

Chelus fimbriatus (Schneider 1783) – Matamata Turtle

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SUMMARY. – *Chelus fimbriatus*, the matamata turtle (Family Chelidae), is the largest member of its pleurodiran family, and is surely the most bizarre turtle in the world. It has an exceedingly rough, tuberculate carapace, a greatly elongated and thickened neck, and a wide, triangular, extremely flattened head, with a tubular nasal extension, reduced anteriorly displaced eyes, and an extremely wide mouth. It is specialized for feeding upon live fish that it sweeps into its mouth by a rapid lateral strike of the neck and jaws, and a vigorous simultaneous expansion of the hyoid apparatus in the neck. It is distributed widely in South America, and currently does not appear to be threatened significantly anywhere in its range.

DISTRIBUTION. – Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname?, Trinidad and Tobago, Venezuela. Distributed widely in lowland tropical rivers of northern South America, including the Amazon, Orinoco, Essequibo, and Oyapoque systems.

SYNONYMY. – *Testudo terrestris* Fermin 1765 (name suppressed), *Testudo fimbriata* Schneider 1783, *Chelus fimbriata*, *Chelys fimbriata*, *Matamata fimbriata*, *Chelus fimbriatus*, *Testudo fimbria* Gmelin 1789, *Testudo matamata* Bruguière 1792, *Emydes matamata*, *Chelus matamata*, *Chelys matamata*, *Testudo bispinosa* Daudin 1801, *Chelys bispinosa*, *Matamata bispinosa*, *Chelys boulengerii* Baur 1890.

SUBSPECIES. – None recognized. Orinoco and Amazon populations have been identified as morphologically distinct from each other, but have not been named.

STATUS. – IUCN 2007 Red List: Not Listed (= Least Concern, LR/lc) (assessed 1996, needs updating); CITES: Not Listed. Colombia Red List: Near Threatened.

Taxonomy. – The matamata was first described over 250 years ago, under the pre-binomial descriptor *Testudo terrestris major putamine echinato et striato, sive raparapa* by Barrère (1741), with the credible type locality “Cayenne” (at that time more probably the country of French Guiana rather than the capital city of the same name). This name was shortened to *Testudo terrestris* by Fermin (1765), a name

subsequently invalidated by Opinion 660 of the ICZN (International Commission on Zoological Nomenclature 1963). The same opinion established *Testudo fimbriata* Schneider 1783, as the valid name, an epithet that pre-dated the alternative names *Testudo matamata* Bruguière 1792 and *Testudo bispinosa* Daudin 1801. The species was transferred to the new genus *Chelus* by Duméril (1806). This publication, in



Figure 1. *Chelus fimbriatus* from the Amazon basin in South America. Photo by Peter C.H. Pritchard.



Figure 2. *Chelus fimbriatus* from Leticia, Colombia. Photo by Peter C.H. Pritchard.

both German and Latin, utilized the forms *Chelus* (in Latin) and *Chelys* (in the German text), and confusion over which spelling should be considered valid prevailed for a long time, with the *Chelys* defenders generally prevailing until Zug (1977) finally re-examined and analyzed Duméril's original text.

Chelys boulengeri Baur 1890 was based upon a skull obtained from commercial sources of unknown origin. Baur considered this to represent a new species in that it had a horny beak (i.e., rhamphotheca), a feature that Boulenger had noted as absent in *C. fimbriatus*. But in fact all matamatas have a horny beak, although it has much less of a palatal extension than in most turtles.

Other scientific names that have been proposed for the matamata (listed by Pritchard and Trebbau 1984, and Fritz and Havas 2006) are based upon misspellings or casual recombinant forms. Merrem (1820) used *Matamata* as a generic name.



Figure 3. Hatchlings of *Chelus fimbriatus* from the Amazon population (note stripes under neck and plastral markings. Photo by Peter C.H. Pritchard.

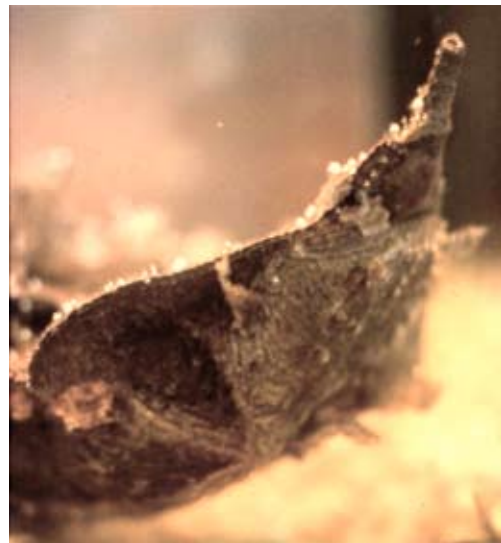


Figure 4. Heads of *Chelus fimbriatus*. Photos by Anders G.J. Rhodin (top, from Leticia, Colombia), Peter C.H. Pritchard (middle), and Russell A. Mittermeier (bottom).

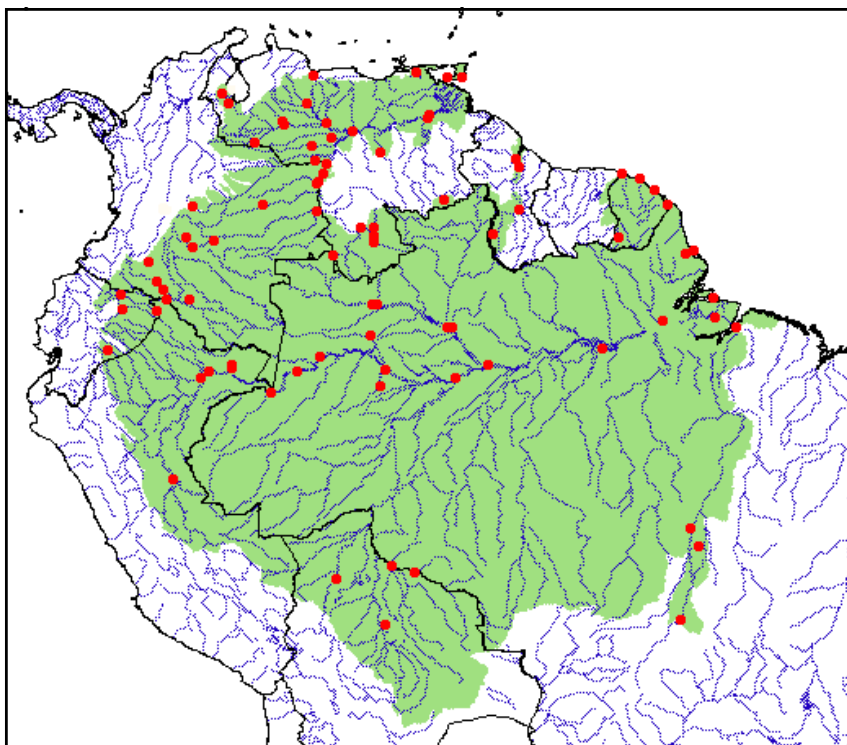


Figure 5. Distribution of *Chelus fimbriatus* in northwestern South America. Red points = museum and literature occurrence records based on published records (Iverson 1992) plus more recent and author's data; green shading = projected distribution based on GIS-defined hydrologic unit compartments (HUCs) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs (Buhlmann et al., unpubl. data), and adjusted based on author's data.

No subspecies of *Chelus fimbriatus* have been proposed, but geographic variation was claimed by Schmidt (1966), who reported differences between specimens from Colombia, Peru, and Brazil. However, Schmidt's analysis was weakened by a small sample size of only five specimens, lack of precise locality data (listed merely by country), and use of specimens that probably all came from the greater Amazon system rather than from the several separate river systems known to be inhabited by the species. The reported differences included those of coloration of the carapace, plastron, and head, the shape of the nuchal scute, the texture of the carapace, the shape of the skull, the form of the "ear flaps," and the configuration of the intergular scute.

Fretey (1977) identified individuals attributable to all three of Schmidt's groups in his series of eight French Guiana specimens, and noted that one known to be from Amapá, Brazil, would have been adjudged as Peruvian by Schmidt's criteria, and a known Peruvian specimen would have been declared Colombian.

Pritchard and Trebbau (1984) made comparisons between large series of matamatas from the Orinoco and the Amazon systems, and concluded that those from the Orinoco were characterized by oval shells and little or no black pigment on the (usually bright pink) underside of the neck; whereas, those from the Amazon had the carapace parallel-sided or even slightly constricted, and had a pair of bold black bars running the length of the underside of the neck, replaced by a median black bar under the chin. These

authors also examined the intergular configuration of 15 Venezuelan specimens, finding a wide range of variation even in the 12 individuals from a single locality in Estado Cojedes.

These differences were confirmed by Sánchez-Villagra et al. (1995), who also added that the plastron of Orinoco specimens was generally unpigmented, whereas that of Amazonian specimens was typified by heavy pigmentation. They also demonstrated that the percentage of individuals in which the intergular failed to separate the gulars was almost identical in the Orinoco and Amazon samples (39 vs. 38%). The few exceptions to the generalizations about pigmentation and shape of Orinoco vs. Amazonian matamatas came largely from zones of probable intergradation, e.g., the upper Río Negro in southern Venezuela, a part of the Amazon system connected to the Orinoco via the Brazo Cassiquiare. Moreover, the specimens I have examined from "Guyana" (but probably including some individuals brought over the Brazilian border from the adjacent Rio Branco system) were of the "Orinoco" rather than the "Amazon" morphotype in both form and coloration. This is also the case with a Rio Branco specimen (USNM 064154) examined by Sánchez-Villagra. Interestingly, 14 of a series of 15 live adults from Guyana that I examined had the intergular failing to separate the gular scutes. On the other hand, the descriptions of French Guiana specimens offered by Fretey (1977) suggest that these are of the "Amazon" rather than the "Orinoco" (including Guyana) form.

These data suggest that one could possibly justify the recognition of two subspecies of *C. fimbriatus*—one in the Orinoco and Essequibo systems of Colombia, Venezuela, and Guyana, and one in the Amazon system of Brazil, Peru, Colombia, Ecuador, and Bolivia, and including the Oyapoque region of French Guiana. Intergradation between the two forms may occur in the upper Río Negro of Venezuela and Colombia and Brazil, and the northern form also penetrates into the Rio Branco in northern Brazil, a tributary of the Amazon. Genetic phylogeographic analysis would help to elucidate and further identify any evolutionarily significant units or possible separate subspecies or species within what is now considered a single wide-ranging taxon.

As regards the relationships of *Chelus*, the genus is clearly a member of the pleurodiran family Chelidae (characterized, inter alia, by the strong lateral processes on the cervical vertebrae, the presence of an intergular scute, the absence of quadratojugals and mesoplastra, and the anteroventral origin of the emargination of the temporal region). But it is also a highly distinctive and specialized taxon, and its relationships within the family are not immediately obvious. Pritchard (1984) presented the argument that *Chelus* is most closely related to *Hydromedusa*, and that the latter was more distantly related to the superficially similar *Chelodina*, that had unique apomorphies including the single frontal bone and the loss of the parietosquamosal arches. On the other hand, Kasper (1903) and Frair (1964) argued that *Chelus* was most closely allied to *Phrynops* (= *Hydraspis*, *Batrachemys*); whereas, Gaffney (1977) placed *Chelus*, *Chelodina*, and *Hydromedusa* in a Subtribe Chelina, with Infratribe Hydromedusad created to receive the latter two genera.

Wood (1976) described two fossil species of *Chelus*, *C. colombianus* and *C. lewisi*, from the Miocene of Colombia and Venezuela, respectively. These species have subsequently been identified in late Miocene deposits of Acre, Brazil (Bocquentin and Rancy 1987; Bocquentin and Rodrigues dos Santos 1989). The fossil species had been described as being differentiated from the extant species by: 1) form and location of the intergular scute; 2) height and thickness of the carapacial tubercles; 3) ratio of bridge length to plastron length; and 4) the greater overall size—commonly over 50 cm, sometimes over 60 cm carapace length (Sánchez-Villagra 1992). However, after extensive analysis, Sánchez-Villagra (1992), suggested that the fossil species were not well differentiated from each other, with the only character that survived scrutiny being the posteriorly expanded carapace of *C. lewisi*, a character that was distinctly variable in the living species.

Description. — The shell is broad and low, variable in outline (usually oval or parallel-sided), with an exceedingly rough, sculptured surface in all except the oldest individuals. Moreover, the carapace has three knobby, tuberculate keels, each reaching a peak at the areola of each of the vertebral and costal scutes. The tip of vertebral 4 is the highest point of the carapace, and a deep trough is present between the median and each of the lateral keels. The nuchal scute is

broad and sculptured, hourglass-shaped or parallel-sided. Vertebral 1 is much wider than others in the series, the others decreasing in width towards the small vertebral 5. The margin of the carapace is sinuous or serrated, more strongly so posterior to the bridge. The marginal series is nearly uniform in height. The anterior extensions of the carapace and plastron are expanded but flattened rather than convergent, leaving a widely gaping anterior shell opening. The bridge is short (only about 25% of plastral width — much shorter than in the fossil species of *Chelus*), and the posterior buttresses are embedded into the visceral surface of pleurals 4—an unusually anterior position.

On the plastron, this short bridge corresponds to an unusually short interabdominal seam. The intergular scute is very variable in size and shape, and may or may not separate the gulars. Occasionally, a small median scute is present immediately posterior to the intergular. The interfemoral seam is the longest along the midline of the plastron. The posterior plastral lobe is narrow, with posteriorly converging, nearly straight sides. The anal notch is well developed; angular in juveniles, rounded in adults.

The head is extremely broad and flat, with the nostrils placed at the tip of a narrow, doubly-cylindrical, fleshy tube. The eyes are exceedingly small and anteriorly located. There is an extensive flap of skin behind the eye and above the tympanum on each side. The mouth is extremely wide in anterior aspect but shorter in lateral view. There are two short, flat papillae on the lower jaw directly beneath the orbits, as well as a transverse series of four complex skin flaps across the throat at the level of the tympanic membranes. The neck is long and very thick and muscular, with coarsely papillose skin and a series of flat, branched skin flaps along each dorsolateral margin.

The limbs are rather small and weak, and the digits are short and only slightly webbed. There are five claws on each forefoot and four on each hindfoot. All the limbs, as well as the tail, are liberally provided with rough, pointed scales separated by tough, papillose skin.

The bones of the carapace are moderately thick, especially along the ridges. The nuchal bone is hexagonal and, unusually among chelids, the neural bones are well developed and comprise a continuous series, typically of seven elements, sometimes 6 or 8. Neural 1 is elongate, and the mid-series neurals are approximately square, but often wider than long. Pleurals 8 meet on the midline, the junction forming the posterior slope of the posterior, highest vertebral tubercle. Sutures in this section of the shell are often highly asymmetrical. Peripherals number 11 pairs, the middle ones being penetrated externally by the triangular rib tips. Inter-costal fontanelles persist to a carapace length (CL) of 15–20 cm. A single, well-developed musk duct passes through the corners of each bridge, close to the sutural connection with peripherals 5 and 7. The free proximal rib-ends loop well away from the pleural bone in which each is embedded, providing a “tunnel” on each side for the powerful longissimus dorsi muscles. The entoplastron is variable in shape but longer than wide, and is crossed by the humero-pectoral

seam and sometimes by the posterior tip of the gulars and/or the intergular. In juveniles, plastral fontanelles are present behind the entoplastron; at the median junction of the hyo- and the hypoplastra; and between the hypo- and the xiphiplastra.

The skull is broadly triangular and extremely flattened; the upper surface is strongly concave in lateral profile. The orbits are very small, each less than half the vertical height of the cavum tympani. Nasal bones are absent and the premaxilla is single—both unique features among chelids. The temporal arch is moderate and is formed by the parietals contacting the squamosals. The supraoccipital process is greatly reduced. The exoccipitals are in broad contact above the foramen magnum. The rami of the lower jaw join mesially in a symphyseal suture, but never fuse. The hyoid apparatus is huge—each of the four rami is comparable in size and shape to a ramus of the lower jaw.

The head is dorsally a rich chestnut-brown, with the sculptured section directly over the parietal bones darker than the remainder of the head. A narrow, continuous dark line runs along the dorsal midline of the neck, and there is an interrupted or blotchy dark line on either side of the neck. There is a light area extending from the orbit down to the edge of the maxilla on each side. These markings continue below the mandible and diverge posteriorly on the skin between the mandibles to terminate below the tympanic membranes. The underside of the neck is often bright pink in color, with a pair of paramedian black bands in Amazon specimens but usually only small, obscure dark dots, or no markings at all, in those from the Orinoco or Essequibo. In hatchlings, the plastron is often red; in adults, it may be almost unmarked in Orinoco specimens but may be uniformly dark, or with dark radiating markings, in those from the Amazon.

The matamata is probably the largest chelid at least as regards average adult size, although close rivals include the Australian *Chelodina expansa* and *Elusor macrurus*. While males rarely exceed 40 cm in CL, adult females are typically larger than this. Wood (1976) found 19 unsexed adults to range between 31.1 and 40.4 cm CL, and I can offer no ready explanation for the turtles in this series being in general smaller than those field-collected specimens documented below (see discussion of sexual dimorphism), apart from the possibility that it was biased towards males. Many observers, familiar with good numbers of medium-size matamatas, have failed to realize how large adult females may be—Fretey (1977) considered two individuals of 36.5 and 39.8 cm CL to be of exceptional size and seemingly very old (although a third, 44.9 cm individual really was unusually large), and Dixon and Soini (1977) considered a 43.7 cm CL Peruvian specimen to be “extremely large”; whereas, it may in fact have been close to the average for adult females (see below). Nevertheless, some authors have exaggerated the maximum size, and there seems to be no basis for the claim of Beadnell (1948) that a matamata was “about a yard long”, nor for Goeldi’s (1906) claim of specimens 125 cm CL and 225 cm in total length.

The largest individual measured by Pritchard and Trebbau (1984), PCHP 1209 from Puerto Ordaz, Venezuela, measured 46.1 cm CL, and the largest of 105 measured by Sánchez-Villagra et al. (1995) was 46.0 cm CL (CEBHPs/n). These were exceeded by the largest of a series of 15 live adults from southern Guyana, that had a maximum CL of 46.4 cm, and a mass of 11.45 kg; the heaviest of this series was a 44.7 cm female with a mass of 11.70 kg. Barrio and Narbaiza (1999) reported a matamata from Puerto Ayacucho, Venezuela (EBRG 3596) with straight CL of 48.2 cm. Barrio-Amoros and Manrique (2006) reported a larger individual, also female, from the Río Apure, with CL length of 52.6 cm (midline 50.2 cm), and mass of 17.7 kg. The specimen was released alive.

Fiasson’s (1945) report of a 53 cm matamata requires some discussion. Elsewhere in his paper, Fiasson used the phrase “il est toujours question de la longueur de la carapace”, so we can be confident that the dimensions referred to CL, not to total length. A measurement over the curve is possible, but the shell of the matamata is so flat that this would only add a couple of cm to the length. Yet Fiasson’s report of a tortoise (*Chelonoidis carbonaria*) measuring 46 cm in length (longer than any known Venezuelan specimen of this species) but only 17 cm in width does lower his credibility.

Perhaps the matter may be settled by consideration of an extremely large skull (PCHP 2156), 15.0 cm wide, from San Carlos de Río Negro, Venezuela. In that a series of 10 adult Orinoco female matamatas with mean CL of 43.1 cm had mean skull width of 12.25 cm (maxima being 45.0 cm CL and 13.0 cm skull width), linear extrapolation would estimate a carapace length of 52.8 cm for PCHP 2156. If we used for comparison a series of nine southern Guyana adult females, whose mean CL was 44.25 cm and mean skull width 12.01 cm, we find an even greater estimated shell length for PCHP 2156, i.e., 55.27 cm—a length that places it in a league with typical fossils of *C. colombianus* and with the largest *C. lewisi* (Sanchez-Villagra 1992).

Hausmann (1968) found that captive-produced hatchlings weighed 15 g, increasing to 30 g within 2 months. Métrailler and Le Gratiot (1996) reported that hatchlings were about 49 mm in CL and 34 mm wide, with a mass of 15–19 g. Specimens estimated to be six months old had a mass of about 60 g, with CL of approximately 80 mm.

Sexual dimorphism is not especially marked in the matamata, but males are somewhat smaller, on average, than females, have longer tails with a more distally located vent, and tend to have a plastral concavity in the region of the junction between the femoral scutes. They are also characterized by frequent extreme sinuosity (asymmetry) of the midline sulcus in this area of the plastron.

A series of 12 adult males from Guyana had mean CL of 39.2 cm (range 37.4–41.9 cm), whereas 10 females had a mean CL of 44.4 cm. Average relative carapace width (CW) in the two samples was virtually identical; CL/CW 1.307 for the males, 1.298 for the females. In a series of 14 live adult males from Rancho La Trinidad, Estado Cojedes, Venezuela, the mean CL was 35.8 cm (range: 31.1–39.6 cm), whereas

the 9 females averaged 43.2 cm (range 40.8–45.0 cm). The observation that, in both of these series, males were both smaller and more numerous than females is in accord with the generalization proposed by Lovich and Gibbons (1990), stating that, in a given turtle species, the sex that reaches maturity earlier will not only remain smaller, on average, than the opposite sex, but will also outnumber it.

Sánchez-Villagra (1992) confirmed the tail-length sexual criterion mentioned above in his series of 105 museum specimens of extant *Chelus*, but found the plastral concavity to be rather variable, with some females displaying a certain concavity (e.g., MHNLS s/n), whereas some males had a more or less flat plastron (e.g., MCZ 4441). I can confirm this difficulty, finding that some of the largest females have a distinct concavity in the region of the mid abdominal and femoral region—sometimes with separate concavities in each of these areas—and that the tail length of adult males is quite variable.

Distribution. — The distribution of *C. fimbriatus* was mapped by Pritchard and Trebbau (1984) and by Iverson (1992) and includes parts of the nations of Colombia, Venezuela, Guyana, French Guiana, Brazil, Ecuador, Peru, Bolivia, and the island of Trinidad. More specifically, it includes the greater part, perhaps all, of the lowland parts of the Orinoco and Amazon River systems, and also the middle and upper Essequibo system of Guyana. Moreover, it occurs in Amazon flood or overflow areas west of Marajó Island through Amapá, Brazil, and the Oyapoque River of eastern French Guiana at least as far as Cayenne. Individuals found west of the Oyapoque may be current-driven, non-breeding individuals, as may be those that are occasionally found on the coast of Trinidad. Fretey (1977) suggested that many Cayenne specimens may have been brought to that city by human agency from Brazil, although he also recorded individuals from the mouth of the Sinnamary River and even from the swamps of the Mana River in northwestern French Guiana. Métrailler and Le Gratiet (1996) reported that, in French Guiana, matamatas had been observed in the east in the Oyapock and Approuague rivers, in the swamps of Kaw, and more rarely in the Kourou, Sinnamary, and Mana rivers, and at St-Jean. The species was also known from the old Marianne Polder and at Remire (J. Moonen, pers. comm.). The species may be absent from Suriname (Hoogmoed 1979), though there is one old and questionable record from there (Müller 1878). Pritchard and Trebbau (1984) mentioned a personal communication suggesting that the species may occur in the Maracaibo Basin, and this was indicated, with a query, on Iverson's 1992 range map. Rueda-Almonacid et al. (2007) reported confirmation of the presence of the matamata in Lake Maracaibo.

Habitat and Ecology. — The matamata is a highly aquatic, lowland tropical species, found equally in forested areas and in savannah river habitats such as those of the Rupununi in Guyana and the Venezuelan llanos. The species apparently occurs throughout the Amazon and Orinoco river systems, whereas in the Essequibo system of Guyana it occurs primarily in the far interior above the rapids, being scarce in

the middle Essequibo and absent near the coast. Pritchard and Trebbau (1984) reported that the matamata occurs in a variety of aquatic habitats, but the preferred situations are still waters of oxbow lakes and quiet inlets and ponds, and relatively small, slow-moving creeks. Individuals are regularly (and presumably passively) discharged from the mouth of the Orinoco, and some such turtles are washed up alive on the southern coast of Trinidad (H. Boos, pers. comm.), at times with numerous small barnacles on the shell testifying to the animal having survived marine conditions for a period of at least some weeks (pers. obs.). It was possibly through such oceanic transport that the species colonized the Essequibo River of Guyana.

The habitat of the matamata in Colombia was characterized by W. Lamar (pers. comm.) as follows: "I have collected adults by day, always sitting in mud adjacent to the steep aggrading bank of a llanos river; at night I have snagged them with long lines, although never have they ingested the bait... they hook themselves in a foot as they pass by. They seem to be most active during the dark of the moon. Juveniles are to be found in shallow eddies that offer some protection and, importantly, that have sandy substrates with numerous dead leaves partially embedded." Pritchard and Trebbau (1984) observed that the matamata, a rather weak swimmer, may avoid direct exposure to the current in riverine situations by taking refuge beneath undercut banks or beside or beneath submerged logs.

The matamata is an extremely specialized feeder, and the various somewhat bizarre modifications of the head and neck are all aspects or components of the unique adaptations for the detection and ingestion of moving prey (i.e., small fish) under conditions where vision is unimportant or inapplicable, such as night time or opaque silty waters. The modifications include the development of numerous skin flaps, tassels, and fringes in the cephalic region, that have been shown by Hartline (1967) to be extensively innervated and to be moved passively in response to minor perturbations of water near the head. Furthermore, the extreme size and wide separation of the tympanic membranes suggest further sensitivity to underwater vibrations, together with the ability to detect the direction of such disturbances. The extraordinary flattening of the head presumably facilitates the rapid, lateral feeding strike of the animal, a movement accompanied by rapid opening and closing of the extremely wide mouth and a powerful inrush of water (and prey) generated by the explosive expansion of the massive hyoid apparatus and the hypertrophied neck musculature. The latter is described in detail by Poglayen-Neuwall (1966). Pritchard (1984) discussed the various specializations of chelonians for piscivory, including a detailed account of *Chelus* and its feeding mechanism, anatomical specializations, and phylogenetic relationships. Functionally and ecologically, *C. fimbriatus* may be considered to play a similar role to the North American alligator snapping turtle (*Macrochelys temminckii*), as there are strong parallels between the two species, including the diet (live fish), feeding strategy (lie in wait), large size, strongly tuberculate carapace, and crypsis.

However, the head and mouth structures and the mechanisms for seizing or ingesting live prey are profoundly different in the two species.

Under typical conditions, where visibility approaches zero, the approach of potential prey to the head of the turtle is presumably fortuitous and dependant upon movements of the prey rather than the predator. However, under captive conditions where water clarity may permit location of prey by sight, the turtle may (literally) take active steps to facilitate prey capture. Fretey (1977) described the actions of a captive matamata, in a long aquarium, that positioned itself so that fish swimming the length of the tank could not avoid coming within striking range, and Holmstrom (1978) described “herding” behavior by captive matamatas, housed in an elongate, crescentic pool, that would slowly patrol the length of the pool with the body angled in such a way as to block most of its width. Fish would be confined into a progressively smaller space at one end of the tank, and ultimately would be forced to attempt to dash past the turtle, an action that often resulted in a successful catch by the turtle.

Despite the attention that has been paid to the feeding mechanisms of *Chelus* under captive conditions, almost no data are available to document the species of fish captured under natural conditions, with the exception of the observation by Métrailler and Le Gratiet (1996) that the most commonly taken prey species in French Guiana was the characin, *Erythrinus erythrinus*, typically with a length of between 20 and 25 cm. In view of the feeding response being a reflex reaction to a typically unseen disturbance, it is probable that prey selection occurs only to the extent of a rough evaluation of the size of the potential prey, there presumably being a lower and upper limit to the size of a proximate organism that would stimulate the feeding response, and with any fish in the habitat that fell between these size extremes being potential prey. In captivity, individuals may initially prefer live prey, but they usually adjust quite rapidly to ingestion of dead or chopped fish. Whether they ever take carrion under natural conditions is unknown.

Hausmann (1968) found that, in captivity, two matamatas grew from approximately 8 cm CL to 25–30 cm in nine years. Scute annuli are sometimes quite distinct, especially in specimens from savannah or llanos areas, where the food supply (i.e., live fish) is highly concentrated during the dry season, but so dispersed during the wet season that successful feeding may be rare enough as to cause seasonal cessation of growth. Examination of the scutes of certain individuals from the Orinoco (Venezuela) led Pritchard and Trebbau (1984) to conclude that a 28.1 cm CL individual was five years old, and an 18.6 cm individual was 5.5 years old, suggesting at least that growth rates may be quite variable. Examination of the annuli of three adult males from southern Guyana suggested that a 37.4 cm specimen was 14 years old, with significantly slowed growth during the last two years; that a 37.9 cm specimen was 16 years old, with the last five annuli very narrow and suggestive of slow growth; and that a 37.5 cm specimen was 11 years old, with no evidence of

slowing of growth. The age of other males was estimated as 10 yrs (38.8 cm); 11 yrs (39.1 cm); 12 yrs (38.0 cm); 15 yrs (40.0 cm); and 18 yrs (40.8 cm). The four females on which annuli were countable gave estimated ages of 13 yrs (43.8 cm); 15 yrs (44.1 cm); 20 yrs (43.5 cm); and 20 yrs (46.4 cm).

The potential longevity of the matamata is unknown. Slavens and Slavens (1990) documented survival of an individual for 12+ yrs at the Fort Worth Zoological Park (Texas), and Bowler (1977) reported survival of a wild-caught adult male matamata for 16+ yrs (and still alive) at the Turtle Back Zoo in New Jersey, but presumably they can live much longer than this.

The courtship of *Chelus* has not been described. Medem (1960) reported that nesting of *Chelus* occurred in October in the Colombian Amazon, and in November–December in the Rio Putumayo, with 12–28 eggs being laid per clutch, in river beaches or on high ground near the banks of small creeks. Twenty eggs were laid by a captive at the National Zoological Park (Washington D.C.), and 32 were laid by a recently acquired Guyana female at the Bronx Zoo in 1992. The eggs are hard-shelled and almost perfectly spherical. Fretey (1977) reported egg diameters of 34–40 mm, and Goeldi (1906) found that five Brazilian eggs averaged 37.2 x 34.3 mm.

The eggs may take a very long time to hatch—Hausmann found they required an average of 208 days, and Heinroth (1943) gave the captive incubation time as 9–10 months. In the wild, incubation and hatching are very probably quicker than this, in that, in many parts of the range, nest sites are liable to be inundated by floodwaters within just a few weeks or months of deposition; possibly hatching is stimulated by contact of the egg with rising waters, as it is with *Carettochelys* in rivers of New Guinea and northern Australia, and without such contact emergence may be very delayed. Nevertheless, there is evidence that the species nests very early in the dry season—October or November in Venezuela, according to Gonzalez Ortiz (in Mondolfi 1955), which might allow for a full five to six months before waters rose again.

In Venezuela, according to E. Mondolfi (pers. comm.), matamatas nest in clayey sand in steep river banks, rather than in open sandbanks. W. Lamar (pers. comm.), confirmed this, observing that, in Colombia, matamatas “utilize steep banks of leafy sand, rather than the usual sand beaches. In order to negotiate the grade, they climb in a sideways fashion. The nest site itself is nearly impossible to locate, although Indians (Guahibo, Curripaco, and Cuiva) unerringly locate them. The aforementioned applies to rivers; no doubt occupants of lagunas nest elsewhere.”

According to R. Augustus, a Warrau resident for much of the year in the Almond Beach area in northwestern Guyana, the matamata turtle occasionally emerges from the sea to nest on this beach. This occurs in the early dry season, after sea turtle nesting has finished. The ocean in this area is, at times, virtually freshwater, depending upon current patterns and the massive outflow from the adjacent Orinoco Delta. Such observations would lend support to the hypothesis that

the Essequibo system received its population of *Chelus* by marine transport from the Orinoco rather than through the close apposition of Amazonian and Essequibo tributaries in the southern Rupununi. This theory is further suggested by the close similarity between the Orinoco and the Essequibo matamatas, and their differences, especially in coloration and carapace outline, from those of the Amazon.

Few data are available on natural predation. At Karanambo, Guyana, on the Rupununi River, D. McTurk (pers. comm.) reported that adult matamatas are regularly brought ashore and sometimes killed by giant river otters. PCHP 2828, the bony shell of a 38.8 cm CL adult male matamata from Karanambo, was a victim of river otters. In Estado Cojedes, Venezuela, all but 5 of the 24 individuals we caught in a dry-season llanos pool had some kind of minor, healed mutilation—missing toes in almost all cases, and occasionally a missing foot, proboscis, or cephalic skin flap. Numerous predatory fish (including abundant *Serrasalmo* sp., the piranha) shared the habitat, and it is possible that the observed mutilations had been effected by these fish.

Population Status. — No quantitative data are available on matamata populations. Throughout most of its range, the species is generally rarely seen, or encountered only by chance on a one-by-one basis. However, this may be an artifact of a cryptic life style rather than rarity or low density per se. I encountered an unusual concentration of this species in a series of dry-season pools, part of the seasonally flowing Río Tinaco, a tributary of the Orinoco at Rancho la Trinidad, Estado Cojedes, Venezuela. At this locale, we caught 11 large individuals in the first landing of our seine, and in the course of 24 hours we caught 24 adults at the same site.

The size of some commercial shipments of matamatas suggests that commercial collectors may have discovered means of catching matamatas in quantity. For example, although the species is generally thought to be rare in Guyana, and there are very few museum specimens in existence from that country, an estimated 60 adult matamatas were commercially exported to the United States from Guyana in 1992, and about a decade earlier several hundred juvenile specimens had been illegally imported into California, where they were confiscated, deposited at the Los Angeles Zoo, and redistributed from there to zoos and other collections.

W. Lamar (pers. comm.) reported that, in Colombia, ornamental fisheries personnel collect large numbers of juvenile matamatas in their nets, especially in the vicinity of Puerto Inírida (Guainía) and around Caño Cabuyaro, a tributary of the Upper Meta (Meta/Casanare).

Threats to Survival. — The matamata, being a cryptic species of wide distribution and little esteemed for human consumption, does not appear to be under immediate threat. In most areas where it occurs, alternative species of turtle are available, especially *Podocnemis* and *Chelonoidis*, both of which are universally esteemed as food. The matamata is so malodorous when newly caught, so peculiar in appearance, and with such an unusual distribution of edible meat

(concentrated primarily in the neck, the limbs being small and weak) that most tribal or rural people in Venezuela, for example, dismiss it as “la fea” (the ugly one), and eat other, more normal looking turtles. However, in former times and other places, this may not have been the case. Sonnini and Latreille (1801) reported that the matamata was so avidly sought for its flesh around the Ile de Cayenne that it had become scarce and could not be found in abundance any closer than 25 leagues to the south of Cayenne.

As a living curiosity, the matamata is keenly sought by aquarists and turtle hobbyists in Europe and the United States. Such interest is centered primarily upon young specimens. Shipments totalling about 60 large adults exported from Guyana to Florida in 1992 were initially priced at retail at about \$1400 US per animal, but sales were not brisk, since the market for such expensive and large turtles was quickly saturated.

Conservation Measures Taken. — None, although it is theoretically protected by comprehensive wildlife protection laws and bans on export trade in Colombia, Venezuela and Brazil. In a few cases, matamata populations may be subject to nominal protection through their presence in National Parks or other protected areas (e.g., Xingu in Brazil, Manu in Peru, Iwokrama in Guyana, and Canaima in Venezuela).

Not listed on the IUCN Red List, nor in the CITES appendices. Included under Category NT (Near Threatened) in the Colombia Red List (Castaño-Mora 2002). Not listed in the Venezuela Red List (Rodríguez and Rojas-Suarez 1999). The matamata is protected by French legislation in French Guiana, but enforcement is inadequate (Métrailler and Le Gratiot 1996).

Conservation Measures Proposed. — None are considered urgent at this time, although certain factors, especially international trade in live animals and severe environmental degradation, should be monitored.

Captive Husbandry. — There are numerous matamatas in captivity, including hundreds of individuals in private hands. Slavens and Slavens (1990) recorded 117 individuals in captivity in the late 1980s. Captive husbandry presents no special demands, beyond provision of water of appropriate depth for the animal to be able to reach up to the surface to breathe without being forced to swim, and provision of live fish until the animal is willing to take dead or chopped prey. Matamatas seem to survive temperatures well below those they would ever encounter in the wild, but the lower limits of thermal tolerance have not been documented. Captive reproduction has not been achieved frequently, but has been reported by Heinroth (1943) and by Hausmann (1968). Much earlier, Duméril and Bibron (1835) noted that there were several matamatas from Cayenne in the natural history collection of the Pantheon (Paris), one of which had produced eggs, and at least one of these had hatched in that the hatchling was also present as a liquid-preserved specimen in the collection.

Current Research. — Marcelo Sánchez-Villagra of the Universidad Simon Bolívar (Sartenejas, Venezuela) is undertaking comprehensive, but primarily morphological,

studies of both the living and extinct species of *Chelus*. His initial findings have already been presented in the form of a thesis (Sánchez-Villagra 1992).

Wayne Hill of Winter Haven, Florida, has recently acquired a captive group of adult matamatas and several juveniles, for the purpose of behavioral observations and captive reproduction.

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