Article

urn:lsid:zoobank.org:pub:AC004567-7D4D-4508-A082-AA2635A734C2

Taxonomic validity of *Mesoclemmys heliostemma* (McCord, Joseph-Ouni & Lamar, 2001) (Testudines, Chelidae) inferred from morphological analysis

FLAVIO B. MOLINA[1,2], FABIO A. MACHADO[1,3] & HUSSAM ZAHER[1,4]

[1]*Museu de Zoologia, Universidade de São Paulo, Avenida Nazaré 481, Ipiranga, São Paulo, 04263-000, SP, Brazil.*

[2]*Universidade de Santo Amaro, Campus I, Rua Prof. Enéas de Siqueira Neto, 340, Cidade Dutra, São Paulo, 04829-300, SP, Brazil. E-mail: fbmolina@uol.com.br*

[3]*Programa de Genética e Biologia Evolutiva, Universidade de São Paulo, Rua do Matão, trav.14, Cidade Universitária CP 11.461, CEP 05422-970, SP, Brazil. E-mail: macfabio@gmail.com*

[4]*Corresponding author. E-mail: hussam.zaher@gmail.com*

Abstract

Mesoclemmys heliostemma (Testudines: Chelidae) was described based on five vouchered specimens and nine live specimens from the western Amazon basin. Some authors questioned its status as a valid species, suggesting that it represents a junior synonym of *M. raniceps*. Here, we report on eight additional specimens from eastern Peru and northern Brazil, and provide descriptive statistics of morphological characters for hatchlings, juveniles, and adults of *M. heliostemma, M. raniceps*, and *M. gibba*. We also test for group differences through univariate and multivariate statistical analyses, and discuss some advantages of this methodology. Our data suggest that all three taxa are morphologically divergent, and that *M. heliostemma* is a valid species.

Key words: taxonomy, range extension, morphometrics

Introduction

The genus *Mesoclemmys* (Testudines: Chelidae) includes ten species of freshwater side-necked turtles that are distributed from northern Colombia to northeastern Argentina (Bour & Zaher, 2005). Four species are present in the Amazonas River basin: *M. gibba* (Schweigger, 1812), *M. nasuta* (Schweigger, 1812), *M. raniceps* (Gray, 1855), and *M. heliostemma* (McCord, Joseph-Ouni and Lamar, 2001). These turtles are bottom dwellers that live preferentially in lentic waters, being found mainly in small forest streams, creeks, ponds, and muddy swamps (Medem, 1960; Dixon & Soini, 1977; Mittermeier *et al.*, 1978; Pritchard & Trebbau, 1984; Métrailler & Le Gratiet, 1996; Vogt *et al.*, 2009; Ferronato *et al.*, 2011). *Mesoclemmys heliostemma* seems to prefer water bodies on high, non-flooded forest areas (McCord *et al.*, 2001; Cisneros-Heredia, 2006). All four species are primarily nocturnal and carnivorous, usually eating fishes, tadpoles, and a large variety of invertebrate species like insect larvae and crustaceans (Mittermeier *et al.*, 1978; Pritchard & Trebbau, 1984; Métrailler & Le Gratiet, 1996; Rueda-Almonacid *et al.*, 2007). *Mesoclemmys raniceps* is a mollusk specialist, eating mainly on gastropods (Fachin-Teran *et al.*, 1995). Vegetal material seems to be occasionally ingested, at least by *M. gibba*, *M. nasuta*, and *M. raniceps* (Mittermeier *et al.*, 1978; Métrailler & Le Gratiet, 1996; Rueda-Almonacid *et al.*, 2007; Vogt *et al.*, 2009).

Mesoclemmys heliostemma was described in 2001, based on specimens from localities in northeastern Peru, eastern Ecuador and southern Venezuela (McCord *et al.* 2001). The species is sympatric with *M. gibba* and *M. raniceps* (McCord *et al.* 2001; Bour & Zaher 2005) and is morphologically similar to the latter (McCord *et al.* 2001). According to McCord *et al.* (2001), *M. heliostemma* can be distinguished from *M. raniceps* by possessing a narrower head (head width represents 25% of carapace length in juveniles), a broader parietal roof (parietal width represents 15% of head width in juveniles, presumably 10-12% in adults), a more substantial parieto-squamosal arch, an intergular scute narrower than the gular scutes, a flatter shell, a more rounded carapace (maximum width at marginal 7th), and the 11th pair of marginal scutes equal to or wider than the supra-caudal pair. These authors also

highlighted the presence, in some juveniles, of bright yellow-orange facial bands, extending from the tip of the nostrils to the scales dorsal to the tympani, in a somewhat V shaped form.

From the diagnosis provided by McCord *et al.* (2001), juvenile head color pattern, head width, and parietal width seem to be the most important diagnostic characters for *M. heliostemma*. The head pattern of *M. raniceps* and *M. gibba* is remarkably distinct. In *M. raniceps*, a dorsal pair of black lines is present from the eyes to the occipital region, and a lateral pair is present from the nostrils to the tympanic region (Bour 1973; Lescure & Fretey 1975; Bour & Pauler 1987). In *M. gibba*, no band or line is seen, but many gray or beige spots are present (Pritchard & Trebbau 1984; Bour & Pauler 1987). However, head coloration as a diagnostic character is limited only to young and some juvenile specimens of *M. heliostemma* since it is lost in subadults and adults (McCord *et al.* 2001). Head and parietal width are important characters for identifying *Mesoclemmys* species (Luederwaldt 1926; Zangerl & Medem 1958; Bour 1973; Pritchard & Trebbau 1984; Bour & Pauler 1987; McCord *et al.* 2001; Bour & Zaher 2005), but McCord *et al.* (2001) did not analyze ontogenetic variation. As they pointed out, only small to large juveniles of *M. heliostemma* were analyzed in their study. According to their description of *M. heliostemma*, the final impression is that it is very difficult to distinguish subadults and adults of *M. heliostemma* and *M. raniceps*.

Rueda-Almonacid *et al.* (2007) questioned the validity of *Mesoclemmys heliostemma*. They suggested that the head color pattern that distinguishes the species might be related to altitudinal variation, representing a color morph of *M. raniceps*. According to these authors, further studies are necessary to investigate the relationship between both species, a conclusion endorsed by other authors (TTWG 2007; Vogt 2008). Accordingly, Artner (2008) considered *M. heliostemma* as a subspecies of *M. raniceps* (*M. raniceps heliostemma*) due to the remarkable similarities shown between adults of the two species.

Here, we provide descriptive statistics of ranges of measures and classical ratios of morphological characters for hatchlings, juveniles, and adults of *M. heliostemma*, *M. raniceps*, and *M. gibba* in order to evaluate whether or not these taxa are morphologically divergent and whether *M. heliostemma* is a valid species. We also test for group differences through univariate and multivariate statistical analyses and discuss advantages of this methodology. Finally, we provide new geographical records and a detailed description of head color variation found in our specimens of *M. heliostemma*.

Material and methods

We examined a total of 58 specimens of the following taxa: 36 *Mesoclemmys gibba* (3 hatchlings, 11 juveniles and 22 adults), 14 *M. raniceps* (4 hatchlings and 10 adults), and 8 *M. heliostemma* (7 juveniles and 1 adult) from the following Brazilian institutions (see also Appendix 1): Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Paraense Emílio Goeldi, Belém (MPEG); Museu Nacional do Rio de Janeiro (MNRJ); Universidade de Brasília (CHUNB); Museu de História Natural do Capão da Imbuia, Curitiba (MHNCI); and Universidade Federal do Mato Grosso, Cuiabá (UFMT).

We measured the following morphological characters: straight line carapace length (CL), from anterior border of nuchal scute to posterior contact between supracaudal scutes; carapace width (CW), at its widest point; shell height (SH), at its highest point; head width (HW), between tympana; parietal width (PW), at its narrowest point across the lateral edges of the dorsal parietal roof; 11th marginal scute width (M11), at posterior border; supra caudal scute width (SC), at posterior border; intergular scute width (IG), at anterior border; and gular scute width (GU), at anterior border. Measurements were taken with a vernier caliper to the nearest 0.1 mm (measures smaller than 155 mm) or 1.0 mm (measures larger than 155 mm). Age classes (hatchlings, juveniles, and adults) were considered in accordance to Bury (1979) and Burke *et al.* (2000), and the sex of each adult individual was determined based on tail size. Head color pattern of each individual was codified according to the Munsell color system, using a practical guide of color charts (Munsell 2000) that provides a satisfactory color standard necessary for technical accuracy (Miller 1958). The system comprises a combination of values for color (hue), saturation (value), and chroma (noted as: hue value/chroma), that together form the color designation. These combinations received specific common names (*e.g.* 10YR 4/2 is called dark grayish brown). Munsell system has been employed in several herpetological researches (*e.g.* Buchanan 1994; Heinen 1994; Weiss 2002; Baird *et al.* 2007; Weiss *et al.* 2012).

All morphometric variables were log-transformed prior the statistical analysis in order to account for deviances from normality and to linearize the allometric relationship between variables. All log-transformed variables were inspected through quantile-quantile plots and did not show substantial departure from normality. Individuals with missing value were excluded from the statistical analysis that demanded that variable.

To investigate the ontogenetic differences between groups, we employed covariance analyses (ANCOVA) for each metric variable using CL as a covariate to control for differences in overall size and, therefore, for different ontogenetic stages.

We used a principal component analysis (PCA) using the within-group variance-covariance matrix of the log-transformed variables to evaluate the multivariate difference between groups. This analysis assumes that this matrix was the same for all three species. This procedure also allows for the calculation of a common first PC that accounts for all variation that can be attributed to size differences (Bookstein 1989). The projection of the original observations on a plane that is orthogonal to this axis of size variation (PC1) produces variables that are size-free and can be evaluated in subsequent analyses (Burnaby 1966). The resulting size-corrected variables were analyzed through a Linear Discriminant Analysis (LDA), and the consistency of the results was evaluated through a leave-one-out, cross-validation procedure. Only individuals without missing data were analyzed in this way.

Results

### Descriptive data analysis

Carapace length varied as follows: 43.40 to 205.0 mm for *Mesoclemmys gibba*; 56.45 to 337.5 mm for *M. raniceps*; and 66.15 to 242.0 mm for *M. heliostemma*. Other measures (CW, SH, HW, and PW) are given in table 1.

TABLE 1. Measures (extreme values) of *Mesoclemmys gibba*, *M. raniceps*, and *M. heliostemma* (CL = carapace length; CW = carapace width; SH = shell height; HW = head width; PW = parietal width).

	M. gibba	*M. raniceps*	*M. heliostemma*
CL (mm)	43.40–205.00	56.45–337.50	66.15–242.00
CW (mm)	32.00–146.50	42.05–235.50	50.15–181.50
SH (mm)	16.15–67.50	19.40–133.00	18.30–69.00
HW (mm)	12.50–35.50	19.50–85.50	19.15–57.40
PW (mm)	5.30–11.50	1.40–5.75	2.20–4.15

The variation of the ratios along the ontogeny can be found in Figure 1. The HW/CL ratio, PW/HW ratio, and PW/CL ratio varied ontogenetically in all three species with hatchlings and juveniles having a proportionately broader head and dorsal parietal roof (Table 2). *Mesoclemmys gibba* has the narrowest head and the broadest parietal roof. The smallest specimen (a hatchling with 43.40 mm in CL) has 0.2903 of HW/CL, 0.4603 of PW/HW, and 0.1336 of PW/CL. The largest adult (a female with 205.0 mm in CL) has 0.1712 of HW/CL, 0.3276 of PW/HW, and 0.0561 of PW/CL. *M. raniceps* has the broadest head and the narrowest parietal roof. The smallest specimen (a hatchling with 56.45 mm in CL) has 0.3463 of HW/CL, 0.1125 of PW/HW, and 0.0390 of PW/CL. The largest adult (a female with 337.5 mm in CL) has 0.2533 of HW/CL, 0.0673 of PW/HW, and 0.0170 of PW/CL. *M. heliostemma* shows intermediate values. The smallest specimen (a juvenile with 66.15 mm in CL) has 0.2895 of HW/CL, 0.1149 of PW/HW, and 0.0333 of PW/CL. The largest adult (a male with 242.0 mm in CL) has 0.2372 of HW/CL, 0.0575 of PW/HW, and 0.0136 of PW/CL.

The CW/CL ratio varied ontogenetically in all three species with hatchlings and juveniles presenting a wider carapace. No difference is evident between the three species; the fact that no specimen of *Mesoclemmys heliostemma* presented a CW/CL smaller than 0.74 can be a consequence of the paucity of adults (only one) in our sampling (Table 3). The smallest *M. gibba* (a hatchling with 43.40 mm in CL) has 0.7373 and the largest one (an adult female with 205.0 mm in CL) has 0.7146. The smallest *M. raniceps* (a hatchling with 56.45 mm in CL) has 0.7449 and the largest one (an adult female with 337.5 mm in CL) has 0.6978. The smallest *M. heliostemma* (a juvenile with 66.15 mm in CL) has 0.7581 and the largest one (an adult male with 242.0 mm in CL) has 0.7500.
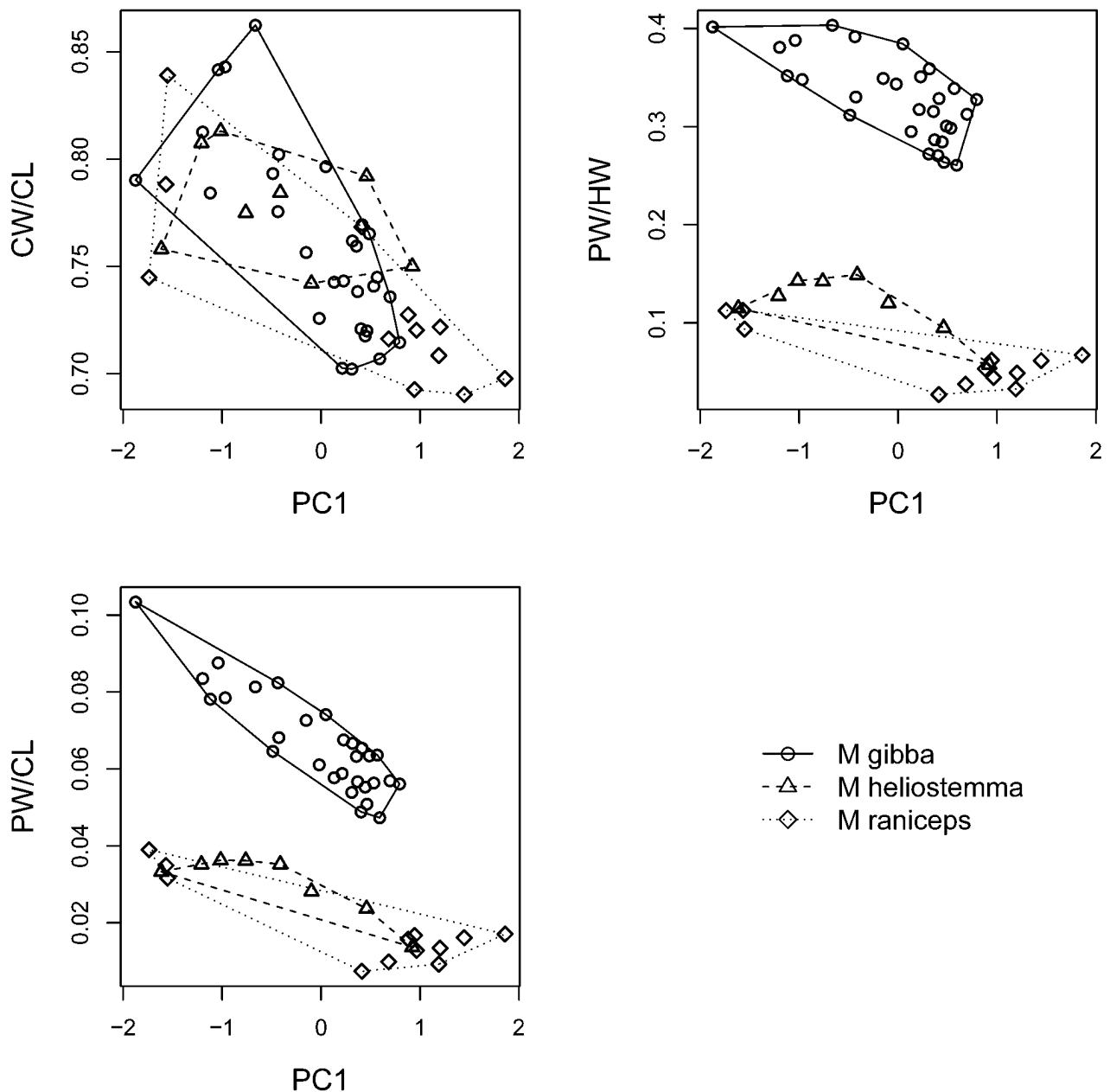
FIGURE 1. Relationship between ratios of measurements along the ontogeny represented by first Principal Component PC1 (see text).

TABLE 2. Range of HW/CL, PW/HW, and PW/CL for hatchlings, juveniles, and adults of *Mesoclemmys gibba*, *M. raniceps*, and *M. heliostemma* (CL = carapace length; HW = head width; PW = parietal width). * = One juvenile could not be measured; ** = Two adults could not be measured.

Species	HW/CL	PW/HW	PW/CL
M. gibba hatchlings	0.2576–0.2903	0.4015–0.4800	0.1034–0.1379
M. gibba juveniles	0.1929–0.2258*	0.3118–0.4033*	0.0646–0.0876*
M. gibba adults	0.1712–0.2110**	0.2607–0.3590**	0.0473–0.0676**
M. raniceps hatchlings	0.3093–0.3463	0.0937–0.1396	0.0316–0.0478
M. raniceps adults	0.2533–0.2947	0.0270–0.0673	0.0074–0.0170
M. heliostemma juveniles	0.2342–0.2895	0.0950–0.1490	0.0236–0.0363
M. heliostemma adult	0.2372	0.0575	0.0136

TABLE 3. Extreme values of CW/CL and SH/CL for hatchlings, juveniles, and adults of *Mesoclemmys gibba*, *M. raniceps*, and *M. heliostemma* (CL = carapace length; CW = carapace width; SH = shell height). * = Two hatchlings could not be measured; ** = One adult could not be measured. *** = One hatchling could not be measured.

Species	CW/CL	SH/CL
M. gibba hatchlings	0.7373–0.7902	0.3151*
M. gibba juveniles	0.7565–0.8624	0.3101–0.3900
M. gibba adults	0.7022–0.7695	0.3103–0.3705**
M. raniceps hatchlings	0.7449–0.8390	0.3070–0.3437***
M. raniceps adults	0.6903–0.7684	0.3043–0.3941**
M. heliostemma juveniles	0.7421–0.8130	0.2663–0.3266
M. heliostemma adult	0.7500	0.2851

No ontogenetic variation was observed in the SH/CL ratio for any of the three species. No difference is evident between *Mesoclemmys gibba* and *M. raniceps*, but *M. heliostemma* was the only species that presented SH/CL smaller than 0.30 (Table 3). The smallest *M. gibba* with a measured SH (a hatchling with 51.25 mm in CL) has 0.3151 and the largest one (an adult female with 205.0 mm in CL) has 0.3293. The smallest *M. raniceps* (a hatchling with 56.45 mm in CL) has 0.3437 and the largest one (an adult female with 337.5 mm in CL) has 0.3941. The smallest *M. heliostemma* (a juvenile with 66.15 mm in CL) has 0.2766 and the largest one (an adult male with 242.0 mm in CL) has 0.2851.

The relationship between IG and GU is variable for all three species. In *Mesoclemmys gibba*, IG is wider than GU in 15 specimens (41.7%), IG is equal to GU in 3 specimens (8.3%), and IG is narrower than GU in 18 specimens (50.0%). In *M. raniceps*, IG is wider than GU in 7 specimens (50.0%), IG is equal to GU in one specimen (7.1%), and IG is narrower than GU in 6 specimens (42.9%). In *M. heliostemma*, IG is wider than GU in 2 specimens (25.0%), IG is equal to GU in one specimen (12.5%), and IG is narrower than GU in 5 specimens (62.5%).

The relationship between M11 and SC is variable for all three species. In *Mesoclemmys gibba*, M11 is wider than SC in 21 specimens (63.6%), M11 is equal to SC in 6 specimens (18.2%), and M11 is narrower than SC in 6 specimens (18.2%) (three specimens were not analyzed). In *M. raniceps*, M11 is wider than SC in 6 specimens (42.9%), M11 is equal to SC in one specimen (7.1%), and M11 is narrower than SC in 7 specimens (50.0%). In *M. heliostemma*, M11 is wider than SC in 4 specimens (50.0%), M11 is equal to SC in one specimen (12.5%), and M11 is narrower than SC in 3 specimens (37.5%).

A comparison of the coloration of the body and the head of *Mesoclemmys raniceps* and *M. heliostemma* can be found on figures 2 and 3, respectively. Among specimens of *M. heliostemma* examined in this study, the V-shaped cephalic mark is complete in the two smallest juveniles (66.15 and 78.20 mm of CL), starting with a vertex over the nostrils, extending back over the eyes and tympani, and ending with the V arms reaching the cranial portion of the neck (Figures 2D and 3D). It is partially visible in five specimens, and indistinguishable in one specimen whose color was completely altered by the long time exposition in alcohol. The analysis of the five specimens with a partial V-shaped mark (88.25 to 242.00 mm of CL) showed that it vanishes in a craniocaudal direction in a way that the last trace of it is a pair of poorly defined pale yellow marks (the V arms) behind the tympani and/or in the cranial portion of the neck (Figure 3C).

V-shaped bands are yellow (2,5Y 8/6) or pale yellow (with three combinations: 5Y 8/4; 2,5Y 8/4; 2,5Y 8/3); top of the head is brown (10YR 4/3), grayish brown (10YR 5/2), dark grayish brown (with two combinations: 2,5Y 4/2; 10YR 4/2), very dark grayish brown (2,5Y 3/2) or dark gray (2,5Y 4/1); side and ventral surfaces of head are dark grayish brown (10YR 4/2), gray (Gley1 5/N), bluish gray (Gley2 5/10B) or dark gray (with two combinations: 2,5Y 4/1; Gley1 4/N); tympani are brown (10YR 5/3), dark grayish brown (10YR 4/2), gray (7,5YR 5/1), greenish gray (Gley1 5/10Y), dark reddish gray (2,5YR 4/1) or dark gray (Gley1 4/N); ramphoteca is yellow (with two combinations: 2,5Y 8/6; 10YR 7/6), olive yellow (2,5Y 6/6) or pale yellow (5Y 8/4); neck is dark grayish brown (10YR 4/2), gray (Gley1 5/N), bluish gray (Gley2 5/10B) or dark gray (with two combinations: 2,5Y 4/1; Gley1 4/N).
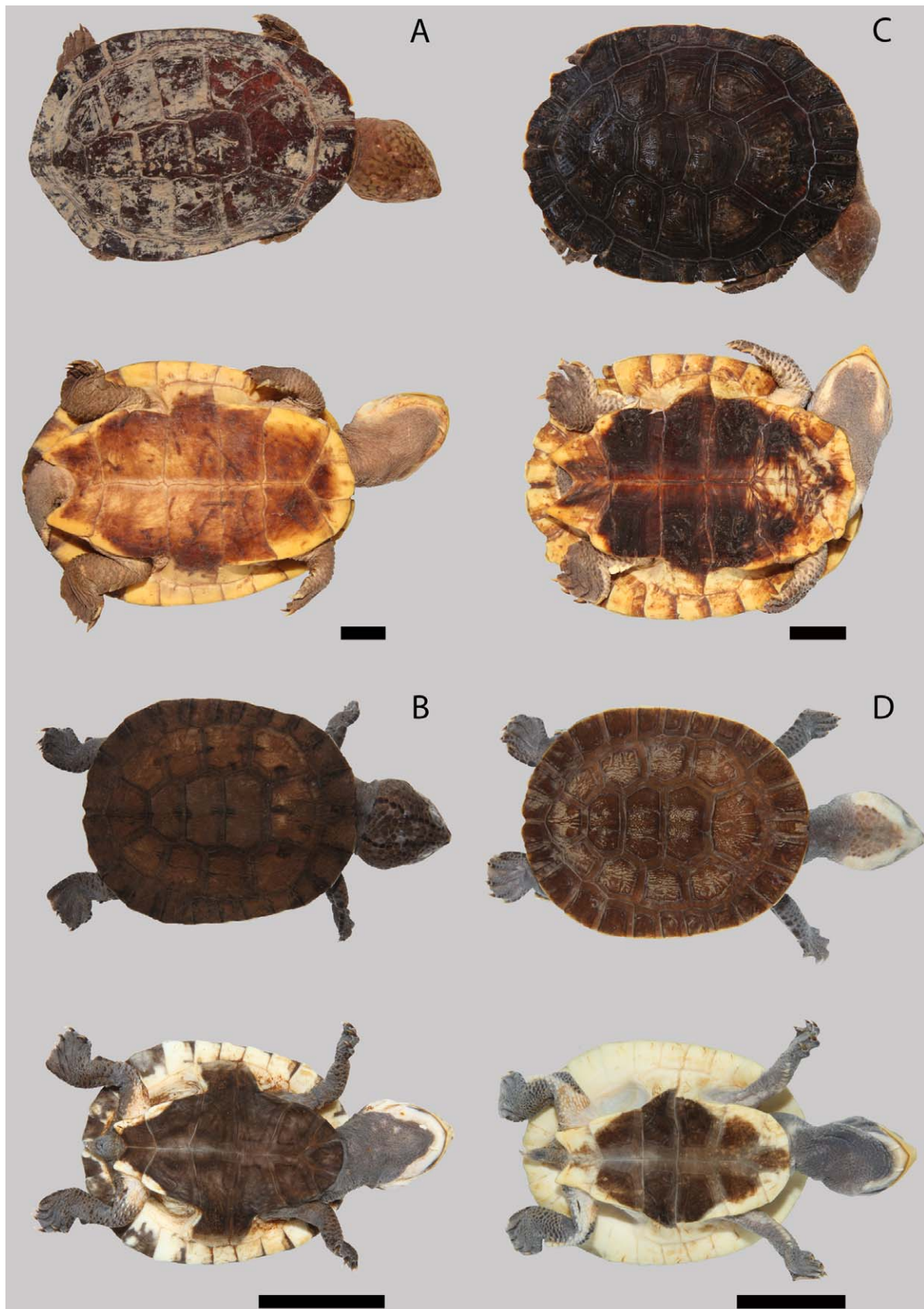
FIGURE 2. Comparison of dorsal and ventral views of *Mesoclemmys raniceps* and *M. heliostemma*. A. Adult of *M. raniceps*, MZUSP 2834 (218.50 mm of CL). B. Hatchling of *M. raniceps*, MZUSP 4388 (63.35 mm of CL). C. Subadult of *M. heliostemma*, MZUSP 2639 (175.50 mm of CL). D. Juvenile of *M. heliostemma*, MZUSP 4377 (78.20 mm of CL). Scale bar 30 mm.

FIGURE 3. Comparison of dorsal, ventral and lateral views of the head of *Mesoclemmys raniceps* and *M. heliostemma*. A. Adult of *M. raniceps*, MZUSP 2834. B. Hatchling of *M. raniceps*, MZUSP 4388. C. Subadult of *M. heliostemma*, MZUSP 2639. D. Juvenile of *M. heliostemma*, MZUSP 4377. Scale bar 10 mm.

Statistical data analysis

The ANCOVAs revealed that HW, PW and SH were significantly different between taxa when the effect of CL was accounted for (Table 4). The inspection of the relationship between the variables shows that, although all taxa can be considered different for HW and PW, only *Mesoclemmys heliostemma* differ in relation to SH (Figure 4). Additionally, although there was a significant interaction between HW and taxa, the slopes does not seem to differ substantially. The slopes, intercepts and significant differences can be found at Appendix 2.
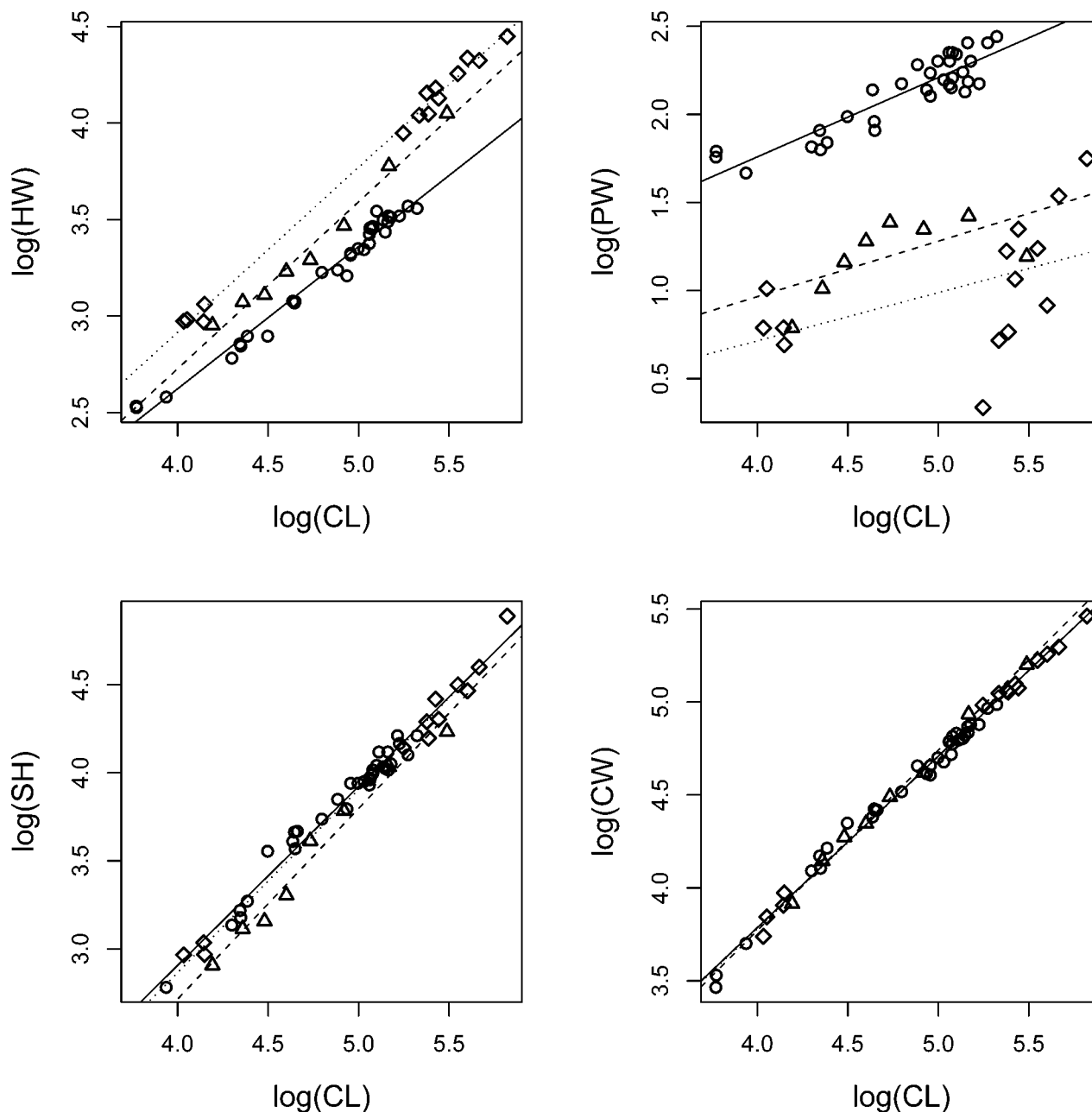
FIGURE 4. Linear relationship between the log-transformed HW, PW, SH and CW with CL for each taxa. Significance of the slopes, intercepts and interactions can be found in table 4. Symbols and lines as in figure 1.

The Principal Component Analysis produced two PCs that explain almost all within-group variation (Table 5). As expected, the first PC has positive weights on all variables, and can be considered as a general measure of allometric size. The PCA shows that there is a large superposition between *Mesoclemmys heliostemma* and *M. raniceps* in the multivariate space, with *M. gibba* differing from the previous groups in the second PC (Figure 5).

The result of the LDA on size-corrected variables shows that, despite the superposition between the 95% confidence ellipses of *Mesoclemmys heliostemma* and *M. raniceps* in the size-corrected LD space, the cross-

validation analysis correctly assigned 100% of the individuals to their *a priori* groups. The first LD axis explains almost all between-group variance (Table 5).

TABLE 4. Results of the ANCOVAs of each variable using CL as a covariate and taxa as factor. *df*—degrees of freedom; *Sum Sq*—sum of squares; *Mean Sq*—mean squares; *F value*—estimated Fisher's F; *P-value*—probability of obtaining a F value as extreme or more as the one observed. Bold P-values indicate tests there were significant at α = 0.05.

| –	–	df	Sum Sq	Mean Sq	F value	P-value
HW	CL	1	10.584	10.584	4865.311	**<.001**
	Taxa	2	1.582	.791	363.548	**<.001**
	CL:taxa	2	.047	.023	10.707	**<.001**
	Residuals	49	.107	.002		
PW	CL	1	.383	.383	10.061	**.02**
	Taxa	2	15.898	7.949	208.666	**<.001**
	CL:taxa	2	.093	.047	1.223	.303
	Residuals	49	1.867	.038		
SH	CL	1	11.707	11.707	2754.216	**<.001**
	Taxa	2	.123	.062	14.495	**<.001**
	CL:taxa	2	.004	.002	.514	.601
	Residuals	47	.200	.004		
CW	CL	1	11.931	11.931	7145.820	**<.001**
	Taxa	2	.003	.002	.965	.388
	CL:taxa	2	.003	.001	.774	.467
	Residuals	50	.083	.002		
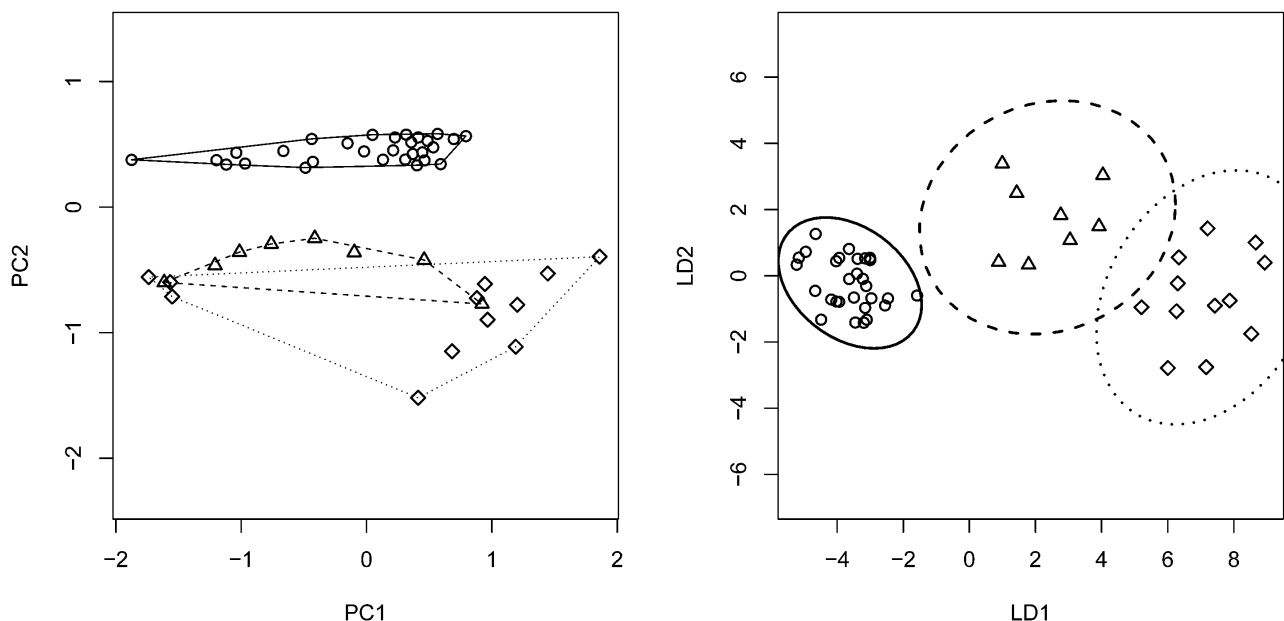
FIGURE 5. Principal component analysis. A. First two Principal Components of the pooled within-group variance-covariance matrix of the log-transformed variable. Lines indicate the convex hulls that encompass all the observations. B. Linear Discriminant functions analysis on the size-corrected variables, depicting 95% confidence ellipses. Symbols and lines as in figure 1.

TABLE 5. Weights of each log-transformed variable on the pooled within-group principal components axes (PC) and size-corrected Linear Discriminant functions (LD), and percentage of variation explained by each axis (within-group and between groups, respectively).

	PC1	PC2	LD1	LD2
CL	0.512	-0.131	-8.133	10.174
HW	0.427	-0.152	18.360	-2.396
PW	0.224	0.968	-2.284	-0.123
CW	0.469	-0.149	-3.863	12.790
SH	0.534	-0.028	5.771	-12.800
%	99.8	0.2	97.1	2.9
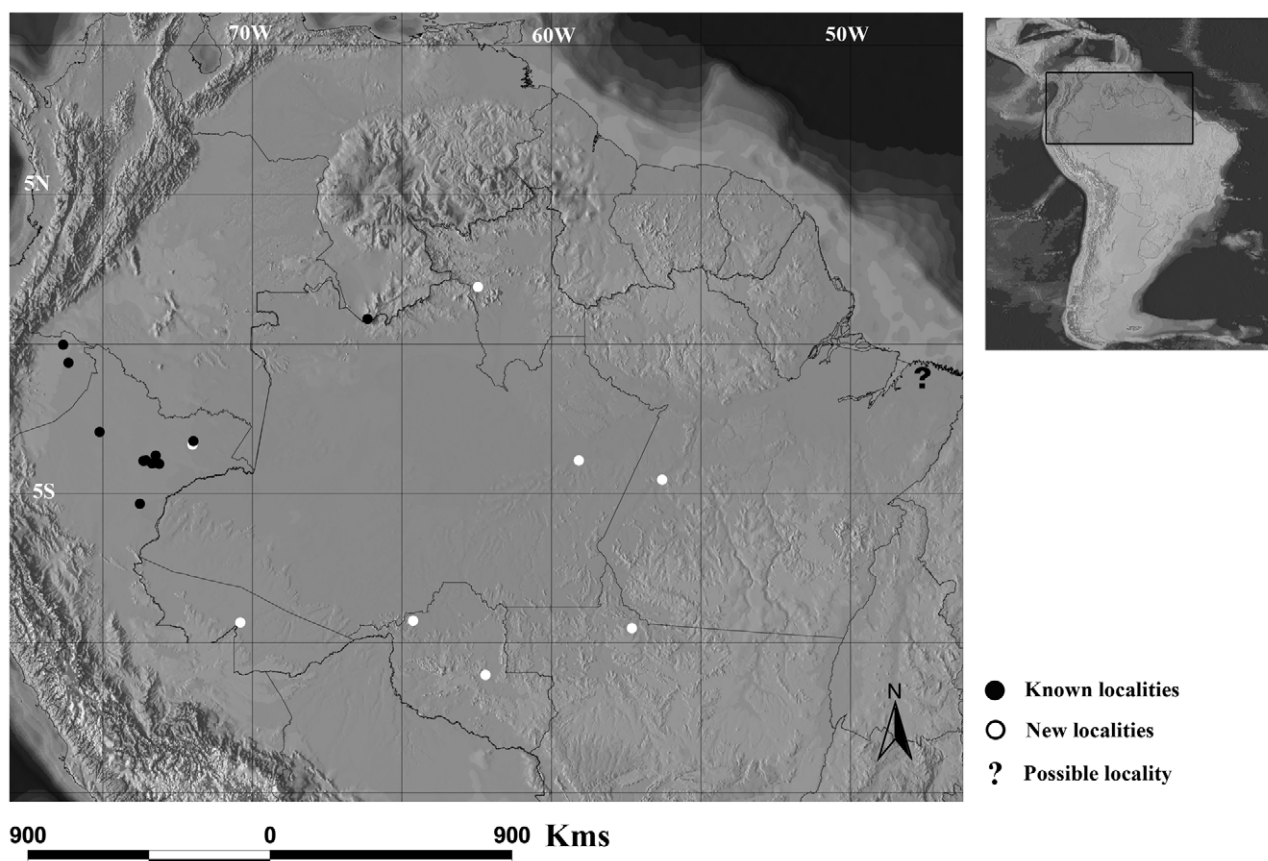
FIGURE 6. Locality records for *Mesoclemmys heliostemma*. Question mark refers to the Igarapé-Açu locality, state of Pará (see text for details).

Geographic distribution

We presented here eight new localities for *Mesoclemmys heliostemma* in the Amazonas River basin: one in northeastern Peru and seven in northern Brazil (Figure 6). The Peruvian specimen MZUSP 2641 (99.55 mm of CL) was collected by Borys Malkin (15-22/05/1966) in Ampiyacu River (a tributary of the left bank of Amazonas River), next to the mouth of Yaguasyacu River, in the Municipality of Estirón, Department of Loreto (03°22'06"S, 72°00'28"W). The Brazilian specimens came from six different states. MZUSP 2918 (88.25 mm of CL) was collected by Carlo Zacquini (17/10/1976) in Jundiá River (a tributary of the right bank of Catrimani River), 12 km upstream from its mouth, in the Municipality of Iracema, State of Roraima (01°54'06"N, 62°28'25"W). MZUSP 2639 (175.5 mm of CL) was collected by the EPA-MZUSP expedition (20/02/1972) in the proximity of the mouth of Canumá River (a tributary of the right bank of Madeira River), in the Municipality of Nova Olinda do Norte, State of Amazonas (03°53'50"S, 59°06'10"W). MZUSP 3022 (242.0 mm of CL) was collected by Miguel T.

MOLINA *ET AL.*

Rodrigues (08/02/1979) at the Uruá Base of Parque Nacional da Amazônia, in front of the Uruá waterfall, on the left bank of Tapajós River (a tributary of the right bank of Amazonas River), Municipality of Itaituba, State of Pará (04°32'50''S, 56°18'20''W). MZUSP 2050 (136.85 mm of CL) was collected by H. Schultz (12/1950) in the proximities of Purus River (a tributary of the right bank of Amazonas River) in the Alto Purus region, Municipality of Santa Rosa do Purus, State of Acre (09°20'S, 70°25'W). MZUSP 4377 (78.20 mm of CL) was collected by Luciana M. Lobo and team (12/02/2010) at the Jirau Hydroelectric Power Plant Station localized on the right bank of Madeira River (a tributary of the right bank of Amazonas River), Municipality of Porto Velho, State of Rondônia (09°16'S, 64°38'W). MPEG 86 (113.60 mm of CL) was collected by Teresa Cristina S. Ávila-Pires and team (18/03/1985) in Santa Helena creek (a tributary of the left bank of Urupá River), Municipality of Urupá, State of Rondônia (11°04'02.45''S, 62°12'56.76''W). MZUSP 3387 (66.15 mm of CL) was collected by Paulo E. Vanzolini and team (24/02/1997) in a small nameless creek belonging to a tributary of the left bank of Bruno River, Municipality of Apiacás, State of Mato Grosso (09°31'05''S, 57°19'27''W).

Discussion

Mesoclemmys heliostemma seems to be easily recognizable from its congeners through their juveniles, which retain a bright yellow-orange V-shaped band that extends from the tip of the nostril to the temporal region, a conspicuous diagnostic character only known to be present in this species. On the other hand, adult specimens are more difficult to diagnose, especially when compared with *M. raniceps*.

Evidence of a yellowish facial band is present in seven preserved specimens of *M. heliostemma*. Only one examined specimen bears no evidence of a facial band, probably as the result of color degradation after more than six decades stored in alcohol. We found poorly defined cephalic marks behind tympani in a subadult female and an adult male, which extend to the cranial portion of the neck in the female (Figure 3C), contradicting the previous view that subadults and adults are always melanic, with no sign of bright head marks (McCord *et al.* 2001). All seven specimens retain a brown or dark gray coloration on the dorsal, lateral, and ventral surfaces of the head, tympani, and neck, while the ramphoteca is yellowish (Figures 2 and 3). Our observations suggest that the fading process of the cephalic V-shaped bands develops in a craniocaudal direction and starts already in the juvenile phase, possibly in specimens with more than 80 mm of CL. The distinction between head color pattern of *Mesoclemmys heliostemma* and *M. raniceps* is evident in figures 2 and 3.

According to McCord *et al.* (2001), both *M. heliostemma* and *M. raniceps* present a broad head, with that of *M. heliostemma* being slightly narrower. These authors also show that *M. heliostemma* has a parietal crest that is intermediate in width between the conditions found in *M. gibba* and *M. raniceps*. Data analyzed here agree with that statement. However, invariant information (*e.g.* ratios) used as character for species identification can also be misleading, even when applied to a determined age class (*e.g.* adults). As already stated by Pritchard and Trebbau (1984) and Bour and Pauler (1987), ontogenetic variation can have a significant influence on the size of the head relative to the carapace and on the size of the parietal roof, and both characters should be evaluated with care. As shown here, HW/CL, PW/HW, and PW/CL ratios varied considerably, even within an age class (Table 2).

Similarly, the relationship between CW/CL, SH/CL, M11/SC, and GU/IG are highly variable between species of *Mesoclemmys* and cannot be used with confidence for species delimitation. McCord *et al.* (2001) found that *M. gibba* and *M. raniceps* have an intergular scute wider than gulars whereas *M. heliostemma* has an intergular scute narrower than gulars. These authors also use the relationship between M11 and SC, stating that in *M. heliostemma* M11 is equal or wider than SC (M11 equal to SC in *M. raniceps*; M11 narrower than SC in *M. gibba*). We found so much variation in these two characters that we do not recommend their use for species delimitation. Additionally, according to Bour and Zaher (2005), adults of *M. gibba* and *M. heliostemma* have CW/CL equal to or larger than 72%, while adults of *M. raniceps* have CW/CL between 68 and 71%. The only adult specimen of *M. heliostemma* measured agrees with that statement. However, our sample counted with 25% of adult specimens of *M. gibba* with narrower carapaces and 60% of adult specimens of *M. raniceps* with wider carapaces than the measures given by Bour and Zaher (2005) (Table 3). Similarly, Bour and Zaher (2005) state that *M. gibba* has a SH/CL equal to or higher than 33% while *M. raniceps* and *M. heliostemma* retain SH/CL lower than 33%. Our data show that some specimens of *M. gibba* (27% of juveniles and 24% of adults) do retain lower shells while a significant number of *M. raniceps* (67% of hatchlings and adults) and one juvenile of *M. heliostemma* (14%) have higher shells (Table 3).

No authors so far used statistical analyses to evaluate morphometric differences between *M. gibba*, *M. raniceps* and *M. heliostemma*. Statistical differences were observed in the regression curves of logarithmized HW and PW on log CL between all three species, even though neither HW nor PW could discriminate between *M. heliostemma* and *M. raniceps* in the inspection of ratios. These differences probably originate because of inherent problems in the use of ratios to discriminate groups. It is widely known that the use of ratios as a way of size-correction is an invalid methodology because it not only fails to erase correlation of the measure with size (*e.g.* Bookstein 1989; Packard & Boardman 1988; 1999; McCoy *et al.* 2006), but also impedes the use of classical parametric statistical analysis (*e.g.* Atchley *et al.* 1976; Anderson & Lydic 1977) and straight-forward interpretations (Packard & Boardman 1988, 1999; Kratochvíl *et al.* 2003). These issues are evident in our analysis, as ratios fail to differentiate groups and show a high negative correlation with PC1, a size measure (plots using CL instead of PC1 are very similar, as both are highly correlated; table 5). This does not mean that some insight cannot be gained by the inspection of ratios alone. For example, SH/CL ratio shows some difference between *M. heliostemma* and the other species, as is evident in the regression of both variables. However, it must be noticed that this ratio shows no ontogenetic variation for this sample, indicating that the relationship between both is isometric, one of the few exceptions that validate the use of ratios as a size-correction method (Bookstein 1989). In fact, the regression between SH and CL shows that the slope between variables is close to 1, indicating that this is actually the case. None of the other variables conform to this exception (Appendix 2).

Our multivariate analysis provides the strongest evidence for the distinction of groups within sampled taxa. The cross-validation analysis of the size-corrected Linear Discriminant Analysis shows a complete discrimination of the groups. Despite that, we advise against the interpretation of the LD coefficients shown, as the multivariate correlation structure could lead to awkward interpretations of the difference between groups. Nevertheless, we encourage future studies on *Mesoclemmys* taxonomy to use both univariate and multivariate approaches, since it has been proven herein to be a powerful taxonomic tool for investigations within the group.

While we find our results compelling, we also consider that a molecular genetic assessment of all species of *Mesoclemmys*, and especially of *M. heliostemma* and *M. raniceps*, is still in urgent need since until now only three out of the ten *Mesoclemmys* species were assessed by molecular means (Vargas-Ramírez *et al.* 2012). Chelonians can show great plasticity in color pattern and morphological data, a factor that could lead to taxonomic inflation, as demonstrated by recent molecular genetic reassessments of morphologically based taxonomic works (Fritz *et al.* 2006a,b, 2007, 2009; Parham *et al.* 2006; Attum *et al.* 2007; Široký & Fritz, 2007).

According to McCord *et al.* (2001), Oversluijs Vásquez (2003), Široký *et al.* (2006), and Cisneros-Heredia (2006), *M. heliostemma* is known to occur in northeastern Peru, eastern Ecuador, and southern Venezuela, with its easternmost record registered to the Venezuelan side of Pico da Neblina (McCord *et al.* 2001). However, the species is more widespread in the Amazonian River basin than previously thought. Our specimens examined expand the range of the species significantly throughout the Brazilian Amazonian basin. The Jundiá River locality (municipality of Iracema, state of Roraima) is the northernmost locality in South America, and is located approximately 430 km (straight line) northeast of the Pico da Neblina locality, while the locality of Uruá Base (municipality of Itaituba, state of Pará) corresponds to the easternmost record in South America, extending the range of the species 1,240 km southeast of the Pico da Neblina locality. The southernmost record is the locality of Santa Helena creek (municipality of Urupá, state of Rondônia) that extends the range of the species *ca.* 1,380 km south of Pico da Neblina. The paratype of *M. heliostemma* (NHM 1904.7.26.1), mentioned but not used by McCord *et al.* (2001) as a valid record for the species, extends even more the easternmost boundary of the species. However, according to these authors, the exact location—"Igape-Assu, state of Pará"—could not be found in any Brazilian gazetteer. We believe that Igape-Assu means Igarapé Açu [as already cited by Pritchard & Trebbau (1984) and Iverson *et al.* (2012)] in reference to a tributary of the right bank of Marapanim River (01°01'16.09"S, 47°41'17.75"W), or the Municipality of Igarapé Açu (01°07'37.20"S, 47°37'04.80"W), a village located at km 112 of the Belém – Bragança railway (Tavares 2008). This record is added as a question mark in Figure 6 due to the uncertainties regarding its exact location.

According to the present knowledge of the species, *M. heliostemma* seems to be sympatric with *M. raniceps* and *M. gibba* in the Iquitos region (Perú; McCord *et al.* 2001) and the Madeira River (Jirau Hydroelectric Power Plant, Brazil), and with *M. raniceps* in the Ampiyacu River (Department of Loreto, Perú).

Acknowledgments

References

Anderson, D.E. & Lydic, R. (1977) On the effect of using ratios in the analysis of variance. *Biobehavioural Reviews*, 1, 255–229.

Artner, H. (2008) The world's extant turtle species, part 1. *Emys*, 15, 4–32.

Atchley, W., Gaskins, C. & Anderson, D. (1976) Statistical properties of ratios. I. Empirical results. *Systematic Biology*, 25, 137–148.

Attum, O., El Din, S.B., Carranza, S., Earley, R., Arnold, E.N. & Kingsbury, B. (2007) An evaluation of the taxonomic validity of *Testudo werneri*. Amphibia-Reptilia, 28, 393–401.

Baird, T.A., Hranitz, J.M., Timanus, D.K. & Schwartz, A.M. (2007) Behavioral attributes influence annual mating success more than morphological traits in male collared lizards. *Behavioral Ecology*, 18, 1146–1154.

Bookstein, F.L. (1989) "Size and shape": a comment on semantics. *Systematic Zoology*, 38, 173–180

Bour, R. (1973) Contribution a la connaissance de *Phrynops nasutus* (Schweigger: 1812) et *Phrynops tuberculatus* (Luederwaldt: 1926). Description d'une nouvelle sous-espèce originaire du Paraguay, *Phrynops tuberculatus vanderhaegei* (Testudinata – Pleurodira – Chelidae). *Bulletin de la Société Zoologique de France*, 98, 175–190.

Bour, R. & Pauler, I. (1987) Identité de *Phrynops vanderhaegei* Bour, 1973, et des espèces affines (Reptilia – Chelonii – Chelidae). *Mesogee*, 47, 3–23.

Bour, R. & Zaher, H. (2005) A new species of *Mesoclemmys*, from the open formations of Northeastern Brazil (Chelonii, Chelidae). *Papéis Avulsos de Zoologia*, 45, 295–311.

Buchanan, B.W. (1994) Sexual dimorphism in *Hyla squirella*: Chromatic and pattern variation between the sexes. *Copeia*, 1994, 797–802.

Burke, V.J., Lovich, J.E. & Gibbons, J.W. (2000) Conservation of freshwater turtles. *In*: Klemens, M.W. (Ed), *Turtle conservation*. Smithsonian Institution Press, Washington, pp. 156–179.

Burnaby, T.P. (1966) Growth-invariant discriminant functions and generalized distances. *Biometrics*, 22, 96–110.

Bury, R.B. (1979) Population ecology of freshwater turtles. *In*: Harless, M. & Morlock, H. (Eds.), *Turtles: Perspectives and Research*. John Wiley & Sons, New York, pp. 571–602.

Cisneros-Heredia, D.F. (2006) Turtles of the Tiputini Biodiversity Station with remarks on the diversity and distribution of the Testudines from Ecuador. *Biota Neotropica*, 6, 153–168.

Dixon, J.R. & Soini, P. (1977) The reptiles of the upper Amazon basin, Iquitos region, Peru. II. Crocodilians, turtles and snakes. *Milwaukee Public Museum, Contributions in Biology and Geology*, 12, 1–91.

Fachin Teran, A., Vogt, R.C. & Gomez, M.F.S. (1995) Food habits of an assemblage of turtles in the rio Guapore, Rondonia, Brazil. *Journal of Herpetology*, 29, 536–547.

Ferronato, B.O., Molina, F.B., Molina, F.C., Espinosa, R.A. & Morales, V.R. (2011) New locality records for chelonians (Testudines: Chelidae, Podocnemididae, Testudinidae) from Departamento de Pasco, Peru. *Herpetology Notes*, 4, 219–224.

Fritz, U., Barata, M., Busack, S. D., Fritzsch, G. & Castilho, R. (2006a) Impact of mountain chains, sea straits and peripheral populations on genetic and taxonomic structure of a freshwater turtle, *Mauremys leprosa*. *Zoologica Scripta*, 35, 97–108.

Fritz, U., Auer, M., Bertolero, A., Cheylan, M., Fattizzo, T., Hundsdörfer, A.K., Martín Sampayo, M., Pretus, J.L., Široký, P. & Wink, M. (2006b) A rangewide phylogeography of Hermann's tortoise, *Testudo hermanni* (Reptilia: Testudines: Testudinidae): implications for taxonomy. *Zoologica Scripta*, 35, 531–543.

Fritz, U., Hundsdörfer, A.K., Široký, P., Auer, M., Kami, H., Lehmann, J., Mazanaeva, L.F., Türkozan, O. & Wink, M. (2007) Phenotypic plasticity leads to incongruence between morphology-based taxonomy and genetic differentiation in western Palaearctic tortoises (*Testudo graeca* complex; Testudines, Testudinidae). *Amphibia-Reptilia*, 28, 97–121.

Fritz, U., Harris, D.J., Fahd, S, Rouag, R., Martínez, E.G., Casalduero, A.G., Široký, P., Kalboussi, M., Jdeidi, T.B. & Hundsdörfer, A.K. (2009) Mitochondrial phylogeography of *Testudo graeca* in the Western Mediterranean: Old complex divergence in North Africa and recent arrival in Europe. *Amphibia-Reptilia*, 30, 63–80.

Gray, J.E. (1855) *Catalogue of shield reptiles in the collection of the British Museum. Part I. Testudinata (Tortoises)*. Taylor and Francis, London, 79 pp.

Heinen, J.T. (1994) The significance of color change in newly metamorphosed American toads (*Bufo a. americanus*). *Journal of Herpetology*, 28, 87–93.

Iverson, J. B., Kimerling, A.J., Kiester, A.R., Hughes, L.E. & Nicolello, J. (2012) *The Emysystem*, The Terra Cognita Laboratory, Corvallis, OR. Available from: http://emys.geo.orst.edu/ (08/08/2012).

Kratochvíl, L., Fokt, M., Rehák, I. & Frynta, D. (2003) Misinterpretation of character scaling: a tale of sexual dimorphism in body shape of common lizards. *Canadian Journal of Zoology*, 81, 1112–1117.

Lescure, J. & Fretey, J. (1975) Étude taxinomique de *Phrynops* (*Batrachemys*) *nasutus* (Schweigger) (Testudinata, Chelidae). *Bulletin du Muséum National d'Histoire Naturelle, Série Zoologie*, 239, 1317–1328.

Luederwaldt, H. (1926) Os chelonios brasileiros com a lista das espécies do Museu Paulista. *Revista do Museu Paulista*, 14, 404–468.

McCord, W. P., Joseph-Ouni, M. & Lamar, W.W. (2001) A taxonomic reevaluation of *Phrynops* (Testudines Chelidae) with the description of two new genera and a new species of *Batrachemys*. *Revista de Biología Tropical*, 49, 715–764.

McCoy, M., Bolker, B., Osenberg, C., Miner, B. & Vonesh, J. (2006) Size correction: comparing morphological traits among populations and environments. *Oecologia*, 148, 547–554.

Medem, F. (1960) Datos zoo-geograficos y ecologicos sobre los Crocodylia y Testudinatas de los ríos Amazonas, Putumayo y Caquetá. *Caldasia*, 8, 341–351.

Métrailler, S. & Le Gratiet, G. (1996) *Tortues continentales de Guyane française.* Privately printed, Bramois, Switzerland, 127 pp.

Miller, R.S. (1958) The Munsell system of color notation. *Journal Mammalogy*, 39, 278–286.

Mittermeier, R.A., Rhodin, A.G.J., Medem, F., Soini, P., Hoogmoed, M.S. & Carrillo de Espinoza, N. (1978) Distribution of the South American chelid turtle *Phrynops gibbus*, with observations on habitat and reproduction. *Herpetologica*, 34, 94–100.

Munsell, (2000) *Munsell soil color charts.* Munsell Color, Grand Rapids, MI, 10 pp., with color plates.

Oversluijs Vásquez, M.R. (2003) Una nueva localidad para la distribución geográfica de *Batrachemys heliostemma* (Reptilia, Chelidae) en la amazonía peruana. *Folia Amazónica*, 14, 189–191.

Packard, G. & Boardman, T.J. (1988) The misuse of ratios, indices, and percentages in ecophysiological research. *Physiological Zoology*, 61, 1–9.

Packard, G. & Boardman, T.J. (1999) The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? *Comparative Biochemistry and Physiology, Part A*, 122, 37–44.

Parham, J. F., Türkosan, O., Sturt, B.L., Arakelyan, M., Shafei, S., Macey, J.R. & Papenfuss, T.J. (2006) Genetic evidence for premature taxonomic inflation in Middle Eastern tortoises. *Proceedings of the California Academy of Sciences*, 57, 955-964.

Pritchard, P.C.H. & Trebbau, P. (1984) *Turtles of Venezuela.* Society for the Study of Amphibians and Reptiles, New York, 403 pp.

Rueda-Almonacid, J.V., Carr, J.L., Mittermeier, R.A., Rodríguez-Mahecha, J.V., Mast, R.B., Vogt, R.C., Rhodin, A.G.J., de la Ossa-Velásquez, J., Rueda, J.N. & Mittermeier, C.G. (2007) *Las tortugas y los cocodrilianos de los países andinos del trópico.* Serie de guías tropicales de campo 6. Conservación Internacional. Editorial Panamericana, Formas e Impresos, Bogotá, Colombia. 538 pp.

Schweigger, A.F. (1812) Prodromus monographiae cheloniorum. *Königsberger Archiv für Naturwissenschaft und Mathematik*, 1, 271–368, 406–458.

Široký, P. & Fritz, U. (2007) Is *Testudo werneri* a distinct species? *Biologia (Bratislava)*, 62, 228–231.

Široký, P., Kamler, M. & Modrý, D. (2006) A new *Eimeria* (Apicomplexa: Eimeriidae) possessing mitra-shaped oocysts, from the Neotropical chelidae turtle *Batrachemys heliostemma* (Testudines: Chelidae), and its comparison with *Eimeria mitraria* (Laveran & Mesnil, 1902). *Memórias do Instituto Oswaldo Cruz*, 101, 555–558.

Tavares, M.G.C. (2008) A formação territorial do espaço paraense: dos fortes à criação de municípios. *Revista Acta Geográfica*, 2008, 59–83.

TTWG (Turtle Taxonomy Working Group) [Bickham, J.W., Iverson, J.B., Parham, J.F., Philippen, H.-D., Rhodin, A.G.J., Shaffer, H.B., Spinks, P.Q. & van Dijk, P.P.]. (2007) An annotated list of modern turtle terminal taxa with comments on areas of taxonomic instability and recent change. *In*: Shaffer, H.B., FitzSimmons, N.N., Georges, A. & Rhodin, A.G.J. (Eds.), *Defining turtle diversity: Proceedings of a workshop on genetics, ethics, and taxonomy of freshwater turtles and tortoises.* Chelonian Research Foundation, Lunenburg, MA, pp. 173–199.

Vargas-Ramírez, M., Michels, J., Castaño-Mora, O.V., Cárdenas-Arevalo, G., Gallego-García, N. & Fritz, U. (2012) Weak genetic divergence between the two South American toad-headed turtles *Mesoclemmys dahli* and *M. zuliae* (Testudines: Pleurodira: Chelidae). *Amphibia-Reptilia*, 33, DOI 10.1163/15685381-00002840.

Vogt, R. C. (2008) *Tartarugas da Amazônia.* O autor, Lima, Peru, 104 pp.

Vogt, R.C., Ferrara, C.R., Schneider, L. & Santos Jr., L.B. (2009) Brazilian Amazonian turtles. Habitat. *Herpetological Review*, 40, 213.

Weiss, S.L. (2002) Reproductive signals of female lizards: Pattern of trait expression and male response. *Ethology*, 108, 793–813.

Weiss, S.L., Foerster, K. & Hudon, J. (2012) Pteridine, not carotenoid, pigments underlie the female-specific orange ornament of striped plateau lizards (*Sceloporus virgatus*). *Comparative Biochemistry and Physiology, Part B*, 161, 117–123.

Zangerl, R. & Medem, F. (1958) A new species of chelid turtle, *Phrynops* (*Batrachemys*) *dahli*, from Colombia. *Bulletin of the Museum of Comparative Zoology*, 119, 375–390.

APPENDIX 1. Specimens Examined.

Mesoclemmys gibba (n = 36)—**BRAZIL:** AMAZONAS: Barcelos, comunidade de Tapera (MZUSP 2640); Lábrea, Rio Ituxí (MPEG 500); Presidente Figueiredo, UHE Balbina (MPEG 124, MZUSP 3115, MZUSP 3140). MARANHÃO: Alcântara (MZUSP 4355). MATO GROSSO: Juína (UFMT 6056). PARÁ: Belém, Parque MPEG (MPEG 265); Belém, Ilha do Mosqueiro (MHNCI 3882); Breves, Corcovado (MZUSP 2684, MZUSP 2685); Curionópolis (MPEG 546, MPEG 547); Marabá, FLONA Tapirapé-Aquiri (MPEG 273); Melgaço, Baía de Caxiuanã (MPEG 548); Paragominas (MPEG 537); Parauapebas, Carajás (MPEG 82, MPEG 83, MPEG89, MPEG 422). RONDÔNIA: Porto Velho, UHE Jirau (MZUSP 4378, MZUSP 4379, MZUSP 4387, MZUSP 4423, MZUSP 4424); Vilhena (CHUNB 9996, CHUNB 9997, CHUNB 9998). RORAIMA: Caracaraí, Rio Jufari (MZUSP 4409, MZUSP 4410, MZUSP 4411, MZUSP 4412, MZUSP 4413); Mucajaí, Rio Apiaú (MZUSP 3318); Rorainópolis, Santa Maria do Boiaçu (MZUSP 3175). Unknown Locality (MPEG 730).

Mesoclemmys raniceps (n = 14)—**BRAZIL:** ACRE: Porto Walter (MZUSP 3007). AMAZONAS: Atalaia do Norte, Rio Itacoaí (MNRJ 2423); Benjamin Cosntant, Rio Javari (MNRJ 1070); Canutama (MZUSP 2834, MZUSP 2838); Manacapuru, Lago do Canabuoca (MNRJ 1068). PARÁ: Belém (MNRJ 4755). RONDÔNIA: Costa Marques, Forte Príncipe da Beira (MZUSP 2136, MZUSP 2138, MZUSP 2139, MZUSP 2140, MZUSP 2141); Porto Velho, UHE Jirau (MZUSP 4388). **PERU:** LORETO: Estirón, Rio Ampiyacu (MZUSP 2642).

Mesoclemmys heliostemma (n = 8)—**BRAZIL:** ACRE: Santa Rosa do Purús, Alto Purús (MZUSP 2050). AMAZONAS: Nova Olinda do Norte, próximo à boca do furo do rio Canumá (MZUSP 2639). MATO GROSSO: Apiacás, igarapé sem nome que corta a trilha do Mutum (MZUSP 3387). PARÁ: Itaituba, PARNA da Amazônia, Base do Uruá (MZUSP 3022). RONDÔNIA: Urupá, Igarapé Santa Helena (MPEG 86); Porto Velho, UHE Jirau (MZUSP 4377). RORAIMA: Iracema, Rio Jundiá (MZUSP 2918). **PERU:** LORETO: Estirón, Rio Ampiyacu (MZUSP 2641).

APPENDIX 2. Slopes and intercepts of the log-transformed variables for *Mesoclemmys gibba* and significant differences of intercept for other taxa.

	HW	PW	SH	CW
Intercept	-1.159	-0.324	-1.159	-0.041
Slope (CL)	1.016	0.737	1.016	0.450
Difference (*M. heliostemma*)	-0.457	-0.408	-0.457	-
Difference (*M. raniceps*)	-0.135	-0.181	-	-