1980

A Diet and Reproductive Study for Selected Species of Malaysian Turtles

Colleen E. Kimmel
Eastern Illinois University

PAPER CERTIFICATE #2

TO: Graduate Degree Candidates who have written formal theses.

SUBJECT: Permission to reproduce theses.

The University Library is receiving a number of requests from other institutions asking permission to reproduce dissertations for inclusion in their library holdings. Although no copyright laws are involved, we feel that professional courtesy demands that permission be obtained from the author before we allow theses to be copied.

Please sign one of the following statements:

Booth Library of Eastern Illinois University has my permission to lend my thesis to a reputable college or university for the purpose of copying it for inclusion in that institution's library or research holdings.

____
Date

I respectfully request Booth Library of Eastern Illinois University not allow my thesis be reproduced because ______________________________

____

____

______________________________ ______________________________
Date Author

pdm

A Diet and Reproductive Study for Selected Species of Malaysian Turtles

(TITLE)

BY

Colleen E. Kimmel

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

Master of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

1980
YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
THIS PART OF THE GRADUATE DEGREE CITED ABOVE

August 1, 1980
DATE

August 1, 1980
DATE

ABSTRACT

Batagur baska, *Callagur borneoensis*, *Cuora amboinensis*, *Cyclemys dentata*, *Orlitia borneensis*, *Siebenrockiella crassicollis*, and *Trionyx cartilagineus* are suggested to be omnivorous by diet analysis. *Cyclemys* and *Orlitia* are the more herbivorous of the seven species examined. *Batagur* and *Callagur* are two closely related sympatric species that appear to have diverged sufficiently to eliminate competition for food resourses, as indicated by Morista's Index of Niche Overlap. Along the Perak River and it's tributaries in West Malaysia, *Batagur* and *Callagur* feed primarily upon the fruit of the berembang tree. In Trengganu (eastern Malaysia), the berembang is absent or rare along the rivers, thus other fruits and leaves make up the diet of these two species. Two other species share similar habitats, *Cuora* and *Siebenrockiella*. They also appear to have eliminated competition for food resourses. *Cuora* tends to be more herbivorous feeding along the shoreline and *Siebenrockiella* more of a scavenger. Little is known about the diet of *Orlitia*. Based on one individual's two fecal samples, *Orlitia* is herbivorous.

Examined for certain reproductive characters were *Cuora amboinensis*, *Cyclemys dentata*, and *Siebenrockiella crassicollis*. *Cuora* appears to be a seasonal nester on the east (involving April, May, and June) and west (including at least October and

and November) coasts of West Malaysia. Nesting occurs during the dry periods; between the northeast and southwest monsoons. Clutch size is small with relatively large eggs and the reproductive potential is at least six eggs per nesting season. Cyclemys is also a seasonal nester (May and June on east coast and at least March on the west coast). They produce one or two clutches of large eggs with a reproductive potential around three to five eggs per season. Siebenrockiella is a seasonal nester in the east coast drainages (prior to June and again in December). It is not conclusive if they are seasonal nesters on the west coast drainages (some activity in January and October). Siebenrockiella lays multiple clutches (as does Cuora) of relatively large eggs with a reproductive potential of six to nine eggs per season. Cyclemys has a slightly different nesting strategy than Cuora and Siebenrockiella. It is suggested that Cyclemys' nesting strategy is to reduce predation of the nesting female. Whereas, Cuora's and Siebenrockiella's strategy is to prevent predation on the eggs. Cuora, Cyclemys and Siebenrockiella compromise with a reproductive strategy found among semi-aquatic, tropical turtles.

ACKNOWLEDGEMENTS

I would like to sincerely thank my advisor, Dr. Moll, for his assistance and guidance throughout the course of this study.

I would also like to thank Dr. Durham, Dr. Andrews, and Dr. Doctor for their review and suggestions of the manuscript.

Finally, I would like to thank Denise Dunn for typing the manuscript.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES cont.

INTRODUCTION

West Malaysia is a small country approximately the size of the state of Illinois, located at the tip of the Malaysian peninsula. Five chelonian families represented by 23 species have been reported for the peninsula and most of these occur in West Malaysia (Moll, 1976).

Relatively little has been written concerning the ecology of this diverse chelonian assemblage. Much of the older literature concerned taxonomy and distribution. Some information on habitat, diet, and reproduction was provided by Cantor (1847), Theobald (1868), Flower (1899), Boulenger (1912), De Rooij (1915), and Smith (1931). Moll (1978, 1980a) described the natural history of the river terrapin, Batagur baska, and in 1980b discussed the habitat and salt water adaptation of the painted terrapin, Callagur borneoensis.

The batagurine emydids comprise 48% of the chelonians present in West Malaysia (Moll, 1976). Most of the emydid species are amphibious (e.g. Cuora, Cyclemys, Notochelys, Siebenrockiella). Heosemys spinosa, although tending to be more amphibious as an adult, is the most terrestrial of the group (Mertens, 1971; Moll, 1976). Batagur baska and Callagur borneoensis are thoroughly aquatic, inhabiting the large rivers of West Malaysia (Smith, 1931; Moll, 1976). Dogania subplana, Pelochelys bibroni, and Trionyx cartilagineus are representatives of the family Trionychidae found in Malaysia (De Rooij, 1915; Smith, 1931; Taylor, 1975; Moll, 1976). Pelochelys bibroni is not strictly a freshwater species but occasionally is seen at sea (Cantor, 1847; Smedley, 1932). Salt water tolerance has not been reported for D. subplana or T. cartilagineus, however, Dogania is the only trionychid regularly found on islands in the area (Smith, 1931) and Trionyx is occasionally captured in estuaries (Moll, personal communication).

The remaining chelonian families, Cheloniidae, Dermochelyidae, and Testudinidae, of West Malaysia will not be discussed in this paper.

A summation of habitat and distribution for the emydids and trionychids of West Malaysia is shown in Table 1.

The primary goals of this study were: (1) analyze and itemize the diets for selected species of West Malaysian turtles, (2) compare the diets of certain species that share similar habitats, and (3) interpret reproductive information in terms of:

(a) size at sexual maturity

(b) timing of the ovarian cycle

(c) egg size

(d) egg length index (ELI)

(e) egg width index (EWI)

(f) clutch size

(g) reproductive effort (RE)

(h) reproductive potential (RP)

TABLE 1. DISTRIBUTIONS AND HABITATS FOR SELECTED SPECIES OF MALAYSIAN TURTLES

SPECIES	DISTRIBUTION
EMYDIDAE	
Batagur baska (Gray)	Bengal, Burma, Malaysia, southern Vietnam, Sumatra.
Callagur borneoensis (Schlegel and Muller)	Borneo, Malaysia, Sumatra
Cuora amboinesis (Gray	Borneo, Malaysia, Philippines, Thailand, Sulawesi.
Cyclemys dentata (Gray)	Burma, Cambodia, India, Malaysia, Philippines, Thailand, Siam.
Heosemys spinosa (Gray)	Borneo, Burma, Cambodia, India, Malaysia, Natuna Islands, Siam, Sumatra, Thailand.
Heosemys grandis (Gray)	Burma, Cambodia, Malaysia, Siam, Thailand.
Notochelys platynota (Gray)	Borneo, Malaysia, southern Vietnam, Sumatra, Thailand.
Orlitia borneensis (Gray)	Borneo, Malaysia, Sumatra.
Siebenrockiella crassicollis (Gray)	Borneo, Burma, Malaysia, Siam, southern Vietnam, Sumatra, Thailand.
TRIONYCHIDAE	
Dogania subplana (Geoffroy)	Borneo, Burma, Java, Malaysia, Philippines, Siam, Sumatra, southern Thailand.
Pelochelys bibroni (Owen)	Bengal, Borneo, Burma, China, New Guinea, Malaysia, Philippines, Siam, southern Vietnam, Sumatra, Thailand, Java, India.
Trionyx cartilagineus (Boddaert)	Borneo, Burma, Cambodia, Java, Malaysia, Siam, southern Vietnam, Sumatra.

HABITAT	REFERENCE
Aquatic: Deep, slow-moving rivers; estuaries; canals.	Boulenger, 1912; Moll, 1980a; Smith, 1931.
Aquatic: estuaries; tidal areas of rivers; canals.	Boulenger, 1912; Moll, 1980b; Taylor, 1970.
Semi-aquatic: lowlands; ponds; marshes; paddy fields, streams.	Boulenger, 1912; Cantor, 1847; DeRooij, 1915; Smith, 1931; Taylor, 1970.
Semi-aquatic: lowland & hill streams	De Rooij, 1915; Flower, 1899; Smith, 1931; Taylor, 1970; Theobald, 1968.
Terrestrial/amphibious: moist, wooded hill and mountain terrain; rice fields; hill streams.	Cantor, 1847; De Rooij, 1915; Smith, 1931; Taylor, 1970.
Semi-aquatic: ponds; ditches; paddy hills and lowlands.	Boulenger, 1912; Flower, 1899; Taylor, 1970.
Semi-aquatic: lowlands; jungle swamps; ponds.	Boulenger, 1912; De Rooij, 1915; Flower, 1899, Taylor, 1970.
Aquatic: slow-flowing rivers; lakes; swamps.	De Rooij, 1915; Moll (pers. commt.)
Semi-aquatic: ponds; marshes; sluggish streams; rice paddies.	Boulenger, 1912; Cantor, 1847; De Rooij, 1915; Flower, 1899; Smith, 1931; Taylor, 1970.
Aquatic: rivers, hill, mountain, or lowland streams.	Boulenger, 1912; De Rooij, 1915; Smith, 1931; Taylor, 1970.
Aquatic: deep, slow moving rivers; estuaries.	Boulenger, 1912; De Rooij, 1915; Flower, 1899; Smith, 1931.
Aquatic: muddy, slow-moving rivers; ditches; ponds; swamps; hill streams.	Boulenger, 1912; Cantor, 1847; De Rooij, 1915; Flower, 1899; Smith, 1931; Taylor, 1970.

METHODS AND MATERIALS

Specimens for this study were collected by Edward O. Moll in West Malaysia from September 1975 to August 1976, and again in the summer of 1978, and now reside in the Sqrugg's Museum at Eastern Illinois University. These collections represent three states, Perak (Pk) of the west coast drainages, Pahang (Pg) and Trengganu (Tg) of the east coast drainages.

Contents of stomach, intestine, and faces were sorted and food items identified. Each food type was measured volumetrically by water displacement for the individual samples. The prey items were categorized into designated food classes (Table 2). For each species food data were combined and expressed as (1) total volume (TV) - the total amount of a certain food type expressed in milliliters, (2) the individual percentage of volume (%IV) - expressed as a percent of the total volume of a given food type found in all samples having that particular food item, (3) total percentage of volume (%TV) - average percentage of total comprised by a given kind of food, as reckoned for all guts examined whether or not they contained that given kind of good, (4) frequency of occurrence (%FO) - percentage of turtles in which a given food item was found (Moll and Legler, 1971). To compare the amount of overlap in diet between species, size class or locality, Morista's index of niche overlap modified by Horn was used (Berry, 1975):

$$C\lambda = 2\sum X_i Y_i / \sum X_i^2 + \sum Y_i^2$$

Where, X_i is the proportion of the i^{th} category (= food class)

TABLE 2. FOOD CLASS DESIGNATIONS FOR FOODS ANALYZED FROM CERTAIN MALAYSIAN TURTLES

Class 1:	Aquatic Sedges and Grasses
Class 2:	Other Leaves and Stems
Class 3:	Algae
Class 4:	Berembang Fruit
Class 5:	Other Fruit Material
Class 6:	Clams
Class 7:	Snails
Class 8:	Insects
Class 9:	Vertebrates
Class 10:	Unidentified Material

utilized by species - size class or locality sample X, and Yi is the proportion of the i^{th} category utilized by sample Y. Cλ will vary from 0 (no overlap) to a maximum of 1 when there is complete overlap and in the same proportion. For this study, X_i is the percent of the total volume of food class i in species - size class or locality sample X, and Y_i is the percent of the total volume of food class i in sample Y.

Reproductive data were analyzed for three species, *Cuora amboinensis*, *Cyclemys dentata*, and *Siebenrockiella crassicollis*. Carapace lengths were measured with vernier calipers to the nearest millimeter. Sexual maturity was determined by examination of the gonads and secondary sexual characteristics. Females were considered mature by the presence of enlarged, yolk-containing follicles, and/or oviducal eggs, and/or corpora lutea. Most of the males examined had previously been labeled mature or immature. However, the criteria for determining sexual maturity in males is presence of secondary sex characteristics (e.g. enlarged tail) or sperm in the epididymides.

Oviducal eggs, enlarged follicles (greater than six millimeters), and corpora lutea were counted and measured with vernier calipers to the nearest 0.1 millimeter. This information was used to determine the following: ELI - egg length index, determined by dividing the mean egg length of clutch by the female's carapace length; clutch size; RE - reproductive effort, determined by dividing the clutch weight by the female's body weight; RP - reproductive potential, as the total number of eggs laid per season, determined from corporalutea, enlarged ovarian follicles and oviducal eggs; timing of the ovarian cycle.

RESULTS OF DIET

The majority of the species examined were omnivorous. The samples were separated by locality for comparison. Diets of two pairs of sympatric species with similar habits (Batagur-Callagur and Cuora - Siebenrockiella) were compared using Morista's index. Dietary data on three additional species are also presented Cyclemys, Orlitia, and Trionyx).

Batagur baska and Callagur borneoensis

Batagur and Callagur are batagurine emydids that co-habit the estuaries of large rivers in West Malaysia. Being closely related to Batagur, Callagur is seemingly a more formidible competitor than other species sharing the tidal areas of large rivers (e.g. Trionyx cartilagineus and Pelochelys bibroni) (Moll, 1980a).

Boulenger (1912) reported Batagur as ominvorous. Smith (1931) later regarded Batagur as herbivorous. Data in Table 3 supports ominvory; vegetation comprised 78.5% of the total samples examined for Batagur, with only 21.5% of the total volume being animal material. The leaves and stems consisted mainly of unknown dicots combined with some aquatic-type sedges identified as Scleria sp. The fruit material is described and identified in more detail in Moll (1980a). Berembang (Sonneratia sp.), a mangrove fruit, was an important fruit consumed by Batagur and comprised 97.76% of the total volume of Perak samples (Moll, 1980a).

Rare along the rivers in Trengganu Berembang was lacking from Batagur's diet in that locality. Other fruit consumed such as, watermelon, grape, padi, and chili peppers, indicate that Batagur

TABLE 3. Composition of fecal samples from *Batagur baska* (12 sub-adult to adult from Perak; one adult and two juveniles from Trengganu).
(Total Volume expressed in milliliters)

	TV	%IV	%TV	%FO
Perak (N=12)				
Leaves and stems	393.50	47.09	45.2	91.7
Fruits	219.05	32.45	25.2	83.3
Clams	257.00	46.92	29.6	58.3
TOTAL	869.55		100.0	
Trengganu (N=3)				
Leaves and stems	192.00	59.20	59.3	100.0
Fruits	132.00	40.69	40.7	100.0
Clams	+	+	+	100.0
TOTAL	324.00		100.0	
TOTAL (N=15)				
Leaves and stems	585.50	50.50	49.1	93.3
Fruits	351.05	30.90	29.4	86.7
Clams	257.00	30.3	21.5	66.7
TOTAL	1193.55		100.0	

tends to feed on human refuse which is dumped into the rivers. The only animal material found were small pelecepod mollusks (10-13 mm in length). These comprised 58.3% of the Perak samples and 29.6% of the total volume. They were found in all three samples (one adult and two juveniles) from Trengganu but in trace amounts. No differences in diet between juveniles and adults were evident.

Boulenger (1912) and De Rooij (1915) recorded Callagur borneoensis as herbivorous. Data in Table 4 suggests ominvory with a preference for vegetation. Plant material comprised 99.1% of the total volume of food consumed as compared to 0.3% animal material. Possibly the animal material consumed was accidental, being consumed along with the vegetation. However, 12 juveniles kept at EIU readily eat meat and presumably would do so in the wild.

The gut of an adult Trengganu specimen (EOM 2390) was packed with fine gravel with only trace amounts of vegetation (T.V.,1.5 ml). The gravel was probably consumed while the animal was scooping up vegetation from shore or river bottom.

Berembang (Table 5) represented 76.1% of the total volume of fruit material consumed by Perak specimens. This fruit appeared to be an important food source for Callagur and Batagur in Perak. Other fruits (e.g. chili peppers, durian) consumed indicate that Callagur, like Batagur, feeds on human refuse discarded into the rivers.

Leaves and stems comprised 10.1% of the total volume of food while grasses and sedges comprised 21.2% (Table 4). Presumably these were consumed along the shoreline. Moll (1980a) stated that Batagur feeds along the shorelines at high tide when shoreline

TABLE 4. Composition of digestive tracts and fecal samples of 18 subadult to adult *Callagur borneoensis* from the Perak river and an adult from the Trengganu River.

	TV	%IV	%TV	%FO
Perak (N=18)				
Leaves and stems	303.9	10.1	10.10	94.4
Grasses and sedges	638.0	59.0	21.20	11.0
Fruits	2042.7	67.8	67.80	100.0
Clams	7.5	7.8	0.20	5.5
Snails	1.0	1.0	0.03	5.5
Insect	2.0	0.4	0.07	11.0
Unidentified	18.0	2.5	0.60	5.5
TOTAL	3013.1		100.00	
Trengganu (N=1)				
Grasses and sedges	1.0	66.7	66.70	100.0
Fruits	+	+	+	100.0
Unidentified	0.5	33.3	33.30	100.0
TOTAL	1.5		100.00	
TOTAL (N=19)				
Leaves and stems	303.9	10.1	10.10	89.5
Grasses and sedges	639.0	59.0	21.20	16.0
Fruit	2042.7	67.8	67.80	100.0
Clams	7.5	7.8	0.20	5.3
Snails	1.0	1.0	0.03	5.3
Insect	2.0	0.4	0.07	10.5
Unidentified	18.5	2.5	0.60	10.5
TOTAL	3014.6		100.00	

TABLE 5. Analysis of fruit and seeds for *Callagur borneensis* from the Perak River (N=18)

	TV	%IV	%TV	%FO
Perak (N=18)				
Berembang (*Sonneratia* sp.)	1553.9	58.0	76.1	94.4
Durian (*Durio zibethinus*)	338.2	36.1	16.6	44.4
Chili (*Capsicum annum*)	2.9	0.2	0.1	33.3
Unidentified	147.7	14.3	7.2	38.9
TOTAL	2042.7		100.0	

vegetation is submerged and accessible.

Certain generalizations can be made from Morista's index (Cλ values) calculated for Table 6B :

(a) Intraspecific overlap is greater than interspecific overlap for Batagur. This is not evident for Callagur, because of the small sample size.

(b) The overlap values are low for Callagur and Batagur where they occur together in Trengganu and slightly higher for Perak.

Table 7 depicts overlap values for Batagur and Callagur separated on age; adults versus juvenile (samples from Perak and Trengganu combined). The high overlap values for Batagur adults and juveniles is expected. The interspecific overlap between Batagur juveniles and Callagur adults (Cλ=.808) is significant. To determine where the overlap is most significant overlap values were calculated for Batagur juveniles of Trengganu (Cλ=.269) and Perak (Cλ=.824) then compared with Callagur adults from Perak. The only significant overlap occurred between Batagur juveniles and Callagur adults of Perak. This could imply competition for a food source between the two species-age groups.

Callagur is the more herbivorous and Batagur more omnivorous. Along the Perak river both species feed primarily on the leaves, stems and fruits (particularly berembang) of shoreline vegetation (especially at high tide).

On the east coast, along the Trengganu River, berembang trees are scarce. Other plants and fruits replace the berembang in the diets of Callagur and Batagur. It appears Callagur feeds on

TABLE 6. A. Percentages of total volume of each food class (Table 2) for each species-locality class sample (Bb-*Batagur baska*, Cb-*Callagur borneoensis*, Pk-Perak, Tg-Trengganu).

FOOD CLASS

(N)	1	2	3	4	5	6	7	8	9	10
Pk-Bb (12)		45.3		15.2	10.0	29.5				
Pk-Cb (18)	21.2	10.1		28.5	39.3	0.2	.03	.07		0.6
Tg-Bb (3)		59.2			40.8	+				
Tg-Cb (1)	66.7				+					33.3

B. Cλ values (Abbreviations in text and Part A)

	Pk-Cb	Tg-Bb	Tg-Cb
Pk-Bb	.420	.741	.002
Pk-Cb		.545	.350
Tg-Bb			.008

TABLE 7. A. Percentages of total volume of each food class (Table 2) for each species-age class sample (A-adult, J-juvenile) of <u>Batagur</u> (Bb) and <u>Callagur</u> (Cb).

FOOD CLASS

	(N)	1	2	3	4	5	6	7	8	9	10
Bb-A	(10)		67.7		7.9	21.1	3.3				
Bb-J	(5)		34.3		36.5	29.0	0.2				
Cb-A	(19)	21.2	10.1		28.5	39.3	0.2	0.03	0.07		0.6

B. <u>Cλ Values</u>

	Bb-J	Cb-A
Bb-A	.762	.554
Bb-J		.808

grasses and sedges while Batagur feeds on more leafy (stems) vegetation. Various other fruits such as, padi, watermelon, durian, and chili peppers were consumed by both species as previously mentioned.

Competition for food does not seem to be significant among the adults of Batagur and Callagur inhabiting the Perak River. The supply of berembang may be sufficient for both species to harvest. The high overlap in the diets of Callagur adults and Batagur juveniles of the Perak River may be a result of the small sample size (only three juvenile Batagur samples from Perak River versus 18 Callagur samples). Further investigation should be conducted to determine the machanisms of co-existence for these two emydids.

Cuora amboinensis and Siebenrockiella crassicollis

Cuora amboinensis is omnivorous (Table 8). Flower (1899) and Smith (1931), stated that Cuora was herbivorous. Boulenger (1912) Boulenger (1912) reported that although Cuora was primarily a vegetarian, it would eat flesh. Data indicates that vegetation predominated Cuora diet. Plant material comprised 84.4% of the total volume consumed and animal material 1.6%. Of the plant material, Cuora seems to prefer grasses and sedges (72.5%TV) that surround its habitat of streams, marshes, and ponds (Table 1). Grasses and sedges also occurred in more individual samples (%FO=68.7) than any other food item. In Pahang, it was the only food consumed. Animal material consists mainly of small aquatic insects (unidentified) and in one sample (EOM 2233) the remains of a spider was

TABLE 8. Composition of food samples from <u>Cuora amboinensis</u> (10 subadult to adult and one juvenile from Perak; three subadult to adult from Pahang; two adults from Trengganu).

	TV	%IV	%TV	%FO
Perak (N=11)				
Leaves and stems	7.5	51.6	2.3	18.0
Grasses and sedges	232.0	94.3	71.0	64.0
Fruit	20.5	12.5	6.3	36.0
Insect	3.0	6.1	0.9	18.0
Fish	3.5	8.8	1.0	9.0
Unidentified	60.4	40.1	18.5	36.0
TOTAL	326.9		100.0	
Pahang (N=3)				
Grasses and sedges	38.6	100.0	100.0	100.0
Trengganu (N=2)				
Leaves and stems	23.5	99.2	35.7	50.0
Grasses and sedges	42.0	100.0	64.0	50.0
Fish	0.2	0.8	0.3	50.0
TOTAL	65.7		100.0	
TOTAL (N=16)				
Leaves and stems	31.0	40.9	7.2	18.7
Grasses and sedges	312.6	95.1	72.5	68.7
Fruit	20.5	12.5	4.7	25.0
Insect	3.0	6.1	0.7	12.5
Fish	3.7	5.8	0.9	12.5
Unidentified	60.4	40.1	14.0	25.0
TOTAL	431.2		100.0	

found (possibly ingested along with vegetation). The few fish vertebrae found indicated a tendency to scavenge or may have been the bait used to trap the animal.

Siebenrockiella crassicollis was reported to be carnivorous by Cantor (1846), De Rooij (1915), and Smith (1931). Table 9 indicates an omnivorous diet. Infact, analysis of 19 guts or fecal samples indicates a predominantly plant diet (78.2% TV). Animal material comprised only 3.7% TV of food stuff. In Perak and Pahang, *Siebenrockiella* fed largely upon leaves and stems as compared to a diet of predominantly algae (29.4%TV) and grasses and sedges (21.1% TV) for Trengganu specimens. An adult female from Perak (EOM 2303) consumed snails ranging in length from 1.9 cm to 2.5 cm (body without shell) and pelycepod mollusks ranging .48 cm - 1.8 cm in width. Wings of a tropical termite and the ventral scutes of a small reptile (0.55 cm x 0.17 cm) were also found. Curiously an adult male (EOM 2280) collected in December from Pahang had consumed termite soldiers, which never leave the colony because they are blind. During that time period, however, heavy rains caused flooding, which possibly washed the termites into the habitat of *Siebenrockiella*. It seems less likely that *Siebenrockiella* found the food on land. Unidentified material is high for Trengganu samples and appeared to have been scooped-up from a mucky bottom. *Siebenrockiella* apparently is more likely to feed in the water than land, and is opportunistic. The leaves and stems found in stomachs seemed partially decayed and may have been eaten by *Siebenrockiella* after falling into its habitat.

TABLE 9. Composition of food samples from *Siebenrockiella crassicollis* (Five adult from Perak; five adults from Pahang; six subadult to adult and three juveniles from Trengganu).

	TV	%IV	%TV	%FO
Perak (N=5)				
Leaves and stems	32.6	94.8	59.0	40.0
Algae	12.6	98.4	22.7	40.0
Fruits	5.6	14.7	10.1	40.0
Insect	+	+	+	20.0
Snail	3.4	77.3	6.1	20.0
Clam	0.4	9.1	0.7	20.0
Unidentified	0.8	11.1	1.4	40.0
TOTAL	55.4		100.0	
Pahang (N=5)				
Leaves and stems	64.6	96.0	90.6	80.0
Grasses and sedges	4.0	100.0	5.6	20.0
Fruit	0.7	1.8	1.0	40.0
Insect	2.0	28.6	2.8	20.0
TOTAL	71.3		100.0	
Trengganu (N=9)				
Leaves and stems	16.0	26.2	7.2	11.0
Grasses and sedges	46.8	69.4	21.1	44.4
Algae	65.2	97.0	29.4	33.3
Fruits	24.5	23.4	11.0	33.3
Fish	7.0	11.5	3.2	11.0
Unidentified	62.4	61.2	28.1	55.5
TOTAL	221.9		100.0	
TOTAL (N=19)				
Leaves and stems	113.2	68.0	32.5	36.8
Grasses and sedges	50.8	71.2	14.6	26.3
Algae	77.8	97.2	22.3	26.3
Fruit	30.8	16.9	8.8	36.8
Insect	2.0	17.5	0.6	10.5
Snail	3.4	77.3	1.0	5.3
Clam	0.4	9.1	0.1	5.3
Fish	7.0	11.5	2.0	5.3
Unidentified	63.2	57.9	18.1	36.8
TOTAL	348.6		100.0	

Table 10 compares the percentages of total volume of each food class and overlap values (Cλ) for all Siebenrockiella and Cuora. Table 11 compares adults and juveniles of each species. Pahang and Trengganu (east coast drainages) samples were combined for statistical purposes and compared to Perak (west coast) samples. The following generalizations can be made from the overlap values:

(a) Intraspecific overlap is higher than interspecific overlap.

(b) Where Siebenrockiella and Cuora occur together, overlap in diet is minimal as indicated by low values.

The minimal overlap between the two species where they occur together may be due to different feeding stratigies: (a) Cuora is less carnivorous than Siebenrockiella, (b) Cuora tends to feed on sedges and grasses more so than Siebenrockiella, (c) Siebenrockiella, is more of a scavenger, whereas Cuora appears to prefer bank vegetation.

Based on two juvenile Cuora and a juvenile Siebenrockiella kept at Eastern Illinois University, Cuora is the more aggressive species and Siebenrockiella is secretive and shy. In contrast, Smith (1931) described Siebenrockiella as a voracious feeder in captivity, and Cuora as dainty eater and timid.

Cyclemys dentata, Orlitia borneensis, and Trionyx cartilagineus

Two gut samples of Cyclemys dentata from Trengganu contained 100% vegetation (Table 12). Leaves and stems comprised 88.9% of the total volume and unidentified fruit and plant material (11.1%TV)

TABLE 10A. Percentages of total volume of each food class for each species-locality class sample (S-*Siebenrockiella crassicollis*, C-*Cuora amboinensis*, Pk-*Perak*, Pt-samples from Pahang and Trengganu combined).

FOOD CLASS

	(N)	1	2	3	4	5	6	7	8	9	10
S-Pk	(5)		59.0	22.7		10.1	0.7	0.1	+		1.4
C-Pk	(11)	71.4	2.3		0.3	6.0			0.9	1.1	18.0
S-Pt	(14)	17.3	27.5	22.2		8.6			0.7	2.4	21.3
C-Pt	(5)	77.3	22.5							0.2	

B. $C\lambda$ Values (abbreviations in text and Part A.)

	C-Pk	S-Pt	C-Pt
S-Pk	.046	.721	.250
C-Pk		.460	.933
S-Pt			.457

TABLE 11 A. Percentages of total volume of each food class for each species-age class sample (S-<u>Siebenrockiella</u>, C-<u>Cuora</u>, A-adult, J-juvenile).

FOOD CLASS

	(N)	1	2	3	4	5	6	7	8	9	10
S-A	(17)	14.1	33.4	23.0		9.0	0.1	1.0	0.6	2.1	16.8
S-J	(2)	30.9				5.1					64.0
C-A	(15)	73.3	8.15		0.2	2.8			1.4	0.05	14.1
C-J	(1)	72.5				18.7				8.8	

B. <u>Cλ VALUES</u>

	S-J	C-A	C-J
S-A	.427	.199	.306
S-J		.593	.434
C-A			.947

comprised the rest. One female (EOM 2381) had eaten 4.5 ml of pink plastic along with a trace amount of sand. Theobald (1868) described _Cyclemys_ as herbivorous, particularly feeding on the fruit of _Ficus glomerata_ (a fig). Smith (1931) claimed _Cyclemys_ is ominovorous but did not describe food items.

Nothing is published concerning the diet of _Orlitia borneensis_. I examined two fecal samples from one individual (EOM 0531). Plants comprised the total volume (Table 12). Fruit, identified as berebang comprised 85.8% of the total volume of food stuff. Like _Callagur_ and _Batagur_, _Orlitia_ inhabits the large rivers and canals of Perak feeding on berembang fruit.

Trionyx cartilagineus is listed as carnivorous by Flower (1899), Boulenger (1912), Smith (1931), Smedley (1932), and Taylor (1970). Flower (1899)stated his _Trionyx_ preferred eating blue mussels rather than fish, frogs, or vegetation. Taylor (1970) reported _Trionyx_ to eat chiefly fish, crustaceans, and amphibians. One female _Trionyx_ obtained from a market in Perak and a fecal sample (EOM 2217) was available for this study. However, the total volume (32 ml) was undiscernible and considered detritus. It could be assumed the material was composed of decaying animal and/or plant material that was scooped from the bottom of a river.

TABLE 12. Composition of food samples for *Cyclemys dentata* (Two adults from Trengganu) and *Orlitia borneensis* (one adult from Perak).

	TV	%IV	%TV	%FO
Cyclemys dentata (N=2)				
Leaves and stems	8.0	88.9	88.9	100.0
Fruit	+	+	+	50.0
Unidentified	1.0	14.3	11.1	50.0
TOTAL	9.0		100.0	
Orlitia borneensis (N=1)				
Leaves and stems	15.5	6.2	6.2	100.0
Fruit	214.2	85.8	85.8	100.0
Unidentified	20.0	10.3	8.0	50.0
TOTAL	249.7		100.0	

DISCUSSION OF DIET

Gauses' law of competitive exclusion works on the premise that no two species can occupy the same niche. Coexistence of two species occupying the same habitat is possible through niche segregation. In the habitat, portions of species' niches can overlap. This area of overlap is where competition would be expected. If competition is minimal the species may coexist. For instance, if interspecific overlap occurs for a particular resource and the resource is abundant (e.g. berembang in Perak) competition may be lacking (Colwell and Futuyma, 1971). If the resource becomes scarce competition may become intense and result in eliminating one of the species or force the utilization of alternate resources. There is the possibility that the resource may be proven to be irrevelent to one or both species.

Batagur and Callagur co-exist in the same habitats, and feed on the abundant berembang fruit in Perak. In Trengganu where berembang is scarce, Batagur consumes a diet of leaves, stems of dicots and mollusks while Callagur feeds predominatley on grasses and sedges. Competition is minimal where food resources are concerned. Further studies into the life histories of these closely related species hopefully will provide insight into how they have diverged within their habitat to eliminate competition.

Cuora and Siebenrockiella also exist in the same habitats. Overlap for food resources again was minimal. Cuora feeds on grasses and sedges while Siebenrockiella consumes algae and scavenges. These two species have seemed to diverge sufficiently to eliminate competition and co-exist.

RESULTS OF REPRODUCTION

Three species, Cuora amboinensis, Cyclemys dentata, and Siebenrockiella crassicollis, were examined to determine: size at sexual maturity (Table 13); egg size; egg length index-ELI; egg width index-EWI; clutch size; reproductive effort-RE; reproductive potential-RP; timing of the ovarian cycles (summarized in Tables 14 and 15).

Cuora amboinensis

The largest specimen recorded had a carapace length of 250 millimeters, although sex and locality were not disclosed (De - Rooij, 1915). Flower (1899) recorded an adult male from Kedah, Malaysia with a carapace length of 216 mm. Data from 11 females, 11 males, and 10 immatures suggests the sexes are similar in size with the adults ranging from 159 mm to 209 mm carapace lengths (Table 13).

Table 14 summarizes findings on the female reproductive cycle. Ovaries of three Pahang (east coast drainage) specimens from December have few enlarged follicles and appear to be in the latent (quiescent) period (Moll, 1979) of the reproductive cycle. An additional Pahang specimen from June was reproductively active with two old corpora lutea, an oviducal egg and sufficient enlarged follicles to produce a third clutch of one. Two May specimens from Trengganu (east coast) are also reproductively active, possessing enlarged follicles, old and new corpora lutea, and one having an oviducal egg. Specimen EOM 2357 had laid two clutches of one egg and had the sufficient enlarged follicles for up to

TABLE 13. Carapace lengthes of Cuora amboinensis, Cyclemys dentata, and Siebenrockiella crassicollis collected in Malaysia.

	Mean ≈ 1SD	Range
Cuora amboinensis		
Females (N)		
Adults (11)	177.4 - 10.0	159.0 - 191.0
Immature (8)	111.4 - 21.0	89.0 - 141.0
Males (N)		
Adults (11)	178.4 - 13.9	159.0 - 209.0
Immature (2)	138.0 - 18.4	125.0 - 151.0
Cyclemys dentata		
Females (N)		
Adults (8)	197.2 - 3.9	191.0 - 202.0
Males (N)		
Adults (4)	188.5 - 9.7	178.0 - 199.0
Siebenrockilla crassicollis		
Females (N)		
Adults (15)	184.4 - 9.0	168.0 - 202.0
Immature (3)	153.0 - 3.6	149.0 - 156.0
Males (N)		
Adults (14)	180.0 - 8.4	169.0 - 198.0
Immature (3)	92.5 - 7.8	88.0 - 101.5

TABLE 14. Seasonal variation of gonadal characters for nine female _Cuora amboinensis_ from West Malaysia;1975-1976, 1978. (Carapace length - Cl; female weight - wt.; Class I follicles, 6-8 mm; Class II, 9-15 mm; Class III, 16-22 mm; Class IV, 23-29 mm; N = new corpora lutea, O = old corpora lutea; mm = millimeter, g = grams).

FOLLICLE SIZE

DATE	SIZE		CLASSES						OVIDUCAL	FIELD
	Cl	wt	I	II	III	IV	N	O	EGGS	NUMBER
October 18***	187	950	-	1	6	-	-	-	-	EOM 2232
November 17***	191	1050	4	1	3	-	1	2	1	EOM 2254
December 2***	183	1000	4	3	-	-	-	-	-	EOM 2275
December 2*	159	700	1	2	1	-	-	-	-	EOM 2276
December 3*	180	800	-	1	1	-	-	-	-	EOM 2278
December 10*	165	900	2	4	-	-	-	-	-	EOM 2281
May 10**	179	1250	4	2	4	1	1	1	1	EOM 2357
May 30**	181	1000	-	7	5	-	1	2	-	EOM 2361
June 2*	171	750	-	1	2	-	1	2	1	EOM 2363

* East coast drainage (Pahang)
** East coast drainage (Trengganu)
*** West coast drainage (Perak)

TABLE 15. Seasonal variation of reproductive characteristics for ten female <u>Siebenrockiella crassicollis</u> from West Malaysia; 1975-76, 1978. (Cl - carapace length in millimeters; wt - weight of female in grams; Class I follicles 6-8 mm; Class II, 9-15 mm; Class III, 16-22 mm, Class IV, 23-29 mm; N = new corpora lutea, O = old corpora lutea).

FOLLICLE SIZE

DATE	SIZE		CLASSES						OVIDUCAL EGGS	FIELD NUMBER
	Cl	wt	I	II	III	IV	N	O		
October 13***	190	900	-	5	1	-	4	-	-	EOM 2224
October 18***	179	700	3	3	-	1	1	1	-	EOM 2228
December 2*	168	650	1	-	-	2	-	-	-	EOM 2273
December 18*	171	1000	4	3	-	1	-	2	-	EOM 2274
January 27***	186	1000	2	-	3	2	2	-	-	EOM 2302
January 28***	198	1050	8	1	3	2	2	2	2	EOM 2303
June 6**	188	1000	3	-	4	2	1	2	1	EOM 2379
June 6**	177	1000	-	-	-	-	6	-	1	EOM 2380
June 23**	185	900	-	-	-	-	5	-	1	EOM 2387
July 20**	170	641	-	-	-	-	1	4	-	EOM 2443

* East coast drainage (Pahang)
** East coast drainage (Trengganu)
*** West coast drainage (Perak)

three more clutches. The remaining May female (EOM 2361) had no oviducal eggs, one fresh and two very old corpora lutea. Sufficient enlarged follicles were present to produce at least one more clutch of up to three eggs.

Based on these limited data it appears Cuora is a seasonal nester in the east coast drainages. The nesting season definitely involves the months of May and June and presumably the month of April. This is a relatively dry period in Malaysia coming between the northeast and southwest monsoons.

Three specimens from west coast drainages (Perak) are from October, November, and December. The October female has no eggs or corpora lutea but does have six enlarging follicles in size class three. The November female with three enlarged follicles (Class III), three corpora lutea and an oviducal egg, has already two clutches and will probably produce at least one more. The December female has no oviducal eggs or corpora lutea and no follicles in either of the upper two size classes.

These scanty data suggest that Cuora also are seasonal nesters on the west coast with December beginning the period of quiescence but again considerable more observation are needed to substantiate this.

Based on numbers of corpora lutea and ovulatory size follicles the reproductive potential is at least six eggs per nesting season (Table 16). The clutch size is small, with all three gravid females having only a single oviducal egg. Egg size is relatively large averaging 47.0 mm in length, an ELI of .261 and EWI of .149. The reproductive effort averaged .019.

TABLE 16. Mean egg length with extremes (millimeters), ELI-egg length index, EWI-egg width index, clutch weight (grams), RE-reproductive effort, RP-reproductive potential (eggs/season) for *Cuora amboinensis*, *Cyclemys dentata*, and *Siebenrockiella crassicollis*.

	Egg Length				Clutch		
	Mean	Extremes	ELI	EWI	Weight	RE	RP
Cuora amboinensis							
EOM 2357	51.0		.285	.151	24.0	.019	7
EOM 2363	44.0		.257	.146	14.5	.019	5
EOM 2254	46.0		.241	-	20.0	.019	6
Mean	47.0		.261	.149	19.5	.019	6
Cyclemys dentata							
EOM 2362	52.7	52.0-54.0	.263	.150	81.5	.065	4
EOM 2381	60.4	59.7-61.5	.305	.143	89.2	.071	3
Mean	56.6		.284	.147	85.4	.068	3.5
Siebenrockiella crassicollis							
EOM 2303	51.5	51.0-52.0	.260	.149	56.0	.053	9
EOM 2380	51.5		.291	.159	24.5	.024	6
EOM 2387	54.1		.292	.171	33.5	.037	5
			.281	.160	38.0	.038	6.7

Cyclemys dentata

Eight adult females and four adult males collected are of similar size. The smallest male and female were 178 mm and 191 mm respectively. Adults ranged from 178 mm to 202 mm carapace lengths (Table 13). The largest known specimen, a female recorded by Smith (1931), was 240 mm in carapace length.

Two east coast specimens were available for the months of May and June. Each possessed corpora lutea, oviducal eggs, and only one had an enlarged follicle (diameter of 18 mm). Both females may have completed their nesting seasons after laying one clutch of three eggs (mean egg lengths of 60.4 mm and 52.7 mm, respectively) but possibly EOM 2362 could lay a single additional egg.

With these scant data it appears Cyclemys' nesting season is nearly completed by the end of May and early June in the east coast drainages of Malaysia.

A west coast (Perak) specimen from March had four old corpora lutea, one new and no enlarged follicles indicating one or more older clutches totaling four eggs, followed by a recent clutch of one at the end of its nesting cycle.

Based on the small sample of corpora lutea and ovulatory size follicles the reproductive potential is around three to five eggs. Clutch size is small with relatively large eggs (mean egg length of 56.6 mm), an ELI of .284, EWI of .147. The reproductive effort averaged .068 (Table 16).

Nesting appears to be seasonal in West Malaysia, involving the months of May and June on the east coast drainages and at least the month of March for the west coast drainages.

Siebenrockiella crassicollis

Data from 15 females, 14 males, and six immatures suggest that sexes mature at the same size and are similar in size throughout life. Adult carapace lengths range from 168 mm to 202 mm, the latter is the largest specimen recorded for Siebenrockiella (Table 13).

Findings on the female's reproductive cycle are summarized in Table 15. Six east coast specimens were examined; three from June, one from July, and two from December. The June and July specimens appear to be near the end of their nesting cycle. All had corpora lutea and only the June females had oviducal eggs (N=3). Only one had enlarged follicles and could continue laying. Of the December females, one had two old corpora lutea and both had ovulatory size follicles, suggesting they may still lay additional eggs.

Nesting appears to be seasonal in the east coast drainages. The nesting cycle appears to enter a latent period beginning in June, some nesting resumes in December. Specimens from the west coast were available from the months of October (N=2) and January (N=2). Table 15 summarizes these reproductive data. All females had corpora lutea and three had ovulatory size follicles.

Of the October specimens, one had laid two clutches of one egg each and the presence of an ovulatory size follicle indicated one more clutch of one egg may be laid before the nesting cycle is completed. The remaining October female appeared to have completed it's nesting cycle with one or more clutches producing a total of four eggs.

The two January specimens were reproductively active. One had two oviducal eggs, two old and new corpora lutea, and two ovulatory size follicles indicating three clutches of two eggs and the probability of at least one more clutch of two eggs. The other female had no oviducal eggs but two fresh corpora lutea and two enlarged follicles of size class four. Both had enlarged follicles of size class three.

From these data its difficult to say if Siebenrockiella is a seasonal nester on the west coast. At least some are reproductive in January and October, further investigation is needed.

The reproductive potential is at least six to nine eggs per season. Clutch size is small, three had single oviducal eggs and one had two. Eggs (N=3) are relatively large averaging 52.4 mm in length (egg data were not available for EOM 2379), an ELI of .281, and an EWI of .160. Reproductive effort averaged .038.

DISCUSSION OF REPRODUCTION

Cyclemys has the highest reproductive effort per clutch and lowest reproductive potential of the three species (Table 16). *Cyclemys* concentrates on producing only one or possibly two clutches of up to three eggs each, during its nesting season. *Cyclemys* appears to be the more aquatic of the three, rarely venturing onto land. The strategy of producing a single larger clutch per season rather than leaving its aquatic environment repeatedly to produce multiple small clutches, may reduce chances of predation. The female being less at home on land is perhaps more susceptable to predation during nesting than the other two species studied.

Cuora is regularly found on land and is well adapted to terrestrial environment (i.e. a plastral hinge). Their strategy of producing multiple small clutches may have selective value in avoiding predation of eggs. The idea being to lay many scattered clutches to ensure the survival of at least a few (not all eggs would likely be found by a predator).

The disadvantage of *Cyclemys* nesting strategy is that predators or some unpredictable environmental conditions can wipe out the entire annual production of an individual by destroying a single nest.

Siebenrockiella's reproductive effort and potential values (Table 16) are intermidiate between *Cyclemys* and *Cuora*. *Siebenrockiella* is known to spend several days out of water hiding in vegetation (Moll, personal communication). Whether or not

Siebenrockiella possesses adaptations to prevent predation on land needs to be proven. This species has a strategy similiar to Cuora's, laying small, multiple clutches scattered throughout the nesting cycle. It is yet to be proven if Siebenrockiella is a seasonal nester on the west coast of West Malaysia.

Because of the monsoons, West Malaysia is seasonally dry and wet, the months varying on east and west coasts. On the west coast March through May and October through December are periods of heavy rain associated with the Northeast and Southwest monsoons. On the east coast October through January is the chief rainy season associated with the Northeast monsoons. Generally, those nesting cycles are selected that allow the offspring to hatch under the most favorable conditions (times when food is abundant and there's less danger of unfavorable climatic conditions). Cuora, Cyclemys, and Siebenrockiella appear to be seasonal nesters, producing offspring during the dry periods in West Malaysia (when chances of egg destruction by flooding are low).

Moll (1979) describes two extreme kinds of reproductive strategy found among chelonians; Pattern I and Pattern II. Pattern I refers to those species that nest communally and lay large multiple clutches of relatively small eggs in well defined nests during definite nesting seasons (e.g. Batabur baska and sea turtles). In contrast, Pattern II are those solitary nesting species that lay small clutches of relatively large eggs with acyclic or continuous nesting periods with little or no nest construction (e.g. Cuora and Cyclemys). Clutch size is correlated with the body size of the turtle; small turtles produce small clutches

(Pattern II) and big turtles lay large clutches (Pattern I). Selection for egg size varies with the ecological parameters (e.g. climate, competition, predation) of the habitat. Of the three species discussed here, Cyclemys tends to lay slightly larger eggs. This possibly results from the fact Cyclemys lays fewer clutches per season than Cuora and Siebenrockiella, thus more energy can be allocated into producing a few fit individuals per season. Production of small clutches of large eggs would result in well developed offspring better able to compete for food resources and to better avoid predation. On the other hand laying large clutches of small eggs to produce as many offspring possible to ensure the survival of a few, by shear weight of numbers rather than quality. These smaller offspring are more susceptable to predation (brought on by cyclic communal nesting on ancestral nesting grounds). Moll (1979) refers to the Pattern I strategy as primitive and Pattern II the more recent strategy.

The extreme strategies are found only in tropical species while temperate species compromise between Pattern I and II (see Fig. 6, Moll, 1979).

Cuora, Cyclemys, and Siebenrockiella tend to generally compromise with Pattern II strategy. Cyclemys appears to be more marginal as it may not lay small multiple clutches, but single slightly larger clutches of large eggs and tends to be more aquatic than Cuora and Siebenrockiella. The latter, lay small clutches of large eggs, indicative of small, semiaquatic specialized, tropical turtles (Moll, 1979).

LITERATURE CITED

Berry, James F. 1975. The population effects of ecological sympathy on musk turtles in northern Florida. Copeia 4: 692-701.

Boulenger, George A. 1912. A vertebrate fauna of the Malay peninsula. Reptilia and Batrachia. London. 294 pp.

Cantor, T.E. 1847. Catalogue of reptiles inhabiting the Malayian peninsula. J. Asiatic Soc. Bengal 16: 607-1078. (Reprinted 1966 by A. Asher Co. Amsterdam.)

Colwell, R.K. and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

De Rooij, Nelly. 1915. The reptiles of the Indo-Australian Archipelago. I Lacertilia, Chelonia, Emydosauria. E. J. Brill, Ltd. 382 pp.

Flower, Stanley S. 1899. Notes on a second collection of reptiles made in the Malay Peninsula and Siam from November 1896 through September 1898. P. Z. S. L., May 16, 1899.

Moll, Edward O. 1976. West Malaysian turtles: utilization and conservation. Herpetologica Rev. 7: 163-166.

------. 1978. Drumming along the Perak. Nat. Hist. 87: 36-43.

------. 1979. Turtles: research and perspectives. John Wiley and Sons, Inc. 695 pp.

------. 1980a. Natural history of the river terrapin, _Batagur baska_. (In press)

------. 1980b. The habitat and salt water adaptation of the painted terrapin, _Callagur borneoensis_. (In press)

------, and J.M. Legler. 1971. The life history of a neotropical slider turtle, _Pseudemys scripta_ (Shoepff), in Panama. Bull. Los Angeles Co. Mus. Nat. Hist. Sci. 11: 102 pp.

Smedley, M.A. 1932. Notes on the herpetological collections in the Selangor Museum. Bull. Raffles Mus. 7: 9-17.

Smith, Malcolm A. 1931. The fauna of British India. Reptilia and Amphibia Vol. I-Loricata, Testudines. Taylor and Francis, LTD, London. 187 pp. (Reprinted 1973 by Ralph Curtis Books, Hollywood, Florida.)

Taylor, Edward A. 1970 The turtles and crocodiles of Thailand and adjacent waters. Univ. Kansas Sci. Bull. 59: 87-179.

Theobald, W. 1868. Reptiles of British Burma. J. Linn. Soc. Zool. 1868: 4-67.