

region (Paratypes of *C. l. loweryi*, formerly LSUMZ 484, 476, 474, and 486); KU 24067, Xilitla region (formerly LSUMZ 613); LSUMZ 472-73, 475, 477-79, 481-82, 485, 485a, 487, Xilitla region (Paratypes of *C. l. loweryi*); LSUMZ 480, Xilitla region (Holotype of *C. l. loweryi*); LSUMZ 488, Ciudad del Maiz; LSUMZ 614, Xilitla region; LSUMZ 4953-54, 4956-57, 6 mi W Ahuacatlán, 5400 ft.; LSUMZ 4958, Birmania, 3 mi S of Valles, 300 ft.; TCWC 29617, 5 mi E El Lobo, 4500 ft.; TCWC 35604, 33.8 mi W Valles, 2500 ft.; UIMNH 51208, Tamazunchale.

Group 8 (*G. ophitrus*): VERACRUZ: BMNH 56.4.17.6, Cordova; NMW 25005, Orizaba; SAM 878, 1.5 mi N Zapotillo; USNM 12245, Mirador; USNM 30206, Orizaba (Holotype of *G. ophitrus*); USNM 118219, Cerro Gordo; USNM 224806, Cuautlan; ZMH R05936, Jalapa.

Group 9 (*G. locephalus*): PUEBLA: UIMNH 19520, Km. 226, Tehuacan; USNM 113216, Cacaloapan; UTA 4715, 1 mi N Cacaloapan, 7400 ft. VERACRUZ: MVZ 76326, 2 mi S Acultzingo.

Group 10 (*G. locephalus*): VERACRUZ: UTA 3360, ca. 2 mi NE Catemaco, north side Lago Catemaco.

Group 11 (*G. locephalus*): GUERRERO: BMNH 19137.19.103, Amula; SCZ 3749, Chilpancingo; MCZ SW Chilpancingo; MCZ 33749, Chilpancingo; MCZ 45006-07, near Chilpancingo; TCWC 8585, 9896, Acahuiztla, 2800 ft.

Group 12 (*G. locephalus*): OAXACA: AMNH 93210, 2 mi E Ixtlan de Juárez, 7000 ft.; AMNH 93211, El Tejocote (ca. 30 mi NW Oaxaca de Juárez), 7600 ft.; AMNH 93212, 2 mi E Ixtlan de Juárez, 7200 ft.; AMNH 100723-27, Tejocotes, 7200 ft.; AMNH 100728, 1.5 mi E Ixtlan de Juárez (Vivero Rancho Tejocote), 7300 ft.; AMNH 102726-30, Disto. de Etla, Tejocotes, 7400-7700 ft.; AMNH 102731, near Tejocotes, Rio Negro, ca. 7000 ft.; AMNH 102732, Tejocotes, Rio Negro, ca. 7000 ft.; AMNH 102733, Disto. de Etla, Tejocotes, 7900 ft.; AMNH 102734, Tejocotes, AMNH 106722-25; Tejocotes, 7500 ft.; AMNH 106726-29, ridge W Tejocotes, 8100 ft.; AMNH 106730-31, Tejocotes, 7200-8000 ft.; AMNH 106733, Tejocotes, 7400 ft.; AMNH 106734-AMNH 106739, Tejocotes, 8000 ft.; AMNH 39, 9 mi N San Juan del Estudiante, 7200 ft.; AMNH 106740-41, 2 mi NE El Estudiante, 7400 ft.; 106742-47, 1.5 mi E Ixtlan de Juárez, 7300 ft.; AMNH 110618-19, 1.5 mi E Ixtlan de Juárez, 7300 ft.; AMNH 110620, Distrito de Ixtlan, 1.4 mi E Ixtlan de Juárez, 7300 ft.; MSB 41654-55, Distrito de Etla, Tejocotes, 7600-7900 ft.; USNM 46748, Valley of Oaxaca, 9000 ft.; UIMNH 63666, 63667-68, 73588-89, Cerro San Felipe; UTA 4232, 5644, 6064-69, 6104-05, 7626, 9858, 10276 (7400 ft.), 12221-26, 13606-10, 19681-84, 22560-73, 27035-38, El Tejocote.

Group 13 (*G. locephalus*): OAXACA: AMNH 68125, Cerro Arenal, near Tenango; AMNH 102735-36,

Juquila, Mixes; MNHN 6135, Tehuantepec; MSB 22753, Distrito de Yauatepec, 9 mi SW San Carlos Yauatepec, 6500 ft.; UCM 44530, Tehuantepec, Lachiguiri, Cerro de Lachiguiri, 7000 ft.; UIMNH 8633, 10 mi SW Miahuatlán; UIMNH 8634, Tenango, near Tehuantepec; UIMNH 19521, Llano Ocotil; UIMNH 35527, Santo Domingo Chontecocatl; UIMNH 46739-34, Cerro Jocal, San Bartolome; UIMNH 46739, Cerro Jocal, San Bartolome, Yauatepec, 5000 ft.; UIMNH 73590, Rio Sal, Lachao, Juquila; UIMNH 73594, Tres Cruces, Tehuantepec; USNM 113217, Tres Cruces; USNM 113218, La Concepcion.

Group 14 (*G. locephalus*): OAXACA: AMNH 66891, El Palmar, Cerro Atravesado; UCM 41063, Sierra Madre, NW Zanatepec; UIMNH 40928, between Cerro Atravesado and Cerro Azul; UIMNH 56865, Sierra Madre, N Zanatepec; UTA 8784, Cerro Baul, ca. 19 km NW Rizo de Oro, Chiapas.

Group 15 (*G. locephalus*): CHIAPAS: AMNH 71596, El Otatal, Tuxtla Gutierrez; UIMNH 52087, Cerro de Sumidero, Tuxtla Gutierrez, 1200 m.

Group 16 (*G. locephalus*): CHIAPAS: UMMZ 94921; Cerro Malé, 3200 m (Holotype of *G. l. austrinus*).

Group 17 (*G. infernalis*): CHIHAUAHA: AMNH 67918, Clarines Mine, ca. 5 mi W Santa Barbara, 6800 ft. (Holotype of *G. locephalus taylori*); AMNH 68295, Santa Barbara, 6300 ft. (Paratype of *G. l. taylori*).

Group 18 (*G. infernalis*): DURANGO: ANSP 20129, Sierra Guadalupe, La Cuchilla Station, 7500 ft.; TCWC 35499, 74.4 mi SW Torreón, Hwy. 31.

Group 19 (*G. cf. locephalus*): DURANGO: UTEP 4562, 2 mi N Pueblo Nuevo, Municipio El Salto, 6000 ft.; UTEP 4563, 6 mi SE Llano Grande, Municipio Durango, 6800 ft. SINALOA: KU 78904, 19.2 km NE Santa Lucia, 1940 m.

Group 20 (*G. cf. locephalus*): COLIMA: MVZ 197549; vicinity of Colima. JALISCO: CM 65825, 40 mi NW Hwy. 80 on Hwy. 200; MVZ 205566, 53 km NW (by Mexico Hwy. 200) of jct. Mexico Hwy. 80.

Other specimens examined: *Gerrhonotus infernalis*: US 39587, El Rio Alamos en Cañon Mulato, Las Margaritas, 3500 ft.; MNHN 5140, 1888.277, Guanajuato; UOMZ 30391, Texas; USNM 3090, Devil's River, Texas (Holotype of *G. infernalis*); USNM 47136, Sierra Encarnacion; ZMB 1154, Texas. *Gerrhonotus locephalus*: AMNH 106732, near summit Cerro Guirone, Disto. Tlacolula, 8100 ft.; ANSP 9026-27, mining districts of Mexico (Syntypes of *Scincus ventralis*); ZMB 1153 (Holotype of *G. locephalus*); MVZ 10323, Oaxaca. *Gerrhonotus lugoi*: ASU 8818, "rastro municipal," 2.7 km SW Cuatro Ciénegas de Carranza, Coahuila, 740 m (Paratype of *G. lugoi*); TCWC 55258, 4.2 mi W Ocampo, Coahuila. *Gerrhonotus ophitrus*: MNHN 1151; locality unknown (Syntype of *G. lemniscatus*).

CRANIAL MORPHOMETRY OF NEW GUINEA CROCODILES (*CROCODYLUS NOVAEGUINEAE*): ONTOGENETIC VARIATION IN RELATIVE GROWTH OF THE SKULL AND AN ASSESSMENT OF ITS UTILITY AS A PREDICTOR OF THE SEX AND SIZE OF INDIVIDUALS

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ABSTRACT: The cranial morphometry of New Guinea crocodiles (*Crocodylus novaeguineae*) was investigated to quantify ontogenetic variation in relative growth of the skull to provide possible demographic insights into commercially harvested populations. Growth attributes were, in general, linear, and univariate statistics provided estimates of size from untransformed values. Curvilinear size (total length) to age transformations were attempted through applications of three growth models: a reparameterized Richards curve, the von Bertalanffy model, and a Brody curve. Satisfactory performance was attained only through the Brody model, with reliable age estimates restricted to smaller (≤ 2 m) individuals. The utility of relative growth ratios to correctly predict the sex of known gender animals was assessed by both parametric (multivariate discriminant analysis—DISCRIM) and nonparametric (binary tree classification analysis—CART) methods. Crossvalidation data sets were created to reduce model biases and to evaluate the correctness of classification rates. CART models consistently showed greater congruence of apparent error rates with true error rates than did DISCRIM models, while the "best fit" models of each method closely paralleled one another in providing conservative overall ability to correctly discriminate gender from measured attributes. Skull growth occurs in three distinctive stages that mimic a saltatory ontogenetic response and are hypothesized to be related to functional foraging responses.

Key words: Cranial morphometry; Crocodiles; Growth; New Guinea

PAPUA New Guinea (PNG; Fig. 1) harbors two species of sympatrically distributed crocodylians: the New Guinea crocodile (*Crocodylus novaeguineae*) endemic to the main island of New Guinea, and the wide-ranging saltwater crocodile (*C. porosus*). Both species are commodities of great economic value as hides and meat, and much effort has been made to improve the biological and economic return of these natural resources (Bolton, 1980, 1981). Trade in live crocodylians or their byproducts is regulated by the Convention on International Trade of Endangered Species of Fauna and Flora (CITES) (King, 1973) because all 23 species of the order Crocodylia (alligators, caimans, crocodiles, gharial, and tomistoma) are classified as endangered or threatened with extinction (Groombridge, 1982; Honegger, 1979). The

more abundant species in PNG is *C. novaeguineae* and it comprises 75-80% of the annual export (>98% of study area exports) of crocodile hides (Anon., 1981; Hall, 1990a,b; Whitaker, 1980; Whitaker and Kemp, 1981). Due to the comparative abundance of this species and the limited availability of *C. porosus* material, *C. novaeguineae* was chosen for this study.

Harvest data of PNG crocodiles provide an indirect measure of size (commercial belly width; see METHODS), but no information on the sex or age of individuals. Gathering data from freshly killed specimens is not feasible due to rapid deterioration of hides and logistic constraints (e.g., remote areas, manpower, and economics). These facts provide a rationale for long-term studies to generate adequate data on wild caught individuals to monitor growth rates and population sex ratios. The costs of such long-term studies have been prohibitive to all but a few external research

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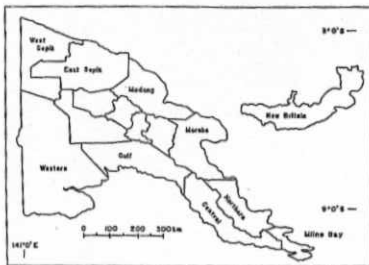


FIG. 1.—Map of Papua New Guinea indicating provinces of crocodile harvest, excluding Manus (2°0'S, 147°0'E), New Ireland (3°0'S, 151°30'E) and the North Solomons (6°0'S, 155°0'E). Right border of map is 153°E.

agencies. In addition, crocodilians are extremely wary animals that develop rapid learning avoidance to capture (Bustard, 1968).

Consequently, we sought to develop a cost-effective, alternative method to address these problems through morphometric sampling of discarded crocodilian skulls from hunter harvests as a practical management tool to aid in monitoring resource use. The objectives of this study were to: (1) examine and quantify ontogenetic patterns in relative growth of the skull in a crocodilian, *Crocodylus novaeguineae*; and (2) assess the utility of the functional patterns of relative growth as a predictor of gender. Such knowledge could permit determination of population structural parameters of future harvests. Thus, demographic trends may be monitored and the potential to manage the resource may be enhanced.

Background

Growth in the Order Crocodylia is generally thought to be indeterminate (Cott, 1961; Jacobsen and Kushlan, 1989), although Brisbin (1990) argues otherwise. Crocodilians exhibit typical size dimorphism, in which males become longer and heavier than females (Neill, 1971). However, this discrepancy may not be apparent where regulated crocodilian harvests occur if the upper size limit is below the point where the divergence between sexes is pro-

nounced (such as in New Guinea where it is about 2.7 m total length for *C. novaeguineae*). Other than size, sexual dimorphism in crocodilians is evident only in socially mature, adult male gharials (*Gavialis gangeticus*) that exhibit a secondary bulbous snout protuberance (Basu, 1980). However, the reliability of this character remains uncertain as a necropsied adult possessing such a feature was found to be female (Martin and Bellairs, 1977). Thus, to date, manual probing of the cloaca (Chabreck, 1963) or vivisection (Magnusson and Hero, 1990) are the only certain means of determining gender in a living individual, except where size dimorphism is apparent.

As a group, crocodilians are long lived (40+ years) vertebrates and dimorphic attributes of growth appear to be expressed in early life by age five (Chabreck and Joanen, 1979; Webb et al., 1978). The disparity of such growth is influenced strongly by incubation temperatures during embryogenesis (Ferguson and Joanen, 1983; Webb and Smith, 1984). Functional changes in the rates and directions of growth for areas of the crocodilian skull are also known to differ according to the age and size of individuals (Dodson, 1975).

We hypothesized that the skulls of New Guinea crocodiles (beyond the early age classes) should also exhibit a dimorphic suite of characters corresponding to the ontogenetic changes in growth of body size with respect to sex. Due to slower female growth rate, the skull of a female crocodile compared to that of an equal length male skull of age X will belong to an animal of age X + t. Thus, the shifts in ontogenetic patterns of relative growth of the skull of comparably sized individuals should be more pronounced in females than males of equivalent size, and become even more disparate as size or age increases. The gender of equal-sized individual skulls is indiscernible with specimens in hand (Fig. 2), but may become apparent when patterns of growth are viewed and analyzed in a multidimensional framework.

The quantitative study of growth in crocodilians is fairly new. Early descriptive investigations on aspects of embryonic

growth include those by Clarke (1891), Deraniyagala (1939), McIlhenny (1934, 1935), Parker (1883), Reese (1908), and Voeltzkow (1902). More recent studies include Bolton (1981), Deeming and Ferguson (1990), Ferguson (1985), Hall (1985b), Magnusson and Taylor (1980), Vásquez Ruesta (1982–1983), and Webb et al. (1983). Growth of posthatching animals has been investigated by several authors. Kramer and Medem (1955) reviewed proportional gross morphology of extant crocodilians as did Wermuth (1964). Other reports on aspects of gross morphological growth focused on a few individual species. These include: *Alligator mississippiensis* (Brisbin, 1990; Chabreck and Joanen, 1979; Dodson, 1975; Jacobsen and Kushlan, 1989; McIlhenny, 1934; Nichols et al., 1976), *Caiman crocodilus* (Ayarzagüena, 1984; Gorzula, 1978; Ouboter and Nanho, 1989; Staton and Dixon, 1975; Thorbjarnarson, 1990), *Crocodylus niloticus* (Cott, 1961; Graham, 1968, 1976; Hutton, 1987a,b), *C. novaeguineae* (Jelden, 1984; Lawson, personal communication; Montague, 1982), *C. porosus* (Banks, 1930; Webb, 1977; Webb and Messel, 1978; Webb et al., 1978), *Crocodylus siamensis* (Müller, 1923, 1927), and *Palaosuchus trigonatus* (Magnusson and Lima, 1991). The works of Greer (1974), Iordansky (1973), Kälin (1933), Langston (1973), Mook (1921a, b), and Parker (1882) were confined to cranial growth in crocodilians. However, the quantitative relationships between size, sex, and age of most crocodilian species remain unknown.

General ontogenetic trends of crocodilian cranial growth have been reported by Brongersma (1941), Iordansky (1973), Kälin (1936, 1955) and Mook (1921b). However, these authors made no quantitative assessment of growth with size, sex, or age. Dodson (1975) later presented allometric coefficients for 27 attributes of cranial growth for *A. mississippiensis*, irrespective of sex or age. Subsequently, Webb and Messel (1978) reported the interorbital width to be a sexually dimorphic character in Australian *C. porosus*. However, the predictive values of their discriminant models to correctly identify gender were

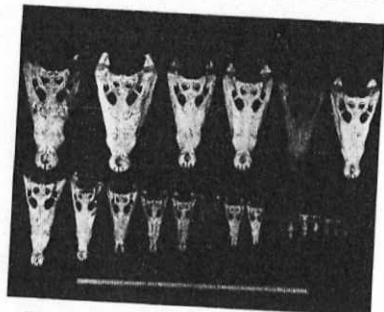


FIG. 2.—Ontogenetic series of *Crocodylus novaeguineae* skulls. Specimens are Louisiana State University Museum of Zoology (LSUMZ) series unless indicated otherwise. Top row (1-r): LSUMZ 44741, 44742, 44740, 44739, 44736, 44738. Bottom row (1-r): LSUMZ 44735, 44734, PMH0152 (senior author's collection), LSUMZ 44733, 44732, 44731, 44730, 44729, 44728, 44727, 44726, 44725, 44724, 44723, 44722, 44721.

low (<60%) except for larger animals; an evident reflection of size dimorphism. Similarly, Montague (1984) reported sexual dimorphism in the midpoint width of the cranial roof in *C. novaeguineae*, but concluded that this trait was an unreliable indicator of sex.

STUDY AREA AND METHODS

Morphometry

Measurements of 425 *C. novaeguineae* (342 skulls and 83 live specimens), taken by a single observer to minimize bias, were recorded during 1980–1982. These include 162 males and 83 females plus 180 individuals of unknown gender. All animals were referable to the southern form of this species (Hall, 1989). Most specimens were collected in Lake Murray District, Western Province, PNG (Fig. 3), while some ($n = 18$) came from Central Province (Brown River, Waigani Swamp), PNG. Lake Murray District is primarily tropical moist forest with pronounced wet (November–May) and dry (June–October) seasons. Annual mean precipitation is 306 cm and 325 cm in Baboa and Pangoa, respectively, in the Lake Murray subdistrict and 258 cm at Bosset in the Middle Fly

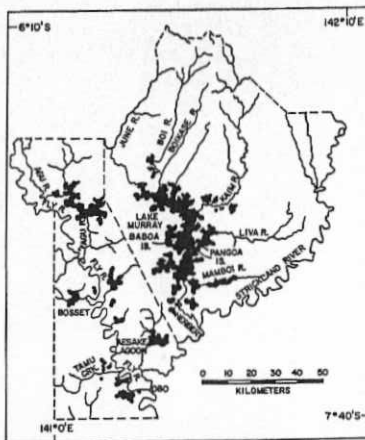


FIG. 3.—Map of Lake Murray District, Western Province, Papua New Guinea indicating the Middle Fly (left) and Lake Murray (right) subdistricts.

subdistrict (Hall, 1990b). Detailed descriptions of the study area have been presented elsewhere (Hall, 1983; Hall and Johnson, 1987).

We obtained data from skulls provided by hunters and from culled short-term captive stock caught from the wild. These sources were pooled for analyses because captive skull growth was indistinguishable from that of wild conspecifics, except for two long-term captive individuals with distinctive anomalies (Hall, 1985a) which were excluded from the analysis. Additionally, two skulls from Western Province (BMNH 86-5-20-1 and 86-5-20-2) were examined at the British Museum (Natural History), London. All skulls were dried at ambient air temperature for at least 30 days prior to inspection. Pre- and post-drying measurements were made on culled captive animals to estimate shrinkage of certain characters. Thus, correction factors can be applied to data that were also obtained from live individuals or from preserved, but uncleaned skulls.

The morphometric measurements taken (Fig. 4), their abbreviations, descriptions,

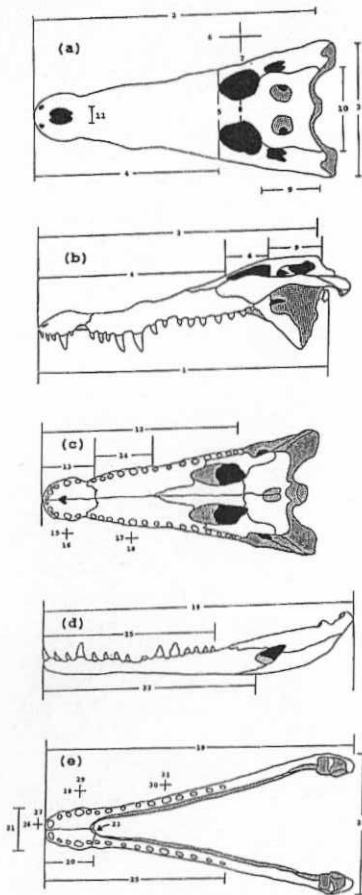


FIG. 4.—Views of *Crocodylus novaeguineae* skull showing measurements taken. (a) Dorsal cranium: 2 = DCL, 3 = CW, 4 = SL, 5 = SW, 6 = OL, 7 = OW, 8 = IOW, 9 = LCR, 10 = WCR, 11 = WN. (b) Lateral cranium: 1 = CL, 2 = DCL, 4 = SL, 6 = OL, 9 = LCR. (c) Palatal cranium: 12 = UM, 13 = PXS, 14 = MXS, 15 = PM4L, 16 = PM4W, 17 = M5L, 18 = M5W. (d) Lateral mandible: 19 = ML, 22 = DL, 25 = LM. (e) Dorsal mandibles: 19 = ML, 20 = LMS, 21 = WMS, 23 = DW, 24 = WSR, 25 = LM, 26 D1L, 27 = D1W, 28 = D4L, 29 = D4W, 30 = D11L, 31 = D11W. See METHODS for explanation.

TABLE 1.—Morphometric and miscellaneous variables recorded on *Crocodylus novaeguineae* indicating their abbreviations, explanation, and the nearest whole unit of measurement. For bilateral categories, growth was assessed unilaterally from the right side, except where damaged. Numbers refer to Fig. 4.

- (1) CL (cranial length, mm). Anterior tip of snout to posterior surface of occipital condyle.
- (2) DCL (dorsal cranial length, mm). Anterior tip of snout to posterior tip of supraoccipital (medial posterior margin of cranial roof).
- (3) CW (cranial width, mm). Distance between the lateral surfaces of the mandibular condyles of the quadrates.
- (4) SL (snout length, mm). Anterior tip of snout to anterior orbital border, measured diagonally.
- (5) SW (basal snout width, mm). Width across anterior orbital borders.
- (6) OL (maximal orbital length, mm).
- (7) OW (maximal orbital width, mm).
- (8) IOW (minimal interorbital width, mm).
- (9) LCR (length of the postorbital cranial roof, mm). Distance from the posterior orbital border to the posterolateral margin of the squamosal.
- (10) WCR (posterior width of the cranial roof, mm). Distance between the posterolateral corners of the squamosals.
- (11) WN (maximal width of external nares, mm).
- (12) PXS (length of palatal premaxillary symphysis, 0.05 mm).
- (13) MXS (length of palatal maxillary symphysis, 0.05 mm).
- (14) UM (length of upper ramus, mm). Anterior tip of snout to posterior margin of distal-most maxillary alveolus.
- (15) PM4L (maximal length of fourth [largest] premaxillary alveolus, 0.05 mm).
- (16) PM4W (maximal width of fourth premaxillary alveolus, 0.05 mm).
- (17) M5L (maximal length of fifth [largest] maxillary alveolus, 0.05 mm).
- (18) M5W (maximal width of fifth maxillary alveolus, 0.05 mm).
- (19) ML (mandible length, mm). Anterior tip of dentary to the posterior tip of the retroarticular process.
- (20) LMS (length of the mandibular symphysis, 1 mm).
- (21) WMS (maximal width across the mandibular symphysis, 1 mm).
- (22) DL (dentary length, mm). Anterior tip of dentary to the anterior external mandibular fenestra.
- (23) DW (dentary width, mm). Lateral interalveolar width of dentary at the posterior margin of the mandibular symphysis.
- (24) WSR (surangular width, mm). Posterolateral width across surangulars at point of jaw articulation.
- (25) LM (length of lower ramus, mm). Anterior tip of dentary to posterior margin of distal most dentary alveolus.

TABLE 1.—Continued.

- (26) D1L (maximal length of first [third largest] dentary alveolus, 0.05 mm).
 - (27) D1W (maximal width of first dentary alveolus, 0.05 mm).
 - (28) D4L (maximal length of fourth [second largest] dentary alveolus, 0.05 mm).
 - (29) D4W (maximal width of fourth dentary alveolus, 0.05 mm).
 - (30) D11L (maximal length of eleventh [largest] dentary alveolus, 0.05 mm).
 - (31) D11W (maximal width of eleventh dentary alveolus, 0.05 mm).
- Other measurements and data recorded, where known, were:
- (32) SVL (snout-vent length, cm). Anterior tip of snout to anterior cloaca.
 - (33) TTL (total length, cm). Anterior tip of snout to posterior tip of tail.
 - (34) BW (commercial belly width, cm). The width across the ventral belly and lateral flank scales between the distal margins of the third transverse row of dorsal scales.
 - (35) BM (body mass, 0.1 kg).
 - (36) Sex.

and the nearest whole unit of value employed are listed in Table 1. Measurements up to 150 mm were taken with 0.05 mm dial calipers. A steel tape was used for larger dimensions. Body mass was weighed on a Salter clock scale. Manual probing of the cloaca (Chabreck, 1963) was used to determine sex.

Ratio indices were used for skull characters to reflect relative growth. The indices used and their methods of calculation are indicated in Table 2. Cranial indices used in this study were modified from Iordansky (1973) by substituting dorsal cranial length (DCL) for cranial length (CL) as an index divisor. The latter measurement includes the occipital condyle which is often broken during collection. Also, DCL is preferable since it can be recorded from living individuals, whereas CL cannot. Mandibular indices were of our own design.

Analyses

Linear regression analysis was used to derive equations for the estimation of DCL from body size measurements or other skull attributes used as independent variables.

TABLE 2.—Relative growth indices used for skull variables of *Crocodylus novaeguineae* indicating abbreviations and methods of calculation.

- (1) RCW (relative cranial width) = cranial width/dorsal cranial length [CW/DCL].
 - (2) RLST (relative length of snout) = snout length/dorsal cranial length [SL/DCL].
 - (3) RWST (relative width of snout) = basal width of snout/snout length [SW/SL].
 - (4) ROL (relative orbital length) = maximal orbital length/dorsal cranial length [OL/DCL].
 - (5) ROW (relative orbital width) = maximal orbital width/maximal orbital length [OW/OL].
 - (6) RWI (relative interorbital width) = minimal interorbital width/maximal orbital length [IOW/OL].
 - (7) RLR (relative length of postorbital cranial roof) = length of postorbital cranial roof/posterior width of cranial roof [LCR/WCR].
 - (8) RWN (relative width of external nares) = maximal width of external nares/dorsal cranial length minus snout length [OL/(DCL - SL)].
 - (9) RPXS (relative length of premaxillary symphysis) = length of premaxillary symphysis/dorsal cranial length [PXS/DCL].
 - (10) RMXS (relative length of maxillary symphysis) = length of maxillary symphysis/dorsal cranial length [MXS/DCL].
 - (11) RLUMR (relative length of upper ramus) = upper ramus length/dorsal cranial length [UM/DCL].
 - (12) RLMS (relative length of mandibular symphysis) = maximal length of mandibular symphysis/mandible length [LMS/ML].
 - (13) RWMS (relative width of mandibular symphysis) = maximal width across mandibular symphysis/maximal length of mandibular symphysis [WMS/LMS].
 - (14) RLD (relative length of dentary) = dentary length/mandible length [DL/ML].
 - (15) RWD (relative width of dentary) = dentary width/dentary length [DW/DL].
 - (16) RWM (relative width of mandible) = maximal width across surangulars at jaw articulation/mandible length [WSR/ML].
 - (17) RLLMR (relative length of lower ramus) = lower ramus length/mandible length [LM/ML].
- For each of the five alveoli measured (PM4, M5, D1, D4, D11) the following ratios were used:
- (18) RL (relative length of alveolus) = maximal alveolus length/dorsal cranial length (for upper alveoli [PM4/DCL; M5/DCL]) or mandible length (for lower alveoli [D1/ML; D4/ML; D11/ML]).
 - (19) RW (relative width of alveolus) = maximal alveolus width/maximal alveolus length (e.g., M5W/M5L).

Slopes and intercepts of regression formulae were compared using *F*-tests to evaluate gender specificity. Coefficients were also calculated for the prediction of body size attributes from DCL by the same method.

We used mark-recapture data from several unpublished studies to derive growth estimates for male *C. novaeguineae* to age nine and females to age 13 (see Hall, 1990b). These values were used to construct growth curves that were fitted to three growth models: a reparameterized Richards curve (Brisbin, 1990; Brisbin et al., 1986), the von Bertalanffy model (Falls, 1965), and a Brody curve (Gates and Dahm, 1989). This latter curve takes the form: $W_t = A[1 - B \exp(-Ct)]$, where W_t represents known body mass or length at time t , A is the final asymptotic length or mass, and B and C are constants. In this study, the maximum confirmed W_t was 335 cm TTL for males and 265 cm for females, while $W_{t=0}$ was 28 cm for both sexes (Hall, 1985b). Due to the superior fit with the Brody curve (see below), growth rates were estimated under three scenarios by that model. In our first pair of Brody growth models, we allowed the asymptote term A to vary freely and seek its own level. Next, growth data were fitted by setting the final asymptote equal to known maximum values of W_t to develop a second set of models. Finally, a third pair of models was constructed with the Brody curve by setting the final asymptote size parameters equal to estimated maximum asymptotic values (see below) of 360 cm TTL (males) and 285 cm (females), respectively.

Gender analysis of relative growth ratios for *C. novaeguineae* was tested by two methodologies to assess the comparative robustness of each approach and its utility for properly classifying observations. A traditional parametric multivariate method, discriminant analysis (DISCRIM; SAS, 1988), was used first followed by a non-parametric binary classification tree analysis program (CART [California Statistical Software, Inc.]; Breiman et al., 1984). The CART methodology offers several impor-

tant advantages over discriminant analysis in that it treats observations with missing values and that it states the decision rules by which classification trees are made.

Both DISCRIM and CART evaluate classification criteria by their performance in the classification of future observations. Initial error count estimates for each method were derived by summing the number of misclassified sex observations from the test data sets and dividing by the total number of observations. The resulting error rates are optimistically biased and referred to as 'apparent' error rates (AER). To evaluate the correctness of these classification rates, crossvalidation data sets were created and then analyzed for each method to reduce model biases and associated variances and to establish 'true' error rates (TER). Cross-validation is a form of jackknifing that treats $n - 1$ out of n training observations (the initial data base) as a learning set; it derives discriminant functions based on these $n - 1$ observations and applies them to classify the one observation left out. Iterations are then performed successively for each of the remaining n training observations and a misclassification rate is calculated as above.

We further analyzed DISCRIM predictor models by using stepwise discriminant analysis (STEPDISC; SAS, 1988). This procedure selects a subset of variables from the original data set to provide a 'best fit' model for discrimination. Similarly, we then used the character variables selected by CART in the initial analysis above to create a new series of comparative 'best fit' models for gender classification.

RESULTS

General Morphology

Linear regression coefficients of body size and skull attributes used as independent variables to predict dorsal cranial length (DCL) are listed in Appendix I (Equations 1-125). Most variables showed a slight allometry with increasing dorsal cranial length. Allometry was most pronounced with respect to body mass (BM) for which logarithmic transformation

(\log_{10}) was made (Eqn. 12-14). Several cranial (snout length [SL; Eqn. 23-25], cranial length [CL; Eqn. 15-18], upper ramus length [UM; Eqn. 59-62]) and mandibular (mandible length [ML; Eqn. 79-82], dentary length [DL; Eqn. 90-92], lower ramus length [LM; Eqn. 100-102]) measurements exhibited near perfect ($r^2 > 0.99$) isometry as predictors of DCL. Correlations of body size and skull measurements with DCL were uniformly high, often extremely so. The fit of regression coefficients (r^2 values) was consistently better for males than females. Variability was most pronounced with respect to interorbital width (IOW; Eqn. 37-39) and dental alveoli (Eqn. 67-78, 103-125).

Predicting Body Size From DCL

The use of DCL as an independent variable to predict body size measurements (second equation) may be accomplished by the regression coefficients in Appendix II (Eqn. 126-139). The observed shrinkage between skull DCL of freshly killed *C. novaeguineae* and the DCL of their cleaned, dried skulls was approximately 4%, which conforms with earlier reports (Montague, 1984). Thus, a correction factor of 1.04 DCL should be used for dried skulls prior to estimating body sizes.

If DCL is an estimated value (first equation) derived from one of the preceding isometric predictors (SL, CL, UM, ML, DL, LM), the standard error of the final body size estimate (E_s) is calculated as follows: $\sqrt{[b_2 E_1]^2 + E_2^2}$, where b_2 is the slope of the second equation, and E_1 and E_2 are the error estimates from the first and second equations, respectively (Webb and Messel, 1978).

The largest live male and female in this study measured 313 and 265 cm total length (TTL), respectively; while the largest male skull measured 455 mm DCL (473 mm pre-shrinkage estimate) which would equate to a TTL estimate of 360 cm. The maximum verified sizes (TTL) of southern form *C. novaeguineae* are 335 cm for males (Montague, 1984) and 265 cm for females (above). The form of this species that occurs in northern New Guinea attains larger

TABLE 3.—Body size and skull attributes (see Table 1) exhibiting sexual dimorphism when used as predictors of dorsal cranial length (DCL) for *Crocodylus novaeguineae*. Comparisons are of estimated sizes (mm)^a for animals the size of the largest female in the study (DCL = 355 mm). Significance levels are inclusive of all individuals in the regression models (see Appendix 1).

Attribute	Predicted size		Percent difference	Significance level
	Female	Male		
SVL	137.1	139.3	+1.6	$P < 0.005$
TTL	261.1	270.4	+3.6	$P < 0.0005$
CL	371.9	376.8	+1.3	$P < 0.05$
CW	171.3	190.2	+11.0	$P < 0.0001$
SW	124.2	135.1	+8.8	$P < 0.0001$
OW	38.0	38.6	+1.6	$P < 0.05$
IOW	31.8	33.4	+5.0	$P < 0.005$
WCR	111.0	114.7	+3.3	$P < 0.005$
WN	25.1	25.8	+2.7	$P < 0.05$
PXS	84.8	80.0	-5.7	$P < 0.05$
UM	269.5	265.5	-1.5	$P < 0.05$
PM4L	11.43	13.58	+20.1	$P < 0.05$
PM4W	10.50	12.61	+20.1	$P < 0.0005$
M5L	14.14	16.12	+14.0	$P < 0.005$
M5W	12.14	15.25	+25.6	$P < 0.005$
ML	425.7	443.1	+4.1	$P < 0.0001$
WMS	54.7	66.1	+20.8	$P < 0.0001$
WSR	194.9	208.4	+6.9	$P < 0.0001$
D1L	11.92	13.15	+10.3	$P < 0.005$
D1W	11.56	12.56	+8.7	$P < 0.05$
D4L	12.42	13.61	+9.6	$P < 0.05$
D11L	11.97	14.52	+21.8	$P < 0.05$
D11W	10.09	12.95	+28.3	$P < 0.01$

^a SVL and TTL in cm.

known TTLs: males = 347 cm; females = 305 cm (Hall, 1990b).

Sexual Dimorphism

Sexual dimorphism was observed in snout-vent length (SVL), TTL, and in 21 of 32 skull attributes (Table 3). These differences varied from slight to pronounced at the size of the largest female in this study (352 mm DCL). Male *C. novaeguineae*

with a comparable-sized DCL possess a longer SVL, TTL, cranial length (CL), and mandible length (ML), but have a shorter premaxillary symphysis length (PXS) and upper ramus length (UM) than females. Males also exhibit greater widths with respect to their cranium (CW), snout (SW), orbit (OW), interorbit distance (IOW), cranial roof (WCR), external nares (WN), mandibular symphysis (WMS), and distance across the surangulars (WSR). However, the most obvious evidence of dimorphism was found in the dentition with the alveoli PM4, M5, D1, D4, and D11 being conspicuously more robust in males. The alveoli PM4, M5, D1, and D4 are pseudo-canines in the genus *Crocodylus*. Their dimorphic character in this species suggests a possible relation to the social ordering of adult males that compete for territories and access to breeding females.

Changes in the directional rates of skull growth indicative of sexual dimorphism commence in *C. novaeguineae* at about 100 cm TTL. Females begin to exhibit proportionally longer skulls than males of equivalent TTL; however, differences in the proportional widths of skulls (males being more robust) are not manifest until a TTL of about 180 cm is attained (Table 4).

Size and Age Relations

Growth estimates for male *C. novaeguineae* to age nine and females to age 13 (Hall, 1990b) were evaluated to derive growth models for predicting size-age relations as indicated in Table 5. The von Bertalanffy model gave a poor fit to our data and grossly underestimated (partic-

TABLE 4.—An example of sexual dimorphism in the directional rate of change of growth in the skull of *Crocodylus novaeguineae*. Dimorphism initiates at about 100 cm total length and comparisons are shown through the length of the largest female in this study.

Total length (cm)	(a)		(b)		Ratio a/b	
	Dorsal cranial length (mm)		Snout width (mm)		Males	Females
	Males	Females	Males	Females		
100	138.97	140.94	38.25	40.79	0.2752	0.2894
150	201.47	206.44	66.66	66.68	0.3309	0.3230
200	263.97	271.94	95.07	92.57	0.3602	0.3404
250	326.47	337.44	123.48	118.45	0.3782	0.3510
265	345.22	357.09	132.00	126.22	0.3824	0.3535

TABLE 5.—Results of growth curve models constructed for *Crocodylus novaeguineae*. In Brody model (1), the final asymptote sizes were allowed to vary freely and seek their own solution. In Brody models (2) and (3), the final asymptotic sizes were specified as indicated and the data were fitted to converge to those points.

Source	Model				
	Brody (1)	Brody (2)	Brody (3)	Richards	von Bertalanffy
Males					
Asymptote TTL (cm)	314	335 (fixed)	360 (fixed)	DNC*	239
Residual df	8	9	9	—	8
Residual mean square	0.13599	1.20317	4.40838	—	8.72493
R ²	0.9999 ^b	0.9999 ^b	0.9998 ^b	—	0.9996 ^b
Females					
Asymptote TTL (cm)	255	265 (fixed)	285 (fixed)	DNC*	220
Residual df	12	13	13	—	12
Residual mean square	5.11505	5.91271	13.21846	—	29.77346
R ²	0.9998 ^b	0.9997 ^b	0.9994 ^b	—	0.9988 ^b

* Did not converge to a solution.

^b $P < 0.001$.

ularly for males) known asymptotic total lengths. Meanwhile, the modified Richards curve failed to converge to solutions when we attempted to estimate unconstrained growth parameters. Ratkowsky (1990) strongly cautioned against the continued use of the Richards model because of its very poor statistical properties in estimation and its high intrinsic nonlinearity. Our results appear to support his admonitions.

The Brody model, however, provided a descriptive fit to our data which resulted in growth curves that closely paralleled known maximum asymptotic sizes (Fig. 5). In our initial scenario (Fig. 5a, d), the final asymptote terms A were allowed to vary freely and seek their own solution. This resulted in predicted final asymptote sizes of 314 cm (males) and 255 cm TTL (females), versus known maximum values of 335 cm and 265 cm TTL, respectively. Figure 5b and e illustrate growth curves generated by setting the final asymptote size parameters equal to known maximum TTLs prior to running the models. Our third pair of Brody growth curves (Fig. 5c, f) was developed using the predicted maximum size estimate of 360 cm TTL for males (see above) and a value of 285 cm TTL for females. This latter value was

may best reflect actual growth, there is little error in predicted age for either sex among models until about age 15 (which encompasses the age classes within the legal size harvest limits for *C. novaeguineae*). However, it is apparent that considerable error could result from attempts to estimate ages for older animals on the basis of growth curve models. For example, Fig. 5g illustrates the range of growth curve confidence limits from our pooled Brody models. Age estimates for a 240 cm TTL female *C. novaeguineae* range from 17–33 years, whereas age estimates of a 300 cm TTL male are 18–31 years.

Gender Classification

The original relative growth data set incorporated a total of 27 ratio indices for a complete skull. These included 15 cranial and 12 mandibular aspects of growth (Table 2).

There was considerable overlap among canonical coefficients in the relative growth data set. Initial discriminant analysis (DISCRIM) results were highly promising (e.g., overall apparent error rate [AER] = 3.6% misclassification with a complete skull), but alarmingly illusory as the crossvalidation true error rate (TER) was 44.8% (Table 6). When the same data set was evaluated by classification tree analysis (CART) the resulting AER (26.1%) provided a realistic estimate of the TER (28.7%). The best overall discrimination resulted from CART

Regardless of which of these scenarios

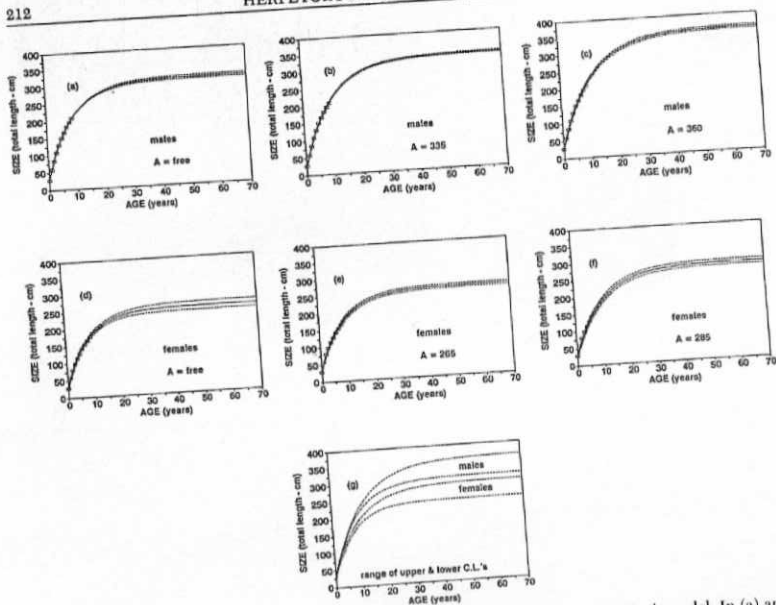


FIG. 5.—Growth curves for *Crocodylus novaeguineae* developed with a Brody growth model. In (a) and (c) the final asymptote sizes *A* were free to vary and seek their own solutions after entering growth data. Curves (b) and (d) were derived by fitting growth data to specified known final asymptote sizes *A* of 335 cm and 265 cm TTL, respectively. Growth data in curves (e) and (f) were fitted to estimated maximum final asymptote sizes *A* of 360 cm and 285 cm TTL (see RESULTS). Panel (g) illustrates the range of growth curve confidence intervals from the preceding (a)–(f). Open squares indicate actual data. Solid lines indicate estimated growth and dashed lines indicate confidence intervals.

TABLE 6.—Comparison of predictive models for gender of *Crocodylus novaeguineae* using discriminant analysis (DISCRIM) and classification tree analysis (CART). AER = apparent error rate, TER = true error rate determined by crossvalidation (see METHODS). *n* = sample size.

Skull type	Gender	Method					
		DISCRIM			CART		
		AER	TER	<i>n</i>	AER	TER	<i>n</i>
Complete skull	M	0.0442	0.2566	113	0.2532	0.2727	154
	F	0.0278	0.6389	72	0.2763	0.3158	76
	M+F	0.0360	0.4478	185	0.2609	0.2870	230
			0.2033	0.2927	123	0.1503	0.1765
Cranium ^a only	M	0.0811	0.3514	74	0.3553	0.4211	76
	F	0.1422	0.3220	197	0.2183	0.2576	229
	M+F	0.1422	0.3220	197	0	0	145
Mandible ^b only	M	0.3391	0.4087	115	0	1	74
	F	0.1667	0.3750	72	1	1	74
	M+F	0.2529	0.3918	187	0.3379	0.3379	219

^a Variables RCW, RLST, RWST, ROL, ROW, RWI, RLR, RWN, RMXS, RFXS, RLUMR, PM4LR, PM4WR, M5LR, M5WR.
^b Variables RLSS, RWSS, RLD, RWD, RWM, RLLMR, D1LR, D1WR, D4LR, D4WR, D11LR, D11WR.

TABLE 7.—Stepwise discriminant analysis results indicating relative growth variables and associated *P* values for 'best fit' predictive models of gender for *Crocodylus novaeguineae*.

Skull type	<i>n</i>	Method			
		Step 1 RWST	Step 2 RLUMR	Step 3 RLR	Step 4 RWSS
Complete skull	185	0.0001	0.0002	0.0006	0.0096
Cranium only	197	0.0001	0.0001	0.0025	N/A
Mandible only	219	N/A	N/A	N/A	0.0001

'fit' models by DISCRIM using the STEPDISC selected variables gave much improved results and better correlations among AER and TER that approximated the CART 'best fit' model consisting of the variables RWST and RLR (Table 8).

Relative Growth Patterns

Relative growth patterns for the skull of *Crocodylus novaeguineae* are shown in Fig. 6. Growth is characterized by three general stages: (I) a hatching phase; (II) a juvenile through middle-aged adult phase; and (III) an old-aged adult phase.

Stage I is maintained through most of the first year of growth until a DCL of 60–70 mm (40–50 cm TTL) is attained. In this stage, the preorbital region of the skull is characterized by a relatively short, robust snout with comparatively narrow external nares. The orbits are enormously enlarged (primarily in relative width) with correspondingly narrow interorbital width; while in the postorbital portion of the skull, the cranial roof assumes the shape of a convex trapezoid in contrast to the concave appearance in subsequent growth stages.

The change from stage I to stage II skull growth is very abrupt, paralleling the 'saltatory ontogeny' model proposed by Balon (1984). The secondary stage is a protracted phase exhibited until animals reach a DCL of about 350 mm (roughly 260 cm TTL). It is in this stage that the crocodylian skull

analysis of the cranium only, where a subset of only two cranial attributes (relative width of snout [RWST] and relative length of cranial roof [RLR]) were selected by the model for classification of gender. The wide disparity between AER and TER was a consistent feature of DISCRIM, while CART results yielded error rates that much more closely paralleled each other. Whether a complete or partial skull was analyzed, fewer observations were misclassified using CART methodology than with DISCRIM when TER was taken into account. Regardless of the method used, better gender classification resulted from use of the cranium than the mandible alone.

Subsequent examination of the original DISCRIM data set by stepwise discriminant analysis (STEPDISC) resulted in reduced model sizes consisting of a maximum of four variables (RWST, RLR, relative upper ramus length [RLUMR], relative mandibular symphysis width [RWSS]) (Table 7). Construction of a series of 'best

TABLE 8.—Comparison of 'best fit' predictive models of gender for *Crocodylus novaeguineae* using stepwise discriminant analysis (STEPDISC—Table 7) and classification tree analysis (CART). AER = apparent error rate, TER = true error rate determined by crossvalidation (see METHODS). *n* = sample size.

Skull type	Gender	Method					
		STEPDISC		<i>n</i>	CART		<i>n</i>
		AER	TER		AER	TER	
Complete ^a skull	M	0.2521	0.2521	119			Below model only
	F	0.2162	0.2432				
	M+F	0.2342	0.2477				
Cranium ^b only	M	0.3200	0.3520	125	0.1503	0.1765	153
	F	0.1600	0.1867	75	0.3553	0.3553	76
	M+F	0.2400	0.2693	200	0.2183	0.2358	229
Mandible ^c only	M	0.3034	0.3034	145			Above model only
	F	0.3649	0.3649	74			
	M+F	0.3342	0.3342	219			

^a Variables RWST, RLUMR, RLR, RWSS.

^b Variables RWST, RLUMR, RLR for STEPDISC; RWST, RLR for CART.

^c Variable RWSS.

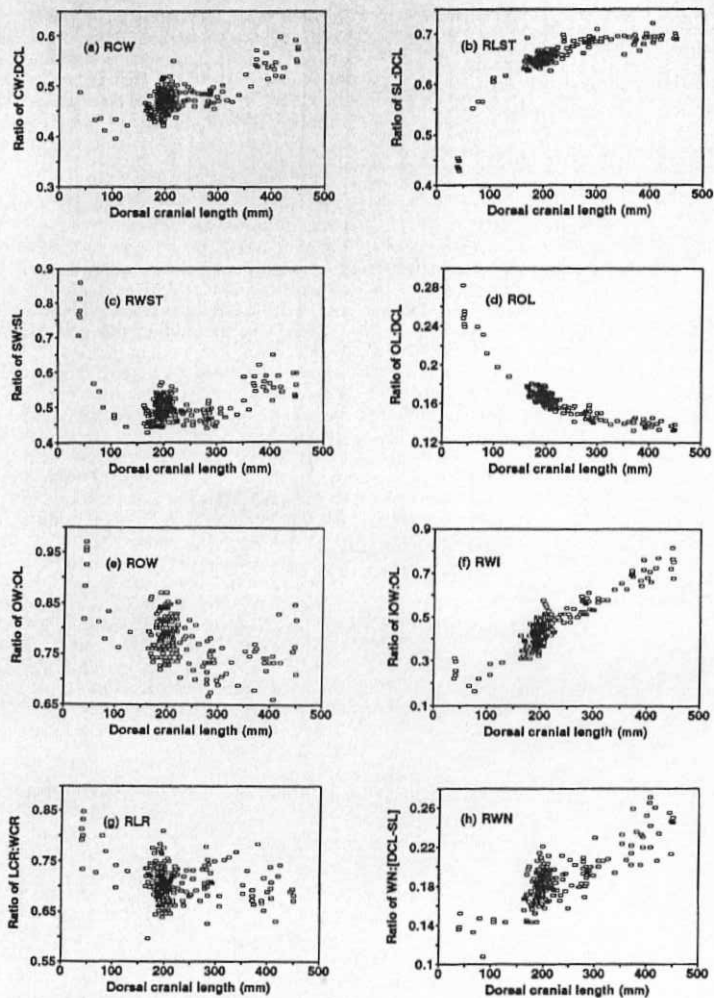
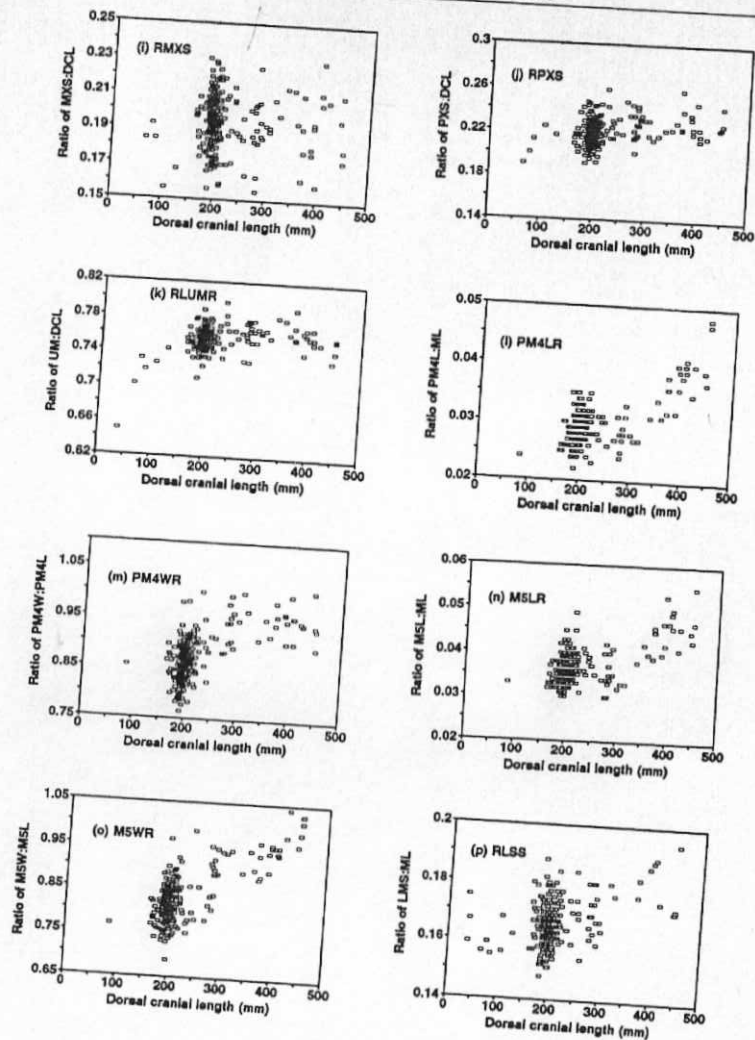
FIG. 6.—Scattergrams of relative growth ratios for *Crocodylus novaeguineae*.

FIG. 6.—Continued.

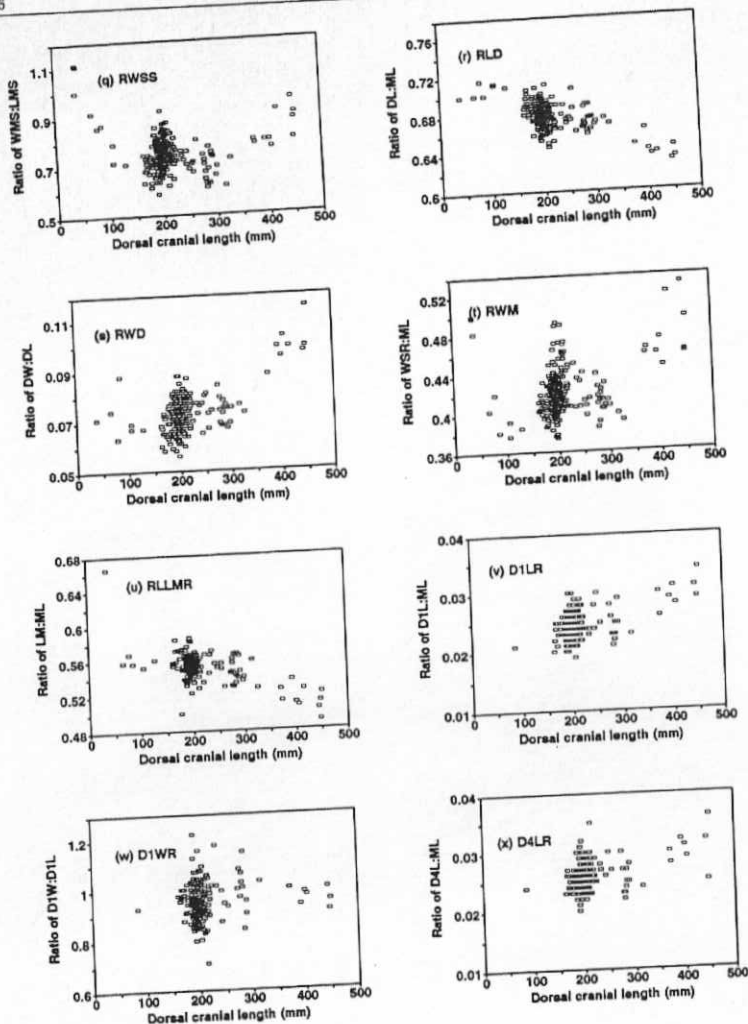


FIG. 6.—Continued.

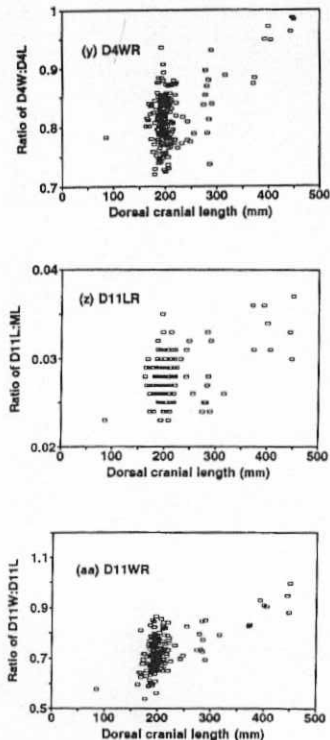


FIG. 6.—Continued.

acquires the proportions of generalized morphology typically associated with the species. The snout becomes relatively long and slender, there is an increase in width in external nares and interorbital distance, the orbits are much reduced in size from stage I, and the cranial roof becomes a concave-shaped trapezoid for the duration of life.

By virtue of size, stage III growth consists predominantly of large adult males and excludes all but the largest females. In stage III, the directional rates of growth undergo another transformation. As the

skull length asymptote is approached, a reversal toward the hatching stage I phase is manifest with respect to the skull becoming increasingly more robust while the snout becomes proportionally shorter. Thus, an individual may exhibit identical relative growth ratios for a given attribute within its life span, but at different stages of growth (e.g., at stages I and III) and at widely differing ages (e.g., hatching and old-aged adult). Hence, some independent measure of size, such as DCL, must be incorporated to lend meaningful interpretation to relative growth data.

DISCUSSION

Relative Growth

Relative growth indices are a useful way to chronicle ontogenetic patterns of growth and to segregate morphologically similar species (e.g., Dodson, 1975; Hall, 1989; Simpson, 1980). Such indices in this study reveal three distinct stages of skull growth in *C. novaeguineae*: a hatching phase (I); a juvenile to middle-aged adult phase (II); and an old-aged adult phase (III).

The abrupt shift in patterns of relative skull growth exhibited by hatching *C. novaeguineae* from stage I to stage II mimics the rapid ontogenetic changes in form and function described by Balon (1984) as a saltatory response. Hatching crocodylians possess a residual embryonic yolk reserve that continues to provide nutrients for growth in the early posthatching period (Whitehead, 1990). In addition to the depletion of yolk reserves during the stage I phase of hatching cranial growth, there is a concomitant dietary shift from an invertebrate prey base toward a gradual inclusion of vertebrate items that form the mainstay of forage for older animals. This is evidenced by structural modifications of the skull from that of hatchlings which principally involve the orbits. Following that stage, there is a diminution of the orbital region and expansion of the external nares throughout growth stages II and III, inferring a greater reliance on olfactory prowess and less on visual acuity in older animals. The shift from stage II to stage III skull growth is not as rapid and

pronounced as from stage I to stage II, but it is in this stage that animals attain the size and are afforded the massiveness and strengthening of the skull through increased robustness to feed on the largest vertebrate prey items available.

Gender Classification

The correctness of classification rates of biological observations by discriminant analysis is strongly influenced by group sample sizes and the distributional overlap among groups. When overlap is high, as in this study, sample sizes must be increased with respect to the number of variables to provide a given level of precision. Williams et al. (1990) recommend that sample sizes be at least two times the number of variables to be measured when among-group overlap is low and substantially more as the overlap increases. Sample sizes of complete skulls in this study ranged from approximately four times the variable number for the general DISCRIM models (Table 6) to 60 times that number for the 'best fit' STEPDISC models (Table 8). As noted earlier, CART methodology maximizes the number of available observations since it treats missing value data, whereas DISCRIM does not. This feature, plus its ease of use and interpretation, makes CART preferable to DISCRIM for classification purposes. More importantly, in this study CART provided consistently lower TER that gave more realistic assessments of model AER than did DISCRIM. However, the choice of methodology is not so clear cut when one compares 'best fit' models since DISCRIM performed nearly as well as CART in that regard, although it entailed the use of three more attributes (LMS, UM, WMS) than the latter method (both used DCL, LCR, SL, SW and WCR).

The fact that aspects of the cranial roof and snout were selected as predictive variables for the classification of gender in both the DISCRIM and CART 'best fit' models suggests that better results might be obtained in future studies through the addition of other measures of the shapes of those variables. Post- and preorbital attributes that may prove of use in further

investigation are as follows: (1) the mid-point width of the cranial roof; (2) the intersuprafenestral width of the parietal; and additional measurements of the snout including (3) the mid-snout width (at the level of the 5th maxillary alveoli); (4) the width at the point of anterior snout constriction (posterior to the external nares); and (5) the maximum premaxillary snout width (at the midpoint of the external nares).

Recent advances in morphological investigation (Bookstein et al., 1985) offer further promise for improvement in the discrimination model results we obtained. However, the use of such methods would require landmark morphometric measurements that we are unable to perform retrospectively. At the time our field measurements were taken, we were unaware of this methodology and did not obtain appropriate measurement for analysis.

Size and Age Relations

Attempts at aging crocodilians usually involve capture-recapture studies, (Chabreck and Joanen, 1979; Gorzula, 1978; Lawson, personal communication; McIlhenny, 1934, 1935; Staton and Dixon, 1975; Webb, 1977; Webb and Messel, 1978; Webb et al., 1978) or observed growth in captivity (Cott, 1961; Montague, 1982). Graham (1968) employed growth annuli in the dentary bone and the weight of the eye lens to determine the age of a sample of harvested *C. niloticus*. However, those methods provided less than satisfactory results. Subsequently, Hutton (1986, 1987c) reported that cross-sections of nuchal scutes from that species provided better resolution and a more reliable method of aging. However, as noted above, considerable margin for error in aging crocodilians still exists. Hutton's (1986) study provided the most rigorous evidence to date of the magnitude of error resulting from attempts to age these reptiles. In that study, the range of errors of individual estimates were about 22% for known-aged crocodiles above age 13, while errors of mean estimates ranged from 15% for 13 year old animals to 9% for a 46 year old individual. Furthermore, aging errors are likely to be greater in fe-

male crocodilians due to lines of arrested growth resulting from reabsorption of calcium from ossified areas during the reproductive cycle (Wink and Elsey, 1986). Thus, as indicated above, use of the growth curves in this study (Fig. 5) will likely produce spurious results for all but the youngest age classes (≤ 15).

The teeth of certain mammalian species exhibit growth annuli and have long been used for aging purposes (e.g., Marsh, 1981). Crocodilian teeth also possess growth zones (Johnston, 1979; Poole, 1961). However, crocodilians have polyphyodont dentition characterized by replacement in irregular sequence and at irregular intervals (Edmund, 1962). These properties render crocodilian teeth unsuitable for aging purposes. We believe, though, that the size of dental alveoli may prove to be a useful indicator of age in crocodilians since growth of an alveolus appears to be continual, except under rare pathological conditions (Hall, 1985a). Further investigation along these lines is required.

CONCLUSIONS

Size estimates of harvested *C. novaeguineae* may be derived with a high degree of accuracy from a complete skull or from fragments thereof. Allometric coefficients are provided for the estimation of dorsal cranial length (DCL) from body and skull attributes, and for the determination of body size attributes from DCL. Best estimates of DCL are obtained from the use of cranial attributes SL (snout length), CL (cranial length), UM (upper ramus length) and mandibular attributes ML (mandible length), DL (dentary length), and LM (lower ramus length).

Sexual dimorphism is subtle but significant with respect to body size (SVL, TTL) and 21 of 32 skull attributes. Differences between the sexes ranged from 1.3% to 28.3% for a given attribute at the size of the largest known female *C. novaeguineae* (Table 3) and were most pronounced in the relative sizes of dental alveoli.

Relative growth indices reveal three distinct stages of skull growth. Stage I is characteristic of hatching crocodiles, stage II of juvenile through middle-aged adults,

and stage III of large, old-aged adults (principally males). Stage I growth abruptly shifts to stage II at about 60-70 mm DCL and mimics a rapid ontogenetic response. The shift from stage II to stage III occurs at about 350 mm DCL and is less abrupt than stage I. Stage III is characterized by a reversal in directional rate of growth, back toward that found in stage I where the relative snout length is decreased and measures of skull width increase.

The use of relative growth indices for the skull of *C. novaeguineae* provided a reasonable means of determining the gender of unknown sex animals by classification through multivariate discriminant analysis (DISCRIM) or through non-parametric binary tree classification (CART). CART methodology provided consistently lower apparent error rates (AER) that correlated better with crossvalidation true error rates (TER) than did those obtained by DISCRIM. However, when 'best fit' models were selected from variables used in general classification models, DISCRIM performed nearly as well as CART. TER was usually greater for females than males regardless of the method or model employed. Suggestions are made for the possible improvement of classification results through the addition of other measures of predictive attributes used by the 'best fit' models.

In conclusion, the use of hunter harvested skulls of *C. novaeguineae* can provide valuable demographic insights to the size structure and sex composition of populations from remote, difficult access locations that are otherwise unlikely to be obtained. This knowledge can offer a cost-effective method for monitoring population trends of future harvests and enhance the management potential for achieving optimal resource use.

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APPENDIX I

Linear regression coefficients for predicting dorsal cranial length (DCL) of *Crocodylus novaeguineae* from body size and other skull parameters by the equation $Y = A + BX$, where A is the Y intercept, B the slope. Equations are expressed separately by gender (M = males, F = females) where they differed by sex ($P < 0.05$), and are combined (M+F) where no such differences were detected. U = sex unknown, TOT = total sample, E_i = standard error of the regression model, r² = coefficient of determination, n = sample size.

Eqn. no.	Predictor X	Sex	A	B	E _i	r ²	n
1	Snout-vent length ^a	M	24.61	2.35	6.46	0.9603	126
2	(SVL)	F	24.37	2.39	6.38	0.9004	70
3		U	-0.73	3.22	3.09	0.9286	27
4		TOT	12.43	2.52	6.70	0.9866	223
5	Total length (TTL) ^a	M	13.97	1.25	6.44	0.9605	126
6		F	9.94	1.51	8.28	0.8726	72
7		U	0.84	1.48	1.52	0.9826	27
8		TOT	7.77	1.30	7.08	0.9852	225
9	Belly width (BW) ^a	M+F	95.41	3.09	11.29	0.8117	206
10		U	22.11	6.09	10.73	0.9832	12
11		TOT	78.91	3.56	13.90	0.8280	218
12	Log ₁₀ Body mass (BM) ^b	M+F	2.04	0.25	0.01	0.8068	189
13		U	2.28	0.52	0.04	0.9141	6
14		TOT	2.00	0.29	0.02	0.9763	195
15	Cranial length (CL)	M	1.55	0.93	2.93	0.9982	151
16		F	-5.02	0.96	2.24	0.9637	75
17		U	2.63	0.93	3.37	0.9976	89
18		TOT	1.92	0.93	3.04	0.9976	315
19	Cranial width (CW)	M	47.67	1.60	7.78	0.9875	151
20		F	19.68	1.94	5.68	0.9507	75
21		U	33.27	1.79	10.02	0.9786	89
22		TOT	44.20	1.66	9.24	0.9777	315
23	Snout length (SL)	M+F	21.40	1.37	2.62	0.9982	229
24		U	19.44	1.37	3.32	0.9982	94
25		TOT	20.69	1.37	3.03	0.9980	323
26	Snout width (SW)	M	54.81	2.20	8.82	0.9849	153
27		F	37.75	2.53	8.23	0.9281	76
28		U	29.01	2.69	13.27	0.9708	94
29		TOT	48.30	2.33	12.54	0.9648	323
30	Orbital length (OL)	M+F	-94.24	8.86	8.58	0.9792	226
31		U	-61.32	8.13	11.14	0.9794	94
32		TOT	-78.24	8.47	10.42	0.9745	320
33	Orbital width (OW)	M	-135.92	12.63	15.76	0.9461	150
34		F	-135.04	12.82	15.86	0.6161	75
35		U	-86.04	11.64	17.40	0.9499	94
36		TOT	-102.00	11.70	19.14	0.9113	319
37	Interorbital width (IOW)	M	77.59	8.22	10.97	0.9756	152
38		F	75.15	8.70	11.59	0.8575	76
39		U	63.14	9.57	18.62	0.9426	94
40		TOT	74.17	8.60	14.82	0.9495	322
41	Length of cranial roof	M+F	26.42	4.10	8.39	0.9817	229
42	(LCR)	U	-8.30	4.91	9.57	0.9848	93
43		TOT	15.44	4.35	10.38	0.9758	322
44	Width of cranial roof	M	27.38	2.83	8.72	0.9852	153
45	(WCR)	F	23.37	2.96	8.23	0.9281	76
46		U	-0.006	3.37	10.95	0.9801	93
47		TOT	20.32	2.98	11.15	0.9721	322
48	Width of external nares	M	47.67	11.81	12.83	0.9681	153
49	(WN)	F	47.65	12.14	11.77	0.8532	76
50		U	20.41	14.91	13.77	0.9643	90
51		TOT	43.99	12.40	15.67	0.9420	319
52	Length of premaxillary	M	15.85	4.20	10.36	0.9775	125
53	symphysis (PXS)	F	44.00	3.63	7.78	0.9075	75
54		U	20.94	4.04	11.90	0.9732	62
55		TOT	21.52	4.08	10.42	0.9711	262

APPENDIX I

Continued.

Eqn. no.	Predictor X	Sex	A	B	E_1	r^2	n
56	Length of maxillary symphysis (MXS)	M+F	19.89	4.70	17.01	0.9121	200
57		U	13.48	4.88	18.65	0.9331	63
58	Length of upper ramus (UM)	TOT	17.66	4.76	17.39	0.9193	263
59		M	-1.07	1.33	2.89	0.9983	125
60	Length of 4th premaxillary alveolus (PM4L)	F	9.77	1.27	3.13	0.9925	75
61		U	6.98	1.27	3.64	0.9976	69
62	Width of 4th premaxillary alveolus (PM4W)	TOT	3.30	1.30	3.50	0.9968	269
63		M	85.54	19.62	12.64	0.9633	145
64	Length of 5th maxillary alveolus (MSL)	F	52.49	26.21	12.56	0.7241	74
65		U	51.12	27.06	16.07	0.9379	59
66	Mandible length (ML)	TOT	82.40	20.71	16.21	0.9216	278
67		M	99.82	20.00	10.98	0.9724	145
68	Length of 5th maxillary alveolus (MSL)	F	69.86	26.86	10.00	0.8251	74
69		U	69.43	26.97	13.63	0.9553	59
70	Width of 5th maxillary alveolus (MSW)	TOT	96.16	21.17	13.94	0.9421	278
71		M	73.86	17.25	12.53	0.9635	147
72	Mandible length (ML)	F	51.91	21.23	12.67	0.7549	75
73		U	53.91	21.19	18.57	0.9173	60
74	Length of mandibular symphysis (LMS)	TOT	72.67	17.93	15.68	0.9266	282
75		M	102.53	16.36	11.89	0.9670	148
76	Width of mandibular symphysis (WMS)	F	64.66	23.66	9.84	0.8522	75
77		U	78.45	21.66	15.84	0.9399	60
78	Dentary length (DL)	TOT	99.91	17.31	15.02	0.9324	283
79		M	19.68	0.75	3.95	0.9952	144
80	Dentary width (DW)	F	7.21	0.81	2.31	0.9953	74
81		U	11.58	0.78	3.34	0.9972	73
82	Width across surangulans (WSR)	TOT	16.67	0.76	3.72	0.9950	291
83		M+F	48.14	3.83	7.32	0.9772	218
84	Length of lower ramus (LM)	U	18.33	4.50	8.14	0.9835	73
85		TOT	38.91	4.04	8.53	0.9737	291
86	Length of 1st dentary alveolus (D1L)	M	71.82	4.24	9.81	0.9701	144
87		F	32.52	5.84	9.68	0.8361	74
88	Length of 1st dentary alveolus (D1W)	U	11.17	6.64	13.65	0.9535	73
89		TOT	62.54	4.65	15.48	0.9135	291
90	Length of 4th dentary alveolus (D4L)	M+F	-0.97	1.23	3.79	0.9936	217
91		U	5.21	1.19	2.76	0.9977	71
92	Length of 4th dentary alveolus (D4L)	TOT	1.21	1.22	3.71	0.9945	288
93		M+F	84.80	9.83	10.88	0.9471	217
94	Length of 4th dentary alveolus (D4L)	U	25.47	15.09	14.49	0.9476	73
95		TOT	72.21	10.86	15.23	0.9137	290
96	Length of 4th dentary alveolus (D4L)	M	54.05	1.43	9.77	0.9795	147
97		F	42.07	1.59	7.89	0.9348	75
98	Length of 4th dentary alveolus (D4L)	U	27.89	1.73	10.65	0.9768	87
99		TOT	48.30	1.50	11.50	0.9657	309
100	Length of 4th dentary alveolus (D4L)	M+F	-5.49	1.54	4.42	0.9926	194
101		U	4.87	1.46	4.83	0.9946	51
102	Length of 4th dentary alveolus (D4L)	TOT	-2.10	1.52	4.68	0.9926	245
103		M	79.07	20.75	10.86	0.9538	141
104	Length of 4th dentary alveolus (D4L)	F	65.01	24.07	11.71	0.7599	74
105		U	51.71	25.65	15.27	0.8704	46
106	Length of 4th dentary alveolus (D4L)	TOT	77.37	21.29	12.50	0.9162	261
107		M	82.30	21.48	9.49	0.9647	141
108	Length of 4th dentary alveolus (D4L)	F	69.71	24.42	9.54	0.8408	74
109		U	62.34	24.70	14.53	0.8827	46
110	Length of 4th dentary alveolus (D4L)	TOT	80.10	21.97	10.89	0.9364	261
111		M	73.89	20.44	13.33	0.9304	141
112	Length of 4th dentary alveolus (D4L)	F	58.40	23.63	11.42	0.7718	74
113		U	44.23	25.59	14.16	0.8885	46

APPENDIX I

Continued.

Eqn. no.	Predictor X	Sex	A	B	E_1	r^2	n
114	Width of 4th dentary alveolus (D4W)	TOT	71.48	21.03	13.43	0.9032	261
115		M+F	99.94	20.19	12.14	0.9219	215
116	Length of 11th dentary alveolus (D11L)	U	56.36	29.24	14.65	0.8807	46
117		TOT	96.36	20.91	13.48	0.9025	261
118	Width of 11th dentary alveolus (D11W)	M	73.75	19.16	10.27	0.9557	141
119		F	22.97	27.49	12.20	0.7398	74
120	Width of 11th dentary alveolus (D11W)	U	52.73	21.70	13.60	0.8841	43
121		TOT	70.43	19.68	12.15	0.9199	258
122	Width of 11th dentary alveolus (D11W)	M	111.08	18.61	11.34	0.9496	141
123		F	73.45	27.62	12.18	0.7404	74
124	Width of 11th dentary alveolus (D11W)	U	75.11	26.28	11.62	0.9154	43
125		TOT	108.24	19.40	12.92	0.9095	258

* cm.

* kg; following predictors in mm.

APPENDIX II

Linear regression coefficients for predicting body size measurements of *Crocodylus novaeguineae* from dorsal cranial length (DCL) by the equation $Y = A + BX$, where A is the Y intercept, B the slope. Equations are expressed separately by gender (M = males, F = females), where they differed by sex ($P < 0.05$), and are combined (M+F) where no such differences were detected. U = sex unknown. TOT = total sample, E_1 = standard error of the regression model, r^2 = coefficient of determination, n = sample size.

Eqn. no.	Predicted value Y	Sex	A	B	E_1	r^2	n
126	Snout-vent length (SVL) ^a	M	-7.03	0.41	2.70	0.9603	126
127		F	-1.94	0.38	2.53	0.9004	70
128	Total length (TTL) ^a	U	1.25	0.29	0.92	0.9286	27
129		TOT	-3.96	0.39	2.64	0.9866	223
130	Belly width (BW) ^a	M	-4.71	0.77	5.04	0.9605	126
131		F	11.89	0.67	5.91	0.8726	72
132	Log ₁₀ body mass (BM) ^b	U	-0.03	0.66	1.02	0.9826	27
133		TOT	-3.88	0.76	5.40	0.9852	225
134	Log ₁₀ body mass (BM) ^b	M+F	-18.53	0.26	3.29	0.8117	206
135		U	-3.23	0.16	1.75	0.9832	12
136	Log ₁₀ body mass (BM) ^b	TOT	-12.54	0.23	3.56	0.8280	218
137		M+F	-6.32	3.20	0.05	0.8068	189
138	Log ₁₀ body mass (BM) ^b	U	-4.07	1.74	0.08	0.9141	6
139		TOT	-6.81	3.41	-0.06	0.9763	195

* cm; DCL in mm.

* kg; using Log₁₀ DCL as a predictor.