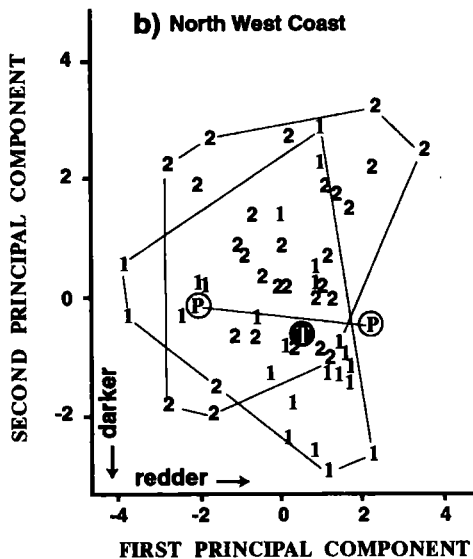
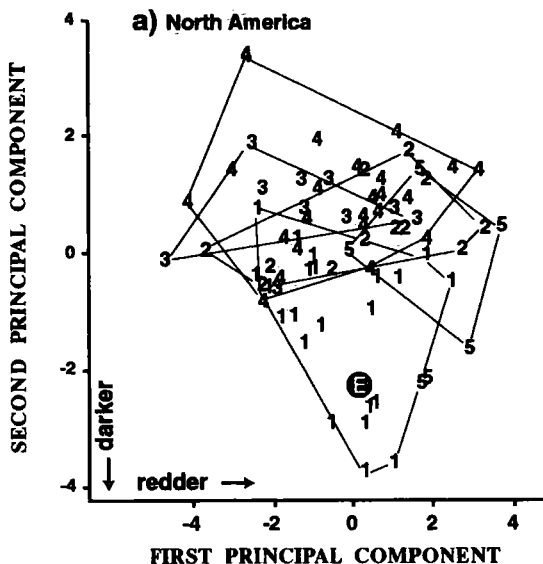
* significant $\alpha p < 0.05$.

Table 2. Probability (≤ 0.05) of difference between the means of color variables for selected South American *Puma concolor* subspecies, including *coryi* and Everglades cats. Variables include measures of hue, saturation, lightness degree of redness, and degree of yellowness for mid-dorsal and mid-lateral region of skin (probability of overall species effect was 0.0001 - MANOVA).

	<i>coryi</i> (n=24)	<i>acrocod</i> (n=4)	<i>arauacan</i> (n=9)	<i>bangsi</i> (n=4)	<i>borben</i> (n=15)	<i>concolor</i> (n=16)	<i>costrac</i> (n=8)	<i>incarum</i> (n=6)	<i>osgoodi</i> (n=4)	<i>pearsoni</i> (n=4)
<i>coryi</i>	1.000	.0001*	.6205	.2953	.0001*	.0001*	.0001*	.0027*	.0107*	.0001*
<i>acrocodia</i>			.0053*	.0856	.0001*	.0036*	.0380*	.0203	.0762	.0001*
<i>arauacanus</i>				.9680	.0001*	.0005*	.0041*	.0239	.0470*	.0003*
<i>bangsi</i>					.0003*	.0083*	.0466*	.0977	.1924	.0218*
<i>borbensis</i>						.0745	.3084	.0046*	.0650	.0001*
<i>concolor</i>							.7781	.0615	.2442	.0001*

* significant $\alpha p < 0.05$.

FLORIDA PANTHER COLOR MEASURES COMPARED WITH OTHER PUMA POPULATIONS



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FLORIDA PANTHER COLOR MEASURES COMPARED WITH OTHER PUMA POPULATIONS

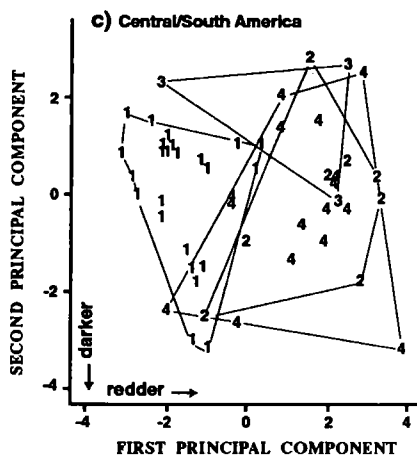


Figure 3. Plots of the first two canonical variables representing color for cougars from North America based on eight color measures. Numbers represent groupings (subspecies) or individuals as follow: (a) 1, *coryi* (Florida); 2, *missoulensis* (Montana, North Dakota, Canada); 3, *hippolestes* (Colorado, Wyoming); 4, *kaibobensis* (Arizona, Utah, Nevada); 5, *mayensis* (southern Mexico, Guatemala); E, Everglades. Note that *coryi* is darker than western and northern inland populations, and darker but not as red as populations from southern Mexico and Guatemala. (b) 1, *coryi*; 2, combined *oregonensis* and *olympus* (Washington, Oregon, Olympic Peninsula); P, Piper cats from Everglades Wonder Gardens; T, test animal (Corbett female). There is virtually no difference between *Puma concolor coryi* and animals inhabiting the northwest coast. (c) 1, *coryi* (Florida); 2, *costaricensis* (Costa Rica, Panama); 3, *osgoodi* (Bolivia); 4, *concolor* (Brasil, Venezuela). Note that *coryi* is as dark as but not as red as tropical subspecies from Panama, Venezuela, and Brasil, although the latter can not be separated from each other. Cougars from mountainous regions of Bolivia are somewhat lighter and less red than the other three groups.

For example, one of the PIPER cats had dorsal and lateral coloration similar to Florida cats, but graded to a bright reddish color along the flank, whereas *coryi* grades to a dull clay color.

PELAGE CHARACTERS AND KINKED TAIL

Methods

Two other pelage features, white flecks and a mid-dorsal whorl, have frequently been observed in the Florida panthers. A third unusual trait is that of the kinked tail, a skeletal feature that is visible externally.

Flecks.— In most Florida cats, the head, neck, and shoulders are irregularly flecked with white hairs (Goldman 1946), a feature noted by Bangs (1899) as "little bunches of white hairs, scattered here and there." A certain amount of white

flecking may be seen on pumas from any part of their range, but it is much more prevalent in the Florida subspecies (Goldman 1946). The density of flecks on any particular animal is correlated with age (Roelke and Wilkins, unpubl. data). They consist of only a few isolated white hairs or small patches on very young animals, but old animals have liberal flecking that extends along the back almost to the hip (Fig 4a). It is generally believed that flecking is caused by ticks, and there are seven species that comprise the ectoparasite fauna of cougars in Florida. Heavy infestations of ticks, especially *Ixodes scapularis*, are associated with open wounds and scars on both live and dead animals (Forrester et al. 1985). Of 318 museum skins examined, only four (two from Brasil, one from Panama, one from Peru) showed the dense flecking seen on Florida cats, although light flecking could occasionally be seen on cougars from throughout their range. This may reflect a sampling error, or unusually high densities of *Ixodes* ticks in Florida compared to other localities. However, it is also possible that panthers in Florida may be more sensitive to the bite of the *Ixoides* tick. Whatever the reason, flecking is consistently more prevalent in the Florida population. As an environmentally induced color change and not a genetically inherited trait, it is not considered a true morphologic character. However, it is useful in recognizing cats from Florida.

Whorl/crooked tail.— The whorl, or cowlick, is a structural reversal of hairs that occurs mid-back and/or at base of the neck. The mid-dorsal whorl can be an abbreviated narrow ridge of only four centimeters, but it is more often a pronounced oblong or tear drop shape up to 30 cm in length (Fig. 4b). The whorl at the base of the neck is chevron-shaped and may be up to 10 cm long (not shown); it is quite distinct from the usual swirl that is caused by the change in direction of hairs in this region. Whorls occur in both sexes and are present at birth, as seen in four fetuses recovered from a car-struck female. Florida animals frequently display the mid-dorsal whorl, sometimes the neck whorl, and in a few instances both appear in the same animal. The mid-dorsal whorl was not mentioned by early describers although it was distinctly present in many of the specimens they examined.

The kinked or crooked tail is the result of a modification of the distal caudal vertebrae. Often the third vertebra from the end is shortened and curved, resulting in a 90-degree bend in the tail (Fig.4c). The last tail vertebra often is truncated and also sometimes curved, resulting in a double kink. The kink is palpable through the skin and is often visible as a curl at the tip of the tail in living animals. The whorl and kinked tail are considered to be genetic markers of the Florida subspecies (O'Brien et al. 1990). The two characters are not linked, as animals occasionally will exhibit one trait and not the other. Skeletons were often not preserved in collections, so the frequency of this trait in older museum specimens could not be determined. However, it is visible in two published photographs panthers shot in the 1940's (Hamilton and Whitaker 1979, pg. 307; Tinsley 1970, p. 23).

FLORIDA PANTHER PELAGE/SKELETAL TRAITS FLECKS, WHORLS AND KINKED TAILS

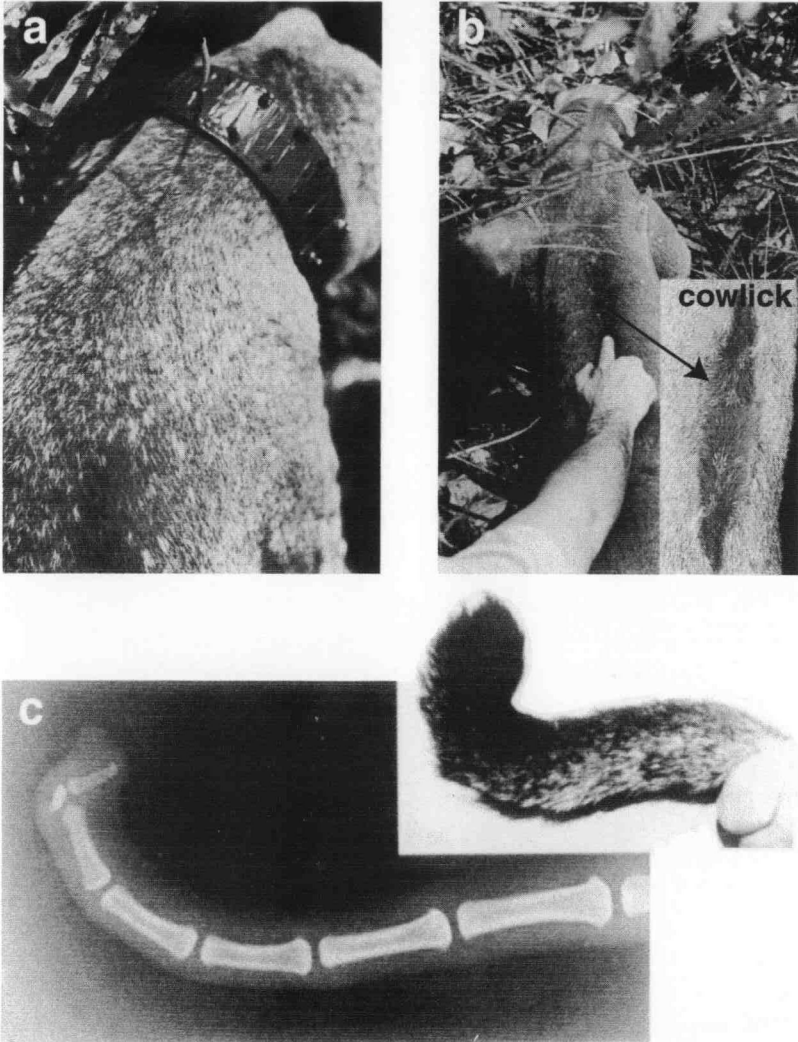
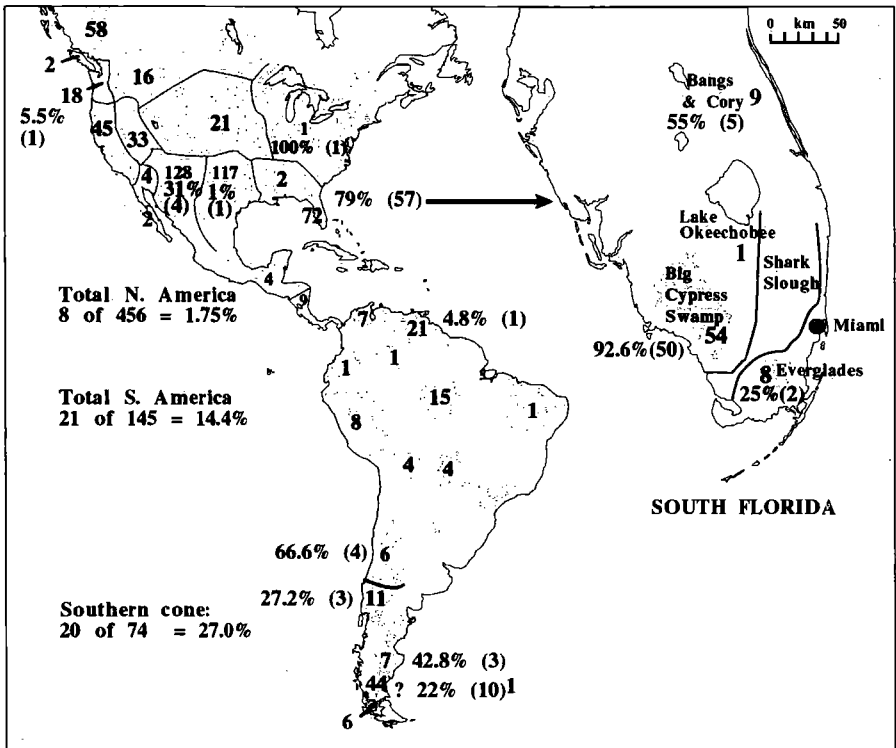


Figure 4. Pelage traits of the Florida panther. (a) flecks shown on an old male where flecking is extensive. (b) mid-dorsal cowlick or whorl. (c) kinked tail, a modification of bones of the tip of the tail, is seen as a curl in the tail of the living animal. Photographs by R. Belden (top) and M. Roelke (bottom).

PRESENCE OF WHORLS IN FLORIDA AND OTHER POPULATIONS OF COUGARS



¹ Localities vague, subspecies undetermined.

Figure 5. Darkened areas represent geographical populations of cougars (subspecies). Numbers represent number of skins examined. Number of specimens displaying mid-dorsal whorl and frequency (%) shown adjacent to population.

The frequency of the whorl in *Puma concolor* was determined by examining 648 skins in museum collections, representing 15 North American and 14 South American subspecies, including the panthers from Florida ($n=49$). Sample sizes for each population varied. In addition to museum skins, live animals (23 Florida, 23 Texas, 50 Colorado) were examined for whorls and kinked tails. At the time the museum skins were examined, the neck whorl had not been discovered, so no quantitative data are available for any population outside of Florida.

Results

Whorl.— The mid-dorsal whorl was found on skins of cougars throughout their range, but in very low frequencies compared to its presence in Florida animals (Fig. 5, 6). It is expressed in six North American subspecies (8 of 456 specimens, or 1.75%) and four South American subspecies (21 of 145, or 14.4%). Among the South American forms, it is more prevalent in subspecies from Chile and Argentina (20 of 74, or 27%) (Table 3, Fig. 5). The trait was present in 12 of 16 historic specimens from Florida, dating back to the late 1800s, but was absent in 4 of 6 type series taken by Bangs in the wilderness west of Sebastian. Among all historic and recent specimens and live captures in Florida, it is more prevalent in the cats from southwestern Florida (92.6%) than in the cats from the Everglades and Palm Beach County, Florida (22.2%) (Table 4). By the mid-1980s when this study was initiated, virtually all cats in the Big Cypress exhibited the whorl, compared to only 2 of 8 cats from the recent Everglades population. It is noteworthy that the only skin known of the eastern puma, *P. c. couguar* (dated 1847 from Greenwich, Rhode Island, in the collections of the Museum of Comparative Zoology [MCZ 42598] Harvard University) did possess a mid-dorsal whorl, whereas the type specimen of *P. c. arundivaga* from Louisiana did not.

Kinked tail.— There is no information available on the occurrence of the kinked tail in other subspecies or in historic *P. c. coryi* because post-cranial skeletons were not preserved. In Colorado, 2 of approximately 50 animals live-captured had kinked tails, but none of the recent Texas cougars ($n=23$) did (R. Armstrong,). As with the whorl, kinked tails occur in very high frequencies

Table 3. Number and frequency of whorl in Florida specimens compared to combined North and South American subspecies.

Locality	Total Examined	Total Whorl	% Frequency of Occurrence
<i>P. concolor coryi</i> ¹	72	57	79.2
Total North America(excluding <i>coryi</i>)	456	8	1.75
Total South America	145	21	14.40
Combined ssp. from Chile ² and Argentina	74	20	27.00

¹ *coryi* includes all Florida specimens and living animals examined, captive specimens included.

² Combined total of Chilean and Argentinean specimens are also presented to illustrate the high frequency of the whorl in this subspecies complex (consisting of four subspecies: *araucanus*, *pearsoni*, *puma*, *patagonica*)

FREQUENCY OF WHORLS AND KINKED TAILS

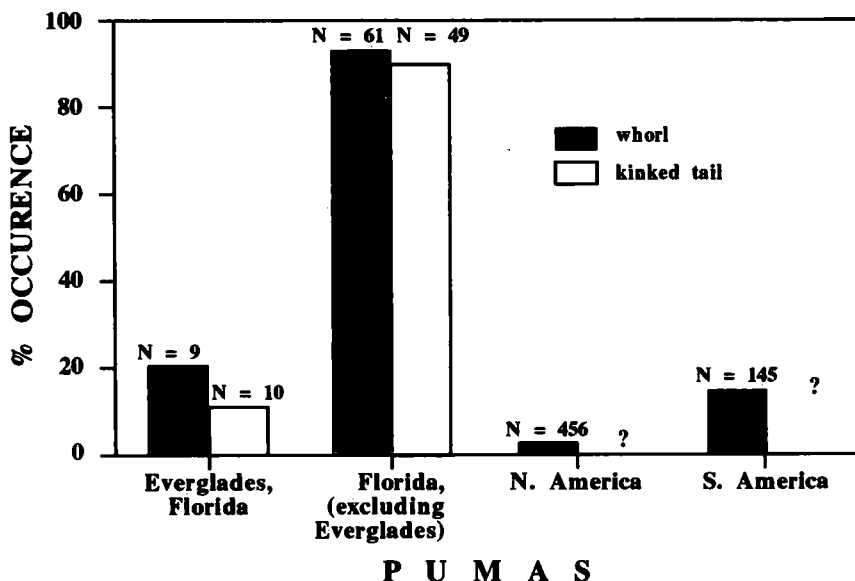


Figure 6. High frequency of whorls/kinked tails in Big Cypress compared to Everglades and puma populations in North and South America. Everglades includes two animals from West Palm Beach, only one of which had a skin.

in the recent specimens and live captures from Florida, and are more prevalent in southwestern Florida (87.8%) than in southeastern Florida (10%) animals (Table 4, Fig. 6).

CRANIAL PROFILE

Methods

According to Goldman (1946), the distinguishing features of the skull of *P. c. coryi* are a broad, flat frontal region, the result of remarkably high-arched nasal bones. He specifically mentions the outline of the nasals "rising to form a distinct convexity..." (p. 236) (Fig. 7a), a trait that has become known as the roman nose.

Table 4. Frequency of occurrence of whorl and kinked tail in specimens and live captures of Florida cougars.

Locality	n	Whorl Present	% Occurrence	n	Kink Present	% Occurrence
Southwest Florida ¹	54	50	92.6	49	43 ³	87.8
Historical Southeast ²	9	5	55.5	post-cranial skeletons not available		
Recent Southeast ³	9	2	22.2	10	1	10.0
Total	72			59		

¹All specimens from Big Cypress and other regions west of Shark Slough.²Specimens taken by Bongo and Cory in the late 1800s³Includes Everglades and two individuals from Palm Beach County, one of which had a skin.

The cranial profile was duplicated with a carpenter's contour gauge. The gauge was placed 1/8" to the left of the midline of the skull. The tip of the nasals and the point at which the contour gauge intersected the temporal line (ridge of bone that curves forward from the sagittal crest towards the post-orbital process) provided two consistent reference points (Fig. 7a). When the images produced by the contour were rotated with reference to a horizontal line (Fig. 7b) and superimposed, the distinctive inflated nasal region of *P. concolor coryi* becomes apparent (Fig. 7c). A total of 338 specimens representing 29 subspecies were measured. Some taxa are represented by a single or few specimens. Each contour was digitized using the mensuration program Sigma Scan. The images were interpolated to increments of 0.05 inches. The contours were normalized on both the X and Y axes; along the X axis to eliminate the variation due to size alone, and along the Y axis to define the highest point on the curve (highest point is Y=1) (Fig. 8) In the final data set, each contour measurement consisted of 20 values, each value representing an increment of 0.05 inches along the profile.

The highest point of the crania of most subspecies is the frontal region, the nasals gradually sloping from there. In the skulls of most *P. c. coryi* the frontal region is flat relative to the highly arched nasals, so the inflated nasal region becomes the highest point on the *P. c. coryi* skulls. This is shown in the comparison of a normalized profile of a Florida panther skull compared to one from Colorado (Fig. 8). The point on the X axis where Y=1.0 (the highest point) then becomes a measure of the degree of inflation at the anterior portion of the cranium. The closer that high point is to X=0, the greater the inflation of the nasals. The means, standard deviation, and minimum-maximum values for the highpoint were calculated and compared. The contour values were not normally distributed. For this reason, and because some classes contained small samples, the Mann-Whitney-Wilcoxon 2-tailed non-parametric test was used to test for differences in the means between (1) males and females, (2) historic *P. c. coryi* and

MEASUREMENT OF CRANIAL PROFILE

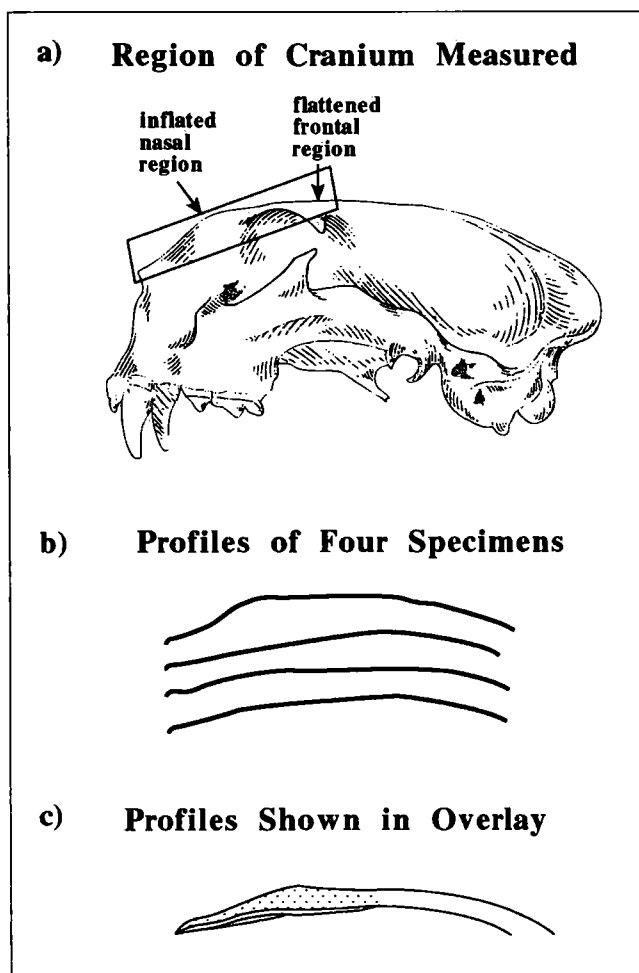


Figure 7. Measurement of cranial profile. (a) outline of Florida panther skull illustrating inflated nasals relative to flattened frontal region and region measured with contour gage placed 1/8" to the left of the midline of the skull; (b) actual contours (from top to bottom) of male *coryi*, compared to cats from New Mexico, Colorado, and Texas; (c) contours overlaid, shaded area is the difference between *coryi* and others.

SKULL PROFILES

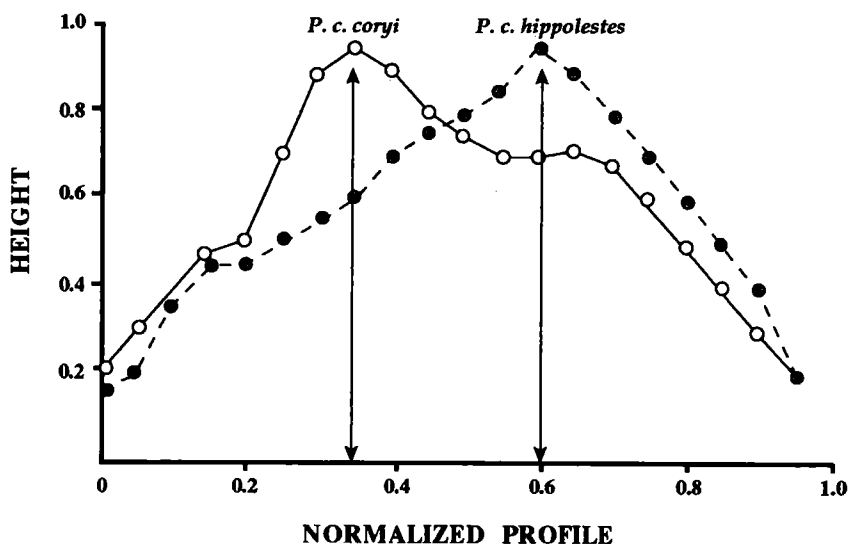


Figure 8. Images of profiles interpolated to increments of 0.05 inches and normalized on both the X and Y axes. The point on the X axis where $Y=1.0$ (the highest point) becomes a measure of the degree of inflation of the anterior portion of the cranium. The closer the high point is to $X=0$, the greater the inflation of the nasals. Shown is the comparison of a normalized profile of a Florida panther skull compared to that of a Colorado animal. This illustrates the inflated anterior portion of the skull of the Florida panther compared to the same area that is more sloping in the Colorado individual.

other pre-defined classes of Florida specimens, and (3) historic *P. c. coryi* and other subspecies.

Results

Hypothesis of no difference between males and females could not be rejected at $\alpha = 0.05$, so sexes were combined in this analysis. When HIST *P. c. coryi* specimens are compared to other subspecies, the differences are significant in 15 of 27 subspecies (Table 5a). Notable differences include the North American subspecies *P. c. azteca* from Arizona, New Mexico ($n=55$, $p=0.028$), *P. c. californica* from California ($n=30$, $p=0.0$), *P. c. hipposlestes* from Colorado ($n=24$, $p=0.0$) and *P. c. stanleyana* from Texas ($n=28$, $p=0.0001$). No significant differences were detected between HIST *P. c. coryi* and North American subspecies *P. c. cougar* of eastern U.S. ($n=4$), *P. c. olympus* ($n=1$) and *P. c. oregonensis* ($n=24$), the latter two from northwestern U.S.. Significant differences were recorded between HIST *P. c. coryi* and three GLADES cats, two PIPER from

Table 5a. Mean, standard deviation, and minimum-maximum values for contour measurements of subspecies ($n = 286$), excluding *coryi*. Figure in last column is probability of differences between means of *coryi* (historic only $n = 18$) and other subspecies ($p \leq 0.05$ Mann-Whitney-Wilcoxon non-parametric 2-tailed test).

Subspecies	n	Mean	Standard deviation	min - max	Z-score	Probability
<i>araucanus</i>	4	.525	.0289	.500 - .550	2.297	0.0216 *
<i>arundivaga</i> ¹	6	.567	.0983	.400 - .650	—	—
<i>azteca</i>	55	.493	.1029	.350 - .700	2.9799	0.0288 *
<i>bangsi</i>	3	.533	.0289	.500 - .550	2.139	0.0325 *
<i>borbensis</i>	8	.475	.0886	.350 - .600	-1.8576	0.0632
<i>browni</i>	1	.600	.0000	.600 - .600	-1.5842	0.1131
<i>cabrarae</i>	2	.525	.0354	.500 - .550	1.6914	0.0908
<i>californica</i>	30	.547	.0890	.350 - .700	-4.1807	0.0000 ****
<i>capricornesis</i>	1	.450	.0000	.450 - .450	0.5940	0.5524
<i>concolor</i>	4	.462	.0479	.400 - .500	1.4415	0.1494
<i>costaricensis</i>	5	.600	.0866	.450 - .650	-3.0032	0.0027 **
<i>cougar</i>	4	.438	.0750	.350 - .500	0.77924	0.4359
<i>greeni</i>	2	.525	.0354	.500 - .550	1.6914	0.0908
<i>hippolestes</i>	24	.546	.0920	.350 - .700	-4.0068	0.0000 ****
<i>incarum</i>	6	.533	.0753	.400 - .600	2.7126	0.0067 **
<i>kaibabensis</i>	22	.539	.0950	.300 - .650	-3.6935	0.0002 **
<i>mayensis</i>	6	.500	.0837	.400 - .600	2.2621	0.0237 *
<i>missoulensis</i>	14	.561	.0789	.350 - .650	-3.7672	0.0002 ***
<i>olympus</i>	1	.550	.0000	.550 - .550	1.3862	0.1657
<i>oregonensis</i>	24	.460	.1021	.350 - .600	-1.6904	0.0910
<i>osgoodi</i>	11	.514	.1206	.300 - .650	2.2949	0.0217 *
<i>patagonica</i>	2	.650	.0707	.600 - .700	-2.2944	0.0218 *
<i>pearsoni</i>	11	.568	.1055	.400 - .750	3.5264	0.0004 ***
<i>puma</i>	2	.525	.0354	.550 - .550	-1.6914	0.0908
<i>schoregori</i>	1	.350	.0000	.350 - .350	-0.71326	0.4757
<i>söderströmi</i>	4	.450	.0913	.350 - .550	-0.95976	0.3372
<i>stanleyana</i>	28	.536	.0941	.350 - .650	3.8647	0.0001 ***
<i>vancouverensis</i>	7	.650	.0500	.600 - .750	-3.8613	0.0001 ***
Total	286					

¹ See table 5b for *arundivaga* (Louisiana) scores.

* $p < 0.05$
 ** $p < 0.01$
 *** $p < 0.001$
 **** $p < 0.0001$

Everglades Wonder Gardens, three historic specimens of Louisiana, and the recent kills from Arkansas and Louisiana ($p < 0.05$). No significant differences can be reported between HIST and RECENT *P. c. coryi* or for four TEST specimens from Florida; namely, the no data specimen from ENP, two Palm Beach females, and the skull found recently in Volusia County (Table 5b).

The consistently high profile values exhibited by historic *P. c. coryi*, followed closely by recent *P. c. coryi*, illustrate that the inflated nasal region in *P. c. coryi*

has the lowest mean value of all groups measured, despite the overlap recorded (Fig. 9). The wide range of values for most subspecies suggests that the failure of the analyses to discriminate between *P. c. coryi* and some of the other groups may be due to small sample sizes.

Everglades cats differed significantly from the HIST cats regardless of small sample size. The two cats from the Everglades do in fact have small rounded crania with flat nasals, more similar to cats from South America. In this case, the flattened nasals represent a real difference from those of both HIST and RECENT *P. c. coryi*.

The failure of the analyses to detect the similarity of the ARUND historic from Louisiana to HIST *coryi* highlights one limitation of the technique; namely the profile scores for three ARUND historical range from 0.4 (inflated nasals) to 0.65 (inflated frontals). The score 0.65 is that of the male type specimen from Louisiana (= *arundivaga*), that has, in addition to the inflated nasals, an enlarged frontal region that obscured the inflated nasals in the normalized profile. The technique was unable to distinguish between actual and relative differences in the conformation of the skull.

Table 5b. Mean, standard deviation and minimum-maximum values for contour measurements of *coryi* classes (n = 49). Figure in last column is probability of differences between the means of *coryi* (historic n = 18) vs *coryi* (recent), Everglades, captive, Test 1, Test 2, Test 3, *arundivaga* (historic) and *arundivaga* test (recent). ($p \leq 0.05$ Mann-Whitney-Wilcoxon 2-tailed non-parametric test).

<i>coryi</i> class	n	Mean	Standard deviation	min - max	Z-score	Probability
Recent	18	.455	.1041	.300 - .600	1.442	0.1493
Piper	3	.567	.0289	.550 - .600	2.4553	0.0141*
Everglades	3	.550	.1000	.450 - .650	2.0794	0.0376*
Historic	18	.411	.0832	.350 - .600		
Test 1 ¹	1	.550	.0000	.550 - .550	1.3862	0.1657
Test 2 ²	2	.500	.0707	.450 - .550	1.4177	0.1563
Test 3 ³	1	.350	.0000	.350 - .350	-0.71326	0.4757
Louisiana (historic)	3	.400	.1323	.400 - .650	2.0275	0.0426*
Louisiana/Arkansas (recent)	2	.583	.0763	.500 - .650	2.4037	0.0162*
Total	52					

¹ Test 1 = GLADES 7040 no data specimen from ENP.

² Test 2 = UF 19077 Canal Point, Palm Beach Co.; UF 23985 Corbett Management area, Palm Beach Co.

³ Test 3 = UF 24042 Skeleton found in Volusia Co.

* $p < 0.05$

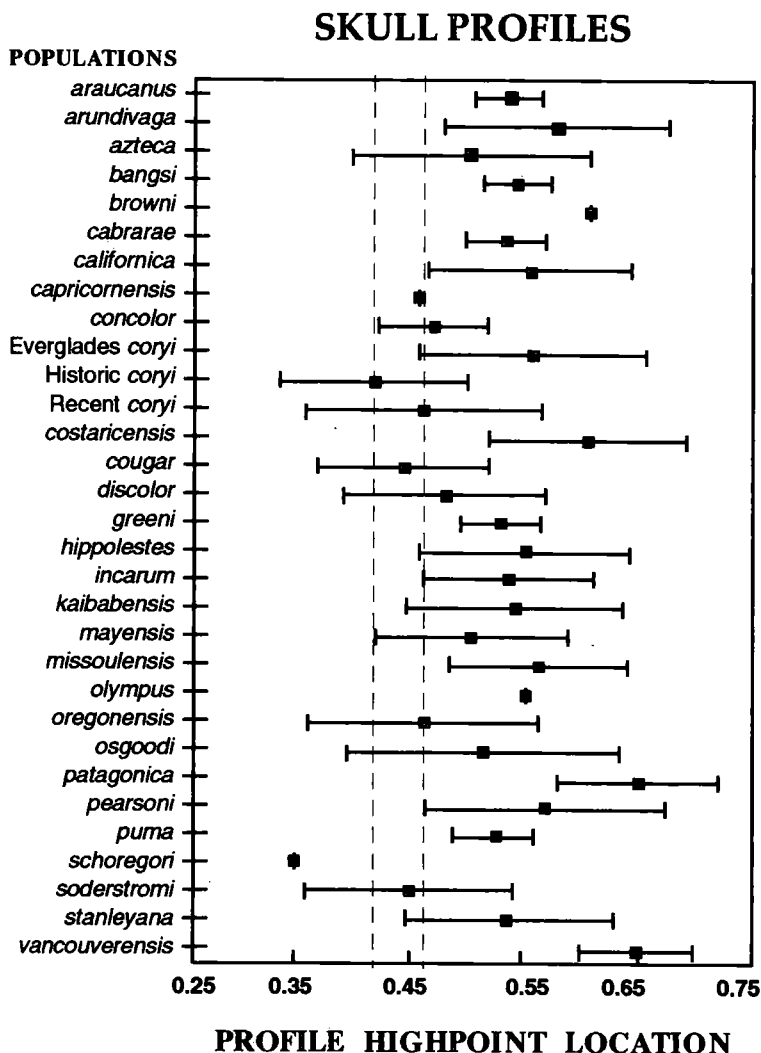


Figure 9. Means and standard deviations for value of X when Y=1.0 (the high point) for all populations measured. Historic *coryi* shows the greatest inflation of the anterior skull, followed by recent *coryi*. The extinct *P. c. couguar*, the eastern cougar, also shows this tendency, as does *oregonensis*, cougars from the northwestern United States.

CRANIAL PROPORTIONS

Methods

Cranial measures provide a suitable method for the study of geographic variation. According to Goldman (1946), the skull of the Florida panther differs from that of western subspecies in a number of proportions. Earlier work showed *P. c. coryi* could be correctly classified with a high level of confidence when compared with other North American subspecies using cranial measurements and statistical methods (Abercrombie 1984, Belden 1986b). Eighteen cranial measurements were taken on adult specimens of *P. c. coryi* (n=55), including historic specimens from Louisiana (n=3) and other North American subspecies (n=183). Lack of sufficient samples of all South American forms and some North American subspecies limited the cranial analysis to the use of six subspecies: *P. c. azteca*, *P. c. californica*, *P. c. coryi*, *P. c. hipolestes*, *P. c. kaibabensis*, *P. c. oregonensis*. There were too few specimens available of the now-extinct *P. c. cougar*, from eastern U.S. to include in this analysis.

Unfortunately, many *P. c. coryi* skulls were damaged, the result of having been shot in the head (older specimens) or hit by cars (recent specimens), resulting in numerous missing values. In all multivariate SAS statistical procedures, observations with missing variables will be eliminated from the analysis. Therefore, even with a sufficient sample of specimens, elimination of damaged individuals and separate analyses by sex would preclude statistical methodology. Missing values were replaced with mean values for a particular variable which was calculated using existing values within the appropriate class (i.e. historic males, historic females, recent males, etc.). Specimens of unknown sex were classified with discriminant-function analysis also using specimens of known sex from the appropriate class (as above) to create a calibration data set. These procedures were necessary only for the Florida data set, since complete skulls of known-sex individuals from other subspecies groups were selected for measurement. Skulls of adult males are not only larger, but more angular and massive. Females are smaller and have a more smoothly rounded brain case and lesser development of sagittal and lambdoid crests (Goldman 1946). The two sexes might, therefore, be described by a different set of variables. Stepwise discriminant analysis selected 11 variables as important for discriminating females and 16 for males.

Geographic variation was explored using PCA. Because no discrete clusters were formed, subsequent CDA was conducted to maximize intergroup differences. Presented here is only one of several analyses conducted, including only three subspecies: Florida and Louisiana specimens (*P. c. coryi*), southwestern U.S. (*P. c. azteca*), and Texas (*P. c. stanleyana*), those groups inhabiting the southern part of the U.S. This was thought to be an appropriate strategy considering the disjunct distribution of *P. c. coryi*, the considerable variation exhibited by the subspecies in North America, and the limited scope of this study. Also, PCA suggested that clinal variation might be a confounding factor that could not be resolved with the

present data set. The objective was to determine if *P. c. coryi* could be discriminated from populations that it most closely resembles and to which it is closest geographically.

Discriminant function analysis examined possible misclassification of specimens ($p < 0.05$), using those specimens with reliable data as the base calibration group. Suspected hybrids (cats from the Everglades), others lacking data or with uncertain data, and those animals that could not be reliably identified as Florida panthers were treated as a test group.

Results

The three groups produced only two canonical variables, which together explained 100% of the variation. Canonical variable I (CV1) explained 81% of the variation for females, and 80% for males, with 19% and 20% respectively being explained by CV2. The measurements contributing to CV1 for females were total length, zygomatic breadth, pterygoid width, and upper carnassial crown length, while width of palate pterygoid width, condyle width, and maxillary tooth row were major contributing variables to CV2. For males total length, zygomatic breadth, condylobasal length, and post-orbital process breadth contributed to CV1, and zygomatic breadth, maxillary tooth row, and palatal width at canines contributed most to CV2 (Table 6). The plots of the canonical variables showed groups much more discrete than with other analyses (Fig. 10). As expected, HIST and RECENT *P. c. coryi* overlapped considerably. A single female Florida cougar was within the range of variation expressed by the Texas group. Test animals fell either on the periphery or outside the range of *P. c. coryi*, as did the two females from the Everglades. The only test animal that could confidently be assigned to *P. c. coryi* was the skull found at the Frampton Wildlife Refuge in Volusia County in 1987.

The results of the discriminant analysis follow the CDA plots in that animals outside the range of variation of *P. c. coryi* were reclassified (Table 7). However, because only three groups were represented, the individual being reclassified was placed in the group it most closely resembled. This confounds the interpretation, but is nevertheless instructive. Cats killed within the last 20 years in Louisiana and Arkansas were reclassified into the Texas subspecies *P. c. stanleyana* and are probably not relicts from the original population inhabiting those states but either new introductions from the west or escaped captive individuals. The two Everglades cats, the Canal Point cat and one Piper captive were reclassified as *P. c. azteca*. The skeleton found in Volusia County was reclassified as *P. c. coryi*. The captive Piper male from Everglades Wonder Gardens, which although well outside the range of variation of *P. c. coryi*, was more similar to it than to any of the other

FLORIDA PANTHER CRANIAL MEASURES COMPARED TO OTHER NORTH AMERICAN POPULATIONS

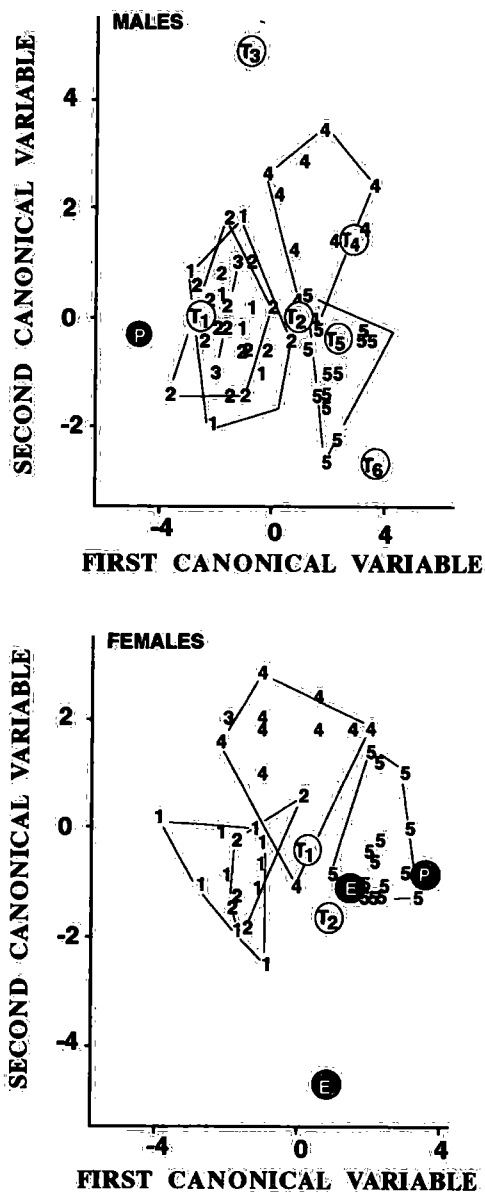


Figure 10. Plots of the first two canonical variables for skull and dental measurements: 1 = Florida historic, 2 = Florida recent, 3 = Louisiana historic, 4 = Texas, 5 = Arizona and New Mexico, E = Everglades, P = Piper (captive), T = Test (of uncertain origin). One observation hidden in each graph.

Table 6. Details of canonical correlation analysis for three subspecies of *Puma concolor* (*coryi*, *stanleyana*, *azteca*). Coefficients having dominant loadings on a standardized variable are shown in bold type and discussed in the text.

	Females		Males	
	Canonical variable		Canonical variable	
	1	2	1	2
Canonical correlation	.89	.68	.87	.66
Eigenvalue	3.70	.87	3.07	.76
Proportion of variance explained	.81	.19	.80	.20
Cumulative proportion explained	.81	1.00	.80	1.00
Standardized canonical coefficients				
Total length	-0.84	-0.59	-1.15	-0.07
Condylbasal length	-	-	1.85	0.05
Zygomatic breadth	0.87	-0.33	1.18	-1.80
Cranium height	-	-	-0.67	0.44
Width of palate	0.50	1.08	0.44	-0.11
Palatal length	-	-	-0.22	-0.80
Maxillary tooth row	-0.49	1.34	0.09	1.14
Mandibular tooth row	-	-	0.62	-0.54
Mastoid breadth	-0.26	0.27	-0.52	-0.04
Post-orbital process breadth	-	-	-1.61	-0.01
Postorbital constriction	0.56	-0.11	0.55	-0.16
Width at canines	-	-	-0.30	1.36
Pterygoid width	0.72	-0.88	-0.01	-0.15
Condyle width	0.15	-0.70	-0.11	0.08
Upper carnassial crown length	-0.74	0.00	-	-
Upper carnassial crown width	-	-	-0.50	-0.54

groups so was reclassified as *P. c. coryi*. It is interesting to note that the historic Louisiana males remained within the *P. c. coryi* sample, however the Louisiana female did not. Both Everglades cats were reclassified.

DISCUSSION AND CONCLUSIONS

Small sample sizes and problematic techniques limit the interpretive value of some of the results. Had it been possible to combine the characters measured, include a broader representation of populations, and have more robust samples, a more cogent picture of the relationship between Florida and other populations

Table 7. Reclassification of specimens of adult male and female Florida cougars according to discriminant function analyses. Specimens of uncertain identity were tested against a calibrated data set of *Puma c. coryi* (n=45), *P. c. azteca* (n=29), and *P. c. stanleyana* (n=21), separate analysis by sex, equal prior probability.

Individual Reclassified	Identity	Reclassified To Class	Posterior Probability
MALES			
LSU 11363	ARK/LA	<i>stanleyana</i>	0.40
LSU 17032	ARK/LA	<i>stanleyana</i>	0.97
MSH 1379	ARK/LA	<i>stanleyana</i>	0.88
UF 12462	Captive	<i>coryi</i>	1.00
ANS 2241	So. Carolina	<i>azteca</i>	0.99
UF 24042	Volusia Co.	<i>coryi</i>	0.99
FEMALES			
EVER 7040	ENP specimen	<i>stanleyana</i>	0.41
UF 19077	Canal Point	<i>azteca</i>	0.78
UF 23985	Corbett	<i>coryi</i>	0.77
UF 24557	Everglades (#27)	<i>azteca</i>	0.97
UF 24563	Everglades (#15)	<i>azteca</i>	0.98

might have emerged. Within the limited scope of the study, however, some conclusions might be drawn.

The geographic races of the cougar, like those of other animals are based on a combination of characters, including size, color, and cranial and dental measures that prevail in areas over which environmental conditions tend to be uniform (Goldman 1946). *Puma concolor coryi*, best known from the Florida population, appears to be well defined based on pelage markings, color, and the cranial profile. None of these characters is unique in itself; however, in combination, they provide a basis to describe the Florida population, whether or not one accepts the concept of a subspecies. Goldman (1946) placed heavy emphasis on the inflated nasals as a distinguishing feature of the Florida panther. Quantitative measures of this trait reinforced Goldman's view of its importance in identifying individuals belonging to the Florida population. Of North American subspecies examined, the Florida population most closely resembles cats from the northwest coast in details of color and cranial profile. This may reflect a similarity of some environmental parameter that prevails over the two geographic areas (for example, high humidity levels) and deserves further investigation.

Two Piper cats from the Everglades Wonder Gardens exhibit significant differences when compared to both the historic and recent specimens of *P. c. coryi*

based on cranial measures and skull contour. The baseline color of one of the Everglades cats was within range of variation of Florida panthers, but qualitative details of the pelage markings would preclude this assignment. These two animals had not been included in the genetic study, but came from the same breeding compound that produced the captive animals released into the Everglades.

Cats of questionable origin or suspect data defied classification. They clustered apart from or on the periphery of the Florida sample. The one exception to this is the skull recovered from Volusia County that could most confidently be assigned to the Florida population. Individuals containing a hybrid strain, with the exception of the Everglades cats, could not be detected within this study, unless it is the single individual that was killed in Canal Point in Palm Beach County, which was not included with genetics study.

The two cats from the Everglades differ significantly from the rest of the Florida cats in cranial profile and in cranial morphology, in addition to the absence of the kinked tail and mid-dorsal whorl. These results are consistent with those of the genetic studies that show the distribution of genetic markers to be strongly partitioned between Big Cypress and Everglades ecosystems. The morphologic differences between the Big Cypress and Everglades cats cannot be explained by geographic separation within Florida either now or in the distant past. This would tend to support the view put forth by O'Brien et al. (1990) that the cats inhabiting the Everglades are descendants of the captive and probably hybrid cats that were released into the Everglades.

The results of genetic work conducted by O'Brien et al (1990) suggest that little genetic mixing has taken place between the Everglades and Big Cypress populations, yet no permanent physiographic barrier exists between the Everglades and Big Cypress systems. Virtually no differences could be detected between the historic *P. c. coryi* morphotype and the recent Big Cypress panthers. The only indication of change is the slightly diminished arched nasal profile in the recent cats. This could be the result of dilution of the character through hybridization, but it may also be a sampling error, or genetic drift as a result of small population size. Considering that perhaps 30 years has elapsed since captive cats were released into the Everglades, the consistent dichotomy between the Everglades cats and Big Cypress cats is open to conjecture.

The Everglades is a vast and complex system, but short term cycles of drought and excessive rainfall do effect water levels in some regions (Duever et al 1994). Shark River Slough, a deep marsh in the western Everglades, when flooded might produce a cyclical but effective barrier limiting dispersal of animals from either side. Radio-collared animals in the Everglades were not documented crossing the Slough until 1989, when a severe drought caused lowered water levels (Bass and Maehr 1991), and then only three of ten monitored animals ever crossed from the Everglades side (Bass 1997). Dispersal around the Slough to the north would be limited by development and habitat fragmentation, while the

Caloosahatchee River is an effective barrier between north and south in the southwestern part of the state (Maehr 1997).

Distribution of panthers in south Florida is limited by the availability of suitable habitat and prey (Smith and Bass 1994). Between 1986 and 1991, radio telemetry studies revealed that female panthers in the Everglades utilized home ranges entirely east of the Slough, as did their female offspring (Bass 1997). In southwest Florida, females remained in or near the home ranges of their probable mothers (Maehr et al 1991). Young female recruitment into natal home range is a pattern repeated in other cougar and felid populations. Due to high home range stability for adult males, vacant home ranges for young dispersing males are limited, and mortality is greatest in subadult and non-resident males (Maehr et al. 1991). High rates of aggressive encounters between males of Florida panthers compared to other cougar populations, and the highest mortality factor of male cougars in Florida (Dunbar 1997), may be a further indication of limited dispersal opportunity as a function of suitable habitat.

A combination of factors that include cyclically high water levels in Shark River Slough, limited habitat availability, and the dynamics of puma behavior could explain the high degree of isolation that existed between the two populations of cougars in south Florida and that would have resulted in a reduction in gene flow and shared morphologic traits. With this recent extended dry period recorded in Florida, the effects of introgression may become more conspicuous as animals cross more freely between the two refuges.

Frequencies of whorls and kinked tails have changed over time. Four of six cats collected and studied by Outram Bangs between 1896 and 1898 did not have a mid-dorsal whorl. Among recent panthers of known origin from the Big Cypress Swamp between 1972 and 1987, all had kinked tails ($n=30$), and 25 of 27 (92%) had the back whorl. In 1986-1987, six panthers were captured in the Everglades National Park (ENP); none had a kinked-tail and only one had the whorl. In 1988 the first BCS animal with a straight-tail and whorl was documented (#25 rogue). By early 1990, four straight-tailed panthers (three of which had whorls) were documented in the BCS and the first cat from ENP (#39) with both the whorl and the kink was captured in ENP (Roelke 1990). This suggests there has been more mixing between the two areas in recent years.

The presence of a mid-dorsal whorl and kinked-tail clearly identifies a cat as being from the native Florida population, regardless of the genetic interpretation. The expression of these traits in the Florida populations in high frequencies has been considered a morphologic indicator of inbreeding and reduced levels of genetic variability. Of six North American subspecies of cougar, Roelke et al. (1993) demonstrated that the authentic Florida panther (excluding Everglades cats) exhibits less variation than any other puma subspecies with the fewest polymorphic loci (P) 4.9%, and low heterozygosity (H) with 1.8%, compared to (P) of 27% and (H) of 1.8-6.7% for other subspecies. This is nearly as low as the level of allozyme variation reported in the cheetah. This condition has undoubtedly resulted from

the loss of habitat and more than 150 years of persecution. Examination of historic specimens of the late 1800s shows that the whorl was not fixed in the population by the late 1800s, as it was missing from four of the original six Bangs specimens, but the frequency was nevertheless high (present in 5 of 9 specimens, or 55%, from the late 1800s).

The process leading to lowered levels of variability and expression of unusual traits might have begun much earlier and be explained in part by the peninsular nature of Florida in which genetic exchange with more northern populations was restricted on three sides. The Florida land mass receded to an even narrower peninsula than it is today when sea levels rose to their present level 8000 BP (Watts and Hansen 1988). Furthermore, climatic changes accompanied by a shift to less productive soils, and a vegetation community dominated by pine flatwoods by 5000 BP might further limit population numbers. Together these would have created conditions that would limit dispersal and intergradation with more northern forms. This view gains some support in the high frequency of the whorl in cats from Chile and Argentina (27% overall, but higher within individual populations) and the peninsular nature of those two countries (Eisenberg and Redford 1982).

The Florida panther exhibits a combination of unique and shared characters that are measurable and quantifiable. Further, the morphotype remains relatively unchanged from the early historic specimens of the late 1800s in spite of a possible introgression with another form. This does not suggest, however, that managed outbreeding is undesirable. The loss of genetic variability and associated problems of lowered reproductive potential and immunological deficiency (Roelke et al. 1993) that threaten this population, in addition to loss of habitat, requires immediate implementation of management decisions, and habitat preservation.

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APPENDIX 1

Florida specimens of *Puma concolor* examined

Catalog No. ¹	Sex ²	Age ³	COND ^{1,4}	BW ^{1,5}	NW ^{1,5}	F ^{1,6}	K ^{1,5}	Date	Comments
USNM 19483*	U	U	S,PSK	A	A	0	NA		Purchase, Wards Scientific
USNM 145264	(F)	2	SK	NA	NA	NA	NA	1859	New Smyrna
USNM 265596	M	4	S,SK	P	A	5	NA	1940	Purchase from E.Ross Allen
USNM 528190 resident	M	4	S	P	P	5	NA	1975?	Confiscated at tanner 1977; belonged to Florida
MCZB 5489	F	4	S,SK	A	P	5	NA	1896	
MCZB 5650	F	3	S,SK	A	A	3	NA	1896	
MCZB 6992	M	4	S,SK	A	A	3	NA	1897	
MCZB 7742T	M	3	S,SK	P	P	3	NA	1898	Type <i>F.concolor coryi</i> (Bangs)
MCZB 7743	F	4	S,SK	R	A	4	NA	1898	
MCZB 7744	(M)	1	!S,SK	A	A	1	NA	1898	
MCZ 31781	(M)	3	SK	NA	NA	NA	NA	1934	near Everglades (city?)
MCZ 10703	(M)	3	SK	NA	NA	NA	NA		"E.Florida", Wyman Collection
MCZ 19855	F	4	S,SK	P	A	4	NA	1922	
MCZ 54423	(F)	1	SK,PSKL	NA	NA	NA	NA	1973	Everglades, NE Flamingo
FMNH 1255T	F	U	!S	P	A	4	NA	1895	Type <i>F.concolor floridana</i> (Cory)
FMNH 14900	F	2	S,SK	P	A	3	NA	1896?	Marked M, but probable F (Cory)
FMNH 14902	(M)	3	S,SK	P	A	4	NA	1896?	Cory specimen
FMNH 50058	F	2	SK	NA	NA	NA	NA	1939	
FMNH 91621**	U	U	!S	P	A	3	NA	1896?	No data, probable Cory specimen
ANSP 15270	(M)	4	SK	NA	NA	NA	NA	1933	
ANSP 16705	(F)	4	SK	NA	NA	NA	NA	1935	
ANSP 16706	(F)	3	SK	NA	NA	NA	NA	1935	
AMNH 100222	(F)	3	SK	NA	NA	NA	NA	1946	
AMNH 144512	M	2	S,SK	P	A	3	NA		
UWZ	(F)	3	SK	NA	NA	NA	NA	1900	
EVER 7040	(F)	3	SK	NA	NA	NA	NA		No data
CCM	U	U	!S	P	A	3	?		Mtd. specimen, Earl Brown Coll., kink present in photo (Kelly's)
UF 9789	M	U	!S,SKL	P	A	4	NA	1972	Glades Co., tail missing
UF 10424	F	2	S,SK,SKL	A	P	3	P	1981	w/4 fetuses G-81-19

Appendix 1 Continued.

Catalog No. ¹	Sex ²	Age ³	COND ^{1,4}	BW ^{1,5}	NW ^{1,5}	F ^{1,6}	K ^{1,5}	Date	Comments
UF 10425	M	F	!ALC	P	A	A	P	1981	Fetus G-81-19
UF 10460	M	F	!ALC	P	A	A	P	1981	Fetus G-81-19
UF 10481	F	F	!ALC	P	A	A	P	1981	Fetus G81-19
UF 10573	F	F	!ALC	P	A	A	P	1981	Fetus G81-19
UF 11852	F	4	S,SK,SKL	A	A	A	A	1979	Captive Everglades Wonder Gdns
UF 11915	F	1+	!S,SK,SKL	P	P	2	P	1979	G-80-4
UF 11927	M	2	S,SK,SKL	P	P	2	P	1980	G-80-15
UF 12004	M	U	!S	P	A	1	NA	1940s	Rug
UF 12462	M	3	S,SK,SKL	A	A	1	A	1981	Captive Everglades Wonder Gdns
UF 12823	U	2	!SK	NA	NA	NA	NA	1940s?	Collected by R. Allen
UF 12827	U	1	!SK	NA	NA	NA	NA	1940s?	Collected by R. Allen
UF 14390	M	3	S,SK,SKL	P	A	2	P	1978	G78-65
UF 14699	(F)	3	PS,SK,PSKL	P	A	3	NA	1940s?	Collected by R. Allen
UF 16374	M	3	SK,SKL	A	A	P	P	1982	FGC #6 "blunt trauma", Skin examined by R. Belden in life
UF 18798	F	3	S,SK,SKL	R	A	P	P	1983	FGC #3 Skin mounted in Tallahassee
UF 18944	M	2?	!S,SK,SKL	R	A	P	P	1983	Palmdale, Glades Co., skull fragmentary, skin not tanned; cowlick could be "coaxed"
UF 19077	(F)	2	SK,SKL	NA	NA	NA	A	1983	Palm Beach Co. illegal kill
UF 19090	F	4	SK,PSKL	P	A	P	P	1983	FGC #5 skin examined by R. Belden
UF 19096	M	4	S,SK,SKL	P	A	5	P	1983	FGC #1
UF 20957	(F)	1+	SK,SKL	NA	NA	NA	P	1985	"Bones"; found by film crew G85-BNZ
UF 20958	F	3	!SK,SKL	NA	NA	NA	P?	1985	G84-26 "squash", specimen mutilated, no record of pelage characters; no kink, but abnormal blunt tail tip
UF 20777	M	5	PS,SK,SKL	P	A	5	P	1984	FGC #2 nasal region destroyed, skin not tanned.
UF 20973	F	1+	SK,PSKL	NA	NA	NA	NA	1985	Butchered female, tail missing G85-C-S
UF 22409	M	4	S,SK,SKL	P	A	4	P	1985	FGC #7 "raccoon"
UF 22529	M	4	S,SK,SKL	P	A	5	P	1985	FGC #4 "tattoo"
UF 23985	F	3	S,SK,SKL	A	A	2	A	1984	Corbett Management Area
UF 23986	M	2	PS,SK,PSKL	P	A	P	P	1987	FGC #10 killed by FGC #12
UF 24042	(M)	3	SK,PSKL	NA	NA	NA	NA	1987	Volusia Co. tip of tail missing
UF 24096	M	3	!S,SK,SKL	P	A	3	P	1988	GFC #13 "big Al", skull fragmented

Appendix 1 Continued.

Catalog No. ¹	Sex ²	Age ³	COND ^{1,4}	BW ^{1,5}	NW ^{1,5}	F ^{1,6}	K ^{1,5}	Date	Comments
UF 24097***	M	1	!S,SK,SKL	A	A	A	A	1988	G88-16 Jefferson Co.
UF 24160	(M)	?	!SKL	NA	NA	NA	P	1979	Gannet Strand
UF 24267	F	5	S,SK,SKL	P	A	5	P	1988	FGC #8
UF 24268	F	3	S,SK,SKL	P	A	4	P	1986	FGC #PCO59
UF 24314	M	4	S,SK,SKL	P	A	4	P	1988	GFC #20
UF 24315	M	3	S,SK,SKL	P	A	2	A	1988	GFC #25 "rogue"
UF 24316	M	2	SK,SKL	P	A	P	P	1988	GFC #24 Highlands Co.; examined in life by M. Roelke
UF 24561	M	2	S,SK,SKL	P	A	2	P	1989	89-64 Corkscrew Sanctuary
UF 24557	F	3	S,SK,SKL	A	A	2	A	1989	GFC #27 Everglades
UF 24563	F	4	PS,SK,SKL	A	A	P	A	1988	GFC #15 Everglades, skin in poor condition
J Billie	M	3	S,SK	P	P	4	P?	1983	Illegal kill; kink discernible in skin; specimen examined at time of trial
UF 24595	M		!S,SK,SKL	P	A	3	P	1989	GFC #33 rabies
UF 24611	M		!S,SK,SKL	P	A	3	P	1990	GFC #35 subadult
UF 24621	M		!S,SK,SKL	P	A	3	P	1990	GFC #30 killed by another male
Total specimens examined = 72: 49 Skins (2 partial); 60 Skulls; 37 Skeletons (6 partial); 4 Fluid preserved									

¹ USNM U.S. National Museum; MCZ Museum of Comparative Zoology; MCZB denotes Bangs' collection; FMNH Field Museum of Natural History; ANSP Philadelphia Academy of Science; UWZ University of Wisconsin; EVER Everglades National Park; CCM Collier County Museum (Florida); UF Florida Museum of Natural History, University of Florida; T=type specimen; COND=Condition; BW=Back Whorl; NW=Neck Whorl; F=Flocks; K=Kink.

² M=male; F=female; (?) male or female based on size of adult individual; U cannot be determined.

³ Age class based on fusion of skull sutures: 1=juvenile or subadult, all sutures open, size small; 2=young adult, sutures distinct and some fusion, size normal; 3=adult, partial fusion of sutures;

⁴ =mature adult, most or all sutures fused; 5=old, sutures indistinct; F=fetus; + indicates intermediate between classes.

⁵ Type of preservation: S=skin, SK=skull, SKL=post cranial skeleton, P=partial, ALC=alcohol.

⁶ Occurrence of pelage and skeletal features: P=present, A=absent, R=rudimentary (see text), NA=not applicable when skin or post-cranial skeleton is not available for inspection.

Category of flecks: 1=<5; 2=5-20; 3=20-50; 4=>50<100; 5=>100; A=absent, P=present, but not evaluated due to poor condition or absence of skin; values are estimated

* USNM19483 deleted from study; purchased from Wards Scientific in Miami, noted specimen importer and supplier; no further data

** FMNH191621 no data, but believed to be Cory specimen FMNH14901 previously mounted and thought discarded; based on color and pelage characters.

*** Specimen not believed to be Florida panther based on color; captive released into north Florida (information from Florida Game & Fish Commission); skull not included in analysis because of young age-subadult

† Skulls included in cranial analysis because missing, juvenile, fragmented or not yet processed;

Appendix 2

Specimens of southeastern *Puma concolor*, outside of Florida, examined

Catalog No. ¹	Sex ²	Age ³	Condition ⁴	Back Whorl ⁵	Neck Whorl ⁵	Flecks ⁶	Kink ⁵	Data	Comments
USNM 137122T	M	3	S,SK	A	A	3	NA	1905	LA, Vidalia; type specimen of <i>F. concolor arundivaga</i> (Hollister)
USNM 1157	(F)	2	SK	NA	NA	NA	NA	1800s	LA, Prairie mer Rouge
USNM 1158	(M)	3	SK	NA	NA	NA	NA	1800s	LA, Prairie mer Rouge
LSU 17032	M	3	SK,SKL	NA	NA	NA	NA	1969	AR, Ashley Co.; tip of tail missing, near LA border
LSU 11363	M	2	S,SK,SKL	A	A	A	A	1965	LA, LaCaddo Parish, near Keithville; skin mtd.; pelage features per M. Haffner LSU; no kink apparent
MSH 1379	M	3	SK	NA	NA	NA	NA	1975	AR, Logan Co.
ANSP 2241	(M)	2	SK	NA	NA	NA	NA	1800s	SC, data questionable

¹USNM U.S. National Museum of Natural History; LSU Louisiana State University; MSH Arkansas Museum of Science and History; ANSP Academy of Natural Sciences of Philadelphia

²M=males; F=female; () male or female based on size of adult individual

^{3,4,5,6} Definitions same as Appendix 1.

Appendix 3

Live animals examined for kinked tail and whorl (1980-1990)¹

Number	Locality	Whorl ²	Kink	Comments
GFC #9	Big Cypress	Yes	Yes	Shot in foot
Big Guy	Big Cypress	R	Yes	White Oak
GFC #11	Big Cypress	Yes	Yes	parent of GFC #19
GFC #12	Big Cypress	Yes	Yes	parent of GFC #19
GFC #14	Everglades	No	No	mother of #16 & #21
GFC #16	Everglades	R	Yes/No	modified kink ³
GFC #17	Big Cypress	Yes	Yes	"Jumbo"
GFC #18	Big Cypress	Yes	Yes	"Jumbette"
GFC #19	Big Cypress	Yes	Yes	Price cat
GFC #21	Everglades	No	No	offspring of #14
GFC #22	Everglades	No	No	offspring of #15
GFC #23	Everglades	No	No	from #15 "Amie"
GFC #26	Big Cypress	R	Yes	Whorl single ridge
GFC #28	Big Cypress	Yes	Yes	
GFC #29	Big Cypress	R	Yes	Whorl single ridge
GFC #31	Big Cypress	Yes	Yes	
GFC #32	Big Cypress	Yes	Yes	
GFC #34	Big Cypress	Yes	Yes	
GFC #36	Big Cypress	Yes	No	
GFC #37	Big Cypress	No	No	First to show no kink or whorl
GFC #38	Big Cypress	Yes	No	
GFC #39	Everglades	Yes	Yes	First to show both kink and whorl
GFC #40	Big Cypress	R	No	
Total		23		

Summary:

Big Cypress		Everglades	
Total	17	Total	6
Whorl absent	1(6%)	Whorl absent	4(66.6%)
Rudimentary	4(23.5%)	Rudimentary	1(16.6%)
Whorl present	12(70%)	Whorl present	1(16.6%)
No kink	4(23.5%)	No kink	5(83.3%)
Kink	13(76.5%)	Kink	1(16.6%)

¹ capture data from R. Belden and M. Roelke, Game and Florida Game and Freshwater Commission² R=rudimentary, approximately 5cm or less, single ridge³ modified kink present at first capture, but absent at later capture. Kink of a different shape (sideways) than those observed in Big Cypress cats; no explanation, unless due to an injury (information from D. Janzen, M. Roelke pers. comm)

APPENDIX 4

Color variables for *Puma concolor (coryi)*. List of all measures for mid-back and mid lateral: V1, V10 = hue; V2, V11 = saturation; V3, V12 = lightness; V19 = degree of red; V20 = degree of yellow for lateral.

Catalogue No.	Class	V1	V2	V3	V10	V11	V12	V19	V20
US 528190	<i>coryi</i>	0.42140	0.38172	28.93000	0.38615	0.37570	48.93000	7.65000	18.04000
US 265596	<i>coryi</i>	0.42266	0.38209	27.43000	0.38656	0.37471	42.42000	7.20000	16.09000
MC 19855	<i>coryi</i>	0.41196	0.37800	27.48000	0.39150	0.37678	45.19000	8.20000	17.89000
MC 86992	<i>coryi</i>	0.41173	0.37938	29.16000	0.48422	0.38006	36.43000	8.84000	17.31000
MC 85489	<i>coryi</i>	0.41435	0.37986	28.37000	0.40158	0.38140	36.29000	8.03000	17.21000
MC 87743	<i>coryi</i>	0.40450	0.37274	25.60000	0.40477	0.38116	34.79000	8.45000	17.02000
MC 87742	<i>coryi</i>	0.41749	0.37673	29.49000	0.400071	0.38057	34.64000	7.78000	16.43000
MC 5650	<i>coryi</i>	0.40565	0.37195	24.84000	0.40755	0.38325	35.58000	8.69000	17.96000
AM 144512	<i>coryi</i>	0.42419	0.38392	30.36000	0.38884	0.37659	46.57000	7.80000	17.92000
FM 14902	<i>coryi</i>	0.42302	0.38768	30.64000	0.40038	0.38427	44.51000	8.35000	20.34000
FM 14900	<i>coryi</i>	0.34076	0.38914	29.58000	0.40016	0.38631	42.84000	7.61000	20.15000
FM 1255T	<i>coryi</i>	0.42736	0.38531	29.25000	0.39062	0.38079	42.87000	6.77000	17.89000
UF 9789	<i>coryi</i>	0.41559	0.38415	32.93000	0.38820	0.37634	45.63000	7.59000	17.52000
UF 22529	<i>coryi</i>	0.42239	9.37523	31.04000	0.38673	0.37541	47.14000	7.65000	17.56000
UF 14390	<i>coryi</i>	0.42094	0.38448	30.39000	0.39548	0.38022	44.94000	8.26000	19.02000
UF 11927	<i>coryi</i>	0.41989	0.38490	8.15000	0.38722	0.37608	48.14000	7.72000	18.04000
UF 12004	<i>coryi</i>	0.43287	0.39457	37.25000	0.39287	0.38354	51.85000	7.66000	21.56000
UF 19096	<i>coryi</i>	0.41287	0.37981	30.26000	0.38384	0.37280	47.39000	7.63000	16.72000
UF 11915	<i>coryi</i>	0.41325	0.37931	30.99000	0.38688	0.37343	44.37000	7.82000	16.41000
UF 10424	<i>coryi</i>	0.42330	0.38549	32.86000	0.38488	0.37401	47.97000	7.65000	17.26000
UF 22409	<i>coryi</i>	0.41857	0.38027	29.72000	0.48283	0.38073	46.22000	7.62000	20.50000
UF 24096	<i>coryi</i>	0.42447	0.38372	29.79000	0.38624	0.37444	47.51000	7.82000	17.40000

Appendix 4 continued.

Catalogue No.	Class	V1	V2	V3	V10	V11	V12	V19	V20
UF 24268	<i>coryi</i>	0.42702	0.38487	31.33000	0.38978	0.37504	45.20000	8.22000	17.33000
UF 24267	<i>coryi</i>	0.41416	0.38203	33.32000	0.38336	0.37185	46.25000	7.62000	16.16000
UF 24314	<i>coryi</i>	0.41583	0.38259	34.83000	0.38149	0.37211	50.83000	7.62000	17.16000
FM 91621	<i>coryi</i>	0.43707	0.38591	27.75000	0.40735	0.38497	45.28000	6.22000	21.75000
UF 11852	captive	0.42582	0.38027	5.91000	0.39663	0.37803	39.25000	8.20000	16.98000
UF 12462	captive	0.43884	0.38656	30.88000	0.38979	0.37478	45.71000	8.35000	17.42000
UF 23985	corbett	0.42496	0.38235	28.52000	0.39149	0.37716	42.88000	7.80000	17.29000
UF 24557	everglades	0.42117	0.38359	26.39000	0.39562	0.37716	42.88000	7.80000	17.29000
UF 24563	everglades	0.38239	0.36295	26.15000	0.38391	0.37007	33.10000	6.84000	14.81000

APPENDIX 5

Sample data set for contour measurement for the type specimen of *P. concolor coryi*. X and Y are the coordinates along the anterior portion of the nasal region; XN and YN are the normalized values. The position on the X axis for which YN=1.000 is the highpoint and marked in bold type.

Catalog	Sex	Status	X	Y	XN	YN
MCZB 7742	M	HIST	0.43750	0.07176	0.05000	0.09289
MCZB 7742	M	HIST	0.87500	0.13107	1.00000	0.16966
MCZB 7742	M	HIST	1.31250	0.21641	0.15000	0.28012
MCZB 7742	M	HIST	1.75000	0.33917	0.20000	0.43902
MCZB 7742	M	HIST	2.18750	0.51020	0.25000	0.66040
MCZB 7742	M	HIST	2.62500	0.68299	0.30000	0.88406
MCZB 7742	M	HIST	3.06250	0.76805	0.35000	0.99416
MCZB 7742	M	HIST	3.50000	0.77256	0.40000	1.00000
MCZB 7742	M	HIST	3.93750	0.69983	0.45000	0.90586
MCZB 7742	M	HIST	4.37500	0.63546	0.50000	0.82254
MCZB 7742	M	HIST	4.81250	0.56039	0.55000	0.72537
MCZB 7742	M	HIST	5.25000	0.52478	0.60000	0.67927
MCZB 7742	M	HIST	5.68750	0.49976	0.65000	0.64689
MCZB 7742	M	HIST	6.12500	0.46806	0.70000	0.60586
MCZB 7742	M	HIST	6.56250	0.43376	0.75000	0.56146
MCZB 7742	M	HIST	7.00000	0.37115	0.80000	0.48042
MCZB 7742	M	HIST	7.43750	0.31526	0.85000	0.40807
MCZB 7742	M	HIST	7.87500	0.21586	0.90000	0.27941
MCZB 7742	M	HIST	8.31250	0.11414	0.95000	0.14774
MCZB 7742	M	HIST	8.75000	0.00259	1.00000	0.00335

APPENDIX 6

Measure of highpoint of contour. Value of XN when YN=1.0 is the highpoint measure for all *P. concolor coryi* (including *P. c. arundivaga*)

Catalog	Subspecies	Sex	Status ¹	XN	YN
US 1157	<i>arundivaga</i>	F	HIST	0.600	1.000
US 1158	<i>arundivaga</i>	M	HIST	0.650	1.000
LSU 11363	<i>arundivaga?</i>	M	TEST	0.650	1.000
LSU 17032	<i>arundivaga?</i>	M	TEST	0.500	1.000
MSH 51375	<i>arundivaga?</i>	M	TEST	0.600	1.000
US 137122	<i>arundivaga</i>	M	TYPE	0.400	1.000
UF 11852	<i>coryi</i>	F	CAPTIVE	0.550	1.000
UF 12462	<i>coryi</i>	M	CAPTIVE	0.600	1.000
UF 24097	<i>coryi</i>	M	CAPTIVE-J*	0.550	1.000
MCZ 54423	<i>coryi</i>	F	GLADES-J*	0.650	1.000
UF 24557	<i>coryi</i>	F	GLADES	0.450	1.000
UF 24563	<i>coryi</i>	F	GLADES	0.550	1.000
AM 100222	<i>coryi</i>	F	HIST	0.400	1.000
ANS 16705	<i>coryi</i>	F	HIST	0.550	1.000
ANS 16706	<i>coryi</i>	F	HIST	0.350	1.000
FM 50058	<i>coryi</i>	F	HIST	0.500	1.000
MCZ 19855	<i>coryi</i>	F	HIST	0.500	1.000
MCZ B5489	<i>coryi</i>	F	HIST	0.350	1.000
MCZ B7743	<i>coryi</i>	F	HIST	0.350	1.000
UF 14699	<i>coryi</i>	F	HIST	0.500	1.000
US 145264	<i>coryi</i>	F	HIST	0.350	1.000
AM 144512	<i>coryi</i>	M	HIST	0.350	1.000
ANS 15270	<i>coryi</i>	M	HIST	0.600	1.000
FM 14902	<i>coryi</i>	M	HIST	0.350	1.000
MCZ 10703	<i>coryi</i>	M	HIST	0.350	1.000
MCZ 31781	<i>coryi</i>	M	HIST	0.350	1.000
MCZB 5650	<i>coryi</i>	M	HIST	0.450	1.000
MCZB 6992	<i>coryi</i>	M	HIST	0.350	1.000
MCZB 7742	<i>coryi</i>	M	HIST/TYPE	0.400	1.000
US 265596	<i>coryi</i>	M	HIST	0.350	1.000
UF 12827	<i>coryi</i>	F	HIST-J*	0.400	1.000
UF 10424	<i>coryi</i>	F	RECENT	0.300	1.000
UF 18798	<i>coryi</i>	F	RECENT	0.450	1.000
UF 19090	<i>coryi</i>	F	RECENT	0.450	1.000
UF 20973	<i>coryi</i>	F	RECENT	0.600	1.000
BILLIE	<i>coryi</i>	M	RECENT	0.500	1.000
UF 11927	<i>coryi</i>	M	RECENT	0.400	1.000
UF 14390	<i>coryi</i>	M	RECENT	0.400	1.000
UF 19096	<i>coryi</i>	M	RECENT	0.350	1.000
UF 22409	<i>coryi</i>	M	RECENT	0.350	1.000
UF 22529	<i>coryi</i>	M	RECENT	0.550	1.000
UF 23986	<i>coryi</i>	M	RECENT	0.600	1.000
UF 24096	<i>coryi</i>	M	RECENT	0.400	1.000
UF 24268	<i>coryi</i>	M	RECENT	0.550	1.000
UF 24314	<i>coryi</i>	M	RECENT	0.600	1.000

Appendix 6 continued

UF 24315	<i>coryi</i>	M	RECENT	0.600	1.000
UF 24316	<i>coryi</i>	M	RECENT	0.400	1.000
UF 24561	<i>coryi</i>	M	RECENT	0.350	1.000
US 528190	<i>coryi</i>	M	RECENT	0.350	1.000
UF 11915	<i>coryi</i>	F	RECENT-J*	0.500	1.000
UF 20957	<i>coryi</i>	F	RECENT-J*	0.600	1.000
GLADES 7040	<i>coryi</i>	F	TEST1	0.550	1.000
UF 19077	<i>coryi</i>	F	TEST2	0.550	1.000
UF 23985	<i>coryi</i>	F	TEST2	0.450	1.000
UF 24042	<i>coryi</i>	M	TEST3	0.350	1.000

* juveniles and subadults eliminated from study

† Status = historic, recent, captive, everglades, test (those animals of questionable identity);

Type=type specimen for subspecies

Appendix 7

Skull measurements used in the cranial analysis of *Puma concolor coryi*.

VARIABLES.

1. **Total Length (TL)** - Anterior tips of premaxillae to posterior point in median line over the foramen magnum.
 2. **Condylobasal length (CBL)** - Anterior tips of premaxillae to posterior pane of occipital condyles.
 3. **Zygomatic breadth (ZYB)** - Greatest distance between outside borders of zygomata.
 4. **Cranium height (CRH)** - Vertical distance from lower border of palatines to height of frontals, at vertical plane of postorbital processes.
 5. **Width of palate (PAW)** - Greatest width of palate between outside margins of carnassial alveoli.
 6. **Palatal length (PAL)** - Anterior tips of premaxillae to posterior edge of palate.
 7. **Maxillary tooth row (MXTR)** - Anterior alveolus of canine to posterior alveolus of carnassial.
 8. **Mandibular tooth row (MDTR)** - Anterior alveolus of canine to posterior alveolus of carnassial.
 9. **Mastoid breadth (MASB)** - Greatest posterior width of skull including outside margins of the mastoids.
 10. **Post-orbital process breadth (POPB)** - Greatest width between the outer points of postorbital processes.
 11. **Postorbital constriction (POC)** - Least distance posterior to the postorbital processes.
 12. **Width at canines (WC)** - Width at outside margins of canine aveoli .
 13. **Interorbital breadth (IOB)** - Least distance between orbits .
 14. **Pterygoid width (PW)** - Least distance at outer edges of pterygoids.
 15. **Condyle width (CW)** - Greatest width of occipital condyles.
 16. **Upper carnassial crown length (UCL)** - Antero-posterior length of crown at cingulum.
 17. **Upper carnassial crown width (UCW)** - Greatest width of carnassial.
 18. **Lower carnassial crown length (LCL)** - Antero-posterior length of crown at cingulum.
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Appendix 8.

Number of *Puma concolor* specimens examined and number possessing a mid-dorsal whorl

Subspecies	N	Locality	Whorl		Source of data ¹
			N	F(%)	
NORTH AMERICA					
<i>arundivaga</i>	2	Louisiana Arkansas	0		USNM, LSU ²
<i>azteca</i>	128	Arizona New Mexico, Mexico	4	3.1	USNM, AMNH, FMNH
<i>brownii</i>	4	Arizona California	0		USNM, MVZ ³
<i>californica</i>	45	California Oregon	0		USNM, MCZ
<i>coryi</i> *	48	Florida	39	81.5	USNM, AMNH, FMNH, ANSP, UF
<i>coryi</i> (?)**	4	unknown origin (incl. captive)	1	2.5	USNM, FMNH, UF
<i>cougar</i>	1	Rhode Island	1	100.0	MCZ
<i>hippolestes</i>	21	Colorado Montana Utah Wyoming British Colombia	0		USNM, FMNH
<i>improcera</i>	2	Baja, California, Mexico	0		MCZ, MVZ ³
<i>kaibabensis</i>	33	Arizona Utah Nevada	1	3.0	USNM, AMNH
<i>mayensis</i>	4	Mexico Belize	0		USNM, FMNH, MCZ
<i>missoulensis</i>	16	Montana	0		USNM
<i>olympus</i>	18	Washington	1	5.5	USNM
<i>oregonensis</i>	58	Oregon Washington	0		USNM
<i>stanleyana</i>	117	Texas	1	1.0	USNM, UF, MR ⁴
<i>vancouverensis</i>	2	Vancouver Island	0		USNM, MVZ ³
SOUTH AMERICA					
<i>araucanus</i>	11	Chile	3	27.2	USNM, FMNH, AMNH, MR ⁵
<i>anthonyi</i>	1	Venezuela	0		AMNH ⁵
<i>acrocodia</i>	4	Brazil (Matto Grosso)	0		USNM, AMNH, FMNH
<i>bangsi</i>	7	Colombia Venezuela	0		FMNH, AMNH, MCZ, EBRG ⁶
<i>borbensis</i> (incl. <i>discolor</i>)	15	Brazil Peru	0		USNM, AMNH
<i>concolor</i>	21	Venezuela Brazil Guyana Surinam	1	4.8	USNM, FMNH, MCZ, EBRG ⁶
<i>costaricensis</i>	9	Costa Rica Panama Venezuela	0		USNM, AMNH, MCZ
<i>greeni</i>	1	Brazil	0		USNM
<i>incarnum</i>	8	Peru		0	USNM, FMNH, AMNH
<i>osgoodi</i>	4	Bolivia Brazil	0		USNM, FMNH
<i>patagonica</i>	6	Argentina	0		USNM, MR ⁴
<i>pearsoni</i>	7	Argentina	3	42.8	USNM, FMNH, CMNH
<i>puma</i>	6	Chile Argentina	4	66.6	USNM, AMNH, FMNH, MR ⁴
<i>soderstromi</i>	1	Venezuela	0		EBRG ⁶
<i>undetermined</i> ***	44	Argentina	10	22.0	BMNH, MCNBR ⁷
TOTAL	648		69		

Appendix 8 Continued.

**coryi* - includes only museum specimens; whorl counted even if difficult to detect, (*i.e.* rudimentary, N=3); see discussion in text regarding presence in live animals

***coryi*(?) - includes purchase (USNM19843); known captives (UF11852 UF12462 Everglades Wonder Gardens, and suspected Cory specimen (FMNH91621 with no data)

***undetermined subspecies, all specimens from Argentina

¹USNM U.S. National Museum; AMNH American Museum of Natural History; FMNH Field Museum of Natural History; MCZ Museum of Comparative Zoology; UF Florida Museum of Natural History; BMNH British Museum of Natural History

²LSU Louisiana State University (M. Haffner, pers. comm.)

³MVZ Museum of Vertebrate Zoology (W. Lidicker, Jr. pers. comm.)

⁴MR Melody Roelke (pers. comm.), based on examination of living animals

⁵AMNH American Museum of Natural History, type specimen (M. Lawrence, pers. comm.)

⁶EBRG Venezuela Estacion Biologica de Rancho Grande (F. Bisbal, pers. comm.)

⁷CMNH Colorado Museum of Natural History (C. Chase, pers. comm.)

⁸MCNBR Museo de Ciencias Naturales "Bernardino Revadavia" (A. Novaro, pers. comm.)

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