Geographic Variation in the Matamata Turtle, *Chelus fimbriatus*, with Observations on its Shell Morphology and Morphometry

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ABSTRACT. – A sample of 126 specimens of *Chelus fimbriatus* was examined for geographic variation and morphology of the shell. A high degree of variation was found in the plastral formula and in the shape and size of the intergular scute. This study suggests that the Amazon population of matamatas is different from the Orinoco population in the following characters: shape of the carapace, plastral pigmentation, and coloration on the underside of the neck. Additionally, a preliminary analysis indicates that the two populations could be separated on the basis of the allometric growth of the carapace in relation to the plastron.

KEY WORDS. – Reptilia; Testudines; Chelidae; *Chelus fimbriatus*; turtle; geographic variation; allometry; sexual dimorphism; morphology; morphometry; osteology; South America

The matamata turtle (*Chelus fimbriatus*) inhabits the Amazon, Oyapoque, Essequibo, and Orinoco river systems of northern South America (Iverson, 1986). Despite a moderately good generic fossil record (Wood, 1976; Bocquentin and Rancy, 1987; Bocquentin, 1988; Bocquentin and Santos, 1989; Sánchez-Villagra, 1992; Sánchez-Villagra et al., 1993, 1995) and the great interest shown in this species by herpetologists, naturalists, and turtle hobbyists (see Pritchard and Trebbau, 1984, for a review), there are no quantitative studies of its morphology and morphometry. Such studies are necessary to understand the individual and geographic variability of this turtle and to clarify the systematics of the fossil species of the genus.

Pritchard and Trebbau (1984) reviewed the few published growth data for South American pleurodires. Geographic variation has been mentioned in some published studies of the matamata, but the limited observations made have sometimes been based upon very small samples (e.g., Medem, 1960; Schmidt, 1966). This paper presents the results of a study of individual and geographic variation and various aspects of the morphology and morphometry of the shell of *Chelus fimbriatus*. Nomenclature of shell elements follows Pritchard and Trebbau (1984).

MATERIALS AND METHODS

A sample of 126 specimens (123 preserved and 3 living) of *Chelus fimbriatus* was examined. The sample embraced almost the entire known geographic distribution of the species (Fig. 1, and list of Specimens Examined). Twenty-one additional specimens from a single locality in the Estado Cojedes, Venezuela, were examined by PCHP and are used here only to show intrapopulational variability in intergular

scute morphology. Measured characters (in all cases straight-line) were: maximum carapace length (CL), carapace width at the level of the sixth marginal scute (CW), and midline plastral length (MPL; LSMV of Medem, 1976). Midseam length of the intergular (IG), gular (G), humeral (H), pectoral (P), abdominal (AB), femoral (F), and anal (AN) scutes was measured along the long axis of the plastron. Instead of measuring the gular scute along one of the contact seams between the gulars and the intergular (as in Lovich and Ernst, 1989), it was measured along the long axis of the plastron, as in Ernst and Lovich (1986). In the method of Lovich and Ernst (1989), the contact between the gulars (when present) is not considered, and a large amount of error is thereby introduced, in addition to the error introduced by the highly variable shape and size of the intergular. Variation in the plastral formula (PF) for each population was quantified using the "measure of plastral variation" (MPV; Lovich and Ernst, 1989) and measures of diversity were calculated using the Shannon-Weiner index (H'; Lovich et al., 1991). We used the Jaccard coefficient as a similarity measure to compare the plastral formulae of the Amazon and Orinoco samples (see Lovich et al., 1991).

Observations made by Medem (1960), Pritchard and Trebbau (1984), and in this work indicate that an analysis of geographic variation should include the following qualitative characters: intergular shape, color pattern on the ventral side of the neck, presence of dark plastral pigmentation, and carapace shape. The shape of the carapace was characterized dichotomously as follows:

– "rectangular," when the distal edges of marginal scutes 4–8 and the central long axis of the carapace are parallel; and

– "oval," when the parallel-sided section of the carapace is restricted to marginals 5–7,
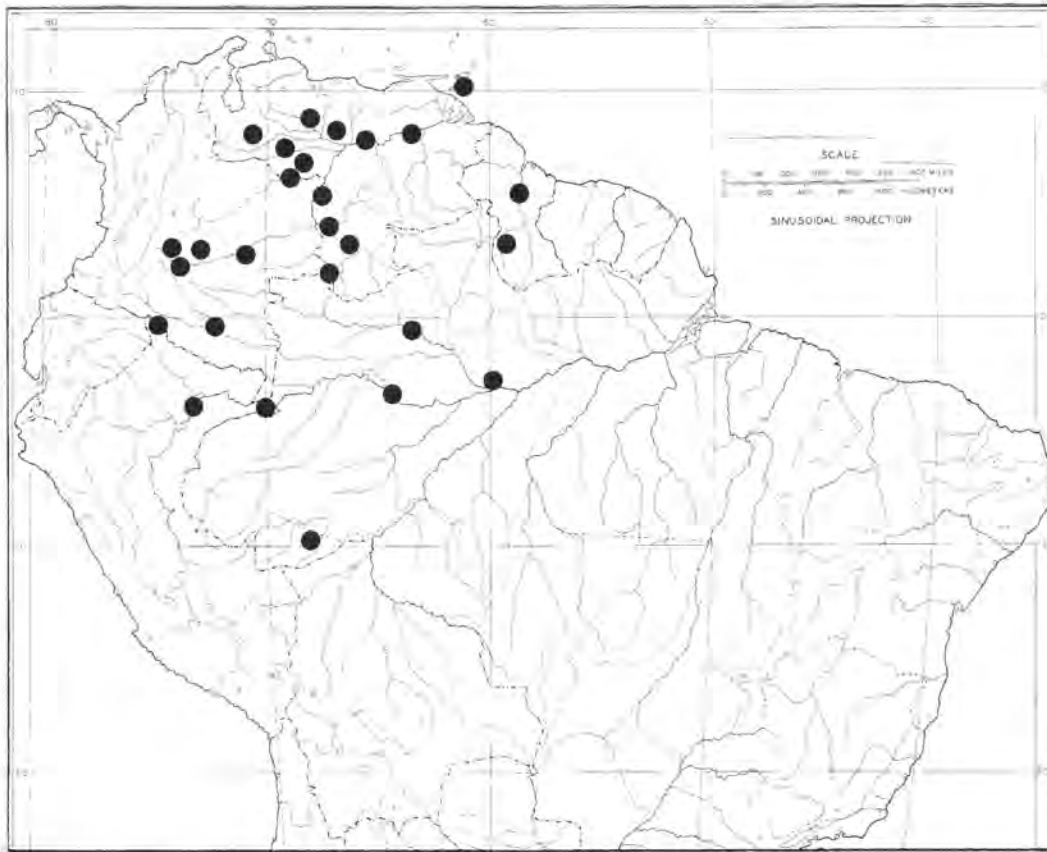
Figure 1. Map of northern South America showing the localities from which specimens were examined. Specimens of uncertain provenance were not included here.

A chi-square test was performed to examine the relationship of the shape of the carapace to the provenance of the specimens (Conover, 1980). Only specimens with CL longer than 145 mm ($n = 108$) were considered for this analysis, since hatchlings and small juveniles do not present a completely ossified shell with a well defined shape. Localities (except for outliers) were classified as belonging either to the Amazon or to the Orinoco river systems. Such division is justified by the observations of Medem (1960), Pritchard and Trebbau (1984), and those in this work. The Amazon and Orinoco hydrographic systems do make contact, with the Brazo Casiquiare in Venezuela the most important connection between the two (Sioli, 1984). Our sample does not include specimens from the Casiquiare.

Preliminary calculations were performed to test for differences between the Amazon and the Orinoco population in proportions of the shell during growth. Analyses of covariance ANCOVA (Sokal and Rholf, 1981) were performed using the statistical package BIOM® (Rholf, 1988). We used midline plastral length, MPL, as the covariate because of its relatively flat configuration, as straight-line carapace length measurements may not reflect hidden growth masked in its convexity and sculpturing (Ernst and Lovich, 1986; Lovich et al., 1990). The dependent variables were CL and CW, so two different sets of tests were performed. Plots of the data showed their relationships to be linear, with logarithmic conversions not necessary. After checking that

the slopes for the two populations were homogeneous in each case, ANCOVAs were performed. All variables were tested and found to be normally distributed.

The sex of many skeletal specimens was uncertain, so rigorous analysis of sexual dimorphism was not possible. Observations were made on the normal range of variation as well as abnormalities in the shell scutes or bones. Sample size for the analyses performed varies since the state of preservation of the specimens was heterogeneous (some consisted of shells without scutes, some were preserved in liquid so the bony sutures could not be seen, etc.). Additionally, the complete sample could not be used for the analysis of geographic variation, as 38 specimens were of unknown locality.

RESULTS

Morphology and Morphometry

Neural Bones. — *Chelus* is unusual among chelids (as is *Hydromedusa*) in having well-developed neural bones forming a continuous series. They are unusually thick, dorsally forming a wide, tuberculate keel. Ventrally the neurals provide part of the concavity on each side of the midline that, together with contributions from the pleurals and the free proximal part of the ribs, constitutes the tunnel-like channel that houses the *longissimus dorsi* muscles.
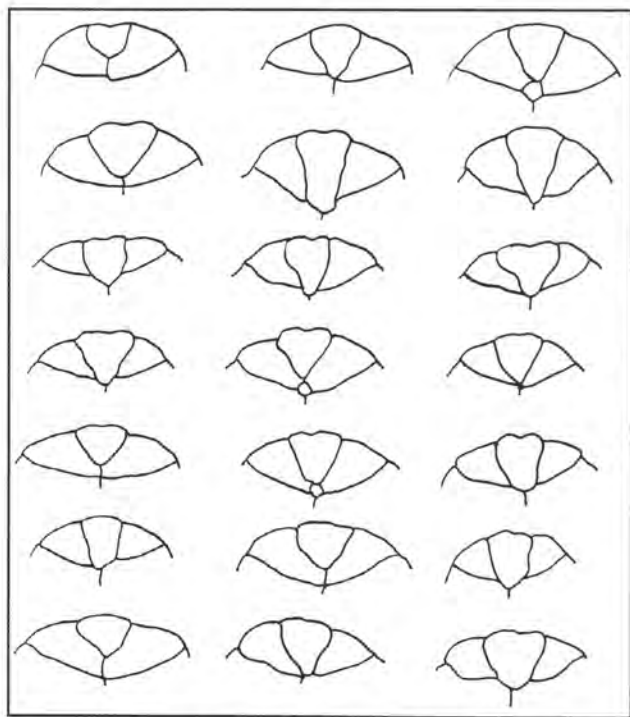
Figure 2. Intergular shape variation in a single population of *Chelus fimbriatus* from Estado Cojedes, Venezuela. The drawings are not to scale.

The typical condition of seven neurals was found in 38 out of 44 (86%) specimens examined. Five individuals in the sample have eight neural bones, either by the transverse division of neural I (PCHP 39, FSM 22266) or of neural VII (AMNH 5911, PCHP 1209) or by the insertion of an azygous element beside neural I (PCHP 38).

Pleural Bones. — The pleural bones of *Chelus* normally number eight pairs (nine on the left side in PCHP 1209 because of a subdivision of the last pleural). Even a single, isolated *Chelus* pleural bone is immediately identifiable by its unique and highly distinctive sigmoid shape. The first pair of pleurals is anteriorly elongated, as are the first neurals, the nuchal bone, and the neighboring peripherals. There is some tendency towards alternation in width of the proximal and distal ends of subsequent pleurals, with pleural III having a widened proximal end (corresponding to the elongated vertebral III), and pleurals II and IV being distally widened.

In one individual (PCHP 1230), represented only by an incomplete set of shell bones, two of the left pleural bones (III and IV) have become completely fused, although all other bony sutures in this relatively small (CL ca. 310 mm) male were unfused. Many of the carapace bones of this specimen showed severe pitting, similar to that illustrated by Zangerl (1969) for the fossil cheloniid *Oligochelone rupeliensis*, but the erosive disease does not appear to have caused this isolated unilateral bony fusion.

In nearly all cases (44 of 48, 92%), the eighth pleurals meet behind the last neural, separating the latter from the single triangular suprapygal. There is no contact between the last pleurals in four specimens (AMNH 5911, AMNH 70638, PCHP 39 (Fig. 3), PCHP 1038), in which the last neural contacts the suprapygal.

Marginal Scutes and Peripheral Bones. — Most of the specimens showed 12 pairs of marginal scutes (86 of 90, 96%). Only four specimens (AMNH 70638, MCNM unnumbered. MCNUSB 426. PCHP 1209) had 13 pairs, in all cases resulting from a division of the twelfth scutes. Speci-

Figure 3. Different shapes of the carapace in Amazon (left) and Orinoco (right) matamatas. **Left:** PCHP 39, from the vicinity of Leticia, Colombia. **Right:** MCNUSB 427, from the Venezuelan Llanos.
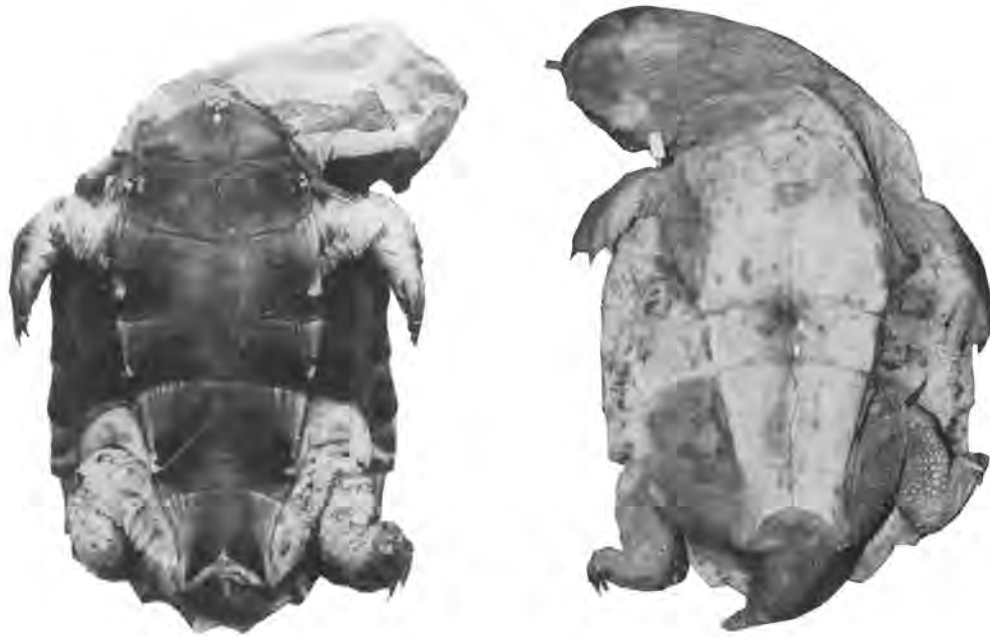
Figure 4. Differences between the Amazon (**Left:** PCHP 3403) and the Orinoco matamata (**Right:** EBRG 2006). The Amazon matamatas present the following characteristics absent in the Orinoco populations: rectangular shape, dark plastral pigmentation, and two dark bands running along the underside of the neck separated by light areas. These differences are consistent throughout growth.

men EBRG 2005 shows 11 marginals instead of 12 on the right side. On the left side there are nine normal marginals, in addition to two very small ones, which correspond to portions of the last marginals of the whole set. In this specimen, as the last marginal scutes are not present, the fifth vertebral scute forms part of the posterior margin of the carapace.

One individual (PCHP 38) represents a case of complete fusion of two bones in an otherwise open-sutured animal. In this individual the sixth right peripheral and the right hypoplastron are represented by a single bone. The fusion was either congenital or occurred very early in life, since loss of a growth zone in the right bridge caused a unilateral deep concavity to form in this area of the shell.

Bridge. — The bridge of *Chelus* is narrow antero-posteriorly, but the buttresses are very strong and unite the plastron firmly and immovably with the carapace. The axillary buttresses are towards the rear of the first pleurals, but the inguinal buttresses, which ankylose with pleurals IV about midway between their anterior and posterior margins, are uniquely far forward.

Maximum Size. — The sample of *C. fimbriatus* examined in this work includes several specimens with CL greater than 400 mm, the largest being CEBHP unnumbered, with a CL of 460 mm. PCHP has recently measured a female matamata from Guyana with a CL of 464 mm. A matamata skull from San Carlos de Río Negro, Amazonas State, Venezuela (PCHP 2156), measures 150 mm in maximum width. The head width of ten adult females from the Orinoco system (CL = 408 to 450 mm; mean = 431 mm) ranged from 115 to 130 mm (mean = 122.5 mm). Assuming similar proportions between the average of these ten females and PCHP 2156, the latter could have had an estimated carapace length of 528 mm but may also simply have been abnormally megacephalic.

Intergular Scute and Plastral Formula. — In 66 out of 120 specimens examined (55 %) the intergular scute separates the gulars. If samples are examined according to locality, the following results are found: of 29 specimens from the Amazon system, 16 (55.2 %) had the intergular separating the gulars; of 41 from the Orinoco system, 23 (56.1 %) had the same characteristic.

There is significant intrapopulational variability in the shape and relative size of the intergular scute. Figure 2 illustrates such variation from a single population at Hato La Trinidad, Estado Cojedes, Venezuela.

The matamata exhibits extensive variation in its plastral formula. Table 1 presents the 42 plastral formulae (PF) found in a sample of 95 matamatas. However, this documented variation represents only 0.83% of the hypothetical maximum variation assuming random arrangement (5040 permutations, not including ties). Measures of variation in the PF are summarized in Table 2 according to locality and for the total sample. The Jaccard coefficient for the comparison between the Amazon and Orinoco populations was 0.109. The measures of plastral variation for the entire sample of 95 matamatas are MPV = 0.44 and H' = 1.529. In spite of the considerable variation in the PF of the specimens examined, certain midseam scute lengths ranked consistently: the femoral was always the longest and the gular the shortest (with one exception); the anal was second shortest in 76 of 95 specimens (80%). This suggests that the variabil-

Table 1. Plastral formulae (PF) in a sample of matamatas (*Chelus fimbriatus*). See abbreviations for the plastral scutes in the text.

Plastral Formula	Amazon	Orinoco	Unknown	Total
F > IG > AB > P > H > AN > G	1	5	0	6
F > H > P > AB > IG > AN > G	3	1	2	6
F > P > AB > IG > H > AN > G	1	2	2	5
F > IG > P > AB > H > AN > G	0	2	3	5
F > H > IG > P > AB > AN > G	0	3	2	5
F > H > P > IG > AB > AN > G	1	1	3	5
F > H > AB > P > IG > AN > G	3	1	0	4
F > P > IG > H > AB > AN > G	2	0	2	4
F > P > IG > AB > H > AN > G	1	0	3	4
F > P > H > IG > AB > AN > G	2	0	2	4
F > IG > H > P > AB > AN > G	0	1	2	3
F > P > AB > H > IG > AN > G	3	0	0	3
F > AB > P > H > AN > IG > G	0	3	0	3
F > IG > H > AB > P > AN > G	0	2	0	2
F > IG > P > H > AB > AN > G	2	0	0	2
F > IG > P = AB > AN > H > G	0	2	0	2
F > H > P = AB > IG > AN > G	0	2	0	2
F > P > H > AB > IG > AN > G	1	0	1	2
F > P > AB > H > AN > IG > G	0	0	2	2
F > AB > IG > P > H > AN > G	0	1	1	2
F > AB > H > P > IG > AN > G	1	0	1	2
F > AB > P > IG > H > AN > G	0	2	0	2
F > IG > H = P > AN > AB > G	1	0	0	1
F > IG > P > H > AN > AB > G	1	0	0	1
F > H > IG > AB > P > AN > G	1	0	0	1
F > H > P = IG > AB > AN > G	0	1	0	1
F > H > P > AB > AN > IG > G	0	0	1	1
F > H = P > IG > AN > AB > G	0	0	1	1
F > H = P > AB > IG > AN > G	1	0	0	1
F > H = P > AB > AN > IG > G	0	0	1	1
F > H > AB > IG > P > AN > G	0	1	0	1
F > H > AB > P > AN > IG > G	1	0	0	1
F > P > IG > AB > AN > H > G	0	1	0	1
F > P > IG > AN > H > AB > G	0	1	0	1
F > P > IG = H > AN > AB > G	0	1	0	1
F > P > H > AB > AN > IG > G	0	1	0	1
F > P > AB > H > AN > G = IG	0	1	0	1
F > P = AB > H > IG > AN > G	1	0	0	1
F > AB > IG > P = H > AN > G	0	1	0	1
F > AB > H > IG > P > AN > G	0	0	1	1
F > AB > H > P > AN > G > IG	0	1	0	1
F > AB > P > H > IG > AN > G	0	0	1	1

Table 2. Measures of variation in plastral formulae (PF) of the matamata sample organized by locality. Refer to text for computational details and abbreviations.

|	Amazon	Orinoco	Unknown	Total
Sample size	27	37	31	95
Plastral formulae	18	23	-	41
MPV	0.67	0.62	-	0.44
H'	1.205	1.299	-	1.529

system (EBRG 8867: Los Paragüitos, Río Meta, Apure State, Venezuela; EBRG 5020: Santa Bárbara, Departamento Atabapo, Amazonas State, Venezuela). Two Amazonian specimens with confirmed localities in which the ventral neck coloration could be seen demonstrated the pattern of dark stripes (FSM 52499, FSM unnumbered).

Strong pigmentation of the plastron was found in all eight specimens from the Amazon river system where this character could be seen clearly. This strong pigmentation contrasts with the paleness of the plastron characteristic of all the Orinoco specimens examined (Fig. 4).

Figures 5A and 5B illustrate the relative growth of the CL and CW against the MPL for the Amazon and the Orinoco samples. The slopes in the two cases were homogeneous; both the F values for the MPL vs. CL case ($F = 1.785$; d.f. = 44) and the MPL vs. CW case ($F = 2.892$; d.f. = 48) were non-significant, so the null hypotheses of homogeneity of slopes were not rejected. On the other hand, the null hypothesis that there are no differences between sample means was rejected in each case. For the case of MPL vs. CL, the F value was 11.815 (d.f. = 44; $P < .005$); the F value for the MPL vs. CW case was 20.573 (d.f. = 48; $P < .001$). These preliminary results suggest that there are significant differences between the Amazon and Orinoco populations in their carapace–plastron allometry.

ity in the PF of *C. fimbriatus* is due to different combinations of lengths in the humeral, pectoral, and abdominal scutes, and to the highly variable shape and size of the intergular scute.

Geographic Variation

Carapace Shape, Neck Coloration, Plastral Pigmentation, and Relative Growth. — There is a strong correspondence between the carapace shape of the matamatas examined and their provenance (chi-square, $\chi^2 = 30.4 > \chi^2_{0.001} = 10.83$). Twenty-one of 25 Amazonian specimens are "rectangular," and 37 of 44 Orinoco specimens are "oval" (Figs. 3 and 4).

The color pattern on the ventral side of the neck could be seen in 15 specimens from the Orinoco river system, and 13 of these lacked the pattern of dark stripes described by Pritchard and Trebbau (1984) for Amazonian matamatas (Fig. 4). The other two Orinoco specimens (both very young, see discussion) were from localities adjacent to the Amazon

DISCUSSION

Sexual Dimorphism. — Sexual dimorphism in the matamata is noteworthy, although we could not perform a rigorous study. Pritchard and Trebbau (1984) reported that male matamatas have slightly longer tails than females. Most of the specimens we examined were shells, so this character alone could not be used in the determination of sex. Furthermore, this is a characteristic that can be used only in a relative way, and tail length in the adults examined was not unequivocally bimodal. We have also observed that the degree of concavity in the plastron is not a reliable sex determinator in the matamata. Some females show a concavity (e.g., MHNLS unnumbered) and some males show a rather flat plastron (e.g., MCZ 4441), although in some cases the concavity is deep enough to be reasonably certain that the specimen was male, especially when a long tail was also present. Pritchard and Trebbau (1984) reported that females are generally slightly larger than males, and PCHP found that, in the Estado Cojedes sample of 21 specimens, adult females were all over 400 mm in CL and males were all shorter than 400 mm. Nevertheless, males occasionally reach
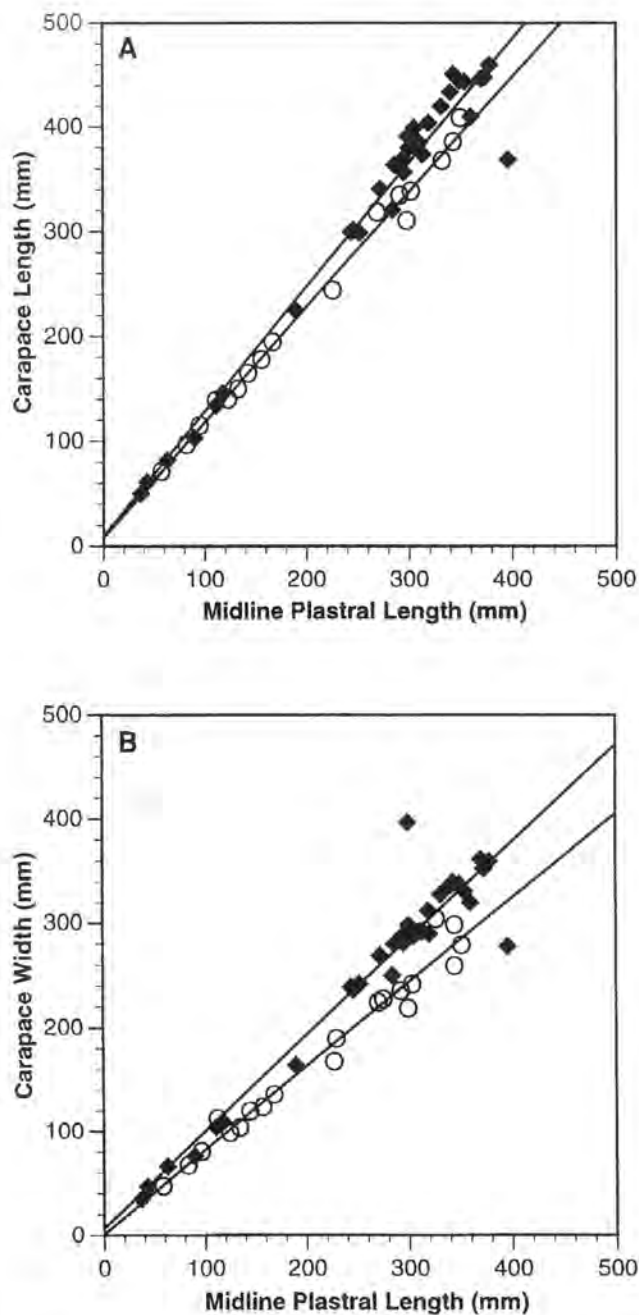
Figure 5. Relationship of midline plastral length (MPL) with **A**. Carapace length (CL); **B**. Carapace width (CW) for the Amazon (○) and the Orinoco (◆) samples of *Chelus fimbriatus*.

extreme size. In most Australian chelid species the females are larger than males, except for *Pseudemydura umbrina* (Berry and Shine, 1980) and the new genus and species from southern Queensland, *Elusor macrurus* (Cann and Legler, 1994). In the case of *Platemys platycephala*, a South American chelid, the males average slightly larger than females (Pritchard and Trebbau, 1984). Our preliminary data suggest that female matamatas are larger than males (Sánchez-Villagra, 1992).

The distance between a xiphiplastral tip and the closest point of the carapace and the width across the xiphiplastral tips are variables that have been useful in establishing sexual

dimorphism in some turtles. Sánchez-Villagra (1992) failed to find any difference between the sexes for these variables in *C. fimbriatus*. The posterior shell opening is very wide and deep in *C. fimbriatus*, so adaptations in this regard to facilitate oviposition (in females) or copulation (in males) are perhaps unnecessary. Only with a larger sample of matamatas of known sex will it be possible to make detailed studies of sexual dimorphism as in Gibbons and Lovich (1990) and Lovich and Gibbons (1992).

Size. — The greatest size reached by *Chelus fimbriatus* is a question of some interest, since Wood (1976) based the two known fossil species of the genus, in part, upon their reaching a distinctly greater size than *C. fimbriatus*. Our data and the review of Pritchard and Trebbau (1984), show that Wood's series of 19 specimens of *C. fimbriatus* underestimated the maximum size actually reached by the living species (see also Sánchez-Villagra et al., 1995).

Goode (1967) gave carapace lengths of five adult *Chelodina expansa* (an Australian chelid) that ranged from 350 mm to 423 mm, with an average of 374 mm. Pritchard and Trebbau (1984), quoting Cann's (1978) record of CL = 480 mm for a specimen of this species, concluded that *Chelodina expansa* was the world's largest chelid. However, having now established that a CL of about 450 mm is quite common in mature *Chelus fimbriatus*, with a documented maximum of 464 mm, and a possible maximum of 530 mm (Fiasson, 1945, and estimation of CL of PCHP 2156), it is possible that *C. fimbriatus* may be the largest living chelid. Some fossil *Chelus* were considerably larger than this, the largest recorded being a specimen of *C. colombianus* (MPV 120) with a CL of 680 mm (Sánchez-Villagra et al., 1995).

Cann (1978) stated that a particularly large specimen of *Chelodina expansa* weighed 10 kg, although Goode (1967) gave 5.5 kg as a "not unusual" weight for a *C. expansa* of typical adult length (CL = 381 mm). The largest living matamata measured here, a female of CL = 441 mm, weighed 10.6 kg (a specimen of CL = 410 mm weighed 8.6 kg), and PCHP has recently weighed an 11.7 kg live female matamata from Guyana of CL = 447 mm.

Intergular Scute and Plastral Formula. — The results of this study of the intergular scute agree with the conclusions of Hoge (1952), Fretey (1977), and Pritchard and Trebbau (1984), with regard to the high variability of this character, both intra- and inter-populational, and its lack of taxonomic value.

Pritchard and Trebbau (1984) and Ernst and Barbour (1989) have pointed out that the femoral scute is always the longest when considering the plastral formula (PF) of *C. fimbriatus*, an observation which has been corroborated in this work.

Variation in the PF for our total sample of *C. fimbriatus* (H': 1.529) is similar to that found for *Platemys platycephala* (H': 1.409) by Lovich and Ernst (1989), the only other chelid for which this information is available. The degree of similarity of the plastral formulae between the Amazon and

Orinoco samples, as measured by the Jaccard coefficient, is lower than that found on average by Lovich et al. (1991) for different species of *Clemmys* of the same sex. What these comparisons mean in terms of their utility for taxonomy or systematics awaits a better understanding of the degree of morphological variation in PF across chelonian taxa. A discussion of the limitations and problems of using these indices was presented by Lovich et al. (1991).

Geographic Variation. — Pritchard and Trebbau (1984) reviewed the literature on geographic variation in the matamata and found differences in the overall shell shape of Amazon and Orinoco specimens. Medem (1960) recognized a character that has been used in this work to distinguish the Amazon and the Orinoco matamatas, namely the presence in the former of two very strong black bands running along the underside of the neck, separated by light (often red) areas.

It is noteworthy that several specimens did not fit the pattern of geographic variation described above (see below for specimen numbers). Some of them have locality records that show they came from wildlife trade centers, in which case the alleged origin may not exactly represent the site of capture. For example, ICN 6411 comes from Leticia, Colombia, which for years was an export center for reptiles from a large area of southern Colombia and adjacent countries.

Most of the specimens that do not follow the overall pattern of geographic variation come from localities close to the contact between the Amazon and Orinoco systems. Examples include: MCZ 4468 (Rio Negro, Brazil), EBRG 2004 (Puerto Ayacucho, Venezuela), and HM unnumbered (Río Capanaparo, Venezuela). Most of these specimens show a mosaic of "Amazon" and "Orinoco" characters, and the presence of such intermediates suggests a subspecific relationship between the two forms. A formal description of these subspecies is in progress by PCHP and MRSV, who will incorporate additional data to document this distinction.

Even though plastral pigmentation is a character that varies ontogenetically (MRSV, *pers. obs.*), there is certainly a difference between the Amazon and the Orinoco matamatas in this regard for both juveniles and adults. Six specimens of unknown locality (ICN 1769, PCHP 3403-4, 3406, 3631, and USNM 104338) show all the characteristics that distinguish Amazon matamatas from Orinoco ones (Fig. 4). This fact alone obviously cannot be used to confirm the pattern of geographic variation presented here, since the specimens are of unknown locality. However, it is significant that all of them present the three characteristics of the Amazon population together, rather than as a mosaic of features. The most important current connection between the Amazon and the Orinoco systems, the Casiquiare (which links the Río Negro with the Orinoco), is perhaps quite recent in origin (see Pilleri and Gihr, 1977). On the other hand, some have suggested that these systems were connected throughout the Tertiary (e.g., Pilleri and Gihr, 1977), but these authors do not give any explanation or argument on which this hypothesis might be based.

The differences between the Amazon and Orinoco samples in the allometric growth of the shell should guide future research in this area. Our results are interpreted as preliminary since the two samples examined were relatively small.

Acknowledgments

SPECIMENS EXAMINED

Specimens from the following collections were examined: Colombia: Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN); Museo Paleontológico de Villavieja, Huila Department (MPV); Venezuela: Acuario de Valencia, Carabobo State (ACV); Colección Estación Biológica Hato Piñero, Cojedes State (CEBHP); Estación Biológica de Rancho Grande, Aragua State (EBRG); Hato Masaguaral, Guárico State (HM); Museo de Ciencias Naturales de Caracas, Caracas D. F. (MCNC); Museo de Ciencias Naturales Mataclara-Manfauna, Cojedes State (MCNM); Museo de Ciencias Naturales de la Universidad Simón Bolívar, Miranda State (MCNUSB); Museo de Historia Natural La Salle, Caracas D.F. (MHNLS); Museo del Instituto Oceanográfico de la Universidad de Oriente, Sucre State (UOIO); Parque del Este Rómulo Betancourt, Caracas D.F. (PERB); USA: American Museum of Natural History, New York (AMNH); Florida Museum of Natural History, University of Florida, Florida (FSM); Museum of Comparative Zoology, Harvard University, Massachusetts (MCZ); Peter C.H. Pritchard, personal collection, Oviedo, Florida (PCHP); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

Bolivia: Santa Fé, Departamento Beni: AMNH 97151; **Brazil**: Amazon River: USNM 222550; Manaos, Amazonas: USNM 28974; Tefé, Amazonas: MCZ 4441; Rio Amazonas: MCZ 1238; Rio Branco: USNM 064154; Rio Negro: MCZ 4468; São Paulo: MCZ 2545 (uncertain); unknown locality: MCZ 4028, PCHP 1910; **Colombia**: Araracuara, Amazonas: ICN 1764; Leticia, Amazonas: FSM 21977, ICN 1768, 1772, 1774, 6411, 6452, PCHP 36-39; Barranquilla: FSM unnumbered (uncertain); Alto Río Guaviare, Guaviare: ICN 1776; San José del Guaviare, Guaviare: ICN 1763, 1766, 1775, 1778-80; Hacienda Guadalajara, Meta: ICN 6450; La Macarena, Caño Losada, Meta: ICN 1777; La Macarena, alto Río Guayabero, Meta: ICN 1765, 1767; Río Guejar, Viso El Piñal, Meta: ICN 1781; Puerto Leguízamo, Río Putumayo, Putumayo: ICN 1770, 1773; unknown locality: FSM 52499; **Guyana**: Essequibo River, Rockstone: PCHP 1823; Rupununi River, Karanambo: PCHP 2828; **Peru**: Caño Shanso, S. of Río Ampiyacu, Loreto: USNM 101103; Iquitos, Loreto: AMNH 58143, 58145; N. of Itaya, Loreto: AMNH 70597; unknown

locality: PCHP 1037-39; **Surinam**: unknown locality; MCZ 4696; **Trinidad**: Blanquizales Swamp: PCHP 1824; **Venezuela**: *Amazonas*: near Cerro Duida, La Esmeralda: PCHP unnumbered; Puerto Ayacucho, Agualinda, Carretera El Burro: EBRG 2004; San Carlos de Río Negro: PCHP 1210, 2156; Santa Bárbara, Departamento de Atabapo: MHNLS 5020; unknown locality: HM unnumbered A; *Apure*: Caño Guaritico, El Samán: MCNUSB 427; Caño Macanillal, Hato El Frío: captured and released individual; Mata de Silva, Hato El Frío: MCNUSB 426; Río Capanaparo, Médano Alto: EBRG 1051-52; Río Capanaparo, San Luis: HM unnumbered; Río Meta, Los Paragüitos; MHNLS 8867; *Barinas*: Reserva Forestal de Ticoporo, Campamento Río Quiú: EBRG 2048; unknown locality: PERB unnumbered; *Bolívar*: Caicara: AMNH 43298, 43305; 4 km N. of Río Villacoa, Río Orinoco: EBRG 2005-7; cu. 35 km S. of Ciudad Guayana: PCHP 1209; *Cojedes*: Hato La Trinidad, Río Tinaco: PCHP 1229-30, 1335-37, 2157-58, 2444-46, Hato Piñero, El Baúl: Pedro Borges personal collection unnumbered; Caño San Jerónimo, El Baúl: CEBHP unnumbered A-C, MCNM unnumbered A-B; unknown locality: ACV unnumbered A-B (alive); *Guarico*: Distrito Miranda, Río Guariquito: MCNC 6998; **Unknown Locality**: AMNH 5911, 58142, 58144, 70638, 81878, 114711, FSM 22266, 56891-92, 60342, 63849, 67620, FSM unnumbered, HM unnumbered B, MHNLS unnumbered A-C, PERB unnumbered A-B, PCHP 40, 42-43, 3265, 3403-4, 3406, 3631, UOIO unnumbered, USNM 065507, 075323, 102883, 104338, 117454-55, 301989-92.

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