

Variation in Geographic Isolates of the New Guinea Crocodile (*Crocodylus novaeguineae* Schmidt) Compared with the Similar, Allopatric, Philippine Crocodile (*C. mindorensis* Schmidt)

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The New Guinea crocodile (*Crocodylus novaeguineae* Schmidt) is a palustrine crocodile endemic to mainland New Guinea. Populations are broadly distributed below 600 m elevations in two major regions, and are represented as northern and southern forms which are separated by central highlands. Based on examination of 692 specimens, these forms differ in palatal structure and cervical squamation, as well as in reproductive biology. A diagnosis of the northern (New Guinea) and southern (Papua) region forms is provided and both forms are compared with the similar, but allopatric, Philippine crocodile (*C. mindorensis* Schmidt). The *C. novaeguineae* forms each differ from *C. mindorensis* in their cervical squamation and palatal structure. *Crocodylus mindorensis* is also distinctive with respect to the number of dorsal midbody scales and in several aspects of the relative growth of the skull. These data lend convincing support to Schmidt's long disputed classification and provide evidence of an independently evolving form within New Guinea.

TWO crocodile species are native to New Guinea—the endemic New Guinea crocodile (*Crocodylus novaeguineae*) and the wide-ranging saltwater crocodile (*C. porosus*). The central highlands of New Guinea effectively divide both species into northern and southern mainland populations, except for a few coastal populations of *C. porosus*. This cordillera serves as a barrier to gene exchange between *C. novaeguineae* from the northern (New Guinea region) and southern (Papua region) tiers.

While examining aberrant southern *C. novaeguineae* skulls (Hall, 1985a), I compared them with Schmidt's (1928) type description of the species from northern New Guinea and observed several discrepancies. Earlier, Neill (1971) had noted interregional phenotypic differences in *C. novaeguineae* and speculated that the species might not be monotypic. Through further study, I observed that southern and northern tier *C. novaeguineae* differed consistently in palatal structure, cervical squamation, and reproductive biology.

A similar, but distinct species, the Philippine crocodile (*C. mindorensis*) was also described by Schmidt (1935). However, disagreement on its classification persists as the species has been assumed to be conspecific with *C. novaeguineae* by Wermuth (1953) and Wermuth and Mertens (1961). European authorities have vacillated be-

tween their early opinion of subspecies level for *C. mindorensis* (Wermuth and Mertens, 1961), to species rank (Wermuth and Mertens, 1977), and back again (Wermuth and Fuchs, 1978). Furthermore, the Convention on International Trade in Endangered Species of Fauna and Flora (CITES—Wermuth and Mertens, 1981, 1985), regards *C. novaeguineae* and *C. mindorensis* as conspecifics, while the International Union for the Conservation of Nature and Natural Resources (IUCN—Groombridge, 1982) considers them to be distinct species. This latter view is supported by recent protein electrophoretic analysis that indicates these two taxa are genetically separable (Densmore, 1983) and that *C. mindorensis* is most closely genetically allied with the mugger crocodile (*C. palustris*). It should be noted though that this finding was based on samples from only a single individual of each species. Additionally, the implied genetic affinities have yet to be assimilated with data on the morphological and reproductive differences between these taxa.

The main purpose of this paper is to quantify my observations on variation in geographic isolates of *C. novaeguineae*. Secondly, I also examined specimens of *C. mindorensis* to see if a clearer morphological basis for its separation from *C. novaeguineae* was possible.

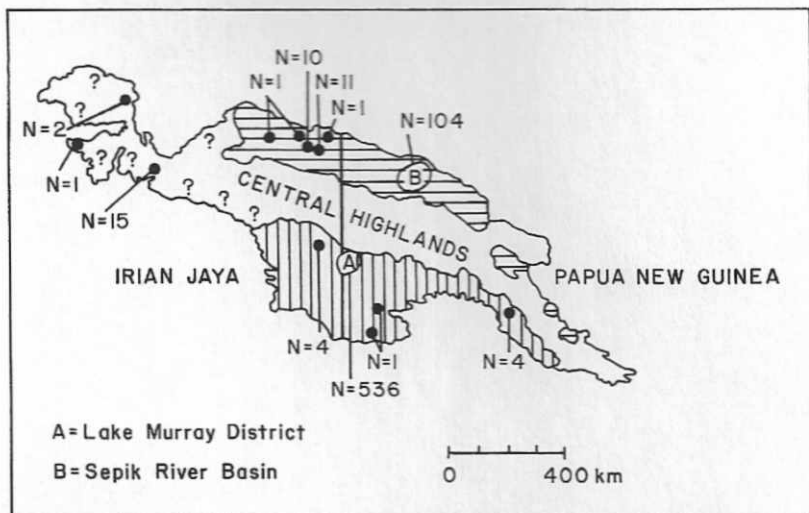


Fig. 1. Locality of specimens of *Crocodylus novaeguineae* examined in this study. Horizontal lines indicate range of northern form *C. novaeguineae*; vertical lines indicate range of southern form.

METHODS

I examined a broad geographic array of *C. novaeguineae* ($n = 692$) harvested by local inhabitants as well as museum specimens and captive animals removed from the wild as juveniles (Figs. 1–2). Within Papua New Guinea (PNG—the independent eastern half of New Guinea) the following areas were represented: Western Province, 538 specimens (250 live, 21 preserved, 267 skulls); Central Province (Brown River and Waigani Swamp), 4 specimens (1 preserved, 3 skulls); and East Sepik Province (Sepik River drainage—Ambunti to Wewak), 104 specimens (84 live, 12 preserved, 8 skulls). Specimens examined from Western Province included one each from Balimo and Boze. The remainder (536) were from Tamu Creek, Aesake and Bosset lagoons, and the following river systems: Agu, Boi, Boikase, Fly, Herbert, June, Liva, Mamboi, and Strickland. Within Irian Jaya (the Indonesian, western half of New Guinea) specimens were examined from the Berap River (1 skull), Digoel River (2 preserved), Fakfak (1 preserved), Grime River (10 skulls), Jamoer Lake (15 preserved), Lake Sentani (1 preserved), Mamberamo River (1 preserved), Oransbari (1 skull and hide, 1 preserved), Tami River (7 preserved, 4 skulls), and Tanah Merah (2 preserved).

Museum specimens of *C. novaeguineae* and *C. mindorensis* examined are indicated in Appendix

I. Institution acronyms follow Leviton et al. (1985), plus North Dakota State University, Fargo (NDSU).

The comparative scale characters assessed follow Brazaitis (1974) and are listed under Table 1. Nuchal scales were not counted, but their general appearance was noted for diagnostic purposes. Also, the outermost dorsal midbody scale was often not contiguous with its adjacent element, although the remainder in the series were in paired contact. Some authors (Ross and Mayer, 1983) have regarded such scales as part of the flank squamation. Nevertheless, I considered them to belong to the midbody series since they were heavily ossified and possessed a strong medial keel, typical of the dorsal armor.

Morphometric cranial indices used in this study (Table 2) were modified from Iordansky (1973), while mandibular index use was my own design. The measurements used (Figs. 3–7), their abbreviations, and the nearest unit of value employed were:

- (1) DCL (dorsal cranial length). Anterior tip of snout to posterior tip of supraoccipital (medial posterior margin of cranial roof). 1 mm.
- (2) CW (cranial width). Distance between the lateral surfaces of the mandibular condyles of the quadrates. 1 mm.
- (3) SW (basal snout width). Width across anterior orbital borders. 1 mm.

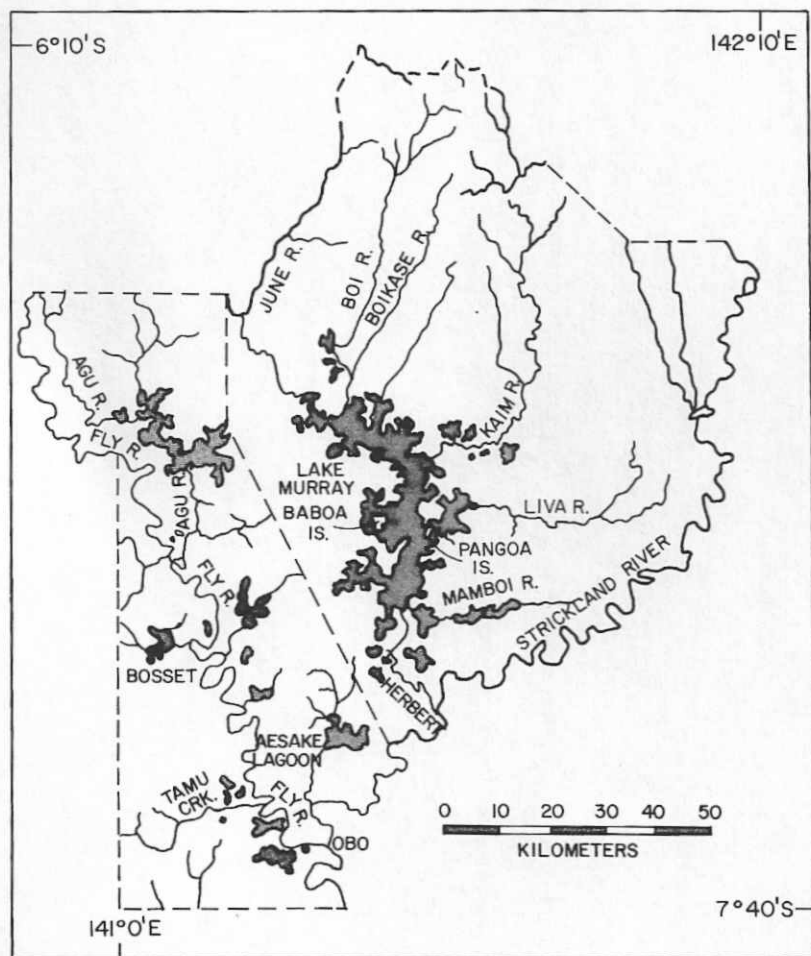


Fig. 2. Enlarged map of area A, Figure 1. Specimens of southern form *Crododylus novaeguineae* were collected throughout the lengths of the depicted lake and river systems within Lake Murray District, Western Province, PNG.

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|---|---|
| (4) SL (snout length). Anterior tip of snout to anterior orbital border. 1 mm. | (12) WMS (maximal width across the mandibular symphysis). 1 mm. |
| (5) IOW (minimal interorbital width). 1 mm. | (13) LMS (length of the mandibular symphysis). 1 mm. |
| (6) OW (maximal orbital width). 1 mm. | (14) DW (dentary width). Lateral intervalveolar width of dentary at the posterior margin of the mandibular symphysis. 1 mm. |
| (7) OL (maximal orbital length). 1 mm. | (15) DL (dentary length). Anterior tip of dentary to the anterior external mandibular fenestra. 1 mm. |
| (8) LCR (length of the postorbital cranial roof). Distance from the posterior orbital border to the posterolateral margin of the squamosal. 1 mm. | (16) WSR (surangular width). Posterolateral width across surangulans at point of jaw articulation. 1 mm. |
| (9) WCR (posterior width of the cranial roof). Distance between the posterolateral corners of the squamosals. 1 mm. | |
| (10) WN (maximal width of external nares). 1 mm. | |
| (11) ML (mandible length). Anterior tip of den- | |

TABLE 1. SCALE CHARACTER* COMPARISONS ($\bar{x} \pm SE$, RANGE IN PARENTHESES) BETWEEN NORTHERN AND SOUTHERN FORM *Crocodylus novaeguineae* AND POOLED DATA COMPARED WITH *C. mindorensis*.

	PO	TDR	DMS	DCV
<i>C. novaeguineae</i> (northern form)	4.26 \pm 0.06 (4-7) n = 105	16.91 \pm 0.03 (16-17) n = 97	9.94 \pm 0.04 (8-11) n = 97	18.14 \pm 0.05 (17-20) n = 97
<i>C. novaeguineae</i> (southern form)	4.65 \pm 0.05 a (3-6) n = 292	16.96 \pm 0.03 (11-18) n = 272	9.90 \pm 0.02 (9-10) n = 272	18.49 \pm 0.04 a (16-22) n = 272
<i>C. novaeguineae</i> (pooled data)	4.53 \pm 0.04 (3-7) n = 397	16.95 \pm 0.03 (11-18) n = 369	9.91 \pm 0.02 (8-11) n = 369	18.40 \pm 0.04 (16-22) n = 369
<i>C. mindorensis</i>	6.00 \pm 0.00 b (6) n = 9	17.09 \pm 0.09 (17-18) n = 11	11.73 \pm 0.19 b (10-12) n = 11	18.20 \pm 0.13 (18-19) n = 10

* PO = no. of postoccipital scales, TDR = no. of transverse dorsal rows, DMS = no. of dorsal midbody scales, DCV = no. of double caudal verticils, SCV = no. of single caudal verticils, TVR = no. of transverse ventral rows.

a— $P < 0.0001$, b— $P < 0.0001$, two-tailed t-test (Ott 1977).

(17) PXS (length of premaxillary symphysis). 0.05 mm.

(18) MXS (length of maxillary symphysis). 0.05 mm.

Details on methods used in studying *C. novaeguineae* reproductive biology are given in Cox (1985), Hall (1985b), and Hall and Johnson (1987).

RESULTS

Palatal structure.—The length of the palatal PXS in southern form *C. novaeguineae* exceeded that of MXS (Fig. 7), a condition opposite that of the northern form and similar to that of *C. mindorensis* (Wermuth, 1953; Schmidt, 1956). The

mean difference of these lengths (MXS-PXS) was highly significant ($t = 5.63$, $P < 0.0001$) between southern and northern form *C. novaeguineae* ($n = 290$). A comparative subsample of paired similar-sized skulls (DCL, range 150–395 mm) of both forms ($n = 22$) for juveniles, subadults, and adults revealed this trait to be independent of the size of the individual ($t = 4.03$, $P < 0.005$) and indicated a joint non-overlap of 85% in mean MXS-PXS length (coefficient of difference = 1.01; Mayr, 1969). Data on the sex of northern form skulls were lacking, but the palatal structure as described for southern form animals was typical of both sexes. Of 269 southern form skulls, 88% exhibited the palatal pattern ascribed herein, vs 67% for northern form skulls ($n = 21$). A correct grouping rate of 0.772 into proper geographic form was attained using the relative difference in MXS-PXS length, after adjusting for unequal sample sizes.

The effects of diet, spacing, and handling by

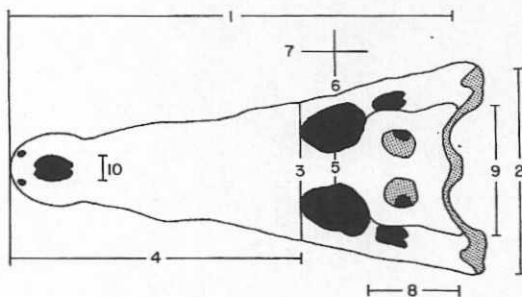


Fig. 3. Dorsal view of *Crocodylus novaeguineae* cranium showing measurements taken. 1 = DCL, 2 = CW, 3 = SW, 4 = SL, 5 = IOW, 6 = OW, 7 = OL, 8 = LCR, 9 = WCR, 10 = WN. See METHODS for explanation.

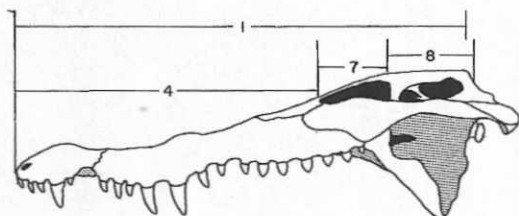


Fig. 4. Lateral view of *Crocodylus novaeguineae* cranium showing measurements taken. 1 = DCL, 4 = SL, 7 = OL, 8 = LCR. See METHODS for explanation.

TABLE 1. EXTENDED.

SCV	TVR
18.10 ± 0.22 (8-21) n = 97	25.02 ± 0.10 (23-28) n = 97
17.73 ± 0.08 (10-20) n = 272	25.23 ± 0.06 (22-28) n = 272
17.83 ± 0.08 (8-21) n = 369	25.18 ± 0.05 (22-28) n = 369
16.90 ± 0.59 (14-20) n = 10	24.33 ± 0.88 (23-26) n = 3

humans had no apparent influence on palatal formation of animals removed from the wild and reared in captivity. Such skulls were visually indistinguishable from skulls of crocodiles harvested in the wild.

Squamation.—The pattern of cervical squamation differed diagnostically between southern and northern form *C. novaeguineae* and each form differed from *C. mindorensis* as well (Fig. 8). The postoccipital series (PO) in *C. novaeguineae* consists of a single transverse row of enlarged scales, 4-6 in number, divided medially into lateral pairs or trios. Specimens of southern form *C. novaeguineae* usually (62%, n = 292) exhibited narrow discontinuity between one or more laterally paired postoccipitals. The converse, in which laterally paired postoccipitals are contiguous with one another mediolaterally, was the prevalent condition (79%, n = 105) for northern form *C. novaeguineae* $\chi^2 = 52.93$, 1 df, $P < 0.005$.

The cervical nuchal cluster (NU, Fig. 8) in *Crocodylus*, except *C. cataphractus*, is composed of four large scutes in a square, mediolaterally flanked by two smaller scutes (King and Brazaitis, 1971). Brazaitis (1974) noted that the nuchals in *C. novaeguineae* tend to be separated from each other along the midline. However, when present, I found that lateral discontinuity of the NU was restricted to the anterior pair. Anteromedial nuchal separation was nearly universal (92%) in southern form *C. novaeguineae* while contiguous pairing was the more frequent

TABLE 2. COMPARATIVE RELATIVE GROWTH SKULL INDICES* ($\bar{x} \pm SE$, RANGE IN PARENTHESES) OF *Crocodylus novaeguineae* AND *C. mindorensis*. See METHODS for explanation of measurements.

Character	n	<i>C. novaeguineae</i>	<i>C. mindorensis</i>	Sig. level ^a
DCL	12	229.6 ± 20.4 (150-388)	227.7 ± 20.6 (140-387)	n.s.
RWST	12	47.1 ± 0.9 (44.3-55.7)	57.5 ± 1.0 (51.9-66.3)	0.0001
RLST	12	66.2 ± 0.5 (64.0-69.3)	63.3 ± 0.6 (59.2-66.4)	0.001
RCW	4	45.2 ± 0.8 (43.4-47.3)	46.4 ± 1.4 (43.9-49.8)	n.s.
RWI	12	44.7 ± 3.3 (30.8-66.7)	53.1 ± 3.5 (34.5-70.5)	0.10
RLR	12	72.6 ± 0.9 (67.2-77.4)	76.8 ± 1.1 (71.2-84.2)	0.01
ROL	12	15.9 ± 0.4 (13.9-17.7)	15.8 ± 0.4 (13.4-18.4)	n.s.
ROW	12	76.0 ± 1.1 (71.1-84.6)	76.1 ± 2.0 (65.9-91.3)	n.s.
RWN	12	17.6 ± 0.6 (14.8-20.6)	19.2 ± 0.7 (16.7-23.1)	0.10
RWSS	3	67.4 ± 2.9 (62.9-72.7)	96.3 ± 8.1 (87.1-112.5)	0.05
RWD	3	6.5 ± 0.2 (6.2-6.8)	8.5 ± 0.3 (7.9-8.9)	0.01
RWM	3	42.3 ± 2.6 (40.2-48.0)	39.6 ± 1.1 (38.1-41.7)	n.s.

* DCL = dorsal cranial length; RCW (relative cranial width) = (cranial width × 100)/dorsal cranial length; RWST (relative width of snout) = (basal width of snout × 100)/snout length; RLST (relative length of snout) = (snout length × 100)/dorsal cranial length; RWI (relative interorbital width) = (minimal interorbital width × 100)/maximal orbital length; RLR (relative length of postorbital cranial roof) = (length of postorbital cranial roof × 100)/posterior width of cranial roof; ROL (relative orbital length) = (maximal orbital length × 100)/dorsal cranial length; ROW (relative orbital width) = (maximal orbital width × 100)/maximal orbital length; RWN (relative width of external nares) = (maximal width of external nares × 100)/dorsal cranial length minus snout length; RWSS (relative width of mandibular symphysis) = (maximal width across mandibular symphysis × 100)/maximal length of mandibular symphysis; RLSS (relative length of mandibular symphysis) = (maximal length of mandibular symphysis × 100)/mandible length; RWD (relative width of dentary) = (dentary width × 100)/dentary length; RWM (relative width of mandible) = (maximal width across surangulars at jaw articulation × 100)/mandible length.
a—Two-tailed t-test (Ott, 1977).

condition (60%) found in the northern form ($X^2 = 119.61$, 1 df, $P < 0.005$).

Four types of postoccipital-nuchal patterns existed for the range of postoccipital scales. Combinations were either both contiguous (C-C) or discontinuous (D-D); with contiguous postoccipitals and discontinuous nuchals (C-D); or, vice-versa (D-C; Fig. 9). The two *C. novaeguineae* forms were strongly bi-modal in their PO-NU

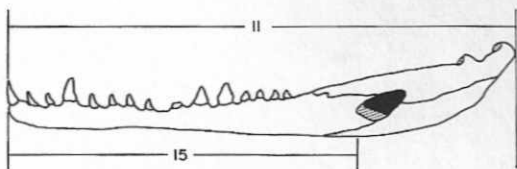


Fig. 5. Lateral view of *Crocodylus novaeguineae* mandible showing measurements taken. 11 = ML, 15 = DL. See METHODS for explanation.

patterns, but opposite in conformation of their most common modes. The prevalent mode in southern form *C. novaeguineae* was D-D (61%) with 4-6 PO, while the northern form exhibited a major modal pattern of C-C (50%) with 4 PO. Few individuals (7% of southern and 11% of northern animals) possessed the major mode of each other. The greatest overlap in PO-NU patterns occurred in the minor mode of C-D (southern form = 31%; northern = 30%). The remaining pattern of D-C was rare (2% in southern *C. novaeguineae*, but nearly as frequent (10%) as D-D in northern animals. Discrimination of individuals into geographic form on the basis of PO-NU patterns was possible in 0.757 instances, after correcting for unequal sample sizes. The expected distribution of PO-NU patterns and the predominant geographic form for equal sample sizes are as follows: C-C = 0.283 (0.885 northern), D-D = 0.356 (0.851 southern), C-D = 0.305 (0.511 southern), and D-C = 0.057 (0.849 northern).

Additionally, the mean number of postoccipitals differed between southern and northern form *C. novaeguineae* ($t = -4.51$, $P < 0.0001$). Many southern animals (42%) exceeded the primary mode of four while that infrequently occurred in northern animals (11%). After adjusting for unequal sample sizes, 80% of the *C. novaeguineae* examined grouped the correct

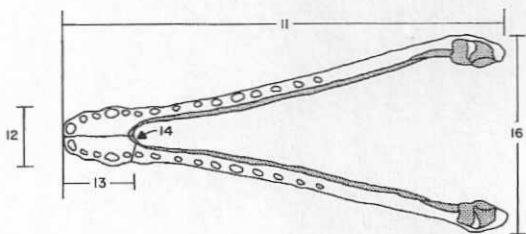


Fig. 6. Dorsal view of *Crocodylus novaeguineae* mandibles showing measurements taken. 11 = ML, 12 = WMS, 13 = LMS, 14 = DW, 16 = WSR. See METHODS for explanation.

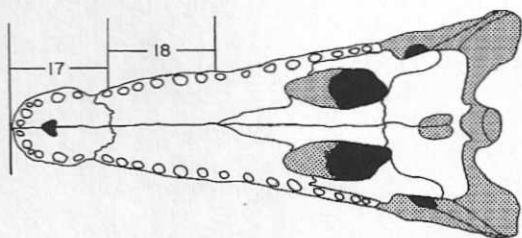


Fig. 7. Palatal view of northern form *Crocodylus novaeguineae* cranium illustrating premaxillary (PXS = 17) and maxillary (MXS = 18) symphyses.

geographic form on the basis of postoccipital counts alone, when the modal value of four was exceeded ($n = 135$).

These forms differed from *C. mindorensis* in that, while *C. mindorensis* exhibited narrowly discontinuous postoccipitals as in southern form *C. novaeguineae*, it showed contiguously paired anterior nuchals that were more common to northern form *C. novaeguineae*. A modal pattern of six postoccipitals occurred in *C. mindorensis*, a condition frequent in southern form *C. novaeguineae*. Additionally, *C. mindorensis* possessed a double row of nucomarginal scales that were more pronounced and less irregularly spaced than in either *C. novaeguineae* form.

Meristic features of *C. novaeguineae* and *C. mindorensis* are presented in Table 1.

Morphometry.—Relative skull measurements did not differ between forms for similar-sized individuals of *C. novaeguineae*, and were pooled for comparison with *C. mindorensis* (Table 2). The skull of *C. novaeguineae* was notably less robust than that of *C. mindorensis*, especially in the relative widths of the snout and the mandibular symphysis. It also differed in having a greater relative SL; narrower relative interorbital, external nares, and DW, and a shorter relative LCR. The comparative shapes of the palatines and posterior frontal provide other bases for the identification of these species (Schmidt, 1935, 1956).

The largest *C. novaeguineae* skull of nearly 400 examined was that of a southern form male (LSUMZ 44741) from the Agu River northwest of Lake Murray. That skull had a snout-supraoccipital length of 450 mm and belonged to an animal with an estimated total length of 3.4 m. The skull length of female *C. novaeguineae* apparently does not exceed 355 mm (TL approx. 2.7 m). Maximum verifiable lengths for *C. novaeguineae* are 3.35 m in males (Montague, 1984)

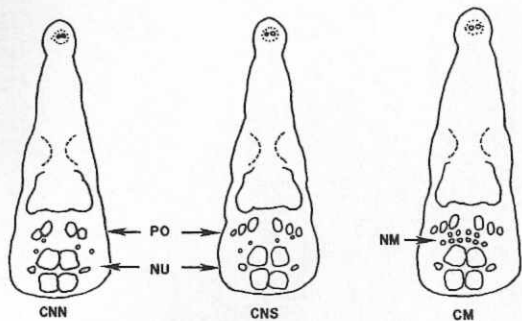


Fig. 8. Cervical scalation of *Crocodylus novaeguineae* and *C. mindorensis*. Left—northern form *C. novaeguineae* (CNN), middle—southern form *C. novaeguineae* (CNS), right—*C. mindorensis* (CM). Note narrow discontinuity of laterally paired postoccipitals (PO) and anteromedial separation of nuchals (NU) in southern form *C. novaeguineae*. Also note the prominence of nuchomarginal rows (NM) in *C. mindorensis* and their reduction in *C. novaeguineae*.

and 2.65 m in females (Hall and Johnson, 1987). Maximum length does not differ between northern and southern forms, based on examination of 1969–80 harvest data (Hall, unpubl.). Unsubstantiated lengths of 4.27 m (14 ft; McKay, 1976) and 5.0 m (Wermuth and Fuchs, 1978) have been reported for *C. novaeguineae*. However, I believe such claims to be of misidentified *C. porosus*. Maximum known length of *C. mindorensis* is 3.02 m (FMNH 52361).

A differential diagnosis of the taxa herein discussed follows.

Crocodylus novaeguineae.—PO 4–6; lateral pairs either contiguous mediolaterally or not. Smaller nuchomarginal scales separate PO from NU, but are indistinct and irregularly spaced compared to *C. mindorensis*. NU contiguous or with anteromedial separation. Transverse dorsal midbody scales 10. Skull slender; MXS either < or > PXS. Palatines flare anteriorly, constrict posteriorly. Posterior frontal with medial projection. Lacrimal ridge, swelling over fifth maxillary alveoli, and cranial convolutions less pronounced than in *C. mindorensis*. Two forms:

northern form—PO normally 4; contiguity typical of lateral pairs. NU generally contiguous. MXS > PXS.

southern form—PO 4–6, often >4; narrow mediolateral discontinuity usually present between one or more lateral pairs. NU separated anteromedially. MXS < PXS.

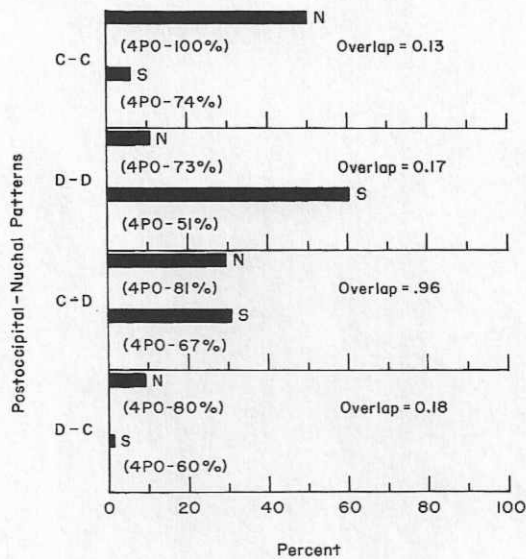


Fig. 9. Postoccipital-nuchal patterns of northern (N) and southern (S) form *Crocodylus novaeguineae*. Patterns were either both contiguous (C-C) or discontinuous (D-D); with contiguous postoccipitals and discontinuous nuchals (C-D); or, vice-versa (D-C). The percent of individuals with the modal number of four postoccipitals (PO) is given below each bar. The overlap for each pattern between northern and southern forms is indicated to the right.

Crocodylus mindorensis.—PO 6; narrow mediolateral discontinuity present between one or more lateral pairs. PO separated from NU by two rows of nuchomarginal scales. NU contiguous. Transverse dorsal midbody scales 12. Skull robust; MXS < PXS. Palatines flare anteriorly and posteriorly. Posterior frontal lacks medial projection. Lacrimal ridge, swelling over fifth maxillary alveoli, and cranial convolutions more pronounced than in *C. novaeguineae*. No subspecies recognized.

Reproductive biology.—Northern and southern form *C. novaeguineae* differ strikingly from each other in aspects of their reproductive biology. Size at hatching ranges from 26–32 cm for southern form *C. novaeguineae*, about 5 cm longer than hatchling northern form (Hall, 1985b). This difference is probably attributable to the different reproductive strategies of these forms in which significantly fewer ($\bar{x} = 21.8$ vs 35.4), and larger ($\bar{x} = 104$ g vs 73 g), eggs are laid by southern form females, although the average and maximum clutch masses of the two forms are similar (Hall and Johnson, 1987). Also,

southern form *C. novaeguineae* build nests and oviposit in the wet season, synchronous with sympatric nesting *C. porosus*; whereas, the northern *C. novaeguineae* form is a dry season nester that is largely temporally segregated from sympatric reproductive *C. porosus* (Cox, 1985). Comparative data for wild *C. mindorensis* were lacking.

Distribution.—Both forms of *C. novaeguineae* are widespread and locally common, inhabiting lowland palustrine and riverine environments ranging from sea level to about 600 m (Fig. 1). Within PNG, the southern form is found from Robinson Creek near Abau, Central Province, westward to the Fly River, Western Province, which forms a common border with Irian Jaya (Whitaker, 1980a; Ross, 1986). The northern PNG form extends from Madang Province westward through East and West Sepik Provinces. The three easternmost northern coastal PNG populations (those in the Markham River delta of Morobe Province and in the Musa and Mambare River drainages of Oro Province) are tentatively regarded as northern form *C. novaeguineae*, but their affinity remains to be determined since no specimens were available for examination. In Irian Jaya, Van der Zon and Mulyana (1978) reported northern form *C. novaeguineae* occurring throughout the Mamberano basin and the southern form to range as far west as the Lorenz River. However, collections have been made as far west as Fakfak in that region (M. Hoogmoed, pers. comm.). More recent records from northern Vogelkop ("bird's head," extreme western New Guinea; BPBM 3942, BPBM 5842) are southern form *C. novaeguineae*. Although the distribution of this species is poorly known from Vogelkop, I speculate that northern form *C. novaeguineae* may not be present there as the central highlands of New Guinea bisect the island east of the Vogelkopian isthmus. Earlier, Wermuth and Mertens (1977) gave the Aru Islands as being within the range of this species. That record was based on an erroneously identified *C. porosus* (Ross, 1986). Recent investigations by Whitaker (1980b) support the contention that *C. novaeguineae* is endemic to the island of New Guinea proper. *Crocodylus mindorensis* is an endangered species known from the Philippine islands of Busuanga, Jolo, Luzon, Masbate, Mindanao, Mindoro, Negros, and Samar (Groombridge, 1982; Ross and Alcalá, 1983; Ross, 1986).

DISCUSSION

The fact that the genus *Crocodylus* is extremely conservative in its biochemical and immunological composition (Densmore, 1983), coupled with the morphological similarities of most taxa (King and Brazaitis, 1971; Brazaitis, 1974), contributes to the problem of crocodylian classification and results in the misidentification of individuals, even by experts with specimens in hand (Brazaitis, 1971; Ross and Ross, 1974; Ross, 1986). A further difficulty is that most taxonomic descriptions are not quantitative and are generally based on few specimens, sometimes entirely lacking type specimens or supporting data (Fuchs, 1974; Fuchs et al., 1974a, 1974b).

Schmidt (1928, 1935) described *C. novaeguineae* and *C. mindorensis* on the basis of two and four skulls, respectively. Both of the former and one of the later specimens had been lying in museum collections for over two decades and were initially regarded as atypical *C. porosus*. However, their validity as new taxa was more readily accepted once Schmidt expanded his descriptions as more specimens became available to him (1932, 1956). The two species named by Schmidt are still poorly represented in museum collections and study of them has subsequently been obfuscated when researchers failed to grant their distinction (Wermuth, 1964; Cohen and Gans, 1970).

The results of this study clearly vindicate Schmidt's judgment that a sound morphological basis exists for the recognition of *C. novaeguineae* and *C. mindorensis* as distinct species. This position is reinforced by recent electrophoretic evidence (Densmore, 1983), despite the fact that the technique often failed to discriminate between species of the genus *Crocodylus*.

The only previous study to examine variation of a crocodylian species throughout its range focused on squamation (Ross and Roberts, 1979). However, their results were inconclusive because of a lack of specimens from the central portion of the range of *Alligator mississippiensis*.

In discussion of intraspecific variation of *C. porosus*, Wermuth and Fuchs (1985, sheet A-306.002.001.009) state that "it does not seem to be justified to discern geographical subspecies before the variability within the whole distributional area has been investigated." Although they recognize that principle, they have not adhered to it in their own studies (Fuchs,

1974; Fuchs et al., 1974a, 1974b). In addition to the confusion caused by these authors regarding the classification of *C. novaeguineae* and *C. mindorensis*, they created further disarray by their unjustified partitioning of *C. cataphractus*, *C. niloticus* and *Caiman crocodilus* (Frair and Behler, 1984). Further, the hide illustrated as *C. n. novaeguineae* in Wermuth and Fuchs (1981) upon which the morphology is described is not of that species (it appears to be a PNG *C. porosus*).

Although molecular analysis was not attempted herein, my morphological results lend quantitative support to Neill's (1971) supposition that phenotypic variation exists in geographic isolates of *C. novaeguineae*. Some sources of variation are relatively consistent within those isolates and provide a basis for the identification of individuals as to region of origin. Such differences appear to be independent of the sex, age, size, and habitat of individuals. Geographic variation in external body structures of southern form *C. novaeguineae* from varying habitats does not occur between drainage systems shown in Figure 2 (Montague, 1984), although it is not known whether such variation exists elsewhere. A large body of data documents the striking differences in nesting strategies of these allopatric and reproductively isolated forms. Further investigation, especially greater detailed hide morphology and the incorporation of molecular techniques, may yield more persuasive evidence for the partitioning of *C. novaeguineae* and lead to recognition of the southern form as a new taxon. In this regard, the companion studies of C. A. Ross (unpubl.) on the Indopacific palustrine *Crocodylus* complex may prove of special value.

APPENDIX I: INSTITUTION SPECIMENS EXAMINED

Crocodylus novaeguineae.—southern form: AMNH (2 preserved: 111642, 82536); BPBM (1 skin and skull, 1 preserved: 3942, 5842); BMNH (2 skulls: 86-5-20-1, 86-5-20-2); LSUMZ (25 embryos: 44674-44698; 21 preserved: 44699-44714, 44716-44720; 22 skulls: 44721-44742); NDSU (1 skull: 4864); PNGM (10 skulls: PMH series 0098, 0243, 0246, 0247, 0329, 0434, 0436, 0443, 0459, 0464); RMNH (19 preserved: 21912-21920, 21923-21927).

Crocodylus novaeguineae.—northern form: AMNH (skull: 64425); BMNH (13 preserved: 1969-662-1969-673, 1978-2177; FMNH (7 skulls: 2854, 13092, 14016, 14039, 14040, 14043, 14048); RMNH (15 skulls: 21817-21831; 6 preserved: 21906-21911).

Crocodylus mindorensis.—BMNH (preserved: 77-12-13-20); FMNH (4 skulls: 11135, 11137, 19891, 21904; 5 skins and skulls: 52357-52362); USNM (2 preserved: 228408, 229290).

Note Added in Proof.—Data on squamation used in this study were collected prior to publication of the methods employed by Ross and Mayer (1983). Hence, we differ with respect to counting dorsal midbody scales as noted in the METHODS. It was not possible to reanalyze my data on that scale character to conform with their approach, but I encourage future workers to adopt their methodology as a uniform stand. If one considers the dorsal midbody series to consist only of those scales lying in medial contact (as Ross and Mayer did) then the number typically found in both northern and southern form *C. novaeguineae* is 8, while the typical number for *C. mindorensis* is 10.

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