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Reproductive Biology and Hatchling Morphology of the Amazon Toad-headed Turtle (*Mesoclemmys raniceps*) (Testudines: Chelidae), with Notes on Species Morphology and Taxonomy of the *Mesoclemmys* Group

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Abstract. – *Mesoclemmys raniceps* is a medium-sized aquatic turtle widely distributed throughout the northern Amazon Basin in South America. Little information has been published about its reproductive biology. Because there is a significant problem identifying juveniles of this species found in the wild, and a controversy concerning the taxonomic status of the *Mesoclemmys nasuta* group, we incubated eggs from known females from known localities at controlled and ambient temperatures. We describe the hatchlings produced. The eggs hatched after an incubation period of 249 d at 28°C. Incubation experiments found both *M. raniceps* and *Mesoclemmys heliostemma* phenotypes hatching from the same clutch of eggs, suggesting that these taxa are conspecific. *Mesoclemmys wermuthi* had been incorrectly synonymized with *M. nasuta* and later absorbed by *M. raniceps* when *M. raniceps* was elevated to species status, resulting in the confusion of *M. raniceps* being different from *M. heliostemma*. *Mesolemmys wermuthi* is a distinct species separate from *M. raniceps*; however, *M. wermuthi* is preceded by *Hydraspis maculata*, which was synonymized with *M. raniceps* and is available for this species as *Mesoclemmys maculata*.

Key Words. – Chelidae; *Mesoclemmys* group; Amazon Toad-headed Turtle; taxonomy; *Mesoclemmys raniceps*; *Mesoclemmys heliostemma*; *Mesoclemmys wermuthi*; *Mesoclemmys maculata*; morphology

Resumo. – *Mesoclemmys raniceps* é um quelônio de água doce com tamanho médio amplamente distribuído no norte da bacia amazônica na América do Sul; são poucas as informações publicadas acerca da biologia reprodutiva. Sempre houve um significativo problema na identificação dos juveneis dessas espécies encontradas na natureza e uma controvérsia sobre o *status* taxonômico de grupo *Mesoclemmys nasuta*. Nós incubamos ovos de fêmeas conhecidas com suas localidades conhecidas em temperaturas controladas e em temperatura ambiente. O período de incubação foi de 249 dias a 28°C. Experimentos de incubação encontraram tanto fenótipos de *M. raniceps* quanto de *Mesoclemmy sheliostemma* eclodindo da mesma ninhada, sugerindo que essas espécies são coespecíficas. *Mesoclemmys wermuthi* foi incorretamente sinonimizado com *Mesoclemmys nasuta* e, mais tarde absorvido por *Mesoclemmy sraniceps* quando *M. raniceps* foi elevada ao *status* de espécie, resultando numa confusão de *M. raniceps* sendo diferente de *M. heliostemma*, *M. wermuthi* é uma espécie distintamente separada de *M. raniceps*, no entanto, *M. wermuthi* é precedida por *Hydraspis maculata* que foi sinonimizada com *M. raniceps* e está disponível para esta espécie como *Mesoclemmys maculata*.

Palavras-chave. – Chelidae; quelônios; *Mesoclemmys* grupo; taxonomia; *Mesoclemmy raniceps*; *Mesoclemmys heliostemma*; *Mesoclemmys wermuthi*; *Mesoclemmys maculata*; morfologia.

There are 10 species of *Mesoclemmys* described from South America, three of which have extremely restricted ranges and are Critically Endangered (Turtle Taxonomy Working Group [TTWG] 2017). There are few data available regarding incubation period and morphology of hatchling *Mesoclemmys raniceps*. Because the ranges of the species in the *Mesoclemmys nasuta* group are not well defined, and even the status of the species in this group is not certain, it is important to define and describe the morphological differences of the hatchlings of the following sympatric species: *M. raniceps*, *Mesoclemmys wermuthi*, *Mesoclemmys nasuta*, *Mesoclemmys gibba*, and

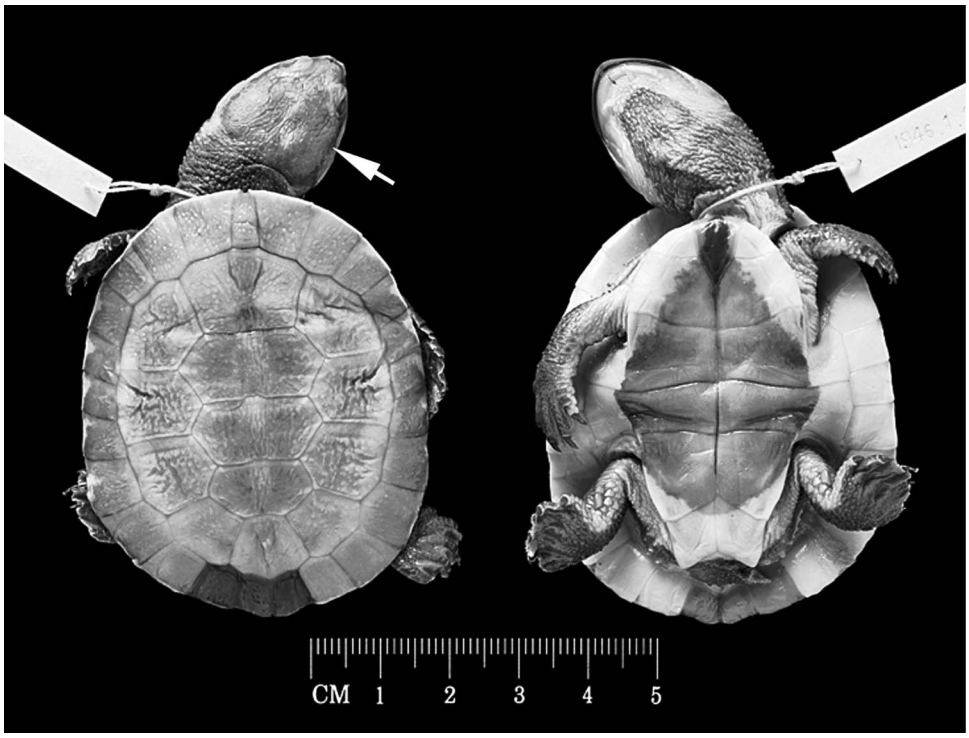

Figure 1. Holotype of *Hydraspis maculata* NHMUK 1946 (British Museum of Natural History) with carapace and plastron aspects. The arrow on the right side of the head in the carapace view points out the distinct black postorbital stripes present, which are a distinctive feature of *Mesoclemmys wermuthi* used to distinguish them from *Mesoclemmys raniceps*. Photo from Rivas et al. (2015), courtesy of P. Campbell and CCB.

Mesoclemmys heliostemma (Rueda-Almonacid et al. 2007; Brito et al. 2012; TTWG 2017).

Emys nasutus was described by Schweigger (1812) from specimens from the Guianas. Gray later described *Hydraspis raniceps* in 1855 as a new species from specimens collected in Pará, Brazil (Gray 1855), but this species was later considered a junior synonym of *nasuta* for over 100 yrs (Bour 1973). Gray (1873) described *Hydraspis maculata* as a distinct species different from *H. raniceps*, noting differences others had not, but Boulenger (1889) synonymized *H. maculata* with *H. nasuta*. Mertens (1969) described another species in this group, *Phrynops wermuthi*, from Iquitos, Peru, from pet trade animals that reached Germany. He even kept paratypes alive for many years noting the ontogeny of color patterns. Mertens did not examine the holotype of *Hydraspis maculata*, which is obviously the same species and not a synonym of *M. raniceps*, as suggested by Bour (1973). Bour (1973) described *Mesoclemmys vanderhaegei* from Paraguay and commented on the status of *M. nasuta*.

Later Bour and Pauler (1987) tried to establish the identity of 5 related species of *Mesoclemmys*, those of *M. vanderhaegi*, *M. nasuta*, *M. gibba*, *M. nasutus*, and *M. raniceps*. McCord et al. (2001) described *M. heliostemma* as a species different from *M. raniceps*, mainly using specimens from Iquitos, Peru. However, they did not compare it with *M. raniceps* sensu stricto, instead following the taxonomic decision of Bour (1973) and calling the specimens from Iquitos *M. raniceps*, while in fact they were a different species, *M. wermuthi* (Iquitos was the type locality of the type series that Mertens used in his description). This resulted in the confusion of describing this new species, which is within the variation of *M. raniceps* in Brazil using head color patterns of hatchlings and juveniles. Gray (1873) was correct; we have studied photographs of the holotype of *H. maculata* (Fig. 1) and it has the distinguishing characteristics of *M. wermuthi* and should not have been placed in the synonymy of *Rhinemys nasuta* by Boulenger (1889). Nearly a century later, Bour and Pauler (1987) placed it in the list of synonyms of *P. nasutus* (now *M. nasuta*). McCord et al. (2001) and the TTWG (2017) followed the taxonomy of Bour and Pauler (1987); however, Bour and Zaher (2005) reidentified the specimen as *M. raniceps*, based on morphology and head color pattern and the presence of a black stripe on each side of the head, extending from the snout through the eyes and terminating at the posterior edge of the tympani (Fig. 1). Both head coloration and the black stripe are important diagnostic characters distinguishing *Phrynops* (*Mesoclemmys*) *wermuthi* (Mertens 1969) from *M. nasuta* (Bour and Pauler 1987) or later in the synonymy of *M. raniceps*. The holotype of *M. maculata* shows in particular the postocular black stripe extending from each orbit and yellow along the mandibular region separating it from *M. raniceps* sensu stricto. Thus what was originally described as *Phrynops* (*Mesoclemmys*) *wermuthi* by Mertens (1969) is actually *M. maculata*, not *M. raniceps*. We have examined

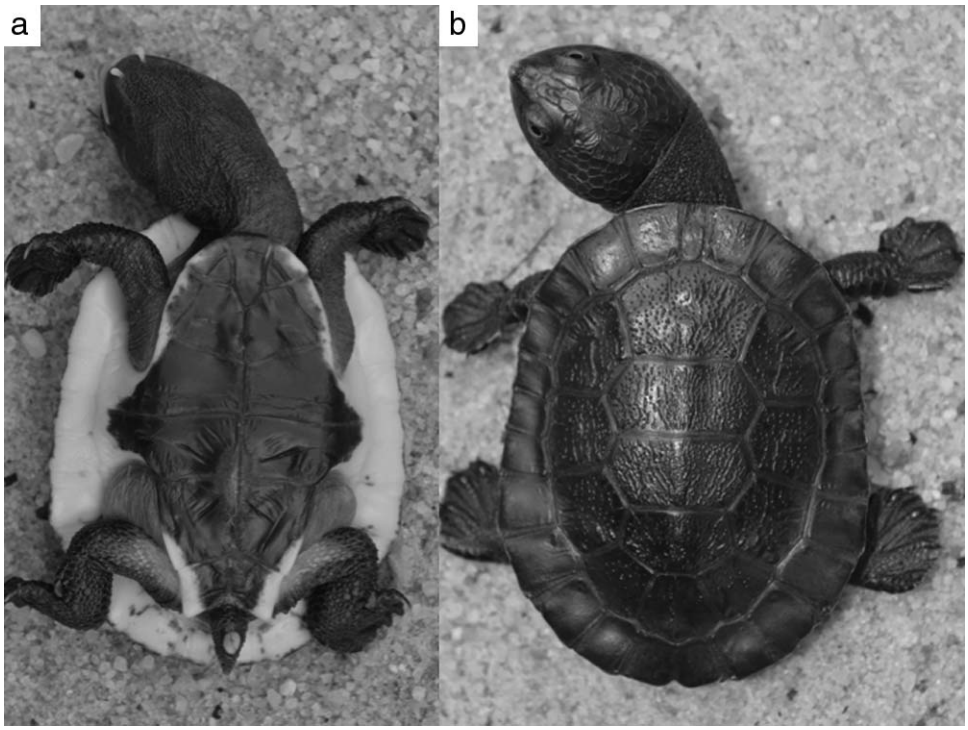

Figure 2. (a) Ventral and (b) dorsal view of hatchling of *Mesoclemmys raniceps* from eggs incubated in the laboratory in Manaus from a female from the Canoas River, Amazonas, Brazil. Photos by F.A.G.C.

photos of the holotype of *Hydraspis* (*Mesoclemmys*) *raniceps* (Gray 1855) and it does not have the postocular black stripes characteristic of *M. wermuthi*. We now have tissues from these species and are beginning to compare them through microsatellite data. The results will determine whether or not *M. heliostemma*, *M. nasuta*, *M. raniceps*, and *M. wermuthi* are distinct species. One of the authors of *M. heliostemma*, after inspecting photographs of *M. raniceps* from Brazil, agrees that *M. heliostemma* is conspecific with *M. raniceps* (W. Lamar, pers. comm. to R.C.V., March 2019).

In summary, first *M. nasuta* was described with a poorly defined range in the Amazon Basin, later restricted to Surinam; *M. raniceps* was described from Pará, Brazil, but assumed to be a junior synonym of *M. nasuta*; *Hydraspis maculata* was described but placed in the synonymy with *nasuta* and later in synonymy with *raniceps*; *Mesoclemmys wermuthi* was described but was soon relegated to a subspecies of *M. nasutus*, *M. nasutus nasutus*, being only in Amapa and the Guianas, and *M. nasutus wermuthi* throughout the Brazilian Amazon to Peru. Later, *M. raniceps* was resurrected and assumed to include all the range except for Amapa and the Guianas, which was allocated to *M. nasuta*. *Mesoclemmys wermuthi* was assumed to be a junior synonym of *M. raniceps* and forgotten about. Even though *M. raniceps* was described from specimens from Pará, there were very few specimens available and no one realized that *M. wermuthi*, which was described from Iquitos, was not synonymous with *M. raniceps*; thus *M. heliostemma* was described after comparing it only to *M. wermuthi* (which the authors assumed to be a synonym of *M. raniceps*). Hence the confusion as to whether *M. heliostemma* is a valid species or not. Our objective was to describe the hatchlings of *M. raniceps* from known parents, such that the field identifications of these species are accurate and range maps for these species can be validated.

Here we report the incubation period for *M. raniceps* compared with those published for other species of *Mesoclemmys*. We also describe the coloration and morphology of the hatchlings produced from known females of *M. raniceps* at specific constant temperatures in the laboratory (Figs. 2–4) and oscillating ambient temperatures in our indoor terrarium in Manaus at ambient temperatures (Figs. 5 and 6) and describe sexual dimorphism for these species (Fig. 7). We also include photos of adults and juveniles of *M. wermuthi* from Iquitos, Peru (Fig. 8); *M. nasuta* from French Guiana (Fig. 9); *Mesoclemmys gibba* from Pará and Amazonas states (Fig. 10); both hatchlings and adults of *M. raniceps* from Amazonas state (Figs. 2–7); and a *M. heliostemma* paratype from Iquitos as an adult and juvenile as well as hatchlings from Amazonas state (Fig. 11).

We have included these photos to aid in the identification of these species so that the distribution of these species can be better understood; up until now all individuals collected in Brazil have been identified as *M. raniceps* or *M. heliostemma*. Keller et al. (2016) published locality records of turtles from the Madeira River in an article for which one of us (R.C.V.) identified the *Mesoclemmys* for her as being *M. raniceps* or *M. gibba*. The identifications were erroneous, as R.C.V. did not

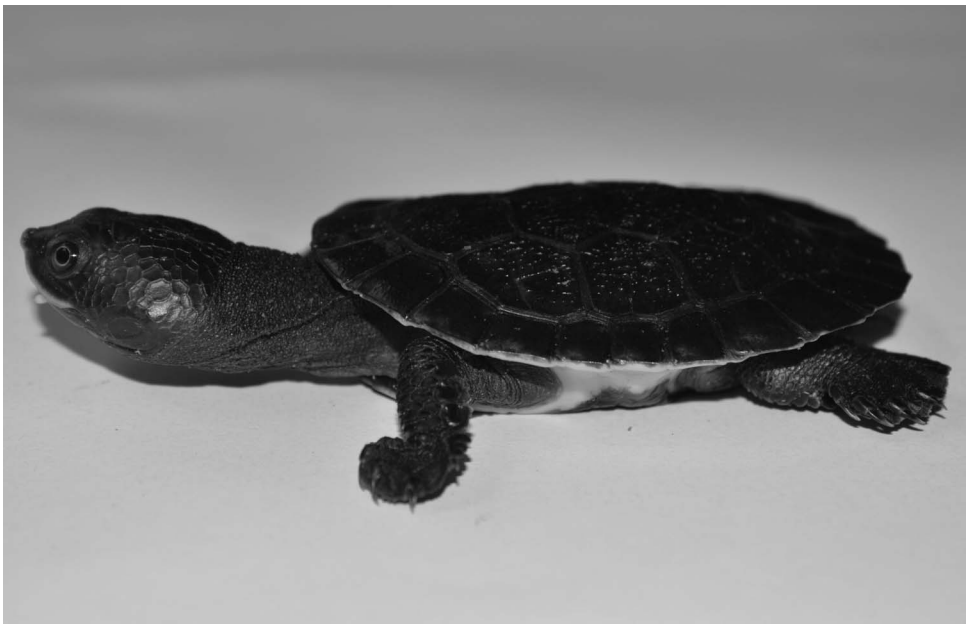

Figure 3. Lateral view of hatchling of *Mesoclemmys raniceps* from eggs incubated in the laboratory in Manaus from a female from the Canoas River, Presidente Figueiredo, Amazonas, Brazil. Photo by F.A.G.C.

realize that *M. wermuthi* was considered a valid species found in Brazil. Since then, R.C.V. has revised his identification of these photos, changing some of the identifications of *M. raniceps* to *M. wermuthi* based on the subtle head coloration. Molina et al. (2012) published an elegant morphological study separating what they thought was *M. raniceps* from *M. heliostemma*; however, they used *M. wermuthi* rather than *M. raniceps* sensu stricto. We are in complete agreement with their study, only the species names have to be changed. They definitively showed that *M. maculata* (*wermuthi*) is distinct from *M. raniceps* (*heliostemma*) (Fig. 12).

Recently, Brito et al. (2019) published a list of all the known and new localities of *M. raniceps* sensu stricto in

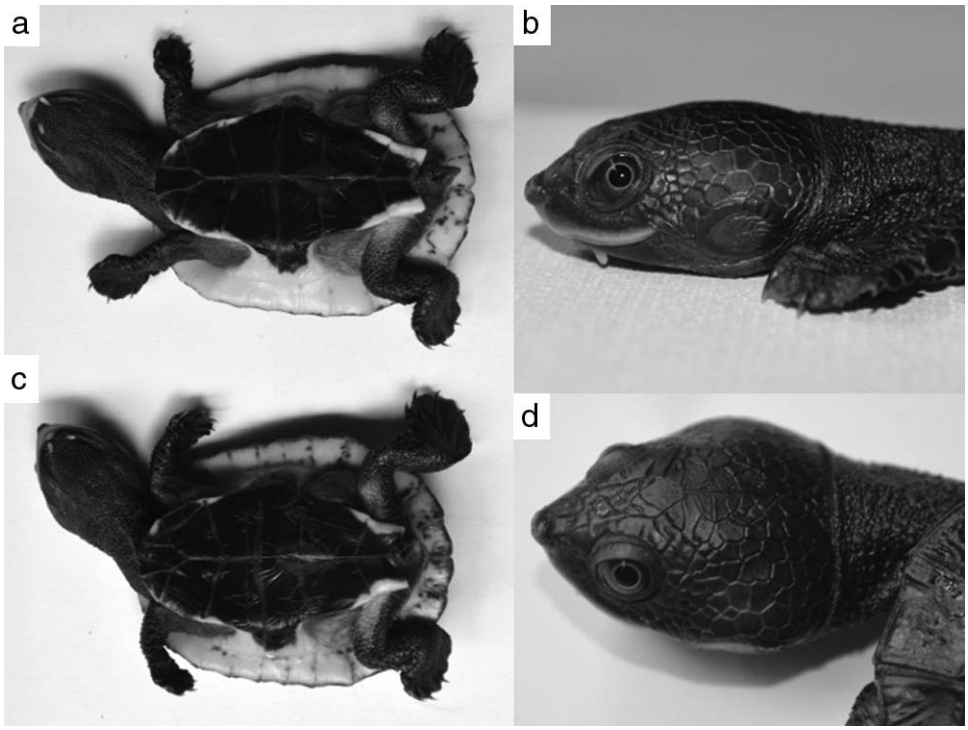

Figure 4. (a and c) Details of the plastron of 2 hatchlings; (b) lateral view of head; and (d) dorsal aspect of the head of *Mesolemmys raniceps* from eggs incubated in the laboratory in Manaus from gravid females from the Canoas River, Amazonas, Brazil. Photos by F.A.G.C.

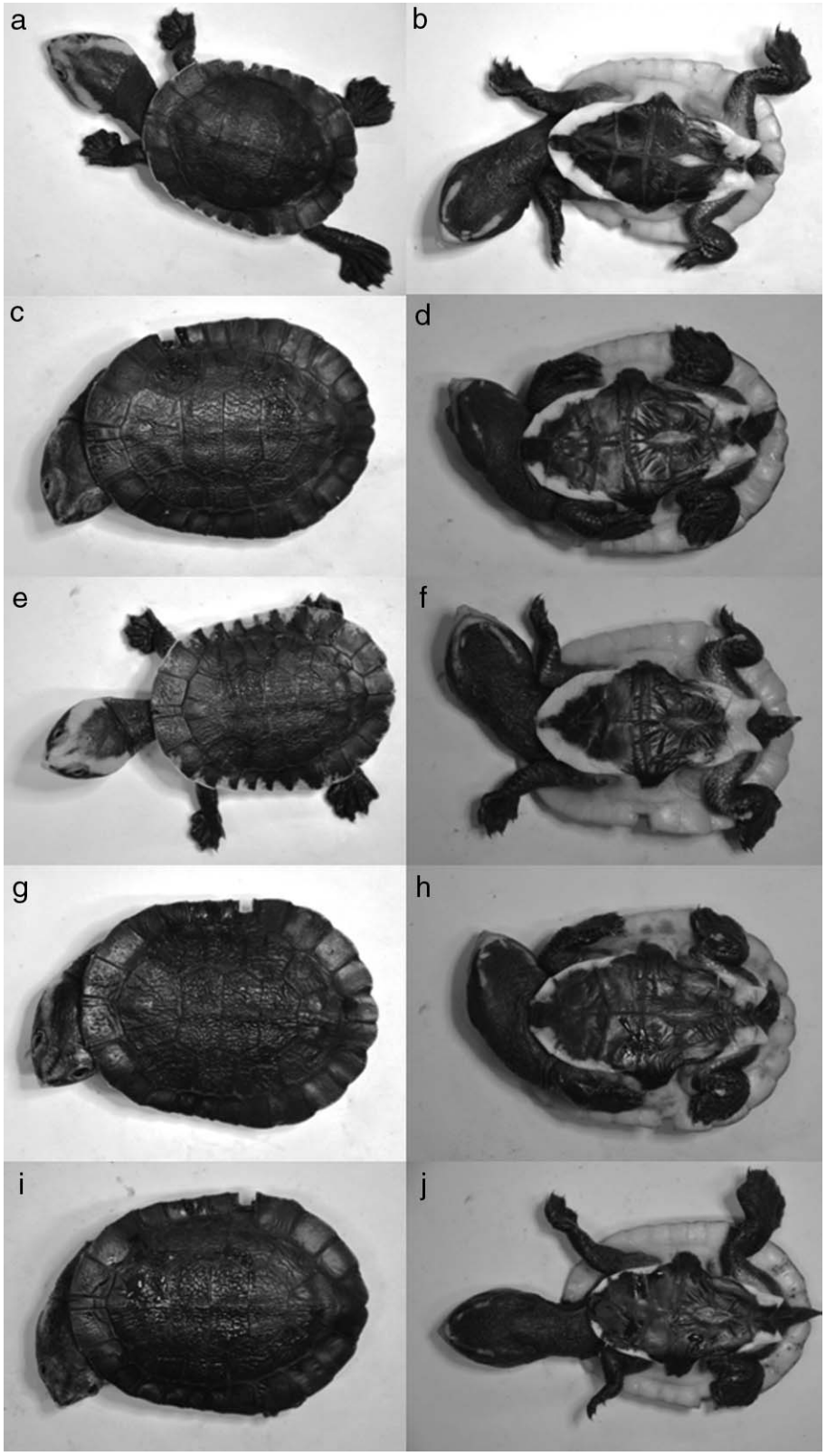

Figure 5. Dorsal and ventral view of 5 hatchlings of *Mesoclemmys raniceps* hatched in CEQUA in December 2018 in Manaus, Amazonas, Brazil. The left column (dorsal aspect) is the same individual as in the right column (ventral aspect). Note the presence of the yellow markings (=white and/or gray in these images) on the dorsolateral regions of the head (a, b, and e, f), characteristics of the phenotype formerly called *Mesoclemmys heliostemma*, now considered to be within the variation of *M. raniceps*. Photos by R.C.V.

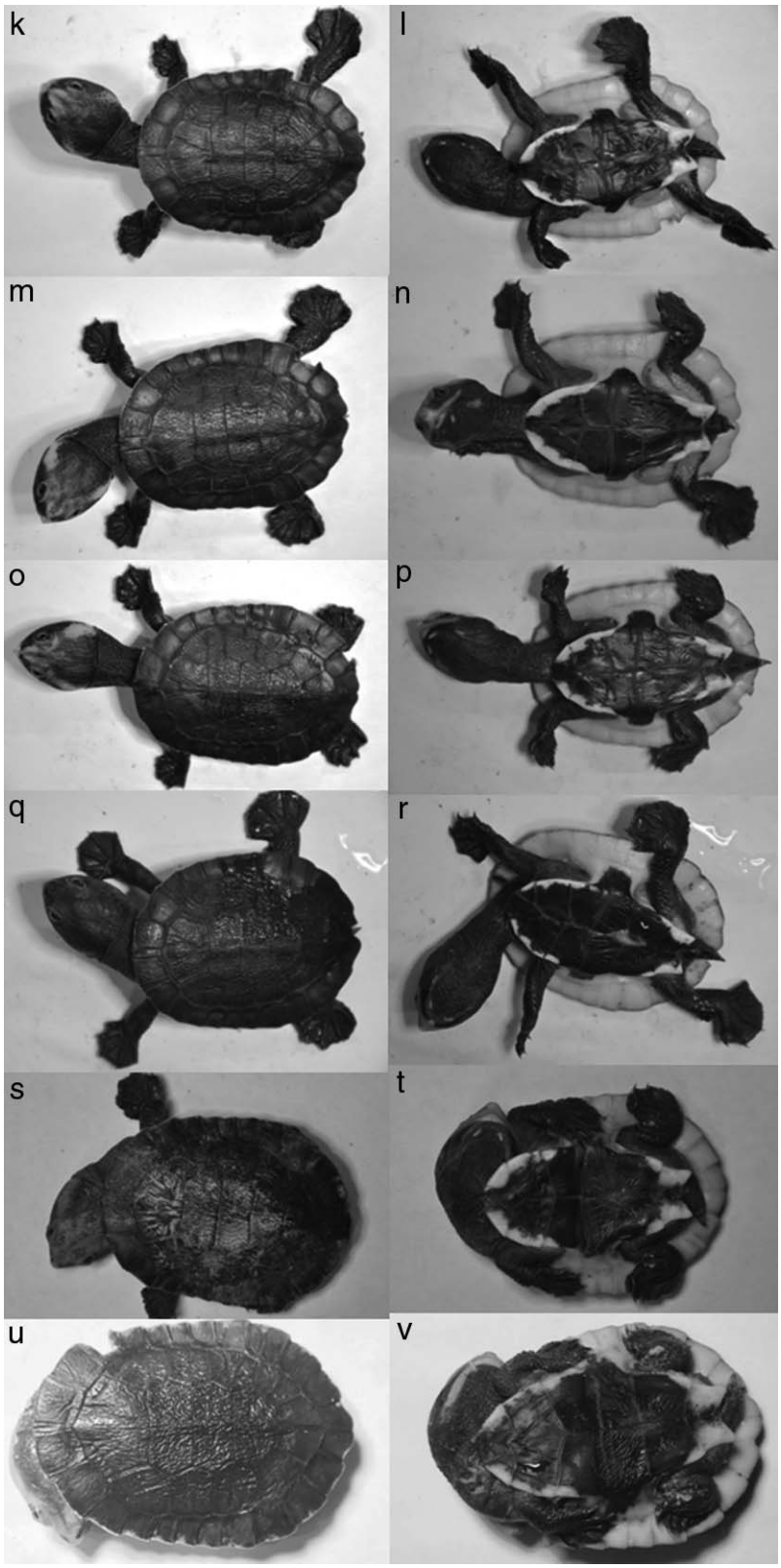

Figure 6. Dorsal and ventral view of 6 hatchlings of *Mesoclemmys raniceps*, hatched in CEQUA in December 2018 in Manaus, Amazonas, Brazil. The left column (dorsal aspect) is the same individual as in the right column (ventral aspect). Note that just one hatchling (q and r) has an entirely black head similar to the other hatchlings of *M. raniceps* in Figure 5. All of the others (k, l, m, n, o, p, s, t, u, and v) exhibit characteristics of the phenotype formerly called *Mesoclemmys heliostemma*, now considered to be within the variation of *M. raniceps*. Photos by R.C.V.

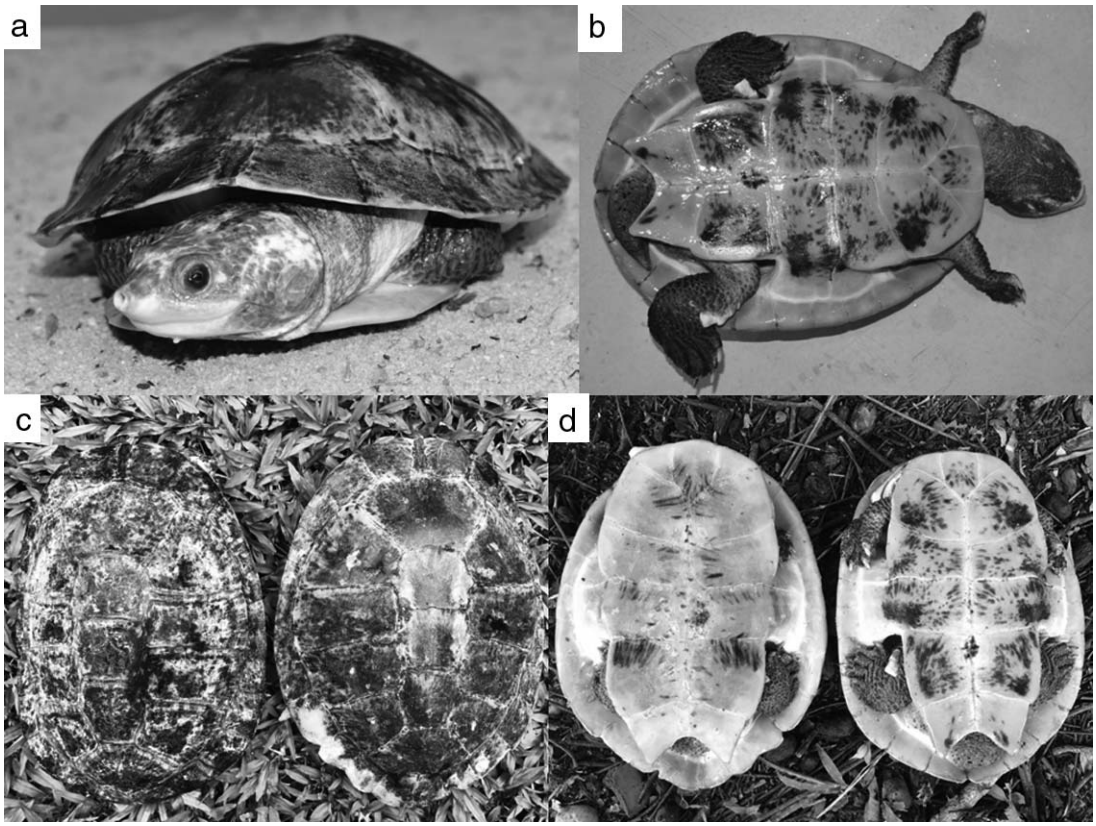

Figure 7. (a) Head of adult female, view of details of the head with white spots characteristic of adult individuals of *Mesoclemmys raniceps*, from the Canoas River, Presidente Figueiredo, Amazonas, Brazil. (b) Enlarged white tibia scales present in adult males of *M. raniceps* from the Canoas River, Presidente Figueiredo, Amazonas, Brazil. (c) Dorsal view of adult male (left) and adult female (right) *M. raniceps* from the Canoas River, Presidente Figueiredo, Amazonas, Brazil. (d) Ventral view of adult female (left) and adult male (right) *M. raniceps* from the Canoas River, Presidente Figueiredo, Amazonas, Brazil. Note that the greatest difference is in the width of the carapace. Photos by F.A.G.C.

Brazil, adding many new localities (including 3 new localities from the state of Pará) and verifying the identity of the others as *M. raniceps* rather than as *M. maculate* (*wermuthi*). Although there have been some recent publications reporting on the reproduction of *M. raniceps* in captivity (Gaibazzi 2005; Schilde 2008; Böhm 2009), the origin of these pet trade turtles is unknown, but it is probably Iquitos. In these 3 publications, we conclude that they are reporting on *M. maculata* (*wermuthi*), a species which has been in the designer pet trade in Europe for over 50 yrs, rather than *M. raniceps*, as determined from the excellent photos published in these articles.

METHODS

Gravid females were collected from the Guaporé River at Costa Marques in the state of Rondônia, Brazil, in June 1989 and the eggs were incubated in the laboratory there. Males and females were collected from the Canoas River near Presidente Figueiredo in the state of Amazonas, Brazil, in June 2016 and 2017. In both localities, turtles were collected in 1-m-diameter baited fyke nets (Vogt 1980).

Once a turtle was determined to be gravid by noting the presence of hard-shelled eggs by palpation in the inguinal cavity, eggs were obtained by induction of oviposition via injection of 10 units of oxytocin (per kilogram of total mass of the gravid female turtle) into the inguinal cavity following Ewert and Legler (1978). Eggs were incubated in humid, fine-grain vermiculite (proportion 1:1 vermiculite:water) in plastic bowls within clear thin plastic bags at 28°C, and within 200-l thermal boxes equipped with aquarium heaters in 4-l glass jars with water and aquarium aerators; temperature fluctuated less than ± 0.5°C (Vogt 1993). Data loggers (Onset®) were used to monitor the temperature in the incubators over the incubation period. In 2018, 2 females from Canoas River were determined to have shelled eggs and were allowed to nest in a terrarium in Centro de Estudos de Quelônios da Amazônia (CEQUA), a 10 × 10-m covered structure with a silica sand substrate with 6, 2-m-diameter and 30-cm-deep pools. They deposited 5 and 7 eggs on 20 May 2018. The eggs were incubated at the ambient temperature, 25°–27°C, in the sand substrate of the terrarium.

Measurements were taken with digital calipers and expressed to the nearest 0.1 mm: straight line maximum carapace length (CL), maximum carapace width (CW), carapace height (CH), maximum plastron length (PL), maximum plastron width taken at the ventral suture of the marginal scutes (PW), maximum head width (HW),

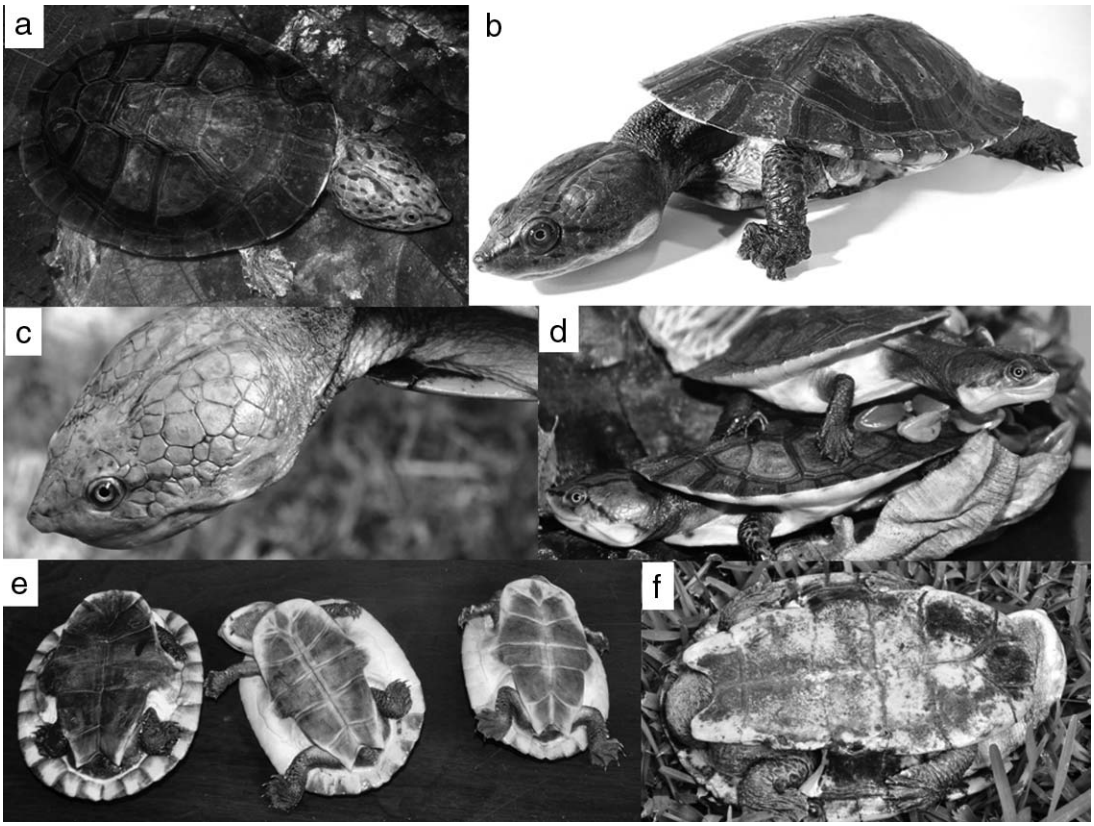

Figure 8. (a) Dorsal view of *Mesoclemmys maculata* (*wermuthi*) from Yanamono. Photo by B. Lamar. (b) *Mesoclemmys maculata*, Amazonian Toad-headed Turtle, January 2019. Photo by B. Lamar. (c) *Mesoclemmys maculata* (*wermuthi*) adult male from Loreto, Peru. Note the presence of faint black lines extending posteriorly from the orbit dorsally and in the direction of the lighter-colored tympanum as well as the scattered faint speckles which are bolder in the juveniles. Photo by R.C.V. (d) *Mesoclemmys maculata* (*wermuthi*) juveniles from Iquitos, Loreto, Peru. Note the distinct black lines extending posterior from the eye to above the yellow (=gray in this image) tympanum and another extending dorsally. Photo by R.C.V. (e) *Mesoclemmys maculata* (*wermuthi*) juveniles from Iquitos, Loreto, Peru. Note the variation in the dark plastron coloration. Photo by R.C.V. (f) *Mesoclemmys maculata* (*wermuthi*) adult male from Loreto, Peru. Note the light-colored underside of the jaw, the yellow (=gray in this image) plastron mottled with black, and the enlarged dark black tubercles on the hind limb. Photo by R.C.V.

maximum head height (HH), head length taken from the tip of the snout to the posterior edge of the tympanum (HL), intergular scute width taken at the anterior edge (IGW), gular length taken at the midline (IGL), and bridge length (BL) taken at the anterior- and posteriormost junctions of the ventral sutures with the marginal scutes. The following plastral scute measurements were taken at the midline: intergular scute length (IGL), humeral scute length (HSL), pectoral scute length (PSL), abdominal scute length (ASL), and anal scute length (ASL; see Iverson and Lewis 2018 for standardized measurement techniques). Body mass (BM) was determined on a digital electronic balance to the nearest 0.1 g.

RESULTS

Mesoclemmys raniceps is sexually dimorphic; males are smaller than females, with mean carapace lengths of 279.0 and 281.0 mm, respectively (n = 5 adult males and 4 adult females; Fig. 7a, c, and d). Adult males have prominent enlarged white scales on the external border of the skin covering the tibia while these scales are reduced in females (Fig. 7b). Seven eggs hatched 13 December 2018 and 4 hatched 31 December 2018, after 201 and 225 d of incubation, respectively. Enlarged white scales were apparent on the tibiae of 6 of the 11 hatchlings that hatched in the terrarium in December 2018 (Figs. 5f and 6v). This suggests that sex may be discernible at hatching. Ten of these hatchlings had the vivid yellow head markings characteristic of *M. heliostemma* and one had the completely black head coloration characteristic of *M. raniceps* (Figs. 5 and 6). The anterior portion of marginals 3–9 were light yellow in some individuals and brighter yellow in some individuals (Fig. 5a, e, o, and u).

Clutch size ranged from 4 to 7 eggs measuring 39.8–43.6 × 29.6–37.0 mm and weighing 26.5–35.9 g (Table 1). Gravid females have been found from May through August in the wild in Amazonas, Pará, and Rondônia states, Brazil. Incubation period ranged from 220 to 249 d in the laboratory under constant temperatures and from 201 to 225 d under fluctuating ambient temperatures.

Hatchlings means were 59.4 mm CL, 45.1 mm CW, 45.0 mm PL, 34.0 mm PW, 18.4 mm HW, and 21.5 g BM. The hatchlings from the Guaporé River, Rondônia, Brazil

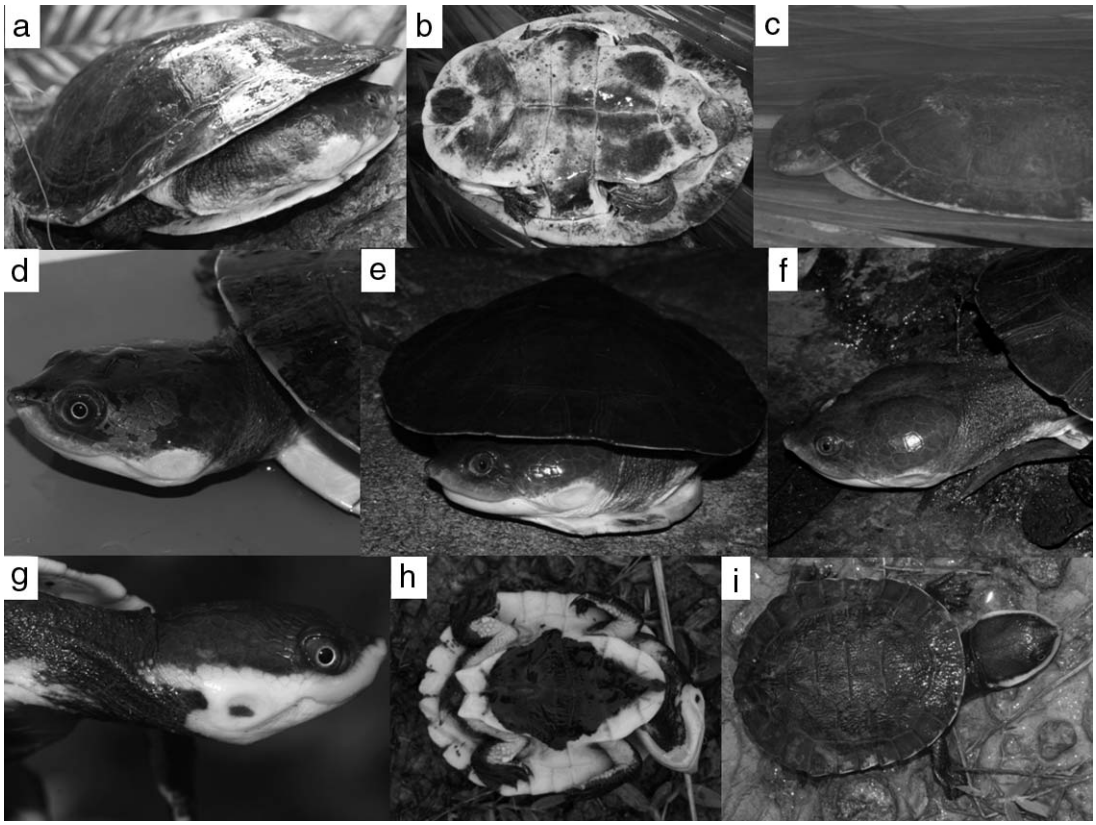

Figure 9. (a) *Mesoclemmys nasuta* adult female from Guiana, Chelonian Research Institute. Note the light-colored underside of the jaws and the yellow side of the head, including the tympanum, and the lack of any black line extending posteriorly from the orbit. Photo by R.C.V. (b) *Mesoclemmys nasuta* adult female from Guiana, Chelonian Research Institute. Note the light-colored plastron mottled with dark brown (=charcoal in this image). Photo by R.C.V. (c) Lateral view of *Mesoclemmys nasuta* adult from French Guiana. Photo by M. Dewynter. (d) Lateral view of head of *M. nasuta* subadult from French Guiana. Photo by M. Dewynter. (e) View frontal of *M. nasuta* subadult from French Guiana. Photo by M. Dewynter. (f) Details head of *M. nasuta* adult from French Guiana. Photo by M. Dewynter. (g) Lateral view of head of *M. nasuta* hatchling from French Guiana. Photo by M. Dewynter. (h) Ventral view of *M. nasuta* hatchling, French Guiana. Photo by M. Dewynter. (i) Dorsal view of *M. nasuta* hatchling, French Guiana. Photo by M. Dewynter.

in 1989 averaged 57.0 mm CL, 40.0 mm CW, 45.0 mm PL, and 21.0 mm HW (Table 2). The hatchlings averaged 20% of the CL of the adult female. The head width is relatively large, measuring 30% of CL. After 35 d the hatchlings measured 63.1 mm CL, 48.0 mm CW, 50.2 mm PL, 36.9 mm PW, 19.3 mm HW, and 25.7 g BM.

The hatchlings differed in morphology and coloration pattern from the adults. The dorsal surface of the head was covered by large, irregular-sized scales; two prominent, yellow chin barbels were present. The nares and part of the mandible surface were light brown in color. The carapace was uniformly dark brown, nearly black (Figs. 2b and 3), and limbs and head were completely black. The plastron had a black, irregular central region surrounded by a burnt yellow coloration (the extremities of the ventral gular, humeral, femoral, and anal scutes) and the plastron bridge was also yellow (Fig. 4a, c). The plastron formula of the hatchlings was as follows: femoral > intergular > abdominal > pectoral > humeral > anal. Ten of these hatchlings from 11 eggs that hatched in the terrarium in our laboratory had the vivid yellow head markings characteristic of *M. heliostemma* (Figs. 5 and 6) and 1 had the completely black head coloration characteristic of *M. raniceps* (Fig. 6q–r).

In Fig. 12, we plotted our data for *M. raniceps* hatchlings with the analysis of linear regression of the data presented by McCord et al. (2001) for *M. heliostemma*, and those data used by Molina et al. (2012) in an attempt to validate the status of *M. heliostemma*, with our data of the hatchlings of *Mesoclemmys raniceps*. There were no statistical differences comparing percent relationship of HW/CL with carapace length (ANOVA, $F_{2,17} = 2.35$, $p > 0.05$), demonstrating that what they called *M. heliostemma* is a color variant of *M. raniceps*.

DISCUSSION

According to the accepted taxonomy of this group, we found 2 different species emerging from the same clutch of eggs. Vogt (1993) showed the pitfalls of relying on head coloration markings for species designations in the *Graptemys pseudogeographica* complex. It is curious that no one wanted to doubt a species that could be identified only by hatchling coloration and that when they became adults they were indistinguishable from *M. raniceps* sensu stricto. These data in themselves are sufficient to place *M.*

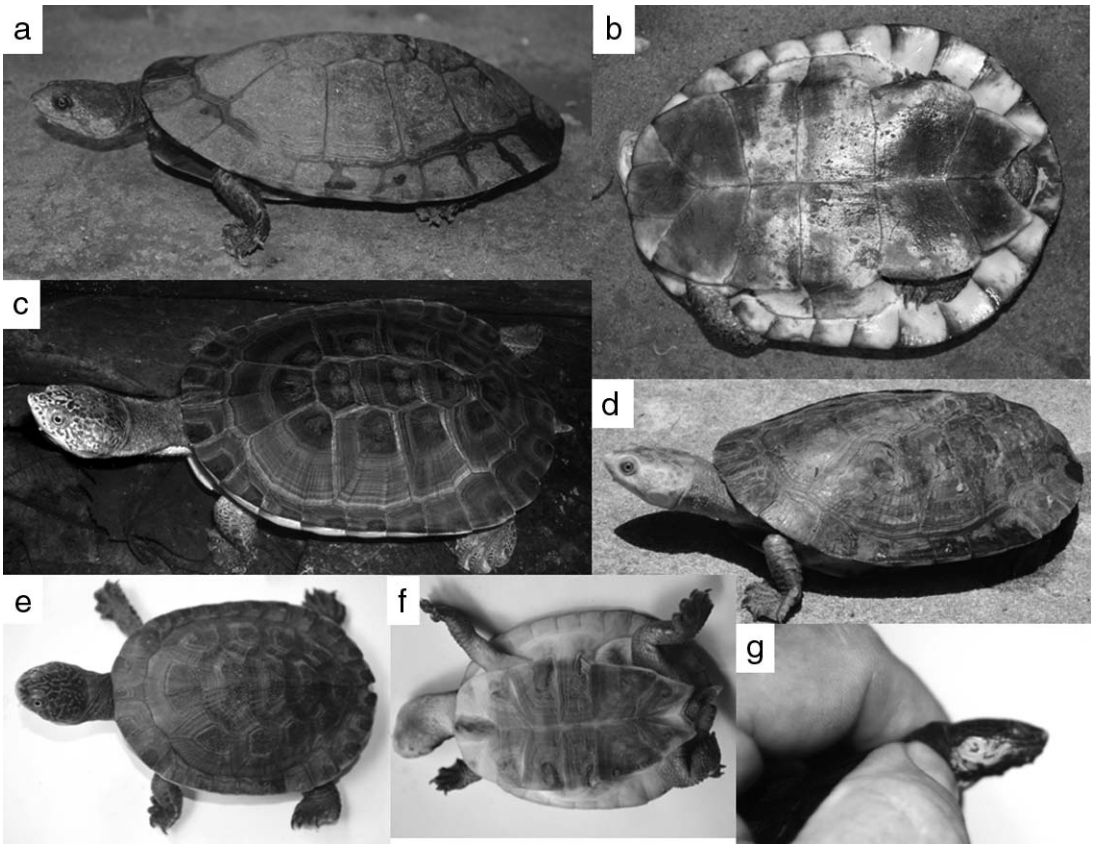

Figure 10. (a) Lateral view *Mesoclemmys gibba* adult male from Juruti, Pará, Brazil. Note the size of the head, smaller relative to other *Mesoclemmys* spp. Photo by F.A.G.C. (b) Ventral view of *M. gibba* adult male from Juruti, Pará, Brazil. Photo by F.A.G.C. (c) Dorsal view of *M. gibba* juvenile from Iquitos, Peru. Photo by B. Lamar. (d) Lateral view *M. gibba* adult from Santarem, Pará, Brazil. (e and f) Dorsal and ventral view of *M. gibba*, juvenile from Tefe, Amazonas, Brazil. Photos by F.A.G.C. (g) Details of head view of *M. gibba*, hatched in laboratory at temperature 26°C, from female collected in Aripuanã River. Note the bright orange (=gray in this image) coloration of the mandibular and tympanic region; this coloration is lost within a year. Photo by R.C.V.

heliostemma in synonymy with *M. raniceps*. We are also studying the genetics of this species group to examine the relationship of *M. heliostemma* and *M. raniceps*.

Sexual dimorphism in *M. raniceps* is similar to that reported for the other species of *Mesoclemmys* (*M. gibba*, *M. vanderhaegei*, *M. zuliae*, *M. dahli*, *M. tuberculata*, and *M. hogei*) in that males are smaller than females and the base of the tail to the cloacal opening is longer and thicker in males than in females (Fig. 7). The enlarged scales on the tibia are also found in other species of chelids (e.g., *Myuchelys* spp., *Elseya* sp.) as well as in *Mesoclemmys* (e.g., *M. tuberculata*). However, in other chelids, the scales are neither as enlarged nor do they have colors different from the leg coloration (S. Thompson, *pers. comm.,* April 2019). In *M. raniceps* the tibial scales are white in males (Fig. 7b) and in *M. hogei* they are red-orange in males. *Mesoclemmys maculata* (*wermuthi*) males do not have white enlarged scales on the tibia (Fig. 8f); the enlarged scales are black.

Number and mass of eggs are similar to published data for the range of this species in Andean countries (Rueda-Almonacid et al. 2007), with 4 to 7 eggs. Clutch size in *M. raniceps* is greater than that reported for *M. gibba* and *M. tuberculata* and fewer than in *M. vanderhaegei*, *M. dahli*, *M. zuliae*, and *M. hogei* (Table 3). The eggs of *M. raniceps* are smaller and rounder than those of *M. gibba*, which are more elongated but similar in length to those of *M. hogei*, although the eggs of *M. hogei* are nearly spherical, making comparisons difficult (Moreira 2002; R.C.V., unpubl. data, 2008). Small Amazonian chelid turtles tend to have larger but fewer eggs per clutch, such as *M. gibba* (2–4 eggs) and *Platemys platycephala* (1 egg, 51 × 26 mm; Rueda-Almonacid et al. 2007). This disproportional relationship between the size of the female and the size of the eggs is expected in these turtles because they have relatively small limbs, heads, and tails, leaving a larger volume available for eggs in the body cavity (Vitt and Congdon 1978; Shine 1992). The mean incubation period for *M. raniceps* was 249 d, whereas *M. dahlia* hatched in 120 d and *M. vanderhaegei* in 300 d (Table 3). Incubation periods in many tropical turtles, including *Mesoclemmys*, are controlled by soil humidity and temperature. They do not begin embryonic development immediately after oviposition as do most emydid turtles. Most of these species have embryonic aestivation in which the embryo remains at an early embryonic stage until environmental cues, usually the drying of the nest substrate, to initiate embryogenesis (Vogt 2008; see Legler

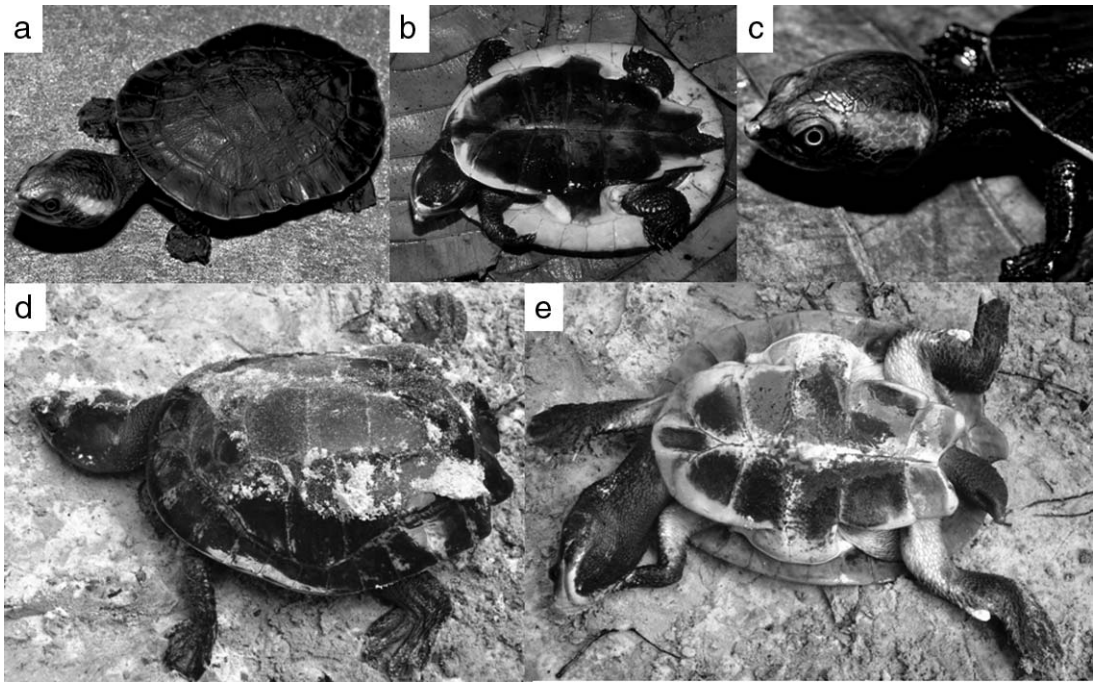

Figure 11. (a, b, and c) Dorsal, ventral, and detail of head views of *Mesoclemmys heliostemma* hatchlings (paratype RMNH 31998; Leiden Museum, The Netherlands). Photos by B. Lamar. This same turtle as an adult male is depicted in panel e. (d) Adult male from Iquitos, Loreto, Peru, in the house of Carlos Rivero; as a juvenile, this specimen was a paratype of this species by McCord et al. (2001). Note black head without vestiges of any yellow (=gray in this image) pattern and the tympanum colored black. Photo by R.C.V. (e) *Mesoclemmys heliostemma* adult male from Iquitos, Loreto, Peru, in the house of Carlos Rivero. Note the plastron marked with a black central pattern, the head with no vestiges of any yellow (depicted as white or gray in this image) pattern except the yellow (white in this image) ventral mandibular region, the tympanum colored black, and the ridge of white enlarged scales on tibia. Note that as a hatching this turtle had cream colored enlarged scales on the tibia in panel b above. Photo by R.C.V. Note that *Mesoclemmys raniceps* sensu stricto males have enlarged white scales on the tibia, whereas *Mesoclemmys maculata* (*wermuthi*) males have black enlarged scales on the tibia.

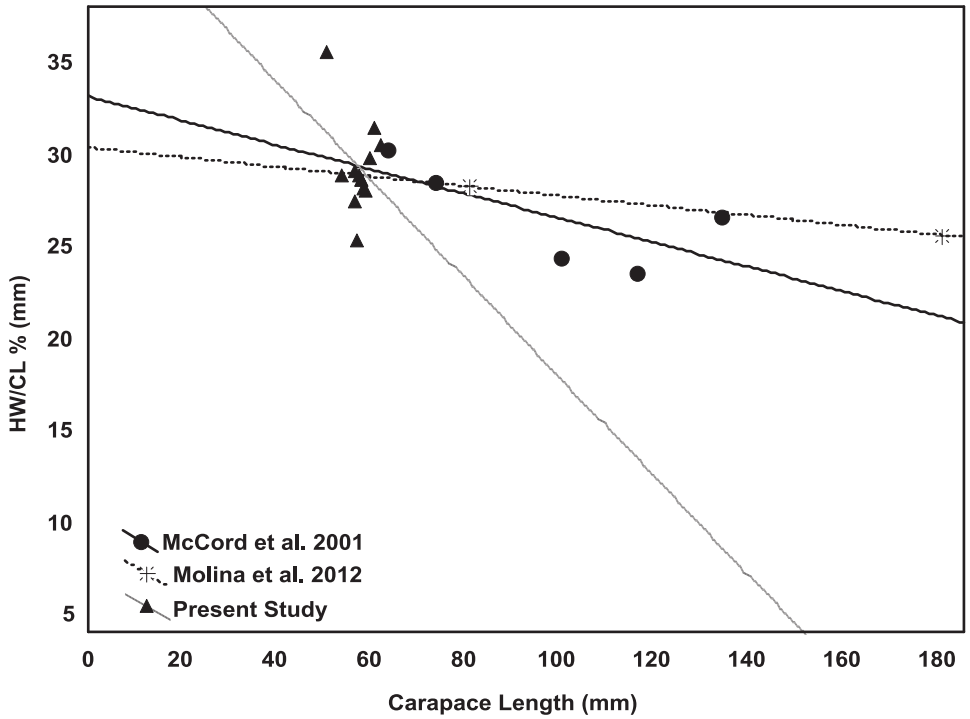

Figure 12. Analysis of linear regression of the data presented by McCord et al. (2001) for *Mesoclemmys heliostemma* and those data used by Molina et al. (2012) in an attempt to validate the status of *M. heliostemma* with our data of the hatchlings of *Mesoclemmys raniceps*. There are no statistical differences comparing percent relationship of HW/CL with carapace length (ANOVA, $F_{2,17} = 2.35$, $p > 0.05$), demonstrating that what they called *M. heliostemma* is a color variant of *M. raniceps*.

Table 1. Morphometric data (absolute values, in mm) for *Mesoclemmys raniceps* females and eggs (means, in mm and g). F4 and F5 are from the Guaporé River; all others are from the Canoas River.

	Carapace length	Carapace width	Plastron length	Body mass
F1	286.0	211.0	241.0	2300
F2	287.0	212.0	241.0	2000
F3	283.0	217.0	243.0	2200
F4	262.0	189.0	228.0	2300
F5	265.0	187.0	203.0	2100
	Egg length	Egg width	Egg mass	Clutch size
F1	41.2	29.8	26.5	4
F2	—	—	—	7
F3	—	—	—	5
F4	43.6	37.0	35.9	6
F5	39.8	34.1	28.1	6

Table 2. Morphometric data for *Mesoclemmys raniceps* hatchlings (absolute values, in mm and g). Only H14 is from Guaporé River; all others are from Canoas River, Amazonas.

Hatchling	Carapace length	Carapace width	Plastron length	Plastron width	Head width	Body mass	Year
H1	60.1	45.1	45.0	33.0	18.3	—	2017
H2	58.8	45.2	45.0	35.0	18.5	21.5	2017
H3	54.8	41.6	42.7	29.5	15.0	16.0	2018
H4	52,0	36.0	41.0	29.0	15.0	15.0	2018
H5	56.0	37.7	42.0	27.0	16.0	17.8	2018
H6	55.4	36.0	41.0	27.0	14.0	16.8	2018
H7	55.6	42.1	42.8	30.5	16.0	18.0	2018
H8	56.8	40.5	42.4	30.1	16.0	18.0	2018
H9	57.9	42.7	43.3	30.0	16.0	19.0	2018
H10	49.2	37.6	42.0	28.5	17.5	16.0	2018
H11	58.0	43.8	45.4	32.9	17.3	22.0	2018
H12	55.0	41.5	44.0	29.0	16.0	17.0	2018
H13	56.0	38.3	42.0	28.4	16.0	17.0	2018
H14	57.0	40.0	45.0	—	21.0	—	1989

Table 3. Comparison of reproductive data for *Mesoclemmys* ssp. ↓ = smaller; ↑ = larger; * = unpublished data for this species; NR = not reported.

Species	Clutch size (no. of eggs)	Mean size of eggs (length × width in mm; mass in g)	Nesting period	Incubation period	Male × female	Author
M. raniceps (Amazon Toad-headed Turtle)	4–7	41.6 × 34.0; 30.6	May–Aug	220–249	↓↑	Present study
M. gibba (Gibba Turtle)	2–4	49.0. × 33.0; 25.0	Jul–Nov	178–200	↓↑*	Mittermeier et al. (1978), Rueda-Almonacid et al. (2007), Pritchard and Trebbau (1984), Barrio and Narbaiza (2008)
M. vanderhaegei (Vanderhaege's Toad-headed Turtle)	1–14	34.0 × 27.0; 14.0	Jan–Jul	300	↓↑	Rueda-Almonacid et al. (2007), Brito et al. (2009), Marques et al. (2014)
M. zuliae (Zulia Toad-headed Turtle)	7–10	35.0 × 30.0; NR	Dec–Mar	—	↓↑	Rueda-Almonacid et al. (2007)
M. dahli (Dahl's Toad-headed Turtle)	5–12	28.0 × 24.0; NR 36.0 × 29.0; 16.0	Sep–Oct	120	↓↑	Rueda-Almonacid et al. (2007), Páez et al. (2012), Forero-Medina et al. (2013)
M. tuberculate (Tuberculate Toad-headed Turtle)	1	31.0 × 20.0; 11.0	Oct	—	↓↑	Corazza and Molina (2004), Santana et al. (2016)
M. hogei (Hoge's Side-necked Turtle)	5–7	41.6 × 41.4; NR	Mar–Apr	>120	↓↑	Moreira (2002)

Table 4. Morphological measurements (in mm and g) of *Mesoclemmys raniceps* hatchlings (INPA-H37495) from the municipality of Manaus, Amazonas State, Brazil, with proportions in relationship to the length of the carapace (%CL). Comparison with the morphometric measurements of *Mesoclemmys gibba* and *Mesoclemmys tuberculata* (Ferronato et al. 2010; Santana et al. 2015) is also given, along with a relationship of these measurements to the carapace length (%CL) for all 3 species. The %CL of the hatchlings of *M. raniceps* was calculated from the measurements taken 35 d after hatchling.

	M. raniceps (present study)				*M. tuberculata* Santana et al. (2015)		*M. gibba* Ferronato et al. (2010)	
	Hatchling 1	Hatchling 2	%CL		$n = 1$	%CL	$n = 2$	%CL
Carapace length	63.1	63.2	—	—	47.1	—	53.8	—
Carapace width	48.9	47.1	74.5	77.5	35.7	75	41	76.2
Plastron length	50.5	50.0	79.1	80.0	42.8	90.0	43	79.9
Plastron width	37.4	36.5	57.8	59.3	28.9	61.0	33.9	63.0
Carapace height	17.3	17.9	28.3	27.4	14.7	31.0	16.6	49.0
Bridge length	11.6	12.4	19.6	18.4	11.1	23.0	10.0	18.6
Head length	22.5	23.3	36.9	35.7	—	—	—	—
Head height	12.4	12.0	19.0	19.7	—	—	—	—
Head width	19.4	19.2	30.4	30.7	15.1	32.0	15	27.9
Intergular scute	9.9	9.4	14.9	15.7	6.5	13.0	9.4	17.5
Humeral scute	7.2	6.8	10.8	11.4	7.2	15.0	6	11.2
Pectoral scute	7.6	6.7	10.7	12.1	5.8	12.0	6.1	11.3
Abdonimal scute	7.9	7.8	12.3	12.5	7.0	14.0	8	14.9
Femoral scute	10.1	9.5	15.0	16.0	8.4	17.0	8.4	15.6
Anal scute	6.7	6.8	10.8	10.6	5.5	11.0	6	11.2
Body mass	27.2	24.2	—	—	14	—	20	—

and Vogt 2013 for a discussion of this phenomenon). After the hatchling is fully formed within the egg, the hatchlings of many species remain within the egg until hatching is elicited by other environmental cues, usually the rise in humidity of the nest substrate due to rains. In this way eggs are protected from drowning should rivers oscillate in depth during the early nesting season; similarly, hatchlings remain in the egg until the rains begin, signaling that they might have ponds with water nearby, whereas if they did not wait for the rains they might not have any place with water to go to (Vogt 2008).

Mesoclemmys raniceps head width is 30% of carapace length, the same as that reported for *M. n. nasuta* (Pritchard and Trebbau 1984), while head width is 28% of carapace length in *M. gibba* (Ferronato et al. 2010) and 32% in *M. tuberculata* (Santana et al. 2015). The relationship of the ventral pectoral scute to the carapace length was 11% in these hatchlings, similar to the proportion found for *M. raniceps* in 1989 (12%) and to the proportions reported for *M. tuberculata* (12%) and *M. gibba* (11%; Table 4).

Studies reporting information on the reproductive biology of species are important because they contribute to the conservation of freshwater turtles (Vogt 1994). Even though the present study has a limited amount of data, it is important to describe the hatchlings of these species in order to aid proper identification of juveniles collected in field inventories and to avoid publishing erroneous species lists and describing erroneous species. It is of great importance that studies on the reproductive biology of *Mesoclemmys* spp. are performed, especially with individuals and experiments from the wild, for later comparison with the present work.

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