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CHELID TURTLES OF THE AUSTRALASIAN ARCHIPELAGO: II. A NEW SPECIES OF *CHELODINA* FROM ROTI ISLAND, INDONESIA

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ABSTRACT. A new species of *Chelodina* (Testudines: Pleurodira: Chelidae) is described from Roti Island, west of Timor, East Nusa Tenggara Province, in the southeastern Indonesian Archipelago. The species is endemic to Roti, a small and relatively xeric island. It is most similar and most closely related to *Chelodina pritchardi* from Papua New Guinea and *C. longicollis* from Australia, less closely related to *C. novaeguineae* and *C. reimanni* from New Guinea.

INTRODUCTION

The side-necked turtles of the family Chelidae that inhabit the Australasian Archipelago of eastern Indonesia and Papua New Guinea remain one of the least well known turtle faunas of the world. Until recently only two species of the snake-necked genus *Chelodina* were known from the regions north of Australia: *Chelodina novaeguineae* Boulenger, 1888 and *Chelodina siebenrocki* Werner, 1901. Since 1975, systematic studies have revealed an additional three species: *Chelodina parkeri* Rhodin and Mittermeier, 1976, *Chelodina reimanni* Philippen and Grossman, 1990, and *Chelodina pritchardi* Rhodin, 1993. The last of these, from the Kemp Welch River of southeastern Papua New Guinea, was described in the first paper of this series on the chelid turtles of the Australasian Archipelago. In this second paper of the series, I describe another new species of *Chelodina*, this time from Roti Island, west of Timor in southeastern Indonesia.

The first species of *Chelodina* to be described from anywhere in the Australasian Archipelago was *C. novaeguineae* Boulenger,

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Figure 1. Distribution of *Chelodina* subgeneric group "A" in northern Australia, New Guinea, and southeastern Indonesia. 1. Distribution of *Chelodina mccordi* on southwestern Roti Island, Indonesia. 2. Australian distribution of *C. novaeguineae* (sensu lato) in Northern Territory and Queensland. 3. Distribution of *C. pritchardi* in Papua New Guinea. 4. New Guinean distribution of *C. novaeguineae* in Irian Jaya and Papua New Guinea. 5. Approximate distribution of *C. reimanni* in Irian Jaya, Indonesia. Major watershed limits in New Guinea and Australia indicated as thick lines; thin dotted lines mark the 200 meter water depth limits around the eastern Indonesian islands as well as the continental Sahul Shelf surrounding Australia and New Guinea.

1888, which came from the southern New Guinea coastal region of what is now designated as the Western Province of Papua New Guinea. It is distributed throughout southern lowland New Guinea including extreme southeastern Indonesian Irian Jaya and southwestern Papua New Guinea. Similar forms of *Chelodina novaeguineae* (sensu lato) also occur in northern Queensland and northeastern Northern Territory in Australia (Fig. 1), although these forms probably represent separate and distinct taxa (J. Cann, personal communication to W. P. McCord). Soon after the original description of *C. novaeguineae*, Lidth de Jeude (1895) de-

scribed three specimens of this species from the island of Roti (originally spelled "Rotti"), west of Timor in southeastern present-day Indonesia. These specimens were collected on Roti in 1891 by Dr. Herman F. C. Ten Kate and donated to the Leiden Museum. Though extremely isolated from the rest of the range of *C. novaeguineae*, this locality has subsequently been duly noted in the distribution of *C. novaeguineae* without any further attempts at critical systematic comparison of its population to the populations in the New Guinean and Australian portions of the range. From the zoogeographic isolation of Roti, I long suspected that this population, if natural, must certainly represent a separate and distinct species, though probably closely related to *C. novaeguineae* (*sensu stricto*).

Unfortunately, Roti has become a difficult place to visit for field studies, due in part to the political upheaval on neighboring Timor, associated with the recent incorporation of Portuguese East Timor into Indonesia. For many years I attempted unsuccessfully to travel to Roti. A few years ago, I was fortunate to meet Dr. William P. McCord, who maintains an enormous collection of live turtles and whose primary interest is the diversity of species in the genus *Chelodina*. Dr. McCord, through his collection contacts in Indonesia (notably Mr. Frank Yowono), had recently succeeded in obtaining a series of 16 *Chelodina* from Roti. When I examined them, my original conviction that the Roti animals would be different from mainland New Guinean and Australian *C. novaeguineae* was confirmed.

Subsequent to my analysis of the McCord collection of Roti animals I obtained on loan two of the original specimens collected in 1891 by Dr. Ten Kate on Roti and still present in the National Museum of Natural History in Leiden. A comparison of those specimens with the description by Lidth de Jeude (1895) confirms that they are the original specimens, and that they are also the same taxon as McCord's specimens obtained from Roti by Frank Yowono. Both Leiden specimens also bear tags with the manuscript name "*Chelodina rottiensis* Brongersma." This name must now be considered a *nomen nudum*, as it was never published or described, but clearly Dr. Brongersma also deserves mention and credit for having previously recognized the distinctiveness of this new taxon from Roti. I thank him and Dr. Hoogmoed for releasing

the specimens and relinquishing claims to the formal description.

These 18 specimens of *Chelodina* from Roti Island were then critically compared to a series of 43 *Chelodina pritchardi* from southeastern Papua New Guinea, 51 *C. novaeguineae* from southwestern Papua New Guinea and adjacent Irian Jaya, 10 *C. novaeguineae* from northern Australia, 54 *C. longicollis* from eastern Australia, 12 *C. reimanni* from southeastern Irian Jaya, Indonesia, and 7 *C. steindachneri* from western Australia, for a total study series of 195 specimens. Analysis of external morphology and cranial osteology demonstrated that this isolated Roti population of *Chelodina* is indeed a new and distinct species of *Chelodina* subgeneric group "A" (sensu Goode, 1967). It is more similar to *C. pritchardi* of Papua New Guinea than it is to either New Guinean or Australian populations of *C. novaeguineae*. It now gives me great pleasure to formally describe this new species of *Chelodina* and to name it in honor of Dr. William P. McCord who succeeded in obtaining the series of animals that made confirmation and description of the new species possible.

TAXONOMY

Chelodina mccordi, sp. nov.

(Figs. 2–5)

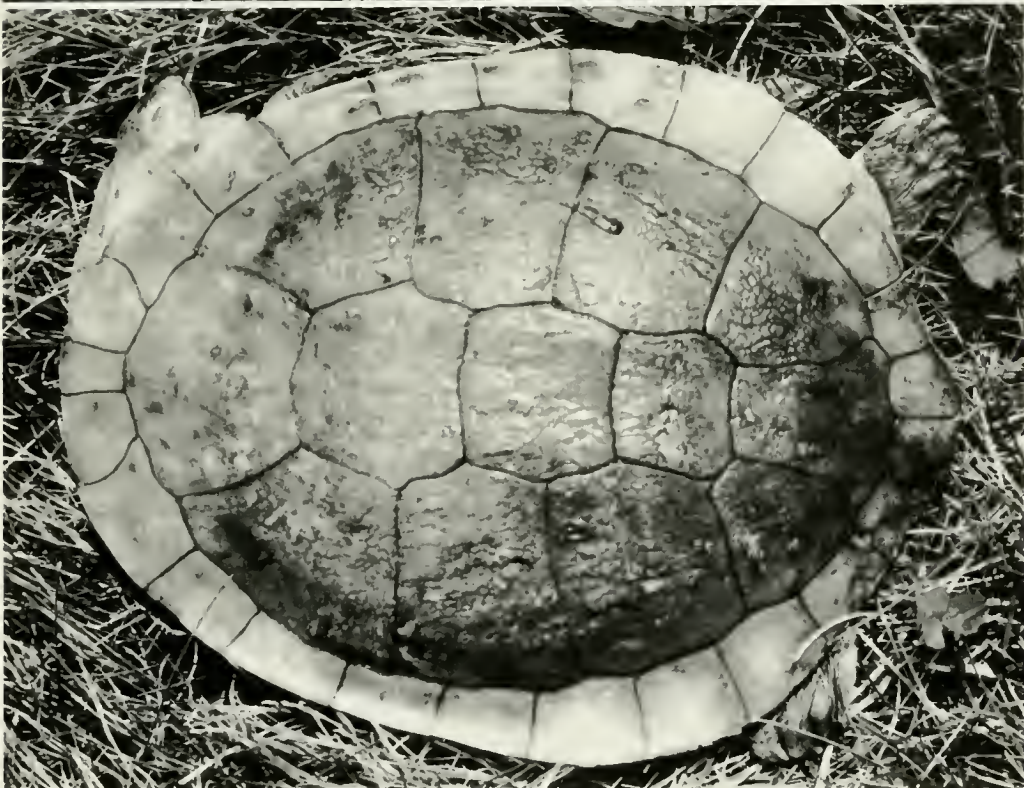
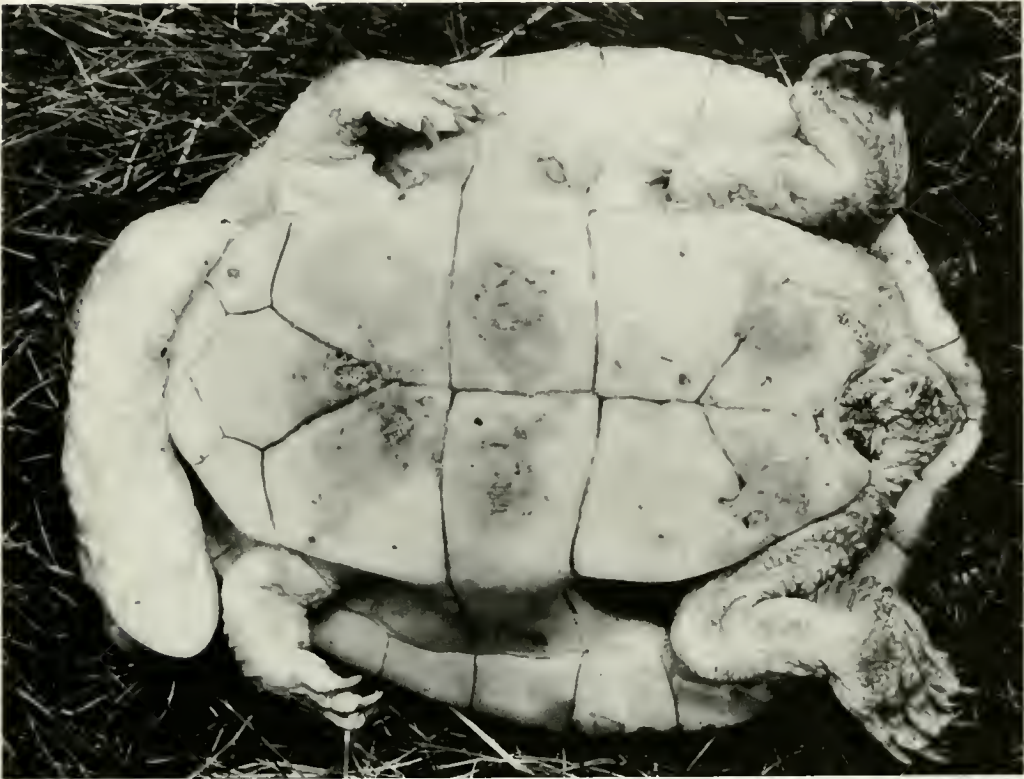
Chelodina novae guineae (partim) Ten Kate, 1894:689

Chelodina novae-guineae (partim) Lidth de Jeude, 1895:119; De Rooij, 1915:315

Holotype. MCZ 176730 (Fig. 2), alcohol-preserved adult female of 197.5 mm carapace length, purchased from native villagers by Frank Yowono in Kupang, western Timor, originally collected on Roti Island, East Nusa Tenggara Province, Indonesia; specimen is formerly from the private live collection of William P. McCord, and also bears old tag AGJR 450 from the personal preserved collection of Rhodin.

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Figure 2. Holotype of *Chelodina mccordi* (MCZ 176730), adult female measuring 197.5 mm carapace length, from Roti Island, Indonesia.



Paratypes. MCZ 176731, alcohol-preserved adult male of 153 mm carapace length, purchased from native villagers by Frank Yowono in Kupang, western Timor, originally collected on Roti Island; specimen is formerly from the private live collection of William P. McCord, and also bears old tag AGJR 364 from the personal preserved collection of Rhodin; MCZ 176732 (Fig. 3), alcohol-preserved adult female of 194 mm carapace length, purchased from native villagers by Frank Yowono in Kupang, western Timor, originally collected on Roti Island; specimen is formerly from the private collection of William P. McCord, and also bears old tag AGJR 368 from the private preserved collection of Rhodin; RMNH 10187 (Figs. 4–5), skeletal preparation of shell, skull, and limbs of adult of unknown sex (but probably female) of 179.5 mm carapace length, collected by Dr. Herman F. C. Ten Kate on “Rotti” [Roti Island, Indonesia] in 1891, originally described by Lidth de Jeude (1895) as a specimen of *Chelodina novaeguineae* Boulenger, 1888.

Referred Specimens. RMNH 4349, collected by Dr. Herman F. C. Ten Kate on “Rotti” [Roti Island, Indonesia] in 1891, originally described by Lidth de Jeude (1895) as a specimen of *Chelodina novaeguineae* Boulenger, 1888; AGJR 365–7, 369, 448–9, 452–7, 460, purchased from native villagers by Frank Yowono in Kupang, western Timor, originally collected on Roti Island, Indonesia, and formerly from the private live collection of William P. McCord. Personal specimens available on loan through the Chelonian Research Foundation, and eventually to be deposited at the Museum of Comparative Zoology.

Distribution. Known only from Roti Island, located about 20 km southwest of the western end of Timor in the Lesser Sunda Islands in the Province of East Nusa Tenggara of the southeastern Indonesian Archipelago (Fig. 1). Not known to occur on Timor itself. No current localities on Roti Island precisely documented as yet, but collectors indicate that the species is most readily found in rice paddies. Most rice paddies are located in the southwestern half of the island west and north of the village of Tudamedea, and along the cross-island road between Tudamedea and Ba’a. In addition, there are some limited rice paddies and small lakes in the northeast peninsular region of the island where the species might also occur, but a large portion of the rest of the island is relatively



Figure 3. Lateral head view of *Chelodina maccordi* (Paratype MCZ 176732), adult female.

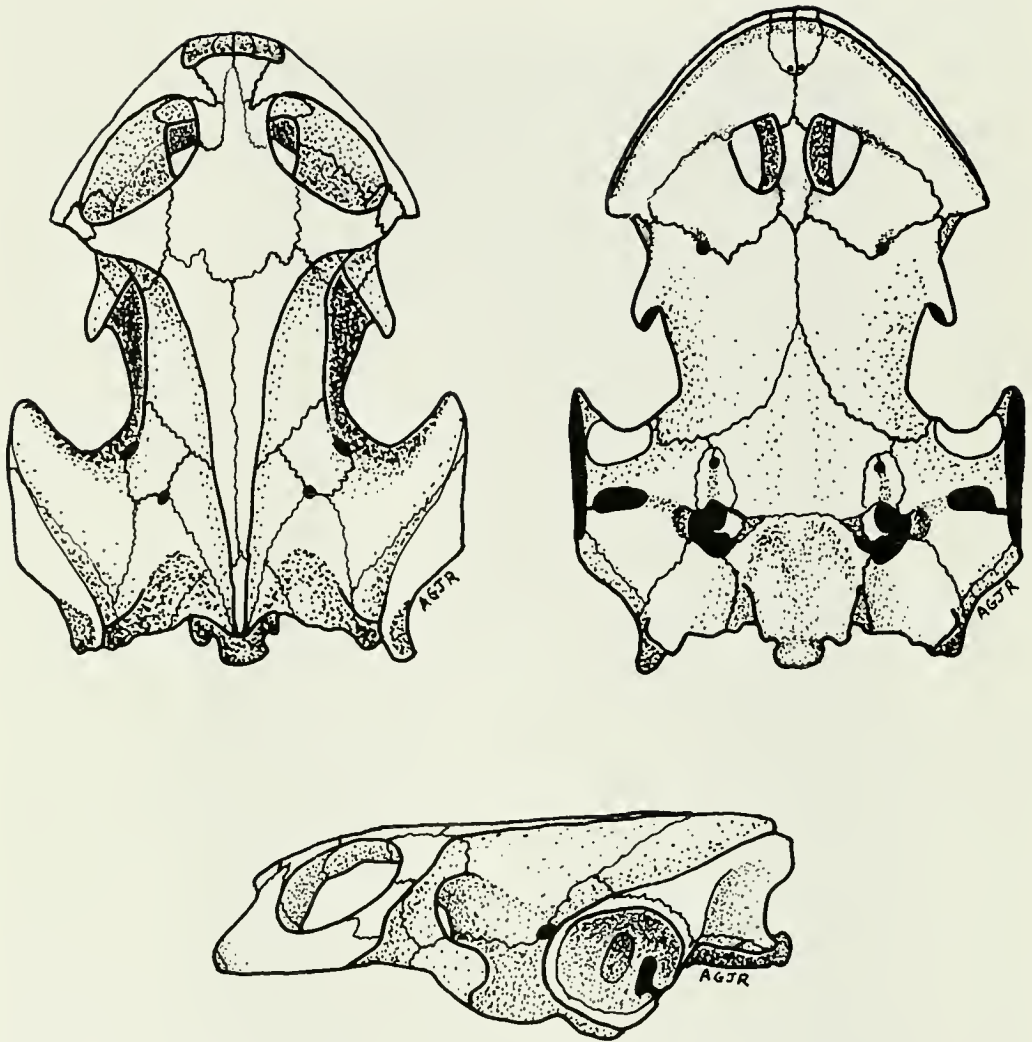


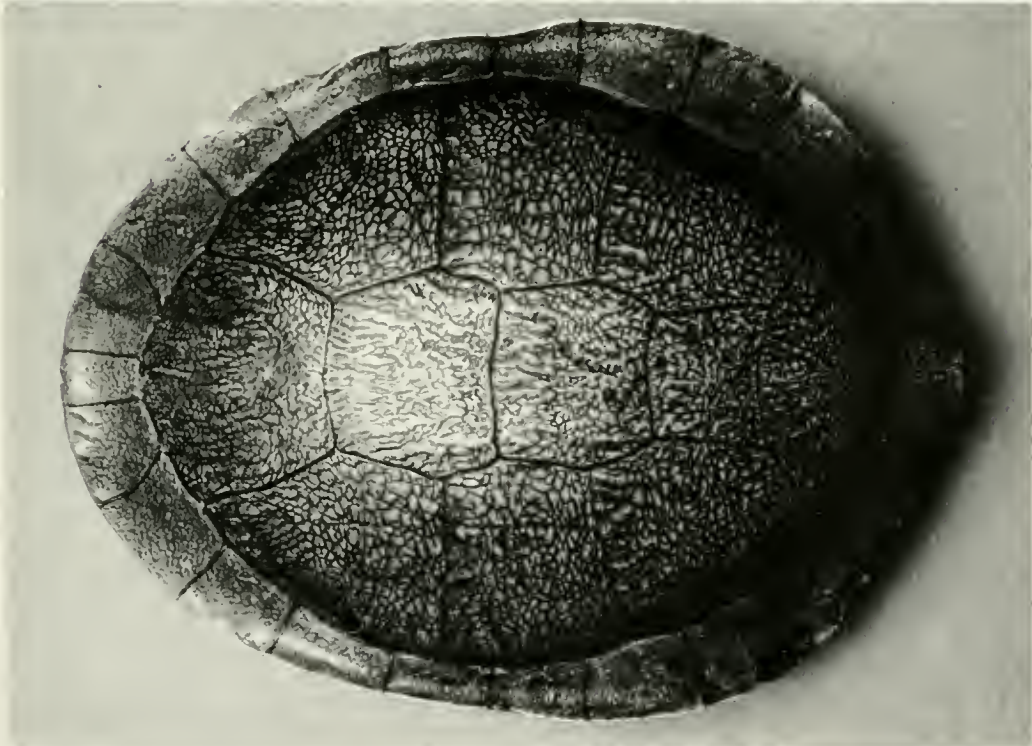
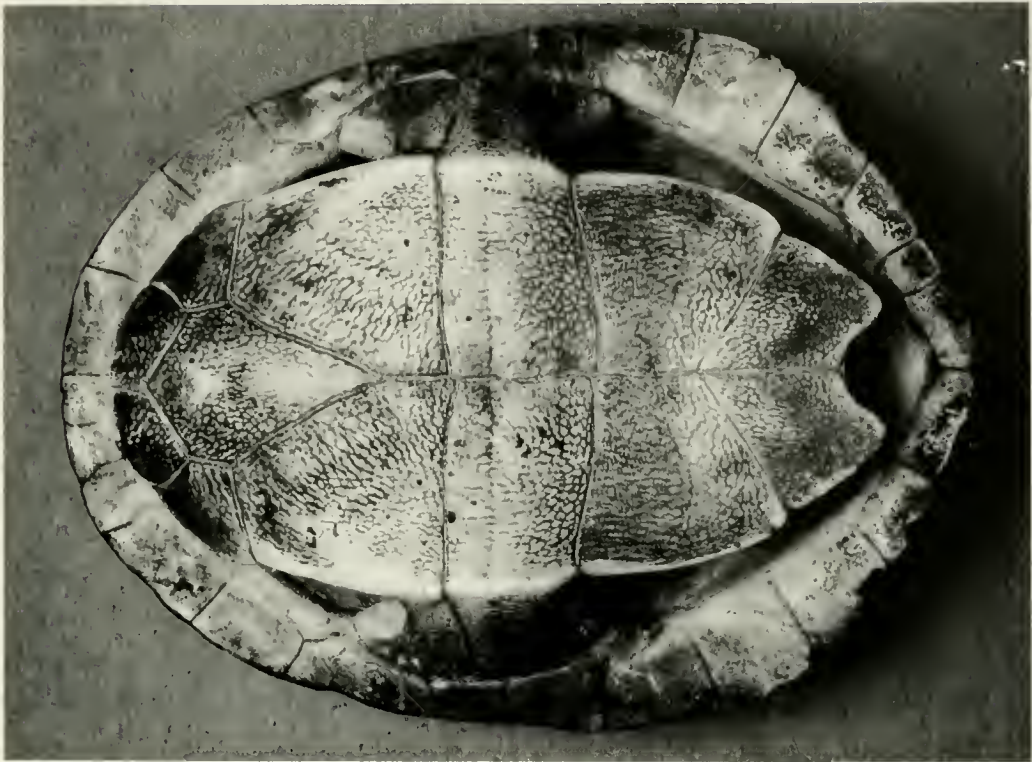
Figure 4. Dorsal, ventral, and lateral views of skull of *Chelodina mccordi* (Paratype RMNH 10187, adult of unknown sex measuring 179.5 mm carapace length) from Roti Island, Indonesia.

xeric with little surface water. The total area of Roti Island is only about 1,214 km², while the highest elevation reaches 444 m.

Type Locality. The collection locality of the holotype specimen obtained by Yowono from Roti Island cannot be stated precisely.

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Figure 5. Shell of *Chelodina mccordi* (Paratype RMNH 10187), originally collected in southwestern Roti in 1891 by Dr. Herman F. C. Ten Kate and described by Lidth de Jeude (1895).



However, a review of the natural history and travel writings of Dr. Ten Kate, who collected three specimens in 1891, including one of the paratypes, and a careful study of older and modern maps of Roti can help further restrict the probable type locality. Dr. Ten Kate states in his travelogue (Ten Kate, 1894:688–689) that he observed a small specimen of *Chelodina novae guineae* [= *Chelodina mccordi*] that fishermen had just caught on 7 September 1891 at the inland freshwater lake “Danau Naloek (Naroek)” near lake “Danau Linggoe” [*Danau* = *Lake* in Bahasa Indonesian]. Danau Naloek was reached approximately three fifths of the way along a four and a half hour trip while Dr. Ten Kate traveled from “Ti-Kanakétoe” (also referred to as simply “Ti”) [= modern Danaheo, or Danahoe, along the southwestern shore, 4 km south of Tudameda] to “Baä” [= modern Ba’a along the northern shore]. The locality “Danau Naloek” does not appear on modern maps, but Dr. Ten Kate mentions that he followed Dr. Wichmann’s earlier route through the area, and Wichmann (1892) shows the lake “Danu naluk” on his map about halfway between Ti and Baä, which he also indicates by their more modern names of Danoheoh and Namudale [= Namodale, a suburb of Ba’a]. Dr. Ten Kate further states that Danau Naloek was located in the middle of dry rolling grassland, and that shortly after leaving the lake he entered forested landscape at “boschrijke . . . Lóameko” where he crossed the administrative border between Dengka and Lelain. This provincial boundary still occurs on modern maps with the villages of Busalangga and Longgo [probably = Danau Linggoe] just west of there, at approximately the three fifths point along the Danaheo-Ba’a road. It is therefore reasonable to state that the species occurred at Danau Naloek in the Busalangga region in 1891 and to assume that Dr. Ten Kate probably collected or obtained at least one of his paratype specimens there. Therefore, the type locality of *Chelodina mccordi* is hereby restricted to Danau Naloek, near Busalangga, ca. 11 km northeast of Tudameda and ca. 8 km southwest of Ba’a, elevation ca. 115 m, southwestern Roti Island (10°48’S, 123°00’E), East Nusa Tenggara Province, Indonesia.

Diagnosis. A medium-sized isolated Rotinese snake-necked chelid turtle of *Chelodina* subgeneric group “A” (sensu Goode, 1967 and Burbidge *et al.*, 1974) with relatively wide head, wide

TABLE 1. FEATURES DISTINGUISHING FOUR SPECIES OF *CHELODINA* SUBGENERIC GROUP "A". FOR MERISTIC BASIS OF DISTINGUISHING FEATURES, SEE TABLES 3 AND 5 AND FIGURES 4–6. PLUSSES AND MINUSES FOR THE INTERMEDIATE CATEGORIES INDICATE SLIGHT DIFFERENTIATION BETWEEN THE TWO SPECIES IN THAT CATEGORY.

Feature	<i>longicollis</i>	<i>pritchardi</i>	<i>mccordi</i>	<i>novaeguineae</i>
External				
Carapace width	Interm.	Wide	Wide	Narrow
Head width	Narrow	Narrow	Wide	Wide
Plastron width	Wide	Interm.	Narrow	Narrow
Marginal 1 width	Wide	Wide	Narrow	Interm.
Composite ratio	Low	Interm. (–)	High	Interm. (+)
Osteology				
Triturating width	Narrow	Interm. (–)	Interm. (+)	Wide
Skull depth	Shallow	Interm.	Interm.	Deep
Skull width	Narrow	Narrow	Wide	Wide
Robusticity	Low	Interm. (–)	Interm. (+)	High

carapace, narrow plastron, narrow first marginal, wide skull, intermediate triturating surface width, intermediate skull depth, and intermediate to mildly increased skull robusticity. Most similar to *C. pritchardi*, but differentiated from it by the much narrower first marginal, relatively wider second marginal, wider head, narrower plastron, wider skull, and very slightly increased skull robusticity. Also similar to *C. novaeguineae*, but differentiated from that taxon by the wider carapace, slightly narrower first marginal, significantly narrower triturating surface width, shallower skull, and significantly decreased skull robusticity.

In most morphological respects *C. mccordi* is intermediate between *C. novaeguineae* and *C. longicollis*, and most similar to *C. pritchardi*, especially in juvenile and subadult stages. See Table 1 for a summary of differences among *C. mccordi*, *C. pritchardi*, *C. longicollis*, and *C. novaeguineae*.

Etymology. The specific epithet is a patronym honoring Dr. William P. McCord, a veterinarian with a deep interest in turtles, who was instrumental in securing the large study series demonstrating the distinctiveness of the species.

Related taxa. *Chelodina mccordi* is most similar to the following five chelid taxa from New Guinea and Australia, all members of *Chelodina* subgeneric group "A": *Chelodina longicollis* (Shaw,

1794), *Chelodina novaeguineae* Boulenger, 1888, *Chelodina pritchardi* Rhodin, 1993, *Chelodina reimanni* Philippen and Grossman, 1990, and *Chelodina steindachneri* Siebenrock, 1914. Type localities and specimens for these species are listed in the first paper of this series (Rhodin, 1993).

DESCRIPTION

External Morphology

Carapace. Carapace of *C. mccordi* moderately rugose and broadly oval, width averaging 77.9% of length [Fig. 6(1)A], moderately wider posteriorly at about marginals 6–7, with slight expansion of marginals 6–8. Moderately prominent lateral marginal recurving from about marginal 4 through 7, often partially involving marginals 3 and 8 as well. Somewhat less prominent recurving in smaller specimens. Moderate supracaudal ridging with slight adjacent concavity of marginal 11. No vertebral knobs, keel, or ridging. Slight vertebral flattening and shallow midline furrow in larger females, smoothly convex in smaller females and males. No supracaudal notch or marginal serrations. Dorsal nuchal long and broad, not projecting anterior to carapace margin. Ventral underlap of nuchal also relatively long and broad. Vertebral 1 widest, then 2, 3, 5, and 4 in descending order of width in normal specimens. Basic external measurements of *C. mccordi* presented in Table 2, differences from *C. pritchardi*, *C. novaeguineae*, and *C. reimanni* presented in Table 3 and Figure 6 (parts 1 and 2).

Many individuals with altered vertebral and costal pattern with supernumerary or fused scutes. Five of 18 specimens have 6 vertebral scutes, three with a small intercalated supernumerary scute between V3 and V4, one between V2 and V3, and one between V4 and V5. Two specimens have three symmetrical costals on each side, one has three costals on one side, four on the other. This deformity creates a very wide fifth vertebral, indicating a fusion of the fourth costals with V5. The larger Leiden specimen (RMNH 10187) originally collected by Dr. Ten Kate has this deformity with a symmetrical pattern of three costals on each side and a very wide fifth vertebral (Fig. 5). Lidth de Jeude (1895) interpreted this as a normal pattern. One of Yowono's specimens

TABLE 2. BASIC EXTERNAL DIMENSIONS OF *CHELODINA MCCORDI*, ALL MEASUREMENTS IN MM. CL = CARAPACE LENGTH (STRAIGHT-LINE IN MIDLINE); CW = CARAPACE WIDTH (GREATEST); CD = CARAPACE DEPTH (GREATEST IN MIDLINE); PL-M = PLASTRON LENGTH (IN MIDLINE); PL-T = PLASTRON LENGTH (TOTAL, INCLUDING ANAL SPURS); PW = PLASTRON WIDTH (AT AXILLARY NOTCH); HW = HEAD WIDTH (TYMPANIC); J = JUVENILE; F = FEMALE; M = MALE; U = UNKNOWN SEX.

Specimen Number	Sex	CL	CW	CD	PL-M	PL-T	PW	HW
RMNH 4349	j	99.5	73.0	31.0	76.0	81.0	43.5	18.6
AGJR 460	f	150.0	118.0	49.0	119.5	126.0	70.0	25.1
AGJR 455	m	150.5	114.5	49.5	117.5	124.5	67.0	26.3
AGJR 454	m	151.0	116.5	47.0	115.5	123.5	66.0	25.0
MCZ 176731	m	153.0	120.5	47.5	116.5	125.0	67.0	26.0
AGJR 449	m	155.0	123.5	51.5	121.5	128.0	73.0	25.3
AGJR 367	f	159.0	121.0	52.0	124.0	131.0	71.0	26.3
AGJR 456	m	162.5	127.5	53.5	120.5	130.5	70.0	25.0
AGJR 369	u	163.0	125.0	52.0	123.0	132.5	71.0	—
RMNH 10187	u	179.5	140.0	60.0	138.0	147.0	81.5	28.7
AGJR 457	f	180.0	137.0	60.0	138.0	147.0	80.0	28.7
AGJR 448	f	181.5	143.5	63.5	139.0	146.5	81.5	27.8
AGJR 366	f	182.0	142.5	60.0	145.0	153.0	84.5	27.9
MCZ 176732	f	194.0	152.0	67.0	153.0	162.0	85.0	30.5
MCZ 176730	f	197.5	156.0	67.5	150.5	159.5	86.5	29.6
AGJR 452	f	202.0	159.0	73.0	161.5	171.0	93.0	31.2
AGJR 365	f	206.0	162.0	72.0	161.0	171.0	92.0	31.8
AGJR 453	f	213.0	162.0	77.5	162.5	172.0	95.0	32.8

(AGJR 368) has this identical deformity, and another (AGJR 365) has it on one side only. Five specimens have markedly reduced fourth costals, often on one side only, giving a slightly wider asymmetrical fifth vertebral. One of the specimens with this deformity is the smaller Leiden specimen (RMNH 4349) originally collected by Dr. Ten Kate.

Width relationships of marginal scutes 1 and 2 distinctive, with M1 much narrower than M2 as measured along the V1-C1 scute border. M1 typically half as wide as M2. In *C. pritchardi* M1 is wider or subequal to M2, and in *C. novaeguineae* M1 averages about 80% of the width of M2 (Fig. 7).

Carapace slightly less broad in *C. mccordi* than in *C. pritchardi*, but significantly broader than in *C. novaeguineae*. Lateral marginal recurving typical for *C. mccordi*, not present in *C. pritchardi*,

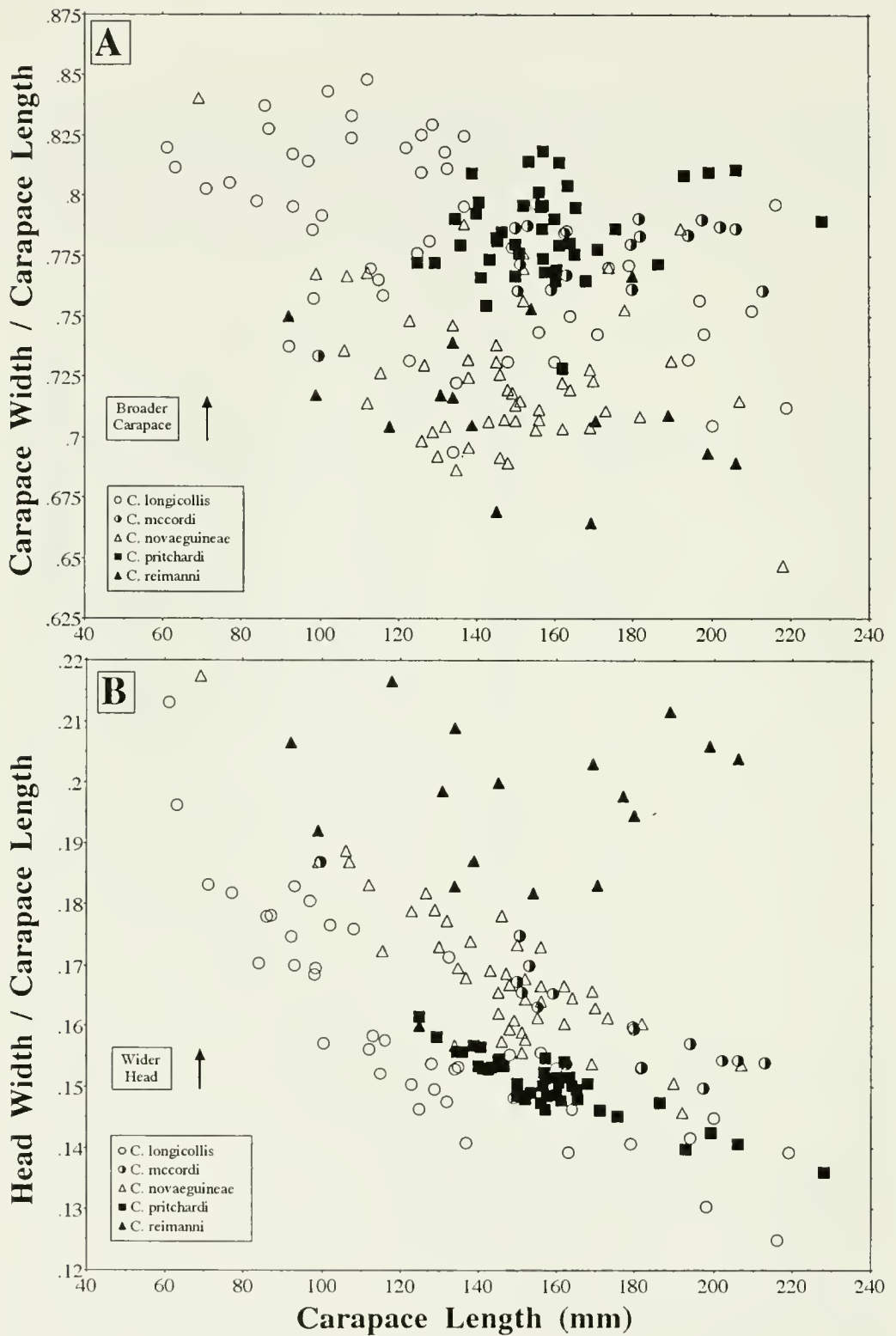


Figure 6. (Part 1). Shell morphometrics. Graphs plotting morphometric variation for four species of *Chelodina* subgeneric group "A", showing the relationships of: A. carapace width ratio (Carapace Width/Carapace Length); B. head width ratio (Head Width/CL).

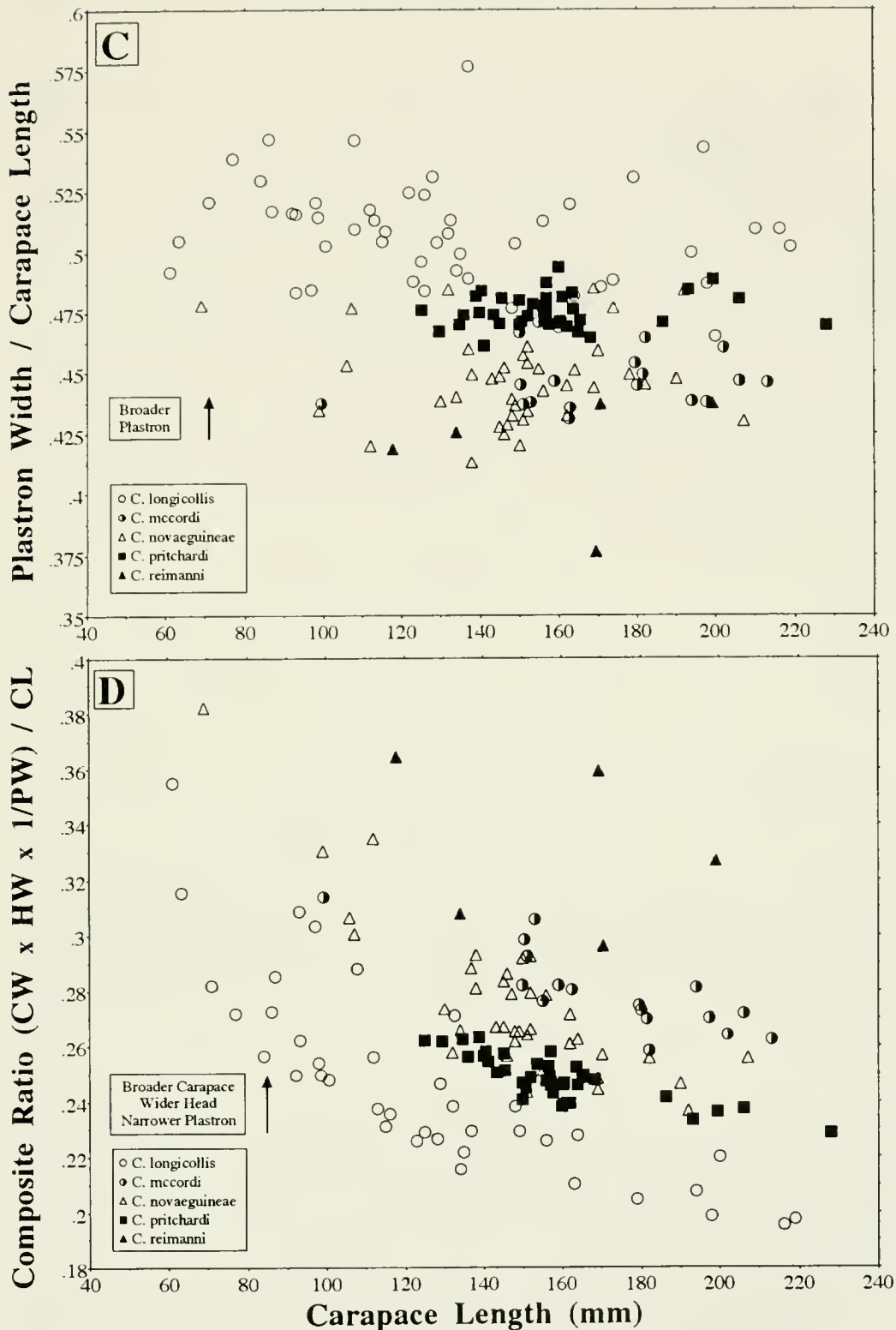


Figure 6. (Part 2). Shell morphometrics. **C.** plastron width ratio (Plastron Width/CL); and **D.** composite ratio of $(CW \times HW \times 1/PW)/CL$ expressed as a trivariate product; all versus Carapace Length. Note the position of *C. mccordi* as most similar to *C. pritchardi* in terms of carapace width (A), but most similar to *C. novaeguineae* in terms of head width (B), plastron width (C), and composite ratio (D).

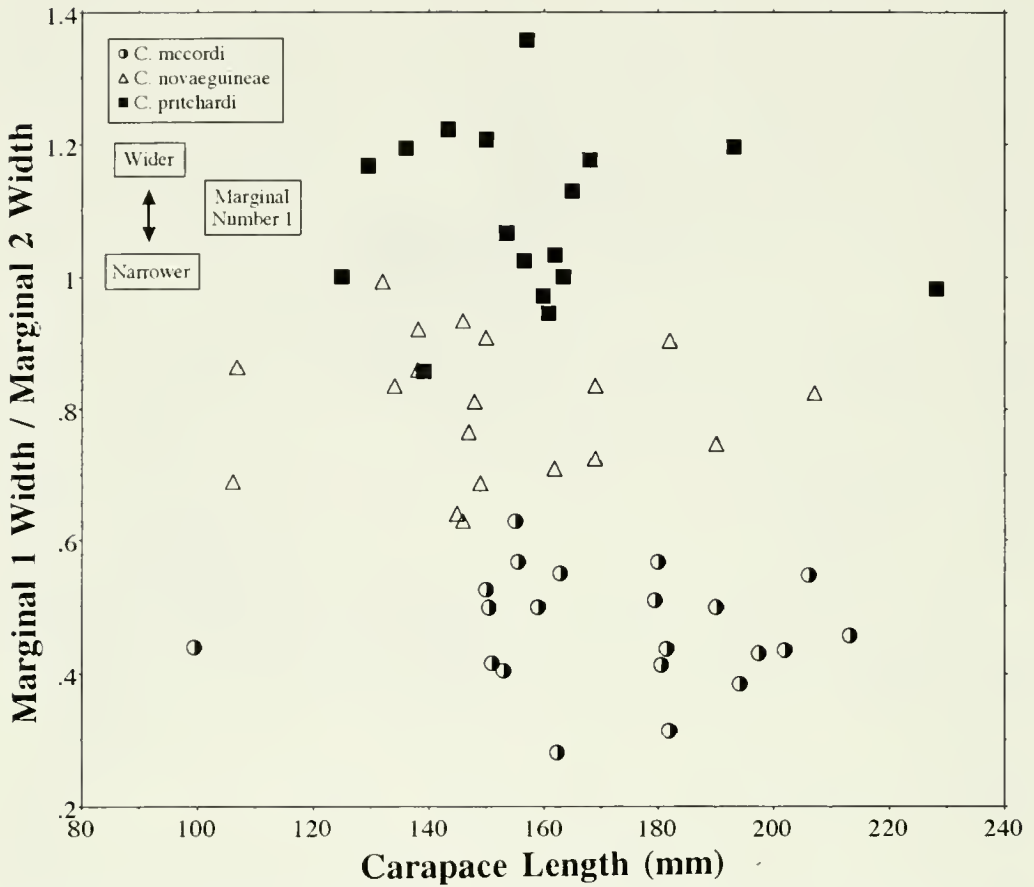


Figure 7. Shell morphometrics. Graph plotting morphometric variation for M1/M2 ratio (marginal number 1 width/marginal number 2 width) versus carapace length for *Chelodina mccordi*, *C. pritchardi*, and *C. novaeguineae*, showing that *C. mccordi* has M1 about half as wide as M2, *C. pritchardi* has M1 slightly wider or subequal to M2, and *C. novaeguineae* has M1 about 0.8 times as wide as M2.

not present or only very minimally developed in *C. novaeguineae*. Supracaudal ridging with adjacent mild marginal concavity also typical for *C. mccordi*, not present in *C. pritchardi* or *C. novaeguineae*.

Carapace moderately deep in large specimens, relatively flatter in younger ones. No sexual dimorphism in carapace depth of specimens examined, with like-sized males and females with same carapace depth. Older females of larger body size all with deeper shells. Carapace depth in *C. mccordi* slightly deeper than in either *C. pritchardi* or *C. novaeguineae*.

Color variable, with most specimens having a distinctive light

grayish-brown carapace unusual for *Chelodina* subgeneric group "A". Some specimens darker chestnut brown, more typical of the color seen in *C. novaeguineae* and *C. pritchardi*. Carapace scutes moderately rugose with retention of concentric growth lines only in small specimens.

Plastron. Plastron broad, axillary width averaging 57.9% of midline plastral length. Anterior lobe moderately broad, similar to *C. novaeguineae*, but not as broad as *C. pritchardi* [Fig. 6(2)-C]. Slight expansion of anterior plastral lobe at posterior edge of humeral scutes, similar to *C. pritchardi*. Anal notch moderately deep, no sexual dimorphism noted. Intergular broad, long, and without marginal contact. Plastral scute medial length formula $Ig > An \geq Abd > Fem > Pec > Gul$. *C. pritchardi* usually with $Pec \geq Fem$, *C. novaeguineae* with either $Pec > Fem$ or $Fem > Pec$. No axillary or inguinal scutes.

Plastron color light yellowish-white with many specimens having thin irregular light-brown areas along the plastral sutures. Original specimens of Dr. Ten Kate with oxidized plastrons, all of Yowono's specimens without oxidation. Plastron most similar to *C. pritchardi*, but generally with more pigment. Hatchlings with a beautiful orange and gray pattern covering plastron and ventral soft parts, gradually fading with growth (McCord, personal communication).

Head and Soft Parts. Head with small irregular scales covering temporal skin, smooth over parietal and interorbital roof. Neck with low soft tubercles, generally more similar to *C. pritchardi* than the slightly more prominent, firmer tubercles in *C. novaeguineae*. Soft parts light to moderate gray dorsally, whitish ventrally, generally lighter in color than in either *C. pritchardi* or *C. novaeguineae*. Hands and feet with four claws each.

Head width moderately wide, similar to the relatively broad-headed *C. novaeguineae*, significantly wider than the narrow-headed *C. pritchardi* and *C. longicollis* [Fig. 6(1)B], and narrower than the broad-headed *C. reimanni*. Head width not as wide as in the broad-headed members of *Chelodina* subgeneric group "B" (*C. expansa*, *C. rugosa*, *C. siebenrocki*, *C. parkeri*, and *C. oblonga*). Relative narrowing of the head ontogenetically.

A few specimens of "*C. novaeguineae*" said to come from Roti, but provided without reliable data, have broad heads most similar

TABLE 3. MEANS AND STANDARD DEVIATIONS FOR SHELL MEASUREMENT RATIOS OF THREE *CHELODINA* SPECIES. ABBREVIATIONS AS IN TABLE 2. DATA BASED ONLY ON SPECIMENS OF CARAPACE LENGTH GREATER THAN 100 MM. *C. NOVAEGUINEAE* INCLUDES ONLY NEW GUINEAN SPECIMENS, NOT AUSTRALIAN ONES. M1 = WIDTH OF MARGINAL NUMBER 1, M2 = WIDTH OF MARGINAL NUMBER 2; FOR THIS MEASUREMENT ONLY, *C. PRITCHARDI* N = 17 AND *C. NOVAEGUINEAE* N = 19.

Ratio	<i>C. pritchardi</i> (n = 43)	<i>C. mccordi</i> (n = 17)	<i>C. novaeguineae</i> (n = 51)
CW/CL	.785 ± .018	.779 ± .012	.723 ± .028
PW/PL-M	.610 ± .012	.579 ± .010	.576 ± .018
HW/CL	.150 ± .005	.160 ± .007	.167 ± .010
CD/CL	.328 ± .014	.335 ± .015	.327 ± .021
M1/M2	1.089 ± .129	.465 ± .090	.803 ± .105

to *C. reimanni* and extremely deep robust shells of a dark black color. These distinct animals appear to represent a different taxon and have been excluded from this analysis of *C. mccordi*, awaiting further confirmation of their probably disparate geographic origin.

Size and Sexual Dimorphism. The largest specimen of *C. mccordi* recorded is a female of 213 mm carapace length. The largest male examined has a carapace length of 162.5 mm, indicating probable sexual dimorphism, with females larger than males. Calculating the sexual dimorphism index according to the method of Gibbons and Lovich (1990) yields an SDI value of approximately 1.31 for *C. mccordi*. The SDI for *C. pritchardi* is 1.22, that for New Guinean *C. novaeguineae* 1.37. The maximum size recorded for *C. pritchardi* is 228 mm, and for New Guinean *C. novaeguineae* 218 mm (Rhodin, 1993). However, in general, and for most specimens representing typical mature adults, *C. mccordi* is significantly larger than New Guinean *C. novaeguineae*, slightly smaller than *C. pritchardi*, and significantly smaller than Australian *C. novaeguineae*, which reaches carapace lengths of 279 to 300 mm (Cann, 1978; Rhodin, 1993).

Osteology

Skull. The description of skull osteology is based on the examination of 36 skulls of *Chelodina* subgeneric group "A". Of these, 4 are *C. mccordi*, 6 *C. pritchardi*, 7 *C. longicollis*, 15 *C. novaeguineae* (12 from New Guinea, 3 from Australia), 2 *C. stein-*

TABLE 4. BASIC SKULL MEASUREMENTS FOR *CHELODINA MCCORDI*. SL = SKULL LENGTH (SNOUT–OCCIPITAL CONDYLE); SWT = SKULL WIDTH, TYMPANIC MAXIMUM; SWM = SKULL WIDTH, MAXILLARY MAXIMUM; SDM = SKULL DEPTH AT POSTERIOR EDGE OF MAXILLAE; SD = SKULL DEPTH IN MIDLINE BETWEEN SUPRAOCCIPITAL SPINE AND BASISPHENOID; IOW = INTER-ORBITAL WIDTH, MINIMAL; OW = ORBITAL WIDTH, SHORT AXIS; PtW = PTERYGOID WIDTH, MINIMAL; TW = TRITURATING WIDTH, MAXILLARY (MEASURED IN MIDLINE FROM TOMIAL EDGE TO ANTERIOR CHOANAL BORDER). REFER TO TABLE 5 AND FIGURES 8(1) AND 8(2) FOR ANALYSIS OF SKULL MEASUREMENT RATIOS.

Specimen Number	SL	SWT	SWM	SDM	SD	IOW	OW	PtW	TW
AGJR 449	35.5	24.5	20.2	8.8	10.0	3.7	8.4	11.9	4.7
RMNH 10187	40.1	27.7	22.9	9.5	11.0	4.3	8.9	13.2	5.7
AGJR 452	43.6	30.1	25.6	10.1	12.1	4.9	9.5	14.2	6.6
AGJR 453	45.5	32.0	25.9	10.6	13.4	5.5	9.6	14.5	7.1

dachneri, and 2 *C. reimanni*. Refer to Tables 4 and 5 and Figure 8 (parts 1 and 2) for additional skull measurements and ratios, and Figure 3 for skull illustrations of *C. mccordi*. Comparative figures of skulls of *C. pritchardi*, *C. novaeguineae*, *C. reimanni*, and *C. longicollis* are in Rhodin (1993).

The skull of *C. mccordi* is a typical *Chelodina* subgeneric group “A” type skull, not overly elongate, flattened, or wide as in subgeneric group “B”. It is strikingly similar to *C. pritchardi* and differs markedly from *C. novaeguineae*. Like in *C. pritchardi*, the skull of *C. mccordi* is differentiated from *C. novaeguineae* by its relative lack of robusticity. *C. novaeguineae* has wide and robust

TABLE 5. MEANS AND STANDARD DEVIATIONS FOR SKULL MEASUREMENT RATIOS OF THREE *CHELODINA* SPECIES. ABBREVIATIONS AS IN TABLE 4. *C. NOVAEGUINEAE* INCLUDES ONLY NEW GUINEAN SPECIMENS, NOT AUSTRALIAN ONES.

Ratio	<i>C. pritchardi</i> (n = 6)	<i>C. mccordi</i> (n = 4)	<i>C. novaeguineae</i> (n = 15)
SWT/SL	.648 ± .013	.694 ± .006	.687 ± .024
SWM/L	.553 ± .006	.574 ± .009	.532 ± .032
SD/SL	.290 ± .009	.282 ± .009	.320 ± .018
TW/SL	.144 ± .005	.145 ± .010	.194 ± .009
PtW/SWT	.522 ± .014	.472 ± .014	.461 ± .018
IOW/OW	.470 ± .037	.503 ± .056	.570 ± .055

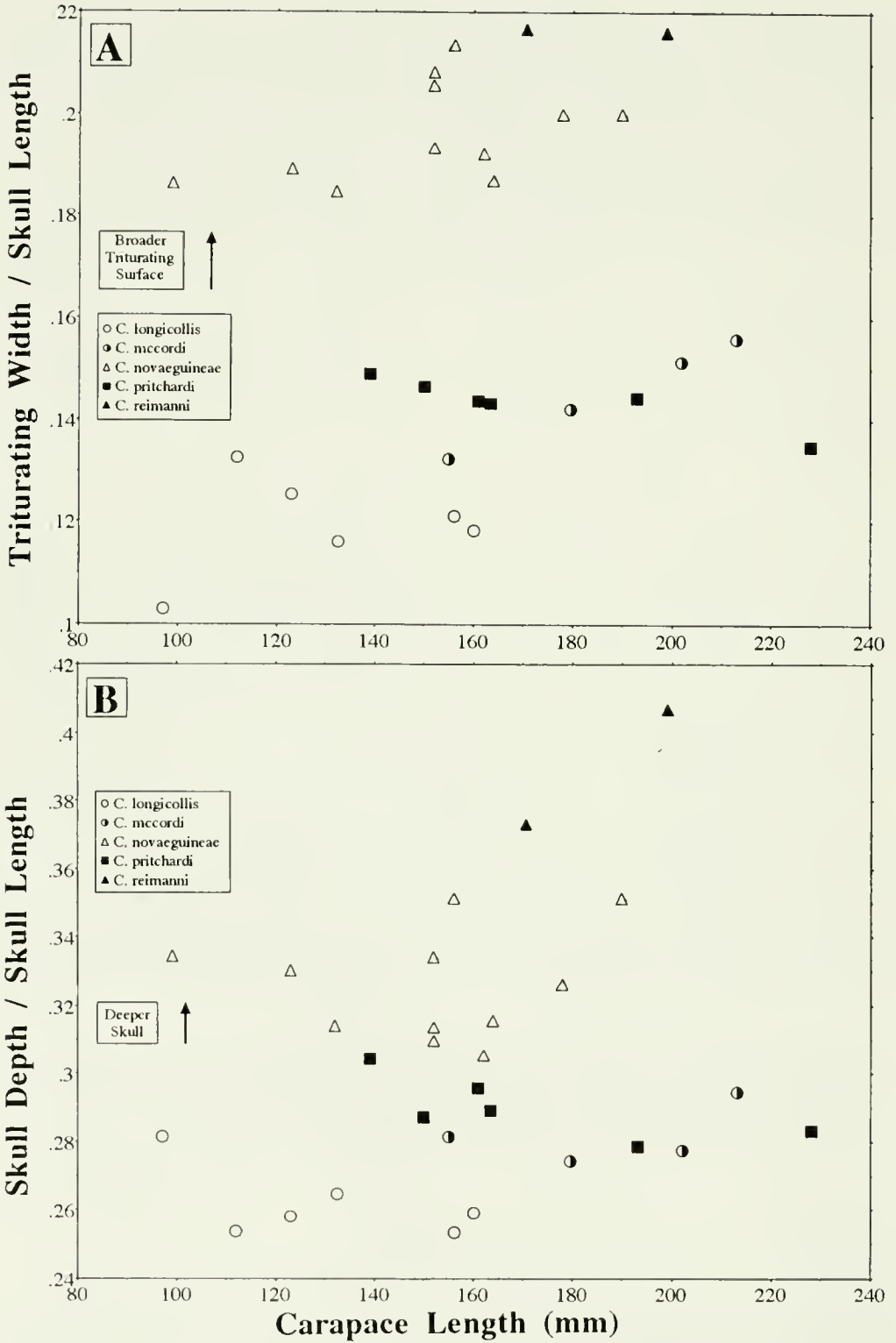


Figure 8. (Part 1). Skull morphometrics. Graphs plotting morphometric variation for four species of *Chelodina* subgeneric group "A", showing the relationships of: A. maxillary triturating width ratio (TW/Skull Length); B. skull depth ratio (SD/SL).

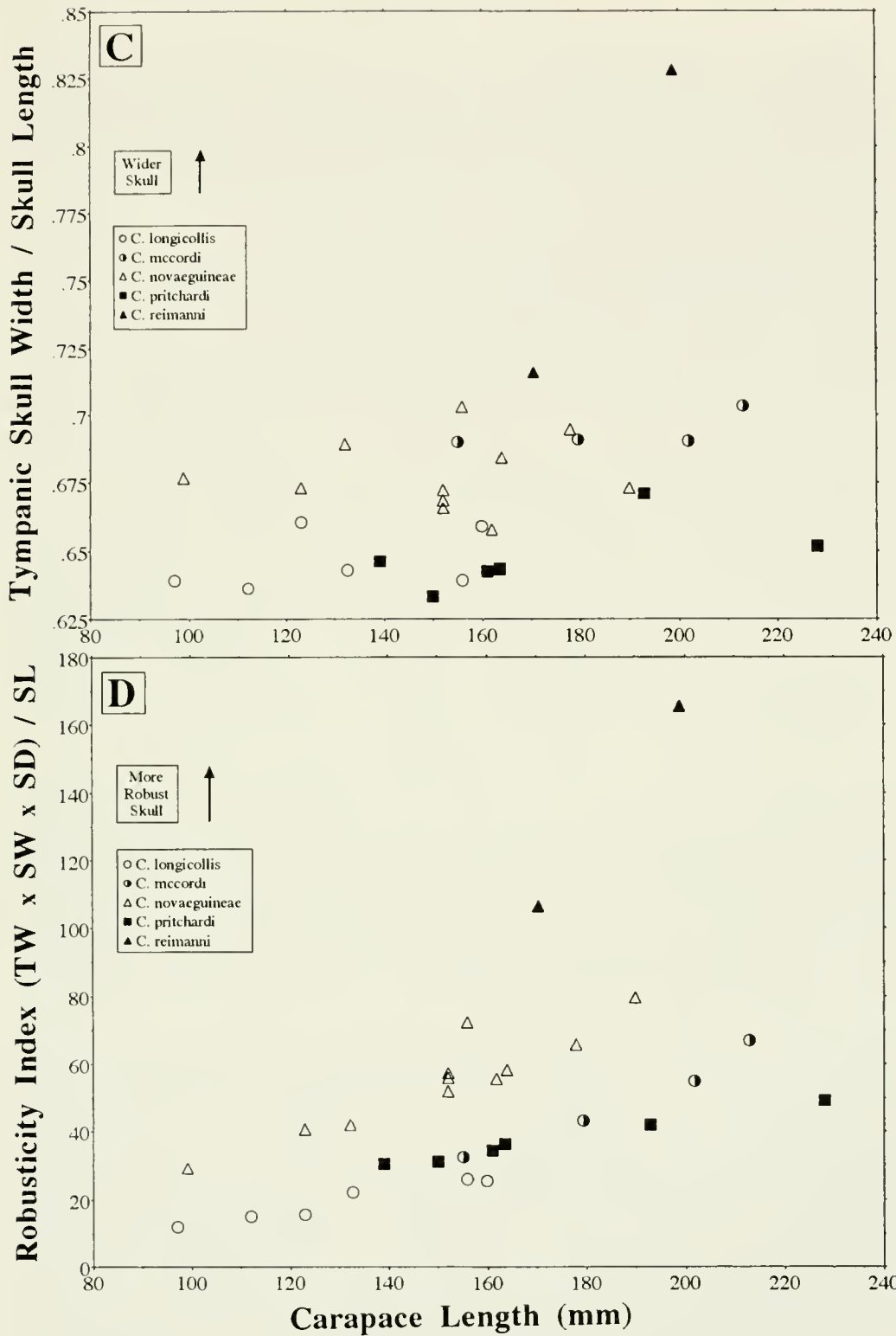


Figure 8. (Part 2). Skull morphometrics. C. tympanic skull width (SWT/SL); and D. composite graph of Robusticity Index (TW × SWT × SD)/SL expressed as a trivariate product; all versus Skull Length. Note the position of *C. mccordi* as most similar to *C. novaeguineae* in terms of tympanic skull width (C), but most similar to *C. pritchardi* in terms of triturating width (A), skull depth (B) and composite Robusticity Index (D).

maxillary and mandibular triturating surfaces, with correspondingly wide and robust horny rhamphothecae. *C. longicollis* has very thin triturating surfaces, whereas both *C. pritchardi* and *C. mccordi* have surfaces that are intermediate and similar to each other, though *C. mccordi* tends to have slightly wider surfaces in larger specimens [Fig. 8(1)A]. *Chelodina novaeguineae* has a deep skull, *C. longicollis* a shallow skull, and *C. mccordi* and *C. pritchardi* have skull depths that are intermediate and similar to each other [Fig. 8(1)B]. Skull width as compared to skull depth is greater in both *C. mccordi* and *C. novaeguineae*, while *C. longicollis* and *C. pritchardi* have relatively narrower skulls [Fig. 8(2)C]. *Chelodina mccordi* has an intermediate-sized parietal roof, like *C. pritchardi*, not as large as *C. longicollis* or as reduced as *C. novaeguineae*. The pterygoid trochlear processes are minimally divergent and unflared in *C. mccordi*, as they are in *C. pritchardi*, lacking the extreme flaring and prominent divergence seen in *C. novaeguineae*. The skull depth and supraoccipital crest height are similar in *C. pritchardi* and *C. mccordi*.

The Robusticity Index (see Rhodin, 1993) for the skull of *C. mccordi* is very similar to *C. pritchardi*, but shows a slight increase in skulls of larger specimens, related to slightly increased triturating width and skull depth, and moderately increased skull width in the larger specimens. Both of these species have skulls that are much more robust than *C. longicollis* and much less robust than *C. novaeguineae* [Fig. 8(2)D], with *C. mccordi* generally slightly more robust than *C. pritchardi*.

Overall, the skull of *C. mccordi* seems to represent a phylogenetic intermediate step in a transformation series leading from *C. pritchardi* to *C. novaeguineae*. *Chelodina mccordi* retains narrow triturating surfaces, though they are slightly widened, and a shallow skull; but has developed significantly increased skull width with slightly increased skull robusticity. These features correlate with an increase in temporal muscle mass, intermediate between the relatively reduced mass in *C. pritchardi* and the markedly increased mass in *C. novaeguineae*. Evidently *C. mccordi* has developed the need for moderately increased mandibular adductor force generation in its jaw closure mechanism, but has not reached the point of requiring massively enlarged opposing triturating crushing surfaces.

From skull morphology, one would predict that *C. mccordi* is a generalized carnivore or omnivorous scavenger, intermediate between the presumed specialized molluscivorous *C. novaeguineae* and the more limited piscivorous or carnivorous *C. pritchardi*.

Cervical Spine. Central cervical articulation pattern is (2(3(4(5)6)7(8) in 4 specimens (2 by direct exam, 2 by radiographic investigation), the only known pattern for all Chelidae as described by Williams (1950). Atlanto-axial (C1-C2) cervical morphology in *C. mccordi* identical to the pattern in other *Chelodina* subgeneric group "A".

Shell. No neural bones in 2 specimens, all pleurals meeting in the midline. Axillary buttress moderately robust, articulating with lateral first pleural and posterior third peripheral; inguinal buttress less robust, articulating with postero-lateral edge of fourth and antero-lateral edge of fifth pleurals, as well as anterior seventh peripheral. Suprapygal relatively wide, contacting tenth peripheral. Broad contact between first peripherals and first pleurals.

Ecology and General

Reproduction. Radiographs or dissections were performed on the females in the series, with one female demonstrating multiple small ovarian follicles bilaterally, as well as enormous paired cloacal bursae (one on each side). No eggs were noted. Reproductive parameters have not yet been fully documented for the species, but McCord (personal communication) has hatched several clutches of eggs from captive individuals. Average clutch size is 8–9 eggs, with oval eggs similar in shape to *C. longicollis* and *C. pritchardi*, but slightly larger than for either of those species, and slightly smaller than the eggs of *C. reimanni*, which are larger and more rounded. The eggs have hatched in about 2 months when incubated at about 82°F.

Growth. The smallest specimen of 99.5 mm carapace length shows three concentric growth rings. The rings are clearly visible on the costal scutes and allow for measurements of growth. The first ring encompasses the indistinguishable original scute and subsequent growth in the first season; the second ring, growth through the end of the second season; and the third ring, growth until capture. By measuring the corresponding costal-vertebral

suture lengths for each of the rings it is possible to create a ratio of costal length to carapace length for each ring and thereby calculate the carapace length of the animal at the end of each growth season. By this method, this specimen (RMNH 4349), which is now 99.5 mm long at the end of its third and last growing season, was approximately 73.5 mm long at the end of the second season, and 51.0 mm long at the end of the first season. The actual original hatchling scute is no longer visible, but extrapolation from the regression curve created by the first three values yields an expected hatchling size of about 32.0 mm (Fig. 9). This predicted hatchling size is within the range of hatchlings of other species of *Chelodina* I have examined: *C. parkeri* at 35.0 mm, *C. siebenrocki* at 35.0 mm, *C. rugosa* at 32.0 mm, *C. oblonga* at 30.0 mm, and *C. longicollis* at 28.8 mm. It is of course not known whether the growth rings are reflective of an annual cycle, but Roti has well defined wet and dry seasons, and it appears likely that this specimen is therefore about three years old.

Predation. Five large females display evidence of possible previous crocodile encounters. Four animals have what appear to be typical healed tooth holes and bite striations on the carapace, one has the hind portions of the carapace missing with resultant deformed regenerated scar tissue. The saltwater crocodile *Crocodylus porosus* is the most likely predator, but freshwater crocodiles may also occur in the Roti area (Ross, 1986). Native collectors also indicate that many specimens receive carapacial damage from farmers' plow blades in the rice paddies where the species is known to occur (McCord, personal communication).

Sympatry. No other freshwater turtles are known to occur on Roti, but the semi-aquatic emydid turtle *Cuora amboinensis* may well occur on the island, having previously been recorded on Timor (Iverson, 1986). In addition, the trionychid aquatic soft-shell turtle *Amyda cartilaginea* may occur on either Roti or Timor. Iverson (1986) records the nearest confirmed locality as Lombok Island just east of Bali, but *Trionyx cartilagineus newtoni* Ferreira, 1897, was described as having been obtained on Timor, and may represent evidence for a population in this area.

DISCUSSION

The occurrence of a population of chelid turtles on Roti Island in Indonesia comes as a relative surprise because of the known

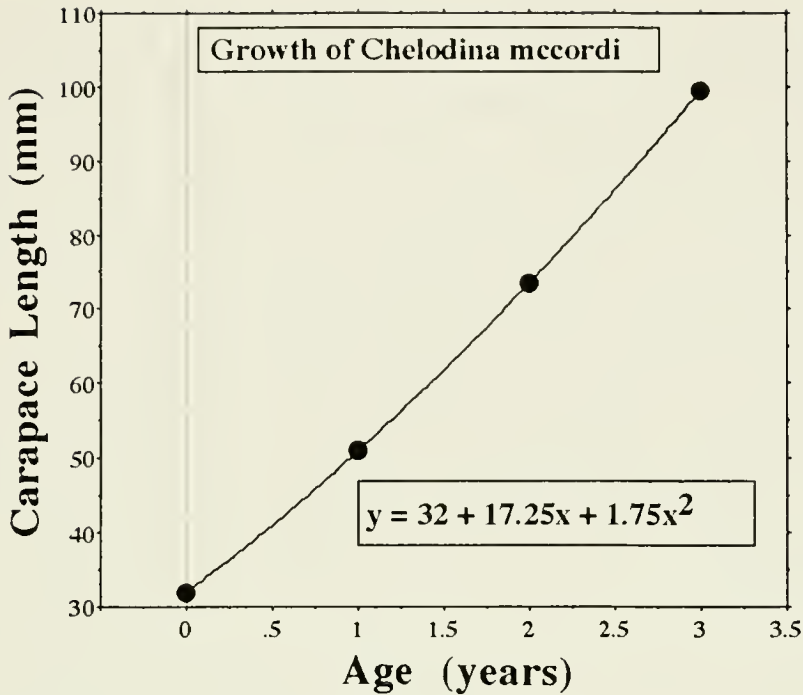


Figure 9. Graph showing probable growth of individual specimen of *C. mccordi* (RMNH 4349) as calculated by measurements of costal scute growth rings. Actual size of specimen recorded as last data point on graph; sizes at age 1 and 2 calculated from growth rings; size at age 0 extrapolated from the curve.

zoogeography of the family. Other than in South America, no other natural populations of chelid turtles have been recorded outside of continental Australia and New Guinea and islands on their contiguous Sahul Shelf. Although *Elseya novaeguineae* has been recorded in the Palau Islands in the northwestern Pacific (Aoki, 1977), that record probably represents an introduction. In addition, I have seen photographs of a specimen of *Emydura subglobosa* purportedly from New Britain in northeastern oceanic Papua New Guinea, which also probably represents an introduction. McCord (personal communication) has obtained specimens of this population of *Emydura subglobosa* collected in the vicinity of Rabaul, a major commercial center with a huge natural products market where exotic species introductions would come as no major surprise.

The collection of specimens of *C. mccordi* on Roti by Dr. Ten Kate back in 1891 and now by Frank Yowono about 100 years later confirms the presence of an established viable breeding population of this taxon. The demonstrated similarity in morphology

of the original 1891 specimens and of the recently collected specimens confirms the identity and the source of the two series.

The marked morphological differences in *C. mccordi* from geographically proximate New Guinean and Australian *C. novaeguineae* argue strongly against recent introduction via human trade. In like manner, the significant similarities of *C. mccordi* with the more geographically distant southeastern New Guinean *C. pritchardi* argues against a recent introduction.

A more likely scenario to explain the presence of *C. mccordi* on Roti is the possibility that both *C. pritchardi* and *C. mccordi* represent relict populations of ancestral *Chelodina* subgeneric group "A" stock, living on the outlying periphery of the previously exposed margins of the continental Sahul Shelf during earlier periods of lower sea levels and shelf emergence (Jongsma, 1970; Douth, 1972; Galloway and Loffler, 1972). During one of the periods that the Sahul Shelf was fully exposed to its 200 meter depth (Fig. 1), *C. mccordi* or its ancestor could potentially have reached Roti by rafting across the narrow deep oceanic channel that would have then separated the island from the northwestern shore of the exposed shelf. In addition, *C. pritchardi* could have reached southeastern Papua New Guinea across what would then have been a more broadly exposed Torres Strait land-bridge. Subsequently, with the partial submergence of the shelf the two species were left as peripheral, isolated, relict populations while the continental Australo-New Guinean form evolved into what is now *C. novaeguineae*. That large continental population then eventually became secondarily split by the much later appearance of Torres Strait separating New Guinea from Australia (occurring about 8,000 years ago), when sea levels rose to their present levels. This hypothesis is partially supported by the evidence found in skull morphologies, which suggests that both *C. mccordi* and *C. pritchardi* are intermediate between the primitive *C. longicollis* and the derived *C. novaeguineae*. In addition, it suggests a long period of isolation of both *C. mccordi* and *C. pritchardi* from "continental" *C. novaeguineae* stock. Further, it raises the possibility that New Guinean and Australian forms of *C. novaeguineae* may also be differentiating, as suggested by findings of slight differences in skull osteology between these two geographic isolates (Rhodin, 1993).

The time frame for this hypothesized phylogenetic scenario is hard to specify. The oldest known fossil of *Chelodina* is from the Early to Middle Miocene (ca. 28 million YBP) of northwestern Queensland, Australia (Gaffney *et al.*, 1989), and is very similar to modern representatives of the genus. It is certainly conceivable that much of the dispersal suggested above could have taken place during Late Miocene and Early Pliocene times (12–28 million YBP) when large land-bridge connections were present between New Guinea and Australia (Doutch, 1972; Galloway and Loffler, 1972). During this time there may even have existed some short-lived land-bridges between Australia and the southeastern Indonesian islands such as Timor and Roti (Doutch, 1972). Interestingly, one species of marsupial mammal from Australia (the cuscus, *Phalanger orientalis*) is found on Timor, also suggesting possible previous connections between the two areas (Cox, 1970), though Glover (1971) states that the cuscus probably represents an introduction by prehistoric man sometime later than 13,500 YBP (earliest evidence of man on Timor).

In addition, Jongsma (1970) has shown that the Sahul Shelf was fully exposed down to a depth of 200 meters as recently as the Illinoisan-Riss glaciation, about 170,000 years ago. Later, sea levels were again down to about 160 meters during the most recent Wisconsin-Wurm glaciation about 18,000 years ago. During these recent times, the Torres Strait land-bridge served as a continual connection between New Guinea and Australia between at least 80,000 and 8,000 years ago (Chappell, 1976).

It is therefore likely that *C. mccordi* reached Roti during one of several distinct times: 1) Late Miocene to Early Pliocene times, ca. 12–28 million YBP; 2) Illinoisan-Riss glaciation, ca. 170,000 YBP; 3) Wisconsin-Riss glaciation, ca. 18,000 YBP; or 4) introduced by prehistoric man sometime later than ca. 13,500 YBP. Other periods of potential dispersal probably also occurred between the Pliocene and Recent periods.

The phylogenetic relationships within *Chelodina* subgeneric group "A" have already been hypothesized and discussed by Rhodin (1993). Within the group, I regard *C. steindachneri* as the most primitive, with the group becoming more specialized and derived in a series that progresses through *C. longicollis*, *C. pritchardi*, and *C. novaeguineae* to *C. reimanni*, the most derived mem-

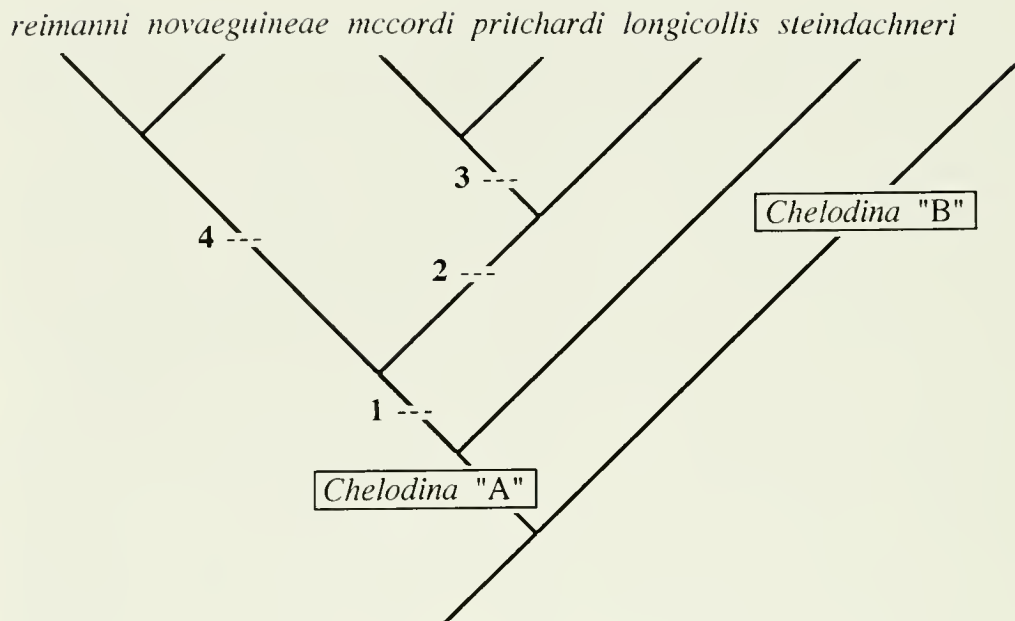


Figure 10. Hypothesized phylogenetic relationships of the six currently recognized species of *Chelodina* subgeneric group "A". The monophyly of *Chelodina* "A" follows Georges and Adams (1992). Characters supporting the intrageneric nodes are as follows: Node 1: partial or complete loss of chelid foramen; Node 2: wide parietal roof, narrow triturating surfaces, parallel pterygoids; Node 3: partial reduction in parietal roof width, slightly widened triturating surfaces; Node 4: narrow parietal crest, flaring pterygoids, wide triturating surfaces, deep robust skull.

ber of the group. Within this phylogeny, *C. mccordi* appears to be most closely related to *C. pritchardi* (Fig. 10), sharing the derived features of lack of chelid foramina and partially narrowed parietal roof, as well as the plesiomorphic features of a shallow skull, decreased robusticity, narrow triturating surfaces, and parallel pterygoid processes. The two species *C. reimanni* and *C. novaeguineae* share the derived features of a narrow parietal crest, flaring pterygoid processes, wide triturating surfaces, deep skulls, increased robusticity, and loss of chelid foramina.

In view of the isolated occurrence of *Chelodina mccordi* on the very small island of Roti, where available habitat may be limited, and human utilization pressures are perhaps heavy, an investigation into the population and survival status of the species needs to be undertaken. Basic ecological and life history data on the species are also extremely limited and further investigation is needed. Finally, the application of modern methods of molecular

phylogenetic analysis to the species should be pursued to help confirm or falsify the hypothesized relationships presented here.

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APPENDIX

Comparative material examined of *Chelodina longicollis*, *C. novaeguineae*, *C. pritchardi*, *C. reimanni*, and *C. steindachneri* all listed in Appendix in first paper of this series (Rhodin, 1993). See text for specimens of *C. mccordi* examined. Collection acronyms utilized in present paper are as follows:

AGJR = personal collection of Rhodin; MCZ = Museum of Comparative Zoology; RMNH = National Museum of Natural History, Leiden.

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