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MORPHOLOGICAL VARIATION IN THE SPECIES <u>Caiman crocodilus</u>: WITH CONSERVATION AND LEGAL IMPLICATIONS

By

Sima S. Pandya

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

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ABSTRACT

MORPHOLOGICAL VARIATION IN THE SPECIES <u>Caiman crocodilus</u>: WITH CONSERVATION AND LEGAL IMPLICATIONS

By

Sima S. Pandya

Five proposed subspecies of <u>Caiman crocodilus</u> occur from southern Mexico to northern Argentina. As with all modern species within the Crocodylia, overall morphology within the genus has been highly conserved. This has made identification at the subspecific level extremely difficult. To address subspecific identification within <u>C. crocodilus</u>, twelve morphological characteristics were examined from 379 preserved museum specimens collected across the entire range of the species. I investigated two competing hypotheses to explain the distribution of morphological variation using linear discriminant function analysis. Two groups were discriminated based on the major river systems in South America. Of the twelve variables, ratio of head width and snout length (HW/SL), mandible pattern (MP), nuchal cluster rank (NCr), dorsal scale rows (DSR), total keeled and unkeeled rows (TKUR), ventral scale rows (VSR), and ventral scale rows at mid-body (VSRM) had significant univariate <u>t-test</u> values (p < 0.05) for discriminating between the two subspecies.

Copyright SIMA SHIRISH PANDYA 1997 To my mother and father, both of whom were great inspirations to me and who, if still living today, would be truly proud.

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BACKGROUND

In Darwin's <u>Origin of Species</u>, he drafted the foundation for a branch of study known as evolutionary systematics. Scientists have been investigating the relationship between taxonomic groups of organisms based on genealogy and the amount and nature of their evolutionary change ever since. In the 1930's and 1940's the focus of systematics shifted from higher taxa (macrotaxonomy) to the level of species and populations (microtaxonomy). The goal of these scientists was to classify organisms according to similar characteristics in order to undertake comparative studies and formulate generalizations about the organisms. Just as Hennig (1969) warned; these comparisons of taxonomic groups in evolutionary studies can only be valid if the initial groupings are correctly defined. It is for this reason that the discipline of classification is considered a prerequisite for sound biological work (Mayr, 1974).

The objectives of my systematic study on <u>Caiman crocodilus</u> are 1) to determine if differentiation at the subspecific level can be supported based on a series of morphological characters and; 2) to determine the basis for the differences between the groups if distinct subspecific differences exist. To address these objectives I evaluated available information concerning <u>C. crocodilus</u> ecology, trade, and evolution

ECOLOGY

Diet

Magnusson et al. (1987) observed that the diet of <u>C. crocodilus</u> in the Amazon shifted as the snoutvent length (SVL) of the individual increased. The author concluded that <u>C. crocodilus</u> eats mainly terrestrial invertebrates when smaller and fish and mollusks when larger in size. In this study, the stomach contents of 105 specimens were examined for terrestrial vertebrates and invertebrates, fish, shrimp, crabs, and mollusks. Juvenile caiman primarily consumed terrestrial invertebrates along with a small percentage of shrimp. Terrestrial invertebrate consumption declined from over ten per individual in the smaller size classes (SVL<40cm) to less than three invertebrates per individual in the larger size classes (SVL>40cm). Adult caiman consumed large numbers of fish and mollusks. Terrestrial vertebrates such as snakes, lizards, mammals, and birds were found in the stomachs of all size classes in low frequency (Magnusson et al., 1987).

During a 4.5 year study in the central Venezuela llanos, smaller <u>C. crocodilus</u> consumed a greater number of invertebrates but depended on fish as a major food source when adult. Seasonal shifts in the consumption of all food items reflected its availability. Caiman preyed upon greater numbers of mammals and snails during the late dry season and greater quantities of crabs during the wet season. The increase in fish consumption during the early dry season was most likely due to the greater concentration of caiman and fish in permanent water holes (Thorbjarnarson, 1993a). Beetles, frogs, fish, crabs, and shrimp were also found to be common food sources for <u>C. crocodilus</u> in the savanna lagoon system in Venezuelan Guyana (Gorzula, 1978).

Fishing Behavior

Schaller and Crawshaw (1982) investigated the fishing behavior of the Paraguayan Caiman (C. crocodilus yacare) in the Pantanal of Brazil. Throughout the study period, the caiman exhibited two main variations of sit-and-wait predation. Both fishing techniques required the animal to lie motionless on the surface of the water or on the bottom of a shallow pond. When motion by a fish was sensed, the caiman lunged forward or snapped sideways in an attempt to capture the fish in its mouth. In the first technique, two caiman were observed positioned across a stream perpendicular to the shore. They were able to divert the normal river flow towards their waiting jaws and act as a weir. In the second technique, caiman floated on the surface of the water parallel to the shore. By slowly moving sideways towards land, the caiman herded the fish into a smaller area. Then, with a slight arching of its body toward the shore, the fish were trapped where the caiman could catch them more easily (Schaller and Crawshaw, 1982).

Thorbjarnarson (1993b) conducted an intensive study of caiman ecology and behavior in the central Venezuelan llanos. Caiman were observed snapping at prey from stationary positions, herding fish against the shore, and acting as a weir across narrow rivers or canals. Peak fishing activity occurred early in the dry season and coincided with reduced water and increased fish concentration. Fishing behavior

declined during the late dry season. Throughout the study, caiman were observed using a variety of foraging techniques to capture prey (Thorbjarnarson, 1993b).

Individual size of caiman studied was the leading explanation for the consumption of different prey items. In general, larger caiman primarily ate fish while smaller caiman foraged on terrestrial invertebrates and shrimp. Frogs, crabs, and other food items were consumed by all size classes depending on availability in various habitats. Therefore, no major differences in habitat selection, feeding or breeding behavior have been reported among populations of caiman that could account for the subspecific differences.

Habitat Selection

In the savanna lagoons of Venezuelan Guayana, <u>C. c. crocodilus</u> were observed near the edges of temporary lagoons during the wet season (July to December) and crowded in the center of permanent lagoons during the dry season (January to June). Sub-adults and adults migrated from these two habitats during the wet season but appeared to return to established territories. Vegetation was used during the dry season as additional protection (Gorzula, 1978). Additional studies on habitat selection by caiman in savanna areas have been completed by Alvarez del Toro (1974), Rivero Blanco (1974), Ayarzaguena (1983), Stanton and Dixon (1975, 1977), and Magnusson (1985).

Ouboter and Nanhoe (1988) investigated the habitat selection of <u>C. crocodilus</u> in the swamp and swamp-forest habitat of northern Suriname. Observations were conducted in the Coesewijne river area from 1982 to 1984. Caiman were counted at night, captured and marked, and equipped with radiotransmitters in order to track their movement. Habitat selection was determined by the density of caiman measured in each area type. Many caiman were positioned on mudbanks at the mouth tributary of the rivers and appeared to prefer shallow water near gradually sloping shore. Higher caiman densities were recorded near aquatic vegetation and sections of the river bordered by swamps. Swamps and aquatic vegetation may provide additional protection for the animals (Ouboter and Nanhoe, 1988).

Herron (1994) investigated habitat selection of <u>C. crocodilus</u> in Cocha Cashu lake, located in the Amazon drainage basin of Peru. Water depth, temperature, and vegetation types were recorded across the lake and linear regression was used to relate these factors to caiman density. Habitat selection depended upon the body size of the individual and vegetation cover. Smaller caiman were found in areas with more

shallow slopes while larger individuals inhabited areas with steeper sloped bottoms. Vegetation provided additional protection for all sizes of caiman from predators such as jaguar and giant otters (Herron, 1994).

Caiman are generalist feeders and appear adaptive to new habitats. They inhabit every major type of wetland in the low altitude neotropics. Caiman have replaced the Orinoco crocodile in many rivers and streams of the Venezuelan llanos as the crocodile populations were decimated by the demand for hides. Caiman even have been reported living in roadside ditches and cattle watering troughs (Thorbjarnarson, 1991).

Breeding Behavior

Caiman breeding ecology has been well studied in the llanos of Venezuela and Colombia, a savanna located in the northern and western region of the Orinoco river drainage. The llanos is characterized by two well-defined seasons; a wet season from May to November and a dry season from December to April. During the dry season, <u>C. crocodilus</u> are forced to conjugate in permanent water holes and this results in an increase in stress and mortality in many age classes. Caiman dispersed again to temporary water following the first significant rainfall in May. Males secured breeding territories and mated from June to July. Since widespread flooding occurred in the area from June to October annually, females began building nests (late July) and laying eggs (from the middle to late August) after the initial heavy rainfall. Nests were constructed from live and dead vegetation on elevated areas to minimize flooding. Twenty to thirty eggs were laid in the nest cavity to incubate for 70 to 90 days, depending on temperature. The females then opened the nest, allowing the hatchlings to escape, and led them to permanent water before the upcoming dry season. Dry season conditions such as crowding and dehydration led to high mortality of the young caiman during the first few years (Thorbjarnarson, 1991).

Cintra (1988) studied nesting behavior of <u>C. crocodilus yacare</u> in the Pantanal of Brazil over a period of three breeding seasons. In the Pantanal, Paraguayan caiman mate during the dry season (August to November). Females build nests and lay eggs beginning in January (wet season) and incubation of the eggs continues for 100 days (Cintra, 1988). Crawshaw and Schaller (1980) observed that females lay eggs after the first peak in water level, suggesting that rainfall may trigger this behavior. Nests consisted of twigs, leaves, and bark piled into a small mound and increased the ambient temperature surrounding the

eggs to more than 29°C. A circular chamber in the center of the nests held from 18 to 38 eggs incubated at 30°C-35°C for approximately 70 days. Nests were located near a water source (approximately three meters) and females were observed guarding the nests. Flooding of nests and predation by monkeys, foxes, raccoons, jaguars, opossums, armadillos, and lizards accounted for approximately 48.5% and 42% mortality for the 1984 and 1985 breeding seasons, respectively. The hatching period ran from March to April with the peak activity occurring from March 30 to April 10 (Cintra, 1988).

In Costa Rica, <u>C. crocodilus</u> built their nests in dense forest adjacent to rivers or canals rather than in open grasslands that may flood quickly. Mound nests were positioned against tree trunks on thick vines at the highest level of the river banks. In Costa Rica, caiman nested in the early wet season (mid to late July) and began to lay eggs between early September and October. Wet season nesting increased the availability of resources to the hatchlings. Internal nest temperature ranged from 30.5°C - 32.8°C, and eggs incubated for about 80 days. During the 1988 and 1989 breeding seasons, 13 of 32 nests found were destroyed by flooding and four additional nests had been subjected to some degree of predation. Females were frequently observed guarding the nests and displayed defensive behaviors to ward off danger (Allsteadt, 1994).

A small study in the Mapurite river system of the Venezuelan Guayana observed five nests over a period of three years. Hatching in these nests occurred between October and November. An additional nest made out of leaves and twigs was examined and found to contain 24 eggs incubated at 31.4°C. The young caiman remained together for 18 months and were defended by various adult caiman that responded to the distress calls (Gorzula, 1978).

Maternal Care

<u>C. crocodilus</u> is one of many crocodilian species that exhibit maternal care. A clutch of 22 young <u>C. crocodilus yacare</u> were observed with their mother for six months after hatching. The mother remained in a forest-surrounded bay in an area where maximum water depth was approximately 40 cm. The water in the 70 X 12 meter study area was clear and supported many small aquatic plant species. During the day (0530 hrs to 1700 hrs) the hatchlings remained within one meter from the female adult and were assumed to be resting. After 1700 hrs the family moved up the inlet and foraged for insects at the water's surface and

to a depth of 15 cm. Hatchlings ventured up to 100 m from their mother during the night, but returned to their resting site between 0530 hrs and 0550 hrs. The mother displayed attack behavior against any intruder attempting to approach the hatchling area. Maternal care is assumed to prevent predation and increase the survivability of hatchlings (Cintra, 1989).

HISTORY OF TRADE

The Crocodilian Skin Trade

Historically, crocodiles have been used for food, medicine, and religious worship. The skin trade began as a result of European expansion into previously remote areas after the Industrial Revolution. Commercial use of the American Alligator (Alligator mississippiensis) began in the late 1700's and increased during the Civil war (1861-1865). Alligator leather was manufactured into boots, travel bags, belts, and card cases. Some trading firms sold up to 60,000 skins to manufacturers in New York annually. By 1900, the demand for Alligator products was too great to be met by U.S. supplies and the industry began exploring additional sources in Mexico and South America. Large tanneries, open in Europe, increased the demand for skins. Caiman skins were still considered inferior to Alligator and Crocodile skins at this time and were not commercially harvested. As the demand continued to grow, the industry secured a new supply of crocodile leather from African and Asian sources. Eventually, the demand for American Alligator skins pushed the population number near extinction and, in 1943, only 6,800 skins were traded from Florida. In 1943, Florida passed legislation to prohibit alligator hunting during breeding season and taking individuals smaller than 1.2 meters. Commercial trade in Alligator skins from Florida increased again to 25,000 in 1947 as the population started to rise. By 1969, the United States placed the American Alligator on the Endangered Species List (Ross, 1989).

The Caiman Skin Trade

Commercial hunting for caimans began in South America in the late 1950's. The black caiman (Melanosuchus niger) was the most sought after species because its skin lacked osteoderms (bony plates in the scales) and more closely resembled Alligator and Crocodile skin than the other caiman species. <u>C.</u> <u>crocodilus</u> hunting in the Amazon began in Venezuela and rapidly spread over much of the continent.

During the 1950's, approximately 5-10 million caiman hides were harvested annually; in the 1960's the annual harvest was 6-8 million. In the 1980's, skins from <u>C. crocodilus</u> comprised over 60% of the world wide skin market (Brazaitis, 1989).

The decimation of crocodilian populations during the 1960's forced many tanneries and brokers out of business. In response, countries began to pass legislation to protect the remaining populations. In 1960 and 1968, Colombia and Bolivia, respectively, banned export of the black caiman and many or all subspecies of <u>C. crocodilus (Ross, 1989)</u>. In Venezuela, caiman harvest greatly reduced population numbers and a total ban on commercial trade was established in 1972. Populations quickly rebounded and caiman became locally abundant by the 1980's (Thorbjarnarson, 1991). In 1978 and 1979, unregulated caiman hunting in Suriname quickly reduced that population, but the hunting laws enacted in the 1980's proved hard to enforce (Ouboter and Nanhoe, 1989). Commercial trade of caiman skins in Brazil and Paraguay in the late 1970's and early 1980's was banned in response to widespread illegal harvesting that was decimating populations across South America. Effective enforcement of the legislation was a major problem for many South American countries and as a result the illegal trade increased to sustain the supply of raw skins to the remaining tanners (Ross, 1989).

The annual trade of <u>C. crocodilus</u> skins from the Convention on International Trades in Endangered Species (CITES) annual reports (1983 to 1991) is summarized in Figure 1. World trade in <u>C.</u> <u>crocodilus</u> skins from 1980-1984 totaled over 2,380,566 (Villalba-Macias, 1986). Trade in caiman skins from countries in its natural range totaled over 239,802 skins in 1987 and 178,510 skins in 1988 (Luxmoore, 1990; Luxmoore and Collins, 1994; Collins and Luxmoore, 1996).

Current <u>Caiman crocodilus</u> Skin Trade (1992-1993)

The current trade in <u>C. crocodilus</u> skins is vastly different from what it was between 1960 and 1980. While problems still exist, the trade is now largely regulated and sustainable. Net export of hides, primarily from Colombia and Venezuela, reached 410,375 in 1992 and 648,847 in 1993. Brazilian production is also increasing as 75 registered ranches work to become operational. Historically, caiman skin harvest has been three to four times larger than the "classic" skin trade (skins that lack osteoderms such

as Alligator and many species of Crocodile). This ratio is predicted to increase by the end of the century. Trade in <u>C. crocodilus</u> is now greater than one million skins per year (Collins and Luxmoore, 1996).

Both the South American economy and the species have benefited from the shift to legal and regulated trade in the 1990's. Today, the caiman skin industry is at the same level of organization that the classic skin trade was only 10 years ago. Management programs are being developed in many countries and uniform conservation and trade regulations are being implemented throughout the natural range. Public awareness of the benefits of sustainable use is increasing to a level that will aid both conservation and industry. The major exporting countries (Colombia, Venezuela, Nicaragua, and Brazil) and the major importing countries (France, Italy, Switzerland, Japan, and the United States) are leading the way toward improving the management of this natural resource (Collins and Luxmoore, 1996).

EVOLUTION

Crocodilian Evolution And Distribution

Reptiles first appeared, in the late Paleozoic era, three hundred million years ago. The oldest crocodilian fossils found in Europe, South America, and Africa date back nearly 230 million years. Crocodilians are the only living representatives from the Archosaurian complex, "The Ruling Reptiles," which includes early crocodilians, dinosaurs, flying reptiles [Pterosaurs] and an assortment of early Mesozoic forms [thecodontians]. The Mesozoic era (245-265 mybp) is called the "Age of Reptiles." During this era reptiles were dominant and extremely diverse (Ross, 1989).

The evolution of all crocodilians can be traced through five suborders: Archeosuchia, Protosuchia, Sebecosuchia, Mesosuchia, and Eusuchia. The suborder Archeosuchia is composed of two families, the Proterochampsidae and the Notochampsidae. <u>Proterochampsa barrionuevoi</u> is the first known fossil crocodile, and it is from the Upper Middle Triassic period of what is now western Argentina. <u>Notochampsa</u> and <u>Erythrochampsa</u> are known from the Upper Triassic of South Africa. The genus <u>Proterochampsa</u> has many features linking it to early thecodontians and it shares a flattened head, fused external nares, and long snout with modern crocodilians. This genus is believed to an important link in the evolution from early crocodilians (Sill, 1968).

The suborder Protosuchia flourished in the late Triassic and early Jurassic. It includes one genus, <u>Protosuchus</u>, which was a deep-skulled, short-snouted crocodilian that probably originated in South America during the middle Triassic (Sill, 1968). The Protosuchia were small (1 meter) and lizard-like in appearance. Most Protosuchia were terrestrial and all possessed bony armor along the back and tail. This characteristic has been conserved by modern crocodilians (Ross, 1989). Bernard Krebs, a Swiss paleontologist, linked crocodilians to ancestral thecodontians because of their shared unique ankle joint structure permitting the foot to swivel or twist sharply during a form of locomotion called the "high walk." The peg-and-socket structure of the crocodilian ankle allows the animal to move quickly over land. During the high walk, the body is lifted completely off the ground and the limbs are bent outward from the body (Ross, 1989).

The suborder Sebecosuchia consists of two families, the Baurusuchidae and the Sebecidae. The Baurusuchidae is found in the late Cretaceous of Brazil and the Sebecidae probably evolved from it. The Sebecidae most likely originated in the middle or late Jurassic from primitive members of the suborder Mesosuchia. Evidence suggests that the Sebecosuchia originated in the western hemisphere, expanded worldwide by late Cretaceous, and disappeared by the end of the Miocene. The Sebecosuchia were characterized by a deep, narrow skulls and may even have descended from the Protosuchia (Sill, 1968).

The suborder Mesosuchia is the next major line of crocodilian evolution from the Protosuchia. Fossil records from the early and middle Jurassic age are unavailable and little is known of this lineage. Only two of the eight families from the suborder Mesosuchia are represented by fossil remains. Both the families, Metriorhynchidae and Teleosauridae, were specialized forms adapted to marine life and distributed around the world (Sill, 1968).

The remaining families of Mesosuchia, found in late Jurassic and Cretaceous deposits, already possessed many characteristics common to modern crocodilians (Sill, 1968). Adaptation to aquatic life and evolution from herbivore to piscivore led to a trend toward snout elongation in crocodilians. Second, an increase in the size of the bony palate has provided crocodilians extra strength and protection while capturing larger prey. The secondary bony palate separates the mouth from the respiratory structures, allowing the animal to breathe while the mouth is open under water (Ross, 1989). Development of large

pterygoid flanges, closure of the otic notch, and loss of antorbital fenestra accompanied the evolution of the bony palate (Sill, 1968). Finally, the evolution of vertebral shape is used to determine crocodilian lineage. Early crocodilian vertebrae were biconcave at both the anterior and posterior surfaces and the vertebrae were amphicoelous. Vertebrae in living crocodilians are concave on the anterior surface and convex on the posterior surface. This modern procoelous vertebral form provides increased flexibility of the spinal column (Ross, 1989).

Modern characteristics found in the family Goniopholidae suggest that it was either in the central line of crocodilian evolution or closely related to it. The Goniopholidae appeared in North America, Europe and Asia during late Jurassic (Figure 2). Two additional families, Theriosuchidae and Atoposauridae, lived in Europe and Asia during late Jurassic, but were probably minor offshoots of the Goniopholidae. Fossils from another family, the Pholidosauridae, appear in upper Jurassic sediments of Europe and Asia, but the family is thought to have become extinct by middle Eocene. The remaining two families from the suborder Mesosuchia (Libycosuchidae and Notosuchidae) existed for only a short period of time and were found only in North and South America, respectively. They represented minor offshoots from late Cretaceous forms (Sill, 1968).

The earth's land masses were united as one land mass (Pangaea) through the end of the Paleozoic era when changes in the polarity of the earth's magnetic field, plate tectonics, and sea-floor spreading began to shape the modern continents. The initial breakup of Pangaea most likely began in middle to late Triassic but Briden (1967) presents evidence suggesting that the extreme South Atlantic may have opened slightly during the Permian. As a result of North Atlantic and Pan-Atlantic rifts, the continents of Laurasia and Gondwana were created by the end of the Jurassic; Laurasia consisted of North America, Europe and Asia and was positioned north of the second major plate, Gondwana. Gondwana, divided by water, was composed of South America, Africa, Antarctica, and Australia. A third plate, supporting India, separated from Gondwana by the Afro-Indian rift, was located west of the African continent (Dietz and Holden, 1970).

Beginning in late Jurassic and continuing until the Miocene period, Europe had an abundance of crocodilians. Most of the evidence points to Europe as the site of the origin of modern crocodilians.

Eusuchia, the modern crocodilian suborder, evolved during the Cretaceous as continents migrated into their present locations. The first of five families, the Hylaeochampsidae, appeared in Europe in the early Cretaceous period and served as a precursor for the families Gavialidae and Crocodylidae (Figure 2). The Crocodylidae represents the main line of crocodilian evolution since the late Cretaceous (Sill, 1968).

Within the family Crocodylidae there are three subfamilies: the Gavialinae, the Crocodylinae, and the Alligatorinae. The subfamily Gavialinae is represented by just one species, <u>Gavialis gangeticus</u>, that is known from as far back as the Miocene. Its range once included North and South America, Africa, and Asia, but it is now restricted to the northern part of India (Ross, 1989). The subfamily Crocodylinae consists of the genera <u>Crocodylus</u>, <u>Osteolaemus</u>, and <u>Tomistoma</u> and has thrived since it first appeared in the fossil records of the late Cretaceous. The subfamily originated in Europe or Eurasia and spread worldwide by early Tertiary (Figure 2) (Sill, 1968).

The subfamily Alligatorinae includes the genera <u>Alligator</u>, <u>Caiman</u>, <u>Paleosuchus</u>, and <u>Melanosuchus</u> (Ross, 1989). The subfamily arose in North America or Central Asia and expanded outward through the connection between Asia and North America. By Eocene, Alligatorinae reached Europe and were present there until the atmosphere began to cool during the Oligocene. By early Tertiary, alligatorines reached South America from North America and from there underwent a secondary radiation to occupy much of their present distribution (Figure 3) (Sill, 1968).

Caiman crocodilus Evolution

Knowledge of plate tectonic activity during the Cenozoic era helps explain the emergence of <u>C</u>. <u>crocodilus</u> in Central and South America. North and South America were separated by a large body of water ("Panamanian portal") throughout the Mesozoic and there was no migration of the Alligatorinae into South America before this time (Savage, 1966). During the Cretaceous, tectonic plates supporting North and South America moved westward and closed the Caribbean region slightly (Dietz and Holden, 1970). In the Paleocene, a land bridge (the "Isthmian Link") was formed by volcanic activity that raised a broad area of central Nicaragua to northern Colombia above sea level for approximately 12 million years. This bridge permitted the first radiation of the Alligatorinae and the Crocodylinae into South America. During this time, the area from the central United States to South America is believed to have been tropical, having higher average temperature and precipitation levels than today. By the end of the Paleocene, the Isthmian Link submerged again and isolation of South America continued through the Eocene to the Pliocene. During this period, a second radiation of the Alligatorinae occurred in South America (Savage, 1966). There were two known genera of the Alligatorinae in South America by Oligocene and there were four known genera of the Alligatorinae by Miocene. Alligatorine representation in the Pliocene fauna of South America included present-day <u>Caiman</u>, <u>Melanosuchus</u>, and <u>Paleosuchus</u> (Sill, 1968). The extensive network of islands available from late Miocene forward facilitated the northern migration of <u>C. crocodilus</u> into its northern range of southern Mexico. The Isthmian Link connecting North and South America was fully restored again by early Pliocene (Savage, 1966).

The Geology of South America

A thorough investigation of the evolution and distribution of <u>C. crocodilus</u> in South America requires knowledge of the geologic history of the continent. Major geologic regions were established through tectonic activity prior to the Paleozoic. These regions are: the Guiana shield, the Brazilian shield and the Coastal Brazilian shield; the Amazon, Parnaiba, and Parana river basins; the Andean Belt, Pampean ranges, Patagonian' region, the Llanos region, and the Chaco. Much of continental South America was engulfed by sea water during the Paleozoic. By the end of the Permian, the sea had recessed from all but the northwestern and southern regions of South America (Harrington, 1962).

Like the Sierra Nevada in western North America and the Appalachian mountains in eastern North America, the Andes Mountains were created by movement of large lithospheric plates across the earth's surface. The South American continent is suspended on the western edge of the South American Plate and is adjacent to the Nazca Plate to the West. The Peru-Chile trench lies at the junction between the South American plate and Nazca plate. West of the Nazca Plate lies the Pacific Plate (Figure 4). Sedimentary rocks, which form the foundation of the continental edge, were deposited during the Paleozoic. In the Cretaceous, the Nazca Plate moved eastward away from the East Pacific Ridge and plunged into the Peru-Chile trench, submerging itself under the South American plate. The rising temperature near the earth's core melted the edge of the undersliding Nazca Plate and magma rock surfaced to form a volcanic arc. Large amounts of magma, from intense volcanic activity, pierced through the surface of existing

sedimentary rock beds and formed enormous batholiths (regions of igneous rock) which remain exposed in the western ridges today (James, 1973).

Triassic orogenies uplifted many areas of South America forcing the sea water to recede further. Invasions by sea water in localized areas of the Venezuelan-Peruvian, Chilean, and Patagonian basins continued through the Cretaceous as a result of fluctuating elevations in topography. Marine sediments were deposited in these basins throughout the Mesozoic. The Colombian-Peruvian basin was finally filled in during late Cretaceous by continental deposits from the uplifting mountains and the sea was forced to leave this area for the last time. The Ecuadorian portal, the connection from the Pacific Ocean inland, was preserved throughout the Cretaceous. The Caribbean and Patagonian basins began to rise above sea level, restricting marine water to narrow stretches west of the rising Coast Cordillera (Harrington, 1962).

Great geologic changes occurred during the Tertiary of South America. In the Eocene, the eastern Cordillera of Colombia, the Perija Range, parts of the Caribbean range, and the Northern Range of Trinidad were uplifted. Rising mountains to the west deposited thick layers of continental beds in the Colombian-Peruvian basin. Uplift of the Principal Cordillera (Cordillera Occidental) in southern Peru and western Bolivia deposited continental debris in the area now known as the Altiplano (Figure 5). In the Oligocene, the Ecuadorian portal closed, which ended the water connection from the Pacific Ocean to the Colombian-Peruvian basin. The Caribbean-Venezuelan mountain region was uplifted and continental sediments created shallow areas of marine and brackish-water. The Altiplano of southern Peru and western Bolivia received additional continental sediment as the Principal Cordillera was uplifted further (Figure 5). Finally, the Patagonian basin was uplifted with the Coast Cordillera forcing the sea to retreat from the basin for the last time. Additional sediments filled in the lower areas and created the extra-Andean Patagonia region (Harrington, 1962).

The Eastern Cordillera of Colombia and the Central and Eastern Cordilleras of Bolivia were uplifted by the beginning of the Miocene (Figure 5). Tectonic activity at the end of middle Miocene, created the paleo-Amazon river, which fed into the paleo-Orinoco river and drained toward the Caribbean into Maracaibo. Additional activity in late Miocene shifted the Amazon and Orinoco river flow toward the East and established the water connection with the Atlantic Ocean (Hoorn et al., 1995). The Orinoco River

and its tributaries still retain a connection to the Amazon River near the Venezuelan-Brazilian border. During peak rainfall these areas are covered by continuous water.

Tectonic activity in the Miocene altered the flow of rivers in northern Bolivia. The Guapore, Itenes, Mamore, Beni, and Madre de Dios rivers and their tributaries flowed southward and emptied into the Pilcomayo and Paraguay rivers prior to the Miocene. As a result of the uplift of the Bolivian Andes, massive amounts of sediment were deposited into central Bolivia and raised the area. The increase in elevation of the rivers redirected the water flow northward. The rivers and their tributaries mentioned above now empty into the Amazon river basin (Figure 6) (King, correspondence).

Continental sediment continued to accumulate in the Altiplano of western Bolivia. Initial uplift of the eastern Cordillera of Venezuela and further uplift in Colombia created the present-day Llanos region. The western Cordillera of Bolivia, Peru, and the Chilean-Argentine Puna experienced volcanic activity. Finally, the Bolivar geosyncline, located in northwestern Venezuela, was uplifted in the Pliocene. Sea water was restricted to the lower Atrata and lower Magdelena rivers. The last major Andean uplift occurred at the end of the Pliocene. At this time the Precordillera of western Argentina and Bolivia and the eastern part of the Cordillera Real of Ecuador was uplifted (Figure 5) (Harrington, 1962).

Evolutionary Hypotheses

The Andes Mountains are the longest mountain chain in the world; spanning over 66 degrees of latitude and responsible for the establishment of a variety of climates and environments across western South America. The creation of the Andes mountains has affected wind and river flow, rain accumulation, and has restricted the movement of many lower-altitude species. Tectonic activity and climatic changes during the Cenozoic created many environments that are utilized by a rich and varied fauna across South America (Duellman, 1979b). The present structure of the Andean mountain range, which began 10 to 15 million years ago in northern Chile and southern Peru, occurred in discrete periods until the Pliocene or Pleistocene time (James, 1973).

The changes caused by the creation of the Andes Mountains may help explain the evolution of subspecific differences within <u>C. crocodilus</u>. Major tectonic activity in the Andes Mountains has been suspended since the Pleistocene. Prior to this time (Paleocene), the first radiation of Alligatorinae migrated

to South America across a temporary land bridge from the North. Isolation of South America resumed from the end of Paleocene to early Pliocene.

Subspeciation of <u>C. crocodilus</u> may have occurred subsequent to the Andean uplift if the individuals in Central America and northwestern Venezuela and Colombia were isolated from the rest of the individuals in South America. This would imply that a subspeciation event occurred recently, probably following the radiation of caiman into Central America in the Pliocene.

Subspeciation of <u>C. crocodilus</u> may have occurred following the initial radiation of Alligatorinae into South America (Paleocene). If <u>C. crocodilus</u> differentiated prior to the major Central Andean uplift this would place a hypothesized secondary radiation during the time of continental isolation (Paleocene to Miocene). Sill (1968) reported the existence of two known genera of the Alligatorinae in South America by Oligocene and four known genera of the Alligatorinae by Miocene. Subspecific differentiation of <u>C.</u> <u>crocodilus</u> during this time of great speciation would certainly be plausible. Trade Data 1983-1993



Figure 1 Annual trade in Caiman crocodilus skins by region from 1983-1993.



Figure 2 Hypothesized evolutionary path of the family Crocodylidae and the sub-family Crocodylinae showing approximate time of geologic appearance (Sill, 1969). G, Goniopholidae; H, Hylaeochampisidae; C, Crocodilinae; T, Tomistominae.



Figure 3 Hypothesized evolutionary path of the sub-family Alligatorinae and the genus <u>Caiman</u> showing approximate time of geologic appearance. C, Crocodilinae; A, Alligatorinae; c, <u>Caiman</u>.



Figure 4 Plate tectonic map of South America illustrating the position of the lithospheric plates and trenches responsible for the formation of the Andes Mountains.



Figure 5 Map of South America illustrating the individual mountain ranges comprising the Andes Mountains.



Figure 6 Enlarged map of Bolivia and surrounding countries illustrating the river systems that were redirected into the Amazon River as a result of the uplift of the Central Andes.

MORPHOLOGICAL STUDY OF Caiman crocodilus

INTRODUCTION

Accurate identification of crocodilian skins and products is essential to the work of law enforcement, agents of the skin industry, and conservationists (Brazaitis, 1986). Crocodilians provide a major source of leather for handbags, shoes, wallets, belts, luggage, watchbands, key chains, and a variety of novelty items. During the 1980's, more than 1.5 million crocodilian skins were harvested each year and it was estimated that caiman skins comprised over 60% of the world market in crocodilian skins (Brazaitis, 1989). Due, in part, to the increase in registered South American caiman ranches, approximately 1.2-1.5 million <u>C. crocodilus</u> skins could enter the market annually before the end of the century (Collins and Luxmore, 1996).

The trade of caiman skins, for the most part, is the impetus for many population studies to date. The demand for better management by the international community has forced countries to evaluate this natural resource and to implement sustainable use programs. Initiating sound management requires that the investigators collect basic information on caiman biology, ecology, and distribution.

<u>C. crocodilus</u> is one of the two species in the genus <u>Caiman</u>. Since 1758, the zoological classification of this taxon has been subject to much debate. More than a dozen subspecific divisions have been proposed between 1758 and 1965 (Kuhn, 1973). Currently there are five recognized subspecies: <u>C. c. crocodilus</u>, <u>C. c. apaporiensis</u>, <u>C. c. fuscus</u>, <u>C. c. yacare</u>, and <u>C. c. chiapasius</u>. The Apaporis River caiman (<u>C. c. apaporiensis</u>) is currently listed as endangered on the U. S. Endangered Species list, and on appendix I of the Convention on the International Trade in Endangered Species (CITES) (Brazaitis, 1973). The Paraguayan or Yacare caiman (<u>C. c. yacare</u>) is also considered endangered by the United States, and importation of this species into the country is prohibited. <u>C. c. fuscus</u> and <u>C. c. crocodilus</u> are listed on appendix II of CITES and commercial trade in their skins is also regulated by CITES (Brazaitis, 1986).

To establish legal control of commercial trade as a conservation mechanism, the international body connected to CITES must be able to properly identify skins from the different subspecies of <u>C. crocodilus</u>. CITES and the U.S. Endangered Species Act requires that each species or population be listed by common and scientific nomenclature. Recovery plans, mandated by legislation, are based on distribution information and diagnostic or taxonomic identification. Crocodilian identification is based on the morphology of skulls, skins, and dentition. (Brazaitis, 1973). To date, no definitive method of differentiating among subspecies of <u>C. crocodilus</u> has been demonstrated when only skulls or skins are available. An accurate method for subspecific determination will lead to better understanding of present distribution and breeding habits, and will assist in the conservation of the species.

To address subspecific identification, morphological variation across the entire range of <u>C</u>. <u>crocodilus</u> was investigated. Former studies have examined variation across limited geographical areas, and this is the first study of this magnitude. To determine boundaries for the possible subspecies, variation in twelve morphological variables was recorded or measured. Two hypotheses, based on possible geographic and geologic isolating events, were considered when assigning the data into <u>a priori</u> groups for linear discriminant function analysis. The null hypothesis for this study states that there are no significant differences among populations of C, crocodilus in Central and South America.

Hypotheses Tested

Hypothesis I states that the Andes mountain range isolated the population of caiman in Central America and northwestern South America from that in rest of the continent. To test this hypothesis, specimens were divided into two groups according to individual sites of collection. Group 1 included all specimens from northwest of the Cordilleras de Marida and de la Costa of Venezuela, and west of the Cordillera Oriental of Colombia (Figure 7). Group 2 included all specimens collected southeast of these mountain ranges.

Hypothesis II states that <u>C. crocodilus</u> subspeciation occurred following the initial radiation of the Alligatorinae into South America (Paleocene) and prior to the Central Andean uplift (Miocene). For this hypothesis, specimens were divided into two groups according to the former boundaries of the major river drainages in South America. <u>C. crocodilus</u> are believed to have migrated into Central America from

northern South America after late Miocene (Savage, 1966). Group 1 for this hypothesis included all specimens collected in areas draining into the Orinoco and Amazon rivers, and all specimens collected in Central America. The Bolivian rivers Guapore, Itenes, Mamore, Beni, and Madre de Dios flowed South into the Pilcomayo and Paraguay rivers prior to the Miocene. Group 2 included all specimens collected in Bolivia and south of the Amazon River system in the Parana, Paraguay, Pilcomayo, and Uruguay Rivers and their tributaries (Figure 8).

MATERIALS AND METHODS

General Methods

Three hundred and seventy-nine preserved specimens were obtained from every known museum collection of <u>C. crocodilus</u> housed in the United States (see Specimens Examined). Only whole, undamaged, alcohol preserved specimens with complete collection information were retained for analysis. While this sample of specimens represents material from within the entire natural range of <u>C. crocodilus</u>, <u>C. c. apaporiensis</u> was not represented; this taxon is thought to be extinct in the wild (Brazaitis, 1984). Localities represented by museum specimens are illustrated in Figure 9.

Morphological Data

Twelve morphological characteristics were examined on each specimen. Characteristics were chosen with reference to the existing literature concerning the identification of living, preserved, and tanned specimens (Brazaitis, 1973; Brazaitis, 1989; Brazaitis and King, 1983; King and Brazaitis, 1971). The twelve variables selected for analysis are defined below:

Ratio of head width to snout length (HW/SL). Head width was measured across the angle of the jaws.
Snout length was measured from the end of the snout to the bridge of the eyes (Figure 10). All measurements were recorded to the nearest tenth of a centimeter using vernier calipers.

2) Mandible pattern (MP) was partitioned into three states based on degree of pigmentation. Character state 1 was no pigmentation on either upper or lower jaw, character state 2 was faint pigmentation on either
(upper or lower) jaw, and character state 3 was dark pigmentation or blotches present on both the upper and lower jaws (Figure 11).

3) Lateral scale pattern (LP), partitioned into three states based on number of scale rows, included degree of keeling, and ratio of keeled to unkeeled scale rows. Pattern state 1 was assigned to lateral rows of large oval scales alternating with a network of irregular shaped small scales and creases. Rows of large scales were completely and heavily keeled and organized into horizontal rows. State 2 was assigned to lateral rows of large scales that appeared randomly keeled. Scale rows were not completely keeled but rather resembled an inverted arched pattern. State 3 was assigned to lateral rows of scales not usually keeled and not organized in horizontal rows (Figure 11).

4) Total number of keeled and unkeeled lateral rows (TKUR).

5) Proportion of keeled to unkeeled lateral rows (KLr; Figure 12), ranked (Table 5).

6) Length and width of the three largest lateral scales. The proportion of scale width to scale length was calculated for each lateral scale, and the average proportion for all three scales was analyzed (AVEL/W) (Figure 13).

7) Nuchal cluster pattern. Thirty-nine different character states were identified (Figure 14); each was assigned a corresponding number (NCr) (Table 6).

8) Number of dorsal scale rows (DSR); counted from the posterior edge of the nuchal cluster to the rear margin of the hind limbs (Figure 15).

9) Number of ventral scale rows (VSR); counted from the first horizontal row after the ventral crest to the last complete row anterior to the anal opening (Figure 16).

10) Ventral scales at mid-body (VSRM); defined as the number of transverse scales across the venter half way between the insertions of front and hind legs (Figure 17).

11) Number of double and single keeled scale rows (SRTAIL) on the dorsal portion of the tail posterior to the anal opening (Figure 18).

12) Number of tail inclusions (TIr). Counted on the ventral side of the tail between the anal opening and the seventh scale row on the tail, inclusions are defined as smaller scales placed between rows of existing larger scales. Many specimens had no tail inclusions, so to eliminate zeros from the data set the number of

tail inclusions was ranked with "1" representing zero, "2" representing one, and "3" representing 2, ect. (Figure 19).

Statistical Analysis

Data were analyzed using linear discriminant function analysis in the package SAS (For Windows, version 6.08). The morphometric data met assumptions for univariate normality and from this I assumed multivariate normality. Statistical significance was predetermined at alpha equal to 0.05. Because discriminant function analysis requires <u>a priori</u> groups be defined for analysis, all <u>a priori</u> groups were defined according to hypothesis I or hypothesis II (see Hypotheses Tested).

Each variable was tested for significance within hypothesis II using a univariate <u>t</u>-test. This additional test showed which variables were responsible for increasing the discriminating power. These variables should be used in all future morphological identification attempts.

RESULTS

Discriminant Analysis

Hypothesis I-- The possibility that the Andes Mountain Range acted as an isolating mechanism does not fully explain the present distribution of morphological variation within <u>C. crocodilus</u>. Using twelve morphological variables, 105 of the 125 (84%) specimens assigned to the northern population (Group 1) were correctly classified, and 221 of the 254 (87%) specimens assigned to the southern population (Group 2) were correctly classified. The misclassification rate for Group 1 was 16%, while the misclassification rate for Group 2 was 13%. Using the geographic location of the Andes Mountain Range to set <u>a priori</u> groups produced 53 (14%) incorrectly classified specimens (Table 1).

Hypothesis II-- The same twelve morphological variables clearly partitioned the <u>C. crocodilus</u> data set when considered in accordance with the geology and geography of two major river systems in South America. Two hundred and fifty-eight of the 266 (97%) specimens collected in Central America, the Orinoco and the Amazon river systems (Group 1) were correctly classified based on the variables. One hundred and eleven of the 113 (98%) specimens assigned to the southern population (Group 2) were correctly classified. The misclassification rate for Group 1 was 3%, while the misclassification rate for Group 2 was 2%. Using geographic and geologic data for the river systems in South America to set <u>a priori</u> groupings produced 10 (3%) incorrectly classified specimens (Table 2).

Of the twelve variables, seven characteristics had significant univariate <u>t</u>-values (p < 0.05). The significant characteristics included: ratio of head width to snout length (HW/SL), mandible pattern (MP), rank of nuchal cluster pattern (NCr), dorsal scale rows (DSR), total keeled and unkeeled lateral rows (TKUR), ventral scale rows (VSR), and ventral scale rows at mid-body (VSRM) (Table 3). Using seven morphological variables in a reduced-model discriminant function analysis produced 257 (97%) and 110 (97%) correctly classified specimens for Group 1 and Group 2, respectively.

Further investigation showed that the ratio of head width and snout length (HW/SL) and nuchal cluster rank (NCr) did not significantly increase discriminating power above that of the other five characteristic: the misclassification rates remained unchanged when this datum was excluded. The results of a second reduced-model discriminant function analysis confirmed that two <u>C. crocodilus</u> populations could be discriminated using the variables MP, DSR, TKUR, VSR, and VSRM. In this analysis, the misclassification rate for both Group 1 and Group 2 was 3%; using only five variables resulted in 12 (3%) incorrectly classified specimens (Table 4).

. For mandible pattern (MP), Group 1 was dominated by specimens with character state 1 (no pigmentation) while Group 2 was dominated by specimens with character state 3 (dark pigmentation) for jaw pattern (Figure 20). The discriminating power decreased significantly without the inclusion of this key characteristic. The misclassification rate for Group 1 and Group 2 increased to 15% and 21%, respectively: subspecies determination without the mandible pattern (MP) produced 63 (17%) incorrectly classified specimens.

The number of dorsal scale rows (DSR) ranged from 17 to 20 for Group 1 and Group 2. Two hundred and forty-six of 266 (92%) specimens from Group 1 had either 18 or 19 dorsal scale rows; 109 of 113 (96%) specimens from Group 2 had either 19 or 20 dorsal scale rows. The total number of lateral flank scales (TKUR), ventral scales (VSR), and ventral scales at mid-body (VSRM) are significantly greater in Group 2 than Group 1. Identification of specimens using only the flanks, as suggested by Brazaitis (1984), failed to produce acceptable classification rates in this study. Lateral patterns (LP) and proportion of keeled to unkeeled lateral rows (KLr) were not significantly different between the groups. Total keeled and unkeeled lateral rows (TKUR) analyzed alone produced 179 (47%) incorrectly classified specimens.

DISCUSSION

One of the goals of this study was to investigate morphological variation within the species <u>C</u>. <u>crocodilus</u> in order to more effectively manage the present populations. Challenges of conserving <u>C</u>. <u>crocodilus</u> are similar to many other crocodilian species and proper identification to the subspecific level is a critical element in the legal protection and management of this species. For example, <u>C. crocodilus</u> is one of 15 or more crocodilian species that are commercially harvested for the worldwide market. <u>C. crocodilus</u> skins are a major source of raw and finished material. The present caiman trade has reached over one million skins annually and is three or four times greater than the "classic" skin trade. International trade in crocodilians is regulated by the Convention on the International Trade in Endangered Species (CITES) and additional regulations are imposed by the United States under the Lacey Act of 1900 and the United States Endangered Species Act of 1973 (Brazaitis, 1989). Classification and sub-species identification of <u>C</u>. <u>crocodilus</u> is based on morphological characters and morphological variation among populations has been used as a basis for implementing CITES and regional management plans (Brazaitis, 1984). Large shipments of skins have been seized and confiscated based on one or more of these morphological characters (Brazaitis, 1986).

A second goal of this study was to determine if enough morphological variation existed in <u>C</u>. <u>crocodilus</u> to justify subspecific divisions. Historically, the number of keeled flank scales (KLR) and lateral flank pattern (LP) have been cited as definitive characteristics for differentiating between <u>C. c. crocodilus</u> and <u>C. c. yacare</u>. According to Brazaitis (1984), the northern subspecies of caiman, <u>C. c. crocodilus</u>, has 2-3 complete rows of alternating large and small well-keeled scales and <u>C. c. yacare</u> has four or more rows of equal-sized scales that are scarcely keeled (Brazaitis, 1984). It has been stated that <u>C. c. crocodilus</u> has 18-19 dorsal scale rows (DSR) (Fuchs, 1974) and 20-24 ventral scale rows (VSR) (Wermuth and Fuchs, 1978) while <u>C. c. yacare</u> has 17-18 dorsal scales rows (DSR) and 22-25 ventral scale rows (VSR) (Brazaitis, 1984). Distinct pigmentation on both upper and lower mandibles (MP) of <u>C. c. yacare</u> specimens has been used as a character to differentiate it from <u>C. c. crocodilus</u>; <u>C. c. crocodilus</u> is thought to lose mandible pigmentation one year following hatching (Brazaitis, 1973).

In this study, not one of the morphological characteristics considered by itself could discriminate between populations or subspecies. There was no significant difference in flank patterns (LP) or proportions of keeled to unkeeled lateral scale rows (KLr) in <u>C. crocodilus</u> when examined across the entire range of the species. There was, however, a significant difference in the total number of keeled and unkeeled lateral scale rows (TKUR). All states of jaw pattern (MP) were found in Group 1 and Group 2 even though there was a significant difference in frequency of occurrence between the groups. Thirty-nine different nuchal cluster patterns (NCr) were found between the two groups and this degree of variation is considerably greater than previously documented. The results of the discriminant analysis using five morphological characteristics suggest that two populations or subspecies of <u>C. crocodilus</u> are distributed in concert with the major river systems in South America. This number is significantly less than the number of proposed divisions for <u>C. crocodilus</u> since 1758, or those suggested by Wermuth and Fuchs (1978).

Morphological variation appears to have been present prior to the Miocene. This study supports the theory that the Alligatorinae migrated into South America across the Isthmian Link in the Paleocene, and underwent a secondary radiation prior to the Miocene (Savage, 1966). Between the Paleocene and the Miocene, <u>C. crocodilus</u> emerged and spread to occupy its present range in South America. Morphological variation between specimens living in the Amazon drainages and those in the Paraguay/Parana River drainages developed during this period of continental isolation. When North America and South America became reconnected, individuals from the northern (Amazonian) population of <u>C. crocodilus</u> migrated into Central America and were founders of the population presently known as <u>C. c. fuscus</u>.

For purposes of management, law enforcement, and systematic study, the two northern populations should be treated together. Regional management of the northern subspecies of <u>C. crocodilus</u> will require additional cooperation among the various countries supporting northern populations. Regional management efforts for the subspecies (<u>C. c. yacare</u>) is complicated by the fact that the Bolivian population, once continuous with the southern drainages, is now reproductively connected to the Amazon basin population.

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Additional investigation and management consideration must be implemented in Bolivia in order to maintain variation within these specimens.

Current law enforcement practices must be changed. Subspecific identification of skins from <u>C</u>. <u>crocodilus</u> can no longer be based on one characteristic, but rather must include mandible pattern (MP), dorsal scale rows (DSR), total keeled and unkeeled lateral rows (TKUR), ventral scale rows (VSR), and ventral scale rows at mid-body (VSRM). All five characteristics from a single specimen can be entered, along with the original data set, into a linear discriminant function (LDF) analysis and reliably assigned to either of the two populations. Membership probabilities (the probability of correctly assigning an unknown sample to a group) can be obtained from LDF, and this probability should be used by law enforcement agents to determine the geographic source of <u>C. crocodilus</u> skin shipments.

Correctly identifying subspecies of <u>C. crocodilus</u> by the method illustrated above is complicated by the fact that crocodilian skins are not generally shipped with the head attached. Because mandible pattern (MP) is one of five characteristics demonstrating discriminatory potential, discriminating power is diminished without this datum. Differentiation to a degree acceptable to the courts cannot be made without this characteristic. The only practical way to rectify this situation is to modify shipping procedures and require that dried and salted heads be included when hides are subjected to the tanning process. Another viable option is to find genetic markers that can be used as a definitive means to identify geographic origin of the commercial trade. Genetic investigation, coupled with further morphological study, will help address the myriad of systematic questions identified by this study.



Figure 7 Map of South America illustrating the Andes Mountain ranges used to partition specimens into Group 1 and Group 2 for testing hypothesis I.



Figure 8 Map of South America illustrating major river systems sampled for testing hypothesis II. River systems within Group 1 are illustrated in light gray, Group 2 systems are illustrated in dark gray.



Figure 9 Collection localities of the 379 <u>Caiman crocodilus</u> specimens analyzed by discriminant function analysis. Symbols may represent multiple specimens.



Figure 10 Head width (HW) and snout length (SL). Measurements expressed as a proportion (HW:SL) for analysis.











Figure 11 Character states 1, 2, and 3 defined within mandible pattern (MP) and lateral pattern (LP).



Figure 12 Proportion of keeled to unkeeled lateral scale rows (KLr).



Figure 13 Length and width of the largest lateral scales.

(AVERAGE PROPORTIONAL VALUE OF L:W OF 3 LARGEST SCALES)



Figure 14 Nuchal cluster (NCr) patterns identified. Thirty-nine different character states were identified.



Figure 15 Number of dorsal scale rows (DSR); counted from posterior edge of the nuchal cluster to the last scale row parallel with the rear margin of the hind legs.



Figure 16 Number of ventral scale rows (VSR); counted from first horizontal row following the ventral crest to the last complete row anterior to the anal opening.



Figure 17 Number of transverse ventral scale rows at mid-body (VSRM).



Figure 19 Number of tail inclusions (TIr) counted on the ventral side of the tail between the anal opening and the seventh scale row.

 Table 1 Cross-validation summary (Andes Mountain Range) using linear discriminant function analysis.

From ANDES	1	2	Total	
1	105 (84.0)	20 (16.0)	125 (100.0)	
2	33 (13.0)	221 (87.0)	254 (100.0)	
Total Percent	138 36.4	241 63.6	379 100.0	
Priors	0.50	0.50		
Error Count Estimates for ANDES:				
	1	2	Total	
Rate	0.16	0.13	0.14	
Priors	0.50	0.50		

Number of Observations and (Percent Classified) into ANDES:

Table 2 Cross-validation summary (by river systems) using linear discriminant function analysis.

From GRP	1	2	Total	
1	258 (97.0)	8 (3.0)	266 (100.0)	
2	2 (1.8)	111 (98.2)	113 (100.0)	
Total Percent	260 68.6	119 31.4	379 100.0	
Priors	0.50	0.50		
Error Count Estimates for GRP:				
	1	2	Total	
Rate	0.03	0.02	0.02	
Priors	0.50	0.50		

Number of Observations and (Percent Classified) into GRP:

Variable	Mean	Range	SD	SE	t	DF	Prob>ITI	
HW/SL	1.3		0.28	0.02	7.28	375.0	0.00	*
	1.2		0.11	0.01	5.36	377.0	0.00	*
MP	1.3	1-3	0.51	0.03	-41.71	372.1	0.00	*
	3.0	1-3	0.25	0.02	-32.17	377.0	0.00	*
NCr	21.9		6.66	0.41	4.32	241.2	0.00	*
	19.0		5.79	0.54	4.09	377.0	0.00	*
DSR	18.7	17-20	0.61	0.04	-7.36	296.6	0.00	*
	19.1	17-20	0.42	0.04	-6.40	377.0	0.00	*
TKUR	3.7	2-8	0.66	0.04	-5.81	182.1	0.00	*
	4.2	2-7	0.79	0.07	-6.23	377.0	0.00	*
KLr	14.0		4.09	0.25	1.29	255.5	0.20	NS
	13.4		3.35	0.32	1.19	377.0	0.24	NS
LP	2.0	1-3	0.37	0.02	-1.71	330.8	0.09	NS
	2.0	2-3	0.22	0.02	-1.42	337.0	0.16	NS
VSR	20.8	18-27	1.14	0.07	-10.43	214.6	0.00	*
	22.1	19-25	1.12	0.10	-10.36	377.0	0.00	*
VSRM	13.5	10-17	1.24	0.08	-9.24	206.8	0.00	*
	14.8	12-18	1.27	0.12	-9.33	377.0	0.00	*
TIr	1.1	1-3	0.31	0.02	1.69	335.0	0.09	NS
	1.0	1-2	0.18	0.02	1.39	377.0	0.16	NS
SRTAIL	8.5	5-11	1.29	0.08	-1.04	246.6	0.30	NS
	8.6	6-12	1.10	0.10	-0.98	377.0	0.33	NS
AVEL/W	1.9		0.57	0.04	2.01	228.8	0.04	*
	1.8		0.53	0.05	1.95	377.0	0.05	NS

Table 3 Results of the <u>t-test</u> with river data showing the mean, range, SD, SE, <u>t</u>, DF, and significance (p <0.05) of the twelve variables used in the analysis. Group 1: N=266; Group 2: N=113.

Table 4 Reduced model cross-validation summary by river system using linear discriminant function analysis. Only variables mandible pattern (MP), dorsal scale rows (DSR), total keeled and unkeeled lateral scale rows (TKUR), ventral scale rows (VSR), and ventral scale rows at mid-body (VSRM) were used in the analysis.

From GRP	1	2	Total
1	257	9	266
	(96.6)	(3.4)	(100.0)
2	3	110	113
	(2.6)	(97.4)	(100.0)
Total	260	119	379
Percent	68.6	31.4	100.0
Priors	0.50	0.50	

Number of Observations and (Percent Classified) into GRP:

Error Count Estimates for GRP:

	1	2	Total
Rate	0.03	0.03	0.03
Priors	0.50	0.50	



Figure 20 Distribution of mandible patterns within the major river systems of Central and South America. Group 1 represents specimens from Central America, the Orinoco river system, and the Amazon river system. Group 2 represents the Rivers Parana, Paraguay, and Urguay, and associated driange systems. APPENDICES

APPENDIX A

Specimens Examined

BOLIVIA--BENI: Río Itenez at Versalles (12 37'S, 63 22'W) (UF-A 40163-40165, 40167); 20 km ESE Santa Ana de Yacuma (13 45'S, 65 15'W) (UF-A 40160-40161); Cercado Prov, 40 km N. Trinidad, Estancia La Habana (14 08'S, 65 04'W) (UF-A 40152, 40156, 40158-40159); Itenez Prov, Río Blanco, Bella Vista (13 16'S, 63 41'W) (UF-FGT 3310); Marban Prov, 30 km S. Trinidad on road to San Lorenzo (15 01'S, 64 43'W) (UF-A 40150); Vaca Diez Prov, Lago San José, 12 km NNE Riberalta (10 51'S, 66 01'W) (UF-A 40136-40138, 40140-40141, 40144-40147, 40149), Tumi Chucua, 30 km S Riberalta (10 59'S, 66 06'W) (USNM 280228-280229); Yacuma Prov, 20-25 km E San Borja (14 55'S, 66 20'W) (UF-FGT 3314-3316). SANTA CRUZ: Chiquitos Prov, S Shore Laguna Concepcion, Estancia San Juan (17 31'S, 61 26'W) (UF-A 40050, 40052); Nuflo De Chavez Prov, San Pablo (15 53'S, 63 17'W) (UF-A 40069-40070), Río Zapacos (15 35'S, 63 14'W) (UF-A 40077). BRASIL--AMAZONAS: Manaus (3 08'S, 60 00'W) (AMNH 64855); Río Itacuaí (4 20'S, 70 12'W), 10 mi SE Río Tachitu Junction (LACM 138238-138239). BAHIA: (12 00'S, 42 00'W) (ANSP 9725). GUANABARA: Río de Jâneiro (22 54'S, 43 14'W) (AMNH 31747-31748). MARANHÃO: São João Dos Patos (6 30'S, 43 42'W) (AMNH 62123). MATO GROSSO: Aquadauna, Río Aquadauna (20 12'S, 55 45'W) (UF-A 46178); Caceres, 80 km SE Fazenda Nova Esperança (16 20'S, 57 48'W) (UF-A 46045, 46047-46048, UF-A 46051-46052); Caramujo (15 46'S, 57 45'W) (UF-46030, 46032-46033, 46036); Corumbá (19 01'S, 57 39'W) (UMMZ 103216); Cuiaba (15 35'S, 56 05'W), Río Paraguai (UF-A 46201, 46204); Descalvado (16 45'S, 57 42'W) (FMNH 10824); Río Paraguay below Descalvado (FMNH 9064); Río Paraquai (15 55'S, 57 40'W) (UF-A 46039-46040); Río Sangridorazinho (15 55'S, 57 05'W) (UF-A 46063, 46065-46066); N Río Sepatuba (15 48'S, 57 39'W) (UF-A 46043); Tapirape River (mouth) (10 41'S, 50 38'W) in Araguaya River (UMMZ 103008 [two specimens]); Vila Bella, Río Guapore (14 27'S, 60 06'W) (UF-A 46057, 46059-46060). MATO GROSSO DO SUL: Coxim, Río Taqueri (18 28'S, 54 45'W) (UF-A 46170); Fazenda Pramisone, Río Paraguai (18 27'S, 55 45'W) (UF-A 46166, 46169); Fazenda Sao Vicente, Río Paraquai (18 45'S, 56 40'W) (UF-A 46160-46161); Nabilequa, Fazenda Piuval (19 40'S, 57 40'W) (UF-A 46100, 46103); Nhumini, Río

Paraguai (14 00'S, 56 15'W) (UF-A 46151); Porta Murtinho, Río Paraguay (21 25'S, 57 40'W) (UF-A 46106, 46108-46109, 46194); Region Corumba, Río Paraguai (± 19 12'S, 57 49'W) (UF-A 46188); Río Negro, Río Negro (19 17'S, 55 15'W) (UF-A 46174). PARÁ: Altamira, 50 km (air) S near Cachoeira do Espelho (3 48'S, 52 32'W) (USNM 303485-303487); Belém (1 27'S, 48 29'W) (CM 2974); Óbydos [Óbidos] (1 55'S, 55 31'W) (FMNH 16073, MCZ 2596, 162011-162013); Santarém (0 39'N, 50 05'W) (MCZ 2814); Reserva Biologica Río Trombetas, Igarapé Abui (1 30'S, 56 30'W) (USNM 289094-289095). RONDÔNIA: Costa Marques (12 25'S, 64 10'W) (UF-A 46024, 46028-46029); Guarjara Mirim (10 55'S, 65 15'W) (UF-A 46013, 46018, 46023). COLOMBIA--AMAZONAS: Leticia (4 09'S, 69 57'W) (CAS 91653-91662). ANTIOQUIA: Turbo (8 06'N, 76 43'W) (MCZ 2721); Urabá [Boca] (8 03'N, 76 50'W), Río Currulao (FMNH 63899-63900). ATLÁNTICO: Barranquilla (10 59'N, 74 48'W), Río Magdalena (CU 12809, KU 94579). CHOCÓ: Tagachí (6 13'N, 76 43'W), Río Atrato (LACM 47185-47190); Golfo de Uraba, Unguia (8 01'N, 77 04'W) (FMNH 63901). CUNDINAMARCA: Giradot (4 18'N, 74 49'W) (MCZ 17602-17608). MADGALENA: Cienaga [Grande] (11 00'N, 74 15'W) (FMNH 69890-69891); Don Diego (10 59'N, 73 47'W) (UMMZ 46680). META: Villavicencio (4 09'N, 73 39'W) (MVZ 71377). PUTUMAYO: Río Mecaya (0 28'N, 75 12'W) (FMNH 69679). VALLE: Buenaventura (3 53'N, 77 04'W), Río Raposo (USNM 151748). COSTA RICA--HEREDIA: Puerto Viejo (10 28'N, 84 01'W) (KU 67460). LIMÓN: Puerto Viejo (9 39'N, 82 46'W) (KU 43893); Tortugero (10 35'N, 83 31'W) (UF 10324, UF 10494, UF 10737, UF 21161, MCZ 54997); Zent (10 02'N, 83 17'W) (MCZ 15333-15334). PUNTARENAS: Rincón (8 42'N, 83 29'W) (LACM 38018). CUBA--Isla de la Juventud (=Isla de Pinos [21 45'N, 82 45'W]) (KU 61857). ECUADOR--NAPO: Santa Cecilia (0 03'N, 76 58'W) (KU 107047, 112242, 122199, 126670-126671). PASTAZA: Río Curaray (2 22'S, 74 05'W) at Paracachi (USNM 196276-196277, 211256-211262), Teresa Mama (1 56'S, 77 13'W), Bobonaza Rió (USNM 196275). GUATEMALA--JUTIAPA: Casa Grande, 4 km E at Finca La Trinidad Laguna (14 17'N, 89 54'W) (UMMZ 107839-107843). GUYANA--EAST DEMERARA: Buxton (6 47'N, 58 02'W) (FMNH 26673-26678, 26681-26687); 50 mi above Georgetown (6 48'N, 58 10'W) (USNM 145473). WEST DEMERARA: Dunoon, Demerara River (6 26'N, 58 18'W) (UMMZ 46111). HONDURAS--Río Aguán (15 55'N, 85 41'W) (UF-A 42519-42520); Río Chapagua (15 58'N, 85 43'W) (UF-A 42516-42518); Río

Plátano (15 53'N, 84 41'W) (UF-A 42510). GRACIAS A DÍOS: Laguna de Brus (15 45'N, 84 29'W) Canal Amatingni (UF-A 42509); Laguna Brus (UF-A 42512); Laguna de Tansin, 15 km NW Puerto Lempira (15 19'N, 83 58'W) (LACM 48459-48461, LSUMZ 21718-21719); Palacios (15 55'N, 84 58'W), Laguna Bacalar (UF-A 42504-42507, 42515); Río La Criba, W of Laguna De Ibans (15 52'N, 84 46'W) (UF-A 42513- 42514); Río Patuca (15 47'N, 84 15'W) (UF-A 42508); Río Sico (15 58'N, 84 58'W) (UF-A 42001). LA REGION MOSOUITIA: Río Plátano (15 53'N, 84 41'W) (UF-A 42511). MEXICO--CHIAPAS: Soconusco, Escuintla (15 20'N, 92 38'W) (UMMZ 88262). YUCATÁN: Chichén Itzá (20 40'N, 88 34'W) (MCZ 17581). NICARAGUA--RIVAS: Río Sapoá (11 15'N, 85 36'W) (LACM 38015-38016); San Jefe del Sur, Isla de Ometepe (11 30'N, 85 35'W) (KU 86272). ZELAYA: Rama (12 09'N, 84 13'W), 6 mi W (TCWC 19285-19286). PANAMÁ--BOCAS DEL TORO: Almirante (9 18'N, 82 24'W) (KU 80219); Almirante, 3 km W (KU 108317-108318); Bastimentos (9 21'N, 82 12'W), Isla Bastimentos (KU 96989); Cayo de Agua (9 09'N, 82 02'W) (USNM 148276); Cayos Zapatilla [Grande] (9 16'N, 82 03'W) (KU 96990); Descudo de Veraguas Id (9 15'N, 81 40'W) (USNM 148249-148250); Fish Creek (9 00'N, 82 14'W) (KU 96991-96992). CHIRIQU : Guabalá (8 13'N, 81 44'W), 2 km S (KU 107863). COLÓN: Fort Sherman (9 22'N, 79 57'W) (MCZ 26760); Gamboa (9 07'N, 79 42'W) (UMMZ 98381); Gatuncillo (9 14'N, 79 39'W) (CU 3967 [2 specimens]); Gutún, Esclusas (9 16'N, 79 55'W) (LACM 74403); Toro Point (MCZ 22332-22333). DARIÉN: Boca de Cupe (8 03'N, 77 35'W), 12 km SSW at Río Cupe (KU 96987); Cana (7 56'N, 77 43'W) (USNM 50090-50092); El Real de Santa María (8 08'N, 77 43'W) (KU 80605, 107879; USNM 140610-140611, 211264); Isthmus (9 00'N, 80 00'W) (UMMZ 65917); Ortiga Camp (8 45'N, 78 00'W) along Río Chucunaque (FMNH 170162); Río Chucunaque at Río Ilagandi, 8 km above Río Mortí (8 51'N, 77 59'W) (KU 107870); Río Chucunague near mouth of Río Canglón (8 20'N, 77 40'W) (UMMZ 124209-124212); Río Tuira at Río Monos (9 16'N, 78 08'W) (KU 96993); Río Ucurgantí (8 27'N, 77 48'W), 7 km above mouth (KU 107871-107878); Río Urusela, 2 mi above El Real de Santa María (8 08'N, 77 43'W) (USNM 167225); Yaviza (8 11'N, 77 41'W) (MVZ 83217). LOS SANTOS: Guánico Abajo (7 18'N, 80 26'W) Río Guanico (KU 107864). PANAMÁ: Arraiján (7 46'N, 80 52'W), 8 km WSW (KU 96988); Barro Colorado Isla (9 09N, 79 51'W) (FMNH 179366, 13329, 13402; USNM 165968); Barro Colorado Isla, Wheeler Trail (UMMZ 63729); Panamá Bay (9 01'N, 79 29'W) (USNM 72384-72385);

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Pedro Miguel (9 01'N, 79 37'W) (AMNH 67201); Río Chagres (9 07'N, 79 42'W) (KU 107865-107869). PARAGUAY--ALTO PARAGUAY: 2 km N Bahía Negra (20 15'S, 58 12'W) (UF-C 108, 111, 117); Estancia General Díaz, Laguna General Díaz (21 10'S, 58 32'W) (UF-C 129); Frog Ponds N Laguna General Díaz (UF-C 131); 3 km E Estancia General Díaz (UF-C 133); 7 km ESE Estancia General Díaz, Tajamar 9 (UF-C 137); Puerto Ramos 7 km S Bahía Negra (20 17'S, 58 10'W) (UF-C 72, 77-78, 86, 92). AMAMBAY: Arroyo Chacalalina (=A Chacal) 4 km above mouth, 60 km SSW Bellavista (22 08'S, 56 31'W) (UF-C 142). CENTRAL: Asunción (25 16'S, 57 40'W) (FMNH 9497-9498). PRESIDENTE HAYES: Estancia Golondrina, 30 km W. Villa Hayes, Potrero Doña Cynthia (25 06'S, 57 34'W) (UF-C 63-66, 68); Estancía Juan De Zalazar, Laguna Vicente, 1 km W headquarters (23 06'S, 59 18'W) (UF-C 16, 18); Estancia Juan De Zalazar, Laguna 8 km NE Headquarters Cañadón Cacique, on map on south easternmost Laguna 7.2 km NE Trans Chaco Hwy (UF-C 5-6); Estancia Juan De Zalazar, Juan De Zalazar Tuyá, 3 km SW Headquarters (UF-C 22, 24); Estancia Tingunque, Río Monte Lindo at Retiro Pozo Arias, 18 km S Fortín Avalos Sánchez (23 28'S, 60 07'W) (UF-C 46, 49). MISIONES: Estancia Sarandy, 15 km SSW Santiago (27 09'S, 56 47'W) (UF-C 27-28, 31-33). ÑEEMBUCÚ: Est. 26, 8 km (air) NE Tacuara (25 59'S, 57 31'W) (UF-C 147). PERÚ--LORETO: 10 mi E Leticia, Colombia (4 09'S, 69 57'W) (UF 35084); near Yaguas River, 90 mi NW Leticia, Colombia (3 00'S, 71 00'W) (AMNH 73156); Nauta (4 32'S, 73 33'W) Río Samiyia, Santa Elena (FMNH 109805); Nazareth (3 54'S, 70 46'W), 20 mi above mouth Yavari River opposite Remate De Males Brazilian Village (FMNH 5671); Iquitos (3 46'S, 73 15'W) on Nanay Road (TCWC 48675). MADRE DE DIOS: Madre De Dios (12 36'S, 70 05'W) (FMNH 40004). UCAYALI: Pucallpa (8 23'S, 74 32'W), 28 mi ESE (TCWC 24129-24130); Río Ucayali, Yarina-Cocha (Lake) (8 15'S, 74 43'W) (FMNH 45639, 45641-45649, 56188); Upper Ucayali River (4 30'S, 73 27'W) (AMNH 71090-71092); Yarina-Cocha near Pucalipa (FMNH 45293). SURINAM--PARAMARIBO: Charlesburg Paramaribo (5 50'N, 55 10'W) (AMNH 8149, CM 44424-44425, TCWC 23567-23570, UF 99371); 25 km from Paramaribo, on road to Nickerie (MCZ 154922). TOBAGO--ST. MARY: SE of Goldsborough (11 15'N, 60 40'W) in Goldsborough River (USNM 228138). TRINIDAD--(10 20'N, 61 30'W) (AMNH 72878; FMNH 41676, 53650-53652; USNM 17718). VENEZUELA--APURE: San Fernando de Apure (7 54'N, 67 28'W), 4 km W at Hato La Guanota (TCWC 45392); San Fernando de Apure, 6 km W (TCWC

46238, 47411); Estado Aragua (9 19'N, 64 54'W) (UMMZ 135258). BOLÍVAR: Cerro Guanaco (4 40'N, 63 51'W) (AMNH 25197, 27191, 27375). FALCÓN: Palma Sola (10 36'N, 68 33'W), Río Yaracuy (UMMZ 55954). MONAGAS: Barrancas, 140 km NE (=Delta Amacuro Territory, 9 48'N, 61 08'W) (LACM 31500); Caripito (10 08'N, 63 06'W) (AMNH 65559); La Guanota (10 13'N, 63 32'W), Río Apure (TCWC-LE 15, 19, 21-23, 25-31, 33, 37, 39-40, 42-49, 51); Maturín, 60 km SE (9 19'N, 62 48'W) (LACM 31499). PORTUGUESA: Mun. Nueva Florida (8 57'N, 69 01'W), Santo Domingo (UF 99370). SUCRE: Guaraúnos (10 33'N, 63 07'W), 7 km S, Río Sabacual (KU 167616).

APPENDIX B

Table 5 Keeled vs unkeeled lateral scale row proportions. Each specimen was assigned the corresponding number for analysis (KLr).

Proportion of Keeled To Unkeeled Lateral Rows	Number Assigned	
0:2	1	
0:3	2	
0:4	3	
0:8	4	
1:1	5	
1:2	6	
1:3	7	
1:4	8	
1:5	9	
1:6	10	
2:0	11	
2:1	12	
2:2	13	
2:3	14	
2:4	15	
3:0	16	
3:1	17	
3:2	18	
3:3	19	
3:4	20	
4:0	21	
4:1	22	
4:2	23	
4:3	24	
4:4	25	

APPENDIX C

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Nuchal Cluster Pattern	Number
	Assigned
4-4-4-7	1
4-4-2-2	2
4-4-2-2-2	3
3-4-2-2	4
2-4-4-2	5
2-4-4-3-2	6
2-4-4-2-2	7
2-4-2-2-2	8
2-2-4-2-2	9
1-5-4-4-2	10
1-4-4-2	11
1-4-4-2-2	12
1-4-3-2-2	13
1-2-4-4-2	14
5-5-2-2	15
5-4-4-2	16
5-4-2-2	17
4-4-2	18
4-4-2-3	19
4-4-2-2	20
4-4-1-2	21
4-3-2-2	22
4-2-2-2	23
4-2-2-1	24
3-4-4-2	25
3-4-3-2	26
3-4-2-2	27
3-2-2-2	28
2-4-4-2	29
2-4-2-2	30
2-3-2-2	31
2-2-2-2	32
1-4-4-2	33
1-4-2-2	34
1-2-2-2	35
4-4-4	36
4-4-2	37
4-3-2	38
4-2-2	39

Table 6 Nuchal cluster patterns recorded. Each specimen was assigned the corresponding number for analysis (NCr).

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