

## Catalogue of American Amphibians and Reptiles.

Ross, F.D. 1998. *Crocodylus rhombifer*.

***Crocodylus rhombifer* (Cuvier)****Cuban Crocodile**

*Crocodylus rhombifer* Cuvier 1807:51. Distribution of the species was first associated with Cuba by Duméril and Bibron (1836), who also described the species from life in diagnostic detail. The type locality was restricted to Cuba by Schmidt (1924). Two known syntypes, one at l'Académie des Sciences, Paris, and the other in the Muséum National de Histoire Naturelle, Paris (MNHN), are both currently unlocated (see Remarks). No lectotype has been designated.

*croc rhombifer*: Cuvier 1817:21 (in a footnote).

*Crocodylus (planirostris)* Graves 1819:348. Type locality: "Africa" (in error). The type specimen, in the Museum of Bordeaux, was formerly in the private collection of the Count of Tustal, M. Journu-Aubert, and was brought to France by a naval surgeon associated with the slave trade (Bory St. Vincent 1824). It has long been considered lost (Gray 1867). Synonymy and type locality restriction to Cuba are by Gray (1862).

*Champse rhombifer*: Merrem 1820:36. New genus. Misquoted by Strauch (1866) as *Champses*.

*Crocodylus (Gravesii)*: Bory de Saint Vincent 1824:109. Substitute name for *planirostris* Graves.

*Crocodylus planirostris*: Bory de Saint Vincent 1824:109.

*Crocodylus Gravesii*: Bory de Saint Vincent 1831:132.

*Crocodylus Rhombifer*: Gray 1831b:22; Cuvier 1831:98.

*Crocodylus Planirostris*: Gray 1831b:23.

*Crocodylus (Champsès) rhombifer*: Cocteau and Bibron 1838:41.

*Crocodylus (rhombifer)*: Drapiez 1838:234.

*Crocodylus (Champsès) rhombifer*: Cocteau and Bibron 1841:55.

*Crocodylus (Palinia) rhombifer*: Gray 1844:60.

*Crocodylus Champse rhombifer*: Mayer 1858:315.

*Palinia rhombifera*: Gray 1862:270.

*Crocodylus pristinus* Leidy 1868:178. Type locality, Pleistocene deposits at Ciego Montero, Cienfuegos (formerly Las Villas) Province, Cuba. Holotype (a dorsal vertebra), Academy of Natural Sciences of Philadelphia (ANSP) VP 8598. Synonymy is by Matthew (1918).

*Crocodylus rhombifer*: Velasco 1893:80. Spelling error.

*Crocodylus rhombifer*: Velasco 1895:37. Spelling error.

*Crocodylus rhombiferus*: Reese 1915:2. Spelling error.

*Crocodylus rhombifer*: Stejneger 1917:289. First use of present combination.

*Crocodylus antillensis* Varona 1966:27, figs. 9–11. Type locality, Pleistocene deposits at Cueva Lamas, near Santa Fe, La Habana Province, Cuba. Holotype (posterior skull fragment), Instituto Biología Cuba, IB 101, collected by Oscar Arredondo (OA 368). Paratypes include maxillary, premaxillary, and squamosal bones. Synonymy is by Varona (1966).

*Crocodylus rhombifera*: Das 1994:200. Spelling error.

• **CONTENT.** *Crocodylus rhombifer* is a monotypic species including Pleistocene fossils. Wild hybrids are suspected. For a discussion of captive hybridization between *C. rhombifer* and several other species of *Crocodylus*, see Comments.

• **DEFINITION and DIAGNOSIS.** *Crocodylus rhombifer* is a spotted crocodile with short legs and short toes. The normal crocodylian webbing between the hind toes is very much reduced. The Cuban Crocodile's moderately short head has a greatly reduced and specialized dentition characterized by 12–13 maxillary teeth and, in adult animals, the development of a carnassial bite between the upper and lower jaws. The maximum reported size is 4.9 m, although few animals exceed 3.5 m (Varona 1966). Behavior such as high-walking and maintaining the head elevated while resting are characteristic.

Characteristic dentition includes the carnassial bite in which co-enlarged maxillary upper teeth 4 and 5 and co-enlarged mandibular lower teeth 9 to 11 act in a single, very strong side-by-side opposition that resembles a pair of scissors, especially when employed for cutting tendons while dismembering large prey. The posterior-most maxillary teeth, and also their opposing posterior-most mandibular teeth, are blunt at their tips, and are reduced to a vestigial condition unsuited for major chewing or crushing. Mandibular teeth number 15, premaxillary teeth 5, and maxillary teeth always fewer than 14 (range 12–13 alveoli). Mandibular tooth 10 is the largest after mandibular tooth 4. All allegations of 14 maxillary teeth are false. Some are based on the palatal view in Cuvier (1808: pl. 1, fig. 2; see Comments). The lateral view of the same tooth row (Cuvier 1808: pl. 1, fig. 3) shows 13 maxillary teeth. Other reports of 14 maxillary teeth

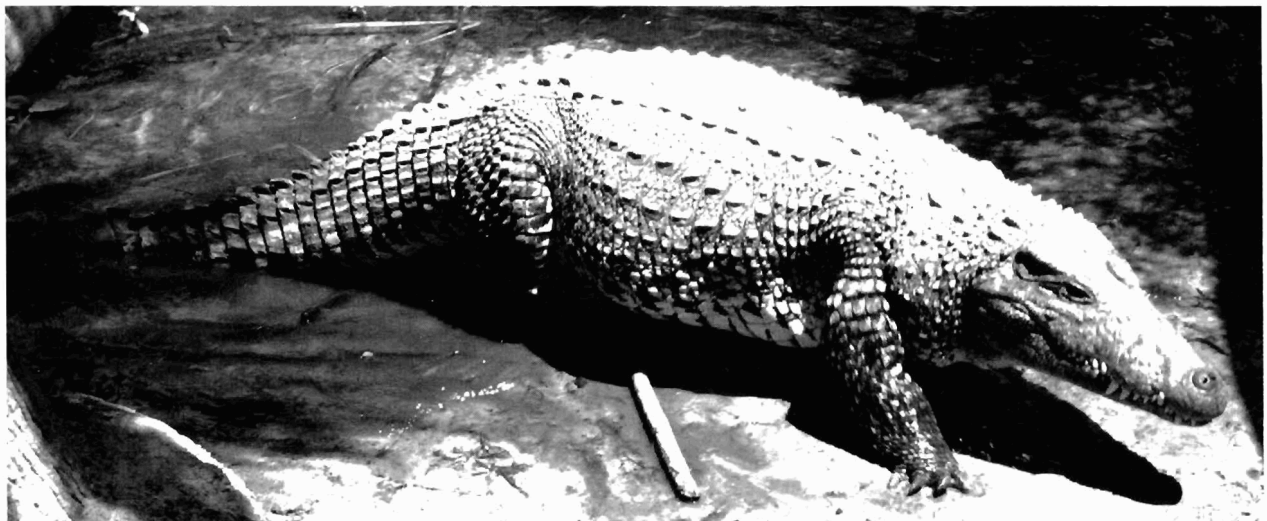
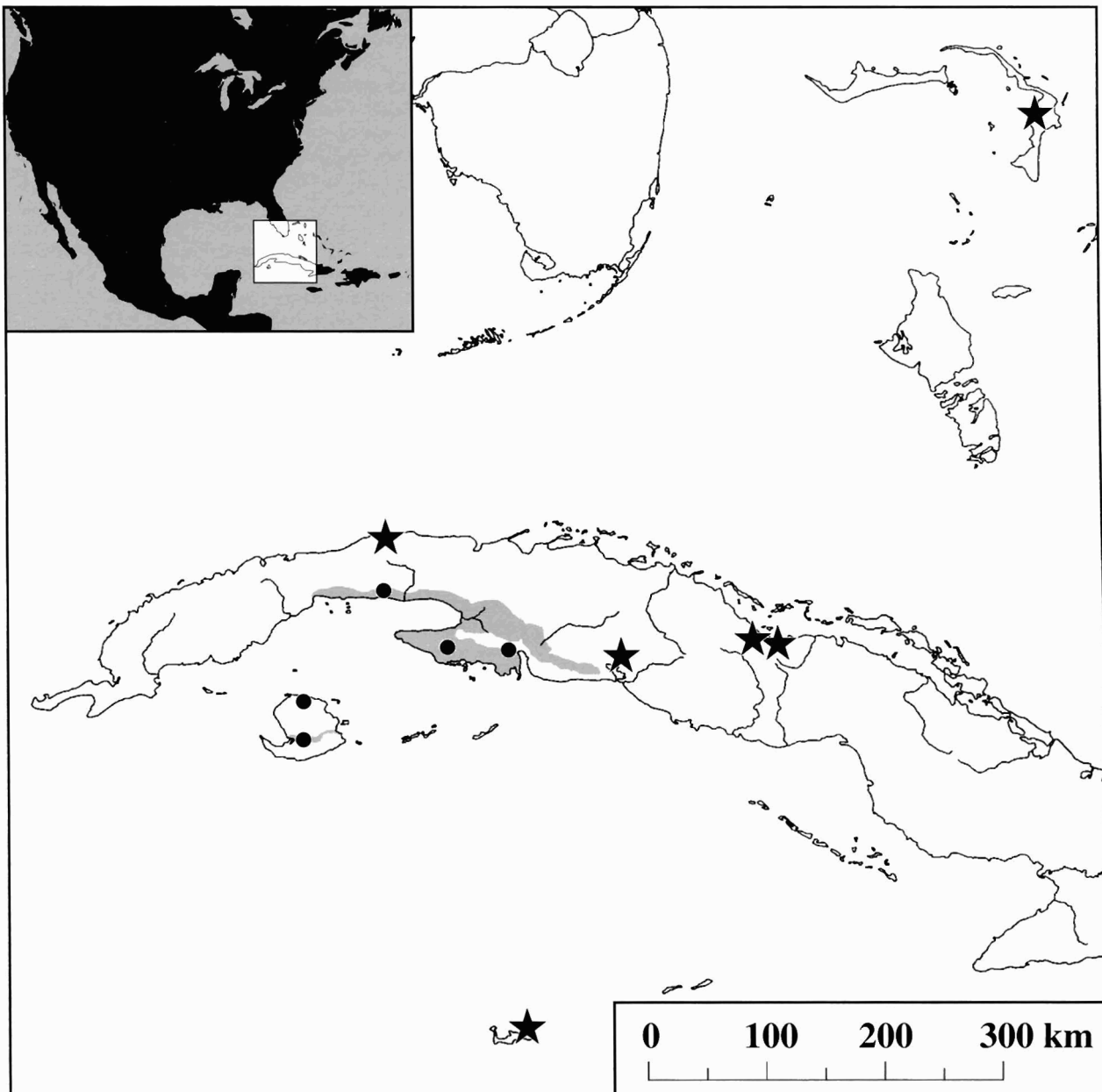


FIGURE 1. Low and evenly keeled dorsal and lateral scalation of a captive adult Cuban Crocodile, *Crocodylus rhombifer* (Cuvier). The high walk posture is characteristic of this species. Photograph by I.L. Brisbin.

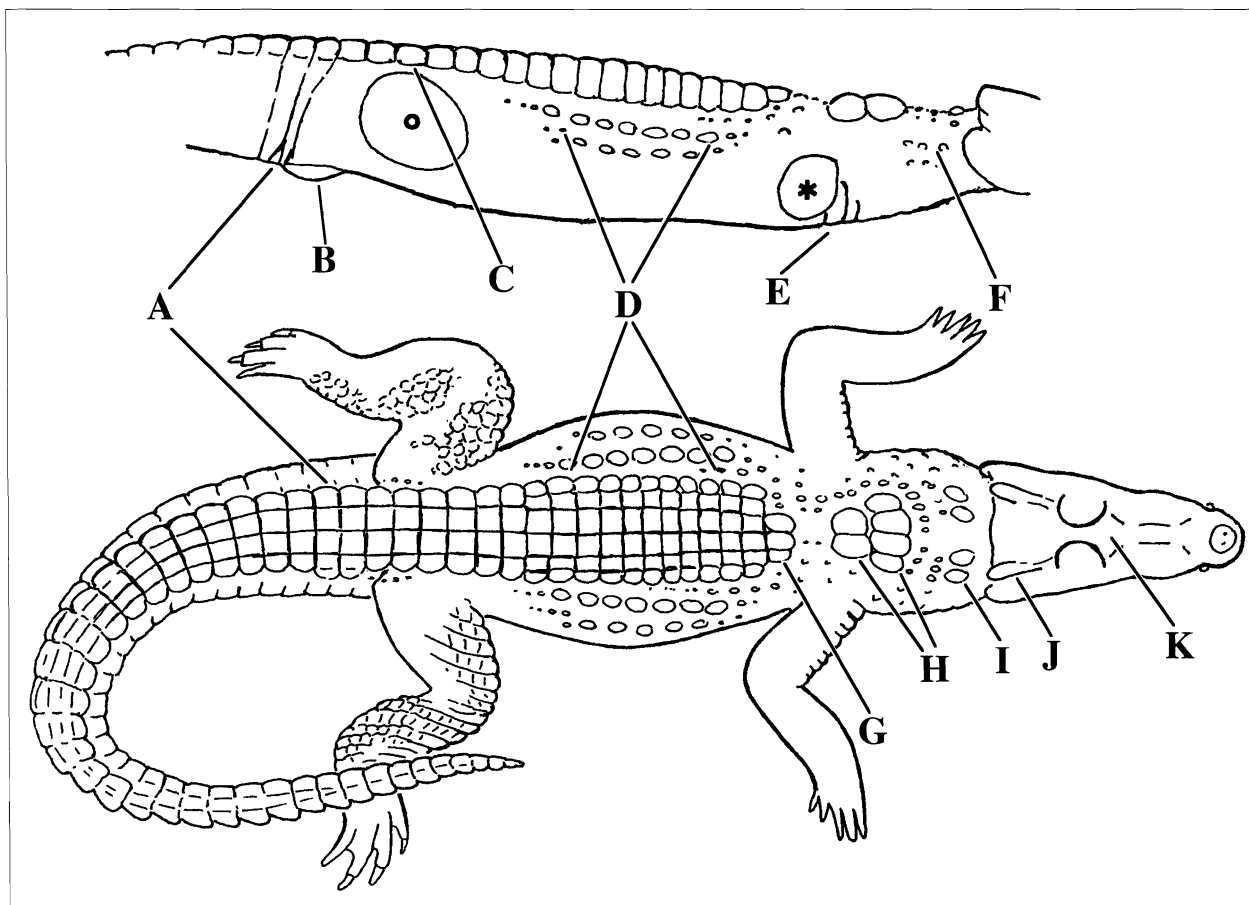
are from Central American *Crocodylus moreletii* mixed in some samples. In addition, some erroneous *C. rhombifer* data in Owen (1853) were reidentified by Gray (1867) to be Asian *C. palustris*. The dentition of *C. rhombifer* most closely resembles a *C. robustus* fossil, from Madagascar, that has 12 maxillary teeth (see Fossil Record).

The dorsal surface of the head has median orbital edges that often are strongly raised at the midlevel of the eyes, and the orbits are large in proportion to skull size when compared with most other *Crocodylus*. A rudimentary bony plate is in the anterior corner of the upper eyelid. Except in very young individuals, the lateral edges of the dorsal postorbital cranial table are usually raised above the center, and the postorbital cranial table widens posteriorly at the back end of the skull. Knobs of the elevated squamosal bone often are highly developed at the posterior and lateral corners of the cranial table in adults. On the snout, in front of the eyes, a minor median hump is often present,

and farther forward, at the level of maxillary teeth 4–5, the median nasal bones are always higher than the lateral maxillary humps in individuals  $>2$  m TL. The width of the snout at the transverse level of the notch for the fourth mandibular tooth is longer than the midline length from the anterior tip of the snout to the level of the notch. Incomplete notch development can very rarely hide the fourth maxillary tooth tip from median dorsal view. The snout tip around the nostrils is short, broad, and dorsoventrally thick. Mandibular tooth 1 rarely pierces the anterior end edge of the premaxillary bone. The mandibular symphysis extends to the level of the 4th teeth on each side when viewed from below with skin; or to the level of mandibular tooth 5, when viewed from above on cleaned lower jaws. Mandibular symphysis length is less than the width of the mandibles at the transverse level of mandibular teeth 4 or 5. The premaxillary–maxillary suture on the palate is essentially transverse, but often a minor median, anterior projection gives it a broad, very



**MAP.** The natural distribution of *Crocodylus rhombifer*, including Pleistocene fossils. The type locality is too imprecise to plot. Dots mark locations of extant populations and stars indicate sites at which fossils have been found. The Isle of Pines currently supports captive and reintroduced populations, whereas those in the Zapata Swamp, Cuba include wild and captive populations.



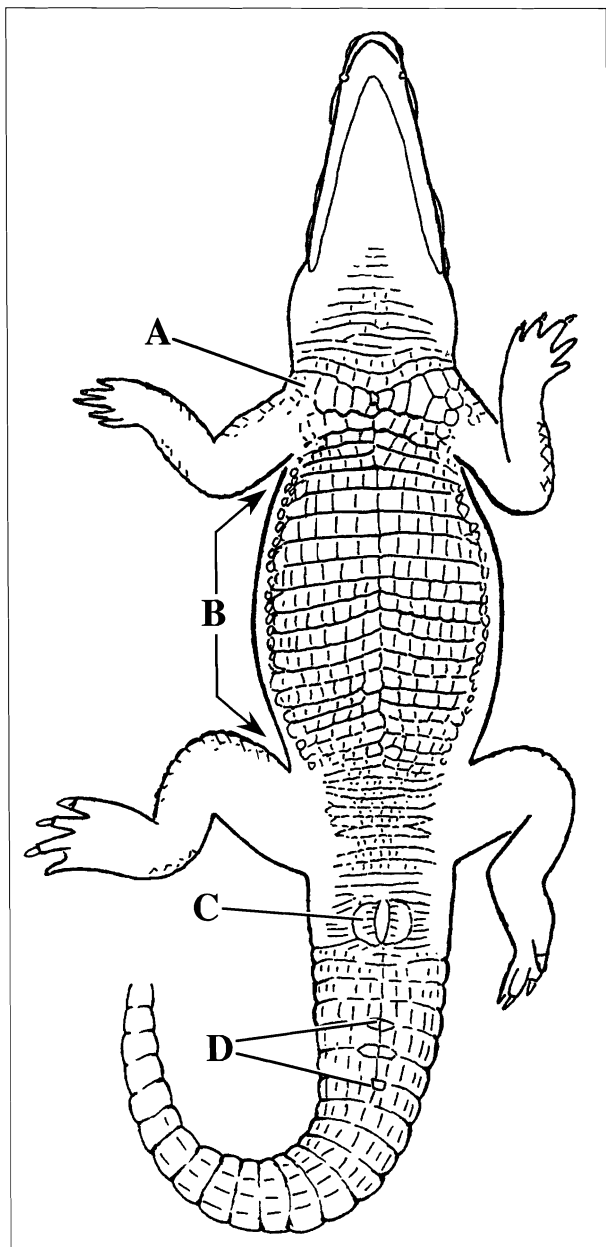
**FIGURE 2.** Partial lateral view (upper drawing) and complete dorsal view of the scalation (lower drawing) of a fluid preserved subadult *Crocodylus rhombifer* in the Zoological Museum of the University of Amsterdam (ZMA 12510) showing: a. the most anterior caudal transverse row of scales to pass posterior to the cloacal region is C-3 (the 3rd caudal row), using the terminology of Ross and Mayer (1983); b. the cloacal region in relation to the hind limb (marked with an open circle); c. the first transverse dorsal precaudal scale row (PC-1); d. lateral body scales form two lengthwise scale rows separated from the contiguous transverse rows of the dorsal armor, and from each other by granular skin; e. the lateral end of the ventral gular collar (also see Fig. 3a) is at the anterior edge of the base of the front leg (marked with a star); f. conical scales on the lateral surface of the neck; g. the 17th precaudal scale row (PC-17); h. the neck shield is PC-20 and PC-21 combined as a transverse row of 2 scales, and PC-22 and PC-23 combined as a transverse row of 4 scales; i. the 26th precaudal transverse scale row (PC-26); j. the squamosal horns of the cranial table; k. the rhomboidal shape that gave *C. rhombifer* its name. Drawings by F.D. Ross.

shallow “W” shape. This projection extends posteriorly to the level of maxillary tooth 1, or slightly beyond, but not to tooth 2 in the maxillary series. The palate is short and appreciably raised above the maxillary tooth row. The mandibles are short and dorsoventrally thickened (see Comments).

The dorsal and lateral scalation of the neck includes small, raised scales surrounding the neck shields. These conically keeled scutes are likely ossified in adult animals and cover the dorsal neck muscles with a protective armor, while still allowing the head to have lateral and vertical movement. The postoccipital transverse scale row, close behind the head, has 4–6 scutes. Using the precaudal terminology of Ross and Mayer (1983), this is scale row PC-26, counting from the base of the tail. The major dorsal neck shield has 6 scutes (nuchal scales) arranged (4 anterior / 2 posterior) in 2 compound transverse rows: PC-22 and PC-23 combined, and PC-20 and PC-21 combined; and, additionally, some specimens also have 1 or 2 scales present in PC-19 as a posterior part of the major neck shield (arranged: 4 anterior / 2 middle / 2 or 1 posterior). The neck and shoulder dorsal body armor are rarely almost continuous when PC-19 through PC-17 are all present. Often PC-18 is absent, and PC-17 has from 0–5 scales. PC-16 often has 6 scales (range: 3–6). Every row between PC-16 and PC-5 has 6 contiguous scales, rarely 4 or 5. The dorsal keel rows on the body

are low, even in size, uninterrupted, and continue well onto the base of the tail. Neither the 18–20 double crest caudal rows nor the more posterior 17 or 18 single crest caudal rows are highly or sharply keeled dorsally. The lateral body scutes have low and essentially continuous keels much like the keels on the dorsal scales, and the lateral rows are separated from each other and from the dorsal armor by granular skin.

The dorsal scales on the limbs often are raised to a central conical peak or a short median point, as opposed to a lengthwise ridge. The cone shape is more developed than in any other living *Crocodylus*. Like the lateral neck scales and the lateral scute rows on the body, the three-dimensional scales on the dorsal and exposed surfaces of the front and rear legs may be a terrestrial adaptation, as is the reduction of the webbing between the short fingers and toes. The dorsal, darkly pigmented, conical scales of the upper and outer surfaces of both the fore and hind limbs are so strongly developed that Lacépède (1833) called them “très-fortes.” The scales on the posterior and ventral edge of the lower legs that are usually flattened into rudder-like or paddle-like keels (= cnemial fringe) in other *Crocodylus* species, are not highly keeled in a lengthwise fashion in *C. rhombifer*. The high degree of cnemial fringe reduction in *C. rhombifer* effectively distinguishes it from all other living *Crocodylus*.



**FIGURE 3.** Ventral view of *Crocodylus rhombifer* scalation (ZMA 12510) showing: a. the gular collar transverse scale row (for lateral view, see Fig. 2e); b. counting near the ventral midline, 31 transverse scale rows occur between the gular collar and the cloacal vent; c. the cloacal vent and associated oval shaped region of granular scales; d. posterior to the cloaca are three small midventral scalation irregularities. Drawing by F.D. Ross.

Ventral scales lack osteoderms, though the condition in very large specimens is unknown. Ventral transverse rows of essentially rectangular belly scales number 29–34 between gular collar and cloacal opening. Scales at the ventral midline usually number 32–34. Scattered and minor midventral scale row irregularities are common on the anterior half of the tail. A single very dark, essentially black integumentary sense organ (follicle gland) is located on each ventral, lateral, and dorsal scale.

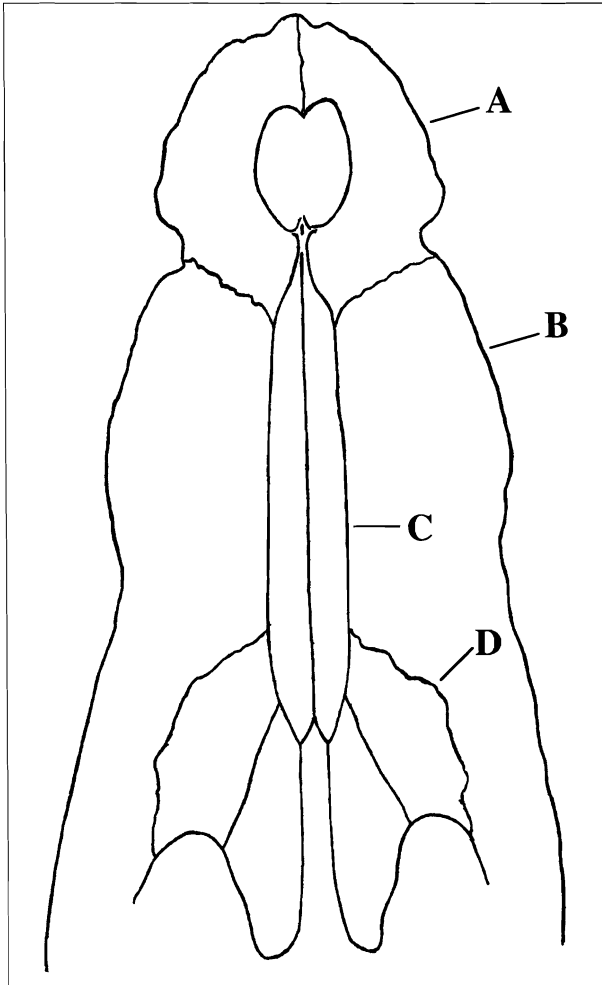
Ventral color is white to yellow, and immaculate near the midline on the belly. A dark lateral pattern is often present on the anterior edges of the lateral-most 4 or 5 belly scales. The dark pigment often extends all the way to the midline on the

posterior part of the tail. The dorsum may be dark, or lighter with 6 dark transverse bands on the body and 8–10 bands on the tail. The dorsal and lateral surfaces of the neck and body are darkly spotted on a lighter background, and dark pigment patches occur on the mandibles. For eye color, see Descriptions.

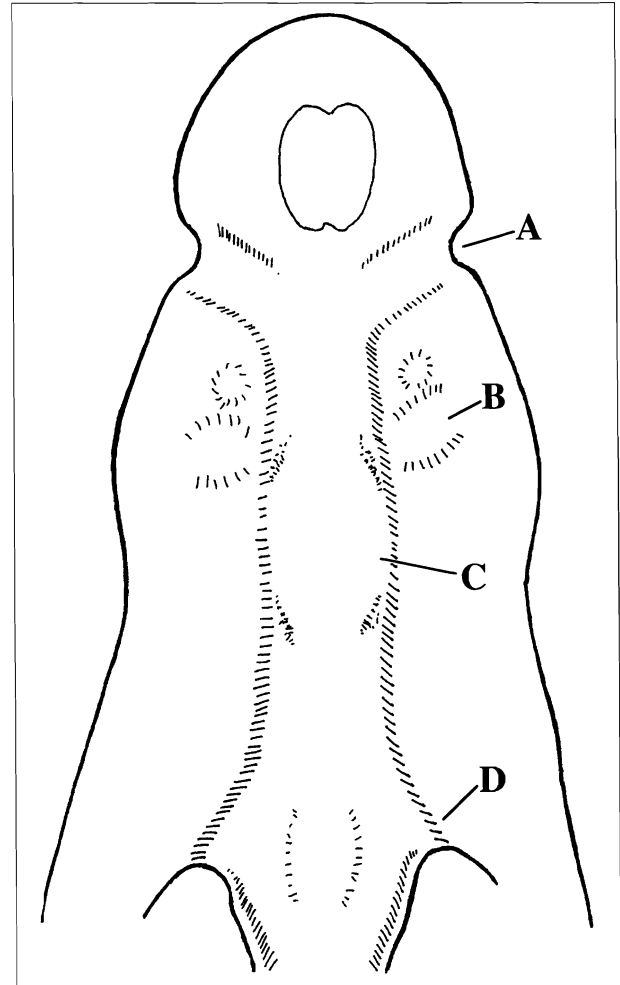
• **DESCRIPTIONS.** Although many of the published descriptions of *C. rhombifer* are listed by topics in Fossil Record and in Pertinent Literature, several groups of references are listed here because they directly support statements in the Definition: **adult total length** (Alderton 1991; Barbour 1914, 1930; Barbour and Ramsden 1919; Boulenger 1889; Brazaitis 1974; Bridges 1968; Cocteau and Bibron 1838; Ditmars 1910; Dow 1990; Edwards 1989; Fuchs 1974; Grenard 1991; Groombridge 1982; Guggisberg 1972; Gundlach 1880; Haltenorth and Trense 1956; Hermes 1987; Herter 1960; Honegger 1968a; Hornaday 1904, 1911; King and Dobbs 1975; Levy 1991; Minton and Minton 1973; Morgan 1994; Neill 1971; Perrero 1975; Pope 1989; Ramos et al. 1994; Reese 1915; Ross and Magnusson 1989; Saint-Girons 1971; Schmidt 1944; Schwartz and Henderson 1991; Sola 1930; Steel 1989; Stone 1989; Trutnau 1986, 1994; Varona 1966, 1969; Vogel 1965; Vokins 1972; Wermuth 1953; Wermuth and Fuchs 1983a; Werner 1933b; Wettstein 1954); **dentition** (Boulenger 1889, Brazaitis 1974, Carpenter and Lindsey 1980, Duméril and Bibron 1836, Iordansky 1973, Mook 1921b, Owen 1845, Rue 1994, Schwartz and Henderson 1991, Steel 1989, Trutnau 1994, Varona 1966, Wermuth 1953); **limb length** (Duméril and Bibron 1836); **presence of palpebral bone** (Duméril and Bibron 1836); **toe length** (Gray 1867, 1872); **voice** (Gundlach 1880, Neill 1971); and **webbing between toes** (Duméril and Bibron 1836, Gray 1867, 1872). Note that the *C. rhombifer* junior synonym *Crocodylus gravesii* data in Owen (1845) suggest that a carnassial is present on that specimen.

Other descriptions of *C. rhombifer* include the following topics: **coloration** (Alderton 1991; Barbour and Ramsden 1919; Boulenger 1889; Brazaitis 1974; Cocteau and Bibron 1838; Dow 1990; Duméril and Bibron 1836; Gray 1862, 1867, 1872; Gundlach 1880; Hornaday 1904; Neill 1971; Neill and Allen 1959; Schwartz and Henderson 1991; Varona 1966, 1986a; Vokins 1972; Wermuth 1953; Wermuth and Fuchs 1983a); **dark spots on the mandible** (Ramos et al. 1994); **eye color** (Gundlach 1880; Neill 1971; Ramos et al. 1994; Trutnau 1986, 1994); **general scalation** (Boulenger 1889; Brazaitis 1974; Cocteau and Bibron 1838; Cuvier 1807; Duméril and Bibron 1836; Fuchs 1974; Gray 1831a, b, 1844, 1862; Gundlach 1880; Günther 1885; King and Brazaitis 1971; Lacépède 1833; Mertens 1943; Ross and Mayer 1983; Schwartz and Henderson 1991; Stejneger 1917; Trutnau 1986, 1994; Varona 1966, 1986a; Wermuth 1953; Wermuth and Fuchs 1978, 1983a, b); **limb scalation** (Gray 1867, 1872); **sexual dimorphism in color** (Vokins 1972); **skull bones and head shape** (Aoki 1983, 1989; Boulenger 1889; Carpenter and Lindsey 1980; Cocteau and Bibron 1838; Cuvier 1807; Dow 1990; Ditmars 1910; Duméril and Bibron 1836; Gray 1844; Gundlach 1880; Günther 1885; Iordansky 1973; Medem and Marx 1955; Mertens 1943; Morgan 1994; Neill 1971; Torre 1939; Varona 1966; Vokins 1972; Wermuth 1953; Wermuth and Fuchs 1978); and **ventral scalation** (Brazaitis 1974; Fuchs 1974; King and Brazaitis 1971; Trutnau 1986, 1994; Wermuth and Fuchs 1983b).

• **ILLUSTRATIONS.** Photographs include: **anterior body** (always including the head and neck and sometimes a front foot)(AAZPA 1984; Brazaitis 1967; Dathe 1974; Grenard 1991; King 1989; Levy 1991; Means 1992; Mielcarek 1983; Minton and Minton 1973; Neill 1971; Neill and Allen 1959; Penny 1991; Petzold 1965; Powell et al. 1996; Rue 1944; Schmidt 1944; Stone 1989; Trutnau 1986, 1994; Varona 1966, 1980), **copulation**



**FIGURE 4.** Dorsal view of part of a Pleistocene fossil skull of a half-grown *C. rhombifer* (AMNH-VP 6185) from the level of the eyes to the anterior tip of the snout. The following bones are indicated: a. premaxillary, b. maxillary, c. nasal, d. lacrimal. Drawing by F.D. Ross.



**FIGURE 5.** Dorsal view of the snout of the same Ciego Montero fossil (AMNH-VP 6185) showing the following surface features: a. the notch that allows the fourth mandibular tooth to stick up outside the snout; b. a small hump to accommodate the base of the fifth maxillary tooth; c. the nasal bones are raised to a major hump between the maxillary bones at the level of the 4th, 5th, and 6th maxillary teeth; d. the lacrimal bone ridge and/or undercutting that runs forward from the usually raised anterior edge of the orbit. When mirrored in bilateral symmetry and in combination with the orbit edges, these form a rhomboidal shaped figure (see Fig. 2k). Drawing by F.D. Ross. The Ciego Montero fossils at the AMNH are for the most part nearly complete, but are all missing pieces, making a drawing of the complete skull very difficult. Photographs of the sample should be published. The least variable part of the skulls in the series is the anterior snout.

(Varona 1966), **fossil skulls** (and/or parts of skulls)(Franz et al. 1995; Morgan 1994; Morgan et al. 1993; Varona 1966, 1984), **hatchlings** (AAZPA 1984, Lanka 1981, Trutnau 1994), **head** (often showing dentition, mandibular color pattern, and eye size)(Aoki 1993; Barbour and Ramsden 1919; Bender 1992, as "alligators;" Betancourt 1970; Brazaitis 1967; Bridges 1968; Felix 1970; Grenard 1991; Harrison 1981; King 1989; Levy 1991; Means 1992; Minton and Minton 1973; Neill 1971; Neill and Allen 1959; Penny 1991; Pope 1955; Rue 1994; Schmidt 1944; Soberon 1995; Sola 1933; Stone 1989; Thorbjarnarson 1992; Trutnau 1986; Varona 1966, 1980, 1986b; Vogel 1965; Werner 1933b, as *C. planirostris* in text; Wettstein 1937), **high walk and resting postures** (Aoki 1993; Betancourt 1970; Dathe 1974; Pough et al. 1998, mistakenly allocated to Australia; Soberon 1995; Thorbjarnarson 1992; Varona 1966), **karyotype** (Chavananikul et al. 1994), **modern skulls** (Mertens 1943, Neill 1971, Varona 1966), **mandibles** (and/or parts of mandibles)(Franz et al. 1995, Mertens 1943, Morgan 1994, Morgan et al. 1993), **mandibular symphysis** (Varona 1984), **proportions and scalation** (Aoki 1993; Barbour and Ramsden 1919; Bender 1992; Betancourt 1970; Dathe 1974; Felix 1970; Grenard 1991; Harrison 1981; King and Ross 1993a; Lanka 1981; Neill 1971; Pope 1955; Soberon 1995; Soberon et al. 1996; Sola 1933; Trutnau 1994; Varona 1966; Vogel 1965; Werner

1933b, as *C. planirostris* in text; Wettstein 1937), and **skins and leather** (Dathe 1974, Fuchs 1974, Wermuth and Fuchs 1983b).

Artists' illustrations include drawings of: **anterior body** (Brazaitis 1974, diagrammatic; Campbell and Winterbotham 1985; Duméril et al. 1873; Grenard 1991; Herter 1960; Ross and Mayer 1983; Steel 1989; Stejneger 1917; Wermuth 1953, 1974; Wermuth and Fuchs 1978, 1983a; Wermuth and Mertens 1961), **coloration** (photographs and a few paintings)(Aoki 1993; Bender 1992, called "alligators;" Brazaitis 1967; Bridges 1968; Cocteau and Bibron 1838; Grenard 1991; Harrison 1981; King 1989; Levy 1991; Means 1992; Penny 1991; Powell et al. 1996; Rue 1994; Trutnau 1986), **head** (often with teeth)(Campbell and Winterbotham 1985; Cocteau and Bibron 1838; Dow 1990; Duméril et al. 1873; Grenard 1991; Herter 1960; Staton 1978; Steel 1989; Wermuth 1953, 1974; Wermuth and Fuchs 1978,

1983a; Wermuth and Mertens 1961), **hind foot webbing** (Cocteau and Bibron 1838), **muscles, arteries, and veins of the throat** (Rathke 1857, 1866), **proportions and scalation** (Dow 1990; Staton 1978; Trutnau 1994; Wermuth 1953; Wermuth and Fuchs 1978, 1983a; Wermuth and Mertens 1961), **retina** (Heinemann 1877), **skulls** (usually with mandibles) (Cuvier 1808, Hoeven 1833, Mook 1921b, Tiedemann et al. 1817, Varona 1966, Wermuth 1953, Wermuth and Fuchs 1983a, Wermuth and Mertens 1961), **venter** (Carmena-Suero et al. 1979; Lanka 1981, including an egg-attachment, "umbilical," scar), and **Zapata Swamp** (Carrillo et al. 1993, Betancourt 1970). Additional illustrations are fairly common in papers dealing with the protected and endangered status of this species (see also Pertinent Literature).

Erroneous and misleading whole animal illustrations (drawings and paintings) include Bory St. Vincent (1831), Ross and Magnusson (1989), Tiedemann et al. (1817), and Wexo (1984). Also, some published photographs of captive and deformed animals show a pathological tooth condition that can occur in any crocodylian, and all descriptions of splayed teeth being characteristic of the Cuban Crocodile are false. The best set of black and white photos of whole animals is in Felix (1970). An otherwise excellent color photograph in Rue (1994) shows an animal with slightly deformed teeth.

• **DISTRIBUTION.** *Crocodylus rhombifer* was apparently recently present in the Cayman Islands, but is now restricted to the freshwater Zapata Swamp (Cienaga de Zapata) of the Zapata Peninsula (Garrido 1980, including a map; Ramos et al. 1994) on the southern coast of Cuba, and to the Lanier Swamp (Lanier's Swamp, Cienaga de Lanier) on the nearby Isle of Pines (Isla de Pinos), which is now called Isla de la Juventud. An additional report of a specimen from Pinar del Rio Province, Cuba, is in Mertens (1972b).

Maps that show both the Zapata Swamp and the Isle of Pines are in Funtanella (1969), Mielcarek (1983), and Varona (1980). A detailed map of just the Isle of Pines is in Todd (1916).

Many sources of information address distribution and habitat (Alderton 1991; Barbour 1914, 1916, 1930; Barbour and Ramsden 1916, 1919; Biddell and Stringer 1990; Boulenger 1889; Brazaitis 1967, 1974; Buide 1967; Carmena-Suero et al. 1979; Carrillo et al. 1993; Cocteau and Bibron 1838; Davies 1994; Ditmars 1910; Dowling 1971; Duméril 1861; Duméril and Bibron 1836; Duméril and Duméril 1851; Fischer 1884; Fuchs 1974; Garman 1887; Garrido and Schwartz 1969; Giebel 1860; Gray 1844, 1862, 1867, 1872, 1873; Grenard 1991; Groombridge 1982, 1987; Guggisberg 1972; Guibé 1970; Gundlach 1875, 1880; Günther 1885; Hallowell 1857; Haltenorth and Trense 1956; Herter 1960; Hoeven 1855; Honegger 1968a, 1979; Hornaday 1904; King and Burke 1989; Köhlmann 1966; Lando and Williams 1969; Levy 1991; Lichtenstein 1856; Lydekker 1896; Mertens 1943, 1972b; Mertens and Wermuth 1955; Mielcarek 1983; Morgan and Patton 1979; Neill 1958, 1971; Orbigny 1844; Ottenwalder and Ross 1992; Penny 1991; Perrero 1975; Pooley 1972a; Pope 1955; Ramos 1989; Ramos et al. 1994; Reinhardt and Lütken 1863; Ross 1998; Ross and Magnusson 1989; Saint-Girons 1971; Schmidt and Inger 1957; Schwartz 1978; Schwartz and Henderson 1991; Smith and Smith 1973, 1976; Sola 1930, 1933; Steel 1989; Stone 1989; Strauch 1866; Sumichrast 1880; Taylor 1969; Thorbjarnarson 1992; Trutnau 1986, 1994; Vaillant 1897; Varona 1966, 1980, 1981, 1983, 1985; Vokins 1972; Webb and Manolis 1989; Wermuth and Fuchs 1978; Wermuth and Mertens 1961; Werner 1909, 1933b; Wettstein 1954; Wiegmann 1834).

Modern specimens with locality data more specific than "Cuba" include AMNH 2024, Santa Clara Province, Aguado,

on the Anabana River; AMNH 57773, Zapata Swamp; AMNH 82943, Isle of Pines or Cayo Cantilles; FMNH 34677, Cuba (1940 Museum Expedition); MCZ 1249, Cienfuegos; MCZ 12081, west coast of Ensenada de Cochinos; MCZ 33600, Zapata Swamp; and USNM 13578, Havana. One fairly large stuffed exhibit specimen at Harvard University (MCZ, no catalog number) is from the Cienaga de Zapata, and is possibly a wild hybrid; it has a head and general coloration like *C. rhombifer*, but the dorsal scalation resembles *C. acutus*.

Errors and problems in distribution records include a Cayo Cantiles specimen (Garrido and Schwartz 1969; Ross and Mayer 1983, hybrid) from the Archipiélago de los Canarreos that possibly originated on the Isle of Pines (G.R. Zug, pers. comm.). All reports from the Archipiélago de los Canarreos (Schwartz and Henderson 1991) were considered to be unsubstantiated by Ross and Magnusson (1989). The specimen (AMNH 82943) was originally identified as an American Crocodile, but many characters suggest that it is a *C. rhombifer*, or possibly a wild hybrid. It has a head like *C. acutus* and dorsal scalation like *C. rhombifer* in several important characters. A vague recent rumor in Campbell and Winterbotham (1985) of Cuban Crocodiles in Hispaniola (Tiburon Peninsula, Haiti) is unverified. The species has twice been wrongly recorded as resident in Central America. Many 19th century distributions erred by confusing *C. rhombifer* with Morelet's Crocodiles, based on a supposed similarity to Hernandez's *Aquez palin*. Ranges involving México, in error, include Cuvier (1832), Reiche (1904a), Troschel (1871), Troschel and Ruthe (1859), Wiegmann (1828, 1829, 1834), and Wiegmann and Ruthe (1832). A supposed *C. rhombifer* in the London Zoo (Slater 1872, 1877, 1883, 1896) was likely a Central American Morelet's Crocodile. Later, Barbour and Ramsden (1919) published the completely mistaken idea that the type specimens of Morelet's Crocodile originated in Cuba (Abercrombie et al. 1980). The Cuban Crocodile junior synonym *C. planirostris* was long thought to possibly be from Africa (Chenu and Desmarest 1856, Gray 1831a). An erroneous idea concerning ranges of *C. planirostris*, *C. moreletii*, and *C. rhombifer* is in Werner (1900). Supposed *C. rhombifer* specimens from Java, Indonesia, mentioned by Müller (1923), Müller and Schlegel (1844), and Strauch (1866) are *C. siamensis* (Ross 1992, Ross et al. 1995). According to Gray (1867, 1872), a *C. palustris* from Bengal was erroneously called *C. rhombifer* by Owen (1853).

The population on the Isle of Pines was formerly more widespread and its range included the northern coastal region (Hornaday 1904). The Isle of Pines population is currently threatened by introduced caimans (Varona 1983). This population of *C. rhombifer* was feared extinct by Wermuth and Mertens (1977) and Ramos et al. (1994), but it has subsequently been bolstered by reintroductions described in detail by Soberon et al. (1996).

The most comprehensive work on Recent *C. rhombifer* in the Cayman Islands is Morgan (1994), which includes maps of fossil sites on Grand Cayman and Cayman Brac. Other Cayman Islands sources include Barbour (1914), Garman (1888), Morgan and Patton (1979), Seidel and Franz (1994), and Williams (1964). The Cayman Islands were called *Caimanes* (Islas Caiman), incorporating the Amerindian word *caiman*. The Cayman Islands were visited by the English fleet of Sir Francis Drake in 1586, and the Cuban Crocodile was apparently the only crocodylian inhabiting the Cayman Islands in the early years of European exploration, including the very early visit by the Portuguese fleet of Columbus in 1503 (Morgan 1994).

• **FOSSIL RECORD.** At least four fossil localities occur on the Island of Cuba. The most productive site is Ciego Montero (Barbour 1945; Barbour and Ramsden 1919; Brown 1913; Leidy

1868; Matthew 1918; Mook 1921b, 1921c; Morgan 1994; Neill 1971; Schuchert 1935; Steel 1989; Varona 1966, 1984). Other Cuban fossil sites include Cueva Lamas (Furrazola 1969, including map; Steel 1989; Varona 1966, 1984), the Pleistocene *C. rhombifer* site at Casimba(s) de Jatibonico (Barbour 1945, Barbour and Ramsden 1919, Brown 1913, Neill 1971, Schuchert 1935, Steel 1989, Varona 1984), and the Caves of Cueiba at Sierra de Remedios (Varona 1984). Two fossil sites are known outside of Cuba and outside the current range. One is in the Cayman Islands, British West Indies (Davies 1994; Morgan and Patton 1979; Morgan et al. 1993, including age 860–375 YBP; Penny 1991; Ross and Magnusson 1989; Seidel and Franz 1994), and the other is on Abaco Island, Bahamas (Franz et al. 1995, including age 2700–2900 YBP; Ramos et al. 1994). Fossil sites on Grand Cayman (B.W.I.) and Cayman Brac (B.W.I.) are discussed in detail and located on maps in Morgan (1994), which also includes radiocarbon dates and a review of other fossils, including the specimen from the Bahamas.

Information about fossils includes the following, listed by topic: **fossil localities and history of Cuban Crocodile paleontology** (Alderton 1991; Brown 1913; Franz et al. 1995; Mook 1921c; Morgan et al. 1993; Schuchert 1935; Steel 1989; Varona 1966, 1984), **Pleistocene ground sloths as food** (Barbour 1945, Barbour and Ramsden 1919, Brown 1913, Leidy 1868, Neill 1971, Steel 1989), **skull** (Barbour and Ramsden 1919; Brown 1913; Franz et al. 1995; Matthew 1918; Mook 1921b; Morgan et al. 1993; Ross and Magnusson 1989; Varona 1966, 1984), **taphonomy and geologic age** (Barbour 1945, Barbour and Ramsden 1919, Brown 1913, Franz et al. 1995, Hedges 1996, Morgan et al. 1993, Ross and Magnusson 1989), **teeth** (Leidy 1868, Morgan 1994, Morgan and Patton 1979, Morgan et al. 1993), and **vertebrae** (Leidy 1868, Varona 1984).

Skulls of Pleistocene fossils are sometimes twice as long as the largest modern skulls studied, and data from fossils were included in Definition. Fossils examined include ANSP-VP8598 (vertebrae), Ciego Montero; AMNH-VP 6179a (skull), Ciego Montero; AMNH-VP 6179b (skull), Ciego Montero; AMNH-VP 6181 (skull), Ciego Montero; AMNH-VP 6185 (skull), Ciego Montero; AMNH-VP 6187 (skull and vertebrae and mandibles generally associated with the skulls), Ciego Montero; and USNM 216197 (skull), Grand Cayman Island.

The assertion (Morgan 1994) that *C. rhombifer* was the only species of crocodylian inhabiting the Cayman Islands at the time of Columbus and Drake, although based on a fossil record devoid of fully adult animals, is probably true. However, the other *Crocodylus* species currently inhabiting the Greater Antillean Region, *C. acutus*, does not occur in any of the *C. rhombifer* fossil sites in Cuba, the Cayman Islands, or Abaco Island, Bahamas. The absence of *C. acutus* from a *C. rhombifer* fossil site is to be expected. The time of arrival of *C. acutus* in the Cuban region, including the Cayman Islands and the Bahamas, deserves further attention, and Williams (1989) has substantiated the general need for an intensive search for old fossils in the entire West Indian Region.

The ancestry and relationships of *C. rhombifer* are not yet understood. The unsupported assertion (Sanderson 1941) that the Morelet's Crocodile forms a link between *C. rhombifer* and *C. acutus*, and that this is evidence of a former connection between Cuba and the Yucatán Peninsula, is likely false. Actually, *C. rhombifer* is very different from the other three living species of New World *Crocodylus* (Densmore and White 1996), and statements about Cuban Crocodiles being directly and very closely related to Morelet's Crocodiles (Schmidt 1928, Sill 1968, Underwood 1954) are in error. Fossil junior synonyms of *C. rhombifer* were cited as ancestors of the modern Cuban Crocodile by Alderton (1991), Balouet (1989), and Langston (1965). A persistent argument claims that the Cuban Crocodile is a small

animal (Reese 1915, for example, claimed a 7 ft maximum total length for *C. rhombifer*) and therefore is different from the Pleistocene freshwater crocodile of Madagascar (Reese 1915, for example, claimed a 30 ft maximum total length for *C. robustus*). This is false because the Cuban Crocodile was a very much larger animal during the Pleistocene. Some fossil *C. rhombifer* may have been well >20 ft in total length. The *C. rhombifer* fossil skulls at the AMNH are so large that they suggest that, before the arrival of *Homo sapiens* in the Greater Antilles and before the demise of the Cuban Ground Sloth which *C. rhombifer* used to eat, the Cuban Crocodile may have grown to a greater total length than that achieved by the Madagascar fossil species. A complication is that the published and often repeated total length of *C. robustus* probably originated with an exaggerated estimate. The data for *C. robustus* reported in this account is from the MCZ fossil which was figured and described by Barbour (1918) and by Mook (1921a). Both *C. robustus* and at least some *C. rhombifer* can have twelve maxillary teeth and possess a carnassial, and this dentition differentiates the two species from all other modern *Crocodylus* species. Further, they both have raised horns on the squamosal bones of the cranial table and both species have short snouts elevated along the dorsal midline. They also both possess the character of having the palate appreciably raised above the alveoli of the maxillary teeth. According to Gasparini (1981), fossil crocodile skull fragments from Argentina include triangular shaped postorbital dorsal cranial tables with squamosal horns that resemble *C. rhombifer*. If it can be shown that the fossils from Cuba and Madagascar are closely related, it would greatly contribute to our understanding of crocodylian relationships (also see Comments).

• **PERTINENT LITERATURE.** Because they had very few specimens for study, early anatomists rarely addressed *Crocodylus rhombifer*. Huxley (1860), Jaeger (1828), and Kälin (1933), for example, were unable to examine a skull. Modern anatomists, especially in Cuba and in Eastern European nations that were behind the Iron Curtain, have had the opportunity to study the captive population at the crocodile rearing stations in the Zapata Swamp, and have added immeasurably to our knowledge of the species.

Subsequent citations are organized by topic: **anesthesiology** (Lloyd et al. 1994), **behavior** (including copulation, general habits, and temperament) (Barbour and Ramsden 1919; Betancourt 1970; Brazaitis 1969a; Cocteau and Bibron 1838; Coy-Otero and Hernandez 1982; Ditmars 1910; Gundlach 1880; Harrison 1981; Hornaday 1904; Neill 1971; Olivares 1899; Penny 1991; Perrero 1975; Steel 1989; Trutnau 1986, 1994; Varona 1966, 1986b, 1987), **blood, hematocrit, and cardiac puncture** (Benitez et al. 1976; Blanco and González 1974; Carmena-Suero et al. 1979; Castellanos 1973a, 1973b, 1977, 1979; Perez-Beato and Granado 1978; Slonimski 1935; Tourn et al. 1994), **cannibalism and predation by vultures at the Zapata farm** (Honegger 1975b, Whitaker 1979a), **capture method** (Sola 1933), **chromosome, DNA, and protein electrophoretic studies** (including analyses of hybridization) (Betancourt et al. 1973, Chavananikul et al. 1994, Davis et al. 1996, Densmore 1983, Densmore and Owen 1989, Densmore and White 1996, Gatesy and Amato 1992, Granado 1983, Granado and Berovides 1975, Perez-Beato and Granado 1978), **cladograms** (Brooks and O'Grady 1989, based on parasites; Densmore 1983; Densmore and Owen 1989; Densmore and White 1996; Gatesy and Amato 1992; Greer 1970, based on nesting habits; a cladogram based on classical characters by Duméril and Bibron 1836 was reproduced and incorrectly attributed by Norell 1989), **cloacal sex organs** (Brazaitis 1969b, Gundlach 1880), **comparison of skull with *C. acutus* and *C. moreletii*** (Morgan 1994), **comparison with *C. moreletii***



(Duméril 1852), **ecology** (including habitat descriptions and some nesting data)(Barbour 1914, 1916; Barbour and Ramsden 1919; Behler 1978; Bolton 1989; Campbell 1972; Carrillo et al. 1993; Davies 1994; Garrido 1980; Hornaday 1904; Magnusson 1992; Mertens 1934; Morgan 1994; Morgan and Patton 1979; Neill 1958, 1971; Neill and Allen 1959; Ottenwalder and Ross 1992; Pooley 1972a; Powell et al. 1996; Ramos et al. 1994; Schmidt 1951; Steel 1989; Trutnau 1986, 1994; Varona 1987), **egg-attachment** (“umbilical”) **scar** (Lanka 1981), **eggs** (Brazaitis and Watanabe 1988b; Gómez and Gonzáles 1970; González and Cabrera 1973; Ikai et al. 1983; Thorbjarnarson 1996; Trutnau 1986, 1994; Whitaker 1979a,b), **embryos and hatchlings** (Odum 1993), **eye** (Fleishman et al. 1988, Heinemann 1877, Krause 1893), **fat** (Gundlach 1880), **food** (sometimes wrongly inferring a diet of turtles based on the rounded tips of the much reduced and probably weak teeth at the back of the mouth)(Brazaitis 1969a; Carmena-Suero et al. 1979; Carpenter and Lindsey 1980; Grenard 1991; Groombridge 1982; Harrison 1981; Larsson and Wihman 1989; Levy 1991; Luxmoore et al. 1985; Neill 1971; Penny 1991; Pope 1955; Powell et al. 1996; Ross and Magnusson 1989; Rue 1994; Skoczylas 1978; Sola 1930; Trutnau 1986, 1994; Varona 1966; Vokins 1972; Webb and Manolis 1989), **geographic juxtaposition with other crocodiles** (Werner 1933a), **growth** (Dowling and Brazaitis 1966; Duméril 1861; Lanka 1981; Neill 1971; J.P. Ross, pers. comm.; Schwartz and Henderson 1991, likely a false claim that females are larger than males; Sola 1930; Trutnau 1994; Vokins 1972; Wermuth 1964), **human use of fat and meat consumption** (Gundlach 1875, 1880; Luxmoore et al. 1986; Pooley 1971; Ramos 1989, Ramos et al. 1994), **jaw and hyoid** (Schumacher 1973), **keys and diagnoses** (Barbour and Ramsden 1919; Boulenger 1889; Brazaitis 1974; Cope 1900; Fuchs 1974; King and Brazaitis 1971; Medem and Marx 1955; Ota 1966; Reiche 1904b; Schmidt 1924; Schwartz and Henderson 1985; Sola 1930; Stejneger 1917; Trutnau 1994; Wermuth 1953; Wermuth and Fuchs 1978, 1983a,b; Wermuth and Mertens 1961), **leather industry** (Collins 1996, 1998; Luxmoore 1990, 1991, 1992, 1994; Ottenwalder and Ross 1992; Ramos 1989; Ramos et al. 1994; Sola 1930; Thorbjarnarson 1992), **limb anatomy** (Meers 1995, Müller and Alberch 1990), **mark-recapture study at the Isle of Pines** (Soberon et al. 1996), **metallo-protease inhibition by ovomacroglobulin** (Ikai et al. 1985), **musk glands** (Gundlach 1880, Neill 1971), **nesting** (Campbell 1972; Carrillo et al. 1993; Greer 1970; Grenard 1991; Gundlach 1880; Larsson and Wihman 1989; Levy 1991; Minton and Minton 1973; Neill 1971; Odum 1993; Ottenwalder and Ross 1992; Ouboter and Nanho 1987; Rue 1994; Schmidt 1924; Steel 1989; Thorbjarnarson 1992, 1996; Trutnau 1986, 1994; Varona 1966, 1987; Webb and Manolis 1989; Wettstein 1954), **parasites and veterinary treatment** (Brooks and O’Grady 1989, Coy-Otero and Barus 1979, Coy-Otero and Hernandez 1982, Groschaft and Barus 1970, Honegger 1975b, Perez-Benitez et al. 1980, Perez-Vigueras 1956, Perez et al. 1976, Sardinias et al. 1980, Schwartz and Henderson 1991, Zajicek and Mendez 1969), **protection status, habitat scarcity, captive stock, captive breeding, and threats to survival of *C. rhombifer* due to hybridization with *C. acutus*, and due to predation by introduced Central American *Caiman crocodilus fuscus*** (AAZPA 1984; Alderton 1991; Allen 1969; AZA 1996; Barbour 1976; Behler 1978; Beltz 1989; Berry 1994; Betancourt 1970; Bezuijen 1996; Bolton 1989; Brazaitis 1967, 1974; Brazaitis and Watanabe 1983, 1985a, 1985b, 1986, 1987a, 1987b, 1988a; Bustard 1984, 1986; Campbell 1977; Campbell and Winterbotham 1985; Carrillo 1994; Conway 1986; Dathe 1974; Davenport 1984a, 1984b, 1985; Davies 1994; Dow 1990; Downes (1973, bibliography); Formozov 1994; Geissler and Jungnickel 1989; Gorzula 1996; Grenard 1991; Groombridge 1982, 1987, 1992; Guggisberg

1972; Hakansson 1994, 1995; Harrison 1981; Honegger 1968a, 1968b, 1971a, 1971b, 1973, 1975a, 1975b, 1979, 1993, 1994; Honegger and Hunt 1990; Honegger and Zeigler 1991; Howell 1990; IUCN 1990; King 1974a, 1974b, 1989, 1990; King and Brazaitis 1971; King and Burke 1989; King and Dobbs 1975; King and Ross 1992a, 1992b, 1992c, 1993a, 1993b, 1994a, 1996; King et al. 1979; Klös and Lange 1986; Lang 1987; Lanka 1981; Levy 1991; Luxmoore 1992; Luxmoore et al. 1985, 1986, 1991; Magnusson 1986; McMahan 1993; Means 1992; Mertens 1951, 1968, 1972a, 1972b; Messel 1994; Mielcarek 1983; NRC 1983; Odum 1993; Ottenwalder and Ross 1992; Penny 1991; Petzold 1965; Pham Van Muoi 1995; Pooley 1971, 1972a, 1972b, 1972c, 1972d; Powell 1971, 1973a, 1973b, 1974a, 1974b; Ramos 1989; Ramos et al. 1994; Richter 1973; Ross and Magnusson 1989; Ross 1991, 1992, 1998; Rue 1994; Schouten 1992; Schwartz et al. 1978; Schwartz and Henderson 1991; Sebastian 1994; Slavens 1980, 1981, 1982; Slavens and Slavens 1990; Soberon 1995; Steel 1989; Stone 1989; Stubbe et al. 1981; Suvanakorn and Youngprapakorn 1987; Thang 1994; Thorbjarnarson 1991, 1992; Trutnau 1986, 1994; Turner 1977; Vaillant 1897; Varona 1966, 1969, 1976, 1980, 1981, 1983, 1986a; Vogel 1965; Vokins 1972; Webb and Manolis 1989; Wermuth 1976; Whitaker 1979a, 1979c; and numerous articles in the International Zoo Yearbook), **protein biochemistry** (Ikai et al. 1983), **reproductive problems** (Benitez et al. 1974), **sex ratios and population density** (Ramos et al. 1994, Thorbjarnarson 1997), **sexual dimorphism** (Casas-Andreu and Guzman-Arroyo 1970, Varona 1966), **size of reproductive females** (Thorbjarnarson 1996), **skins as stuffed curios or handbags** (Carrillo 1994, Dathe 1974, King and Ross 1994a, Messel 1994, Pooley 1971), **synonymies** (non-fossil)(Boulenger 1889; Cocteau and Bibron 1838; Duméril and Bibron 1836; Gray 1867, 1872; Mertens and Wermuth 1955; Mielcarek 1983; Mook 1959; Schwartz and Thomas 1975; Strauch 1866; Sumichrast 1884; Trutnau 1994; Wermuth 1953; Wermuth and Mertens 1961, 1977; Werner 1933b), **tagging and aerial surveys** (Carrillo et al. 1993, Soberon et al. 1996), **throat anatomy** (O’Donoghue 1917; Rathke 1857, 1866), **vision** (Fleishman et al. 1988).

• **REMARKS.** Of the two known syntypes, the one at l’Académie des Sciences, Paris, was nearly complete. The MNHNP specimen, a skull figured in Cuvier (1808, see Comments), was removed from what Gray (1867, 1872) called a mutilated skin. MNHNP 966, in a catalog by Duméril, may be a syntype (C.A. Ross, pers. comm.).

Captive Cuban Crocodiles are socially dominant over *C. acutus* in enclosures. The former is also dangerous in captivity because it has a well deserved reputation for jumping (Varona 1966, Ross 1998). However, in the early days of European exploration of the Cuban region, the American Crocodile was the more aggressive species toward people in the wild (Dampier 1729, Humboldt 1856).

The Greek word *rhombos* (rhomboidal geometric figures with four equal sides and without right angles) incorporated into the trivial name (see Etymology) refers to the dorsal surface of the skull, and in detail to the bony preorbital ridges (and/or undercutting) that are laterally connected to raised anterior edges on the orbits, and extend forward on the lacrimal bones. Many specimens, especially very young animals, exhibit only part of the character, and the rhombus is always imaginary at the anterior and posterior ends along the dorsal midline of the skull. The rhombus in *rhombifer* (synonyms include “Rhombic Crocodile” by Gray 1831b, *Crocodile rhombifère* by Duméril and Bibron 1836, *le Crocodile Rhombifère* by Duméril and Bibron 1836, *le Cr. rhombifère* by Duméril 1852, *Crocodile rhombifer* by Orbigny 1844, *Crocodilo rombifero* by Cocteau and Bibron 1838, and *Cocodrillo rombifero* by Wermuth and Fuchs 1983a)



is a dorsal skull character, and the original name in French, *le crocodile a losange* (Cuvier 1807), refers to the skull rhombus. Synonyms include *le crocodile à losange* by Cuvier (1808) and Vaillant (1897), *Le Crocodile a losange* by Tiedemann et al. (1817), *das Krokodil mit der Raute* by Tiedemann et al. (1817), *Krokodil Chamsi rautiger* by Merrem (1820), “lozenged crocodile” by Cuvier (1831), *crocodile à losanges* by Lacépède (1833), *Rautenkrokodil* by Giebel (1860) and Richter (1973), and *Ruitkrokodil* by Grzimek (1973). Thus, the name “Lozengescaled Crocodile” (Gosse 1851) (synonym, “Square-shielded Crocodile” by Gray 1831a) is in error, even though rhomboidal scales are seen on the legs in *C. rhombifer*. The names “Aque Palin” (Gray 1844) and “Cuban Palinia” (Gray 1867) both incorrectly associate the taxon with México, as did Fischer (1884, *Das mexikanische Krokodil*), and Krause (1893, *dieses mexikanischen Crocodils*). The use of the name “Mexican Crocodile” by Sclater (1872, 1877, 1883, 1896) is probably a *C. moreletii*, and the longevity records in Flower (1925, 1929) are for the same London Zoo animal(s), likely from Central America.

The common name “Cuban Crocodile” is derived from Guibé’s (1970) *le Crocodile de Cuba*. Synonyms include *Crocodile du Cuba* by Wermuth and Fuchs (1978), *Crocodrill de Cuba* by Wermuth and Fuchs (1983a), *Cocodrillo de Cuba* by Wermuth and Fuchs (1983a), *Cocodrillos cubanos* by Casas-Andreu and Guzman-Arroyo (1970), “Cuban crocodile” by Castellanos (1977), *cocodrillo cubano* and *cocodrillo di Cuba* by Ross (1990, in an Italian translation of Ross 1989), *Cubaanse krokodil* by Hoogmoed and Ross (1993), *Cuba Croco* by Fuchs (1974), *Cuba croco* by Wermuth and Fuchs (1983b), *Le Crocodile de la Havane* by Duméril (1861), *das kubanische Krokodil* by Mertens (1934), *Kubakrokodil* by Mertens (1951), *Kuba-Krokodil* by Haltenorth and Trense (1956), *krokodyl kubánsky* by Felix (1970), *krokodyl kubansky* (Czech) by Lanka (1981); *krokodyl kubansky* (Polish) by Mielcarek (1983); *Kuba-Kroko* by Wermuth and Fuchs (1983b), and *Kuba-croco* by Fuchs (1974). Use of “Cuban Crocodile” (= pure *C. rhombifer*) in this account follows Vesey-Fitzgerald (1968) and Ross (1989). Davies (1994) suggested “Freshwater Cuban Crocodile.” Other common names include Japanese spellings in Aoki (1993) and Ota (1966) and one in Russian in a table of contents associated with Castellanos (1979). Cuban names include *Cocodrillo*, per Gundlach (1875) and the synonym *crocodrillo* by Schmidt and Inger (1957). Other Cuban names are *criollo* by Varona (1966), *legítimo* by Varona (1966), *cocodrillo perla* by Varona (1966, synonym: “Pearly Crocodile” by Grenard 1991), and *zoquendo* (Buide 1967, synonym: *zaquendo* by King and Brazaitis 1971 and *Caimán Zaquendo* by Wermuth and Fuchs 1978).

African slaves in early Spanish Cuba called *C. rhombifer* “Cayman’s cousin” (Stoddard 1909). Wild hybrids (*C. rhombifer* x *acutus*) were named “Cocodrillo mixturado” (Varona 1966) and “mixturals” (Harrison 1981). Fossil junior synonyms of *C. rhombifer* do not have published vernacular names. The junior synonym *C. planirostris* was named “Crocodile planirostre” (Graves 1819), *Crocodile de Graves* (Bory St. Vincent 1824), “Flat-headed Crocodile” (Gray 1831a), and “Graves’s Crocodile” (Gray 1844).

• **ETYMOLOGY.** The species name *rhombifer* is derived from two Latin words, *rhombus* and *fero*, which are combined to mean “rhomb-bearer” (Redfield 1865).

• **COMMENTS.** The Cuban Crocodile has a long history. Reports of two species of crocodiles in Cuba were made by the early explorers, William Dampier (1729) and Alexander von Humboldt (1856), although neither actually saw a Cuban Crocodile. Humboldt’s boat sailed through the Archipelago de los

Canarreos and in 1801, Humboldt visited the town of Batabanó on the southern coast of Cuba (Funtanella 1969, including a map). He attempted to get a specimen of *C. rhombifer* in 1804, while in Havana (Humboldt 1856).

The dorsal armor description in Cuvier (1807) distinguished *C. rhombifer* from the American Crocodile by dorsal scalation characters. The drawings of the skull in Cuvier (1808: pl. 1, figs. 1–5) have, however, been challenged in the literature as possibly being a *C. acutus* by Günther (1885), who said that “the skull on which Cuvier founded *C. rhombifer* may prove to be nothing but a short-snouted *C. americanus*.” Earlier, Huxley (1860) said that the *C. rhombifer* skull in Cuvier (1808) resembled the American Crocodile “in the great convexity of its nasal region, but differs from it in the greater breadth of the skull and in the strong converging preorbital ridges, which appear to be limited to the lacrymal bones. If the figures are to be trusted, however, there are other very important distinctive characters about the cranium of this species, for Cuvier’s figure ..., which gives a view of the palate, shows the premaxillary-maxillary suture forming a nearly straight transverse line.” The illustrations in Cuvier (1808) have been reprinted many times in various editions of Cuvier’s works. Huxley (1860: vol. 9, p. 102 and pl. 331) referred to “Oss. Fossiles” in a different pagination of Cuvier (1808) printed in 1836 (p. 70, pl. 231, figs. 1–5). See also Literature Cited.

The need for finding the syntypes is extreme in the case of *C. rhombifer*, because some of the type figures in Cuvier (1808) are likely very slightly in error. One documented example of an error in a type figure of a crocodile is in Ross and Ross (1987). The illustration in Cuvier (1808: pl. 1, fig. 2) shows partly the wrong number of maxillary teeth (with 14 teeth on one side in the drawing) and shows, instead, on one side, the correct number for the American Crocodile (14 maxillary teeth are normal for *C. acutus*). The relative sizes of maxillary teeth 4, 5 and 6 in Cuvier (1808: pl. 1, fig. 2) are indistinguishable from observed variation in *C. acutus*. The mandible figured in Cuvier (1808: pl. 1, figs. 3–4) is not as dorso-ventrally thickened, particularly posteriorly, as it perhaps should be in a true Cuban Crocodile. The transverse suture in Cuvier (1808: pl. 1, fig. 2) is at the level of the first maxillary tooth, as opposed to being at the level of the back of the first tooth as it is in the Morelet’s Crocodile illustration in Ross (1987), or even farther posteriorly as it is in *C. acutus*. Huxley (1860) was correct in saying that the palatal premaxillary-maxillary suture shape in Cuvier (1808: pl. 1, fig. 2) eliminates *C. acutus*.

The *C. robustus* fossil at Harvard University also has a palate with the premaxillary-maxillary suture truly forming a nearly straight transverse line, as do some *C. rhombifer*, including the Pleistocene fossils, and, to only a slightly lesser extent, some very large skulls of *C. acutus* (see Varona 1966, unless that specimen is a misidentified Cuban Crocodile). The mandible with the big *C. acutus* skull in Varona (1966) more closely resembles the mandible of a fossil *C. rhombifer* in Morgan et al. (1993) than Cuvier’s (1808) figure. The lacrimal ridges in the dorsal view in Cuvier (1808) resemble many *C. rhombifer* and some *C. acutus*. The same dorsal view of the syntype skull (Cuvier 1808: pl. 1, fig. 1) shows the nasal bones raised above the bony humps accommodating the bases of maxillary teeth 5, and this is a very reliable character for positively identifying *C. rhombifer* >2 m TL. The skull shown in Cuvier (1808) must be a true *C. rhombifer*. Although Cuvier (1807) probably failed to distinguish *C. rhombifer* from *C. niloticus* and *C. siamensis*, no ambiguity exists regarding the validity of the taxon because the *C. rhombifer* illustrations in Cuvier (1808) show an identifiable Cuban Crocodile, and Duméril and Bibron (1836) identified living animals known to have originated in Cuba as being conspecific with the syntypes of *C. rhombifer* Cuvier (1807, 1808).

The use of the word "type" in two checklists (Schwartz and Thomas 1975, Schwartz and Henderson 1991) is as a subject heading. A specimen in the British Museum of Natural History (BMNH) that was described by Gray (1844, 1867) and possibly other material in the MNHN (Paris), collected by Ramón de la Sagra, are available as neotypes. The dentition of the BMNH specimen (collected by de la Sagra and received from the MNHN) should be determined and reported. Data pertinent to the maxillary dentition of the BMNH specimen could disagree with Cuvier's (1808: pl. 1, fig. 2) drawing in missing the extra 14th maxillary tooth (it should have 12–13 maxillary teeth).

Mook (1921b), in reference to the Ciego Montero fossils and also about modern *C. rhombifer*, said that "in studying a collection of Pleistocene crocodiles from Cuba, considerable difficulty in the determination of species was encountered, through the wide range in some characters of the skulls, coupled with close similarities in other characters. It was first thought that many of the differences were of specific value, but closer study has suggested that they are due rather to individual variation or age variation or, more probably, both." Problems still are encountered when some few very large skulls need species level identification. For example, Staton (1978) called Carnegie Museum (CM) 9997 a Cuban Crocodile, but C.A. Ross (pers. comm.) questioned that identification (it may be a very large American Crocodile). Similarly, a very large *Crocodylus* skull from Cuba (MCZ 17728) was originally identified (in Cuba) as *C. rhombifer*, but later redetermined (by me) as *C. acutus* on the basis of the premaxillary-maxillary suture extending posteriorly to the level of the second maxillary teeth and because it lacks the Cuban Crocodile's squamosal horns. However, the alveolus for maxillary tooth 4 is larger than the 5 alveolus, a strong *C. rhombifer* character. Nevertheless, 14 maxillary teeth occur on both sides and the cranial table is flat and rectangular. Another very large "*C. acutus*" skull was illustrated in Varona (1966). Problems like these probably inspired Mook to study individual, geographic, and age variation. One error is that Staton (1978) called MCZ 17728 a skin of *C. rhombifer*, but it is not a skin (it is a skull). The locality data in Staton (1978) also are wrong (it is not from the Isle of Pines; apparently confusion occurred with MCZ 17718).

The living *Crocodylus rhombifer* population is classified as "Endangered" by the Crocodile Specialist Group of the International Union for the Conservation of Nature and Natural Resources, Species Survival Commission (Ross 1998), and wild individuals were thought to number no more than a few thousand by Ramos et al. (1994). A more recent estimate is 3,000–6,000 individuals in 300 km<sup>2</sup> of the southwestern part of the Zapata Swamp (Ross 1998). Documentation of the historical recovery of this population is in Chabreck (1982). The species is currently restricted in distribution to a few hundred square kilometers of habitat in one or two permanent freshwater swamps in the Cuban region. Large captive populations in Cuba and on the Isle of Pines are successfully breeding (Ross 1998), and a coordinated captive breeding effort exists for approximately 100 specimens held in zoos in the USA (Brazaitis 1996) and a few zoos in Europe (International Zoo Yearbooks, Vokins 1972). A studbook records captive breeding in Europe and North America (King and Ross 1990, Ross 1998). Restocking of formerly occupied wild habitat on the Isle of Pines was proposed (Soberon 1995) using captive breeders in the Habana Zoo (Luxmoore 1992) that are probably Zapata Swamp stock. Escaped farm stock of *C. rhombifer* are restocking the Isle of Pines (Soberon et al. 1996). The now wild *Caiman crocodilus* on the Isle of Pines are thought to have been pets, as opposed to farm stock (Luxmoore 1992, David 1994). Management of *Caiman crocodilus* relative to *Crocodylus rhombifer* on the Isle of Pines has been proposed (Soberon et al. 1996). The modern popula-

tion of caimans is probably unrelated to several very early and likely mistaken reports (Gray 1840, Reinhardt and Lütkin 1863) of the species from Cuba (Barbour 1914).

At one point it was estimated that captive hybrids between *C. acutus* and *C. rhombifer* were more numerous than pure *C. rhombifer* in Cuba (Webb and Manolis 1989). Captive hybridization between *C. rhombifer* and *C. niloticus* has been reported (Davis et al. 1996, King and Ross 1992a). Hybridization between *C. rhombifer* and *C. palustris* is also suspected (Davis et al. 1996). The captive production of hybrids with *C. acutus* in Cuba has completely stopped since 1976 (Ramos 1989, Ross 1998) and, as much as possible, all of the hybrids have been removed from the gene pools of the now separated species (Soberon et al. 1996, Ross 1998). The propagation of hybrids between *C. rhombifer* and *C. siamensis* in South East Asia remains an unsolved problem (C.A. Ross, pers. comm.; Honegger and Hunt 1990; King and Ross 1994b; Thang 1994). The *C. rhombifer* x *siamensis* hybrids in Vietnam will be difficult to identify because of many strong morphological similarities (including color, scalation, and squamosal horns) between the Siamese Crocodile and *C. rhombifer*. DNA microsatellite markers like those reported in Davis et al. (1996) may help identify South East Asian hybrids and parental stock. Uncompromised Cuban Crocodile stock may possibly be available in Thailand for comparison (C.A. Ross, pers. comm.; Suvanakorn and Youngprapakorn 1987). The sale of commercial hides from *C. rhombifer* x *siamensis* hybrids could benefit the pure stocks of Cuban Crocodiles in Vietnam (Gorzula 1996), but it will have to be from registered CITES farms, because the hybrids are Appendix 1 animals (King and Ross 1996).

Data from a sample of 69 juvenile stuffed Cuban Crocodiles (all CITES confiscations) in the National Museum of Canada (CMN 35001) were included in the Definition, because they appear to be pure *C. rhombifer*, as opposed to captive hybrids (Schueler, pers. comm.).

The survival of *C. rhombifer* in the Cuban region is greatly to the credit of the Cuban scientific community. Existing wild populations and natural habitat must continue to be protected, and possibly expanded (King and Ross 1992b, Ross 1998). Excluding his many contributions to the Crocodile Specialist Group Newsletter, Luis S. Varona, in the period 1964–1986, authored 41 papers about Cuban animals, eight of which were about crocodilians, including an officially anonymous 1969 article that announced that "more than 3,000 wild Cuban Crocodiles have been rounded up in their native swamps and placed in protected enclosures or 'corrals' in one of the swamps" and that hybridization between Cuban Crocodiles and *C. acutus* at the Cuban government-sponsored farm threatened the *C. rhombifer* stock (Woods 1989). Dr. Varona has been considered the authority on *C. rhombifer* for many years (Powell 1975, Ross 1997).

Cold War politics seriously hampered research on crocodile biology and conservation in Cuba (Ramos 1989). The results of many Cuban studies of *C. rhombifer* were published in periodicals and reports that are very hard to find in North America and Western Europe. Many of the most detailed reports about the Zapata Swamp round-up, the Zapata Swamp farms, and subsequent veterinary research and reproduction studies appeared in Central and Eastern European journals. Publications by authors from communist (or formerly communist) countries not seen but cited in this paper are Benitez et al. (1974), Benitez et al. (1976), Betancourt et al. (1973), Blanco and González (1974), Castellanos (1973b), Gómez and González (1970), González and Cabrera (1973), Granado (1983), Granado and Berovides (1975), Lanka (no date), Perez et al. (1976), Perez-Vigueras (1956), Ramos (1970), and Varona (1981). Two Mexican spelling errors in the synonymy at the head of this account, attrib-

uted to Velasco (1893, 1895), were quoted from Smith and Smith (1973, 1976).

Text accompanying the photo by Jessie Cohen in the now hard-to-find American Association of Zoological Parks and Aquariums (AAZPA) Newsletter (1984) indicated that on 2 and 3 August, seven Cuban Crocodiles (*Crocodylus rhombifer*) hatched at the National Zoological Park (NZP), Washington, D.C., after an incubation period of 78 days. The female laid 29 eggs on 16 May and 25 were artificially incubated, seven proving to be fertile. The hatchlings averaged 27.4 cm and 67.3 g at birth. Both parents were wild-caught. The female had been on loan from the Wilhelma Zoo, Stuttgart, Germany since 1981 and the male had been at NZP since 1975.

For quotations of several complete items from 1971–1990 issues of the IUCN-SSC Crocodile Specialist Group Newsletter and data summaries of others, see Ross (1997). Many of the older Newsletter issues are very rare in libraries.

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