VARIATION AND SYSTEMATICS OF THE MALAYAN SNAIL-EATING TURTLE, *MALAYEMYS SUBTRIJUGA* (SCHLEGEL AND MÜLLER, 1844)

by

Timothy R. Brophy
A Dissertation
Submitted to the
Graduate Faculty
of
George Mason University
in Partial Fulfillment of
The Requirements for the Degree
of
Doctor of Philosophy
Environmental Science and Public Policy

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Date: _______________________________________ Fall Semester 2002
George Mason University
Fairfax, VA

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Master of Science
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DEDICATION

This dissertation is dedicated to my children, Timmy and Emily,
who have made this entire project worthwhile.

ACKNOWLEDGEMENTS

This study would not have been possible without specimen loans or access from the following museum curators, technicians, and collection managers: C.W. Meyers and C.J. Cole, American Museum of Natural History, New York; C. McCarthy, British Museum (Natural History), London; J.V. Vindum, E.R. Hekkala, and M. Koo, California Academy of Sciences, San Francisco; E.J. Censky, Carnegie Museum of Natural History, Pittsburgh; P.C.H. Pritchard and G. Guyot, Chelonian Research Institute, Oviedo, FL; K. Thirakhupt and P.P. van Dijk, Chulalongkorn University, Bangkok, Thailand; A. Resetar, Field Museum of Natural History, Chicago; D.L. Auth, Florida Museum of Natural History, University of Florida, Gainesville; G. Koehler, Forschungs-Institut und Natur-Museum Senckenberg, Frankfurt, Germany; C.H. Ernst, George Mason University; H. Ota, Kyoto University Zoological Collection, Kyoto, Japan; J. Mariaux, Museum d'Histoire Naturelle, Geneva, Switzerland; R. Bour, Muséum National d'Histoire Naturelle, Paris, France; J.P. Rosado, J.E. Cadle, and L.A. Thomas, Museum of Comparitive Zoology, Harvard University, Cambridge; R.A. Nussbaum and G. Schneider, Museum of Zoology, University of Michigan, Ann Arbor; Mumpuni, Museum Zoology Bogor, Bogor, Indonesia; M.S. Hoogmoed, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; G.R. Zug and R.V. Wilson, National Museum of Natural History, Washington, D.C.; R.L. Bezy, J.A. Seigel, and D. Kizirian, Natural History Museum of Los Angeles County, Los Angeles; E. Stoeckli, Naturhistorisches Museum Basel, Basel, Switzerland; K. Grossenbacher, Naturhistorisches Museum Bern, Bern, Switzerland; F. Tiedemann and R. Gemel, Naturhistorisches Museum Wien, Vienna, Austria; R.W. Murphy and R. MacCulloch, Royal Ontario Museum, Toronto, Canada; U. Fritz, Staatliches Museum für Tierkunde, Dresden, Germany; R. Hirayama, Teikyo Heisei University, Ichihara Chiba, Japan; H. Silva, University of Kansas Natural History Museum, Lawrence, KS; K. Lim, C.M Yang, and P.K.L. Ng, Zoological Reference Collection, School of Biological Sciences, National University of Singapore, Singapore; J. Hallerman, Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Hamburg, Germany; F. Glaw, Zoologische Staatssammlung München, Munich, Germany; J.B. Rasmussen, Zoologisk Museum, Kobenhavns Universitet, Copenhagen, Denmark. Special thanks goes to Robert V. Wilson of the National Museum of Natural History (Smithsonian Institution) for endless hours of loan processing on my behalf. I would also like to thank Marinus Hoogmoed and Franz Tiedemann for their wonderful hospitality during my visits to Leiden and Vienna, respectively.

Many thanks go to Kerry Hansknecht for taking most of the photographs in this dissertation. I also thank Tom Akre for many late nights spent studying for comps, discussing turtle conservation and evolution, and for being a great friend.

I would also like to express my sincerest gratitude to my dissertation committee. I thank Dr. Carl Ernst for his willingness to take a chance on me, and for his guidance, patience, and tender heartedness. I thank Dr. George Zug, one of the most objective scientists I have ever met, for his constructive criticisms and for always having my best interests in mind. I thank Dr. John Miller for endless hours of statistics in his office and over the phone. I thank Dr. Jay Shaffer for his insights on animal taxonomy and evolution. This study would not have been possible without the assistance of these four selfless men.

I thank the Chelonian Research Foundation, the Chicago Herpetological Society, and George Mason University for financial support during various stages of this project.

Finally, this study would have been impossible without the love and support of four special people. I thank my children, Timmy and Emily, for their unconditional love and for the sacrifices they have made during this study. I cannot express in words my gratitude to my wife Michele. This project would have been absolutely impossible without her love and support (financial, emotional and spiritual). She deserves at least half of this degree. I hope our life together is better because of the sacrifices you have made during this six year period. Lastly, I give all honor and glory to my Lord and Savior Jesus Christ, who has given me a peace that passes all understanding (Phillipians 4:6-7) and has established my thoughts throughout this project (Proverbs 16:3).

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ABSTRACT

VARIATION AND SYSTEMATICS OF THE MALAYAN SNAIL-EATING TURTLE, *MALAYEMYS SUBTRIJUGA* (SCHLEGEL AND MÜLLER, 1844)

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Allometry, sexual dimorphism, and geographic variation were studied in the Malayan snail-eating turtle, *Malayemys subtrijuga* (Schlegel and Müller, 1844), using regression and discriminant function analyses. Allometry was evident in *M. subtrijuga* from the Chao Phraya River Basin. Shell shape changed in males as carapace length increased more than shell width and height, whereas females showed proportional changes. This difference in allometric growth yielded sexually dimorphic adults. Females attained larger sizes and had relatively wider and higher shells than males. Discriminant function analysis of shell and head-stripe characters revealed a clear pattern of geographic variation that was consistent with the topography of Southeast Asia and the poor dispersal abilities of these turtles. Two morphologically distinct groups of *Malayemys* occur allopatrically in lowland areas of mainland Southeast Asia, and each requires recognition as a distinct species. Turtles from the Mekong River Basin retain the name *Malayemys subtrijuga* (Schlegel and Müller, 1844), whereas those from the Chao Phraya and Mae Khlong basins, coastal areas of southeastern Thailand, and the Malay Peninsula are assigned the name *Malayemys macrocephala* (Gray, 1859). Both species are potentially threatened by overcollection and habitat destruction, and should be protected separately. Finally, discriminant function analysis of shell and head-stripe characters suggested that *M*. *subtrijuga* on Java were derived from the Mekong River Basin.

Chapter 1 – Background and Objectives

Because of recent changes in Asian economics, many Asian turtle and tortoise species are at serious risk from uncontrolled commercial exploitation (Behler, 1997). Several casualties of such exploitation have already been reported. The following species have either vanished from the wild or are considered commercially extinct: *Cuora aurocapitata*, *C. zhoui*, *C. pani*, *C. mccordi*, *C. flavomarginata*, and *Chinemys reevesii* (Behler, 1997; Salzberg, 1998). Several others are at serious risk in nature including *Cuora trifasciata*, *Batagur baska*, *Callagur borneoensis*, *Orlitia borneoensis*, *Pelochelys bibroni*, and *Chitra* spp. (Behler, 1997). During a July 1997 trip to China, William P. McCord visited turtle markets in Guangzhou and Shenzhen. He estimates that 10,000 turtles were seen in these two markets over a two-day period. This translates into a conservative estimate of 2.6 million turtles being sold in China each year (Salzberg, 1998).

According to John Behler (1997), the turtle crisis in Southeast Asia and southern China is among the most serious facing conservationists today. Asian turtles are being exploited at such a rate that some species are very likely disappearing before they are recognized by biologists. *Malayemys subtrijuga*, the Malayan snail-eating turtle, is one such species that is seriously threatened by commercial exploitation. This chapter begins by giving detailed information regarding the natural history, taxonomic history, and phylogenetic position of *M. subtrijuga* and concludes with the objectives for a morphometric study of allometry, sexual dimorphism, and geographic variation in this species.

Natural History

Malayemys subtrijuga, the Malayan snail-eating turtle, is a small batagurid turtle reaching maximum sizes of 220 mm carapace length (Srinarumol, 1995). The carapace is dark brown to mahogany with black areoli, a yellow rim, and three discontinuous keels. The plastron and lower marginals are yellow with large dark blotches on each scute. The black head is proportionally large and adorned with several yellow or cream-colored stripes that extend onto the neck. Limbs are gray to black with a narrow yellow outer border (Ernst and Barbour, 1989; van Dijk and Thirakhupt, in press).

Malayemys subtrijuga inhabits lowland freshwater habitats including ponds, canals, streams, swamps, marshes, and wet rice fields (Smith, 1931; Taylor, 1970; Nutaphand, 1979; Ernst and Barbour, 1989; Srinarumol, 1995; van Dijk and Thirakhupt, in press). It is usually found at the margins in warm shallow water, where it spends most of its time foraging (van Dijk and Thirakhupt, in press). The Thai name for this species (“Tao Nao”) means ricefield terrapin, indicating its fondness for that habitat (Nutaphand, 1979; Srinarumol, 1995).

Malayemys subtrijuga is a diurnal bottom feeder that locates its prey by smell (van Dijk and Thirakhupt, in press). It is primarily a mollusk-eater, as evidenced by its large head, large triturating surface, and powerful jaw muscles (Smith, 1931; Taylor, 1970; Nutaphand, 1979; Ernst and Barbour, 1989; Srinarumol, 1995; van Dijk and

Thirakhupt, in press). Small individuals feed almost exclusively on aquatic snails, but large females also consume freshwater mussels (van Dijk and Thirakhupt, in press). Srinarumol (1995) found the diet of *M. subtrijuga* to be dominated by two freshwater snails, *Filopaludina sumatrensis* (Mesogastropoda: Viviparidae) and *Brotia costula* (Mesogastropoda: Thiaridae). *Malayemys subtrijuga* is also known to consume worms, aquatic insects, leeches, crabs, shrimp, and small fish (Smith, 1931; Taylor, 1970; Nutaphand, 1979; Ernst and Barbour, 1989; Srinarumol, 1995; van Dijk and Thirakhupt, in press).

Malayemys subtrijuga has several parasites and predators. Major ectoparasites include leeches of the Order Acanthobdellida (Srinarumol, 1995). Major endoparasites include two species of nematodes (Family Oxyuridae, Order Ascaridida; and Family Rhabditidae, Order Rhabditida) and one species of fluke (Suborder Prostomata, Order Digenea) (Srinarumol, 1995). Natural predators of *M. subtrijuga* include monitor lizards (*Varanus* spp.) and crows (*Corvus macrorhynchos*) (van Dijk and Thirakhupt, in press).

In the central plains of Thailand, the breeding season of *M. subtrijuga* begins in August (Srinarumol, 1995), and nesting occurs from December to March (van Dijk and Thirakhupt, in press). The nesting season in Cambodia is similar to that of Thailand, as evidenced by the sale of fresh shelled-eggs at a Cambodian market in January (van Dijk and Thirakhupt, in press). Typical clutch size is 3-4 eggs (van Dijk and Thirakhupt, in press), but clutches ranging from 3-10 (Nutaphand, 1979; Srinarumol, 1995) and 8-10 (van Dijk and Thirakhupt, in press) have been reported from Thailand and Cambodia, respectively. It has been hypothesized that clutch size increases with female body size in

Malayemys, with small females (<150 mm CL) laying clutches of 3-4 eggs and large females (>150 mm CL) laying clutches of ≥ 5 eggs (van Dijk and Thirakhupt, in press). The following sizes have been recorded for the white, elliptical, brittle-shelled eggs of this species: 32 x 20 mm (Flower, 1899); 40-45 x 20-25 mm (Smith, 1931); 41.5 x 24.5 mm (Kopstein, 1932); an average of 44 x 22 mm (Ewert, 1979); 32.5-45 mm length and 6.3-15.4 g mass (Srinarumol, 1995); 40.7 ± 2.6 x 21.9 ± 1.2 mm and 10.9 ± 2.8 g (means ± 1 SD, n = 12) (van Dijk and Thirakhupt, in press).

Incubation time (29.5° C and 90% relative humidity in the laboratory) for this species is 164.20 ± 40.33, 161.24 ± 49.64, 200.75 ± 25.95, and 170.57 ± 44.61 days (means ± 1SD) for clutch sizes 3, 4, 5, and 6 respectively; and hatching success is 66.67%, 70.83%, 40%, and 30.89% for clutch sizes 3, 4, 5, and 6 respectively (Srinarumol, 1995). Hatchling size has been reported as 35.3 mm (CL) and 31.1 mm (PL) by Ewert (1979); and as 29.01 ± 1.24 mm (midline PL for male hatchlings; mean ± 1 SD) and 28.21 ± 1.74 mm (midline PL for female hatchlings; mean ± 1 SD) by Srinarumol (1995). Survival rates of captive hatchlings are high for the first three months (first two months=100%; third month=96%) but decrease in subsequent months (fourth month=79%; fifth month=65%) (Srinarumol, 1995). Female hatchlings grow relatively faster during the first five years of life, but sexual dimorphism is most pronounced after sexual maturity is attained (Srinarumol, 1995). This occurs at approximately 100 mm CL in males and 120 mm CL in females (Srinarumol, 1995). *Malayemys subtrijuga* has pronounced sexual dimorphism, with females having larger overall body sizes, proportionally wider carapaces, and shorter, narrower tails. The plastra of both sexes, however, are flat (Ernst and Barbour, 1989; Srinarumol, 1995; van Dijk and Thirakhupt, in press).

Populations of *M. subtrijuga* can be found in virtually all lowland areas of central Thailand, where it is the most commonly found wild turtle (van Dijk and Thirakupt, 2000). In a 10 km^2 study site outside of Bangkok, approximately 400 individuals were found in a few month period with a low occurrence of recaptures (van Dijk and Thirakupt, 2000). Population status outside of central Thailand is poorly documented. *Malayemys subtrijuga* is presumed to be abundant in southern Vietnam (Bourret, 1939; Geissler and Jungnickel, 1989; van Dijk and Thirakhupt, in press), less abundant in peninsular Thailand (van Dijk and Thirakhupt, in press), and rare in Java (van Dijk and Thirakhupt, in press; Peter C. H. Pritchard, pers. comm.).

Taxonomic History

The three syntypes of *Malayemys subtrijuga* (see Appendix A) were collected in Java by H. Kuhl and J. C. van Hasselt, probably in the province of Bantam (former residency in western Java also known as Banten; reinstated as Banten Province in 2000) (Schlegel and Müller, 1844; Hubrecht, 1881). These specimens were sent to the Leyden Museum (presently the Nationaal Natuurhistorisch Museum in Leiden, The Netherlands) where Boie (“1824-1825”) incorrectly identified them as *Emys trijuga* Schweigger, 1812 from the Indian subcontinent (see Hoogmoed, 1982 for discussion of completion date of Boie’s “1824-1825” manuscript). Boie (“1824-1825”) also provided an illustration of one individual (Fig. 1), an adult female currently cataloged as RMNH 6085.

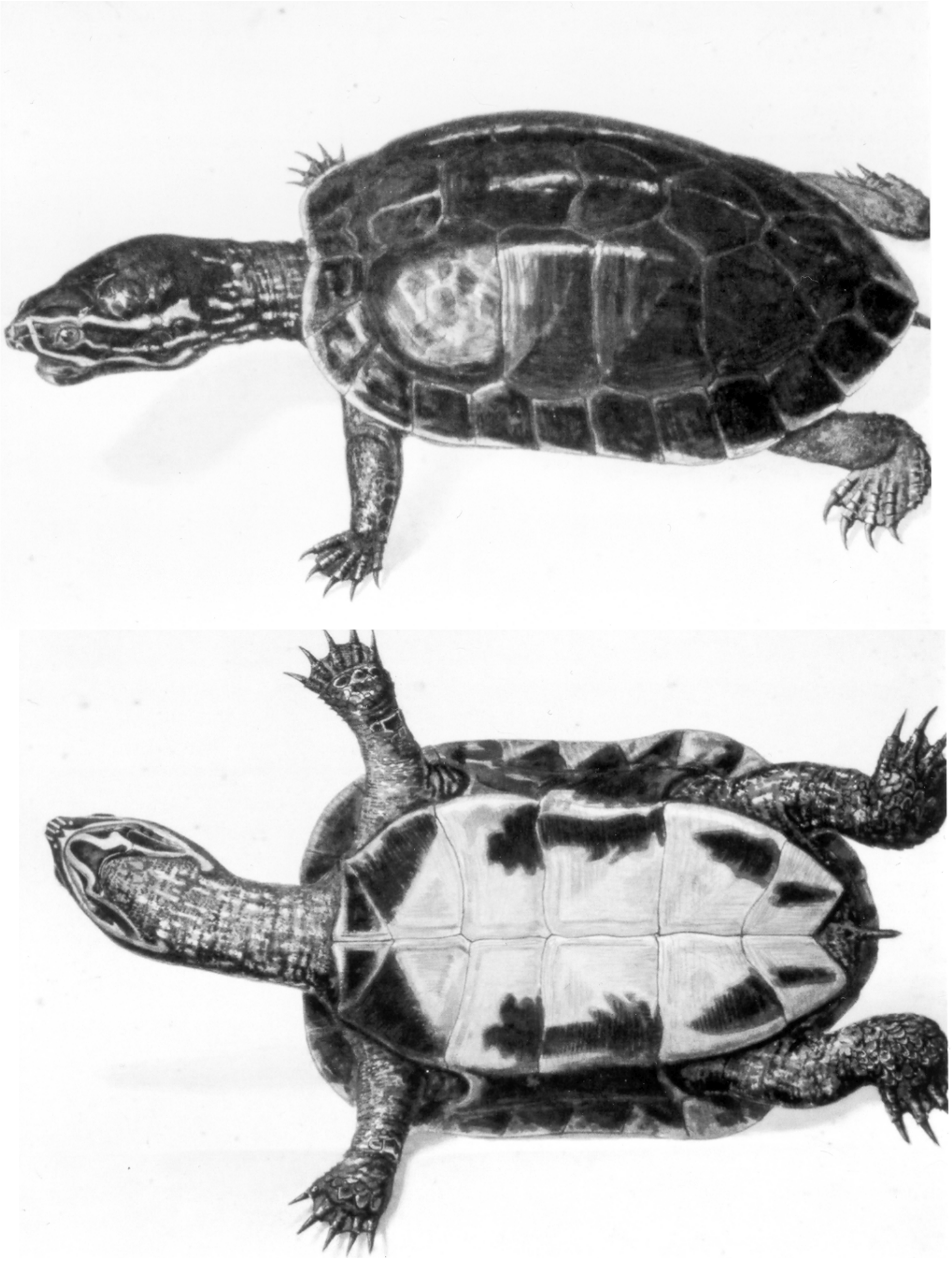

FIGURE 1. Photograph of Plate III from Boie (“1824-1825”) showing one of the three syntypes of *Malayemys subtrijuga*. This turtle is an adult female currently cataloged as RMNH 6085. Boie’s (“1824-1825”) original manuscript, along with color prints, is housed in the archives of the Nationaal Natuurhistorisch Museum in Leiden, The Netherlands.

Temminck and Schlegel (1835:64) gave a short description of these same three specimens (Appendix B) that included the following characteristics: head large; plastron small, mobile; anterior marginal scutes large; first vertebral scute bell-shaped; carapace with yellow border and three prominent keels; plastron solid, flat underneath, angular on sides, truncated anteriorly, notched posteriorly; muzzle protruding; yellow stripes descending obliquely, covering sides of head and muzzle; and jaws covered with large number of spots that disappear towards neck. Temminck and Schlegel, like Boie, made the mistake of uniting these specimens with *E. trijuga* Schweigger, 1812.

Schlegel eventually realized this error and corrected it in Schlegel and Müller (1844). In this publication (Appendix B), the three specimens in the Leyden Museum were given the name *Emys subtrijuga* (Schlegel and Müller, 1844:30). The large head of this species was mentioned, and the type-locality was given as “Java” (probably in Bantam). For a more complete description, reference was given to Temminck and Schlegel (1835). The three syntypes, one stuffed adult male and two stuffed adult females, have since been cataloged as RMNH 6082, 6084, and 6085 (King and Burke, 1989).

In a published account of reptiles collected on Java, Bleeker (1857:239) listed *Cistudo gibbosa* Blkr, n. spec. from Batavia (former name of Jakarta, Indonesia). A specimen bearing that name was eventually sent by Bleeker to the British Museum (presently British Museum of Natural History in London) and in 1889 appeared on a list of *Damonia subtrijuga* found in its collection (Boulenger, 1889:95; “specimen k”). The name *C. gibbosa* is a *nomen nudum* since it was never accompanied by an appropriate description. The citation for this nomen nudum has traditionally (Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977) been given as: *Cistudo gibbosa* Bleeker in Boulenger, 1889:95. However, it should be given as: *Cistudo gibbosa* Bleeker, 1857:239.

Gray (1859:479) described two specimens which he received from M. Mouhot as *Geoclemys macrocephala*. He gave a rather long description of these specimens (Appendix B) that included the following characteristics: shell oblong, depressed, entire, three-keeled, olive-brown; margin yellow-edged; plastron yellow with black triangular spots; head large; crown flat, purplish-brown; two stripes from middle of nose; two stripes from posterior edge of orbit; two close stripes under nostrils to middle of upper jaw; two broad stripes down front of lower jaw; front of forelegs covered with broad band-like scales; first vertebral scute quadrangular, front edge wider, rounded; second through fourth vertebrals six-sided, second longer than broad, fourth broader than long; and fifth vertebral scute subquadrangular. Gray also provided a detailed drawing of one of the specimens (Plate XXI) but misspelled the generic name in the caption (Fig. 2). The type-locality for *G. macrocephala* was given as “Siam” (Thailand), and the two stuffed juvenile syntypes mentioned by Gray have since been cataloged as BMNH 59.7.8.4 and BMNH 59.7.8.5. According to Hubrecht (1881), Gray’s description and drawing of *G. macrocephala* agreed, in almost every detail, with the syntypes and descriptions of Schlegel and Muller’s (1844) *E. subtrijuga*. *Geoclemys macrocephala* has been recognized as a junior subjective synonym of *M. subtrijuga* by several authors

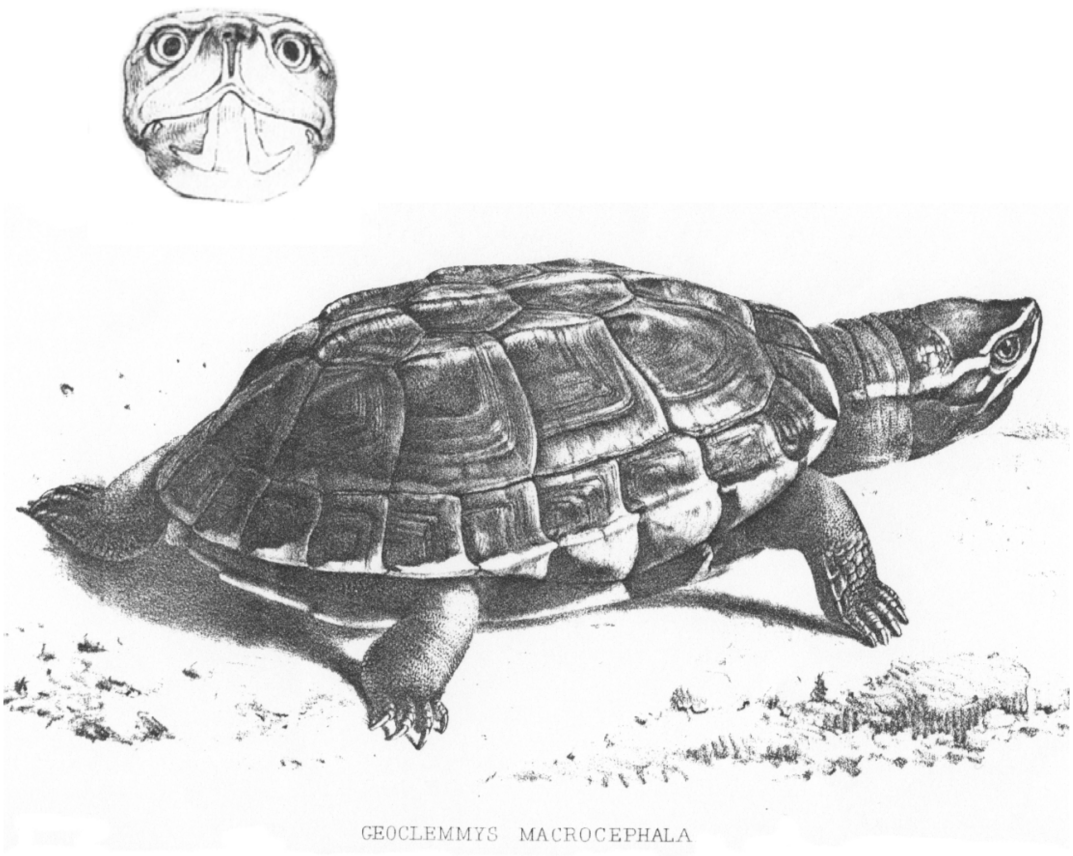

FIGURE 2. Plate XXI from Gray's (1859) description of *Geoclemys macrocephala*. The type locality for this species is "Siam". Notice the mispelling of *Geoclemys* (*Geoclemmys*) in the caption.

(Boulenger, 1889; Smith, 1931; Bourret, 1941; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977; Taylor, 1970).

Strauch (1862:32) reassigned Gray's (1859) *G. macrocephala* to the genus *Clemmys*. His description of the genus *Clemmys* included several characters of both the shell and skull. Strauch gave no description of *C. macrocephala* but simply listed it among 62 species of *Clemmys* from all parts of the world.

Blyth (1863:82) described *Emys nuchalis* based on specimens he received from the Batavia Society in 1844. Blyth included the following characters in his description of *E. nuchalis*: medial nuchal plate large, triangular; next four medial dorsal plates elongate, quadrangular; sixth medial dorsal plate triangular, apex to the front; three dorsal ridges conspicuous in young; posterior border of shell slightly dentate in young; plastron flat, angled laterally; principal pairs of sternal plates about equal, nearly quadrate; in some, second pair of sternal plates much shorter than wide, with third pair correspondingly enlarged; olive-brown color; lateral angles of carapace and plastron yellow; plastron reddish-brown, clouded with black; head black; yellow lines on eye, under eye, behind eye, bordering upper jaw; and yellow markings on lower jaw. The type-locality for *E. nuchalis* was given as "Java?". Smith (1931) listed the Indian Museum as the repository for the type material of *E. nuchalis* but was not more specific. Theobald (1868) stated that three *E. nuchalis* specimens were in the Museum of the Asiatic Society of Bengal in Calcutta: one stuffed adult specimen from Java (received from the Batavia Society); and two stuffed juvenile specimens of uncertain origin (presumably Java; also received from the Batavia Society). According to Das et al. (1998), the three syntypes (ZMZ 824-826) of *Emys nuchalis* are currently housed in the collection of the Zoological Society of India in Calcutta. *Emys nuchalis* has been recognized as a junior subjective synonym of *M. subtrijuga* by several authors (Boulenger, 1889; Smith, 1931; Bourret, 1941; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977; Taylor, 1970).

Günther (1864:31) reassigned Gray's (1859) *G. macrocephala* to the genus *Emys*. Günther's description of the genus *Emys* included the following characters: thorax and sternum solid, entirely bony; carapace depressed, immovable in adult; third and fourth vertebrals broadly united; sternum flat; pectorals subquadrangular; toes broadly webbed; and five strong claws anteriorly, four posteriorly. Günther listed 11 species of *Emys* from British India (that part of India formerly under direct British administration) and gave the range of *E. macrocephala* as Siam and Cambodia.

Gray (1869:194) reassigned *G. macrocephala* (Gray, 1859) to the genus *Damonia*. His description of this new Asiatic genus was based largely on characters of the skull but also included the following: head very large; nose high, truncated; thorax oblong, distinctly three-keeled; vertebral shields six-sided; sternal plates regular; toes strong, with band-like shields; and hind toes longest. Gray listed four species of *Damonia* from the British Museum and gave the range of *D. macrocephala* as Siam and Cambodia.

Gray (1870:41) reassigned Blyth's (1863) *E. nuchalis* to the genus *Bellia*. Gray's description of the Asiatic genus *Bellia* included the following characters: head very large; nose high, truncated; thorax oblong; back three-keeled; vertebral plates elongate, subtrigonal; and toes strong, with transverse band-like shields. This description of *Bellia* is identical in many respects to Gray's (1869) description of *Damonia*. Gray (1870), however, differentiated the two genera accordingly: "*Bellia* has the large head, with dependent lips, of *Damonia*; but the alveolar surface of the upper jaw is not so wide, and the inner nostrils are anterior" (1870:40). Java was given as the range of *B. nuchalis*.

Gray (1870:43) described *Damonia*? *crassiceps* based on a sketch (copy of drawing in the Reeves collection) in the Hardwicke collection at the British Museum (Nos. 19-21) (see Wheeler, 1998). The type-locality of this species was given only as China, and its description included the following characters: shell oblong; vertebral shields broad, six-sided, blackish-brown; margin entire, with broad caudal notch; underside reddish-brown; head very large, acute in front; front of legs with a few small transverse oblong plates. Gray stated that this species differed from *D. megacephala* (*macrocephala*?) by not having markings on the side of the head. Several authors have included *D.*? *crassiceps* as part of the synonymy of *M. subtrijuga* (Smith, 1931; Bourret, 1941; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977; Taylor, 1970;).

Gray (1871:367) described *Damonia oblonga* based on a Batavian specimen purchased from Mr. Edward Gerrard, Jr. Gray gave a lengthy description of *D. oblonga* and compared it with *D. macrocephala* from Cambodia and Siam. He stated that *D. oblonga* was very similar to *D. macrocephala* but differed by being a narrower, oblong form; by having very differently shaped vertebral shields; by having three perpendicular streaks on each side of the nose; and by having a more uniformly black shell (especially the plastron). More specifically, the carapacial shields of *D. oblonga* were described as follows: first vertebral longer than wide, urn-shaped; second vertebral nearly quadrangular, as long as wide; third and fourth vertebrals six-sided; fourth vertebral wider than long, narrow posteriorly; and first costal shield elongate, much larger than same shield in *D. macrocephala* (compare each character with description of *G. macrocephala* above). As mentioned above, the type-locality for *D. oblonga* was given as "Batavia", and the stuffed male holotype mentioned by Gray has since been cataloged as BMNH 71.4.10.2. Several authors (Boulenger, 1889; Smith, 1931; Bourret, 1941; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977; Taylor, 1970) have recognized *D. oblonga* as a junior subjective synonym of *M. subtrijuga*.

Boulenger (1889:94) united each of the following names with *Damonia subtrijuga* (Schlegel and Muller, 1844): *E. trijuga* Temminck and Schlegel, 1835 (non Schweigger, 1812); *E. subtrijuga* Schlegel and Müller, 1844; *G. macrocephala* Gray, 1859; *C. macrocephala* (Gray, 1859); *E. nuchalis* Blyth, 1863; *E. macrocephala* (Gray, 1859); *D. macrocephala* (Gray, 1859); *B. nuchalis* (Blyth, 1863); and *D. oblonga* Gray, 1871. His description of the genus *Damonia* included the following characters: neural plates six-sided, short-sided anteriorly; long axillary and inguinal scutes; inguinal extending to point between fifth and sixth costals; entoplastron intersected by humero-pectoral suture; skull with bony temporal arch; alveolar surfaces broad; choanae post-orbital; small shields on posterior portion of head; webbed toes; and tail short or moderate. Boulenger listed five species of *Damonia* from the British Museum and gave the range of *D. subtrijuga* as Siam, Cambodia, and Java.

Siebenrock (1909:476) reassigned Boulenger's (1889) *D. subtrijuga* to the genus *Geoclemys*. His description of *Geoclemys* was nearly identical to Boulenger's (1889)

Damonia and included the following characteristics: inguinal scutes extending to point between fifth and sixth costals; entoplastron intersected by humero-pectoral scute; alveolar surfaces flat, broad; choanae positioned posterior to orbit; small scales on posterior portion of head; and tail short to moderately long. Siebenrock listed four species of *Geoclemys* and gave the range of *G. subtrijuga* as the Malay Peninsula, Siam, Cochinchina (a former French colony; later that part of southern Vietnam south of 10° 50’ N), and Java.

Lindholm (1931:30) was the first to use the current combination *Malayemys subtrijuga*. He explained that the genus name *Damonia* was preoccupied, as it was used by Robineau-Desvoidy (1847:593) to describe a genus of dipterans (Diptera: Insecta). As a substitute, Lindholm recommended the use of the name *Malayemys* with the monotypic species *M. subtrijuga* (Schlegel and Müller, 1844) from Java and “Hinterindien” (mainland Southeast Asia).

Phylogenetic Position

Even though the nomenclatural history of *M. subtrijuga* is well documented, its phylogenetic position is less certain. *Malayemys subtrijuga* represents a distinct lineage, well defined by several uniquely derived characters (Table 1). This high level of divergence from all other batagurids is the precise reason for the difficulty in assessing its phylogenetic position (Sites et al., 1984). Most authors avoid making a firm phylogenetic conclusion regarding *M. subtrijuga* and simply present its placement on a parsimonious cladogram.

TABLE 1. Uniquely derived characters of *Malayemys subtrijuga*.

Character	Reference
Unique choanal structure; lacks any trace of a papilla or fold lateral to the choana[a]	Parsons, 1960, 1968; McDowell, 1964
Contact between the processus inferior parietalis and the maxillae present with flared process of parietals[b]	Hirayama, 1984
Contact between the jugals and the articular facet of the quadrates present[b]	
Foramen palatinum posterius enclosed by the flared processus inferior parietalis antero-medially, excluded from the fossae orbitalis[b]	
Pterygoid participation onto the articular facet of the quadrates present[b]	
Scapular prong with lateral concavity[b]	
Contact between the medial process of jugals and the processus inferior parietalis present[c]	
Autapomorphic biochemical characters: $+\mathrm{Gtdh}^{120}$, $-\mathrm{Gtdh}^{100}$, $+\mathrm{Ldh\text{-}B}^{116}$, $-\mathrm{Ldh\text{-}B}^{100}$, $-\mathrm{Pep\text{-}D}^{100}$, $+\mathrm{Pep\text{-}D}^{87}$, $+\mathrm{M\text{-}Aat}^{115}$, $+\mathrm{S\text{-}Mdh}^{88}$, $+\mathrm{Me}^{100}$[d]	Sites et al., 1984
Unique karyotype; 2n=50 (8:5:12) with the NOR (nucleolus organizer regions) located interstitially on a large microchromosome[e]	Carr and Bickham, 1986

[a] Unique among Recent turtles (Parsons, 1968)

[b] An unique derived character among testudinoid turtles; considered as acquired only once among testudinoids (Hirayama, 1984)

[c] An unique derived character among batagurids, but shared by some emydids as well (Hirayama, 1984)

[d] Negative loci reflect loss of characters, whereas positive loci reflect the addition of characters (Sites et al., 1984)

[e] Unique among batagurids, but indistinguishable from invariant emydid karyotype (Carr and Bickham, 1986)

Data presented for *M*. *subtrijuga* shows that its uniqueness makes its phylogenetic position extremely obscure. McDowell (1964:261) placed *M*. *subtrijuga* in his *Batagur* complex and noted that it was "quite peculiar in lacking any trace of a papilla or fold lateral to the choana." The choanal structure of *M*. *subtrijuga* is unique among Recent turtles (Parsons, 1960, 1968). Hirayama (1984) found that *M*. *subtrijuga* possessed five characters uniquely derived among testudinoids and one character uniquely derived among batagurids (Table 1). He suggested that *Malayemys* was most closely related to *Chinemys* and *Geoclemys*. Sites et al. (1984) found that *M*. *subtrijuga* had nine autapomorphic biochemical characters (Table 1) and was fixed for a unique electromorph at two of the three most conservative loci used in their study. They concluded (1984:151) that "*Malayemys subtrijuga* is extremely problematic [with respect to assessing its phylogenetic position] and can be hypothesized in any number of clades." Their most parsimonious cladogram, however, placed *M*. *subtrijuga* in closest association with *Ocadia sinensis* and *Kachuga smithi*. Carr and Bickham (1986) found that *M*. *subtrijuga* had a unique karyotype among batagurids but indistinguishable from the invariant emydid karyotype (Table 1). They hypothesized that *Malayemys* has a phylogenetic position somewhere between the *Orlitia* complex (*Orlitia* and *Siebenrockiella*) and the emydids.

Another unique aspect of *M*. *subtrijuga* is its presumed geographic uniformity. This uniformity may be more apparent than real, because analyses of other Southeast Asian turtles have revealed significant regional differentiation (Ernst, 1988; Ernst and Lovich, 1990; McCord and Iverson, 1991, 1992; Iverson and McCord, 1992a, 1992b, 1997; Yasukawa et al., 1996; McCord, 1997). My goal is to test for geographic uniformity and if regional differentiation has occurred to seek vicariant explanations.

Objectives

The primary objectives of this study are to examine geographic variation in *M. subtrijuga* and to describe any new taxa discovered. Fulfilling these objectives will provide valuable taxonomic information and may lead to much needed legal protection for certain overexploited populations. The specific objectives are as follows:

1) To examine allometric variation and sexual dimorphism in populations of *M. subtrijuga*.

2) To examine geographic variation in *M. subtrijuga*.

3) To describe any new taxa resulting from the above analyses.

4) To determine which factors (past geological, ecological, or otherwise) produced and maintained conditions leading to differentiation and speciation.

Chapter 2 – Intrasample Examinations: Size Distribution, Allometry, and Sexual Dimorphism of Shell Characters

Sexual dimorphism and allometry of the turtle shell have been studied extensively (see Mosimann, 1956; Berry and Shine, 1980; Ernst and Lovich, 1986; and Gibbons and Lovich, 1990 for reviews). Sexual dimorphism deals with differences in shape and size of the shell between sexes, whereas allometry focuses on relative growth of parts of the shell in relation to the entire organism. Both are important factors in various types of biological studies. In ecology, these are critical because of the influence of shell shape and size on the habits of turtles (Mosimann, 1958). In physiology and nutrition, they are useful in describing surface area to volume relationships and their subsequent effects on metabolism (Mosimann, 1958). In addition, allometry and sexual dimorphism of the turtle shell have obvious implications for embryology and morphogenesis (Mosimann, 1958) as well as evolution (Berry and Shine, 1980; Gibbons and Lovich, 1990) and taxonomy (Mosimann, 1958).

For purposes of this study, however, I am most interested in sexual dimorphism and allometry as they relate to my larger study of geographic variation in *M. subtrijuga*. A detailed investigation of intrapopulational variation is a crucial first step in any study of interpopulational differences. Without such considerations, critical errors in taxonomic judgement are likely to occur.

The purpose of this chapter is to examine sexual dimorphism and allometric variation in several populations of *M*. *subtrijuga*. Although these aspects have been studied widely in turtles, little attention has been focused on *M*. *subtrijuga*. In fact, this is the first statistical treatment of allometric variation in *M*. *subtrijuga* and only the second statistical examination of its sexual dimorphism.

Materials and Methods

Sample and Character Definitions

An attempt was made to examine all museum specimens from throughout the known range of *M*. *subtrijuga*. Specimens were grouped into regional geographic samples representing major drainage basins for those on mainland Southeast Asia (Kottelat, 1989) and entire islands for those in the Greater Sundas. Sample localities were: Maly, Malay Peninsula including western Malaysia and peninsular Thailand; MKhl, Mae Khlong basin of Thailand; CPhr, Chao Phraya basin of Thailand; SECos, coastal areas of southeast Thailand and Cambodia; Mekg, Mekong basin of Vietnam, Cambodia, and eastern Thailand; Sumt, Sumatra; Java, Java (Fig. 3). The geographic origin of each specimen was based on museum records, and each geographic sample was divided into subsamples based on sex and life stage.

A total of 258 *M*. *subtrijuga* were examined and utilized in all or some of the analyses that follow (see Appendix C and D for specimens examined). The data set consisted of one meristic and 28 mensural shell characters (Table 2). These characters derived from those previously used in morphometric studies of turtles, from those previously used to describe *M*. *subtrijuga*, and from characters newly discovered during

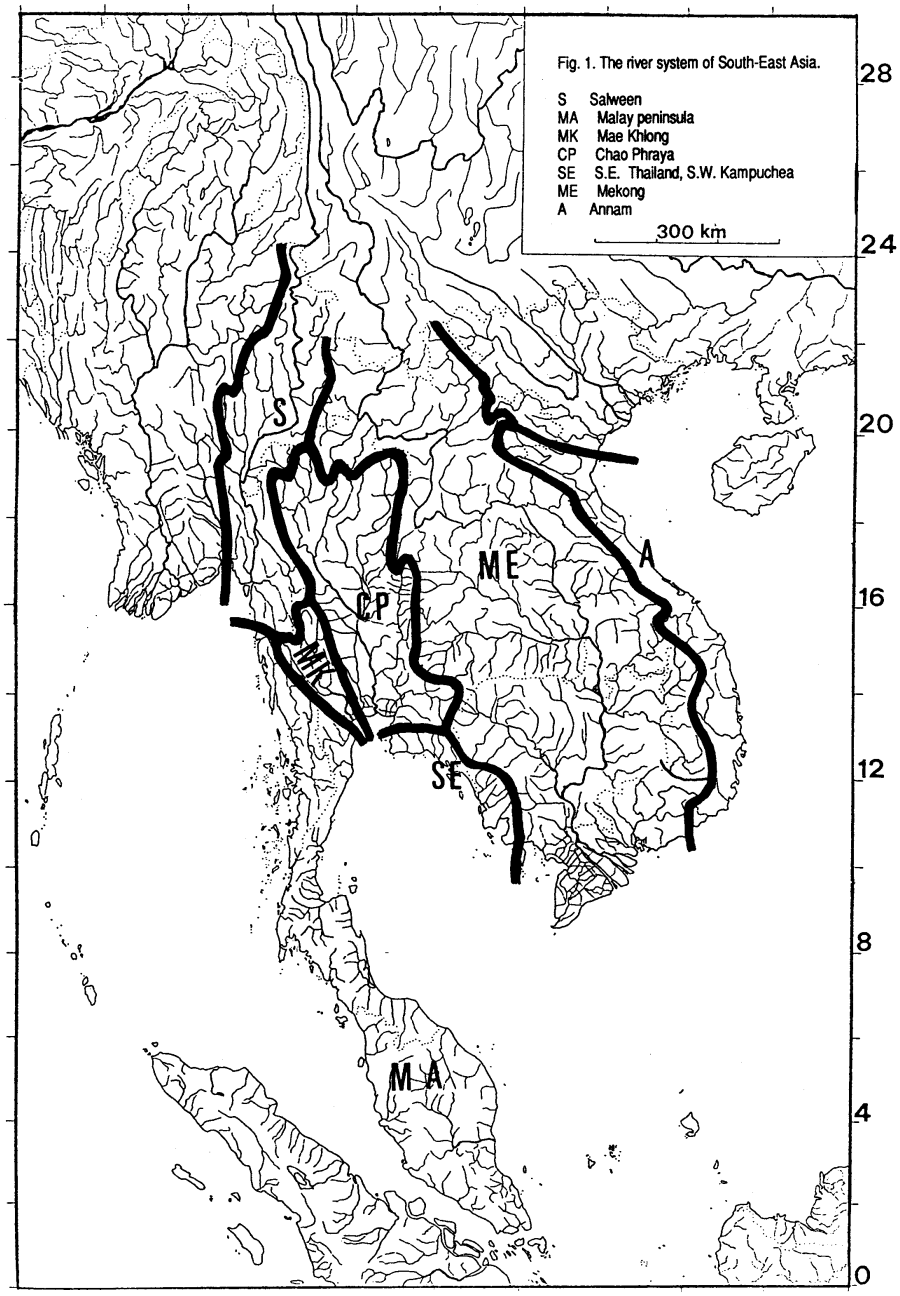

FIGURE 3. Major drainage basins for mainland Southeast Asia. Map adapted from Kottelat (1989). Drainage abbreviations correspond with geographic samples in this study as follows: MA = Maly; MK = MKhl; CP = CPhr; SE = SECos; ME = Mekg.

TABLE 2. Characters and character states of *Malayemys subtrijuga*. Characters are arranged alphabetically by character name abbreviation within the two data types (mensural and meristic). The abbreviations serve as short-hand notations within the text. Character descriptions followed by (A) are used in analyses, whereas those followed by (D) are given for descriptive purposes only. Unless otherwise noted, mensural characters are straight-line measurements. Scute designations are those of Zangerl (1969).

Mensural Characters

AbdL = Abdominal scute length, taken along the midline contact of the paired abdominal scutes. When one of the paired scutes extended farther anteriorly and/or posteriorly than its twin, measurements were taken at a point midway between their extremities. (A)

AnL = Anal scute length, taken along the midline contact of the paired anal scutes. When one of the paired scutes extended farther anteriorly and/or posteriorly than its twin, measurements were taken at a point midway between their extremities. (A)

AnW = Left anal scute width, maximum. (A)

APLL = Anterior plastron lobe length, maximum. (A)

APLW = Anterior plastron lobe width, width across plastron from right to left axilla. (A)

BrL = Left bridge length, taken from axilla to inguinal edge at bridge's minimum dimension. (A)

CL = Carapace length, maximum. (A)

CW = Carapace width, taken at the level of the seam separating vertebrals 2 and 3. (A)

FemL = Femoral scute length, taken along the midline contact of the paired femoral scutes. When one of the paired scutes extended farther anteriorly and/or posteriorly than its twin, measurements were taken at a point midway between their extremities. (A)

FemW = Left femoral scute width, maximum. (A)

TABLE 2. Continued.

GulL = Gular scute length, taken along the midline contact of the paired gular scutes. When one of the paired scutes extended farther anteriorly and/or posteriorly than its twin, measurements were taken at a point midway between their extremities. (A)

GulW = Left gular scute width, maximum. (A)

HumL = Humeral scute length, taken along the midline contact of the paired humeral scutes. When one of the paired scutes extended farther anteriorly and/or posteriorly than its twin, measurements were taken at a point midway between their extremities. (A)

HumW = Left humeral scute width, maximum. (A)

HW = Head width, taken at the anterior margin of the tympanum. (A)

InfSW = Infraorbital stripe (InfS) width, taken at LorS. (A)

PecL = Pectoral scute length, taken along the midline contact of the paired pectoral scutes. When one of the paired scutes extended farther anteriorly and/or posteriorly than its twin, measurements were taken at a point midway between their extremities. (A)

PL = Plastron length, maximum. (A)

Pleu1L = Pleural scute 1 length, maximum. (A)

Pleu1W = Pleural scute 1 width, maximum. (A)

PPLL = Posterior plastron lobe length, maximum. (A)

PPLW = Posterior plastron lobe width, width across plastron from right to left inguinal edge. (A)

SH = Shell height, height of carapace plus plastron taken at the level of the seam separating vertebrals 2 and 3. (A)

Vert1L = Vertebral scute 1 length, maximum. (A)

Vert1W = Vertebral scute 1 width, maximum. (A)

TABLE 2. Continued.

Vert2L = Vertebral scute 2 length, maximum. (A)

Vert2W = Vertebral scute 2 width, maximum. (A)

Vert3L = Vertebral scute 3 length, maximum. (A)

Vert3W = Vertebral scute 3 width, maximum. (A)

Vert5L = Vertebral scute 5 length, maximum. (A)

Vert5W = Vertebral scute 5 width, maximum. (A)

Meristic Characters

InfLor = Infraorbital stripe/loreal seam, whether InfS (1) does not extend superior to LorS, (2) extends only slightly superior to LorS, (3) extends completely superior to LorS but does not join SupS, (4) extends completely superior to LorS and joins SupS. (A)

InfS = Infraorbital stripe, yellow or cream-colored stripe beginning on each side of the snout just behind the nostrils and curving downward and then backward passing below the orbit to the angle of the mouth. (D)

LorS = Loreal seam, seam extending between the nostril and eye on each side of the head, separating the large scale covering the snout and crown and the large scale extending around the upper jaw. (D)

NasS = Nasal stripes, number of narrow stripes extending downward from the nostrils towards the medial notch of the upper jaw plus number of similar stripes running parallel in nasal region. (A)

RLatK = Right lateral keel, position of the right lateral keel as it bisects pleural scute 2, expressed as a proportion. (A)

SupS = Supraorbital stripe, yellow or cream-colored stripe extending posteriorly from the tip of the snout along the canthus rostralis and supraorbital edge to the base of the neck. (D) this study. The condition of bilateral characters was recorded from the right side of the carapace and the left side of the plastron unless damaged. Measurements were taken with dial calipers to the nearest 0.02 mm.

Museum abbreviations followed Leviton et al. (1985) and Leviton and Gibbs (1988) with the following additions: CRI = Chelonian Research Institute, Oviedo, Florida, USA; KUZ = Kyoto University Zoological Collection, Kyoto, Japan; RH = personal collection of Ren Hirayama, Teikyo Heisei University, Ichihara, Chiba, Japan; ZRC = Raffles Museum of Biodiversity Research, Zoological Reference Collection, The National University of Singapore, Singapore.

Sexual Identification and Maturity

Tail morphology was the primary characteristic used for sexual identification in this study. Sexual dimorphism of this character is pronounced in both subadults and adults (Fig. 4), with males having much longer and thicker tails (Ernst and Barbour, 1989; Srinarumol, 1995; van Dijk and Thirakhupt, in press). When tail morphology was not available (shell and skeletal material; some dried specimens), information from museum records sometimes formed the basis of sexual identification. In these instances, preliminary statistical analyses were used to verify sexual identification. In a very few cases, where statistical analyses clearly indicated a misidentification, sexual identification was modified (switched or omitted) with respect to museum records.

Assignment of specimens to appropriate life stages (juvenile, subadult, adult) was based primarily on Srinarumol (1995), who distinguished adults from subadults based on the complete development of testes and ovaries, and subadults from juveniles based on

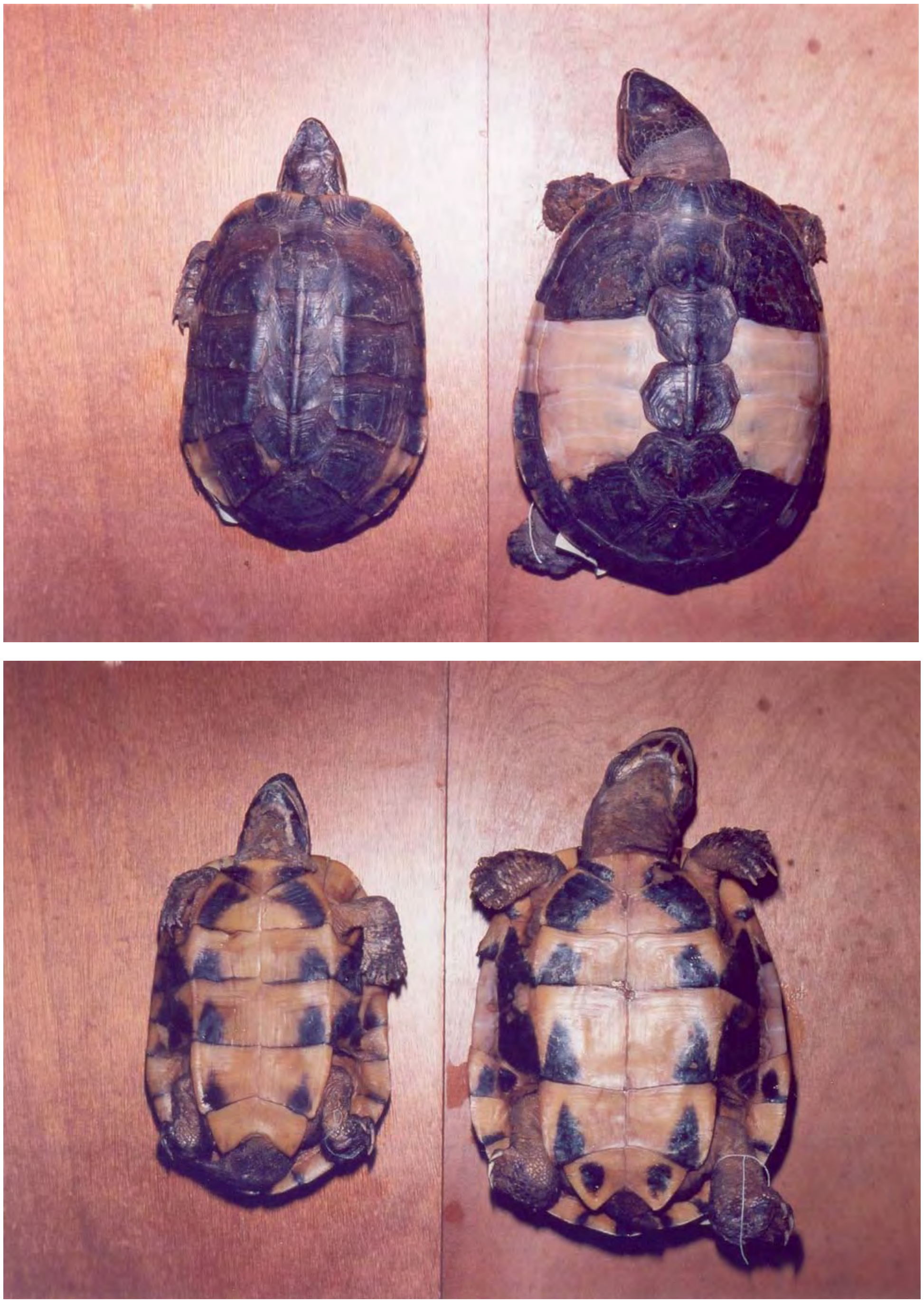

FIGURE 4. Photograph of male (left-CRI 3808) and female (right-CRI 3276) *Malayemys subtrijuga* illustrating morphological differences.

tail morphology. Based on the findings of the current study and those of Srinarumol (1995), life stages were defined accordingly: adult males were all specimens ≥ 98 mm CL that had appropriate tail morphology or sex information from museum records; adult females were all specimens ≥ 114 mm CL that had appropriate tail morphology or sex information from museum records; subadult males were all specimens 68-98 mm CL that had appropriate tail morphology; subadult females were all specimens 85-114 mm CL that had appropriate tail morphology; juvenile females included specimens 68-85 mm CL that had appropriate tail morphology; juvenile males could not be distinguished because all specimens < 68 mm CL lacked sexual dimorphism of tail morphology; juveniles of indeterminate sex were all specimens < 68 mm CL.

Allometry

To test for allometric variation within each geographic sample, CL was used as the independent variable for regression analyses (least squares method) of other shell characters. Non-transformed data (mm) were utilized for all specimens that had a determinable sex (juveniles, subadults, adults), and males and females were analyzed separately. The slope and intercept of each regression equation were tested for differences from zero using Student’s t-tests. Intercepts that were significantly different from zero ($\alpha = 0.05$) indicated differential growth (i.e., allometry) of the character (Mosimann, 1958).

Sexual Dimorphism – Univariate

Sexual dimorphism of shell characters was examined within each geographic sample using the regression analyses detailed above. The regression slopes of each bivariate relationship were compared for males and females using Analysis of Covariance (ANCOVA), with CL as covariate and sex as factor. Significantly different slopes (α = 0.05) indicated sexual dimorphism in the characters regressed against CL (Mosimann and Bider, 1960). In addition, sexual differences in CL were expressed by the sexual dimorphism index (SDI) proposed by Gibbons and Lovich (1990), which is calculated as follows:

$$+f/m, \text{ when } f > m; \text{ or } -m/f, \text{ when } f < m$$

where f and m denote mean CL for adult females and males, respectively.

Sexual Dimorphism – Multivariate

Sexual dimorphism of shell characters was also examined within each geographic sample using multivariate techniques. All 28 mensural shell characters (all except CL; Table 2) were divided by CL, and the resulting ratios comprised the majority of the data set. RLatK (Table 2), also part of this data set, was not divided by CL because it is standardized upon measurement (expressed as a proportion). To minimize the effects of allometric variation, only adult and larger subadult turtles of each sex (males ≥ 80 mm CL; females ≥ 100 mm CL) were compared within each geographic sample.

Using all 29 shell variables, stepwise selection (PROC STEPDISC; SAS, 1989; significance level for entry and removal = 0.30) was used to obtain a set of potential models that would classify turtles relative to their predetermined sex. Each step of this procedure generated a distinct model that was tested for classification accuracy using linear discriminant function analysis (PROC DISCRIM; SAS, 1989). Final selection of the best model (as defined by me) was based on model size and classification accuracy.

The best model gave the most accurate cross-validation results (PROC DISCRIM; SAS, 1989) and had no more variables than the number of individuals in the smallest sample. This protocol was designed to select conservative models that had a low number of variables and a high level of classification accuracy.

Using the best model as defined above, the following procedures were performed for each geographic sample. The probability of correctly classifying each turtle relative to its predetermined sex was calculated using the cross-validation results of linear discriminant function analysis (PROC DISCRIM; SAS, 1989). Shell differentiation between the sexes was graphically summarized by plotting canonical discriminant scores (PROC CANDISC; SAS, 1989).

Results and Discussion

Very few, if any, published studies have examined size distribution, allometric growth, or sexual dimorphism in populations of *M. subtrijuga*. Srinarumol's (1995) thesis examined the population biology of *M. subtrijuga* from the Pathum Thani Province of Thailand, and is the only study that addresses these topics in detail. Only three geographic samples in the current study had sufficient numbers to warrant intrasample examination. All analyses that follow were based on samples from CPhr, Mekg, and Java.

Size Distribution

Frequency distributions of CL (Figs. 5-7) indicated that females were larger than males in all three geographic samples. Adult females averaged 148.60 ± 20.23 (mean ± 1 SD) mm CL in CPhr (Table 3), 163.64 ± 22.23 mm CL in Mekg (Table 3), and 152.83 ±

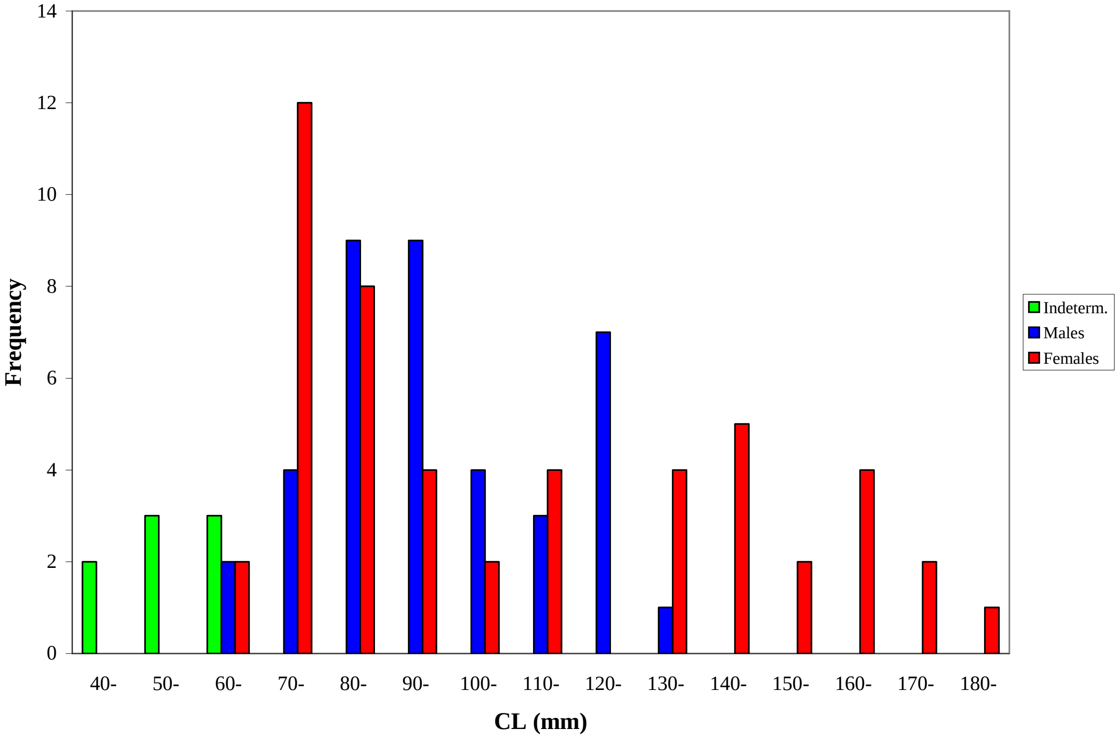

FIGURE 5. Frequency distribution of carapace length for *Malayemys subtrijuga* from the Chao Phraya River Basin. Indeterm. = juveniles of indeterminate sex.

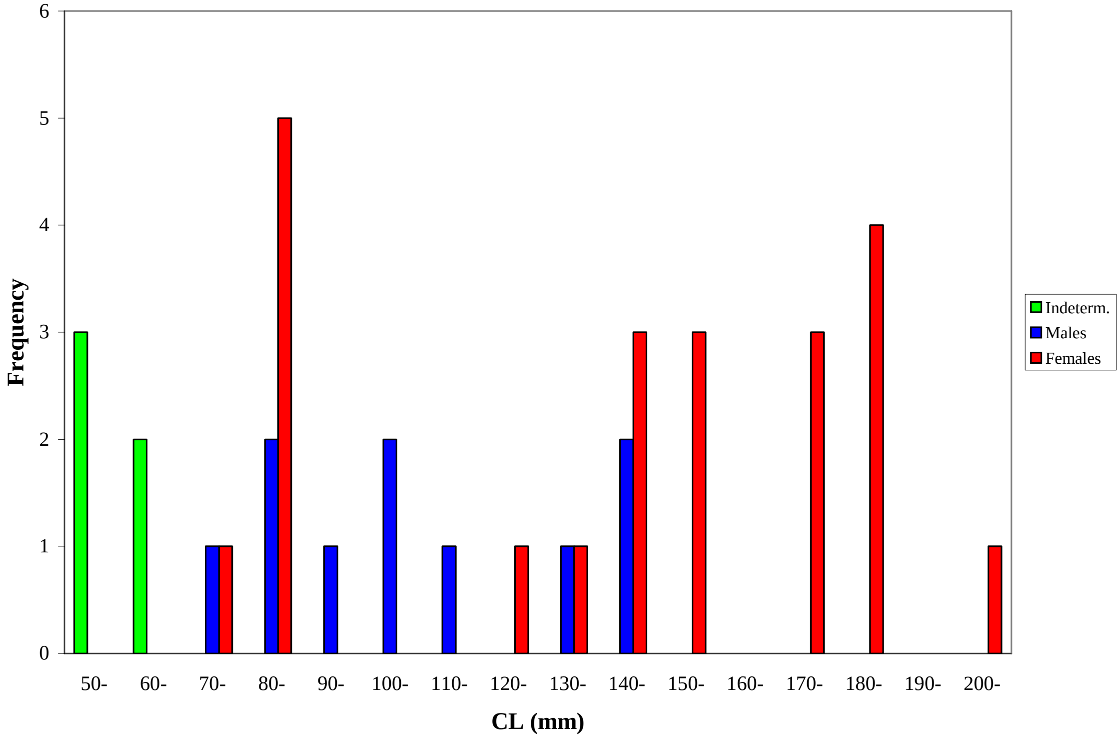

FIGURE 6. Frequency distribution of carapace length for *Malayemys subtrijuga* from the Mekong River Basin. Indeterm. = juveniles of indetrminate sex.

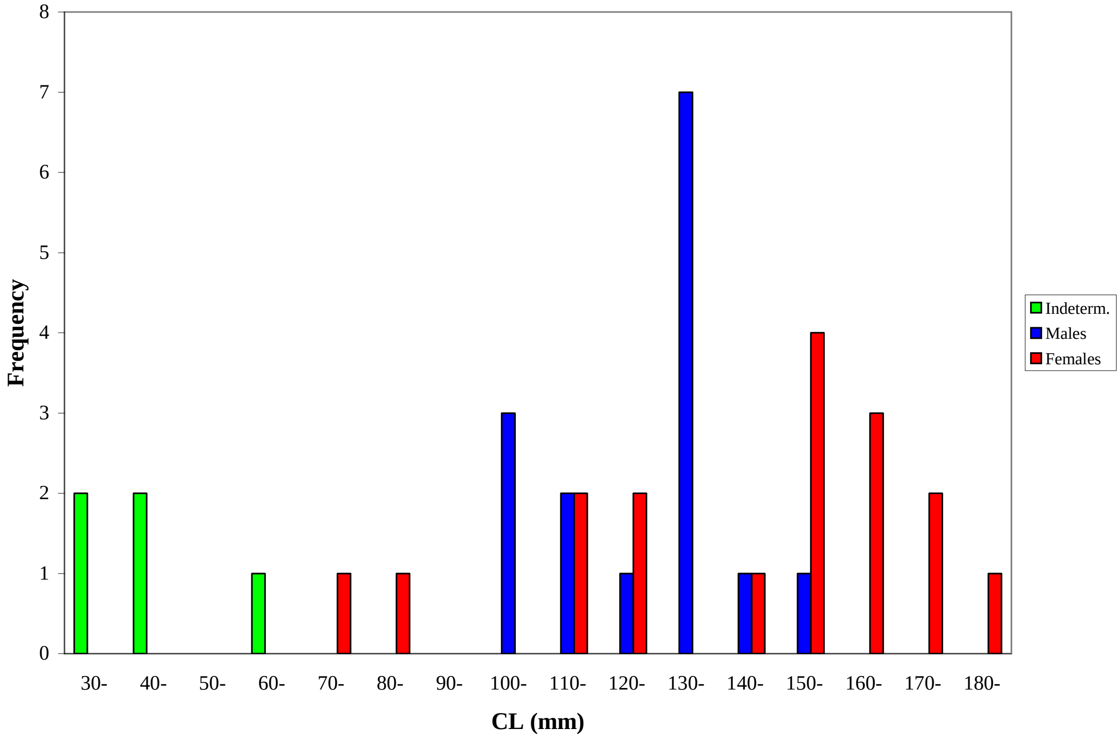

FIGURE 7. Frequency distribution of carapace length for *Malayemys subtrijuga* from Java. Indeterm. = juveniles of indeterminate sex.

TABLE 3. Carapace length (in mm) – mean ± 1 SD, (range), and [n] – for *Malayemys subtrijuga* from the Chao Phraya River Basin, Mekong River Basin, and Java.

Life Stage	CPhr	Mekg	Java
Adult females	148.60 ± 20.23 (114.4-187.0) [21]	163.64 ± 22.23 (121.4-207.0) [16]	152.83 ± 19.75 (118.0-182.4) [14]
Adult males	117.21 ± 9.54 (100.3-131.7) [15]	126.28 ± 18.73 (103.5-149.9) [6]	127.16 ± 15.65 (101.0-151.8) [15]
Subadult females	94.64 ± 9.56 (85.3-113.2) [11]	86.18 ± 0.11 (86.1-86.3) [2]	113.12 ± 0.00 (113.12) [1]
Subadult males	85.74 ± 7.68 (69.7-95.4) [24]	85.53 ± 6.85 (77.0-92.8) [4]	N/A
Juvenile females	75.75 ± 4.63 (68.1-83.4) [18]	79.22 ± 6.04 (70.2-82.8) [4]	80.53 ± 4.88 (77.1-84.0) [2]
Indeterminate juveniles	57.33 ± 9.33 (42.7-67.9) [8]	59.44 ± 5.47 (51.4-65.4) [5]	45.45 ± 12.83 (32.2-65.6) [5]

19.75 mm CL in Java (Table 3). Adult males were considerably smaller and averaged 117.21 ± 9.54 mm CL in CPhr (Table 3), 126.28 ± 18.73 mm CL in Mekg (Table 3), and 127.16 ± 15.65 mm CL in Java (Table 3). Srinarumol (1995) reported that adult females and males averaged 155.48 ± 27.91 mm CL and 112.20 ± 9.83 mm CL, respectively. These are comparable to the results presented above.

Subadult females and males averaged 94.64 ± 9.56 and 85.74 ± 7.68 mm CL, respectively in CPhr (Table 3); and 86.18 ± 0.11 and 85.53 ± 6.85 mm CL in Mekg (Table 3). There were no subadult males in the Java sample and only one subadult female (CL = 113.12 mm). Juvenile females and juveniles of indeterminate sex averaged 75.75 ± 4.63 and 57.33 ± 9.33 mm CL, respectively in CPhr (Table 3); 79.22 ± 6.04 and 59.44 ± 5.47 mm CL in Mekg (Table 3); and 80.53 ± 4.88 and 45.45 ± 12.83 mm CL in Java (Table 3). Juvenile males could not be distinguished because all individuals < 68 mm CL lacked sexual dimorphism of tail morphology. Srinarumol (1995) distinguished between subadults and juveniles and found that males could be identified at carapace lengths ≥ 80 mm and females at carapace lengths ≥ 86 mm.

The assignment of turtles to life stages was done primarily to determine which specimens were appropriate in tests of allometric growth, sexual dimorphism, and geographic variation. Since these life stage assignments were based primarily on Srinarumol (1995), the present data provided little meaningful insight into the specific size boundaries of each life stage.

Allometry

Allometric growth of the shell was evident in *M. subtrijuga* from CPhr (Table 4). Among males, shell shape changed as CL increased proportionally more than shell width (CW, APLW, PPLW), shell height (SH), plastral length (PL and APLL), several scute widths (Pleu1W, Vert1W, Vert2W, Vert3W, HumW, FemW, and AnW), and a few scute lengths (Vert1L, BL, and AnL). For females, CL did not increase proportionally more than shell width or shell height but did increase proportionally more than plastral length (PL and PPLL) and a few scute widths (Vert1W, Vert3W, FemW, AnW) and lengths (BL, AbdL, AnL).

Allometry was less evident in *M. subtrijuga* from Mekg and Java (Tables 5 and 6). No allometry was detected for Mekg males. Among Mekg females, CL increased proportionally more than PPLL and a few scute widths (Vert3W, FemW, AnW). For Java males, CL increased proportionally more than SH, APLW, PPLL, and a few scute widths (Pleu1W) and lengths (BL and FemL). Among Java females, CL increased proportionally more than PPLL and a few scute widths (Vert1W and FemW) and lengths (AbdL). The scarcity of statistical support for allometric growth in Mekg and Java probably resulted from inadequate sample sizes for these regions (see Tables 5 and 6).

Allometry of shell characters is a widespread phenomenon among turtles. I am unaware, however, of any report that examines allometric growth in *M. subtrijuga*. Srinarumol (1995) performed regression analyses similar to those presented here but did not test for differential growth of shell characters. The allometric pattern that emerges for *M. subtrijuga* is one where males grow proportionally longer than wider or higher,

TABLE 4. Allometric relationships of shell characters to carapace length for *Malayemys subtrijuga* from the Chao Phrya River Basin. All slopes are significantly ($P < 0.0001$) different from zero. For significance levels, ns = $P > 0.05$. Character abbreviations follow Table 2.

Character	Sex	N	Linear relation: y = a + bx (in mm)	R^2	Significance levels (P) Intercept (a) (H_0: a = 0)
CW	F	48	CW = 2.43 + 0.75CL	0.98	ns
	M	38	CW = 14.77 + 0.58CL	0.94	< 0.0001
SH	F	42	SH = 2.04 + 0.41CL	0.97	ns
	M	35	SH = 10.30 + 0.29CL	0.94	< 0.0001
Pleu1W	F	48	Pleu1W = 0.29 + 0.27CL	0.98	ns
	M	38	Pleu1W = 4.53 + 0.21CL	0.81	0.0041
Pleu1L	F	48	Pleu1L = -1.12 + 0.25CL	0.98	ns
	M	38	Pleu1L = 1.43 + 0.22CL	0.91	ns
Vert1W	F	47	Vert1W = 3.88 + 0.17CL	0.91	< 0.0001
	M	38	Vert1W = 11.25 + 0.08CL	0.40	< 0.0001
Vert1L	F	47	Vert1L = 0.76 + 0.20CL	0.96	ns
	M	37	Vert1L = 3.45 + 0.17CL	0.93	0.0039
Vert2W	F	47	Vert2W = -1.29 +0.22CL	0.96	ns
	M	35	Vert2W = 5.48 + 0.14CL	0.83	< 0.0001
Vert2L	F	47	Vert2L = -0.83 + 0.19CL	0.98	ns
	M	36	Vert2L = 1.05 + 0.16CL	0.90	ns
Vert3W	F	48	Vert3W = -2.63 + 0.24CL	0.97	0.0001
	M	37	Vert3W = 3.85 + 0.16CL	0.87	0.0040
Vert3L	F	46	Vert3L = 0.90 + 0.18CL	0.96	ns
	M	36	Vert3L = 0.83 + 0.16CL	0.82	ns
Vert5W	F	45	Vert5W = 0.84 + 0.26CL	0.92	ns
	M	38	Vert5W = 0.45 + 0.27CL	0.71	ns
Vert5L	F	43	Vert5L = 1.38 + 0.18CL	0.91	ns
	M	37	Vert5L = -2.37 + 0.23CL	0.83	ns
PL	F	43	PL = -4.43 + 0.92CL	0.99	0.0005
	M	36	PL = 4.89 + 0.80CL	0.99	0.0358
APLW	F	43	APLW = 0.02 + 0.45CL	0.99	ns
	M	36	APLW = 5.37 + 0.38CL	0.95	0.0015
APLL	F	43	APLL = -0.11 + 0.34CL	0.97	ns
	M	36	APLL = 3.97 + 0.29CL	0.92	0.0304
PPLW	F	43	PPLW = -0.67 + 0.45CL	0.98	ns
	M	36	PPLW = 7.21 + 0.35CL	0.94	0.0006
PPLL	F	43	PPLL = -6.71 + 0.61CL	0.99	< 0.0001
	M	36	PPLL = 0.54 + 0.52CL	0.98	ns

TABLE 4. Continued.

Character	Sex	N	Linear relation: y = a + bx (in mm)	R^2	Significance levels (P) Intercept (a) (H_0: a = 0)
BL	F	42	BL = -2.99 + 0.37CL	0.92	0.0007
	M	36	BL = 6.94 + 0.25CL	0.98	< 0.0001
GulW	F	44	GulW = 0.73 + 0.13CL	0.97	ns
	M	36	GulW = 0.67 + 0.13CL	0.93	ns
GulL	F	44	GulL = 1.14 + 0.10CL	0.89	ns
	M	36	GulL = -0.68 + 0.12CL	0.77	ns
HumW	F	44	HumW = 0.001 + 0.22CL	0.98	ns
	M	36	HumW = 1.77 + 0.19CL	0.94	0.0484
HumL	F	44	HumL = -0.11 + 0.12CL	0.87	ns
	M	36	HumL = 1.17 + 0.10CL	0.64	ns
PecL	F	43	PecL = -1.50 + 0.13CL	0.91	ns
	M	36	PecL = 1.51 + 0.09CL	0.44	ns
AbdL	F	43	AbdL = -1.93 + 0.24CL	0.97	0.0149
	M	36	AbdL = 1.73 + 0.19CL	0.86	ns
FemW	F	44	FemW = -1.23 + 0.23CL	0.98	0.0149
	M	36	FemW = 2.51 + 0.18CL	0.94	0.0095
FemL	F	44	FemL = -0.99 + 0.15CL	0.92	ns
	M	36	FemL = -1.00 + 0.16CL	0.78	ns
AnW	F	44	AnW = -1.36 + 0.16CL	0.99	0.0002
	M	36	AnW = 1.40 + 0.13CL	0.91	0.0356
AnL	F	44	AnL = -2.00 + 0.15CL	0.94	0.0014
	M	36	AnL = 3.76 + 0.08CL	0.65	0.0016

TABLE 5. Allometric relationships of shell characters to carapace length for *Malayemys subtrijuga* from the Mekong River Basin. All slopes are significantly ($P \leq 0.01$) different from zero. For significance levels, ns = $P > 0.05$. Character abbreviations follow Table 2.

Character	Sex	N	Linear relation: y = a + bx (in mm)	R^2	Significance levels (P) Intercept (a) (H_0: a = 0)
CW	F	22	CW = -0.45 + 0.76CL	0.98	ns
	M	10	CW = 4.94 + 0.67CL	0.99	ns
SH	F	20	SH = -0.27 + 0.43CL	0.97	ns
	M	10	SH = 8.31 + 0.32CL	0.94	ns
Pleu1W	F	19	Pleu1W = 0.44 + 0.28CL	0.97	ns
	M	10	Pleu1W = 1.68 + 0.24CL	0.98	ns
Pleu1L	F	19	Pleu1L = -0.98 + 0.26CL	0.97	ns
	M	10	Pleu1L = -3.67 + 0.28CL	0.98	ns
Vert1W	F	19	Vert1W = 5.39 + 0.15CL	0.74	ns
	M	10	Vert1W = 6.88 + 0.13CL	0.84	ns
Vert1L	F	19	Vert1L = 1.13 + 0.19CL	0.99	ns
	M	10	Vert1L = -1.91 + 0.23CL	0.97	ns
Vert2W	F	19	Vert2W = -3.04 +0.23CL	0.95	ns
	M	10	Vert2W = 2.20 + 0.17CL	0.88	ns
Vert2L	F	19	Vert2L = -1.54 + 0.19CL	0.96	ns
	M	10	Vert2L = 1.16 + 0.16CL	0.98	ns
Vert3W	F	19	Vert3W = -4.87 + 0.25CL	0.94	0.02
	M	10	Vert3W = 2.20 + 0.17CL	0.85	ns
Vert3L	F	19	Vert3L = -0.51 + 0.18CL	0.92	ns
	M	10	Vert3L = 1.43 + 0.15CL	0.95	ns
Vert5W	F	19	Vert5W = -3.22 + 0.30CL	0.95	ns
	M	10	Vert5W = -8.90 + 0.36CL	0.93	ns
Vert5L	F	20	Vert5L = 0.91 + 0.20CL	0.95	ns
	M	10	Vert5L = -4.04 + 0.26CL	0.95	ns
PL	F	21	PL = -2.46 + 0.90CL	0.98	ns
	M	10	PL = 4.10 + 0.80CL	0.99	ns
APLW	F	20	APLW = -0.88 + 0.46CL	0.99	ns
	M	10	APLW = -1.97 + 0.45CL	0.98	ns
APLL	F	19	APLL = 0.79 + 0.35CL	0.96	ns
	M	10	APLL = 4.39 + 0.30CL	0.96	ns
PPLW	F	20	PPLW = -2.50 + 0.46 CL	0.99	ns
	M	10	PPLW = 1.12 + 0.40CL	0.99	ns
PPLL	F	19	PPLL = -5.17 + 0.57CL	0.98	0.04
	M	10	PPLL = 1.77 + 0.49CL	0.99	ns

TABLE 5. Continued.

Character	Sex	N	Linear relation: y = a + bx (in mm)	R^2	Significance levels (P) Intercept (a) (H_0: a = 0)
BL	F	20	BL = -2.05 + 0.36CL	0.96	ns
	M	10	BL = 5.44 + 0.26CL	0.97	ns
GulW	F	20	GulW = 1.47 + 0.13CL	0.95	ns
	M	10	GulW = 0.64 + 0.13CL	0.96	ns
GulL	F	20	GulL = -0.35 + 0.11CL	0.83	ns
	M	10	GulL = -1.52 + 0.11CL	0.89	ns
HumW	F	20	HumW = -0.30 + 0.22CL	0.98	ns
	M	10	HumW = -0.24 + 0.20CL	0.98	ns
HumL	F	20	HumL = -0.62 + 0.11CL	0.76	ns
	M	10	HumL = 1.98 + 0.09CL	0.84	ns
PecL	F	20	PecL = 1.48 + 0.13CL	0.83	ns
	M	10	PecL = 3.31 + 0.10CL	0.70	ns
AbdL	F	20	AbdL = -3.63 + 0.24CL	0.88	ns
	M	10	AbdL = 0.40 + 0.19CL	0.93	ns
FemW	F	20	FemW = -1.99 + 0.23CL	0.98	0.04
	M	10	FemW = -0.79 + 0.21CL	0.99	ns
FemL	F	20	FemL = 3.17 + 0.12CL	0.74	ns
	M	10	FemL = -0.34 + 0.15CL	0.87	ns
AnW	F	20	AnW = -2.15 + 0.16CL	0.98	0.0069
	M	10	AnW = -1.03 + 0.15CL	0.97	ns
AnL	F	20	AnL = -2.83 + 0.14CL	0.84	ns
	M	10	AnL = 3.52 + 0.08CL	0.77	ns

TABLE 6. Allometric relationships of shell characters to carapace length for *Malayemys subtrijuga* from Java. All slopes are significantly ($P < 0.05$) different from zero except PecL-Males. For significance levels, ns = $P > 0.05$. Character abbreviations follow Table 2.

Character	Sex	N	Linear relation: y = a + bx (in mm)	R^2	Significance levels (P) Intercept (a) (H_0: a = 0)
CW	F	16	CW = 1.30 + 0.74CL	0.98	ns
	M	14	CW = 13.68 + 0.58CL	0.93	ns
SH	F	15	SH = 1.80 + 0.41CL	0.96	ns
	M	12	SH = 12.01 + 0.30CL	0.90	0.0399
Pleu1W	F	16	Pleu1W = -0.74 + 0.28CL	0.98	ns
	M	14	Pleu1W = 6.53 + 0.21CL	0.92	0.02
Pleu1L	F	16	Pleu1L = 0.07 + 0.26CL	0.98	ns
	M	14	Pleu1L = -1.92 + 0.27CL	0.92	ns
Vert1W	F	14	Vert1W = 7.51 + 0.12CL	0.69	0.0118
	M	13	Vert1W = 4.70 + 0.13CL	0.67	ns
Vert1L	F	14	Vert1L = 1.67 + 0.19CL	0.96	ns
	M	13	Vert1L = -1.15 + 0.20CL	0.89	ns
Vert2W	F	14	Vert2W = -0.05 +0.18CL	0.80	ns
	M	13	Vert2W = -0.81 + 0.18CL	0.79	ns
Vert2L	F	14	Vert2L = -2.16 + 0.20CL	0.84	ns
	M	13	Vert2L = 3.37 + 0.14CL	0.74	ns
Vert3W	F	13	Vert3W = -4.56 + 0.23CL	0.86	ns
	M	13	Vert3W = -4.61 + 0.22CL	0.83	ns
Vert3L	F	13	Vert3L = 0.34 + 0.16CL	0.91	ns
	M	13	Vert3L = -0.84 + 0.17CL	0.75	ns
Vert5W	F	13	Vert5W = 1.15 + 0.24CL	0.85	ns
	M	13	Vert5W = 3.39 + 0.23CL	0.69	ns
Vert5L	F	13	Vert5L = 3.91 + 0.17CL	0.86	ns
	M	12	Vert5L = -0.69 + 0.23CL	0.89	ns
PL	F	16	PL = 0.12 + 0.86CL	0.99	ns
	M	14	PL = 10.64 + 0.72CL	0.96	ns
APLW	F	16	APLW = -0.68 + 0.47CL	0.98	ns
	M	14	APLW = 8.56 + 0.36CL	0.93	0.0420
APLL	F	15	APLL = 6.07 + 0.30CL	0.89	ns
	M	14	APLL = 3.48 + 0.30CL	0.89	ns
PPLW	F	15	PPLW = 0.21 + 0.46CL	0.98	ns
	M	14	PPLW = 7.03 + 0.36CL	0.91	ns
PPLL	F	15	PPLL = -8.10 + 0.59CL	0.98	0.0039
	M	14	PPLL = 10.70 + 0.40CL	0.94	0.0324

TABLE 6. Continued.

Character	Sex	N	Linear relation: y = a + bx (in mm)	R^2	Significance levels (P) Intercept (a) (H_0: a = 0)
BL	F	15	BL = -1.92 + 0.34CL	0.97	ns
	M	14	BL = 8.86 + 0.21CL	0.84	0.0343
GulW	F	15	GulW = 1.17 + 0.13CL	0.95	ns
	M	14	GulW = 2.00 + 0.12CL	0.87	ns
GulL	F	16	GulL = 1.78 + 0.11CL	0.76	ns
	M	14	GulL = 6.35 + 0.06CL	0.59	ns
HumW	F	15	HumW = 1.13 + 0.21CL	0.99	ns
	M	14	HumW = 4.52 + 0.17CL	0.83	ns
HumL	F	16	HumL = -1.45 + 0.12CL	0.77	ns
	M	14	HumL = -4.28 + 0.14CL	0.76	ns
PecL	F	16	PecL = 5.01 + 0.08CL	0.31	ns
	M	14	PecL = 1.31 + 0.11CL	0.28	ns
AbdL	F	16	AbdL = -10.28 + 0.28CL	0.87	0.0068
	M	14	AbdL = 2.50 + 0.16CL	0.66	ns
FemW	F	15	FemW = -2.81 + 0.24CL	0.98	0.0254
	M	14	FemW = 0.60 + 0.20CL	0.93	ns
FemL	F	16	FemL = 1.30 + 0.14CL	0.86	ns
	M	14	FemL = 9.11 + 0.07CL	0.23	0.0489
AnW	F	16	AnW = -1.82 + 0.17CL	0.97	ns
	M	14	AnW = -1.70 + 0.16CL	0.90	ns
AnL	F	16	AnL = 0.99 + 0.11CL	0.73	ns
	M	14	AnL = -1.31 + 0.11CL	0.69	ns

whereas females show proportional growth. This allometry yields adult males with relatively narrower, flatter shells and adult females with relatively wider and higher shells.

It is critical to emphasize the interrelatedness of allometric growth and sexual dimorphism. The differences in allometric growth between male and female *M. subtrijuga* produce the sexually dimorphic adults. Such a connection has been demonstrated by other authors working with a variety of turtle species (Mosimann, 1956, 1958; Mosimann and Bider, 1960; Stickel and Bunck, 1989; Ernst et al., 1998). Sexual dimorphism in *M. subtrijuga* will be discussed in the following sections.

Sexual Dimorphism – Univariate

Sexual dimorphism of the shell was evident in *M. subtrijuga* from CPhr. Analysis of Covariance indicated that the regression slopes of males and females differed significantly ($P < 0.05$) in 22 of the 28 characters examined (Table 7). Among these, differences in relative shell width, shell height, and plastral length were most significant ($P < 0.0001$). Females had relatively wider carapaces (CW, Pleu1W, Vert1W, Vert2W, Vert3W), relatively higher shells (SH), and relatively wider (APLW, PPLW, FemW, AnW) and longer (PL, PPLL, BL, AnL) plastra (Figs. 8-21). Srinarumol (1995), using a similar method, found female *M. subtrijuga* to have relatively wider carapaces, longer plastra, and longer midline gular and pectoral lengths.

One character of particular interest was anal scute length (AnL). The present data showed that males from CPhr had relatively shorter AnL than females (Fig. 21; Table 7). van Dijk and Thirakhupt (2000) stated that males are distinguished from females by the

TABLE 7. Comparison of regression slopes (ANCOVA) of shell characters versus carapace length among male and female *Malayemys subtrijuga* from the Chao Phrya River Basin. Regression equations are found in Table 4. For significance levels, ns = P > 0.05. Character abbreviations follow Table 2.

	Male vs. Female Slopes (b) (H_0: $b_{males} = b_{females}$)		
Characters	F	df	P
CW	26.26	1,82	< 0.0001
SH	24.33	1,73	< 0.0001
Pleu1W	12.38	1,82	0.0007
Pleu1L	5.61	1,82	0.0202
Vert1W	21.44	1,81	< 0.0001
Vert1L	5.95	1,80	0.0169
Vert2W	32.40	1,78	< 0.0001
Vert2L	6.21	1,79	0.0148
Vert3W	30.40	1,81	< 0.0001
Vert3L	3.58	1,78	ns
Vert5W	0.19	1,79	ns
Vert5L	8.02	1,76	0.0059
PL	22.17	1,75	< 0.0001
APLW	14.16	1,75	0.0003
APLL	6.87	1,75	0.0106
PPLW	20.02	1,75	< 0.0001
PPLL	22.94	1,75	< 0.0001
BL	51.65	1,74	< 0.0001
GulW	0.00	1,76	ns
GulL	2.40	1,76	ns
HumW	5.10	1,76	0.0269
HumL	0.68	1,76	ns
PecL	5.19	1,75	0.0255
AbdL	9.65	1,75	0.0027
FemW	21.56	1,76	< 0.0001
FemL	0.03	1,76	ns
AnW	18.63	1,76	< 0.0001
AnL	32.57	1,76	< 0.0001

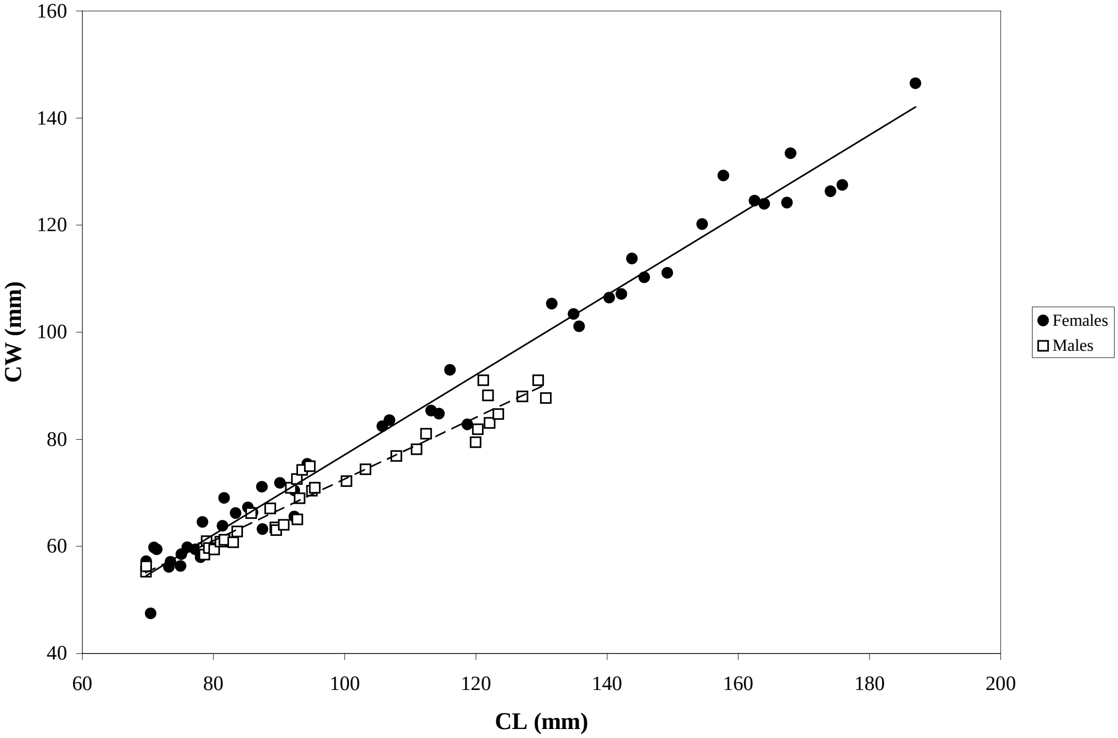

FIGURE 8. Allometry of sexually dimorphic carapace width plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: CW = 2.43 + 0.75CL; Male: CW = 14.77 + 0.58CL; ANCOVA: df = 1,82, F = 26.26, P < 0.0001)

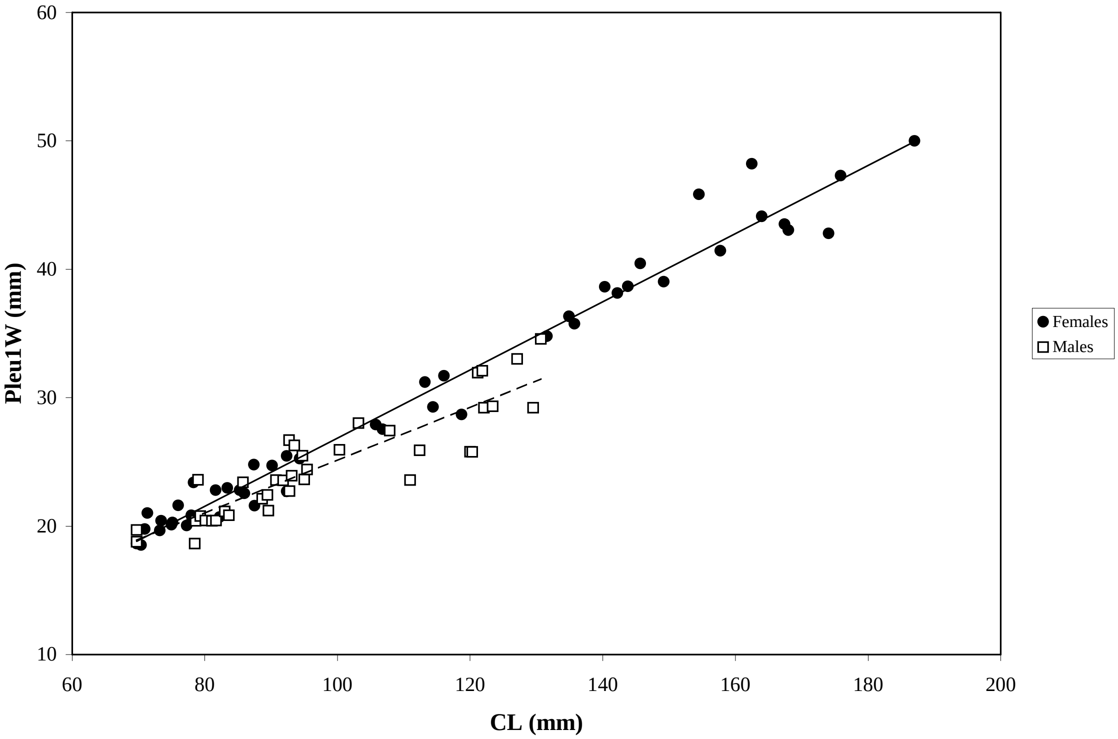

FIGURE 9. Allometry of sexually dimorphic pleural scute 1 width plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: Pleu1W = 0.29 + 0.27CL; Male: Pleu1W = 4.53 + 0.21CL; ANCOVA: df = 1,82, F = 12.38, P = 0.0007)

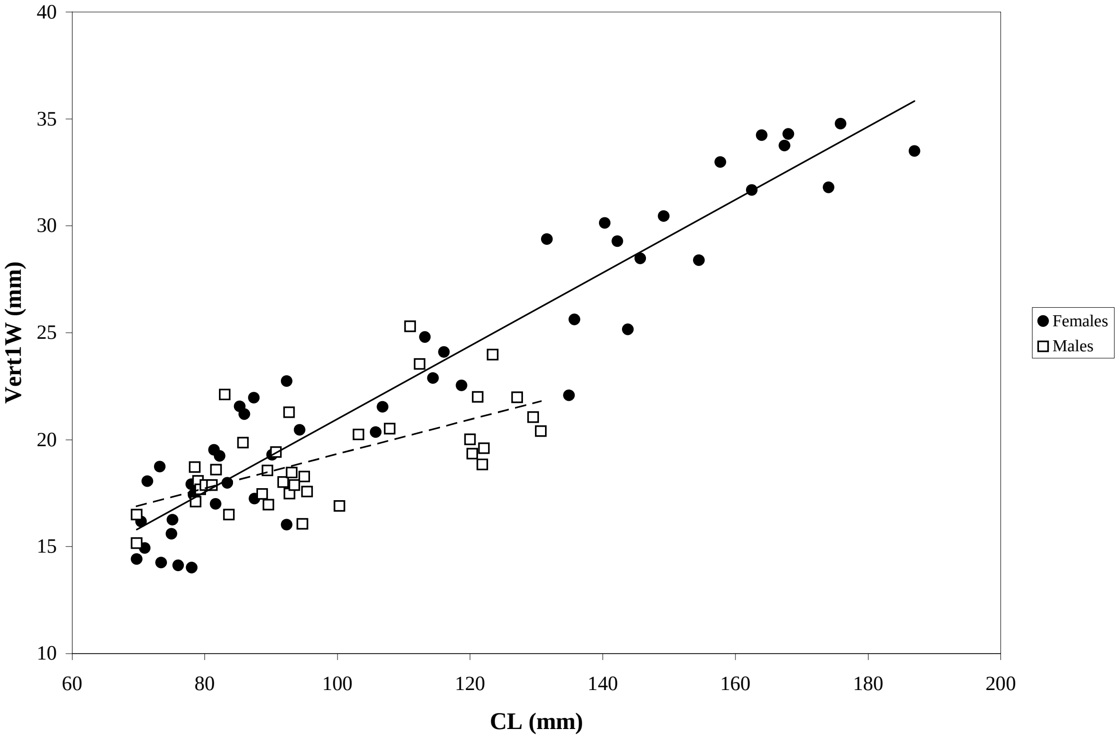

FIGURE 10. Allometry of sexually dimorphic vertebral scute 1 width plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: Vert1W = 3.88 + 0.17CL; Male: Vert1W = 11.25 + 0.08CL; ANCOVA: df = 1,81, F = 21.44, $P < 0.0001$)

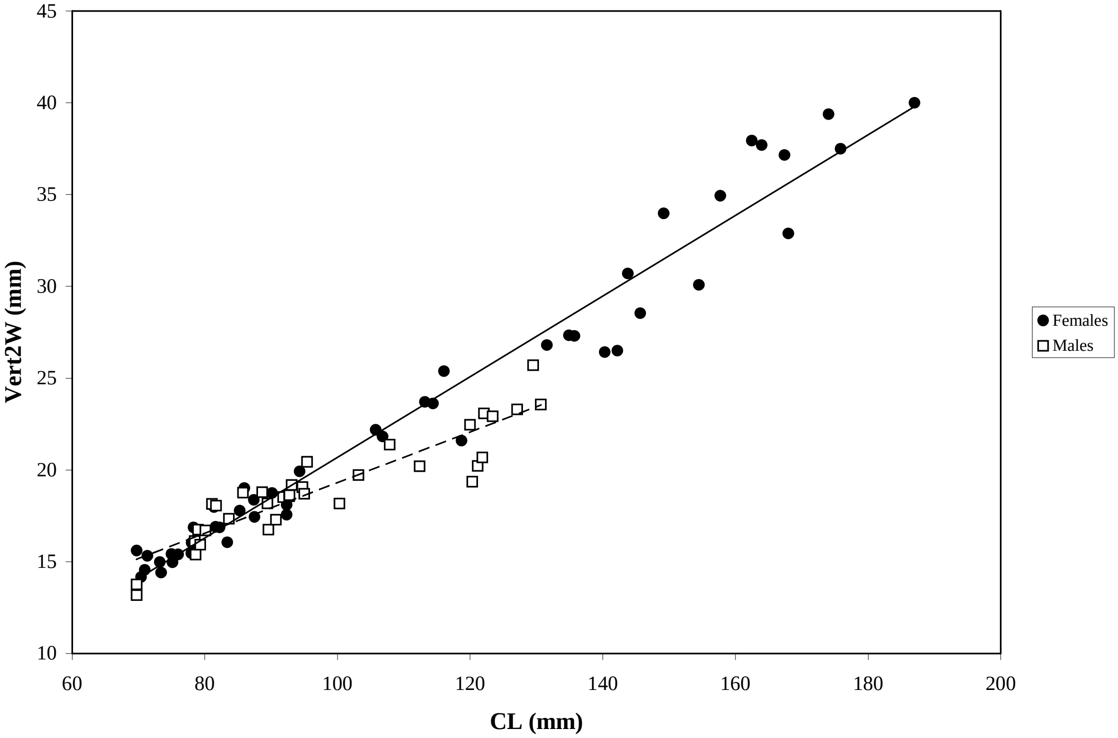

FIGURE 11. Allometry of sexually dimorphic vertebral scute 2 width plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: Vert2W = -1.29 + 0.22CL; Male: Vert2W = 5.48 + 0.14CL; ANCOVA: df = 1,78, F = 32.40, $P < 0.0001$)

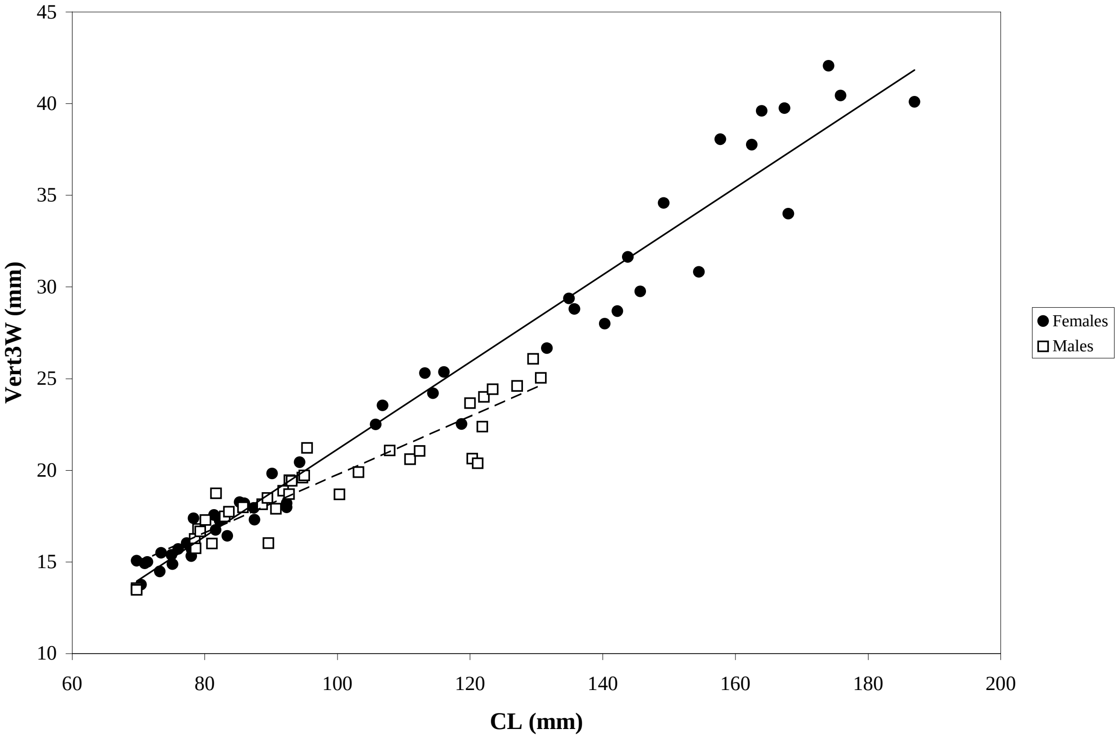

FIGURE 12. Allometry of sexually dimorphic vertebral scute 3 width plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: Vert3W = -2.63 + 0.24CL; Male: Vert3W = 3.85 + 0.16CL; ANCOVA: df = 1,81, F = 30.40, P < 0.0001)

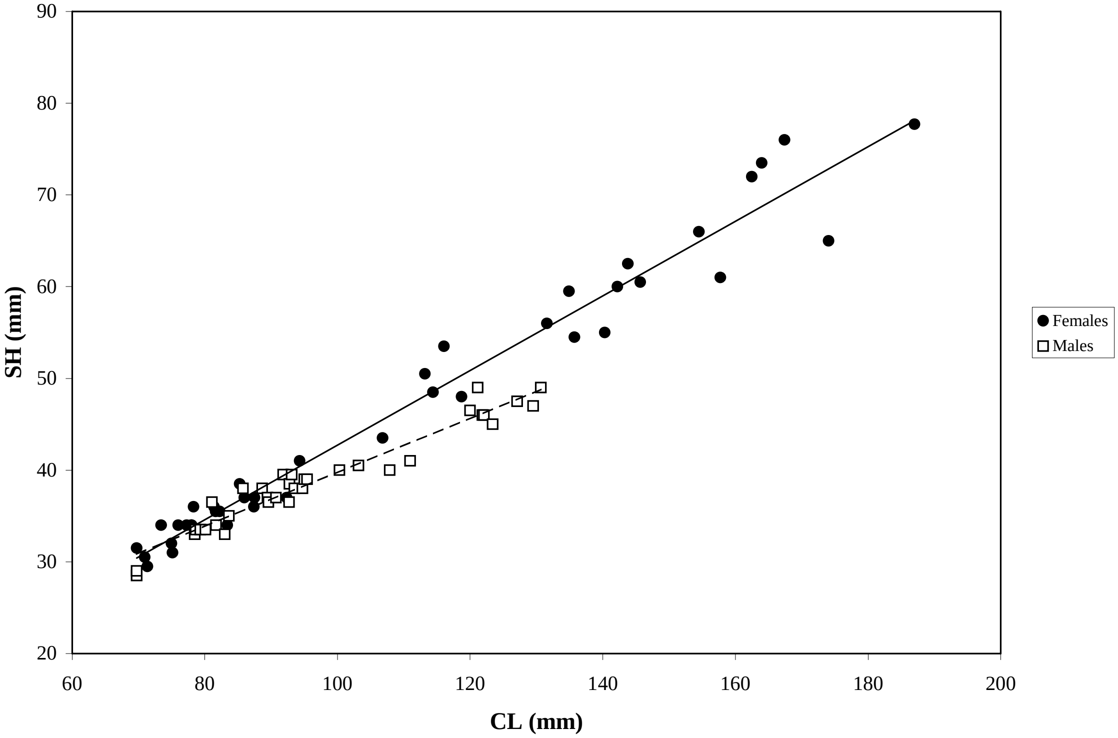

FIGURE 13. Allometry of sexually dimorphic shell height plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: SH = 2.04 + 0.41CL; Male: SH = 10.30 + 0.29CL; ANCOVA: df = 1,73, F = 24.33, $P < 0.0001$)

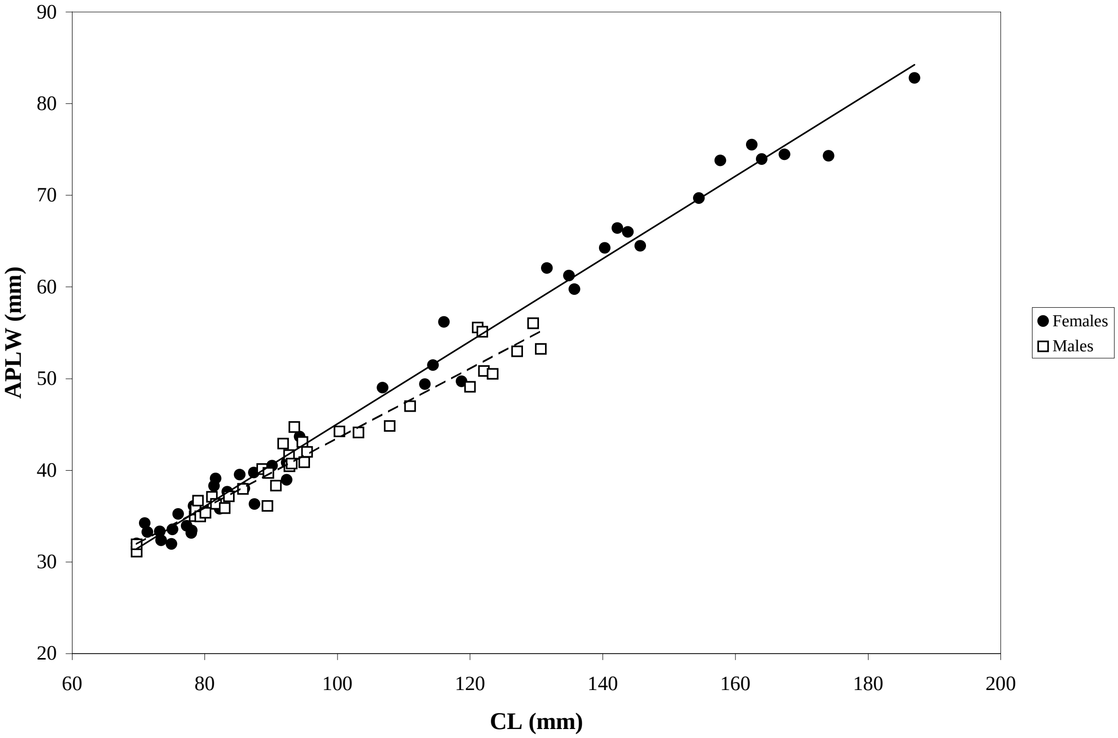

FIGURE 14. Allometry of sexually dimorphic anterior plastron lobe width plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: APLW = 0.02 + 0.45CL; Male: APLW = 5.37 + 0.38CL; ANCOVA: df = 1,75, F = 14.16, P = 0.0003)

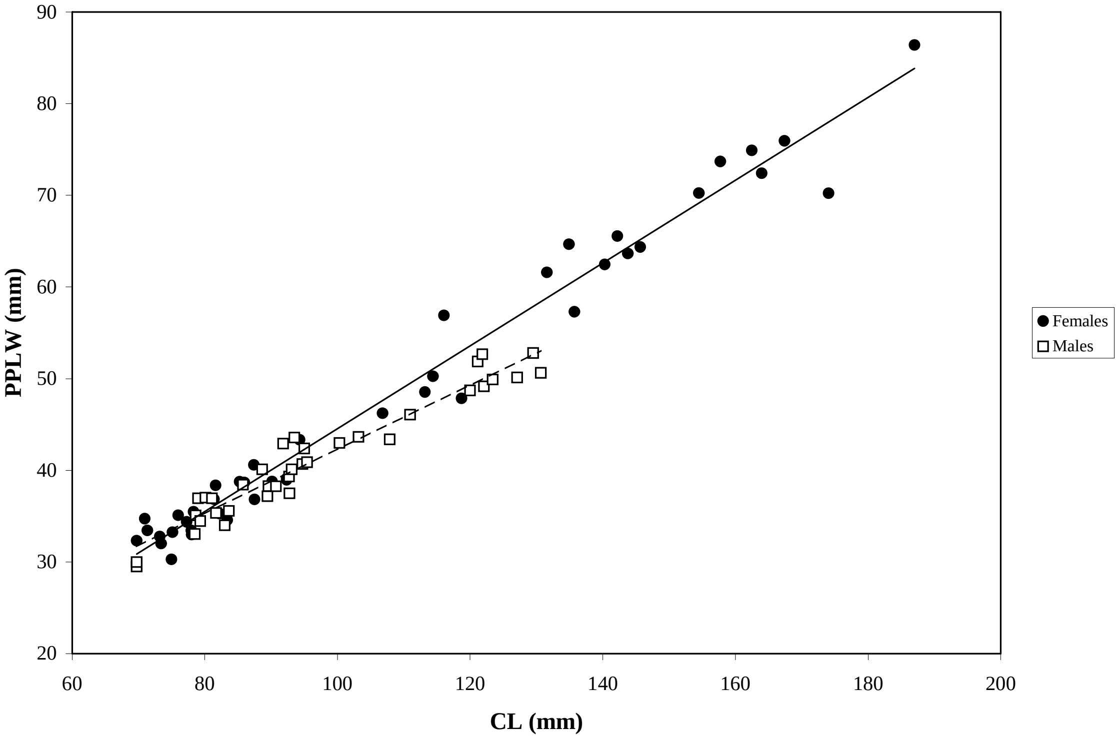

FIGURE 15. Allometry of sexually dimorphic posterior plastron lobe width plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: PPLW = -0.67 + 0.45CL; Male: PPLW = 7.21 + 0.35CL; ANCOVA: df = 1,75, F = 20.02, P < 0.0001)

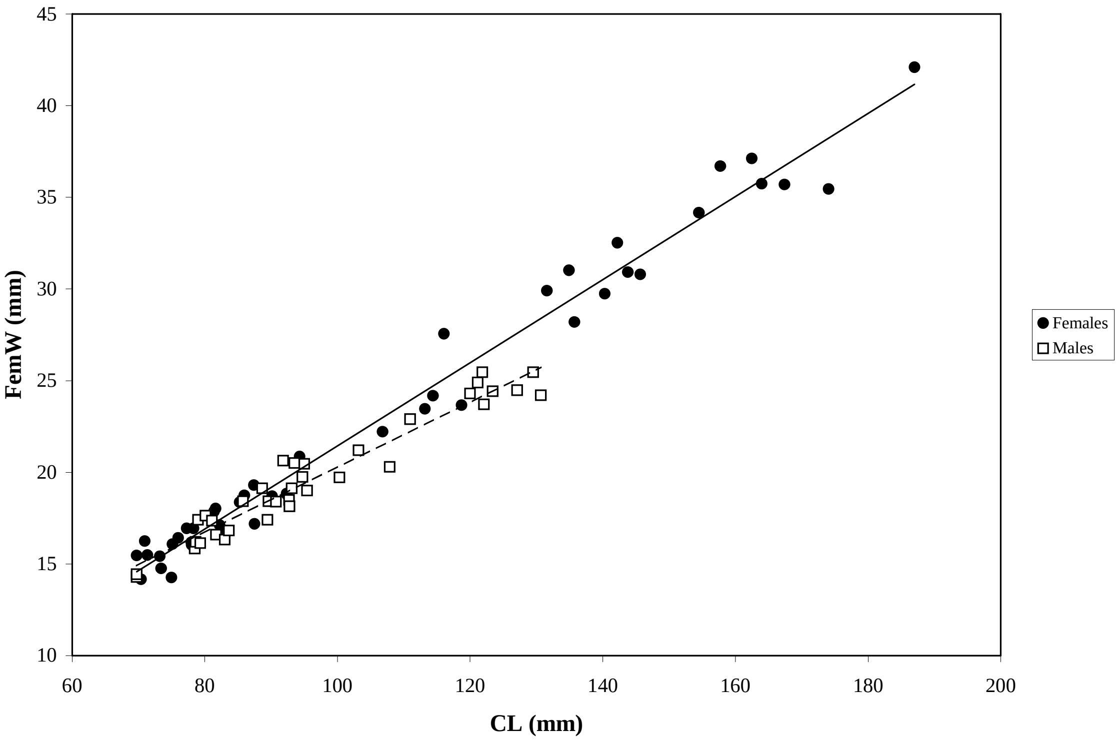

FIGURE 16. Allometry of sexually dimorphic femoral scute width plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: FemW = -1.23 + 0.23CL; Male: FemW = 2.51 + 0.18CL; ANCOVA: df = 1,76, F = 21.56, P < 0.0001)

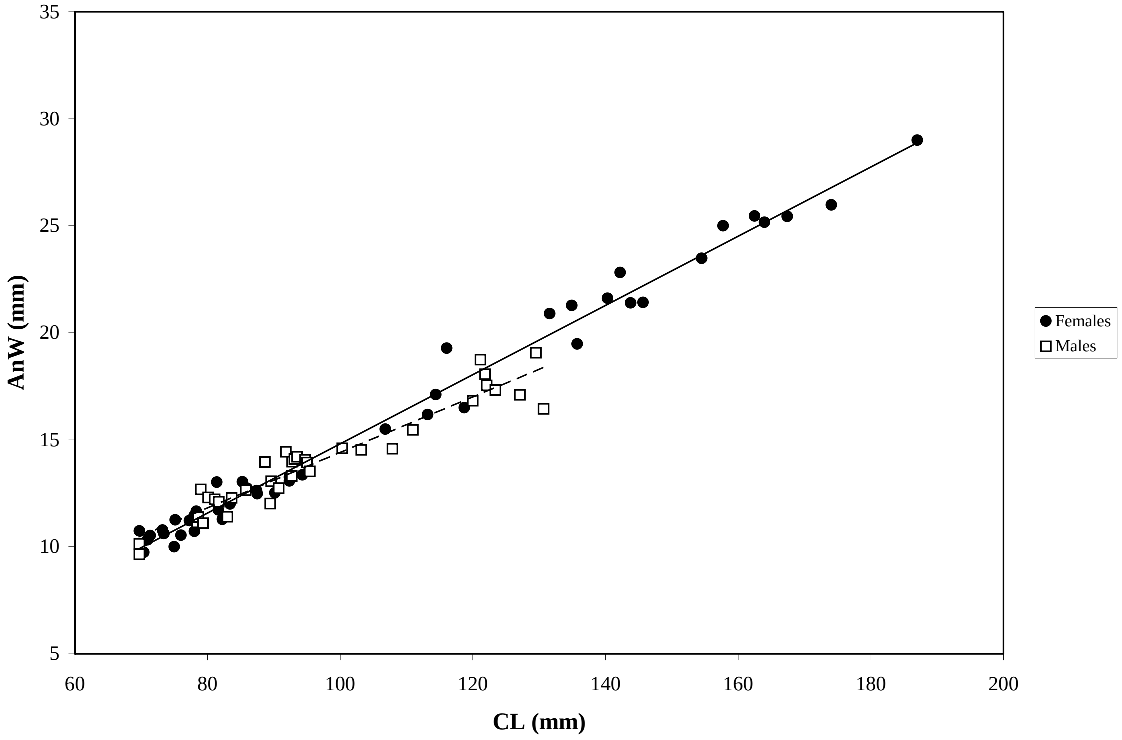

FIGURE 17. Allometry of sexually dimorphic anal scute width plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: AnW = -1.36 + 0.16CL; Male: FemW = 1.40 + 0.13CL; ANCOVA: df = 1,76, F = 18.63, P < 0.0001)

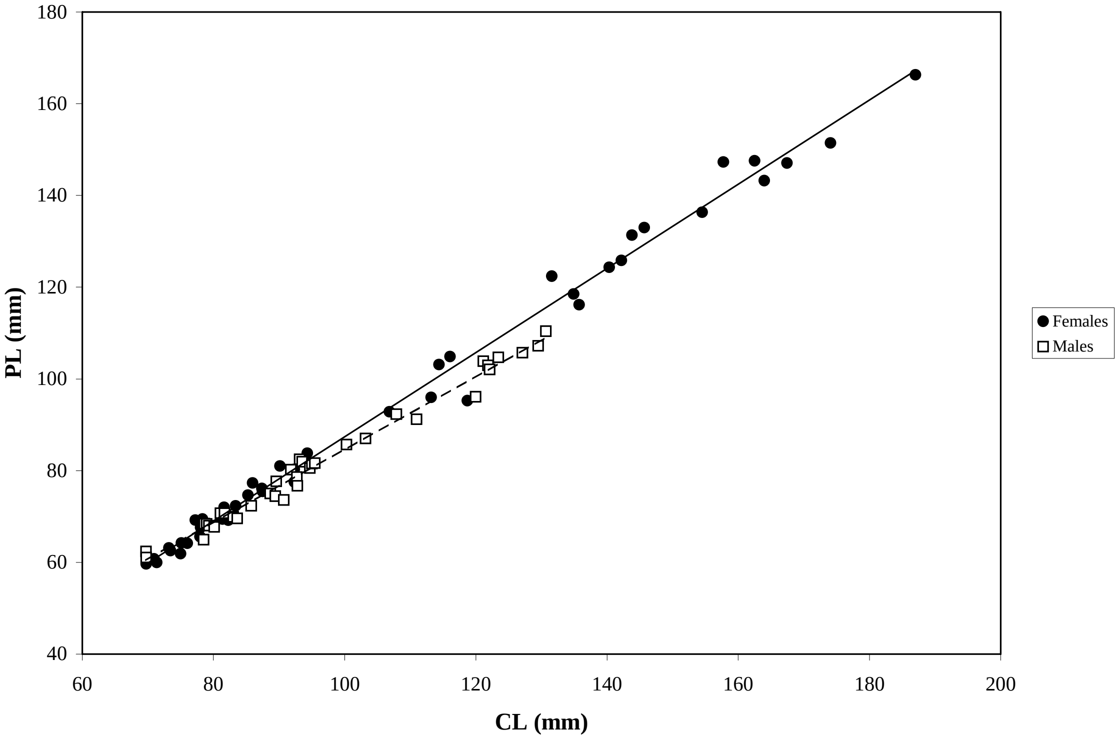

FIGURE 18. Allometry of sexually dimorphic plastron length plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: PL = -4.43 + 0.92CL; Male: PL = 4.89 + 0.80CL; ANCOVA: df = 1,75, F = 22.17, P < 0.0001)

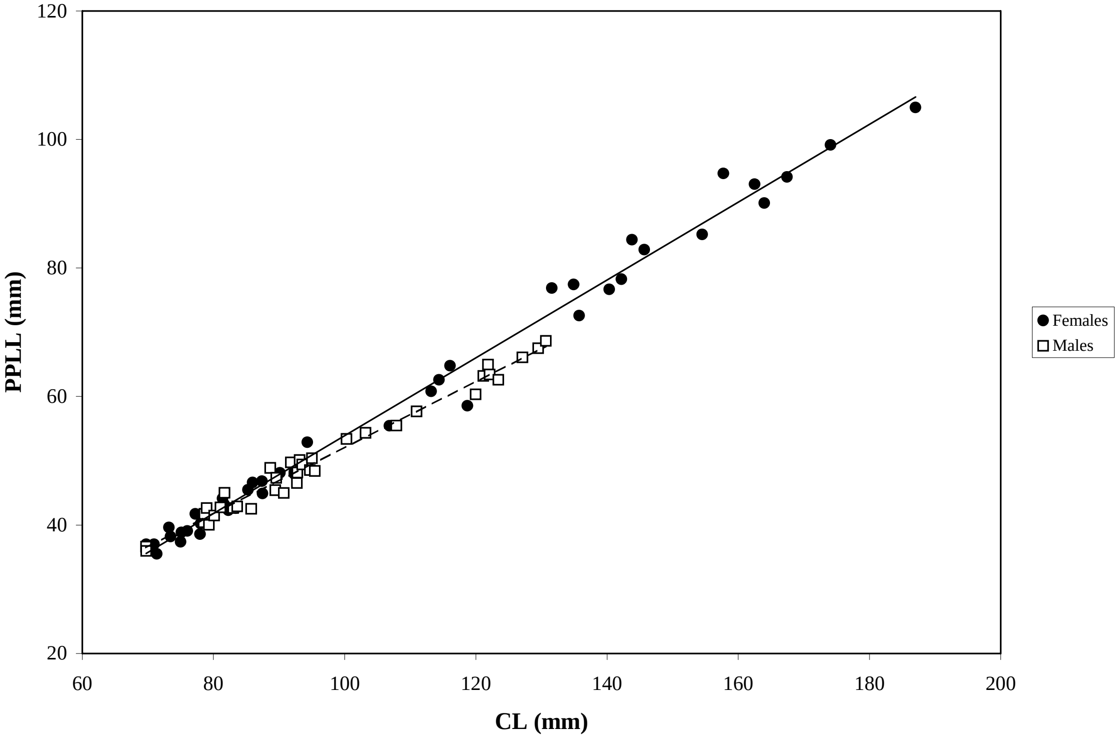

FIGURE 19. Allometry of sexually dimorphic posterior plastron lobe length plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: PPLL = -6.71 + 0.61CL; Male: PPLL = 0.54 + 0.52CL; ANCOVA: df = 1,75, F = 22.94, P < 0.0001)

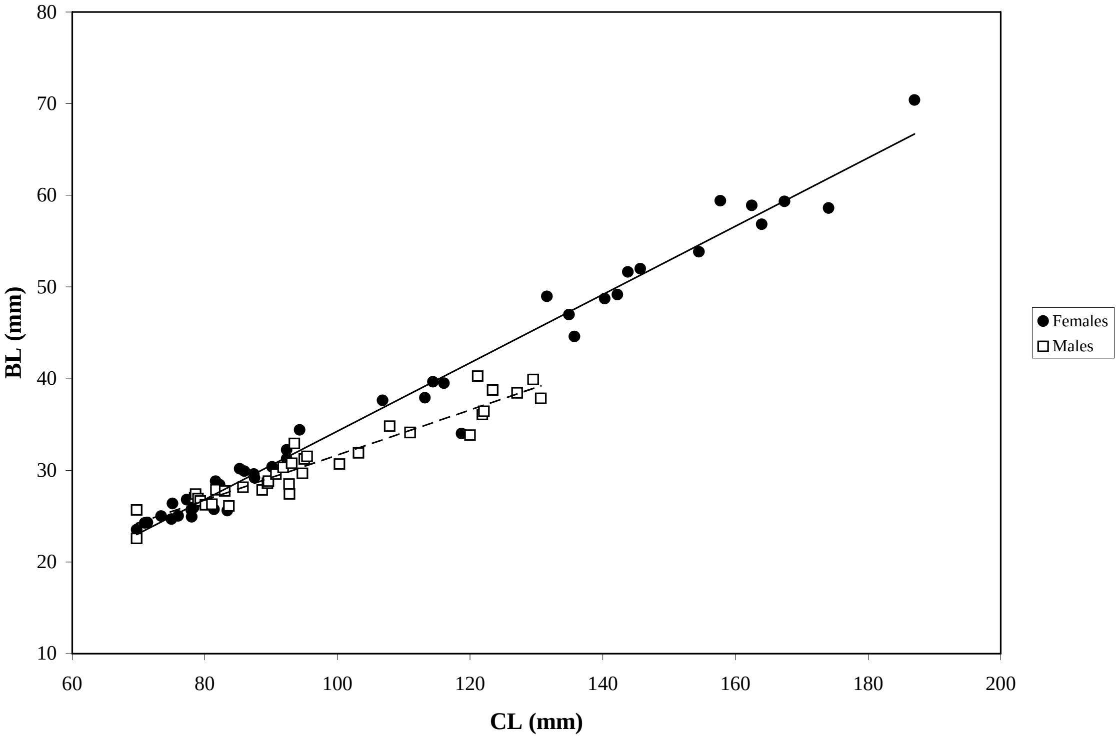

FIGURE 20. Allometry of sexually dimorphic bridge length plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: $BL = -2.99 + 0.37CL$; Male: $BL = 6.94 + 0.25CL$; ANCOVA: df = 1,74, $F = 51.65$, $P < 0.0001$)

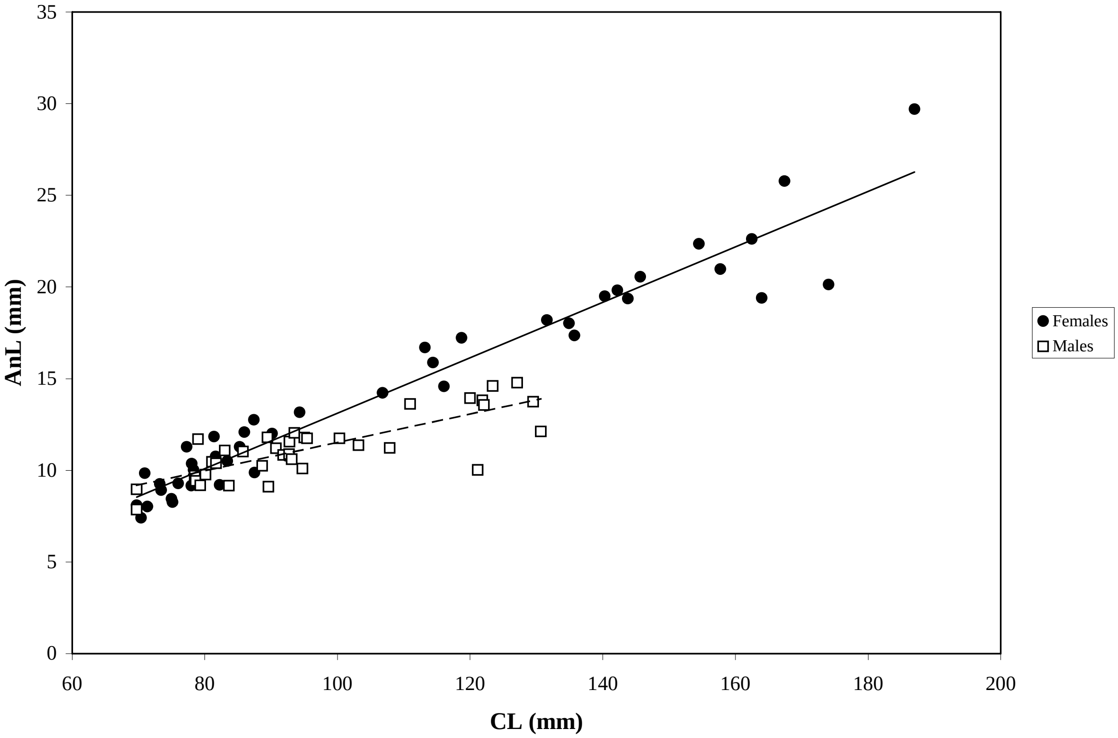

FIGURE 21. Allometry of sexually dimorphic anal scute length plotted as a function of carapace length and sex for *Malayemys subtrijuga* from the Chao Phraya River Basin. (Female: AnL = -2.00 + 0.15CL; Male: BL = 3.76 + 0.08CL; ANCOVA: df = 1,76, F = 32.57, P < 0.0001)

shape of their anal notches. Males have V-shaped notches whereas females have round ones. It is not difficult to imagine that a V-shaped anal notch would correspond to a shorter AnL. The V-shaped anal notch and relatively shorter AnL allow for a longer precloacal distance (Mosimann and Bider, 1960) in males. This is significant because the precloacal region of the tail accomodates the male’s penis (Mosimann and Bider, 1960).

Sexual dimorphism of shell characters, as examined by ANCOVA, was not as evident for *M. subtrijuga* from Mekg and Java. For Mekg, the regression slopes of males and females differed significantly in only four of the 28 characters examined (Table 8). In all four cases, the difference in slopes was barely significant ($P > 0.02$ in all cases). For Java, the regression slopes of males and females differed significantly in 10 of the 28 characters examined (Table 9). Only five of these, however, had P values < 0.01. As was suggested for allometric growth, the scarcity of statistical support (ANCOVA) for sexual dimorphism in Mekg and Java probably resulted from inadequate sample sizes for these regions (see Tables 8 and 9).

Average CL was greater for adult females than it was for adult males in all three geographic samples (Table 3). Therefore, all SDI values were positive (Gibbons and Lovich, 1990). SDI values were +1.27 for CPhr, +1.30 for Mekg, and +1.20 for Java. These are comparable to the SDI value of 1.39 that is derived from Srinarumol’s (1995) data.

Sexual Dimorphism – Multivariate

Sexual dimorphism of the shell was also evident in *M. subtrijuga* from CPhr when examined by multivariate techniques. The best model to classify turtles relative to

TABLE 8. Comparison of regression slopes (ANCOVA) of shell characters versus carapace length among male and female *Malayemys subtrijuga* from the Mekong River Basin. Regression equations are found in Table 5. For significance levels, ns = P > 0.05. Character abbreviations follow Table 2.

	Male vs. Female Slopes (b) (H_0: $b_{males} = b_{females}$)		
Character	F	df	P
CW	3.11	1,28	ns
SH	5.48	1,26	0.0272
Pleu1W	1.23	1,25	ns
Pleu1L	0.66	1,25	ns
Vert1W	0.28	1,25	ns
Vert1L	6.15	1,25	0.0202
Vert2W	3.55	1,25	ns
Vert2L	2.18	1,25	ns
Vert3W	5.29	1,25	0.0301
Vert3L	0.82	1,25	ns
Vert5W	1.96	1,25	ns
Vert5L	4.20	1,26	ns
PL	2.05	1,27	ns
APLW	0.24	1,26	ns
APLL	1.72	1,25	ns
PPLW	3.31	1,26	ns
PPLL	3.76	1,25	ns
BL	6.08	1,26	0.0206
GulW	0.05	1,26	ns
GulL	0.04	1,26	ns
HumW	0.67	1,26	ns
HumL	0.53	1,26	ns
PecL	0.63	1,26	ns
AbdL	1.36	1,26	ns
FemW	1.45	1,26	ns
FemL	0.56	1,26	ns
AnW	0.91	1,26	ns
AnL	2.77	1,26	ns

TABLE 9. Comparison of regression slopes (ANCOVA) of shell characters versus carapace length among male and female *Malayemys subtrijuga* from Java. Regression equations are found in Table 6. For significance levels, ns = P > 0.05. Character abbreviations follow Table 2.

	Male vs. Female Slopes (b) (H_0: $b_{males} = b_{females}$)		
Character	F	df	P
CW	6.65	1,26	0.0160
SH	5.32	1,23	0.0305
Pleu1W	10.84	1,26	0.0029
Pleu1L	0.22	1,23	ns
Vert1W	0.02	1,23	ns
Vert1L	0.20	1,25	ns
Vert2W	0.02	1,23	ns
Vert2L	2.17	1,23	ns
Vert3W	0.05	1,22	ns
Vert3L	0.02	1,22	ns
Vert5W	0.03	1,22	ns
Vert5L	2.23	1,21	ns
PL	8.89	1,26	0.0062
APLW	9.05	1,26	0.0058
APLL	0.00	1,25	ns
PPLW	5.94	1,25	0.0222
PPLL	20.62	1,25	0.0001
BL	13.49	1,25	0.0011
GulW	0.37	1,25	ns
GulL	2.18	1,26	ns
HumW	3.62	1,25	ns
HumL	0.41	1,26	ns
PecL	0.15	1,26	ns
AbdL	4.79	1,26	0.0378
FemW	6.05	1,25	0.0211
FemL	2.92	1,26	ns
AnW	0.28	1,26	ns
AnL	0.03	1,26	ns

predetermined sex contained six of the original 29 shell character ratios. These were AnL/CL, PPLL/CL, RLatK, Vert3W/CL, FemL/CL, and PecL/CL (see Table 2 for character abbreviations). Mean values for these six shell character ratios are presented in Table 10. Using the six variable model, cross-validation results of linear discriminant function analysis correctly classified 93.10% of males and 89.47% of females (Table 11). A histogram of canonical discriminant scores (Fig. 22) also demonstrated shell differentiation between males and females from CPhr. In general, females had positive CV1 (canonical variable 1) scores and males had negative CV1 scores.

Multivariate techniques also detected sexual dimorphism in *M. subtrijuga* from Mekg and Java. The best models contained five and three shell variables for Mekg and Java, respectively. The Mekg model contained CW/CL, HumL/CL, Vert5W/CL, RLatK, and HumW/CL. The Java model contained BL/CL, FemW/CL, and GulW/CL. Mean values for these shell character ratios are presented in Tables 12 (Mekg) and 13 (Java). Cross-validation correctly classified 88.89% of males and 81.82% of females from Mekg (Table 14), and 100% of both males and females from Java (Table 15). Histograms of canonical discriminant scores also demonstrated shell differentiation between the sexes. As was the case with CPhr, females from both Mekg (Fig. 23) and Java (Fig. 24) generally had positive CV1 scores whereas males had negative CV1 scores.

Based on the analyses above, a clear pattern of sexual dimorphism emerges for *M. subtrijuga*. Females attain larger sizes (Figs. 5-7; Table 3) and have relatively wider and higher shells (carapace and plastron) and longer plastra than males (Figs. 8-24; Tables 7-15).

TABLE 10. Shell character ratios – mean ± 1 SE, (range), and [n] – used in discriminant function analysis to classify males and females from the Chao Phraya River Basin. Character abbreviations follow Table 2.

Character	Females	Males
AnL/CL	0.14 ± 0.002 (0.12-0.16) [19]	0.12 ± 0.002 (0.08-0.13) [30]
PPLL/CL	0.56 ± 0.006 (0.49-0.60) [19]	0.52 ± 0.003 (0.50-0.55) [30]
RlatK	0.22 ± 0.007 (0.13-0.25) [23]	0.24 ± 0.003 (0.20-0.25) [32]
Vert3W/CL	0.22 ± 0.003 (0.19-0.24) [23]	0.20 ± 0.002 (0.17-0.23) [31]
FemL/CL	0.14 ± 0.003 (0.12-0.17) [19]	0.15 ± 0.003 (0.12-0.18) [30]
PecL/CL	0.12 ± 0.003 (0.09-0.15) [19]	0.10 ± 0.003 (0.07-0.16) [30]

TABLE 11. Cross-validation results for male and female *Malayemys subtrijuga* from the Chao Phraya River Basin based on linear discriminant function analysis of shell character ratios. Percentages in parentheses.

	Group classification		
Actual group	Males	Females	Total
Males	27 (93.10)	2 (6.90)	29
Females	2 (10.53)	17 (89.47)	19
Total	29	19	48

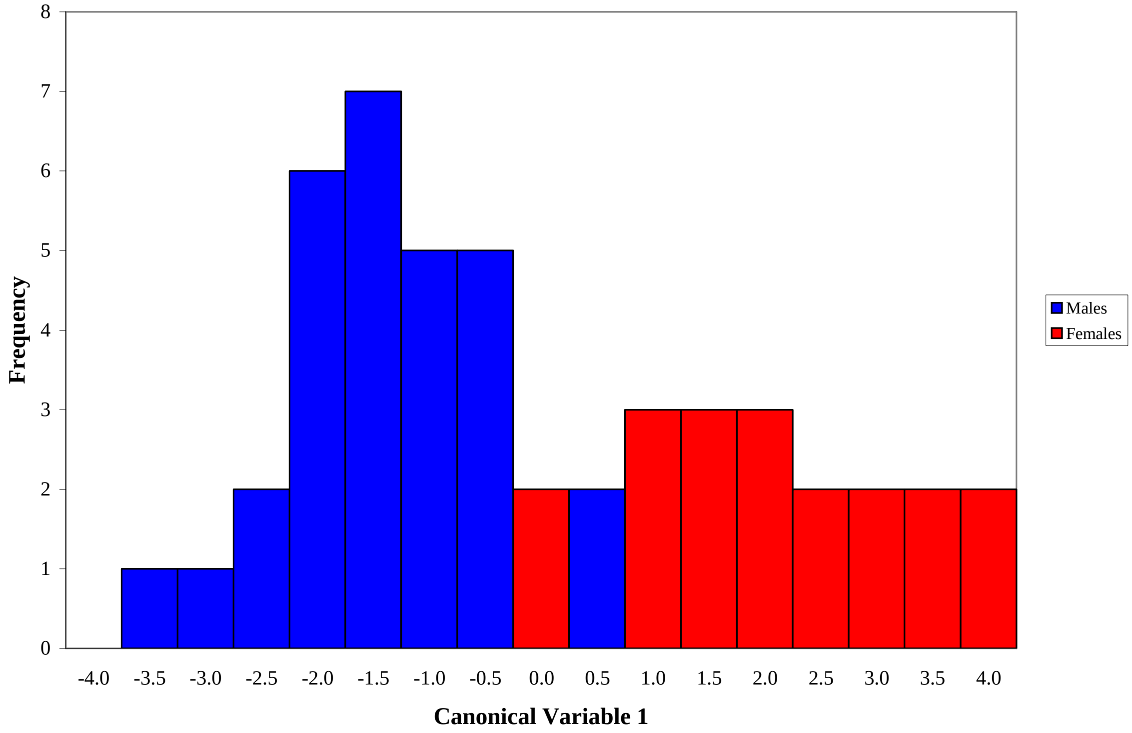

FIGURE 22. Histogram of canonical discriminant scores (canonical variable 1) for male and female *Malayemys subtrijuga* from the Chao Phraya River Basin.

TABLE 12. Shell character ratios – mean ± 1 SE, (range), and [n] – used in discriminant function analysis to classify males and females from the Mekong River Basin. Character abbreviations follow Table 2.

Character	Females	Males
CW/CL	0.75 ± 0.007 (0.71-0.79) [16]	0.71 ± 0.006 (0.69-0.74) [9]
HumL/CL	0.11 ± 0.006 (0.04-0.14) [14]	0.11 ± 0.004 (0.09-0.13) [9]
Vert5W/CL	0.28 ± 0.006 (0.24-0.33) [13]	0.27 ± 0.011 (0.21-0.32) [9]
RLatK	0.22 ± 0.007 (0.20-0.25) [12]	0.22 ± 0.008 (0.20-0.25) [9]
HumW/CL	0.21 ± 0.003 (0.20-0.23) [14]	0.20 ± 0.002 (0.19-0.22) [9]

TABLE 13. Shell character ratios – mean ± 1 SE, (range), and [n] – used in discriminant function analysis to classify males and females from Java. Character abbreviations follow Table 2.

Character	Females	Males
BL/CL	0.33 ± 0.004 (0.31-0.35) [13]	0.28 ± 0.004 (0.26-0.31) [14]
FemW/CL	0.23 ± 0.002 (0.21-0.24) [13]	0.20 ± 0.002 (0.19-0.21) [14]
GulW/CL	0.14 ± 0.002 (0.13-0.15) [13]	0.14 ± 0.002 (0.12-0.14) [14]

TABLE 14. Cross-validation results for male and female *Malayemys subtrijuga* from the Mekong River Basin based on linear discriminant function analysis of shell character ratios. Percentages in parentheses.

	Group classification		
Actual group	Males	Females	Total
Males	8 (88.89)	1 (11.11)	9
Females	2 (18.18)	9 (81.82)	11
Total	10	10	20

TABLE 15. Cross-validation results for male and female *Malayemys subtrijuga* from Java based on linear discriminant function analysis of shell character ratios. Percentages in parentheses.

	Group classification		
Actual group	Males	Females	Total
Males	14 (100.00)	0 (0.00)	14
Females	0 (0.00)	13 (100.00)	13
Total	14	13	27

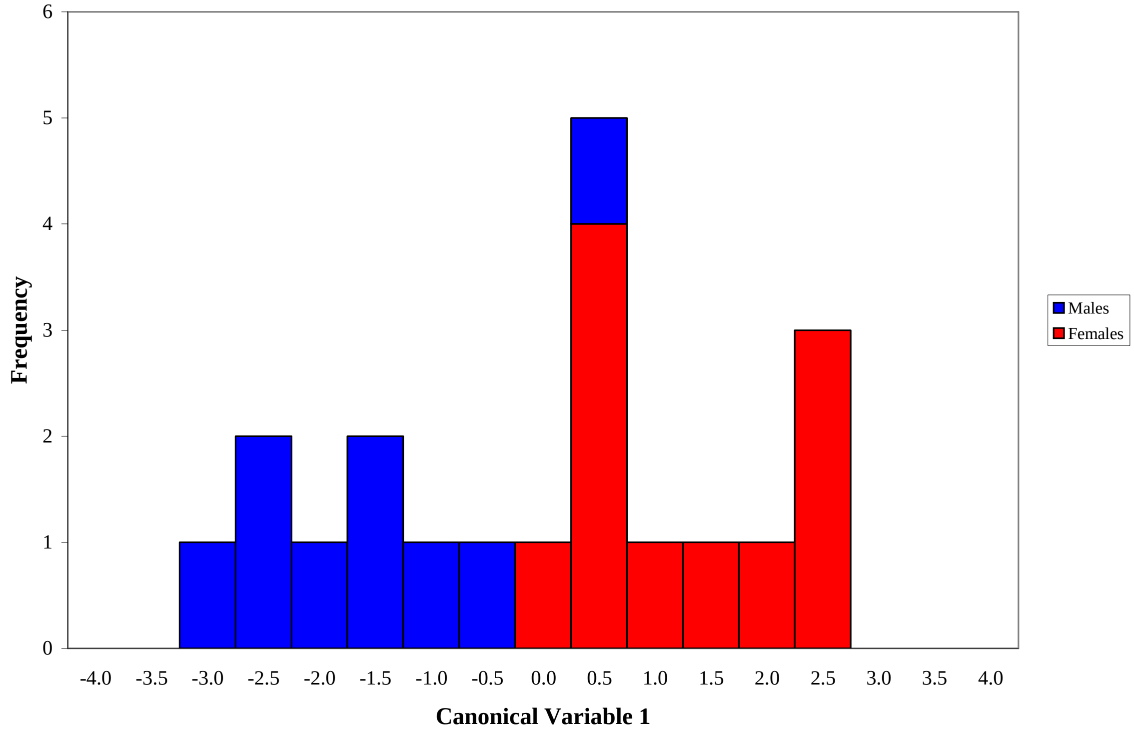

FIGURE 23. Histogram of canonical discriminant scores (canonical variable 1) for male and female *Malayemys subtrijuga* from the Mekong River Basin.

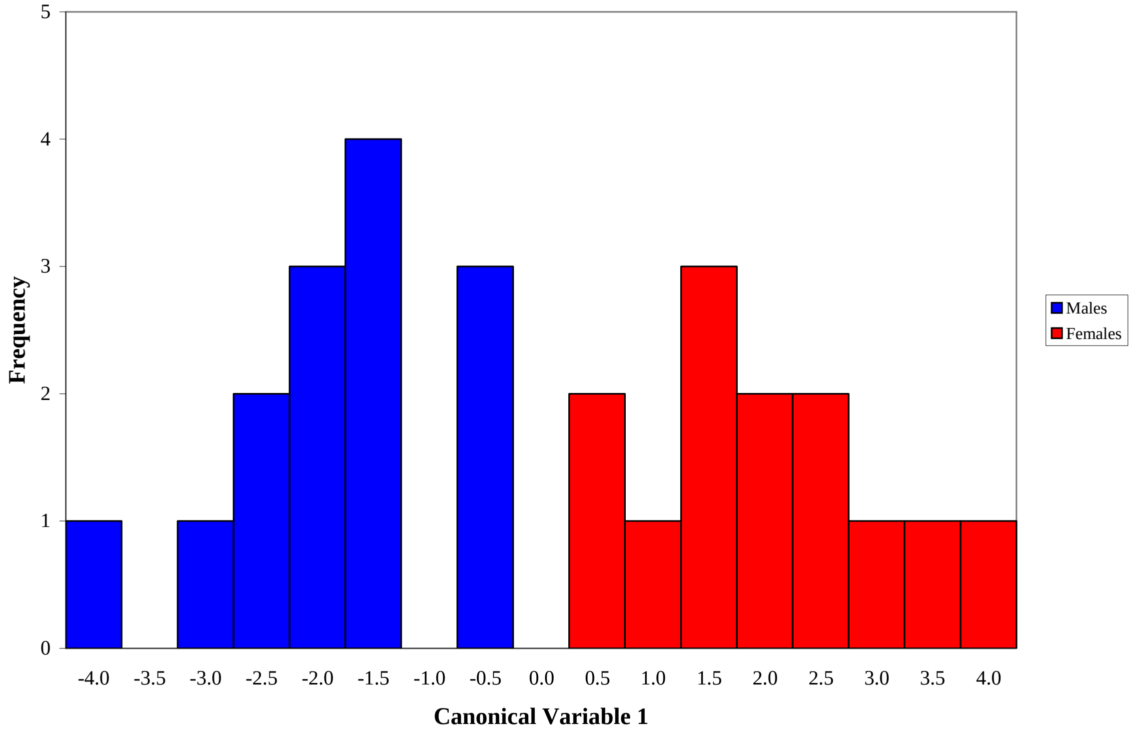

FIGURE 24. Histogram of canonical discriminant scores (canonical variable 1) for male and female *Malayemys subtrijuga* from Java.

Malayemys subtrijuga is a poor-swimming, slow-moving, diurnal bottom-feeder (van Dijk and Thirakhupt, in press). One might expect, therefore, that it follows the sexual size dimorphism (SSD) pattern of Berry and Shine's (1980) "semiaquatic and bottom-walking" group. Larger males of this group have an advantage when it comes to forcibly inseminating females, so males tend to grow larger than females. *Malayemys subtrijuga*, however, probably does not engage in forced insemination because it lacks many of the structures (long, prehensile, spine-tipped tails and specialized patches of roughened scales on rear legs) common to species that employ this mating strategy (Berry and Shine, 1980). Instead, *M. subtrijuga* falls into Berry and Shine's (1980) "aquatic swimmers" category. Males are usually smaller than females in this group either because small size evolves to increase mobility and female location or because selection for increased fecundity results in larger females.

Gibbons and Lovich (1990) predict that the smaller sex in a turtle species will mature at a smaller size and younger age, and that the degree of difference in these factors will lead to the ultimate size difference between the sexes. Although there is a scarcity of data on this topic for *M. subtrijuga*, this is probably the case for this species. Male *M. subtrijuga*, the smaller sex, seem to mature at a smaller size (PL) than females (Srinarumol, 1995). According to Gibbons and Lovich (1990), SSD is the result of a trade-off between the benefits of early maturity (increased matings leading to increased reproductive output) and the negative environmental consequences of small body size (increased risk of predation, dessication and thermal stress). In aquatic habitats, like those inhabited by *M. subtrijuga*, the risks associated with small body size are minimal

(Gibbons and Lovich, 1990). Therefore, small body size is seemingly favored in male *M. subtrijuga* because the benefits of their early maturity outweigh the risks of small body size.

Hypotheses relating to small body size in male turtles deal with only half of the SSD pattern displayed by *M. subtrijuga*. Both Berry and Shine (1980) and Gibbons and Lovich (1990) recognize the importance of fecundity as a factor influencing body size in female turtles. Darwin's "fecundity advantage" hypothesis says that natural selection should favor large body size in females because this would allow them to produce more offspring. For turtles in general, larger female size generally results in more or larger eggs (Gibbons et al., 1982). Such a relationship has also been suggested for *M. subtrijuga* specifically (van Dijk and Thirakhupt, in press). Although fecundity selection could induce an increase in overall female size, it should primarily act on the relative size of the abdominal cavity (Bauwens et al. *in* Mouton et al., 2000). This helps to explain the many relatively wider, higher, and longer shell characters exhibited by female *M. subtrijuga* (Figs. 8-21; Tables 7-9).

Some authors (see Gibbons and Lovich, 1990 for review) have suggested that SSD is a result of ecological forces or natural selection. The most frequently cited ecological cause of SSD is probably competitive displacement (Brown and Wilson, 1956; Dunham et al., 1979). In the displacement model, the sexes evolve to exploit different resources in the environment, thereby reducing competition between them. This model is frequently used to explain situations where larger individuals of a species are able to consume larger food items than their smaller counterparts. Large females of *M.*

subtrijuga consume freshwater mussels, whereas males and other small individuals feed almost exclusively on aquatic snails (van Dijk and Thirakhupt, in press). The weakness of the displacement model in explaining this situation, is that it cannot predict which sex should be larger (Gibbons and Lovich, 1990). Rather than ecological factors being the cause of SSD in *M*. *subtrijuga*, it is more likely that ecological differences between the sexes are simply consequences of sexually selected dimorphism (Shine, 1986).

Based on my data and those of Srinarumol (1995), *M*. *subtrijuga* has SDI values (Gibbons and Lovich, 1990) ranging from +1.20 to +1.39. SDI values for the entire turtle order range from –1.45 to +2.10. When compared to other species that have females as the larger sex (mean SDI for all species where f > m = +1.36; median SDI for all species where f > m = +1.23), *M*. *subtrijuga* displays average SDI values (Gibbons and Lovich, 1990). In summary, the SSD pattern exhibited by *M*. *subtrijuga* is the result of a combination of selective pressures. Selection for increased fecundity produces larger females (Berry and Shine, 1980; Gibbons and Lovich, 1990), whereas selection for early maturity results in smaller males (Gibbons and Lovich, 1990).

Chapter 3 – Intersample Comparisons: Geographic Variation of Shell and Head-Stripe Characters

Taxonomy is the foundation of traditional conservation practices (Avise, 1989; Daugherty et al., 1990; Lovich and Gibbons, 1997). Such practices emphasize protection of rare taxa at the single-species level. Modern conservation programs still adhere to this tradition, because species must be discovered and described before they can be effectively protected (Avise, 1989). As such, many cryptic species are in potential danger of extinction because of faulty taxonomy, unrecognized intraspecific variation, and/or the lack of formal species descriptions. A proactive alternative to single-species conservation is biodiversity conservation at the major landscape and ecosystem level. This type of strategy serves to protect communities that encompass sensitive as well as non-endangered species, including cryptic species (Lovich and Gibbons, 1997). Until such a strategy is implemented on a large scale, however, good taxonomic research remains the best chance of protection for most cryptic species.

“One of the worst mistakes we can make in our efforts to protect biodiversity is to allow the extinction of species because of faulty taxonomy” (Lovich and Gibbons, 1997:427). The tuatara is an excellent example of this perspective. Tuataras have been viewed almost universally as a single species (*Sphenodon punctatus*), and efforts to protect it have been based on this view. Taxonomists in the 1800s (Gray, 1842; Buller, 1877), however, described two extant species (*S. punctatus* and *S. guentheri*), and subsequent research in the past century (Wettstein, 1931, 1943) identified variant types as subspecies of *S. punctatus* (*S. p. punctatus* and *S. p. reischeki*). All of these taxonomic proposals were largely ignored until Daugherty et al. (1990) demonstrated significant morphological and genetic differentiation among living populations and provided strong support for the taxonomic assignments proposed some 50-150 years earlier. Tragically, the failure to recognize this documented taxonomic diversity resulted in the extinction of *S. p. reischeki* and the near extinction of *S. guentheri*. "Perceived monotypy of tuatara apparently forestalled management intervention on behalf of threatened populations, thus contributing to extinction of 10 of the 40 populations (25%) in the past century and the imminent extinction of four more" (Daugherty et al., 1990:177).

Another example where perceived monotypy led to the endangerment of cryptic species is shown by the Alabama map turtle, *Graptemys pulchra*. This turtle was traditionally envisioned as a single species inhabiting several drainage systems in Alabama, Georgia, Florida, Mississippi, and Louisiana (Cagle, 1952). A detailed analysis of morphology and mtDNA haplotypes (Lovich and McCoy, 1992) revealed that *G. pulchra* (*sensu lato*) is actually composed of three species (*G. ernsti*, *G. gibbonsi*, and *G. pulchra*), and all are threatened by pollution, channelization, and restricted distribution (Lovich and Gibbons, 1997). As of 1997, "no conservation plans exist for these species as they were formerly considered to be populations of a single widely distributed taxon" (Lovich and Gibbons, 1997:427).

Malayemys subtrijuga (Testudines: Bataguridae) is a wide-ranging species that has been generally perceived as monotypic (Ernst and Barbour, 1989). It is found in lowland freshwater areas of Thailand, Laos, Cambodia, southern Vietnam, the northern Malay Peninsula, and Java. A detailed study of geographic variation has yet to be completed for this species and is therefore desperately needed to determine whether cryptic taxa exist among its populations. Such a study is particularly urgent because of the ongoing turtle crisis in Southeast Asia. Many Southeast Asian turtle populations are in rapid decline because of serious pressure from commercial exploitation and habitat destruction (Behler, 1997; Thirakhupt and van Dijk, 1997). If overexploited populations of *M. subtrijuga* represent cryptic taxa, it is imperative that they are discovered and described so that the mistakes made with the tuatara and Alabama map turtle can be avoided.

Materials and Methods

Geographic Distribution

Prior to statistical analyses of geographic variation, a detailed table and map were constructed to clearly define the geographic distribution of *M. subtrijuga*. Distribution data from all available museum and literature records were used. Information included country and watershed of origin, specific locality data (if available), latitude and longitude coordinates, museum catalog number, and/or literature reference. No other account of geographic distribution in *M. subtrijuga* is based on such a complete compilation of data (Appendix D; Fig. 29).

Sample and Character Definitions

An attempt was made to examine all museum specimens from throughout the known range of *M. subtrijuga*. Specimens were grouped into regional geographic samples representing major drainage basins for those on mainland Southeast Asia (Kottelat, 1989) and entire islands for those in the Greater Sundas. Sample localities were: Maly, Malay Peninsula including western Malaysia and peninsular Thailand; MKhl, Mae Khlong basin of Thailand; CPhr, Chao Phraya basin of Thailand; SECos, coastal areas of southeast Thailand and Cambodia; Mekg, Mekong basin of Vietnam, Cambodia, Laos, and eastern Thailand; Sumt, Sumatra; Java, Java (Fig. 3). The geographic origin of each specimen was based on museum records, and each geographic sample was divided into subsamples based on sex and life stage.

A total of 258 *M. subtrijuga* were examined and utilized in all or some of the analyses that follow (see Appendix C and D for detailed list of all specimens examined). The shell data set consisted of one meristic and 28 mensural characters, while the head-stripe data set consisted of two meristic and one mensural character (Table 2). These characters derived from those previously used in morphometric studies of turtles, from those previously used to describe *M. subtrijuga*, and from characters newly discovered during this study. The condition of bilateral characters was recorded from the right side of the carapace and the left side of the plastron unless damaged. Measurements were made with dial calipers to the nearest 0.02 mm.

Museum abbreviations followed Leviton et al. (1985) and Leviton and Gibbs (1988) with the following additions: CRI = Chelonian Research Institute, Oviedo, Florida, USA; KUZ = Kyoto University Zoological Collection, Kyoto, Japan; RH = personal collection of Ren Hirayama, Teikyo Heisei University, Ichihara, Chiba, Japan; ZRC = Raffles Museum of Biodiversity Research, Zoological Reference Collection, The National University of Singapore, Singapore.

The head-stripe characters, used in several of the analyses that follow, need further description. The number of nasal stripes (NasS) was counted for each specimen. Nasal stripes were defined as narrow stripes extending downward from the nostrils towards the medial notch of the upper jaw plus those similar stripes running parallel in the nasal region (Fig. 25-26; Table 2). The condition of the infraorbital stripe with respect to the loreal seam (InfLor) was also recorded. Each specimen was given a numerical score as follows: 1 = infraorbital stripe does not extend superior to loreal seam; 2 = infraorbital stripe extends only slightly superior to loreal seam; 3 = infraorbital stripe extends completely superior to loreal seam but does not join supraorbital stripe; 4 = infraorbital stripe extends completely superior to loreal seam and joins supraorbital stripe (Fig 27-28; Table 2). Finally, the width of the infraorbital stripe was measured at the loreal seam (InfSW). This character was then normalized by dividing it by head width (InfSW/HW) (Fig. 27-28; Table 2).

Sexual Identification and Maturity

Tail morphology was the primary characteristic used for sexual identification in this study. Sexual dimorphism of this character is pronounced in both subadults and adults (Fig. 4), with males having much longer and thicker tails (Ernst and Barbour, 1989; Srinarumol, 1995; van Dijk and Thirakhupt, in press). Assignment of specimens to

FIGURE 25. Photographs of *Malayemys subtrijuga* illustrating NasS values of 2 (top-USNM 71480) and 4 (bottom-SMF 52865).

FIGURE 26. Photographs of *Malayemys subtrijuga* illustrating NasS values of 6 (top-MTKD 26087) and 7 (bottom-ROM 37059).

FIGURE 27. Photographs of *Malayemys subtrijuga* illustrating InfLor values of 1 (top-GMU 3520) and 2 (bottom-USNM 71480), and an infraorbital stripe that is relatively wide at the loreal seam (both).

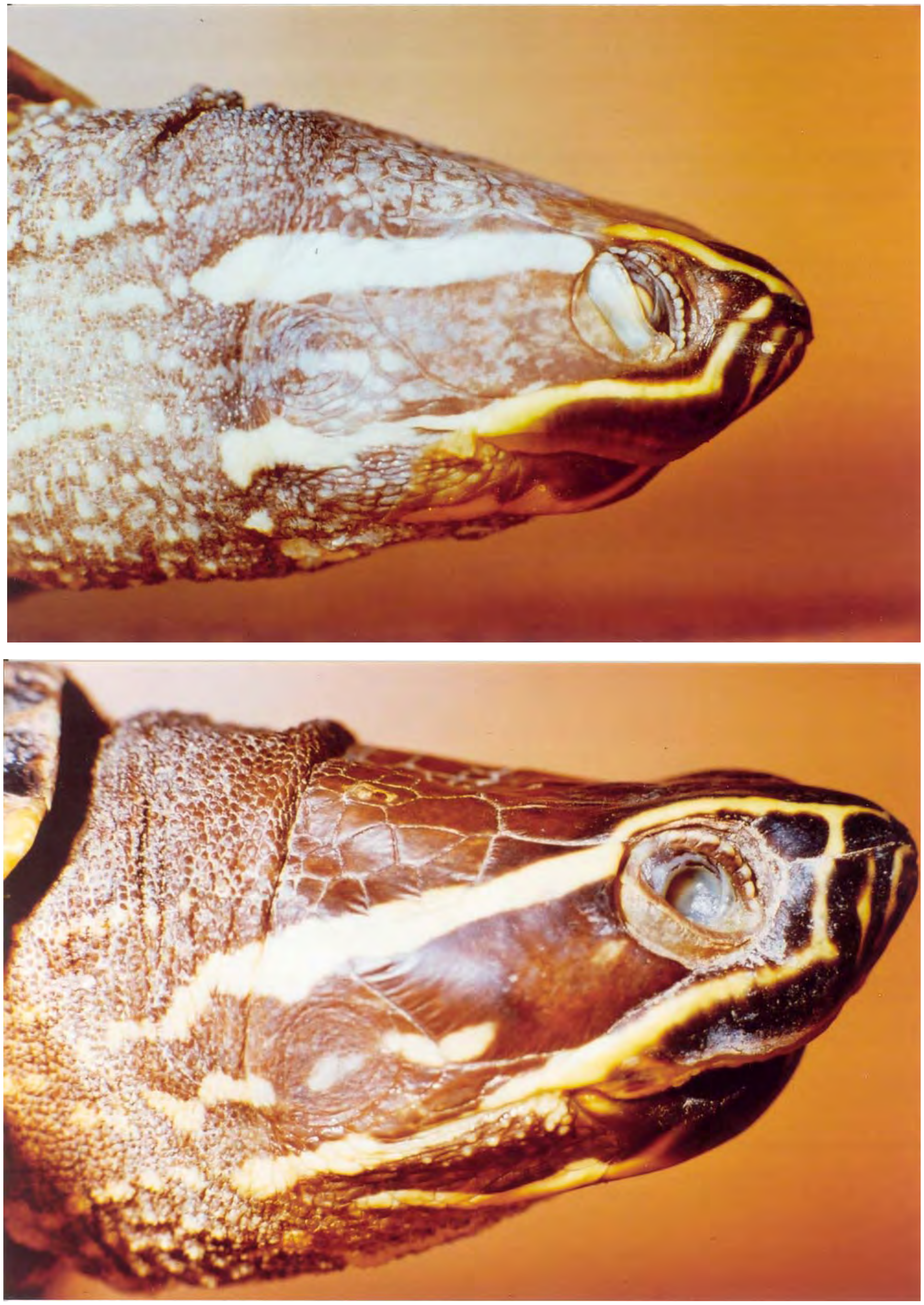

FIGURE 28. Photographs of *Malayemys subtrijuga* illustrating InfLor values of 3 (top-MTKD 23937) and 4 (bottom-MTKD 26087), and an infraorbital stripe that is relatively narrow at the loreal seam (both).

appropriate life stages (juvenile, subadult, adult) was based primarily on Srinarumol (1995) who distinguished adults from subadults based on the complete development of testes and ovaries, and subadults from juveniles using tail morphology (see Chapter 2 for a more detailed discussion of sexual identification and maturity).

Geographic Variation – Shell Characters

Only three geographic samples in the current study had sufficient numbers to warrant intersample comparisons. All methods and analyses that follow pertain to samples from CPhr, Mekg, and Java. Geographic variation of shell characters was examined using multivariate techniques. All 28 mensural shell characters (all except CL; Table 2) were divided by CL, and the resulting ratios comprised the majority of the data set. RLatK (Table 2), also part of this data set, was not divided by CL because it is standardized upon measurement (expressed as a proportion). Preliminary analyses indicated that allometric variation and sexual dimorphism exist in each of the three geographic samples (see Chapter 2). To minimize the effects of these factors, only adult and larger subadult turtles of each sex (males ≥ 80 mm CL; females ≥ 100 mm CL) were utilized, and males and females were analyzed separately.

Using all 29 shell variables for each sex separately, stepwise selection (PROC STEPDISC; SAS, 1989; significance level for entry and removal = 0.30) was used to obtain a set of potential models that would classify turtles relative to their predetermined geographic origin (CPhr, Mekg, and Java). Each step of this procedure generated a distinct model that was tested for classification accuracy using linear discriminant function analysis (PROC DISCRIM; SAS, 1989). Final selection of the best model (as defined by me) was based on model size and classification accuracy. The best model gave the most accurate cross-validation results (PROC DISCRIM; SAS, 1989) and had no more variables than the number of individuals in the smallest sample. This protocol was designed to select conservative models that had a low number of variables and a high level of classification accuracy.

Using the best model as defined above, the following procedures were performed for each sex. The probability of correctly classifying each turtle relative to its predetermined geographic origin (CPhr, Mekg, and Java) was calculated using the cross-validation results of linear discriminant function analysis (PROC DISCRIM; SAS, 1989). Shell differentiation between geographic samples was graphically summarized by plotting canonical discriminant scores (PROC CANDISC; SAS, 1989). Specimens from geographic samples other than CPhr, Mekg, or Java were entered as test data and classified using the best models described above (PROC DISCRIM; SAS, 1989).

Since there is some question as to the status of *M. subtrijuga* populations on Java (ie. natural or introduced), one additional set of multivariate analyses was performed. Using the same shell character-sets as the best male and female models above, the probability of correctly classifying each turtle relative to its predetermined geographic origin was again calculated using the cross-validation results of linear discriminant function analysis (PROC DISCRIM; SAS, 1989). This time, however, models were based on the CPhr and Mekg samples only. Specimens from the Java sample were subsequently entered as test data and classified using these new models.

Geographic Variation – Head-Stripe Characters

Geographic variation of head-stripe characters was also examined using multivariate techniques. NasS, InfLor, and InfSW/HW (Figures 25-28; Table 2) comprised the entire data set. Preliminary analyses were conducted to determine the validity of combining sexes and life stages within each geographic sample. For each geographic sample (CPhr, Mekg, Java), specimens were assigned to the following five categories based on sex and size: males ≥ 100 mm CL; males < 100 mm CL; females ≥ 120 mm CL; females < 120 mm CL; juveniles of indeterminate sex < 70 mm CL. Using the three head-stripe characters above, the probability of correctly classifying each turtle relative to its predetermined sex/size category was calculated using the cross-validation results of linear discriminant function analysis (PROC DISCRIM; SAS, 1989).

Based on the results of the preliminary analyses above, all specimens within each geographic sample were combined regardless of sex or life stage. Using the three head-stripe characters above, the probability of correctly classifying each turtle relative to its predetermined geographic origin (CPhr, Mekg, and Java) was calculated using the cross-validation results of linear discriminant function analysis (PROC DISCRIM; SAS, 1989). Head-stripe differentiation between geographic samples was graphically summarized by plotting canonical discriminant scores (PROC CANDISC; SAS, 1989). Specimens from geographic samples other than CPhr, Mekg, or Java were entered as test data and classified using the head-stripe model described above (PROC DISCRIM; SAS, 1989). Individual means for each of the three head-stripe characters were compared using

Analysis of Variance (ANOVA) followed by the Ryan-Einot-Gabriel-Welsch Multiple Range Test (REGW) with $\alpha = 0.05$ (PROC ANOVA; SAS, 1989).

Results

Geographic Distribution

Distribution records are presented in Appendix D and Figure 29. Based on data from all available museum and literature records, *M. subtrijuga* has been found in the Chao Phraya and Mae Khlong basins of Thailand; portions of the lower Mekong basin in eastern Thailand, southern Laos, Cambodia, and southern Vietnam; coastal areas of southeast Thailand; the Malay Peninsula in peninsular Thailand and northern Malaysia; the Greater Sundan islands of Java and Sumatra; and markets in southern China and northern Vietnam.

Records from the Chao Phraya and Mae Khlong basins of Thailand are abundant. *Malayemys subtrijuga* has been recorded in the Chao Phraya basin from Chon Buri and Bangkok in the south, Chiang Mai in the north, Kamphaeng Phet Province in western Thailand, Phetchabun Province in the eastern portion of the basin, and many areas in between. In the Mae Khlong basin, *M. subtrijuga* has been recorded from Kanchanaburi, Phetchaburi, Ratchaburi, and Samut Songkhram provinces.

Records for *M. subtrijuga* are less abundant from the Mekg basin, but a substantial number still occur. *Malayemys subtrijuga* has been recorded from Amphoe Pak Thong Chai and Nakhon Ratchasima in the Thailand portion of the basin, Pakxe in southern Laos, and Siem Reap and Snoc Tru in Cambodia. Most records for the Mekong basin, however, come from southern Vietnam. *Malayemys subtrijuga* has been recorded

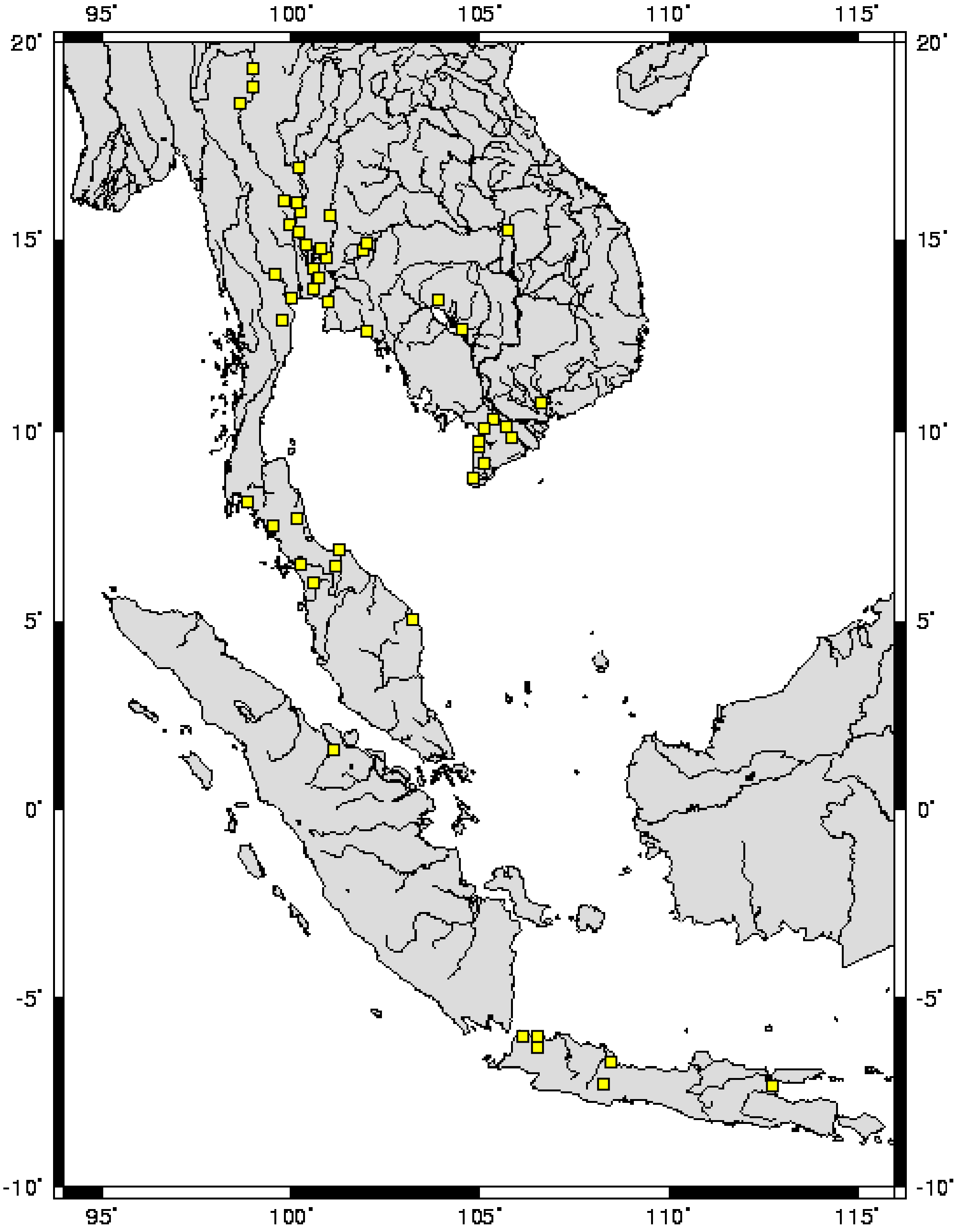

FIGURE 29. Distribution map for *Malayemys subtrijuga* based on available museum and literature records. See Appendix D for more detailed records.

from Ca Mau, Can Tho province, Ho Chi Minh City, Long Xuyen, Nam Can, Phung Hiep, Rach Gia, and the U Minh Region of Ca Mau and Rach Gia provinces.

Fewer records for *M. subtrijuga* are known from other portions of its mainland range. A single record exists for Laem Sing in the southeast coastal areas of Thailand. Records are known from the east coast *Melaleuca* swamps in Terengganu, Malaysia and from the northern Malaysian states of Kedah and Perlis. Several records also exist for peninsular Thailand including Krabi, Pattani, Phatthalung, Trang, and Yala.

Malayemys subtrijuga has also been recorded from several places in Indonesia. It has been found on Java in Banten, Cirebon, Depok, Jakarta, Surabaya, and Tasikmalaya. There is also a single record for *M. subtrijuga* from Duri, Sumatra and a few for “Sumatra” only.

In addition to these Southeast Asian records, *M. subtrijuga* has been found in several markets in China and northern Vietnam. These include records from Guangzhou (Farkas and Sasvári, 1992; Kuchling, 1995; Artner and Hofer, 2001) and Shenzhen (Kuchling, 1995) in southern China and those from Hanoi, Mon Cai, and Lang Son in northern Vietnam (Le Dien Duc and Broad, 1994, 1995).

Geographic Variation – Shell Characters

Geographic variation of shell characters was evident for female *M. subtrijuga*. The best model to classify female turtles relative to predetermined geographic origin correctly classified 88% of all individuals and contained seven of the original 29 shell character ratios. These were Vert5W/CL, PPLW/CL, CW/CL, Pleu1W/CL, Vert3L/CL, AnL/CL, and HumL/CL (see Table 2 for character abbreviations). Mean values for these seven shell character ratios are presented in Table 16. Using the seven variable model, cross-validation results of linear discriminant function analysis correctly classified 89.47% of females from CPhr, 90.91% of females from Java, and 80.00% of females from Mekg (Table 17). Most misclassifications for females (80%) were CPhr individuals classified as Mekg and vice versa (Table 17). A bivariate plot (CV1 vs. CV2) of canonical discriminant scores for females also demonstrated shell differentiation between geographic samples (Fig. 30). Three clusters representing geographic samples were apparent on the plot, with some overlap between the CPhr and Mekg clusters.

Geographic variation of shell characters was also evident for male *M. subtrijuga*. The best model to classify male turtles relative to predetermined geographic origin correctly classified 80% of all individuals and contained five of the original 29 shell character ratios. These were PPLL/CL, AnL/CL, AnW/CL, Vert1L/CL, and Vert5L/CL (see Table 2 for character abbreviations). Mean values for these five shell character ratios are presented in Table 18. Using the five variable model, cross-validation results of linear discriminant function analysis correctly classified 75.86% of males from CPhr, 81.82% of males from Java, and 88.89% of males from Mekg (Table 19). Most misclassifications for males (70%) were CPhr individuals classified as Mekg and vice versa (Table 19). A bivariate plot (CV1 vs. CV2) of canonical discriminant scores for males demonstrated some shell differentiation between geographic samples (Fig. 31). Three clusters representing geographic samples were present on the plot, with some overlap between the CPhr and Mekg clusters.

TABLE 16. Shell character ratios – mean ± 1 SE, (range), and [n] – used in discriminant function analysis to classify females from different geographic samples. Character abbreviations follow Table 2.

Character	CPhr	Java	Mekg
Vert5W/CL	0.26 ± 0.005 (0.22-0.31) [23]	0.25 ± 0.007 (0.22-0.29) [11]	0.28 ± 0.006 (0.24-0.33) [13]
PPLW/CL	0.45 ± 0.005 (0.40-0.49) [19]	0.46 ± 0.004 (0.45-0.48) [13]	0.44 ± 0.005 (0.39-0.46) [14]
CW/CL	0.76 ± 0.006 (0.70-0.82) [23]	0.75 ± 0.007 (0.71-0.80) [14]	0.75 ± 0.007 (0.71-0.79) [16]
Pleu1W/CL	0.27 ± 0.003 (0.24-0.30) [23]	0.28 ± 0.002 (0.26-0.29) [14]	0.28 ± 0.004 (0.25-0.31) [13]
Vert3L/CL	0.18 ± 0.003 (0.15-0.21) [23]	0.16 ± 0.003 (0.14-0.18) [12]	0.17 ± 0.004 (0.15-0.20) [13]
AnL/CL	0.14 ± 0.002 (0.12-0.16) [19]	0.12 ± 0.004 (0.10-0.15) [14]	0.12 ± 0.005 (0.09-0.15) [14]
HumL/CL	0.12 ± 0.003 (0.10-0.15) [19]	0.11 ± 0.004 (0.08-0.14) [14]	0.11 ± 0.006 (0.04-0.14) [14]

TABLE 17. Cross-validation results for female *Malayemys subtrijuga* based on discriminant analysis of shell characters. Percentages in parentheses. Watershed abbreviations follow Chapter 3.

	Group classification			
Actual group	CPhr	Java	Mekg	Total
CPhr	17 (89.47)	0 (0.00)	2 (10.53)	19
Java	0 (0.00)	10 (90.91)	1 (9.09)	11
Mekg	2 (20.00)	0 (0.00)	8 (80.00)	10

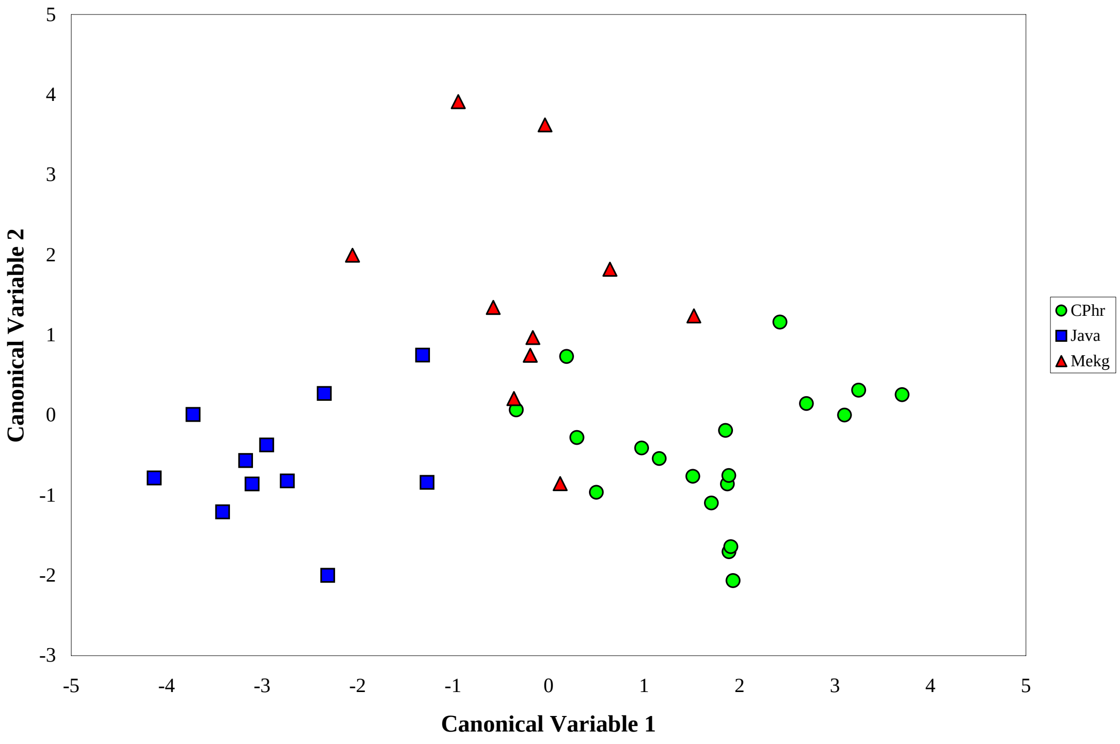

FIGURE 30. Plot of the first two canonical axes for female *Malayemys subtrijuga* based on discriminant function analysis of seven shell character ratios.

TABLE 18. Shell character ratios – mean ± 1 SE, (range), and [n] – used in discriminant function analysis to classify males from different geographic samples. Character abbreviations follow Table 2.

Character	CPhr	Java	Mekg
PPLL/CL	0.52 ± 0.003 (0.50-0.55) [30]	0.49 ± 0.005 (0.46-0.53) [14]	0.50 ± 0.003 (0.48-0.51) [9]
AnL/CL	0.12 ± 0.002 (0.08-0.13) [30]	0.10 ± 0.002 (0.08-0.11) [14]	0.12 ± 0.004 (0.10-0.13) [9]
AnW/CL	0.14 ± 0.001 (0.13-0.16) [30]	0.15 ± 0.002 (0.14-0.16) [14]	0.14 ± 0.002 (0.13-0.15) [9]
Vert1L/CL	0.20 ± 0.002 (0.19-0.22) [31]	0.20 ± 0.003 (0.18-0.21) [13]	0.21 ± 0.004 (0.19-0.23) [9]
Vert5L/CL	0.21 ± 0.003 (0.16-0.25) [31]	0.22 ± 0.003 (0.20-0.24) [12]	0.22 ± 0.005 (0.20-0.24) [9]

TABLE 19. Cross-validation results for male *Malayemys subtrijuga* based on discriminant analysis of shell characters. Percentages in parentheses. Watershed abbreviations follow Chapter 3.

	Group classification			
Actual group	CPhr	Java	Mekg	Total
CPhr	22 (75.86)	1 (3.45)	6 (20.69)	29
Java	1 (9.09)	9 (81.82)	1 (9.09)	11
Mekg	1 (11.11)	0 (0.00)	8 (88.89)	9

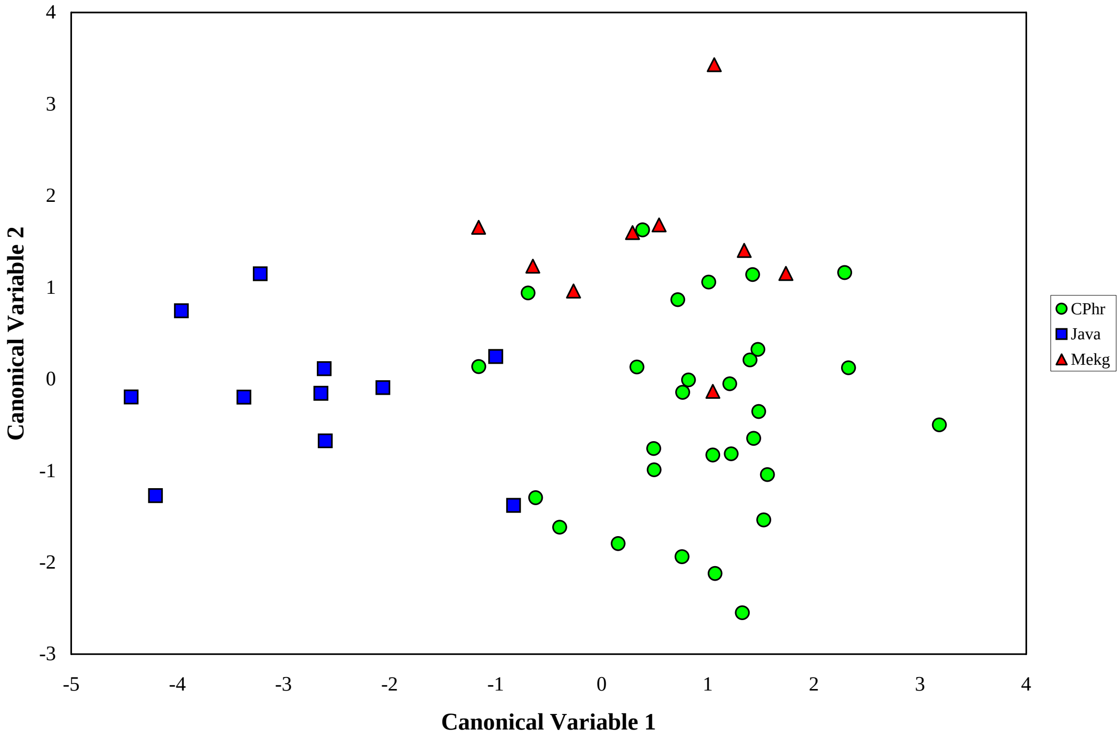

FIGURE 31. Plot of the first two canonical axes for male *Malayemys subtrijuga* based on discriminant function analysis of five shell character ratios.

When specimens from geographic samples other than CPhr, Mekg, and Java were entered as test data in the shell character models (based on CPhr, Mekg, and Java), female *M*. *subtrijuga* from Maly and SECos were classified as CPhr, whereas one from Sumt was classified as Mekg (Table 20). One male *M*. *subtrijuga* from Maly was classified as CPhr, whereas those from Sumt were classified as both CPhr (2 specimens) and Mekg (1 specimen) (Table 21).

When specimens from the Java sample were entered as test data in the shell character models based on CPhr and Mekg only, all Java females (11/11) and 91% (10/11) of Java males were classified as Mekg.

Geographic Variation – Head-Stripe Characters

For geographic variation of head-stripe characters, preliminary analyses verified the validity of combining sexes and life stages within each geographic sample. Within each sample, the cross-validation results of linear discriminant function analysis could not reliably differentiate between the sex/size categories. In fact, there was an extremely low degree of classification accuracy with respect to predetermined sex/size category. Overall classification accuracy was 27% for CPhr, 39% for Java, and 20% for Mekg. The obvious confusion between sex/size categories supported the decision to combine all specimens in each sample regardless of sex or life stage. Combining sexes and size created larger sample sizes and more robust statistical conclusions.

Geographic variation of head-stripe characters was clearly evident in *M*. *subtrijuga*. Using the three character head-stripe model, cross-validation results of linear discriminant function analysis correctly classified 97.73% of turtles from CPhr, 36.36%

TABLE 20. Female *Malayemys subtrijuga* entered as test data in the female shell character model. All specimens have geographic origin other than CPhr, Java, and Mekg. Numbers in parentheses indicate number of specimens. See Appendix D for more detailed information regarding specimens.

Geographic Origin	Classification	Museum Number
Maly (1)	CPhr	USNM 23111
SECos (1)	CPhr	USNM 72212
Sumt (1)	Mekg	NMW 29376.2

TABLE 21. Male *Malayemys subtrijuga* entered as test data in the male shell character model. All specimens have geographic origin other than CPhr, Java, and Mekg. Numbers in parentheses indicate number of specimens. See Appendix D for more detailed information regarding specimens.

Geographic Origin	Classification	Museum Number
Maly (1)	CPhr	BMNH 1903.4131
Sumt (2)	CPhr	NMW 29376.1, 29376.4
Sumt (1)	Mekg	NMW 29376.3

of turtles from Java, and 76.00% of turtles from Mekg (Table 22). The majority of misclassifications here (83%) were Java individuals classified as Mekg and vice versa (Table 22). The CPhr sample formed a clearly distinct group with considerable confusion between the Java and Mekg groups. This observation was reinforced by the bivariate plot (CV1 vs. CV2) of canonical discriminant scores (Fig. 32). CPhr formed a distinct cluster that had almost no overlap with Java or Mekg, wheras the Java and Mekg clusters strongly overlapped.

When specimens from geographic samples other than CPhr, Mekg, or Java were entered as test data in the head-stripe model, all specimens from Maly, MKhl, and SECos were classified as CPhr. Specimens from Sumt were classified as both CPhr (2 specimens) and Mekg (2 specimens) (Table 23).

An examination of individual means for the head-stripe characters also demonstrated the distinctiveness of CPhr (Figs. 33-35; Table 24). CPhr had much lower mean values for NasS (3.1 ± 0.10, mean ± 1 SE) and InfLor (1.5 ± 0.07) and a much higher mean value for InfSW/HW (0.11 ± 0.002) than either Java (NasS = 5.6 ± 0.15; InfLor = 3.5 ± 0.13; InfSW/HW = 0.05 ± 0.003) or Mekg (NasS = 6.2 ± 0.19; InfLor = 3.6 ± 0.14; InfSW/HW = 0.04 ± 0.004) (Fig. 33-35; Table 24). Java and Mekg, however, had very similar mean values for all three head-stripe characters (Figs. 33-35; Table 24). The mean value of NasS for CPhr was significantly different ($p < 0.05$) than the mean values of both Java and Mekg, whereas mean values of NasS were not significantly different between Java and Mekg (ANOVA followed by REGW; Table 24). For both

TABLE 22. Cross-validation results for *Malayemys subtrijuga* based on discriminant analysis of head-stripe characters. Percentages in parentheses. Watershed abbreviations follow Chapter 3.

Actual group	Group classification			
	CPhr	Java	Mekg	Total
CPhr	86 (97.73)	2 (2.27)	0 (0.00)	88
Java	2 (6.06)	12 (36.36)	19 (57.58)	33
Mekg	1 (4.00)	5 (20.00)	19 (76.00)	25

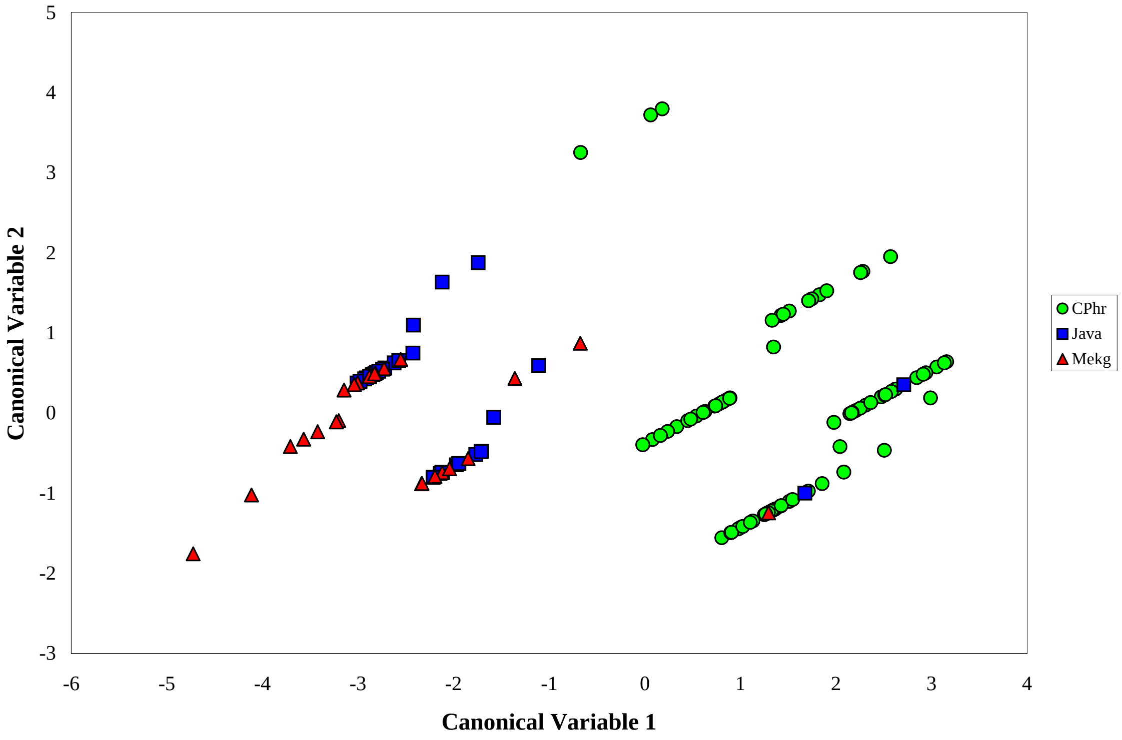

FIGURE 32. Plot of the first two canonical axes for all *Malayemys subtrijuga* based on discriminant function analysis of three head-stripe characters.

TABLE 23. *Malayemys subtrijuga* entered as test data in the head-stripe model. All specimens have geographic origin other than CPhr, Java, and Mekg. Numbers in parentheses indicate number of specimens. See Appendix D for more detailed information regarding specimens.

Geographic Origin	Classification	Museum Number
Maly (6)	CPhr	BMNH 1903.4131 KUZ 36800-801 UF 85286 USNM 22951, 23111
Mkhl (11)	CPhr	CUB 1999.010503-506 CUB 1999.010508-514
SECos (1)	CPhr	USNM 72212
Sumt (2)	CPhr	NMW 29376.3-29376.4
Sumt (2)	Mekg	NMW 29376.1-29376.2

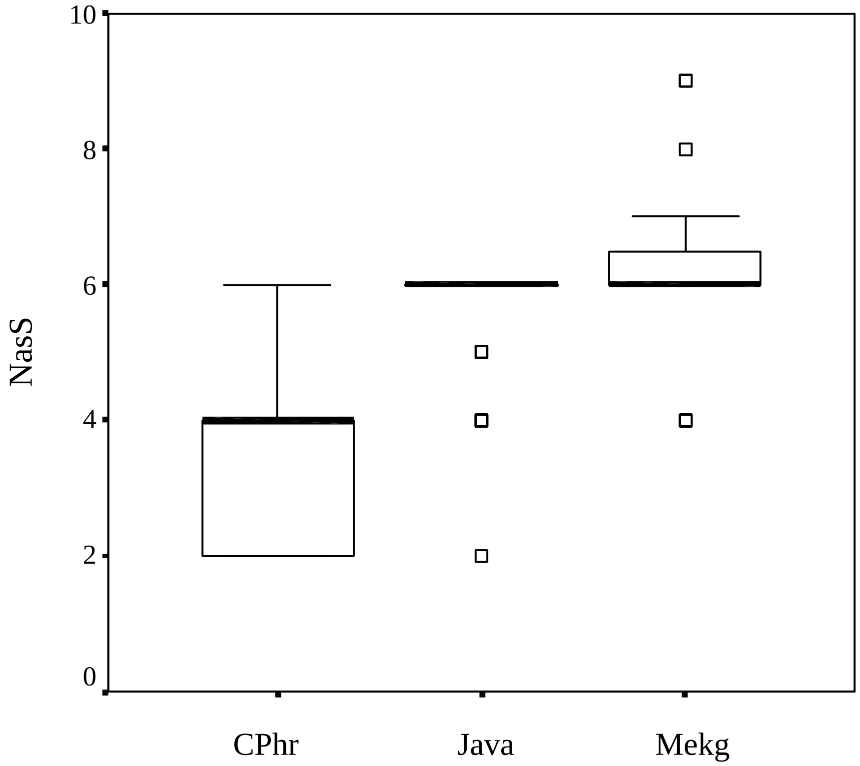

FIGURE 33. Summary plot of NasS for *Malayemys subtrijuga* based on median, quartiles, and extreme values. Boxes represent interquartile ranges and dark lines indicate medians. Whiskers extend to highest and lowest values, excluding outliers. Squares are values more than 3 box lengths from the upper or lower edge of box.

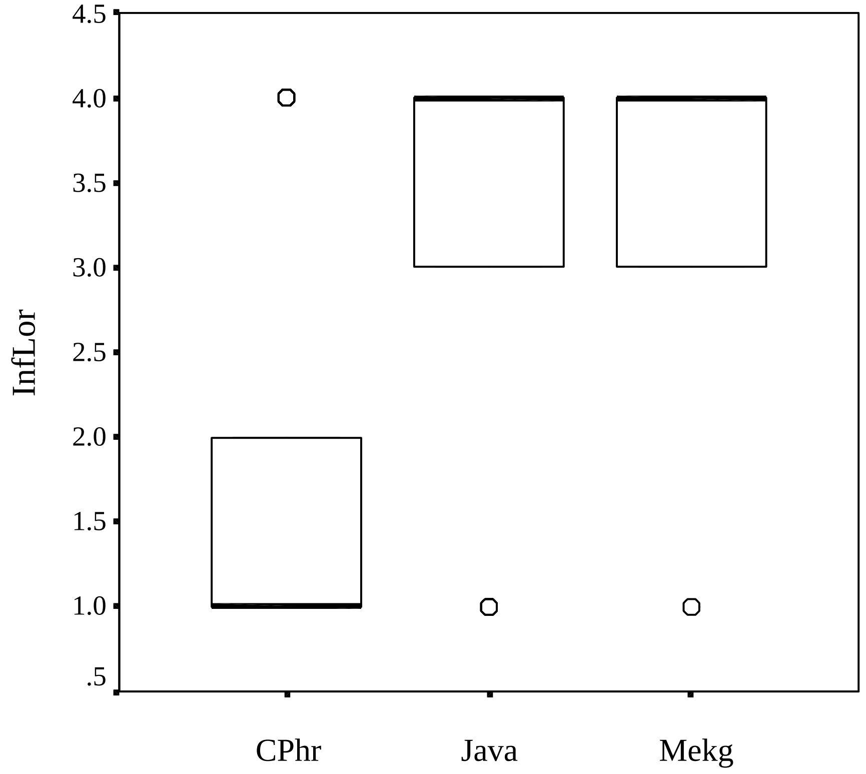

FIGURE 34. Summary plot of InfLor for *Malayemys subtrijuga* based on median, quartiles, and extreme values. Boxes represent interquartile ranges and dark lines indicate medians. Whiskers extend to highest and lowest values, excluding outliers. Circles are values between 1.5 and 3 box lengths from the upper or lower edge of box.

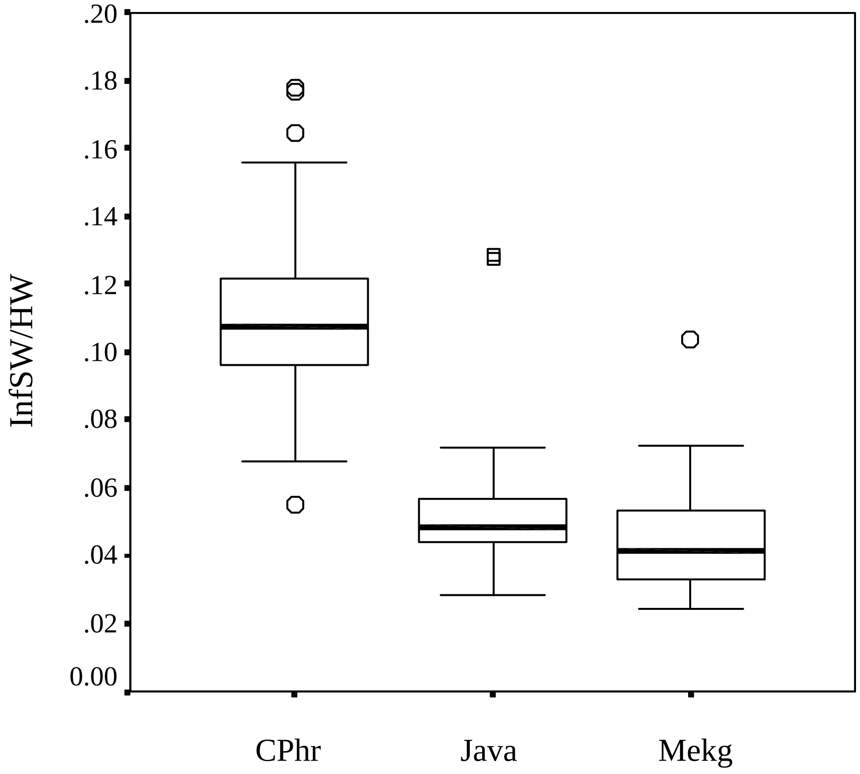

FIGURE 35. Summary plot of InfSW/HW for *Malayemys subtrijuga* based on median, quartiles, and extreme values. Boxes represent interquartile ranges and dark lines indicate medians. Whiskers extend to highest and lowest values, excluding outliers. Circles are cases with values between 1.5 and 3 box lengths from the upper or lower edge of the box. Squares are values more than 3 box lengths from the upper or lower edge of box.

TABLE 24. Head-stripe characters – mean ± 1 SE, (range), and [n] – used in analyses. For each character, means with different superscripts are significantly different ($p < 0.05$). Character abbreviations follow Table 2.

Character	CPhr	Java	Mekg
NasS	3.1 ± 0.10^{a} (2-6) [98]	5.6 ± 0.15^{b} (2-6) [37]	6.2 ± 0.19^{c} (4-9) [35]
InfLor	1.5 ± 0.07^{a} (1-4) [94]	3.5 ± 0.13^{b} (1-4) [35]	3.6 ± 0.14^{b} (1-4) [25]
InfSW/HW	0.11 ± 0.002^{a} (0.06-0.18) [88]	0.05 ± 0.003^{b} (0.03-0.13) [33]	0.04 ± 0.004^{c} (0.02-0.10) [26]

InfLor and InfSW/HW, all pairwise comparisons of mean values were significantly different ($p < 0.05$; ANOVA follwed by REGW; Table 24).

Finally, I had an opportunity to examine photographs of *M*. *subtrijuga* from Siem Reap, Cambodia (Kurt Buhlmann, pers. comm.; Peter Pritchard, pers. comm). All animals for which data could be recovered had six nasal stripes (7 specimens), an InfLor value of ≥ 3 (5 specimens), and an infraorbital stripe that was relatively narrow at the loreal seam (5 specimens). This corresponds to the head-stripe morphology of other specimens from Mekg.

Discussion

A few issues need to be discussed with regards to the observed distribution of *M*. *subtrijuga* (Appendix D; Fig. 29). I will dispose of two simple issues first and then move to a more complex one. Live *M*. *subtrijuga* have frequently been offered for sale in southern Chinese and northern Vietnamese markets. These areas are far outside the suspected natural range of *M*. *subtrijuga* and any individuals found there were most certainly imported (Farkas and Sasvári, 1992; Kuchling, 1995; Artner and Hofer, 2001; van Dijk and Thirakhupt, in press).

The few records that exist for Sumatra are also most likely based on imported specimens. Several herpetofaunal surveys have failed to locate *M*. *subtrijuga* on Sumatra (de Rooij, 1915; van de Bunt, 1990; Fritz and Gaulke, 1997; Gaulke et al., 1998; Shepherd, 2000). During Shepherd’s (2000) survey, people at all levels of the turtle trade were shown pictures of *M*. *subtrijuga* and questioned about its presence on Sumatra. None of the traders had ever seen *M*. *subtrijuga*. Similarly, *M*. *subtrijuga* was the only turtle, included in a list of potential Sumatran species, that did not have a local Sumatran name (Shepherd, 2000). My own results suggest that the specimens of *M. subtrijuga* from Sumatra were of mixed origin and were, therefore, probably introduced (Tables 20, 21, and 23). Based on the scarcity of records from Sumatra and the results of this study and the above surveys, it is clear that *M. subtrijuga* does not occur naturally on Sumatra (Fritz and Gaulke, 1997; Shepherd, 2000; van Dijk and Thirakhupt, in press).

The presence of *M. subtrijuga* on Java is another issue which needs to be discussed. *Malayemys subtrijuga* has been known from Java for almost 200 years (Temminck and Schlegel, 1835; Schlegel and Müller, 1844; Hoogmoed, 1982). In fact, the syntypes of *M. subtrijuga* were collected in Java's Bantam Province (Temminck and Schlegel, 1835; Schlegel and Müller, 1844). There are several lines of evidence, however, that lead me to conclude that *M. subtrijuga* is not native to Java. These come from distributional patterns on Java, the current status of populations of *M. subtrijuga* on Java, the history of human activities in Southeast Asia, and zoogeographic patterns of turtles and other vertebrates.

I will briefly describe the first three evidences and then go into more detail regarding zoogeography. First, the known distribution of *M. subtrijuga* on Java is primarily limited to port cities on the northern coast (Fig. 29). This type of distribution would be expected for an introduced species (Inger, 1966). Second, recent reports have indicated that populations of *M. subtrijuga* on Java are dwindling or extinct (Samedi and Iskandar, 2000; van Dijk and Thirakhupt, in press; Peter C. H. Pritchard, pers. comm.). This may be due in part to the small size of introduced founding populations. Third, history indicates that humans have been moving between Java and the Southeast Asian mainland for many hundreds of years (Schwartzberg and Bajpai, 1992). Since *M. subtrijuga* is commonly used for food (van Dijk and Palasuwan, 2000; van Dijk and Thirakhupt, in press) and religious practices (van Dijk and Palasuwan, 2000; Hendrie, 2000; van dijk and Thirakhupt, in press), it is conceivable that it was brought to Java for these reasons.

The most compelling reason to conclude that *M. subtrijuga* was introduced to Java, however, comes from zoogeography. The distribution of *M. subtrijuga* is curious in that it has been recorded from Java and mainland Southeast Asia but not the intervening areas. Its absence from Sumatra, Borneo, and southern Malaysia suggest a zoogeographical pattern that is inconsistent with that of other vertebrates. Dammerman (1929), in a still pertinent analysis of Javan zoogeography, found only a very small percentage of animals (<10%) from Java and the Southeast Asian mainland, but not the intervening areas. These included only 3% of reptiles and only one species each for amphibians and fish. Those species which did display this curious distribution were typically birds, flying mammals, or human commensals. Zoogeographic studies of amphibians (Inger, 1999), mammals (Lekagul and McNeely, 1977; Corbet and Hill, 1992), and reptiles (Lovich, 1994) yielded similar results.

Analyses of ancient river systems on the Sunda Shelf explain why the curious distribution discussed above is unlikely for *M. subtrijuga*. In the middle Pleistocene, during periods of maximum glaciation, sea levels dropped 120 m in this region (Heaney, 1991; Inger, 1999; Lovich, 1994). During this time, the Sunda Shelf was a vast lowland forest dissected by several major river systems. These river systems served as dispersal corridors for many turtle species (Lovich, 1994; van Dijk, pers. comm.). The North Sunda River linked the east coast of Sumatra and west coast of Borneo to West Malaysia. The East Sunda River linked southern Sumatra with Java and southern Borneo (Burridge, 1992; Voris, 2000). In essence, *M*. *subtrijuga* could not have reached Java from the Southeast Asian mainland without passing through either Borneo or Sumatra. This fact along with zoogeographical analyses like the ones above have led several authors to conclude that *M*. *subtrijuga* was probably introduced to Java (Dammerman, 1929; Ernst et al., 2000; van Dijk and Thirakhupt, in press). I concur and will demonstrate below that populations of *M*. *subtrijuga* on Java were derived primarily from the Mekong River Basin.

At this point, I will discuss the natural range of *M. subtrijuga* and how it relates to patterns of zoogeography in Southeast Asia. *Malayemys subtrijuga* occurs naturally in lowland areas of the Chao Phraya and Mae Khlong basins of Thailand; lowland areas of the lower Mekong basin in eastern Thailand, southern Laos, Cambodia, and southern Vietnam; and southward along the Malay Peninsula in lowland areas of peninsular Thailand and the northern states of Malaysia (Appendix D; Fig. 29).

Once Java is removed from the natural distribution of this species, it becomes clear that *M*. *subtrijuga* is one of the many Indochinese endemics whose populations are primarily found north of the Isthmus of Kra. Lovich’s (1994) analysis of the zoogeography of Southeast Asian turtles suggested that less than 50% of Indochinese turtles are found south of the Isthmus of Kra. The Isthmus of Kra has acted as an effective barrier to migration for many turtle species because it coincidentally lies at the boundary of two distinct climatic regions. To the south of Kra, aseasonal conditions occur with year round rain, tropical evergreen rainforests, and higher temperatures. To the north of Kra, seasonal monsoons occur with mainly deciduous forests and lower temperatures (Lovich, 1994; Rainboth, 1996; Inger, 1966, 1999). Because of the role that rainfall plays in faunal distributions, the Isthmus of Kra is a more effective barrier for fauna moving north (from Sundaic to Indochinese region) than for those moving south (Inger, 1966).

Lovich's (1994) analysis suggested that Southeast Asia consists of two primary faunal regions, a mainland Indochinese region and a Sundaic region (Malay Peninsula, Sumatra, Borneo, and Java). The existence of distinct Indochinese and Sundaic faunas is also supported by the distribution patterns of fish (Kottelat, 1989; Rainboth, 1996), amphibians (Inger, 1966, 1999), and mammals (Lekagul and McNeely, 1977; Corbet and Hill, 1992). Animals that do not occur south of the Isthmus of Kra, like *M. subtrijuga*, may have been poor dispersers, may have arrived at the Sunda Shelf too late (i.e. after the last exposure in the late Pleistocene), or may have gotten caught on the shelf during one of the many times sea levels rose during the Pleistocene (Lovich, 1994).

Based on the results of this study, I conclude that two distinct groups of *Malayemys* occur on mainland Southeast Asia. Populations from central and southern Thailand (CPhr, MKhl, SECos, Maly) differ significantly and consistently from those in eastern Thailand, southern Laos, Cambodia, and southern Vietnam (Mekg). These groups were clearly separated by multivariate analyses of both shell (Table 16-19; Fig.

30-31) and head-stripe characters (Table 22, 24; Fig. 32). *Malayemys* from CPhr, MKhl, SECos, and Maly have four or fewer nasal stripes and an infraorbital stripe that is relatively wide at the loreal seam and does not extend or extends only slightly superior to the loreal seam (Table 24; Fig. 33-35). Conversely, populations from Mekg have six or more nasal stripes and an infraorbital stripe that is relatively narrow at the loreal seam, extends completely superior to the loreal seam, and usually joins the supraorbital stripe (Table 24; Fig. 33-35).

The observed differences between these two groups are consistent with the topography of the region and the poor dispersal abilities of *Malayemys*. The Southeast Asian mainland is a topographically complex region with mountain chains, hills, and lowlands interspersed throughout. The topography of this area was formed in response to the subduction of the Indian subcontinent under the Asian mainland (Lekagul and McNeely, 1977; van Dijk, 1997). This created the Himalayas at the main collision front and buckled other areas around its edges. As a result, the mountain and hill ranges in mainland Southeast Asia stretch in a general north-south direction (Lekagul and McNeely, 1977; van Dijk, 1997). The two distinct groups of *Malayemys* correspond with separate lowland areas that are broadly separated at the boundary between the Chao Phraya and Mekong river basins.

Because of the poor dispersal abilities of *Malayemys*, the boundary between the Chao Phraya and Mekong basins is sufficient to isolate these two groups. Turtles of the genus *Malayemys* are slow-moving, poor-swimming, bottom-feeders that exclusively inhabits lowland freshwater areas. Thirakhupt and van Dijk (1994) clearly stated that

Malayemys is restricted by hilly areas and associated watershed divides and is unable to ascend streams. Similarly, despite intensive searches, *Malayemys* could not be found in any stream in hilly areas (van Dijk and Thirakhupt, in press). The complex topography of mainland Southeast Asia and the poor dispersal abilities of *Malayemys* have effectively isolated these two groups, thereby restricting gene flow between them.

The genus *Malayemys* most likely evolved in Southeast Asia. The ever-changing topography of this region eventually led to the isolation of the two groups of *Malayemys* in separate river basins. The specific events that led to this isolation are unclear. One possible explanation, however, may be found in the reconstruction of former river courses. Gregory (1925) hypothesized that the Upper Mekong River was once connected to the Chao Phraya River through the present-day Mae Nam Yom. This hypothesis is supported by the high degree of ovelap in fish faunas between the modern Chao Phraya and Mekong basins (Kottelat, 1989). This connection may have joined the two groups of *Malayemys*, and its severing may have been the final step in their isolation. Once isolated, divergence probably occurred via natural selection or genetic drift.

The question now arises as to the taxonomic status of these two groups. My goal in this study was to discern evolutionarily independent but genetically cohesive units and to recognize them as taxonomic species (Good and Wake, 1993). There is sufficient evidence (topographical, ecological, and geological) to conclude that that the two groups of *Malayemys* discovered during this study are allopatrically distributed, and that the likelihood of genetic interchange between them is low. Since these groups are currently allopatric, they are, by definition, independently evolving entities that should be afforded full species status (Simpson, 1961; Wiley, 1978, 1980; Frost and Hillis, 1990). These groups may have been geographically isolated for only a short time, and they might resume interbreeding if they come into contact in the future. Since knowledge of future events is impossible, however, inferences about past events must suffice (Good and Wake, 1993). Furthermore, it is assumed that the longer these two groups are isolated and the more differences that evolve between them, the more likely it is that they will remain reproductively independent on recontact (Good and Wake, 1993).

For conservation purposes, it is better to overestimate biological diversity in taxonomy than to underestimate it (Frost and Hillis, 1990; Good and Wake, 1993). This approach is especially crucial in Southeast Asia, where turtles are under tremendous pressure from overcollection and habitat destruction, because decisions about habitat conservation are often made on the basis of biological diversity (Wilson, 1988; Good and Wake, 1993). Similarly, overexploited populations rarely receive legal protection unless they have full species status (Avise, 1989; Iverson and McCord, 1997; Lovich and Gibbons, 1997). I am not advocating a “political species concept” (Good and Wake, 1993), but simply stating that underestimating species diversity does a disservice to both threatened populations and our understanding of biodiversity as a whole.

A valid species name is available for *Malayemys* from the Mekong River Basin. The syntypes for *M. subtrijuga* were collected on Java and described as *Emys subtrijuga* by Schlegel and Müller (1844) (Appendix D). Evidence from various sources, however, suggests that *Malayemys* is not native to Java. The results of this study suggest that *Malayemys* from Java are morphologically identical to those from the Mekong River

Basin and were probably introduced to Java from that region (Table 22; Fig. 32-35). I have examined the type specimens of *M. subtrijuga* (RMNH 6082, 6084, 6085) and conclude that they are representative of *Malayemys* from the Mekong basin. All three specimens have six nasal stripes, an infraorbital stripe that is relatively narrow at the loreal seam (InfSW/HW = 0.0362, 0.0459, 0.0462), and an infraorbital stripe that extends completely superior to the loreal seam and joins the supraorbital stripe (InfLor = 4). In addition, RMNH 6082 and 6085 were classified as Mekg by linear discriminant function analysis of both shell and head-stripe characters (Table 22; Fig. 32). RMNH 6084 was classified as Mekg by linear discriminant function analysis of head-stripe characters (Table 22; Fig. 32), but was not classified at all by the shell character model because of missing data. For the above reasons, *Malayemys* from the Mekong River Basin will retain the name *Malayemys subtrijuga* (Schlegel and Müller, 1844) (Fig. 36).

A valid species name is also available for *Malayemys* inhabiting the Chao Phraya and Mae Khlong basins of central Thailand, the coastal areas of southeastern Thailand, and the Malay Peninsula in southern Thailand and northern Malaysia. Gray (1859) described two specimens from Thailand as *Geoclemys macrocephala*. He gave a lengthy description that included the following diagnostic character for this group: “...two close streaks under the nostrils to the middle of the upper jaw...” (Gray, 1859:479). This corresponds with two nasal stripes from the current study. Examination of the accompanying Plate XXI reveals that *Geoclemys macrocephala* also has a relatively wide infraorbital stripe that does not extend superior to the loreal seam (Fig. 2). The syntypes for this species (BMNH 59.7.8.4-.5) were examined, and it is concluded that they are

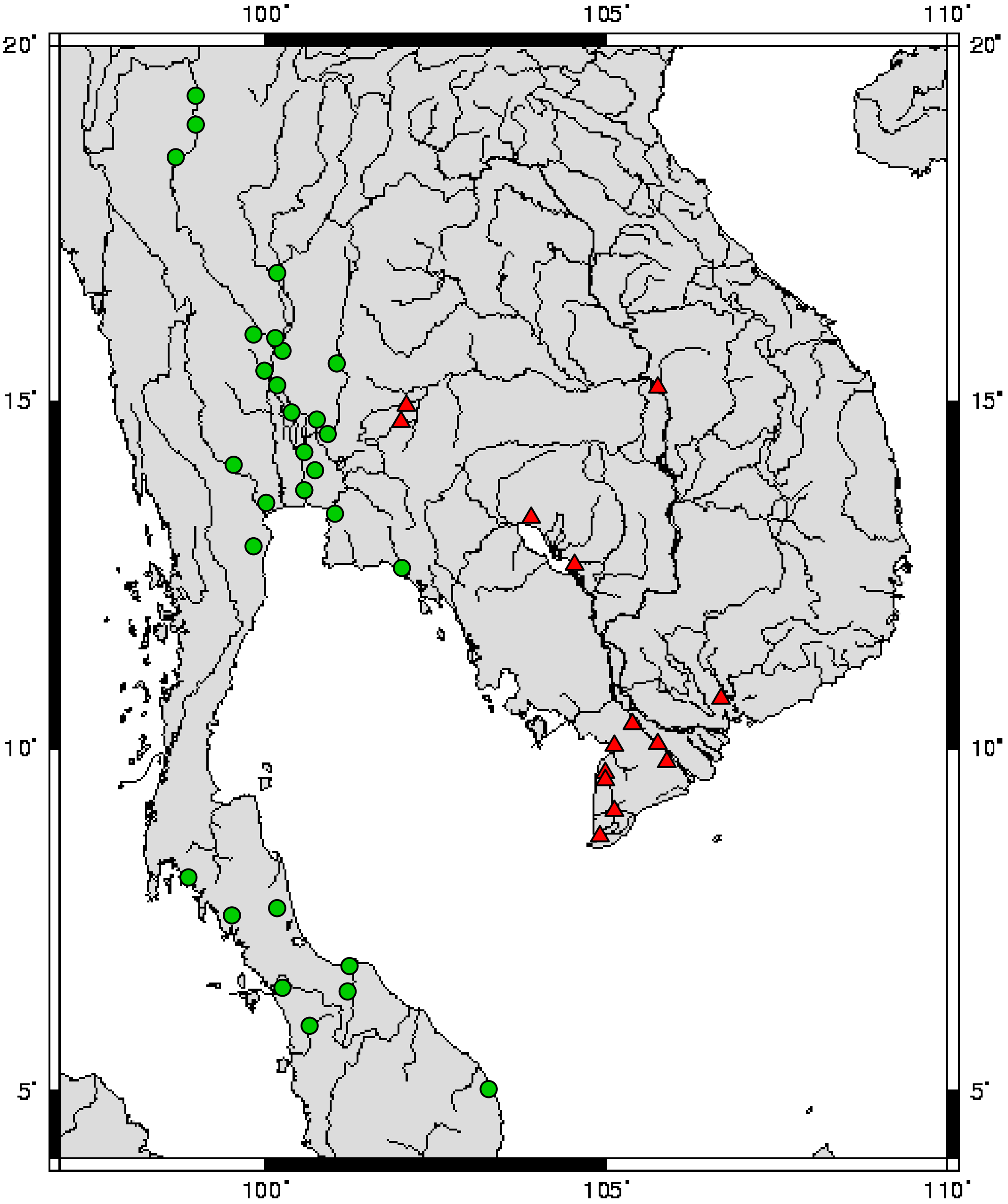

FIGURE 36. Distribution map for *Malayemys subtrijuga* (Schlegel and Müller, 1844) (triangles) and *Malayemys macrocephala* (Gray, 1859) (circles) based on available museum and literature records. See Appendix D for more detailed records.

representative of *Malayemys* from CPhr, MKhl, SECos, and Maly. Both specimens have two nasal stripes, an infraorbital stripe that is relatively wide at the loreal seam (InfSW/HW = 0.0684, 0.0817), and an infraorbital stripe that does not extend superior to the loreal seam (InfLor = 1). In addition, both specimens were classified as CPhr by linear discriminant function analysis of head-stripe characters (Table 22; Fig. 32). BMNH 59.7.8.5 was also classified as CPhr by linear discriminant function analysis of shell characters (Table 17; Fig. 30). For the above reasons, *Malayemys* from CPhr, MKhl, SECos, and Maly are assigned the name *Malayemys macrocephala* (Gray, 1859) (Fig. 36).

Populations of *Malayemys macrocephala* (Gray, 1859) seem to be substantial in central Thailand (van Dijk and Thirakhupt, in press). This species is found in considerable numbers in both the Chao Phraya (van Dijk and Thirakhupt, in press) and Mae Khlong (Thirakhupt and van Dijk, 1994; van Dijk and Thirakhupt, in press) river basins. The IUCN/SSC Tortoise and Freshwater Turtle Specialist Group (IUCN TFTSG) and the Asian Turtle Trade Working Group (ATTWG) (2000) reported its status as not uncommon in Thailand. van Dijk and Palasuwan (2000) reported *Malayemys* populations as stable or in modest decline in Thailand. *Malayemys macrocephala* are less abundant in the southern part of their distribution (van Dijk and Thirakhupt, in press). Only small numbers of this species were found in peninsular Thailand markets during the 1990s (van Dijk and Thirakhupt, in press). In Malaysia, *M. macrocephala* is restricted to the northern states. It is commonly caught in rice fields in Perlis and has been captured in *Melaleuca* swamps on the eastern coast of Terengganu. The only protected habitat of this type in the entire country is at Jambu Bongkok Recreational Forest in Terengganu (Sharma and Tisen, 2000). E. O. Moll found only three *Malayemys* specimens in northern Malaysian markets (van Dijk and Thirakhupt, in press). The IUCN TFTSG and ATTWG (2000) report populations as small and restricted in Malaysia.

Malayemys subtrijuga (Schlegel and Müller, 1844) is vulnerable in Laos, Cambodia, and Vietnam (IUCN TFTSG and ATTWG, 2000). Populations in Laos continue to survive in appropriate habitat but are probably quite reduced. Despite its reduced numbers, *M. subtrijuga* remains one of the most common species in Laos (Stuart amd Timmins, 2000). *Malayemys subtrijuga* is probably the most abundant turtle species in Cambodia, as well (Touch Seang Tana et al., 2000). Trade in this species is high in Cambodia (Touch Seang Tana et al., 2000) and observations of numerous market animals uniformly close to the maximum size suggest that a previously untouched population is now being heavily exploited (van Dijk and Thirakhupt, in press; Peter C. H. Pritchard, pers. comm.). Population sizes in southern Vietnam are considered to be very low (Touch Seang Tana et al., 2000). This is due to the severe reduction of natural habitats and heavy collection for the wildlife trade (Touch Seang Tana et al., 2000). The status of *M. subtrijuga* populations in eastern Thailand is unknown.

All populations of *Malayemys* in Southeast Asia are currently listed as vulnerable (VU A1d+2d) in the 2000 IUCN Red List of Threatened Species but are not listed in CITES. On a regional level, *M. macrocephala* (Gray, 1859) in Thailand and Malaysia are fairly well protected. In Thailand, they are protected by the Wild Animals Reservation and Protection Act B.E. 2535 (revised in 1992) which prohibits all trade in this species, but does allow some local exploitation. They are also potentially protected by numerous wildlife sanctuaries, national parks, and non-hunting areas, although verification of their presence in many of these areas is still needed (Thirakhupt and van Dijk, 1994; van Dijk and Palasuwan, 2000; van Dijk and Thirakhupt, in press). Enforcement of these protections is generally good in Thailand (van Dijk and Palasuwan, 2000). On the national level in Malaysia, the Fisheries Act of 1985 includes protection for turtle species (Sharma and Tisen, 2000). There are also customs laws (Customs Order 88) prohibiting imports and exports of turtles, but they are open to various interpretations because of unclear language (Sharma and Tisen, 2000). Because of the way these Malaysian laws are written, however, the burden of protection lies with the states. Perlis has no legislation whatsoever protecting turtles. Terrengganu (1951) and Kedah (1972) have enacted legal measures for turtle conservation, but these are based on local turtle names that result in confusion and various misinterpretations (Sharma and Tisen, 2000).

Malayemys subtrijuga (Schlegel and Müller, 1844) in the Mekong Basin of eastern Thailand receive the same protections as *M. macrocephala* (Gray, 1859) in central and southern Thailand. *Malayemys subtrijuga* (Schlegel and Müller, 1844) in Laos, Cambodia, and Vietnam, however, are not protected as well. Laos has legislation (Lao Wildlife Management Categories) intended to protect only three kinds of turtles, based on local turtle names, from harvest and trade (Stuart and Timmins, 2000; Stuart et al., 2000). In reality, however, all turtle trade is legal in Laos because no true protection exists (Stuart and Timmins, 2000). Laos has also created national Biodiversity Conservation Areas, but little to no real protection exists in them (Stuart and Timmins, 2000). Cambodia also has legislation (Law No. 33-Dept. Fisheries; Declaration No. 1563-Ministry of Agriculture, Forest and Fisheries; Joint Declaration No. 1563-Ministry of Agriculture, Forest and Fisheries, Ministry of Environment; Government Decision 02-Department of Fisheries) intended to prevent the destruction and trade of wild animals (Stuart et al., 2000; Touch Seang Tana et al., 2000). Vietnam has legislation (Directive 359) that generally restricts trade and export of wildlife (Hendrie, 2000; Stuart et al., 2000). It also has commerce regulations preventing traders from operating without a license (Hendrie, 2000; Stuart et al., 2000). In addition, Vietnam has created 11 national parks and 91 protected areas (Hendrie, 2000). Even though legislation protecting turtles exists in each of these three countries, very little real protection exists because relatively little implementation takes place (Stuart et al., 2000).

There are several factors threatening *Malayemys* in all parts of Southeast Asia. The most significant of these is overcollection for local (Stuart and Timmins, 2000; van Dijk and Palasuwan, 2000; van Dijk and Thriakhupt, in press), regional (Nash, 1997; Stuart and Timmins, 2000; Touch Seang Tana et al., 2000; van Dijk and Palasuwan, 2000; van Dijk and Thriakhupt, in press), and international trade (Farkas and Sasvári, 1992; Le Dien Duc and Broad, 1994, 1995; Kuchling, 1995; Artner and Hofer, 2001; Hendrie, 2000; Sharma and Tisen, 2000; Stuart and Timmins, 2000; Touch Seang Tana etal., 2000). Large females are often collected for consumption of their meat and eggs (van Dijk and Palasuwan, 2000; van Dijk and Thirakhupt, in press). This practice is directly detrimental to both the reproductive output and recruitment of affected populations (Hendrie, 2000; van dijk and Thirakhupt, in press). *Malayemys subtrijuga* is probably the most heavily traded species in Vietnam (Hendrie, 2000), Laos (Stuart and Timmins, 2000), and Cambodia (Touch Seang Tana et al., 2000). Even though populations seem to be somewhat large and stable in many areas, natural populations are unlikely to be sustained under present rates of collection (Hendrie, 2000). *Malayemys*, unlike many other turtles, probably benefited from the spread of wet rice culture in Southeast Asia (van Dijk and Thirakhupt, in press). However, present agricultural trends are potentially dangerous to *Malayemys* populations. These include increased use of pesticides and other agrochemicals (van Dijk and Thirakhupt, in press) and physical injury from modern agricultural machinery (van Dijk and Palasuwan, 2000; vanDijk and Thirakhupt, in press). *Malayemys* is also threatened by growing human populations without adequate sewage and waste disposal facilities (van Dijk and Thirakhupt, in press), increased drought conditions (van Dijk and Thirakhupt, in press), and the ever increasing loss of natural habitat (Hendrie, 2000; Sharma and Tisen, 2000; van Dijk and Palasuwan, 2000). On the east coast of Malaysia, freshwater wetlands are continually being drained for other land uses (Sharma and Tisen, 2000). Finally, *Malayemys* is possibly affected by the use and abandonment of monofilament fishing nets which cause accidental drownings (van Dijk and Palasuwan, 2000).

The future looks grim for populations of *Malayemys* in Southeast Asia, especially those of *M. subtrijuga* in Laos, Cambodia, and Vietnam. High levels of exploitation coupled with poor legal protection are potentially disastrous for these populations. The IUCN TFTSG and ATTWG (2000) recommended that populations of *Malayemys* be listed as vulnerable (VU A1d + 2d) in the 2000 IUCN Red List, an increase of two categories over 1996. This recommendation was made before the included taxonomic proposals which effectively cut the current species in half. The urgency to protect exploited populations in Laos, Cambodia, and Vietnam is greater now than ever before. We can no longer depend on stable populations in central Thailand to preserve this species. Populations in Laos, Cambodia, Vietnam, and eastern Thailand are distinct and must be protected separately. Touch Seang Tana et al. (2000) suggested that Cambodia populations were of medium importance in their likely value to the conservation of this species. In light of the current taxonomic proposals, it is suggested that the importance of Cambodian *M. subtrijuga* has increased tremendously. Populations in southern Vietnam are severely degraded, so those in Cambodia, eastern Thailand, and Laos represent the best chance for the long term survival of this species.

Several recommendations can be made which, if followed, will increase the long term survival of *Malayemys* populations in Southeast Asia. With the exception of Laos, legislation protecting *Malayemys* already exists in the countries discussed above. The problem for protection of *Malayemys* lies in the lack of enforcement of these laws. Enforcement will require additional man power, education of personnel, and monetary funds (Hendrie, 2000; Stuart and Timmins, 2000; Stuart et al., 2000; Touch Seang Tana et al., 2000; van Dijk and Palasuwan, 2000). New laws that protect all turtles are needed in Laos, along with the resources to enforce them (Stuart and Timmins, 2000). Unfortunately for *Malayemys*, most protected areas in Southeast Asia are centered around forested habitats (Thirakhupt and van Dijk, 1994; Stuart and Timmins, 2000). Legal protection of a number of lowland swamps would be of immense conservation value to

Malayemys (Thirakhupt and van Dijk, 1994; Hendrie, 2000; Sharma and Tisen, 2000; Stuart et al., 2000). Population monitoring and life history studies are also needed to identify suitable habitats, determine the current status of *Malayemys*, form workable management plans, and apply appropriate levels of protection for these species (Hendrie, 2000; Stuart and Timmins, 2000; Touch Seang Tana et al., 2000; van Dijk and Thirakhupt, in press). Finally, education and awareness programs on the importance of turtles and the severity of threats against them are desperately needed in Southeast Asia (van Dijk and Palasuwan, 2000; Hendrie, 2000; Stuart and Timmins, 2000; Stuart et al., 2000; Touch Seang Tana et al., 2000). Without the support of the local peoples in this region, all conservation efforts will fail.

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APPENDIX A

Scientific Names Applied to *Malayemys subtrijuga* (Schlegel and Müller, 1844)

Malayemys subtrijuga (Schlegel and Müller, 1844)
Malayan Snail-eating Turtle

Emys trijuga Temminck and Schlegel, 1835:64 (non Schweigger, 1812), description of eventual syntypes, but misidentification.

Emys subtrijuga Schlegel and Müller, 1844:30. Type-locality, "Java". Syntypes, Nationaal Natuurhistorisch Museum 6082, 6084, 6085, one stuffed male and two stuffed females, collected by Kuhl and van Hasselt, date unknown (examined by author).

Cistudo gibbosa Bleeker, 1857:239. *Nomen nudum*.

Geoclemys macrocephala Gray, 1859:479. Type-locality, "Siam". Syntypes, British Museum of Natural History 59.7.8.4 and 59.7.8.5, stuffed juvenile specimens, presented by M. Mouhot, date unknown (examined by C. H. Ernst).

Geoclemmys macrocephala (Gray, 1859). Gray, 1859:Plate 21, misspelling.

Clemmys macrocephala (Gray, 1859). Strauch, 1862:32.

Emys nuchalis Blyth, 1863:82. Type-locality, "Java?". Syntypes, Zoological Survey of India 824, 825, 826, one adult and two juvenile stuffed specimens, received from Batavian Society in 1844 (not examined by author).

Emys macrocephala (Gray, 1859). Günther, 1864:31, preoccupied by *Emys macrocephala* Gray, 1844.

Damonia macrocephala (Gray, 1859). Gray, 1869:194.

Bellia nuchalis (Blyth, 1863). Gray, 1870:41.

Damonia? *crassiceps* Gray, 1870:43. Type-locality, "China". Based on a sketch in the Hardwicke collection at the British Museum (not examined by author).

Damonia oblonga Gray, 1871:367. Type-locality, "Batavia". Holotype, British Museum of Natural History 1947.3.5.30, stuffed male specimen, presented by Edward Gerrard Jr., date unknown (examined by C. H. Ernst).

Damonia subtrijuga (Schlegel and Müller, 1844). Boulenger, 1889:94.

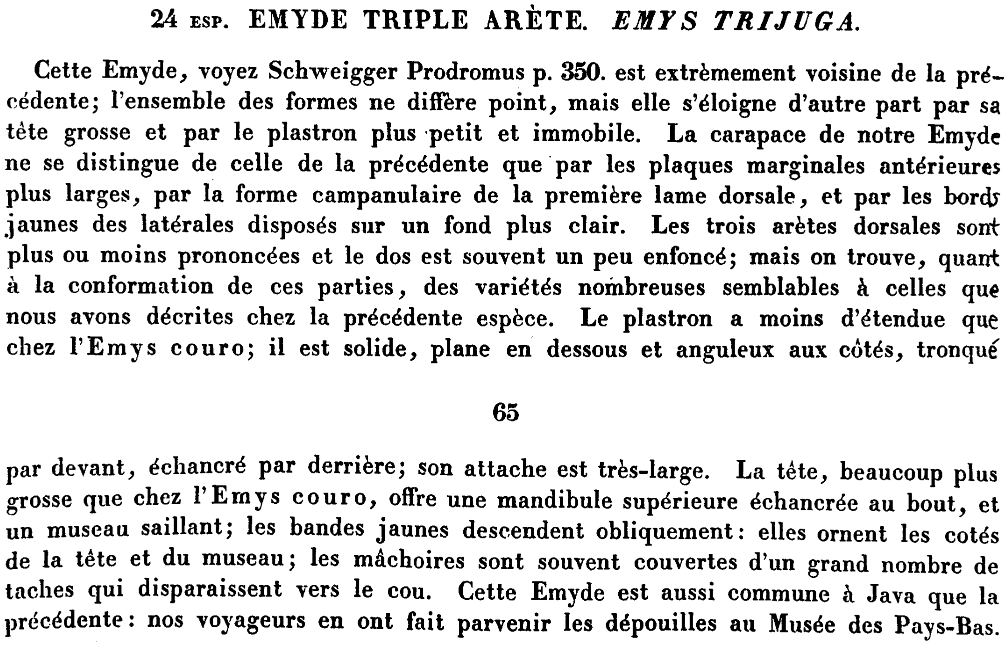
Geoclemys subtrijuga (Schlegel and Müller, 1844). Siebenrock, 1909:476.

Malayemys subtrijuga (Schlegel and Müller, 1844). Lindholm, 1931:30.

APPENDIX B

Three Descriptions Relevant to the Taxonomic History of *Malayemys subtrijuga* (Schlegel and Müller, 1844): Temminck and Schlegel, 1835; Schlegel and Müller, 1844; Gray, 1859

Temminck, C. J., and H. Schlegel. 1835. Volume III, Reptilia, Chelonii. *In* P. F. Von Siebold (ed.), Fauna Japonica sive descripto animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava imperium tenent, suscepto annis 1823-1830 collegit, notis, observationibus et adumbrationibus illustravit, pp. 1-80. J. G. Lalau, Leiden.



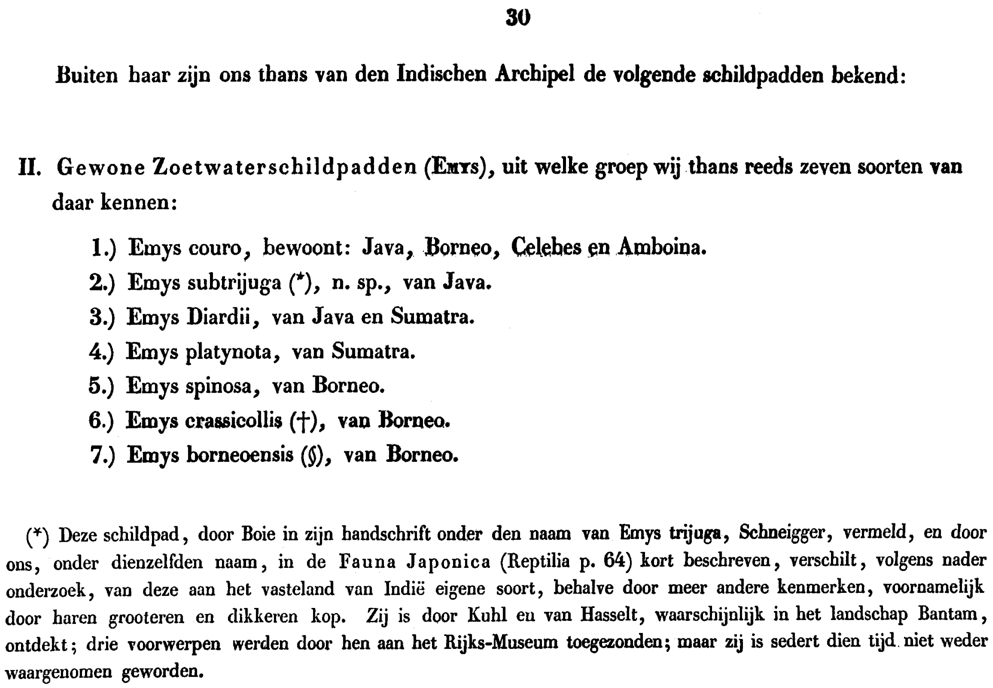
24 ESP. EMYDE TRIPLE ARÈTE. *EMYS TRIJUGA.*

Cette Emyde, voyez Schweigger Prodromus p. 350. est extrèmement voisine de la précédente; l'ensemble des formes ne diffère point, mais elle s'éloigne d'autre part par sa tète grosse et par le plastron plus petit et immobile. La carapace de notre Emyde ne se distingue de celle de la précédente que par les plaques marginales antérieures plus larges, par la forme campanulaire de la première lame dorsale, et par les bords jaunes des latérales disposés sur un fond plus clair. Les trois arètes dorsales sont plus ou moins prononcées et le dos est souvent un peu enfoncé; mais on trouve, quant à la conformation de ces parties, des variétés nombreuses semblables à celles que nous avons décrites chez la précédente espèce. Le plastron a moins d'étendue que chez l'Emys couro; il est solide, plane en dessous et anguleux aux côtés, tronqué

65

par devant, échancré par derrière; son attache est très-large. La tète, beaucoup plus grosse que chez l'Emys couro, offre une mandibule supérieure échancrée au bout, et un museau saillant; les bandes jaunes descendent obliquement: elles ornent les cotés de la tète et du museau; les mâchoires sont souvent couvertes d'un grand nombre de taches qui disparaissent vers le cou. Cette Emyde est aussi commune à Java que la précédente: nos voyageurs en ont fait parvenir les dépouilles au Musée des Pays-Bas.

Schlegel, H., and S. Müller. 1844. Over de Schildpadden van den Indischen Archipel, en beschrijving eener nieuwe soort van Sumatra. *In* C. J. Temminck (ed.), Verhandelingen over de Natuurlijke Geschiendenis der Nederlandsche Overzeesche Bezittingen, 1839-44. Part 3, Zoölogie, Schildpadden, pp. 29-36. Luchtmans and van den Hoek, Leiden.



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Buiten haar zijn ons thans van den Indischen Archipel de volgende schildpadden bekend:

II. Gewone Zoetwaterschildpadden (EMYS), uit welke groep wij thans reeds zeven soorten van daar kennen:

1.) Emys couro, bewoont: Java, Borneo, Celebes en Amboina.
2.) Emys subtrijuga (*), n. sp., van Java.
3.) Emys Diardii, van Java en Sumatra.
4.) Emys platynota, van Sumatra.
5.) Emys spinosa, van Borneo.
6.) Emys crassicollis (†), van Borneo.
7.) Emys borneoensis (§), van Borneo.

(*) Deze schildpad, door Boie in zijn handschrift onder den naam van Emys trijuga, Schneigger, vermeld, en door ons, onder dienzelfden naam, in de Fauna Japonica (Reptilia p. 64) kort beschreven, verschilt, volgens nader onderzoek, van deze aan het vasteland van Indië eigene soort, behalve door meer andere kenmerken, voornamelijk door haren grooteren en dikkeren kop. Zij is door Kuhl en van Hasselt, waarschijnlijk in het landschap Bantam, ontdekt; drie voorwerpen werden door hen aan het Rijks-Museum toegezonden; maar zij is sedert dien tijd niet weder waargenomen geworden.

Gray, J. E. 1859. Description of a new species of freshwater tortoise from Siam. Proceedings of the Zoological Society of London 1859:478-479.

2. DESCRIPTION OF A NEW SPECIES OF FRESHWATER TORTOISE FROM SIAM. BY DR. J. EDWARD GRAY, F.R.S., V.P.Z.S., PRES. ENT. SOC., ETC.

(Reptilia, Pl. XXI.)

The British Museum has received from M. Mouhot, with some other Reptiles, two specimens of a Freshwater Tortoise, which are

decidedly different from any I have before seen. They have somewhat the external appearance, both in shape and markings of the head, of some specimens of *Cistudo amboinensis*, but belong to the genus *Emys*, or rather *Geoclemys*, and not to *Cistudo*.

They are referable to the first division of genus which has the back of the shell three-keeled, and, like the other species of that section, come from Asia.

1. GEOCLEMYS MACROCEPHALA.

The shell oblong, rather depressed, entire, three-keeled, olive-brown; the keels subcontinued, nearly parallel, the middle one higher and more distinct behind; the lateral ones, near the upper edge of the shields, continued, ending abruptly on the hinder edge of the third lateral discal shield; the hinder lateral and central shield only marked with a slight convexity; the margin entire, yellow-edged. The under side yellow, with black triangular spots; the sternum flat, very indistinctly keeled on the side.

Animal blackish-olive. Head large; crown flat, covered with single smooth plate, purplish-brown, with two streaks from middle of the nose, the upper edging the crown, the other the upper part of the beak, and with two streaks from the hinder edge of the orbit, the lower short and interrupted, extended on the temple, the upper broader and continued over the ear along the side of the neck; two close streaks under the nostrils to the middle of the upper jaw, and two broad streaks, dilated behind, down the front of the lower jaw, and continued on the edge of the lower jaw behind; the nape and hinder part of the side of the lower jaw covered with large flat scales; the rest of the neck and legs covered with minute granular scales; the front of the fore-legs covered with broad band-like scales; the toes of the fore- and hind-feet rather short and thick, covered above with broad band-like scales.

Hab. Siam.

The front vertebral plate is quadrangular, the front edge wider, rounded; second, third, and fourth ventral shields six-sided, the second longer than broad, the fourth broader than long; the three hinder sides are longest, the fifth vertebral shield subquadrangular, the front sides being very narrrow, and the hinder side very broad and slightly truncated.

APPENDIX C

Specimens Examined in Analyses of Size Distribution, Allometry, Sexual Dimorphism, and Geographic Variation

Size Distribution

CPhr: Juveniles-AMNH R-92278-79, R-94563; MTKD 17107; UF 111443; UMMZ 65138; USNM 72323; ZSM 55/1956.10; Females-AMNH R-92277; BMNH 1921.4.1.187; CAS 119939; CUB 1992.07.04.6, 1992.11.10.1-.2, 1999.01.05.15, 1999.01.05.17; FMNH 190336; KU 50509-14; MCZ R-20302-03; MTKD 17098, 22275, 34593; NMW 1322; RMNH 10374.2, 11367, 14911.2; SMF 42960, 52867; UMMZ 65140, 65142-43, 65145, 65147-50; USNM 70363, 71480, 79499, 101580, 102994, 104335; ZMUC R25233; ZRC 2.72; ZSM 17/1956.03, 17/1956.06-.12; Males-CAS 98890; CUB 1999.01.05.16, 1999.01.05.18; FMNH 73815, 171927-28, 190337-42; MTKD 22274; NMW 29373.5, 29375; RMNH 4749, 10374.3-.6, 14911.1; SMF 52864-66, 70535; UF 69136; UMMZ 65139, 65144, 65146; USNM 72322, 79454; ZMUC R2505-06; ZSM 17/1956.01-.02, 17/1956.04-.05, 55/1956.02-.03

Java: Juveniles-BMNH 63.12.4.38; MNHN 1905.57; NMW 29373.4; RMNH 3960, 22213; Females-NMW 29371.1-.3; RH 33, 140; RMNH 6084-85; SMF 7532-33, 7535, 58097; USNM 43871; ZMH R00399-400, R03088; ZMUC R25229, R25231; Males-BMNH 71.4.10.2; NMBE 44a/14; NMW 1722, 29371.4; RH 143; RMNH 6082, 28045; SMF 7534, 52792; USNM 43870, 44121-22; ZMUC R25230, R25232; ZSM 2/1949

Mekg: Juveniles-BMNH 60.8.28.6, 61.4.12.17; MNHN 1963.746; ROM 37064, 37066; Females-BMNH 1861.4.12.15; CRI 3231, 3276, 3442-46, 3448, 3807, 3850, 4077; CUB 1991.9.1.2, 1993.01.16.2, 1993.01.16.9; MTKD 22525, 23937, 26087; ROM 37060-61, 37063, 37065; Males-CRI 3447, 3808; MTKD 18811; NMW 29373.3, 29374.1; ROM 37057-59, 37062; ZRC 2.2592

Regression Analyses: Allometry and Sexual Dimorphism of Shell Characters

CPhr: Females-AMNH R-92277; BMNH 1921.4.1.187; CAS 119939; CUB 1992.07.04.6, 1992.11.10.1, 1999.01.05.15, 1999.01.05.17; FMNH 190336; KU 50509-14; MCZ R-20302; MTKD 17098, 22275, 34593; NMW 1322; RMNH 10374.2, 11367, 14911.2; SMF 42960, 52867; UMMZ 65140, 65142-43, 65145, 65147-50; USNM 70363, 71480, 79499, 101580, 102994, 104335; ZMUC R25233; ZRC 2.72; ZSM 17/1956.03, 17/1956.06-.12; Males-CAS 98890; CUB 1999.01.05.16, 1999.01.05.18; FMNH 73815, 171927-28, 190337-42; MTKD 22274; NMW 29373.5, 29375; RMNH 4749, 10374.3, 10374.5-.6, 14911.1; SMF 52864-66, 70535; UF 69136; UMMZ 65139, 65144, 65146; USNM 72322, 79454; ZMUC R2505-06; ZSM 17/1956.01-.02, 17/1956.04-.05, 55/1956.02-.03

Java: Females-NMW 29371.1-.3; RH 140; RMNH 6084-85; SMF 7532-33, 7535, 58097; USNM 43871; ZMH R00399-400, R03088; ZMUC R25229, R25231; Males-BMNH 71.4.10.2; NMBE 44a/14; NMW 1722, 29371.4; RMNH 6082, 28045; SMF 7534, 52792; USNM 43870, 44121-22; ZMUC R25230, R25232; ZSM 2/1949

Mekg: Females-BMNH 1861.4.12.15; CRI 3231, 3276, 3442-46, 3448, 3807, 3850, 4077; CUB 1991.9.1.2, 1993.01.16.2, 1993.01.16.9; MTKD 22525, 23937, 26087; ROM 37060-61, 37063, 37065; Males-CRI 3447, 3808; MTKD 18811; NMW 29373.3, 29374.1; ROM 37057-59, 37062; ZRC 2.2592

Discriminant Function Analyses: Sexual Dimorphism of Shell Characters

CPhr: Females-BMNH 1921.4.1.187; CAS 119939; CUB 1992.11.10.1; FMNH 190336; KU 50509-11, 50514; MTKD 17098, 34593; NMW 1322; RMNH 10374.2, 11367; UMMZ 65140, 65142; USNM 70363, 71480, 79499, 104335; ZRC 2.72; Males-CAS 98890; FMNH 73815, 171927-28, 190337-39, 190341-42; MTKD 22274; NMW 29375; RMNH 4749, 10374.3, 10374.5; SMF 52864, 70535; UF 69136; UMMZ 65139, 65144, 65146; USNM 72322, 79454; ZMUC R2505-06; ZSM 17/1956.01-.02, 17/1956.04-.05, 55/1956.03

Java: Females-NMW 29371.1, 29371.3; RMNH 6084-85; SMF 7532-33, 7535; USNM 43871; ZMH R00399-400, R03088; ZMUC R25229, R25231; Males-BMNH 71.4.10.2; NMBE 44a/14; NMW 1722, 29371.4; RMNH 6082, 28045; SMF 7534, 52792; USNM 43870, 44121-22; ZMUC R25230, R25232; ZSM 2/1949

Mekg: Females-BMNH 1861.4.12.15; CRI 3276, 3442, 3445-46, 3448, 3807, 4077; CUB 1991.9.1.2, 1993.01.16.2; MTKD 22525; Males-CRI 3447, 3808; MTKD 18811; NMW 29373.3, 29374.1; ROM 37057-59, 37062; ZRC 2.2592

Discriminant Function Analyses: Geographic Variation of Shell Characters

CPhr: Females-BMNH 1921.4.1.187; CAS 119939; CUB 1992.11.10.1; FMNH 190336; KU 50509-11, 50514; MTKD 17098, 34593; NMW 1322; RMNH 10374.2, 11367; UMMZ 65140, 65142; USNM 70363, 71480, 79499, 104335; ZRC 2.72; Males-CAS 98890; FMNH 73815, 171927-28, 190337-39, 190341-42; MTKD 22274; NMW 29375; RMNH 4749, 10374.3, 10374.5; SMF 52864, 70535; UF 69136; UMMZ 65139, 65144, 65146; USNM 72322, 79454; ZMUC R2505-06; ZSM 17/1956.01-.02, 17/1956.04-.05, 55/1956.03

Java: Females-NMW 29371.3; RMNH 6085; SMF 7532-33, 7535; USNM 43871; ZMH R00399-400, R03088; ZMUC R25229, R25231; Males-BMNH 71.4.10.2; NMBE 44a/14; NMW 29371.4; RMNH 6082, 28045; SMF 7534, 52792; USNM 43870, 44122; ZMUC R25230, R25232

Mekg: Females-BMNH 1861.4.12.15; CRI 3276, 3442, 3445-46, 3448, 3807, 4077; CUB 1991.9.1.2; MTKD 22525; Males-CRI 3447, 3808; MTKD 18811; NMW 29373.3, 29374.1; ROM 37057-59, 37062; ZRC 2.2592

Discriminant Function Analysis: Geographic Variation of Head-stripe Characters

CPhr: AMNH R-92277-79, R-94563; CAS 119939; CUB 1999.01.05.15-.18; FMNH 73815, 171927-28, 190336-42; KU 50510-14; MCZ R-20302-03, R-20306, R-43083; MTKD 17098, 17107, 22274-75, 34593; NMW 29373.5, 29375; RMNH 10374.3, 10374.5-.6, 11367, 14911.1-.2; SMF 42960, 52864-67, 70535; UF 69136; UMMZ 65138-40, 65142-50; USNM 70363, 71480, 72322-23, 79454, 79499, 101580, 102994, 104335; ZMUC R2505-06, R25233; ZRC 2.72; ZSM 17/1956.01-.12, 55/1956.01-.03

Java: BMNH 63.12.4.38, 71.4.10.2; MCZ R-7819; MNHN 1905.57; NMBE 44a/14; NMW 29371.1-.4, 29373.4; RH 143; RMNH 3960, 6082, 6084-85, 22213; SMF 7532-34, 52792, 58097; USNM 43870-71, 44121-22; ZMH R00399-400; R03088; ZMUC R25229-32; ZSM 2/1949

Mekg: BMNH 60.8.28.6, 1861.4.12.15; CRI 3276, 3447, 3807-08, 4077; MNHN 1963.746; MTKD 18811, 22525, 23937, 26087; NMW 29373.3, 29374.1; ROM 37057-66; ZRC 2.2592

APPENDIX D

Geographic Distribution of *Malayemys subtrijuga* Based on Available Museum and Literature Records

APPENDIX D. Geographic distribution of *Malayemys subtrijuga* based on available museum and literature records. See Chapter 3 for watershed abbreviations.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
CPhr	Thailand	Ayutthaya, Ayutthaya Prov.	14.350 100.550	Flower, 1899
		Bangkok	13.733 100.500	AMNH R-80925, R-92277-79, R-94563; BMNH 98.4.2.2, 1898.11.8.1-.2, 1921.4.1.187, 1929.4.26.4; CAS 98890; FMNH 73815; KU 50509-11; MCZ R-29506, R-20302-03; MTKD 17107, 22274-75, 34593; NMBA #; NMW 29373.5, 29375; RMNH 4749, 14911.1-.2; SMF 42960, 52864-67, 70535; UF 43900, 111443; UMMZ 65138-50; USNM 70363, 71480, 72322-23, 79454, 104335; UMNH 10264-72; ZMH R401-11, R4005-07; ZMUC R2505-06, R25233; ZRC 2.72; ZSM 17/1956.01-.12, 22/1919, 55/1956.01-.03, 807/20; Bocourt, 1866; Flower, 1899; Smith, 1916, 1931; Cochran, 1930; Taylor, 1970
		Bung Borapet, Nakhon Sawan Prov.	15.670 100.243	CUB 1998.04.05.1
		central Thailand	N/A	Smith, 1916

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
		Chai Nat, Chai Nat Prov.	15.183 100.133	Thirakhupt and van Dijk, 1994
		Chiang Mai, Chiang Mai Prov.	18.800 98.983	FMNH 171928, 190336-42; KU 50512-14; MCZ R-43083; MTKD 17098; RMNH 10374.1-.6; USNM 101580; Taylor, 1970
		48 km N Chiang Mai, Chiang Mai Prov.	N/A	USNM 102994
		Chom Thong, Chiang Mai Prov.	18.417 98.733	USNM 79499
		Chon Buri, Chon Buri Prov.	13.400 100.983	Taylor, 1970
		Dang Phraya Fai Mts.	N/A	NMW 1322, 29374.2-.3
		Huai Kasang (creek), 1 km S Ban Phu Toel, Phetchabun Prov.	15.566 101.063	UF 69380
		Klong Dam village, Samut Prakan Prov.	N/A	CAS 119939
		Klong Mae Wong, near Klong Larn National Park, Kamphaeng Phet Prov.	N/A	Thirakhupt and van Dijk, 1994
		Klong Mae Wong, Nakhon Sawan Prov. (coordinates for province)	15.700 100.083	CUB 1992.07.04.6

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
		Lat Yao, Nakhon Sawan Prov.	15.750 99.800	Peter Paul van Dijk, pers. comm.
		Lop Buri, Lop Buri Prov.	14.817 100.617	UMMZ 189186-87
		Nakhon Sawan, Nakhon Sawan Prov.	15.683 100.117	Thirakhupt and van Dijk, 1994
		31 km WNW Nakhon Sawan (Lat Yao?), Nakhon Sawan Prov.	N/A	Thirakhupt and van Dijk, 1994
		Phitsanulok, Phitsanulok Prov.	16.833 100.250	RMNH 25716
		Ping River	N/A	Thirakhupt and van Dijk, 1994
		Rangsit Area (Klong 7), Thanyaburi, Pathum Thani Prov.	14.017 100.733	CUB 1992.11.10.1-.2, 1999.01.05.15-.18; Srinarumol, 1995; van Dijk and Thirakhupt, in press
		8 km N Sara Buri, Saraburi Prov. (ccordinates for Sara Buri)	14.533 100.883	UF 69136
		Saraburi Prov.	14.700 100.867	MNHN 7962
		Sing Buri, Sing Buri Prov.	14.933 100.350	ZMH R3848
		Uthai Thani, Uthai Thani Prov.	15.367 100.050	Thirakhupt and van Dijk, 1994

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
Java	Indonesia, Java	Bantam Prov. (former residency in western Java; type locality)	N/A	RMNH 6082, 6084-85; Schlegel and Müller, 1844; Hubrecht, 1881
		Banten, Banten Prov.	-6.000 106.150	MZB; de Rooij, 1915
		Cirebon, Jawa Barat Prov.	-6.767 108.550	Kopstein, 1938
		Depok, Jawa Barat Prov.	-6.367 106.750	MCZ R-7819; USNM 43870-71, 44121-22; Barbour, 1912; de Rooij, 1915
		Duri, Jakarta Raya Prov.	-6.183 106.77	de Rooij, 1915
		Jakarta, Jakarta Raya Prov.	-6.133 106.750	BMNH 63.12.4.38, 71.4.10.2; MNHN 1905.57; MZB; NMW 29373.4; RH 33, 140-44; RMNH 28045; SMF 52792, 58097; ZMUC R25229-32; Gray 1871, 1873; de Rooij, 1915
		Surabaya, Jawa Timur Prov.	-7.233 112.750	ZMH R399-400, R3088
		Tasikmalaya, Jawa Barat Prov.	-7.333 108.267	MZB
		west Java	N/A	RMNH 22213

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
Java	Indonesia, Java	N/A	N/A	NMW 1722, 29371.1-.4; RMNH 94; SMF 7532-35; ZMZ 824-26; ZSM 2/1949; Bleeker, 1857; Blyth, 1863; Gray, 1870; Boulenger, 1889, 1912; Flower, 1899; Siebenrock, 1903, 1909; Dammerman, 1929; Lindholm, 1931; Smith, 1931; Bourret, 1941; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977; Nutaphand, 1979; Pritchard, 1979; Ernst and Barbour, 1989; Whitten and McCarthy, 1993; Ernst et al., 2000; Samedi and Iskandar, 2000; van Dijk and Thirakhupt, in press
Maly	Malaysia	east coast *Melaleuca* swamps in Terengganu and possibly Kelantan (coordinates for Jambu Bongkok Forest Reserve, Terengganu)	4.917 103.350	Sharma and Tisen, 2000
		northern state of Kedah	6.000 100.667	Lim and Das, 1999; Sharma and Tisen, 2000; van Dijk and Thirakhupt, in press

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
		northern state of Perlis	6.500 100.250	Lim and Das, 1999; Sharma and Tisen, 2000; van Dijk and Thirakhupt, in press
		northern part of peninsular Malaysia	N/A	Bourret, 1941; Ernst et al., 2000; Sharma, 1999
		peninsular Malaysia	N/A	KUZ 36800-01
Maly	Malaysia	N/A	N/A	MSN 6; Nutaphand, 1979; van Dijk, 2000
Maly	Thailand	Krabi, Krabi prov.	8.067 98.917	Mudde, 1991
		lower reaches of Pattani River, Pattani Prov.	N/A	BMNH 1903.4.13.1; Boulenger, 1903, 1912
		Pattani, Pattani Prov.	6.833 101.333	Taylor, 1970
		peninsular Thailand	N/A	Smith, 1916; van Dijk and Thirakhupt, in press
		lower reaches of Phatthalung River, Phatthalung Prov.	N/A	Annandale, 1916
		Phatthalung, Phatthalung Prov.	7.617 100.083	Laidlaw, 1901
		Trang, Trang Prov.	7.500 99.300	USNM 22951, 23111
		Yala, Yala Prov.	6.667 101.167	Laidlaw, 1901

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
Maly	N/A	Malay Peninsula	N/A	UF 85286; Siebenrock, 1909; de Rooij, 1915; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977;
		northern part of Malay Peninsula	N/A	Smith, 1931; Pritchard, 1979
Mekg	Cambodia	Siem Reap, Siem Reap Prov.	13.367 103.850	Kurt Buhlmann, pers. comm. (with photo record); Peter Pritchard, pers. comm. (with photo record)
		Snoc Tru, Kampang Chhnang Prov.	12.517 104.450	MNHN 1963.746
Mekg	Cambodia	N/A	N/A	BMNH 60.8.28.6, 61.4.12.17, 1861.4.12.15; NMW 29374.1; Gray 1861, 1869, 1870; Günther, 1864; Morice, 1875; Tirant, 1885; Boulenger, 1889, 1912; Boettger, 1892; Flower, 1899; Siebenrock, 1903, 1909; de Rooij, 1915; Bourret, 1941; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977; Ernst and Barbour, 1989; Ernst et al., 2000; Touch Seang Tana et al., 2000; van Dijk, 2000; van Dijk and Thirakhupt, in press

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
Mekg	Laos	Pakxe, Champasak Prov.	15.117 105.783	Nash, 1997
Mekg	Laos	N/A	N/A	Ernst et. al., 1998; Stuart et al., 2000; Stuart and Timmins, 2000; Touch Seang Tana et al., 2000; van Dijk, 2000; van Dijk and Thirakhupt, in press
Mekg	Thailand	Nakhon Ratchasima, Nakhon Ratchasima Prov.	15.000 102.100	CUB 1991.9.1.2
		Sakaerat, Amphoe Pak Thong Chai, Nakhon Ratchasima Prov.	14.717 102.017	CUB 1993.01.16.2, 1993.01.16.9
Mekg	Vietnam	Ca Mau, Ca Mau Prov.	9.250 105.167	Le Dien Duc and Broad, 1995; Nash, 1997
		Can Tho Prov.	10.033 105.783	Le Dien Duc and Broad, 1994, 1995
		Ho Chi Minh City, Ho Chi Minh Prov.	10.750 106.667	MTKD 18811, 22525, 26087; ZRC 2.2592; Siebenrock, 1903; Smith, 1931; van Dijk and Thirakhupt, in press; Peter Pritchard, pers. comm.
		Long Xuyen, An Giang Prov.	10.383 105.417	BMNH 1920.1.20, 2544-45
		Mekong Delta, southern Vietnam	N/A	MTKD 23937

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
		Nam Can, Ca Mau Prov.	8.683 104.933	Le Dien Duc and Broad, 1994, 1995
		Phung Hiep, Can Tho Prov.	9.812 105.820	ROM 37057-66
		Rach Gia, Kien Giang Prov.	9.917 105.083	Le Dien Duc and Broad, 1994, 1995
		southern Vietnam	N/A	Morice, 1875; Siebenrock, 1909; Boulenger 1912; de Rooij, 1915; Smith, 1931; Bourret, 1939, 1941; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977; Pritchard, 1979; Ernst and Barbour, 1989; Geissler and Jungnickel, 1989; Ernst et al., 2000; Hendrie, 2000; van Dijk and Thirakhupt, in press
		U Minh Region, Ca Mau and Rach Gia provinces.	9.467 105.033	Le Dien Duc and Broad, 1994, 1995
		U Minh Thuong Nature Preserve, Kien Giang Prov.	9.600 105.083	Safford et al., 1998; Turtle Conservation and Ecology Project, 2001

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
Mekg	Vietnam	N/A	N/A	CRI 3231, 3276, 3442-51, 3703, 3807-08, 3850-54, 4077; NMW 29373.3; Touch Seang Tana et al., 2000; van Dijk, 2000; William McCord, pers. comm.
MKhl	Thailand	Kanchanaburi, Kanchanaburi Prov.	14.033 99.533	Thirakhupt and van Dijk, 1994
		Mae Khlong basin	N/A	Thirakhupt and van Dijk, 1997
		Ratchaburi Prov.	13.533 99.800	Thirakhupt and van Dijk, 1994
		Samut Songkhram Prov.	13.400 100.00	Thirakhupt and van Dijk, 1994; Hutasingh, 1998
		Tharang District, Phetchaburi Prov.	12.750 99.583	CUB 1999.01.05.1-.14; Srinarumol, 1995; van Dijk and Thirakhupt, in press
SECos	Thailand	Laem Sing, Chanthaburi Prov.	12.483 102.067	USNM 72212
Sumt	Indonesia, Sumatra	Duri, Riau Prov.	1.450 101.250	MZB; Iverson, 1992
Sumt	Indonesia, Sumatra	N/A	N/A	NMW 29376.1-.4; Samedi and Iskandar, 2000
N/A	Indonesia	N/A	N/A	NMBE 44a/14; RMNH 3960; van Dijk, 2000

APPENDIX D. Continued.

Watershed	Country	Specific Locality	Latitude/ Longitude	Museum and/or Literature Reference
N/A	Thailand	N/A	N/A	AMNH R-80924; BMNH #, 59.7.8.4-.5, 59.7.8.7, 78.2.14.8; CRI 2760; FMNH 17915-16, 17926-27; LACM 8115; MCZ R-29504, R-55149; MHNG 1531.55-.73; MTKD 3694-95, 9054, 11111-13, 35034; NMW 29374.2-.3; RMNH 25716; SMF 7531, 56091; UF 68969, 85203; UMMZ 128404; Gray, 1859, 1861, 1869, 1870; Günther, 1864; Boulenger, 1889, 1912; Flower, 1899; Siebenrock, 1903, 1912; de Rooij, 1915; Smith, 1931; Bourret, 1941; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961, 1977; Taylor, 1970; Nutaphand, 1979; Pritchard, 1979; Ernst and Barbour, 1989; Ernst et al., 2000; Touch Seang Tana et al., 2000; van Dijk, 2000; van Dijk and Palasuwan, 2000; van Dijk and Thirakhupt, in press

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