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A New South American Freshwater Turtle of the Genus *Mesoclemmys* from the Brazilian Amazon (Testudines: Pleurodira: Chelidae)

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ABSTRACT. – We describe a new species of small chelid turtle from perennial streams in the Araguaia River subbasin near Serra das Andorinhas State Park, São Geraldo do Araguaia, Pará, Brazil. It is morphologically distinct and the smallest known member of the genus *Mesoclemmys*, with an average straight-line carapace length (CL) of 144 mm and maximum recorded CL of 170 mm. The species has a moderate head width of approximately 20% of CL. The carapace and dorsal soft parts are blackish, the plastron is light brownish yellow with a blackish brown central plastral figure, and the ventral soft parts are pale yellow. It has the largest femoral scutes of any *Mesoclemmys* and its plastral contact formula is Intergular > Anal > Humeral > Femoral > Abdominal > Pectoral > Gular. We describe the shell and skull morphology of the new species and performed genetic analysis using mitochondrial DNA (cytochrome *c* oxidase, subunits I [COI] and 16S) to build a phylogenetic tree for the genus, which placed the new species as sister to *M. vanderhaegei*.

KEY WORDS. – *Mesoclemmys* sp. nov.; Amazon basin; biodiversity; taxonomy; freshwater turtles

The South American Neotropics have a rich diversity of freshwater turtles with a high degree of endemism and a high conservation priority (Ennen et al. 2020). Most of the species occur in the Amazon and Orinoco basins, and Brazil is the third-ranked country globally for turtle species richness (Turtle Taxonomy Working Group [TTWG] 2021). In the family Chelidae, there are 21 currently recognized species (TTWG 2017, 2021; Cunha et al. 2021b). In a recent taxonomic revision of the genus *Mesoclemmys*, Cunha et al. (2019) concluded that *M. heliostemma* (McCord et al. 2001) was a synonym of *M. raniceps* (Gray 1856) and that *M. wermuthi* (Mertens 1969), a former synonym of *M. raniceps*, was in fact a valid and separate species (Costa et al. 2021; TTWG 2021). There has been considerable debate concerning the taxonomy of species included in the genus *Mesoclemmys*, one reason being the paucity of data on their biology, with few publications dealing with their natural history, reproductive biology, and taxonomy (Brito et al. 2019; Cunha et al. 2021a, 2021b).

At present, there are 10 species generally recognized in the genus *Mesoclemmys*, widely distributed throughout South America, occurring in Brazil, Bolivia, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, Trinidad, and Venezuela (TTWG 2021). Brazil has 8 species of *Mesoclemmys*: *M. raniceps* from the central Amazon basin in the states of Acre, Amazonas, Pará, Roraima, Rondônia, and Mato Grosso, and possibly extending into southeastern Colombia, Peru, eastern Ecuador, and northern Bolivia; *M. wermuthi* from the upper Amazon basin in the states of Acre, Amazonas, Rondônia, Mato Grosso, and extreme western Pará, and extending into Peru, northern Bolivia, and extreme southeastern Colombia; *M. nasuta* (Schweigger 1812) from the Guiana Shield, Suriname, French Guiana, Amapá, and extreme northeastern Pará; *M. gibba* (Schweigger 1812) in Amazonia extending north into Venezuela and Trinidad, south into northern Mato Grosso, and east into Guyana and Suriname; *M. vanderhaegei* (Bour 1973) occurring in Brazil in Tocantins, Mato Grosso do Sul, Goiás, Minas Gerais, and São Paulo, as well as in the wetlands of

Paraguay and northern Argentina; *M. tuberculata* (Luederwaldt 1926) from the Caatinga of northeastern Brazil in Sergipe, Piauí, Ceará, and Rio Grande do Norte; *M. perplexa* (Bour and Zaher 2005), also from northeastern Brazil in Piauí and Ceará; and *M. jurutiensis* (Cunha et al. 2021b), with an apparently restricted distribution in the lower River Amazonas in western Pará. Additionally, *Ranacephala hogei* (Mertens 1967) from the Atlantic Forest in Minas Gerais, Rio de Janeiro, and Espírito Santo was previously considered a member of the genus *Mesoclemmys* (TTWG 2017), but is now considered to represent a primitive monotypic genus, *Ranacephala* (TTWG 2021), and *M. raniceps*, *M. wermuthi*, *M. nasuta*, and *M. tuberculata*, all with relatively wider heads, are morphologically divergent and referred by some authorities to the genus *Batrachemys* (McCord et al. 2001; Cunha et al. 2019).

The unsettled and poorly defined taxonomy of this genus has impeded studies of the ecology of its component species, complicating, as a result, the concrete and targeted conservation measures needed with the widespread degradation and loss of their habitats that is prevalent in tropical South America today. Here, we provide a description of a new species of *Mesoclemmys* in the *gibba-vanderhaegei* complex from São Geraldo do Araguaia, Pará, Brazil, on the basis of distinct morphological characters and molecular genetic analysis, comparing it to other species of the genus. We generate a phylogenetic tree with sequences obtained from 7 Brazilian congeneric and closely related species (*M. jurutiensis*, *M. raniceps*, *M. gibba*, *M. vanderhaegei*, *M. nasuta*, *M. tuberculata*, and *R. hogei*) and from other tropical Testudines available in Genbank. For comparison, we provide photographs of all the studied Brazilian species that we currently recognize.

METHODS

Specimens Examined for Morphological Measurements. — We analyzed and compared the morphology of 6 specimens (4 adults, 1 subadult, 1 juvenile) of the new species with 40 specimens of 5 other members of the genus: *M. jurutiensis*, *M. gibba*, *M. raniceps*, *M. perplexa*, and *M. vanderhaegei* (Appendix 1). All specimens were deposited in either the Herpetological Collection of the Museu Paraense Emílio Goeldi (MPEG), Belém, Pará, Brazil, or in the Reptile and Amphibian Collection and the Center for the Study of Amazonian Chelonia (CEQUA), both of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil. Morphological data for 15 specimens of *M. vanderhaegei* from the Paraguai River basin were kindly provided by E.S. Brito. Skulls from specimens in several international museums were also examined (Appendix 1).

We measured standard quantitative morphological characteristics and recorded qualitative characters. Primary measurements recorded (all by F.A.G.C.) were maximum

straight-line carapace length (CL), maximum straight-line carapace width (CW), maximum carapace depth (CD), maximum plastron length (PL), plastron width (PW), gular scute length left (GSL), intergular scute length (ISL), gular scute length right (GSLR), humeral scute length (HSL), pectoral scute length (PSL), abdominal scute length (ASL), femoral scute length (FSL), anal scute length (AnSL), head length (HL), head height (HH), and head width (HW) at the midpoint of the tympani. We used analog calipers (Marberg® for the smaller measurements and Haglof® for the larger measurements) to the nearest 0.1 mm; means \pm 1 standard deviation (SD) are provided. All specimens were photographed and radiographic images were taken of 3 of them.

We measured 59 skulls from 10 species: *Mesoclemmys raniceps/wermuthi*, *M. tuberculata*, *M. gibba*, *M. vanderhaegei*, *Ranacephala hogei*, *Phrynops geoffroanus*, *P. hilarii*, *P. williamsi*, *Rhinemys rufipes*, and the new species of *Mesoclemmys*. For each skull we measured CL of the whole animal, midline skull length (SL) from the premaxillaries to the occipital condyle, tympanic skull width (SWT), maxillary skull width (SWM), maxillary skull depth (SDM), posterior midline skull depth at the level of the basioccipital (SDP), interorbital width (IOW), minimum orbital width (OW), minimum parietal roof width (ParW), and maximum pterygoid trochlear processes width (PtW). These specimens were measured by AGJR, except for the single skull of the new species measured by FACG.

Statistical Analysis. — We used the one-way analysis of variance (ANOVA) to test for statistical differences in the ratios of CW, PL, CD, and HW to CL. We used the analysis of covariance (ANCOVA) 1-way test to examine differences in the ratios of CW and CL for each of the five species studied. Prior to these tests, we ascertained that the data followed a normal distribution and were homoscedastic, allowing for parametric statistical analyses. We also tested the data using Levene's Test for equality of variances. The variances were not equal, so we used the Scheffé method post hoc to adjust the significance in examining the differences between pairs of species. We also regressed the ratios CW/CL, HW/CL, and CD/CL on CL using simple linear regression analysis.

For principal component analysis (PCA), we used the ratios CW/CL, CD/CL, and HW/CL in the Program R software. For the analysis of skull data, we used the ratios of SL/CL, SWT/CL, SWT/SL, SWM/SL, SWM/SWT, ParW/SWT, PtW/SWT, IOW/SWM, IOW/OW, and SDM/SWM. The selection of metrics was based on the criteria of variability, responsiveness, and redundancy (Whittier et al. 2007). The variability criterion was used to exclude metrics with low discriminatory power, inadequate to detect differences between samples, and also to exclude metrics with 75% equal value. In addition, we discarded numeric metrics with a range \leq 3 and percentage metrics with a range $<$ 10%. The second criterion tested the responsiveness of the metrics through a PCA using the

Table 1. Data partitions, evolutionary models, and the numbers of base pairs.

Partition	Best model	Sites
1	GTR+G	603
2	K80+I	214
3	F81+I	213
4	HKY+G	213

function `prcomp` in R (R Core Team 2021). Different measurement units were involved; therefore, data were standardized (\log_{10}) and analyses were performed based on the correlation matrix (Hammer et al. 2001). The significant components of the analysis were obtained using the broken stick criterion (Jackson 1993). Metrics that did not have a significant correlation ($p > 0.05$) with any of the significant PCA axes were excluded. The redundancy criterion, in turn, sought to identify pairs of metrics that express similar information. When two metrics were considered redundant (Spearman's $\rho \geq 0.70$), the one with the lower responsiveness-test significance value was removed.

All statistical relationships and analyses were performed following Zar (2014), with Statistica® 7.0 Software and Software R (R Core Team 2021). We recorded the plastral formula described by Lovich and Ernst (1989). Regarding the relationships of morphometric measurements to compare data for taxonomic studies of freshwater turtles, part of the method was based on Thomson et al. (2006).

Genetic Data and Analyses. — We used muscle tissue samples from 8 specimens preserved in absolute EtOH (with 6 of these specimens used for morphological description), deposited in the genetics bank of the Museu Paraense Emílio Goeldi, Belém, state of Pará, Brazil. We obtained total DNA with Promega's Wizard Genomic kit, according to the manufacturer's protocol. We amplified

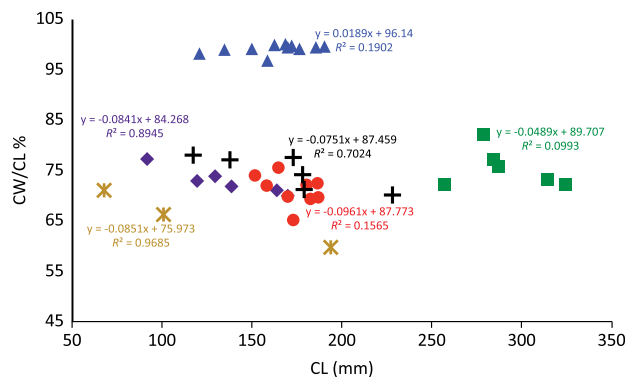


Figure 1. Analysis of linear regression of the carapace width (CW)/carapace length (CL) ratio vs. carapace length (CL) of *Mesoclemmys sabiniparaensis* (diamonds), *M. raniceps* (squares), *M. gibba* (circles), *M. perplexa* (asterisks), all from the data presented by Bour and Zaher (2005); *M. jurutiensis* (crosses) from data presented by Cunha et al. (2021b); and *M. vanderhaegei* (triangles) from unpublished data provided by E.S. Brito. (Color version is available online.)

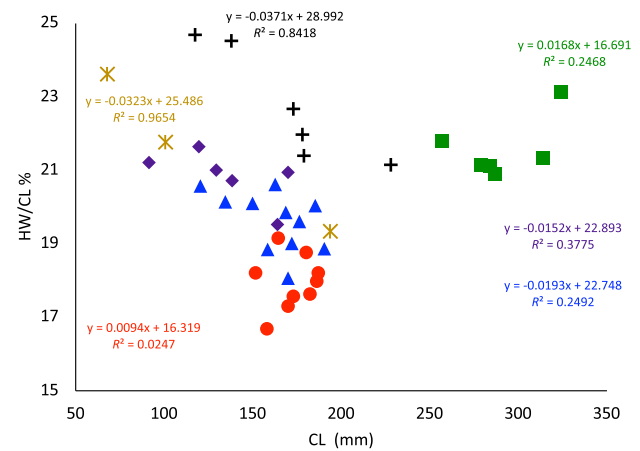


Figure 2. Analysis of linear regression of the head width (HW)/carapace length (CL) ratio vs. carapace length (CL) of *Mesoclemmys sabiniparaensis* (diamonds), *M. raniceps* (squares), *M. gibba* (circles), and *M. perplexa* (asterisks), all from the data presented by Bour and Zaher (2005); *M. jurutiensis* (crosses) from data presented by Cunha et al. (2021b); and *M. vanderhaegei* (triangles) from unpublished data provided by E.S. Brito. (Color version is available online.)

fragments of the COI and 16S gene by polymerase chain reaction (PCR). For the PCRs, a final volume of 15 μ L was used, containing about 30 ng of genomic DNA, 2.4 μ L of dNTPs (1.25 mM), 1.5 μ L of 10 \times Buffer (200 mM Tris-HCl, 500 mM KCl), 1 μ L of MgCl₂ (25 mM), 1 μ L of each primer (0.2 μ M), and 1 U of *Taq* DNA polymerase. The amplification protocol was initiated with 4 min of denaturation at 95°C, followed by 35 cycles of 3 stages: (i) denaturation at 95°C for 30 sec; (ii) annealing at a specific temperature of 47°C to COI and 53°C to 16S; and (iii) extension at 72°C for 60 sec. After completion of the 35 cycles, there was a final extension stage at 72°C for 10 min. We then purified the PCR products using polyethylene glycol and ethanol (Paithankar and Prasad 1991). The sequencing reactions were run

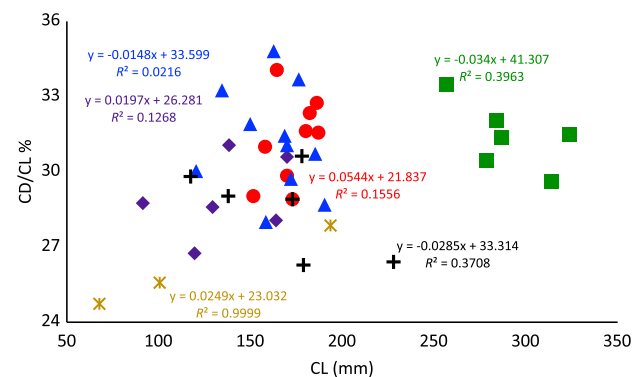


Figure 3. Analysis of linear regression of the carapace depth (CD)/carapace length (CL) ratio vs. carapace length (CL) of *Mesoclemmys sabiniparaensis* (diamonds), *M. raniceps* (squares), *M. gibba* (circles), *M. perplexa* (asterisks), all from the data presented by Bour and Zaher (2005); *M. jurutiensis* (crosses) from data presented by Cunha et al. (2021b); and *M. vanderhaegei* (triangles) from unpublished data provided by E.S. Brito. (Color version is available online.)

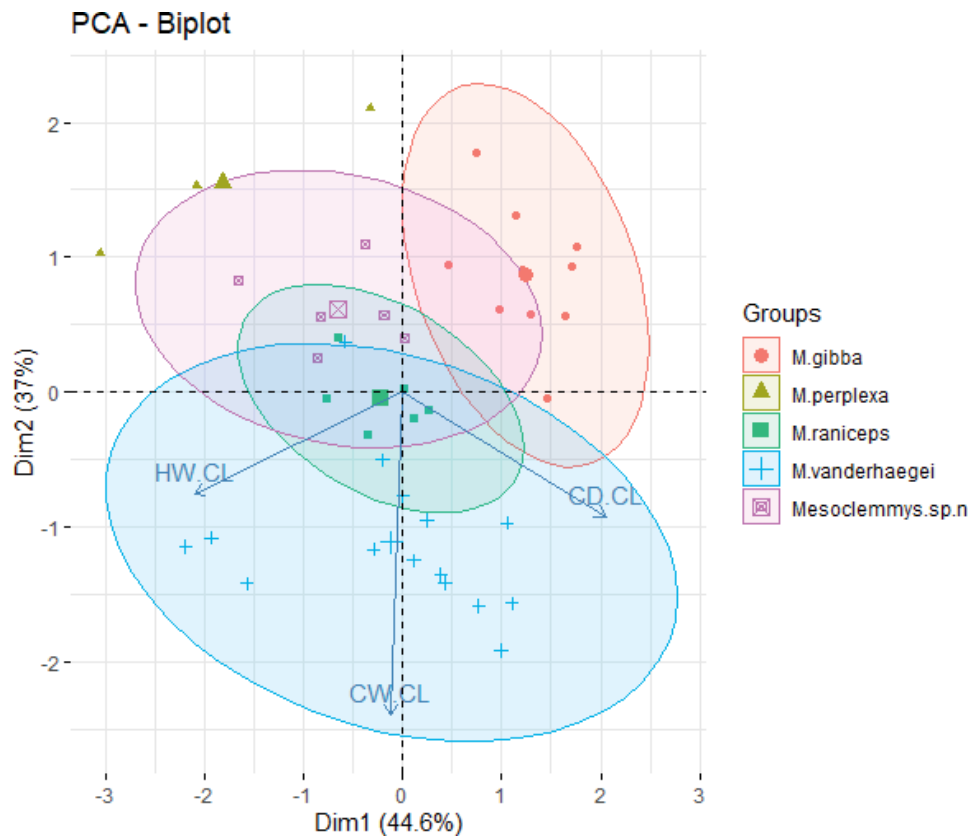


Figure 4. For multivariate analysis of principal components, we used the ratios of carapace width (CW)/carapace length (CL), carapace depth (CD)/carapace length (CL), and head width (HW)/carapace length (CL).

using the BigDye Terminator Sequencing kit v. 3.1 (Life Technologies) and the reaction products were separated and visualized using an ABI 3500xl automatic sequencer (Life Technologies).

Sequence Alignment, Phylogenetic Analyses, and Genetic Distances. — For the phylogenetic reconstruction, we included all the *Mesoclemmys* sequences and those of a number of closely related genera available from GenBank. The DNA sequences were aligned using online Mafft (Katoh et al. 2019). We used the software PartitionFinder (Kimura 1980; Lanfear et al. 2012) to test different partition schemes and select the most appropriate evolutionary model (Table 1). For Partition Finder analyses, we allowed linked branch lengths and used the Bayesian information criterion. Our analysis suggested that the best scheme for our data set was to separate it into 4 partitions. Phylogenetic reconstruction was performed in W-IQ-

TREE online (Trifinopoulos et al. 2016) considering the scheme and model estimated in PartitionFinder. In MEGA (Kumar et al. 2018), we estimated genetic distances between pairs of taxa. We used ABGD (Puillandre et al. 2012) to test the possibility of a new species among the samples analyzed. A phylogenetic tree was created with 20 species of 11 genera of the family Chelidae available in GenBank and concatenated for the two genes studied.

RESULTS

Morphology. — The *Mesoclemmys* from the Serra das Andorinhas State Park in the Araguaia River subbasin is morphologically distinct from all other species of the genus. It shares some morphological features with 4 *Mesoclemmys* from the region (*M. gibba*, *M. perplexa*, *M. raniceps*, and *M. vanderhaegei*), but there is a significant difference in the CW/CL ratio among the 5 species we

Table 2. Factor loadings in multivariate analysis of principal components (PC) using the ratios carapace width (CW), carapace depth (CD), and head width (HW) to carapace length (CL).

	PC1	PC2	PC3
CW/CL	-0.0420684269640431	-0.894495920333646	-0.445092457764939
CD/CL	0.696605417187193	-0.34560906585144	0.628725111910406
HW/CL	-0.716220036160835	-0.28360434077356	0.637649933501144

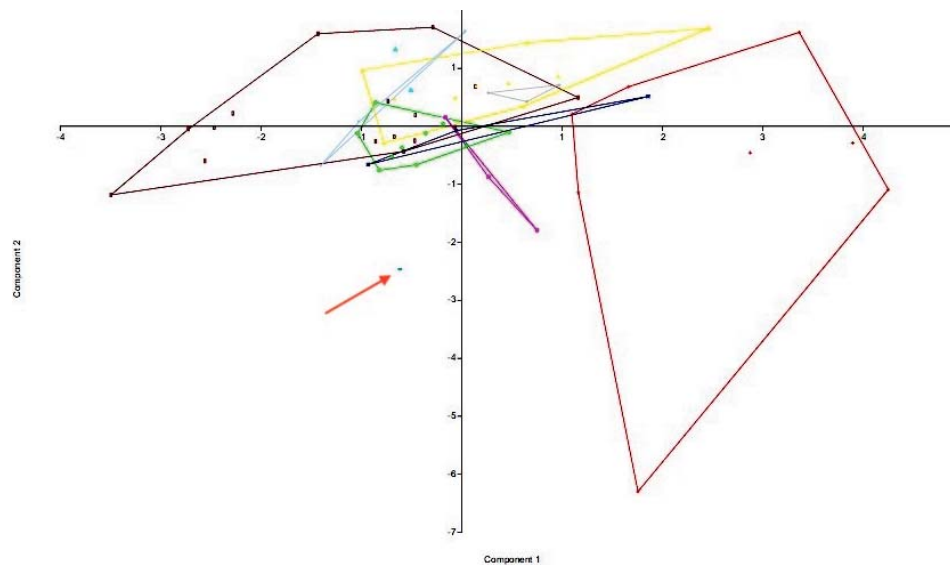


Figure 5. The results of the principal components analysis of skull measurements. Note the arrow showing the position of the new species, *Mesoclemmys sabiniparaensis*. Red polygon: *Mesoclemmys raniceps/wermuthi*; pink polygon: *Mesoclemmys tuberculata*; blue polygon: *Mesoclemmys vanderhaegei*; green polygon: *Mesoclemmys gibba*; light blue polygon: *Ranacephala hoguei*; dark red polygon: *Phrynops geoffroanus*; yellow polygon: *Phrynops hilarii*; blue triangle: *Phrynops williamsi*; and gray polygon: *Rhinemys rufipes*.

studied (ANOVA, $F_{4,35} = 100.8$, $p < 0.01$), and the same is true for the PL/CL and HW/CL ratios (ANOVA, $F_{4,35} = 5.50$, $p < 0.01$; ANOVA, $F_{4,35} = 8.32$, $p < 0.01$). The covariance between the 5 species for each of the paired species is the same and the Serra das Andorinhas State Park specimens differ significantly from each of the other species in ANCOVA: *M. gibba* ($F_{1,6} = 404.1$, $p < 0.01$), *M. perplexa* ($F_{1,6} = 148.3$, $p < 0.01$), *M. raniceps* ($F_{1,6} = 159$, $p < 0.01$), and *M. vanderhaegei* ($F_{1,6} = 463.8$, $p < 0.01$). Regression of CW/CL, HW/CL, and CD/CL on CL for the Serra das Andorinhas specimens and the five *Mesoclemmys* species is shown in Figs. 1–3.

PCA results for shell morphometrics (Fig. 4) were more evident for all species with stronger relationships for PC1 for CD/CL, PC2 for CW/CL, and PC3 for HW/CL (Table 2). The results of the PCA for skull measurements are shown in Fig. 5; the six ratios with the greatest significance were extracted (Table 3).

Genetics. — We analyzed 640 bp for the COI gene and 549 bp for 16S. Fragments homologous to the

sequences were obtained from Genbank for *R. hoguei*, *M. gibba*, *M. raniceps*, *M. tuberculata*, *M. jurutiensis*, and *M. vanderhaegei*. The genetic distance analysis for the COI gene sequences (Table 4) separated the *Mesoclemmys* from Serra das Andorinhas from its sister species, *M. vanderhaegei*, by 4.3%, and from *R. hoguei*, *M. raniceps*, and *M. tuberculata* by $> 10.8\%$ as a result of the different rates of the evolutionary model. For the 16S gene (Table 5), the *Mesoclemmys* from Serra das Andorinhas was genetically distinct by 3.0% from *M. gibba*, by $> 8.0\%$ from *R. hoguei*, and by $> 4.0\%$ for the most part from *M. nasuta*. At higher taxonomic levels, the *Mesoclemmys* from Serra das Andorinhas diverges $> 7.6\%$ from *Phrynops hilarii* (Duméril and Bibron 1835), *Phrynops williamsi* (Rhodin and Mittermeier 1983), and *Platemys platycephala* (Schneider 1792). A maximum likelihood phylogenetic analysis grouped the Serra da Andorinhas *Mesoclemmys* in a monophyletic clade with *M. vanderhaegei*, with 87% statistical support (Fig. 6).

Table 3. Factor loadings in multivariate analysis of principal components (PC) using the ratios of skull measurements of tympanic skull width to carapace length (SWT/CL), tympanic skull width to skull length (SWT/SL), maximum pterygoidal trochlear processes width to tympanic skull width (PtW/SWT), interorbital width to maxillary skull width (IOW/SWM), interorbital width to minimum orbital width (IOW/OW), and maxillary skull depth to maxillary skull width (SDM/SWM).

	PC1	PC2	PC3	PC4	PC5	PC6
SWT/CL	0.4238	-0.5568	-0.1557	0.2626	0.2911	0.5766
SWT/SL	0.5728	0.01962	-0.2116	0.3626	-0.6347	-0.3039
PtW/SWT	-0.1956	0.6431	-0.3231	0.5135	0.04229	0.4222
IOW/SWM	0.3796	0.3536	0.528	-0.3574	-0.2674	0.5028
IOW/OW	0.5424	0.376	0.02998	-0.005066	0.6597	-0.3582
SDM/SWM	-0.1254	-0.09837	0.7395	0.6388	0.06231	-0.1255

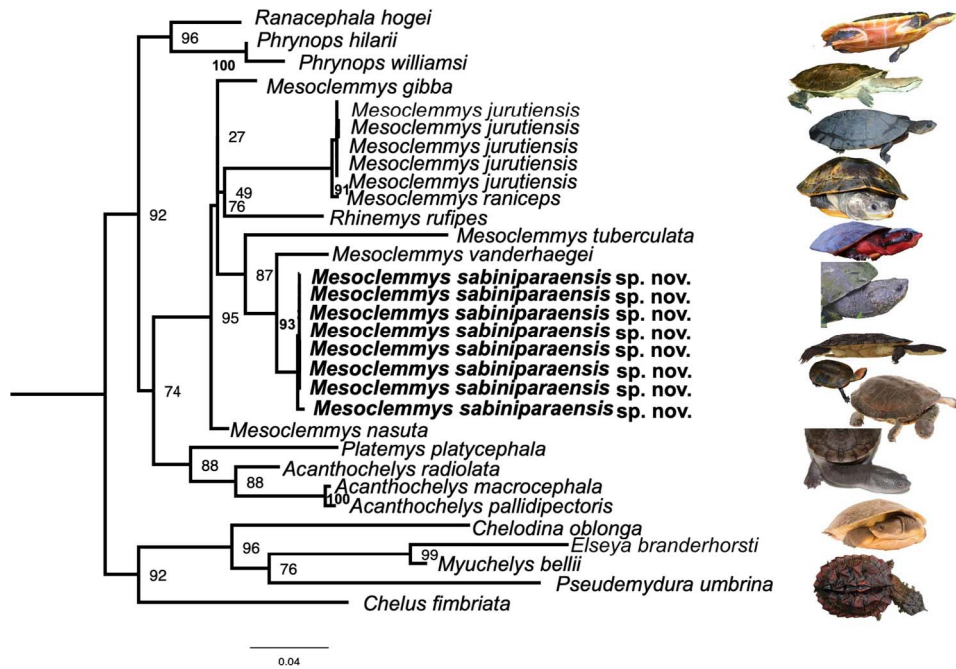


Figure 6. Phylogenetic analysis of maximum likelihood for the new species and other related species available in GenBank. Bootstrap numbers are next to the nodes. Concatenated data (COI and 16S) were used for the analysis and creation of the phylogenetic tree. (Color version is available online.)

having the proportionately smallest abdominal scutes (ASL/CL) and largest femoral scutes (FSL/CL) in the genus (Table 7).

Mesoclemmys sabiniparaensis differs from sympatric *M. gibba* in having a flatter carapace, shell not domed, and the lateral margins of the carapace not upturned; it differs from sympatric *M. raniceps* in having a large pair of barbels under the mandible and lacking the narrow parietal skull roof and prominently bulbous temporal musculature of *M. raniceps*. In addition, *M. raniceps* has a proportionally

wider head (ca. 21%–23% of CL vs. ca. 20% of CL for *M. sabiniparaensis* and ca. 17%–19% of CL for *M. gibba*).

As for the other potentially sympatric members of the genus, *M. sabiniparaensis* differs from *M. perplexa* in having a larger humeral scute (HSL/CL), and a flatter head without raised scales and orbital plaques; it differs from *R. hogei* in having a dark, blackish patch on the central part of the plastron on the humeral, pectoral, abdominal and femoral scutes; and it is much smaller than *M. nasuta*, with adult females having a CL of 129.5 mm, while the CL of

Table 6. Morphometric data (absolute values, in mm) and relationship between morphometric measurements and carapace length (in percentages) for the holotype, allotype, and 2 paratypes of *Mesoclemmys* sp. nov. from the municipality of São Geraldo do Araguaia, state of Pará, Brazil.

		<i>Mesoclemmys sabiniparaensis</i> sp. nov.							
		Holotype MPEG-H1251		Allotype MPEG-H1255		Paratype 1 MPEG-H1254		Paratype 2 MPEG-H1258	
	Code	mm	%CL	mm	%CL	mm	%CL	mm	%CL
Carapace length	CL	119.7	—	138.5	—	129.5	—	91.5	—
Carapace width	CW	87.3	72.9	99.5	71.8	95.7	73.8	70.8	77.3
Plastron length	PL	105.7	88.3	128.9	93.0	115.4	89.1	79.1	86.4
Plastron width	PW	72.6	60.6	84.4	60.9	79.2	61.1	56.7	61.9
Carapace depth	CD	32.0	26.7	43.0	31.0	37.0	28.5	26.3	28.7
Head length	HL	28.6	23.8	27.5	19.8	31.2	24.0	23.7	25.9
Head width	HW	25.9	21.6	28.7	20.7	27.2	21.0	19.4	21.2
Head height	HH	14.4	12.0	34.2	24.6	17.5	13.5	11.9	13.0
Gular scute length left	GSR	12.3	10.2	15.7	11.3	15.9	12.2	11.2	12.2
Intercular scute length	ISL	13.3	11.1	26.8	19.3	22.6	17.4	18.4	20.1
Gular scute length right	GSL	12.8	10.6	17.0	12.2	15.4	11.8	11.1	12.1
Humeral scute length	HSL	14.3	11.9	22.2	16.0	15.6	12.0	10.9	11.9
Pectoral scute length	PSL	13.7	11.4	11.7	8.4	16.0	12.3	9.4	10.2
Abdominal scute length	ASL	13.1	10.9	16.7	12.0	12.2	9.4	9.7	10.6
Femoral scute length	FSL	15.5	12.9	22.8	16.4	20.5	15.8	14.4	15.7
Anal scute length	AnSL	18.9	15.7	18.5	13.3	19.7	15.2	14.1	15.4

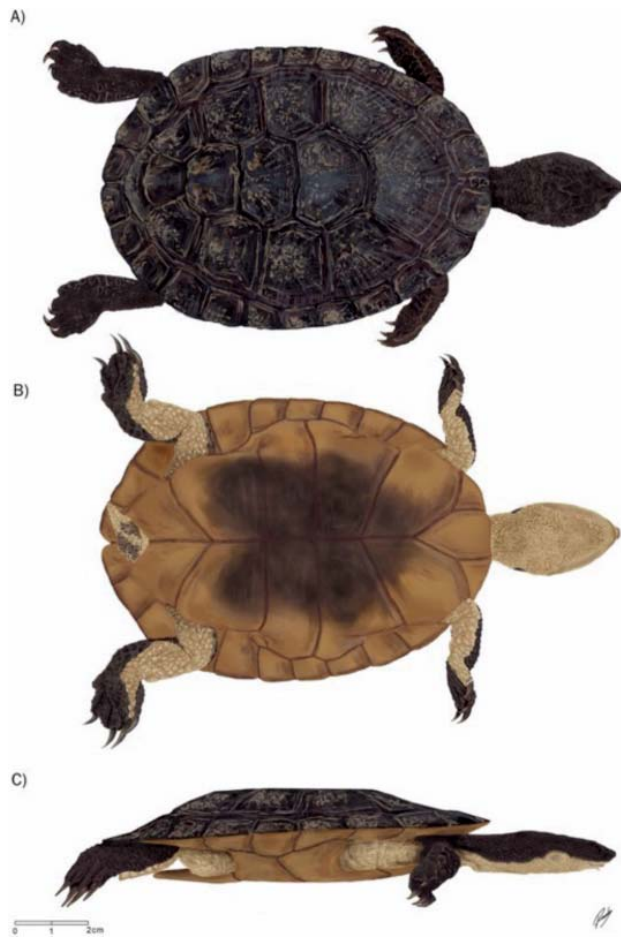


Figure 7. (A) Dorsal aspect, (B) ventral aspect, and (C) lateral aspect of the subadult female holotype of *Mesoclemmys sabiniparaensis* (MPEG-H1251, carapace length = 119.7 mm) from the municipality of São Geraldo do Araguaia, state of Pará, Brazil. Illustrations by Ricardo Ribeiro.

M. nasuta averages 300 mm in adult females and 320 mm for adult males. The head of *M. sabiniparaensis* is narrower and its parietal roof is much wider than in *M. nasuta*. *Mesoclemmys sabiniparaensis* differs from *M. tuberculata* in having larger pectoral scutes and no upturning of the lateral margins of the carapace. Unlike in *M. tuberculata*, the arc of the shell shape of *M. sabiniparaensis* in lateral view is continuous and uniform.

Description of the Holotype. — Maximum carapace length 119.7 mm; carapace width at the 8th marginal scute 87.3 mm; (maximum) plastron length 105.7 mm; plastron width at the 6th marginal scute 72.6 mm; maximum depth of the shell 32.0 mm; length of the head from the tip of the nostril to the last scale on the head 28.6 mm; maximum width of the head at the level of the tympani 25.9 mm; height of the head (across tympani) 14.4 mm; gular length 12.3 mm on the left; lengths of plastral scutes (midline): intergular 13.3 mm; humeral 14.2 mm; pectoral 13.7 mm; abdominal 13.1 mm; femoral 15.5; and anal 18.9 mm. Carapace low and flat, with subtle arching; oval with a smooth surface and an indistinct median keel on the third and fourth vertebral scutes. Longitudinal furrows absent;



Figure 8. [Top] Ventral and dorsal aspect of the subadult female holotype of *Mesoclemmys sabiniparaensis* (MPEG-H1251, carapace length = 119.7 mm). [Bottom] Ventral and dorsal aspect of the adult male allotype *Mesoclemmys sabiniparaensis* (MPEG-H1255, carapace length = 138.5 mm) from the municipality of São Geraldo do Araguaia, state of Pará, Brazil. White line represents 30 mm. Photos by Fábio A.G. Cunha.

lateral margins of the carapace not upturned. Head small; mean head width/head length ratio (HW/HL) 0.90 and mean head width/carapace length ratio (HW/CL) 0.216. Head flattened dorsoventrally, triangular, with large eyes positioned anteriorly and oriented dorso-laterally. Iris black. Snout pointed, mouth small, and a pair of long, separate, pale-yellow barbels present, anteriorly below the mandible. Plastron flat, with intergular scute wider and longer than gular scutes. Plastron scute formula: Intergular > Anal > Humeral > Femoral > Abdominal > Pectoral > Gular. Distal tibial scale evident but weakly developed. Tail small.

Carapace uniformly black. Plastron and ventral carapace a uniform light brownish yellow with dark seams along the margins of the scutes. Center of plastron blackish brown on medial portions of humeral, pectoral, abdominal, and femoral scutes. Base of tail blackish, but tip paler and pinkish. Ventral neck burnt yellow with slightly pinkish tones. Demarcation of dark dorsal head and neck from pale yellow throat sharply and symmetrically defined from the mouth, posteriorly at the level of the tympani on both sides of the neck to its base and along the sides of the head.

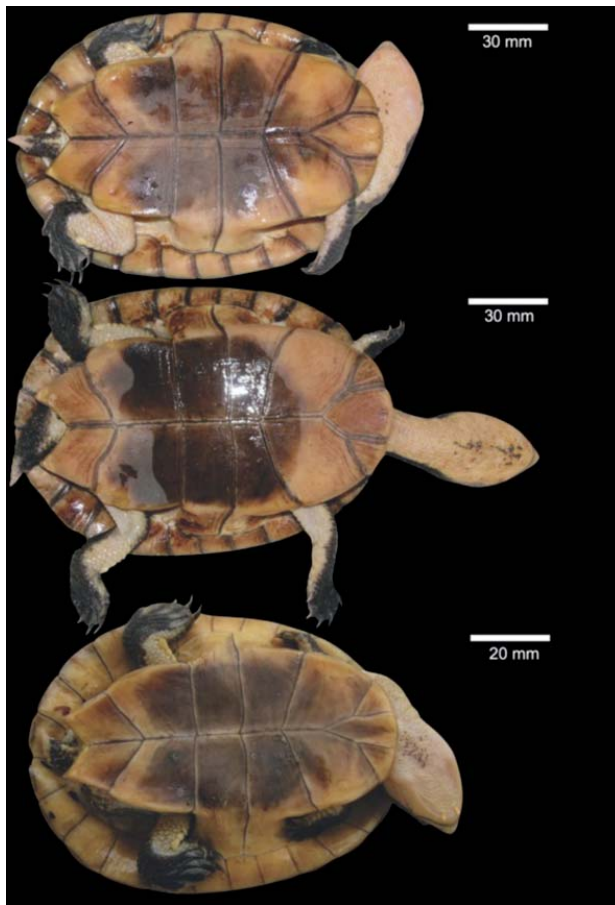


Figure 9. [Top] Ventral view of a female *Mesoclemmys sabiniparaensis* MPEG-H1254 (carapace length = 129.5 mm). [Middle] Ventral view of a male *Mesoclemmys sabiniparaensis* MPEG-H1255 (carapace length = 138.5 mm). [Bottom] Ventral view of the juvenile *Mesoclemmys sabiniparaensis* MPEG-H1258 (carapace length = 91.5 mm). Photos by Marinus S. Hoogmoed.

Bridge between the carapace and the plastron not ossified (Fig. 13).

Description of the Allotype. — Maximum CL 138.5 mm; width of carapace at the 8th marginal scute 99.5 mm; plastron 128.9 mm long and 84.4 mm wide at the 6th marginal scute; maximum depth of the carapace–plastron 43.0 mm; length of the head from tip of snout to the last scale of head 27.5 mm; maximum width of head at the level of the tympani 28.7 mm; height of head 34.2 mm; length of left gular scute of plastron 15.7 mm. Lengths of plastral scutes (midline): intergular 26.8 mm; gular 17.0 mm; humeral 22.2 mm; pectoral 11.7 mm; abdominal 16.7 mm; femoral 22.8; anal 18.5 mm. Carapace low, flat, not dome-shaped, and oval with a smooth surface and 3 indistinct keels on the third and fourth vertebral scutes. Longitudinal furrows absent and lateral margins of carapace not upturned. Head narrow (HW/CL 0.207), flattened dorso-ventrally, and triangular in shape. Large eyes positioned anteriorly and oriented dorso-laterally. Iris uniformly black. Snout pointed, mouth small, and a pair of long, separate, pale-yellow barbels present, anteriorly below the mandible.



Figure 10. [Top] Lateral view of the juvenile paratype of *Mesoclemmys sabiniparaensis* (holotype MPEG-H1258, carapace length = 91.5 mm). Note the shape and dark reddish brown coloration of the carapace. [Bottom] The same specimen detailing the dorso-lateral part of the head with the sharp bilineation. Photos by Marinus S. Hoogmoed.

Carapace uniformly black. Plastron and ventral carapace a uniform burnt yellow but with dark seams along scute margins. Center of plastron blackish brown on interior portions of humeral, pectoral, abdominal, and femoral scutes. Tail large and thick, blackish at base, with pale yellow tip. Neck pale yellow with some black spotting below the chin. Division of dark head and nuchal region and pale-yellow throat sharp and symmetrically defined, from the mouth, posteriorly at the level of

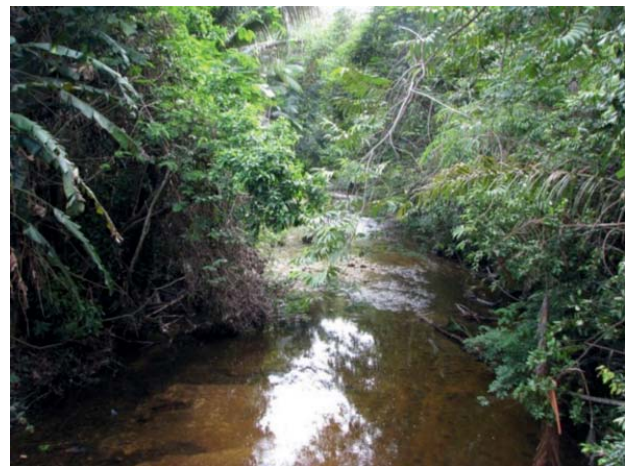


Figure 11. Habitat of *Mesoclemmys sabiniparaensis*, in the Serra das Andorinhas State Park, municipality of São Geraldo do Araguaia, state of Pará, Brazil (WGS84, 06°12'53"S, 48°25'44"W; 110 m above sea level). Photo by Marinus S. Hoogmoed.

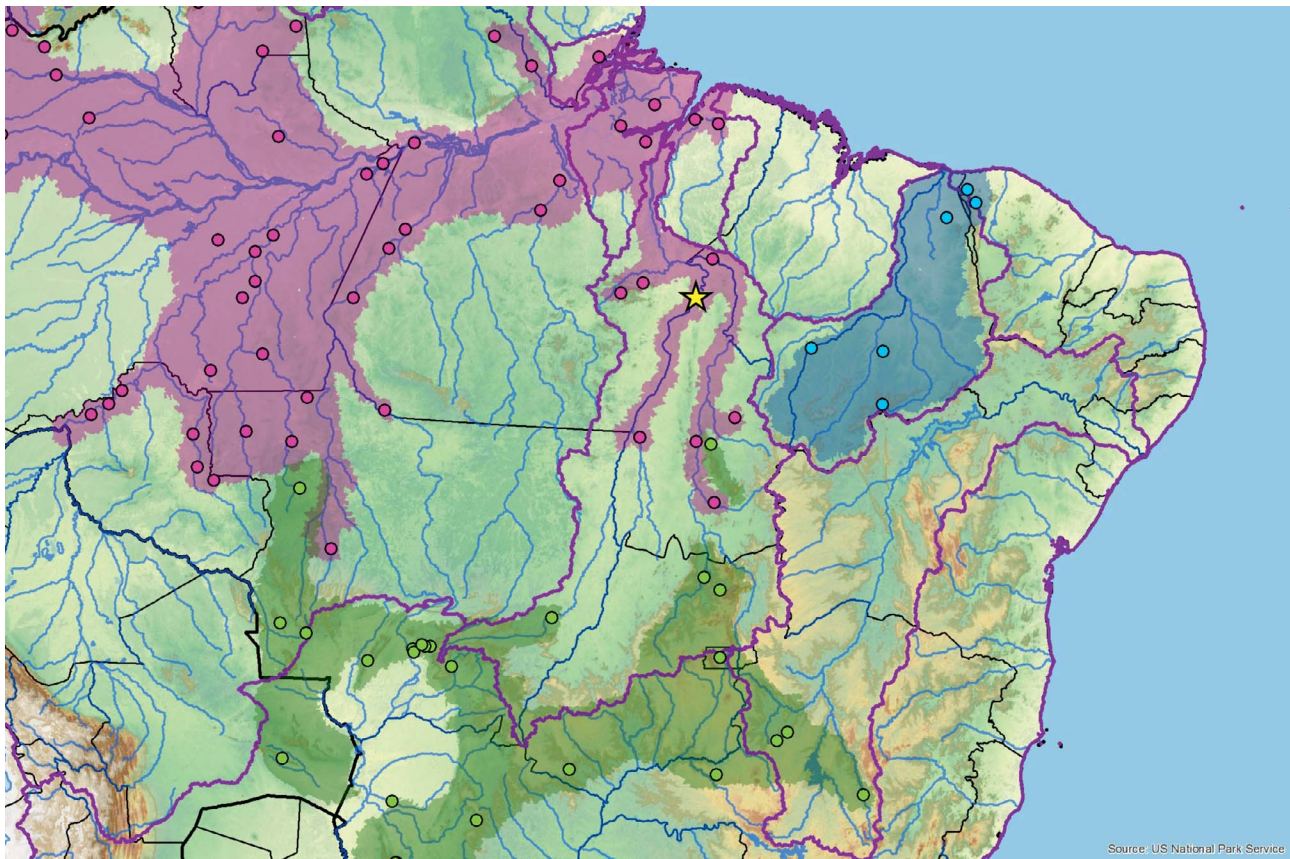


Figure 12. Location where *Mesoclemmys sabiniparaensis* was collected in São Geraldo do Araguaia, Pará, Brazil (yellow star), and currently understood distributions (shadings and dots) of *M. gibba* (purple), *M. vanderhaegei* (green), and *M. perplexa* (blue) as per TTWG (2021) and updated with new distributional information. Purple lines show watershed limits for level 03 World Wildlife Fund hydrobasins (hydrologic unit compartments [HUCs]). Note that *M. vanderhaegei* is endemic to the higher altitude Cerrado biome and apparently excluded from non-Cerrado lower altitude areas such as the Pantanal and lowland regions of the upper Araguaia and Tocantins watersheds.

tympani on both sides of neck to its base, and sides of head.

Juvenile Paratype. — Young specimen (CL 91.5 mm) of *M. sabiniparaensis* differs in coloration of carapace, which is uniformly reddish brown, and dorsum of head, which is blackish, spotted with brown.

Adult Female Paratype. — Skull length 31.0 mm; tympanic width 26.0 mm; minimum parietal roof width 7.1 mm; interorbital width 4.4 mm, minimum orbital width 7.2 mm.

The skull of the new species is relatively narrow as compared with its carapace length, similar to that of *M. gibba* and *M. vanderhaegei*, and narrower than skulls of the *M. raniceps/wermuthi* complex. The tympanic skull width as a percentage of carapace length (SWT/CL) in *M. sabiniparaensis* is 20.1% ($n = 1$), in *M. gibba* it averages 18.3% (range 17.5%–18.9%, $n = 8$), in *M. vanderhaegei* it averages 18.9% (range 18.2%–19.3%, $n = 3$), and in the *M. raniceps/wermuthi* complex it is wider and averages 24.2% (range 20.3%–26.7%, $n = 5$). The skull of *M. sabiniparaensis* is relatively narrow compared with its length; the tympanic skull width as a percentage of skull length (SWT/SL) in *M. sabiniparaensis* is 83.9% ($n = 1$), in *M. gibba* it averages 85.8% (range 83.3%–90.3%,

$n = 10$), in *M. vanderhaegei* it averages slightly more at 87.8% (range 84.1%–94.2%, $n = 3$), and in the *M. raniceps/wermuthi* complex the skull is wider and averages 95.5% (range 85.3%–103.6%, $n = 8$).

The minimum horizontal width of the parietal roof in *M. sabiniparaensis* is relatively wide, similar to that in *M. gibba*, but slightly wider than in *M. vanderhaegei*, and much wider than the narrow parietal ridge present in the *M. raniceps/wermuthi* complex. The parietal roof width as a percentage of tympanic skull width (ParW/SWT) in *M. sabiniparaensis* is 27.3% ($n = 1$), in *M. gibba* it averages 29.5% (range 24.2%–37.8%, $n = 10$), in *M. vanderhaegei* it is slightly narrower and averages 17.3% (range 12.2%–21.5%, $n = 3$), and in the *M. raniceps/wermuthi* complex it is much narrower, no more than a ridge, and averages 4.1% (range 1.8%–6.8%, $n = 6$).

The orbits in *M. sabiniparaensis* are fairly narrowly separated from one another, with a relatively narrow interorbital distance; the orbital separation is wider in *M. gibba*, *M. vanderhaegei*, and especially in the *M. raniceps/wermuthi* complex. The interorbital width as a percentage of orbital width (IOW/OW) in *M. sabiniparaensis* is 61.1% ($n = 1$), in *M. gibba* it averages 70.9% (range 64.9%–76.4%, $n = 8$), in *M. vanderhaegei* it is slightly

Table 7. Morphometric data (means ± standard deviations, in mm) and relationship between morphometric measurements and carapace length (as a percentage of CL) for adults and a juvenile of *Mesoclemmys sabiniparaensis*; for adults and hatchlings of *Mesoclemmys raniceps*; for adults and juveniles of *Mesoclemmys gibba* and *Mesoclemmys perplexa* (all data from Bour and Zaher 2005, except hatchling data for *M. raniceps* from Cunha et al. [2019] and data for *M. gibba* from Ferronato et al. [2010]). * Two turtles measured; NR = not reported.

	<i>Mesoclemmys</i> sp. nov.					<i>Mesoclemmys raniceps</i>					<i>Mesoclemmys gibba</i>					<i>Mesoclemmys perplexa</i>				
	Adults n = 5		Juvenile n = 1		Code	Adults n = 6		Hatchlings n = 2		Code	Adults n = 10		Juveniles n = 2		Code	Adults n = 2		Juvenile n = 1		
	Mean ± SD	%CL	mm	%CL		Mean ± SD	%CL	Mean ± SD	%CL		Mean ± SD	%CL	Mean ± SD	%CL		Mean ± SD	%CL	Mean ± SD	%CL	mm
CL maximum–minimum:	170–119	—	—	—	324–257	—	—	—	—	186–131	—	—	—	—	193–100	—	—	—	—	
Carapace length	144.3 ± 21.8	—	91.5	—	290.8 ± 24.4	—	63.1 ± 0.0	—	—	168.5 ± 17.5	—	58.6 ± 6.7	—	147.2 ± 65.6	—	67.5	—	—		
Carapace width	103.3 ± 13.7	71.9	70.8	77.3	219.3 ± 17.5	75.5	48.0 ± 1.2	76.0	71.4	120.1 ± 11.4	71.4	46.7 ± 7.9	79.4	91.2 ± 34.6	63.0	48.0	71.0	—		
Plastron length	129.3 ± 19.2	89.6	79.1	86.4	249.7 ± 19.3	85.9	50.2 ± 0.3	79.5	90.6	152.6 ± 15.5	90.6	47.4 ± 6.2	80.8	126.1 ± 53.3	86.1	54.2	80.2	—		
Plastron width	86.4 ± 11.6	60.0	56.7	61.9	126.0 ± 29.5	43.0	36.9 ± 0.6	58.5	57.6	97.0 ± 10.4	57.6	37.8 ± 5.4	64.3	94.5	48.0	37.9	56.1	—		
Carapace depth	42.0 ± 7.7	28.9	26.3	28.7	91.2 ± 6.1	31.4	17.6 ± 0.4	27.8	31.2	52.7 ± 6.6	31.2	17.9 ± 1.8	30.6	39.8 ± 19.9	26.7	16.7	24.7	—		
Head length	32.3 ± 8.2	22.4	23.7	25.9	NR	NR	22.9 ± 0.5	36.3	21.6	NR	NR	NR	NR	NR	NR	NR	NR	NR		
Head width	29.8 ± 3.9	20.7	19.4	21.2	62.8 ± 6.9	21.5	19.3 ± 0.1	30.5	17.9	36.2 ± 3.3	17.9	15.2 ± 0.2	26.0	29.7 ± 10.9	20.0	15.9	23.6	—		
Head height	20.8 ± 7.7	14.6	11.9	13.0	NR	NR	12.2 ± 0.2	19.4	11.5	19.3 ± 1.6	11.5	NR	NR	NR	NR	NR	NR	NR		
Gular scute length left	17.9 ± 4.9	12.2	11.2	12.2	33.2 ± 3.0	11.4	NR	NR	11.6	19.9* ± 1.4	11.6	NR	NR	18.1 ± 9.3	12.1	8.0	11.9	—		
Intergular scute length	25.6 ± 8.1	17.4	18.4	20.1	48.9 ± 3.6	16.8	9.6 ± 0.3	15.3	18.4	31.0 ± 3.1	18.4	10.9 ± 2.0	18.4	26.5 ± 10.1	18.3	11.8	17.4	—		
Gular scute length right	18.5 ± 5.2	12.6	11.1	12.1	33.6 ± 3.4	11.6	NR	NR	12.1	20.7* ± 1.4	12.1	NR	NR	NR	NR	NR	NR	—		
Humeral scute length	19.4 ± 4.2	13.4	10.9	11.9	32.6 ± 5.1	11.1	7.0 ± 0.2	11.1	12.1	20.4 ± 3.0	12.1	6.0 ± 0.0	10.3	17.3 ± 8.5	11.6	7.4	10.9	—		
Pectoral scute length	14.2 ± 1.6	9.9	9.4	10.2	31.8 ± 6.8	11.0	7.1 ± 0.6	11.4	10.2	17.3 ± 2.0	10.2	6.5 ± 0.6	11.2	13.1 ± 2.1	9.5	5.5	8.2	—		
Abdominal scute length	16.5 ± 3.8	11.3	9.7	10.6	40.1 ± 5.7	13.8	7.8 ± 0.0	12.4	13.1	22.2 ± 4.0	13.1	8.1 ± 0.1	13.9	19.3 ± 11.4	12.6	8.3	12.3	—		
Femoral scute length	23.9 ± 6.5	16.3	14.4	15.7	44.5 ± 5.4	15.3	9.8 ± 0.4	15.5	14.7	24.8 ± 4.3	14.7	8.2 ± 0.3	14.0	22.9 ± 9.9	15.6	9.0	13.3	—		
Anal scute length	19.3 ± 0.6	13.6	14.1	15.4	31.4 ± 8.6	10.7	6.8 ± 0.0	10.7	10.7	24.3 ± 2.2	14.4	8.3 ± 3.1	13.9	14.9 ± 4.7	10.4	8.1	12.0	—		



Figure 13. Radiograph of the adult female *Mesoclemmys sabiniparaensis* holotype (MPEG-H1251). Note the unossified zone between the carapace and the plastron. Photo by Fábio A.G. Cunha.

greater and averages 77.1% (range 69.2%–85.0%, $n = 2$), and in the *M. raniceps/wermuthi* complex it is much greater with the orbits widely separated, and averages 107.3% (range 85.2%–126.7%, $n = 7$). Fig. 14 shows the skulls of the new species, *M. gibba*, and *M. raniceps*.

The minimum width across the pterygoid trochlear processes is relatively narrower in *M. sabiniparaensis* than in *M. gibba*, *M. vanderhaegei*, or the *M. raniceps/wermuthi* complex. The minimal pterygoid width as a percentage of tympanic skull width (PtW/SWT) in *M. sabiniparaensis* is 30.4% ($n = 1$), in *M. gibba* it averages 48.1% (range 43.1%–56.5%, $n = 10$), in *M. vanderhaegei* it is about the same and averages 47.9% (range 45.8%–50.9%, $n = 3$), and in the *M. raniceps/wermuthi* complex

it is also about the same, averaging 44.7% (range 32.9%–52.0%, $n = 7$).

Common Names. — Sabin’s Side-necked Turtle (English); Perema-bicolor (Portuguese); Perema-do-Pará (Portuguese); Acaçú (local indigenous).

Etymology. — The first part of the specific epithet, *sabini*, is a patronym honoring Andrew Sabin, in recognition of his valuable contributions to species conservation, most especially for endangered amphibians and turtles, and to the protection wildlife habitats around the world. The second part of the epithet, *-paraensis*, refers to the Brazilian state of Pará where the species was discovered. The state of Pará, one of the 27 comprising the República Federativa do Brasil, is the second-largest state of the country. The origin of the name Pará is from the indigenous language of the Tupi-guarani: “*Pa’ra*” meaning river-sea (toponym *τόπος/όνομα*), their name for the Pará River, a right-bank tributary of the Amazonas River, which, when mixing with the Tocantins River, produces a body of water so large it is not possible to see the opposite bank. On the arrival of the Portuguese, the province was given the name of Grão-Pará (mighty river), eventually shortened to Pará (Brazil, Pará 2021a).

DISCUSSION

Inconsistency, uncertainty, and errors in the identification of the species in the genus *Mesoclemmys* are not uncommon (Cunha et al. 2019). We present here the description of a species in this genus that is based on morphometry in combination with a molecular genetic analysis including 8 of the 10 members of the genus (sequences from the genes COI and 16S). *Mesoclemmys sabiniparaensis* is morphologically distinct from other currently recognized members of the genus (Figs. 15–23). Of the two *Mesoclemmys* species with which it is sympatric, *M. gibba* and *M. raniceps*, *M. sabiniparaensis* is easily distinguishable by its bicolored pattern in the soft parts of the body and easily distinguished from *M. raniceps* by its narrower head. This characteristic also distinguishes it from *M. nasuta*.

Mesoclemmys sabiniparaensis is otherwise similar to *M. gibba*, except that the latter has a deeper carapace, a slightly wider head, and lacks the distinctive bicolored pattern. The phylogenetic analysis shows that *M. sabiniparaensis* is sister to *M. vanderhaegei*, the two forming a clade with *M. tuberculata*, and forming a clade with *M. gibba* and *M. nasuta*, sister species on another branch (Fig. 6). Adding *Rhinemys rufipes*, the tree indicates a separation for all these Amazonian species; this corroborates Colston et al. (2020), who also found that *R. hoguei* from the Atlantic Forest was basal, and sister to a branch of two *Phrynops* species, *P. hilarii* and *P. williamsi*. Cytogenetic studies have also shown that the Amazonian *Mesoclemmys* and *R. rufipes* (also Amazonian) are closely related (Viana et al. 2020).

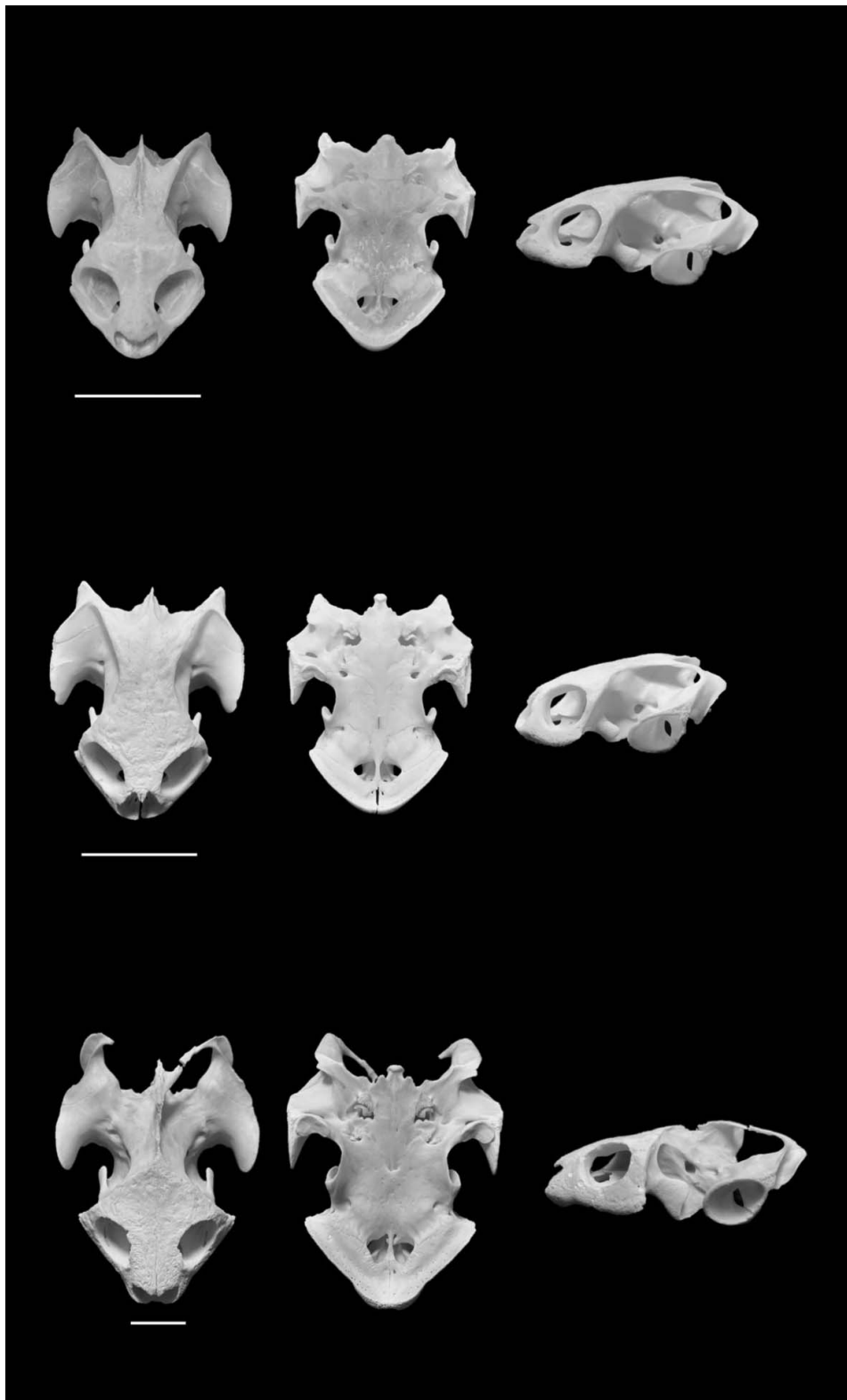


Figure 14. [Top] Dorsal, ventral, and lateral views of skull of *Mesoclemmys sabiniparaensis* sp. nov. from São Geraldo do Araguaia, Pará, Brazil (MPEG-H1254, carapace length 129.5 mm). [Middle] Dorsal, ventral, and lateral views of skull of *Mesoclemmys gibba* from Juruti, Pará, Brazil (INPA-H41288, carapace length 170 mm). [Bottom] Dorsal, ventral, and lateral views of skull of *Mesoclemmys raniceps* from Cachoeira do Aruã, Pará, Brazil (UFOPA-H 2952, carapace length 314 mm). White scale bar = 20 mm. Photos by Fábio A.G. Cunha.



Figure 15. Lateral, ventral, and dorsal views of an adult *Mesoclemmys gibba* from Juruti, Pará, Brazil. Note the size of the head, which is relatively smaller than other *Mesoclemmys* spp. Photos by Fábio A.G. Cunha. (Color version is available online.)

As far as we know, South American chelids show low genetic divergence, as demonstrated by Reid et al. (2011); specifically, the COI gene showed better responses in taxonomy studies when compared with the 16S. However, the joint analysis of the COI gene and 16S presents itself as a good alternative for understanding the phylogenetic structure of the studied turtle species. The delimitation of a new taxon, presented here, is based on the species concept using classical morphological criteria and molecular analyses analyzed in an integrative manner (De Queiroz 2007) and is supported by speciation patterns that are interdependent with spatial–temporal changes in the environment (Thomson et al. 2021).

The species of the genus *Mesoclemmys* have robust morphological characteristics that separate and support systematic delimitations, in addition to other information resulting from multiple taxonomic analytical tools. For some other genera within the Chelidae, the morphological differences can be subtle and sometimes significant morphological differences among species or lineages are difficult to discern (e.g., for the *Phrynops geoffroanus* complex; Carvalho et al. 2022).



Figure 16. Ventral, dorsal, and head views of *Mesoclemmys raniceps* from the Canoas River, Presidente Figueiredo, Amazonas, Brazil. Note the pattern of white spotting on the head, unique among the *Mesoclemmys* spp. Photos by Fábio A.G. Cunha. (Color version is available online.)

The taxonomy of the South American chelids has been quite volatile, most especially for the Amazonian species. Integrative studies have shown that what was believed to be one species was in fact two or more, or even distinct species groups, as was recently published for *Chelus fimbriata* and *C. orinocensis* (Vargas-Ramírez et al. 2020). Some Amazonian species have long remained poorly defined (e.g., Cunha et al. 2019) resolved a taxonomic dispute of 2 decades, clarifying inconsistencies concerning *M. raniceps*, *M. wermuthi*, and the previously recognized *M. heliostemma*, as noted and agreed to by TTWG (2021).

At the time of this description, there are no genetic data available and few morphological data that could be used for *M. perplexa*, other than those used in the original description. With the description of *M. jurutiensis*, Cunha et al. (2021) shed light on some questions concerning the taxonomy of *Mesoclemmys*: there is strong morphological differentiation between sympatric species, the geographic delimitation for the type locality of *M. raniceps* (sensu stricto) needs detailing, and it is necessary to refine all distribution and natural history records for the taxon *M. wermuthi*, now separated from *M. raniceps* (Cunha et al. 2019; TTWG 2021). Despite the low genetic divergences for Amazonian chelid species, it is necessary to consider many other variables that can elucidate taxonomic issues,



Figure 17. Dorsal and ventral view of *Mesoclemmys perplexa*. Lateral head view of *M. perplexa* from the Serra das Flores, Viçosa do Ceará, state of Ceará, Brazil. Note the color of the eye and pale grayish orbital line. Photo by Daniel Loebmann (published in Loebmann and Haddad 2010). (Color version is available online.)

such as ecology, behavior, reproduction, osteology, natural history, and molecular data.

Conservation. — As a group, the Testudines are among the most threatened of all the vertebrates. Wild populations are in severe decline (Rhodin et al. 2018; Stanford et al. 2020). On a global scale, Amazonia is of the highest priority for turtle conservation, considering the immense threats that it is now facing (Mittermeier et al. 2015; Eisemberg et al. 2016; Aleixo et al. 2019; Ennen et al. 2020). There are some areas under particular pressure, facing ongoing and currently accelerating deforestation and environmental degradation (Gomes et al. 2019), as is true of the south of the state of Pará. The loss of forest canopy is a decisive factor in the declines of freshwater turtles (Fagundes et al. 2018) and those dependent on pools and streams in primary forest are extremely vulnerable.

As far as we know, *M. sabiniparaensis* is an Amazonian endemic, restricted to the southeast of the state of Pará, in the direct pathway of the “arc of deforestation,” a northwestward wave of burning and clearance for cattle ranching, subsistence farming, logging,



Figure 18. Ventral view of *Mesoclemmys nasuta* adult from French Guiana. Details of the head of an adult *M. nasuta* from French Guiana. Photograph by M. Dewynter. Lateral head view of an adult female *M. nasuta* from Guiana, Chelonian Research Institute. Note the light-colored underside of the jaw and the yellow patch on the side of the head, including the tympanum, and the lack of any black line extending posteriorly from the orbit. Photo by Richard C. Vogt (published in Cunha et al. 2019). (Color version is available online.)

and soybean plantations (Soares-Filho et al. 2004; Malhi et al. 2008), in a state already with a long history of colonization, forest loss, and environmental degradation. However, a positive note affecting *M. sabiniparaensis* was the creation in 1996 of the 24,000-ha Serra dos Martírios-Andorinhas State Park (PESAM; Brazil, Pará 2021b), where the species occurs.

At a global level, 62% of the world’s freshwater turtle species are under some degree of threat (Rhodin et al. 2018; Stanford et al. 2020). Various forms of pressure negatively affect all ontogenetic stages of species. Hatchlings are marketed as pets, juveniles for commercial purposes, and adults for meat, fats, and eggs as well. This whole scenario, both at a macro level and in small spatiotemporal scales, results in alarming and worrying numbers. To make the scenario even more difficult, many species complexes are still being evaluated as single species, completely disregarding the ecological specificities, ecosystem services, and threats to the habitats and populations of each possibly cryptic species or evolutionarily distinct lineage. Further studies on the taxonomy and natural history of freshwater turtle species are of great importance, especially for regions of the world with an accelerated process of landscape alteration, such as the Amazon and the Brazilian Cerrado.



Figure 19. Ventral and dorsal views of *Mesoclemmys tuberculata* from Areia Branca, state of Sergipe, Brazil. Lateral head view of *M. tuberculata* adult from Tobias Barreto, state of Sergipe, Brazil. Photo by Daniel O. Santana (published in Santana et al. 2016). (Color version is available online.)

With the present discovery, we advance the understanding of the diversity of the fauna of Amazonian chelonians and their distribution areas, thus contributing to the knowledge of the species richness of the Brazilian Amazon, a turtle hotspot and priority region for the preservation of freshwater turtle species. Pending further study, it may become necessary to readjust the interventions and actions of governments and institutes in order to preserve the diversity and richness of these and other Amazonian freshwater turtle species.

ACKNOWLEDGMENTS

The entire procedure for the description of this species complied with national and international legislation for the capture and collection of fauna (Biodiversity System, from Chico Mendes Institute for Biodiversity Conservation). SISBIO/ICMBio provided the collection authorization (N° 59171 FAGC) as well as the Ethics Committee Use of Animals. Likewise, turtles were captured and handled according to the Guidelines for Herpetological Research published by the American Society of Ichthyologists and Herpetologists. This study is part of the doctoral thesis of the first author (F.A.G.C.) at the Graduate Program on Aquatic Ecology and Fishing, Federal University of Pará,



Figure 20. Ventral and dorsal view of an adult *Mesoclemmys vanderhaegei* from Chapada dos Guimarães, state of Mato Grosso, Brazil. Lateral view of *M. vanderhaegei* adult from Chapada dos Guimarães, state of Mato Grosso, Brazil. Photos by Elizângela S. Brito. (Color version is available online.)

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We especially dedicate this contribution to all those who inspired us and are no longer with us, because many researchers, scientists, and conservationists died as a result



Figure 21. Lateral, dorsal, and lateral views of the head details of an adult *Mesoclemmys wermuthi* from Mancio Lima, state of Acre, Brazil. Photos by Tiago L. da Silva. (Color version is available online.)



Figure 22. Ventral and dorsal view of an adult *Mesoclemmys jurutiensis* from Juruti, state of Pará, Brazil. Frontal view of a *M. jurutiensis* adult from Juruti, state of Pará, Brazil. Photos by Fábio A.G. Cunha. (Color version is available online.)

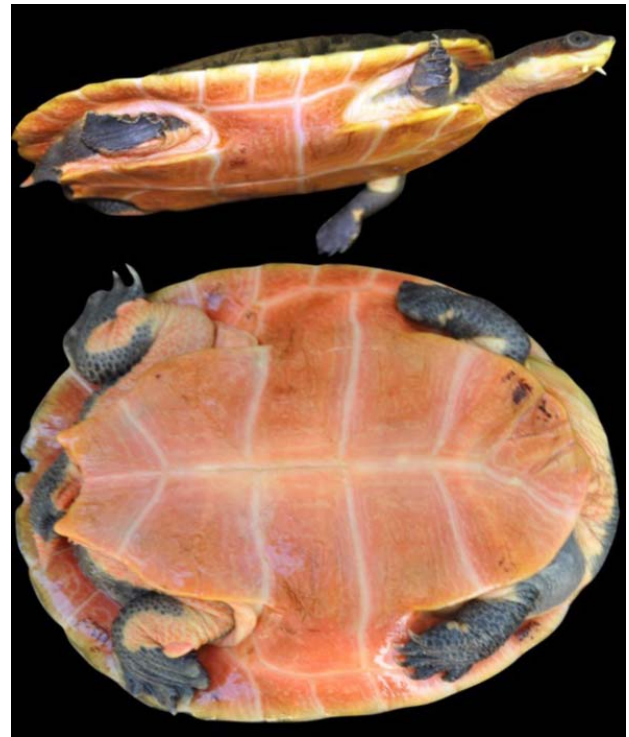


Figure 23. Lateral view of an adult *Ranacephala hogeii* from the Carangola River, state of Minas Gerais, southeastern Brazil. Ventral view of a *Mesoclemmys hogeii* subadult from the Carangola River, state of Minas Gerais, southeastern Brazil. Photos by Richard C. Vogt. (Color version is available online.)

of the pandemic during the months of this work. We dedicate our work in a very special way to the late Aderbal S. Cunha (deceased grandfather of F.A.G.C.), who gave support for this description to happen.

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APPENDIX 1

Ratio Variables. — 1. CW/CL; 2. PL/CL; 3. PW/CL; 4. CD/CL; 5. HL/CL; 6. HW/CL; 7. HH/CL; 8. GSLR/CL; 9. GSSL/CL; 10. ISL/CL; 11. HSL/CL; 12. PSL/CL; 13. ASL/CL; 14. FSL/CL; 15. AnSL/CL; 16. HW/HL; 17. HH/HL; 18. SL/CL; 19. SWT/CL; 20. SWT/SL; 21. SWM/SL; 22. SWM/SWT; 23. ParW/SWT; 24. PtW/SWT; 25. IOW/SWM; 26. IOW/OW; 27. SDM/SWM.

Specimens Examined. — *Mesoclemmys raniceps*: CEQUA/INPA AVID 001.051.326 Canoas River, municipality Presidente Figueiredo, state of Amazonas, Brazil; CEQUA/INPA AVID 039.873.869; CEQUA/INPA AVID 002.373.512 Canoas River, Presidente Figueiredo municipality, state of Amazonas, Brazil; CEQUA/INPA AVID 039.602.301 unknown; CEQUA/INPA AVID 039.778.104; UFOPA-H 2952 Cachoeira do Aruã, Juruti municipality, state of Pará, Brazil. *Mesoclemmys gibba*: INPA-H316 UHE Jari, Laranjal do Jari, Amapá, Brazil; INPA-H12805 Rio Aripuanã, state of Amazonas, Brazil; INPA-H12806 Rio Aripuanã, state of Amazonas, Brazil; INPA-H12807 Rio Aripuanã, state of Amazonas, Brazil; INPA-H17668 Pico da Neblina National Park, state of Amazonas, Brazil; INPA-H24998 city of São Luis, state of Maranhão, Brazil; INPA-H25671 stream on highway BR 310, KM 351, state of Amazonas, Brazil; INPA-H17706 undetermined; INPA-H41287 municipality of Juruti, state of Pará, Brazil; INPA-H41288 municipality of Juruti, state of Pará, Brazil. *Mesoclemmys perplexa*: from state of Piauí, Brazil, from Bour and Zaher (2005), MZUSP 4111; MZUSP 4112; MZUSP 4086. *Mesoclemmys vanderhaegei*: 15 individuals with data kindly provided by Elizângela E. Brito, from the

hydrographic basin of the Rio Paraguai. *Mesoclemmys sabini-paraensis*: Holotype MPEG-H1251 female subadult; allotype MPEG-H1255 male adult; paratype MPEG-H1254 female adult; paratype MPEG-H1252 female adult; paratype MPEG-H1257 female adult; and paratype MPEG-H1258 juvenile; all animals from the municipality of São Geraldo do Araguaia, state of Pará, Brazil. *Mesoclemmys jurutiensis*: Holotype INPA-H41283 male adult; paratype INPA-H41284 female adult; paratype INPA-H41285 juvenile; paratype INPA-H41379 female adult; paratype INPA-H41380 juvenile, all animals from the municipality of Juruti, state of Pará, Brazil, and paratype INPA-H41286 male adult from the municipality of Aveiro, state of Pará, Brazil.

Skulls Examined and Measured. — *Mesoclemmys sabini-paraensis*: MPEG-H1254; *Mesoclemmys raniceps/wermuthi*: MCZ 53300, 120331, 142585, 159025, CRF 307, CRI 440, UFOPA-H 2952; *Mesoclemmys tuberculata*: MCZ 38682, UMMZ 103127, MZUSP 43; *Mesoclemmys gibba*: FMNH

45670–71, MCZ 66028, 159023, UF 57917, 61932, FMNH 45669, UK 148409, CRI 1821, INPA 41288; *Mesoclemmys vanderhaegei*: MCZ 2600, MHNJRJ 3529, MNHN P s/n; *Phrynops geoffroanus*: MZUSP 50, 775, 1027, 2633–37, 2680, MCZ 3743, 34317, 38683, 59200, 146144–45, FMNH 73432; *Phrynops hilarii*: MCZ 145750, UF 56382, 57918, CRF 303, FMNH 222371, 224281, SMF 8010, 33670, 45470–71; *Phrynops williamsi*: ZMB 6858, BMNH 84.2.5.3; *Ranacephala hogei*: CM 3132, MHNJRJ 3145, MZUSP 96; *Rhinemys ruftipes*: MCZ 57395, ZSM 3006/0, MHNJRJ 3527.

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Appendix 2

Cod GenBank COI	Species	Author	Institution	Publication date or deposited date
MZ707089	<i>Mesoclemmys jurutiensis</i>	Cunha, F.A.G., Sampaio, I., Carneiro, J., and Vogt, R.C.	Genomics and Systems Biology, Federal University of Pará, Brazil	Chel. Cons. and Biol. 2021 07 Aug 2017
MF615513	<i>Ranacephala (Mesoclemmys) hogei</i>	Prosdocimi, F., Sarzi, D., Carvalho, D.C., Furtado, C., Gomes, L.C., Coutinho, M., and Drummond, G.	Biodiversity and Genomics Laboratory, Federal Rio de Janeiro University, Brazil	30 Apr 2018
MH273638	<i>Chelus fimbriata</i>	Mulcahy, D.C., Ibanez, R.D., Jaramillo, C.A., Crawford, A.J., Gonzales, G.P., Gotte, S.W., Jacobs, J.F., Ray, J.M., Wynn, A.H., Crombie, R.L., Mcdiarmid, R.W., Zug, G.R., and De Queiroz, K.	Global Genome Initiative, National Museum of Natural History, Smithsonian Institution	Mol. Ecol. Resour. 2011
HQ329590	<i>Acanthochelmys radiolata</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
HQ329630	<i>Mesoclemmys tuberculata</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
KC692464	<i>Platemys platycephala</i>	Nie, L.W., and Hou, H.Z.	College of Life Science, Anhui Normal University	26 Feb 2013
HQ329634	<i>Phrynops williamsi</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
HQ329629	<i>Mesoclemmys raniceps</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
HQ329628	<i>Mesoclemmys raniceps</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
HQ329632	<i>Mesoclemmys vanderhaegei</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
HQ329631	<i>Mesoclemmys vanderhaegei</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
KY486272	<i>Pseudemadura umbrina</i>	Zhang, X., Unmack, P. J., Kuchling, G., Wang, Y., and Georges, A.	Institute for Applied Ecology, University of Canberra	Mol. Phylogenet. Evol. 2017 07 Mar 2017
KY705236	<i>Elseya branderhorsti</i>	Zhang, X.	Institute for Applied Ecology, University of Canberra	Mol. Ecol. Resour. 2011
HQ329601	<i>Myuchelys bellii</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
HQ329637	<i>Rhinemys rufipes</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
KY776451	<i>Chelodina oblonga</i>	Georges, A.	Institute for Applied Ecology, University of Canberra	15 Mar 2017
HQ329588	<i>Acanthochelmys pallidipectoris</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011

Appendix 2. Continued.

	Species	Author	Institution	Publication date or deposited date
HQ329587	<i>Acanthochelys macrocephala</i>	Reid, B.N., Le, M., McCord, W.P., Iverson, J.B., Georges, A., Bergmann, T., Amato, G., Desalle, R., and Naro-Maciel, R.	Forest and Wildlife Ecology, University of Wisconsin	Mol. Ecol. Resour. 2011
Cod GenBank 16S MZ707322	<i>Mesoclemmys jurutiensis</i>	Cunha, F.A.G., Sampaio, I., Carneiro, J., and Vogt, R.C.	Genomics and Systems Biology, Federal University of Pará, Brazil	Chel. Cons. and Biol. 2021
AF113636	<i>Mesoclemmys gibba</i>	Georges, A., Birrell, J., Saint, K.M., McCord, W., and Donnellan, S.C.	Applied Ecology Research Group and CRC for Freshwater Ecology, University of Canberra	Biol. J. Linn. Soc. Lond. 1999
AF113637	<i>Mesoclemmys nasuta</i>	Georges, A., Birrell, J., Saint, K.M., McCord, W., and Donnellan, S.C.	Applied Ecology Research Group and CRC for Freshwater Ecology, University of Canberra	Biol. J. Linn. Soc. Lond. 1999
MF615513	<i>Ranacephala (Mesoclemmys) hogeti</i>	Prosdocimi, F., Sarzi, D., Carvalho, D.C., Furtado, C., Gomes, L.C., Coutinho, M., and Drummond, G.	Biodiversity and Genomics Laboratory, Federal Rio de Janeiro University, Brazil	07 Aug 2017
AY283252	<i>Ranacephala (Mesoclemmys) hogeti</i>	Moral, F.A.F., Paulino, L.C., and Nobrega, F.G.	Research and Development Institute, University of Vale do Paraíba, Brazil	23 Apr 2003
AY283249	<i>Acanthochelys radiolata</i>	Moral, F.A.F., Paulino, L.C., and Nobrega, F.G.	Research and Development Institute, University of Vale do Paraíba, Brazil	23 Apr 2003
KC692464	<i>Platemys platycephala</i>	Nie, L.W., and Hou, H.Z.	College of Life Science, Anhui Normal University	26 Feb 2013
AY283257	<i>Phrynops williamsi</i>	Moral, F.A.F., Paulino, L.C., and Nobrega, F.G.	Research and Development Institute, University of Vale do Paraíba, Brazil	23 Apr 2003
JN999705	<i>Phrynops hilarii</i>	Lourenco, J.M., Claude, J., Galtier, N., and Chiari, Y.	ISEM, Place Eugene Baraillon, University Montpellier	Mol. Phylogenet. Evol. 2012
HQ172156	<i>Chelus fimbriata</i>	Wang, L., Zhou, X., Nie, L., Xia, X., Liu, L., Jiang, Y., Huang, Z., and Jing, W.	College of Life Sciences, Anhui Normal University	Mol. Biol. Rep. 2012
AY283255	<i>Phrynops hilarii</i>	Moral, F.A.F., Paulino, L.C., and Nobrega, F.G.	Research and Development Institute, University of Vale do Paraíba, Brazil	23 Apr 2003
AF113634	<i>Acanthochelys pallidipectoris</i>	Georges, A., Birrell, J., Saint, K.M., McCord, W., and Donnellan, S.C.	Applied Ecology Research Group and CRC for Freshwater Ecology, University of Canberra	Biol. J. Linn. Soc. Lond. 1999