



## Where to set the bar? Recent descriptions inflate species number in South American toad-headed turtles (*Mesoclemmys*)

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Turtles are among the most endangered vertebrate taxa, with an average threat level rivaled only by that of primates (Rhodin *et al.* 2018). For such imperiled groups, knowledge of their exact diversity is of paramount importance, because taxonomy is the foundation for conservation actions. Unfortunately, biodiversity hotspots, such as the Neotropics, are also areas with research knowledge gaps that could potentially magnify the extinction probability of recognized and unrecognized taxa. In some cases, especially in taxonomically poorly known groups facing extinction, researchers often have to do their best with the data at hand in order to minimize the risk of overlooking diversity, and this may result in new taxa being described prematurely (i.e., with insufficient evidence). Of course, this strategy brings the risk that a proposed taxon may later be synonymized following more extensive sampling and more sophisticated analyses. However, even under extreme and challenging scenarios, descriptions with modest data should still be rigorous and maintain the highest standards of scientific analysis. This is especially true today when the scientific community is advocating for better taxonomic practices, higher standards in species delimitation, and providing the best available evidence to support taxonomic hypotheses (TTWG 2007a; Padial *et al.* 2010; Kaiser *et al.* 2013). Within the framework of integrative taxonomy, a powerful approach for species delimitation has been suggested by Padial *et al.* (2010); i.e., using congruence between independent lines of evidence.

Two recent articles by Cunha *et al.* (2021, 2022) each described a newly discovered Brazilian freshwater turtle species: *Mesoclemmys jurutiensis* and *M. sabiniparaensis*, respectively. The South American genus *Mesoclemmys* (family Chelidae) is a poorly studied group of sideneck turtles that has been subject to frequent taxonomic discussions and revisions (McCord *et al.* 2001; Bour & Zaher 2005; Cunha *et al.* 2019; Ettmar 2019; Thomson *et al.* 2021; TTWG 2021). In the descriptions of *M. jurutiensis* and *M. sabiniparaensis*, Cunha *et al.* (2021, 2022) used similar morphological, statistical, and molecular analyses to provide what they described as “strong and robust scientific evidence” to support the validity of their two new species. While we agree that the genus deserves scientific attention and likely comprises additional unrecognized taxa (Ettmar 2019), the evidence presented in these two descriptions was neither strong nor robust, and the conclusions drawn from their extremely limited datasets were very weakly supported. Here, we point out the inconsistencies and methodological shortcomings of Cunha *et al.* (2021, 2022) and discuss why *M. jurutiensis* and *M. sabiniparaensis* were described prematurely and should not be recognized until more robust and reliable data are presented to corroborate their validity. We specifically focus on phylogenetic and morphological evidence.

**Phylogenetic analysis.** Cunha *et al.* (2021, 2022) justified the formal description of *M. jurutiensis* and *M. sabiniparaensis* with the putative phylogenetic distinctness in two mitochondrial gene fragments, namely 16S (16S ribosomal RNA gene) and the barcoding gene COI (cytochrome c oxidase subunit I). The downsides of using only mtDNA to delineate species are widely known: mtDNA is uniparentally inherited, considered a single genetic locus,

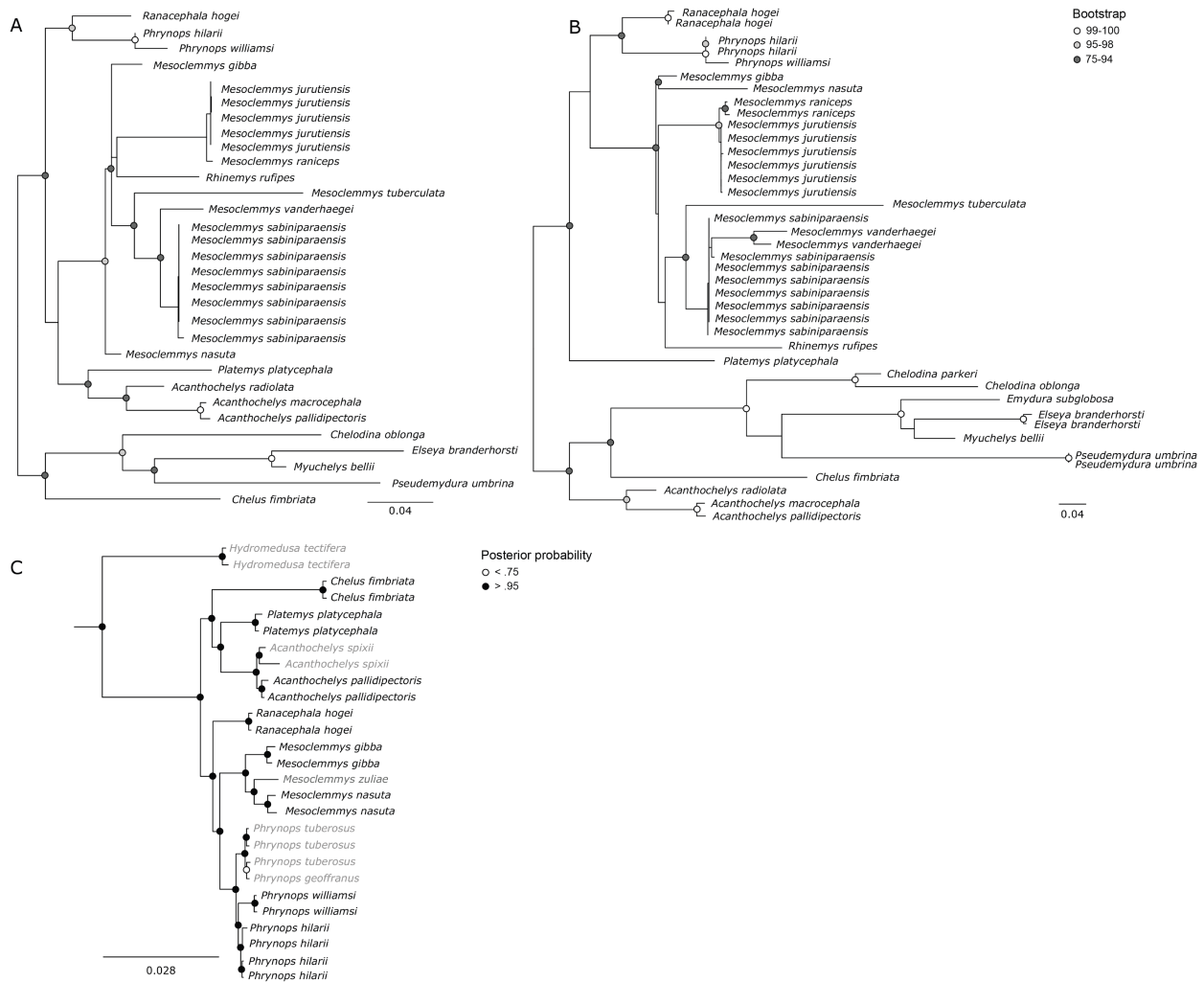
has the propensity to introgress across species borders and to transfer into the nuclear genome, has little use in detecting hybridization, and often yields topologies that do not represent species trees (Moore 1995; Toews & Brelsford 2012; Allendorf 2017; Hillis 2019). Therefore, the exclusive use of mtDNA sequences to delineate species is highly discouraged in modern taxonomy (e.g., TTWG 2007a; Padial *et al.* 2010). In addition, the analyses by Cunha *et al.* (2021, 2022) were based on very restricted taxon sampling, and relevant sequences available from GenBank were not included, even some of their own (GenBank accession numbers MZ707096, MZ707098). Their datasets also suffer from a severe mismatch in species assemblages for the two mitochondrial gene fragments, so that their concatenated alignment represents a patchwork of mostly incomplete sequences (Table 1). Furthermore, there is no explanation of how the actual taxonomic identification of the sequences downloaded from GenBank was done, and it is likely that their dataset was compromised by erroneous species assignments and outdated taxonomic names on GenBank.

**TABLE 1.** Comparison of the COI and 16S datasets used in Cunha *et al.* (2021, 2022). Matching sequence datasets are highlighted in grey. Numbers in columns are sample sizes.

Taxon	Cunha <i>et al.</i> (2021) Formal description of <i>M. jurutiensis</i>		Cunha <i>et al.</i> (2022) Formal description of <i>M. sabiniparaensis</i>	
	COI	16S	COI	16S
<i>M. gibba</i>	–	1	–	1
<i>M. jurutiensis</i>	6	5	5	5
<i>M. nasuta</i>	–	1	–	1
<i>M. raniceps</i>	2	–	1	–
<i>M. sabiniparaensis</i>	–	–	6	8
<i>M. tuberculata</i>	1	–	1	–
<i>M. vanderhaegei</i>	2	–	1	–
<i>P. hilarii</i>	–	1	–	1
<i>P. williamsi</i>	–	1	1	1
<i>R. hogei</i>	1	2	1	1

More concerning is the fact that Cunha *et al.* (2021, 2022) ignored evident signals of lack of support in their weakly resolved topologies, contrary to guidelines for best practices in taxonomy (TTWG 2007b; Kaiser *et al.* 2013). Cunha *et al.* (2021, 2022) also ignored the presence of polytomies, and overlooked the fact that their topologies do not reflect previously revealed relationships identified during the analyses of substantially larger datasets (e.g., Guillon *et al.* 2012; Thomson *et al.* 2021). For example, Cunha *et al.* (2022) did not comment on the fact that in their gene tree even the relationships among the recognized genera do not match the well-resolved phylogeny recently published by Thomson *et al.* (2021) which was based on 15 nuclear genes (Fig. 1). This discordance clearly indicates that their data are inadequate to resolve the species tree of South American chelids.

To re-evaluate the validity of *M. jurutiensis* and *M. sabiniparaensis*, we pooled sequences used in both publications and repeated the genetic analyses done by Cunha *et al.* (2021, 2022; Fig. 1). In addition, we constructed separate, single-marker maximum likelihood phylogenies for the COI and 16S alignments using RAxML 8.2.10 (Stamatakis 2014) and the optimal partition scheme derived from PartitionFinder 2 (Lanfear *et al.* 2012, 2017), the default nucleotide substitution model, and the Bayesian Information Criterion (BIC). Furthermore, we complemented the COI alignment of Cunha *et al.* (2021, 2022) with 11 extra sequences identified in GenBank as *Phrynops geoffroanus*, *P. hilarii*, *M. tuberculata*, *M. heliostemma*, *M. gibba*, and an undetermined *Mesoclemmys* taxon. Using the combined sequence data of Cunha *et al.* (2021, 2022), we were unable to reproduce the topology of their concatenated trees, and nodal support was mostly weak (Fig. 1). This suggests low resolution power of the chosen markers and a negative effect of the patchy sequence alignment (Table 1), particularly the lack of 16S gene sequences for *M. raniceps* and *M. vanderhaegei*, two species closely related to the newly described *M. jurutiensis* and *M. sabiniparaensis*. The detrimental impact of the patchy alignment is supported by the conflicting phylogenetic signal of the two markers when the single-gene trees of Cunha *et al.* (2021, 2022) are compared (Fig. 2).



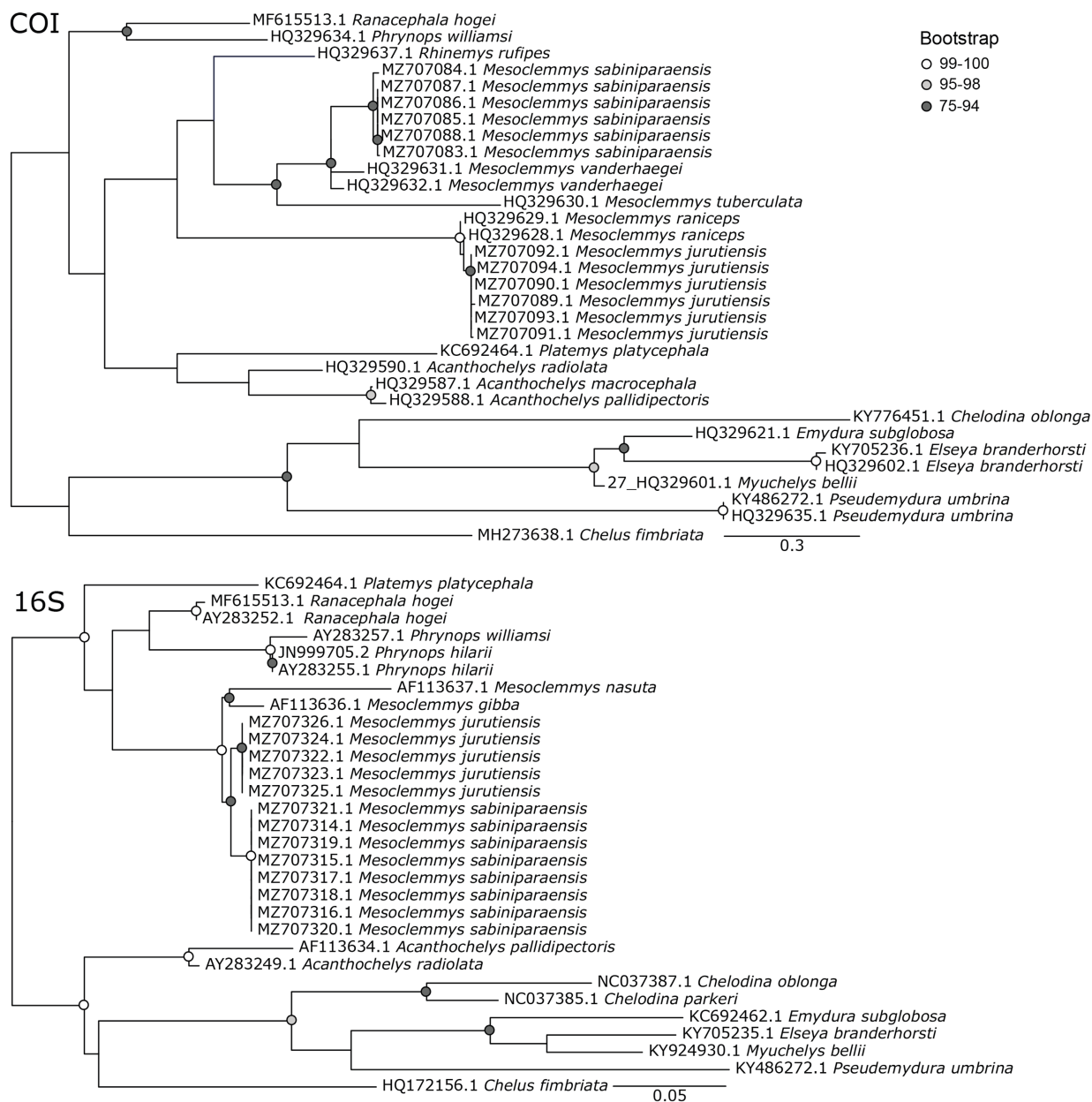
**FIGURE 1.** (A) Maximum likelihood tree redrawn from Cunha *et al.* (2022); (B) maximum likelihood tree using a concatenated alignment (1261 bp; 675 bp COI, 586 bp 16S) combining sequences from Cunha *et al.* (2021, 2022); (C) topology of the corresponding clades redrawn from Thomson *et al.* (2021) derived from a Bayesian analysis of 15 nuclear loci. Taxa not represented in Cunha *et al.* (2021, 2022) are shown in grey. Nomenclature for genera follows TTWG (2021).

We then compared the COI tree of Cunha *et al.* (2021, 2022; Fig. 2) to an expanded COI tree that included additional GenBank sequences for *M. raniceps* and *M. vanderhaegei* and other missing related taxa (Fig. 3). However, this expanded tree still lacks some congeneric taxa like *M. perplexa*, to which *M. sabiniparaensis* was morphologically compared in its original description. We found that neither of the two newly described species was phylogenetically distinct, at least for this mitochondrial marker. The expanded COI tree suggested that *M. raniceps* is paraphyletic with respect to *M. jurutiensis*, and with respect to GenBank sequences labeled as *Mesoclemmys* sp., *M. gibba*, and *M. heliostemma* (Fig. 3). It is important to note that *M. heliostemma* is currently considered a synonym of *M. raniceps* by some authors (but not all), and that *M. wermuthi*, a taxon lacking in the tree, has been recently resurrected from synonymy with *M. raniceps* (Cunha *et al.* 2019; TTWG 2021). Furthermore, our expanded COI gene tree showed almost no genetic differentiation between sequences previously identified as *M. raniceps* and the newly described *M. jurutiensis* (uncorrected *p* distances: 0.7–1.3), *M. heliostemma* and *M. jurutiensis* (uncorrected *p* distances: 0.0–0.5), and *M. raniceps* and *M. heliostemma* (uncorrected *p* distances: 0.7–1.1; Table 2). Finally, our analyses render *M. vanderhaegei* paraphyletic with respect to *M. sabiniparaensis*, indicating that the phylogenetic relationship of these two taxa needs further investigation.

**Morphological analysis.** Cunha *et al.* (2021, 2022) also justified the erection of *M. jurutiensis* and *M. sabiniparaensis* with purported morphological differences, which suggested character congruence with their genetic data, an important criterion used for species delimitation within the framework of integrative taxonomy (Padial *et al.* 2010). However, also with respect to morphology, both publications by Cunha *et al.* (2021, 2022) were compromised by very restricted



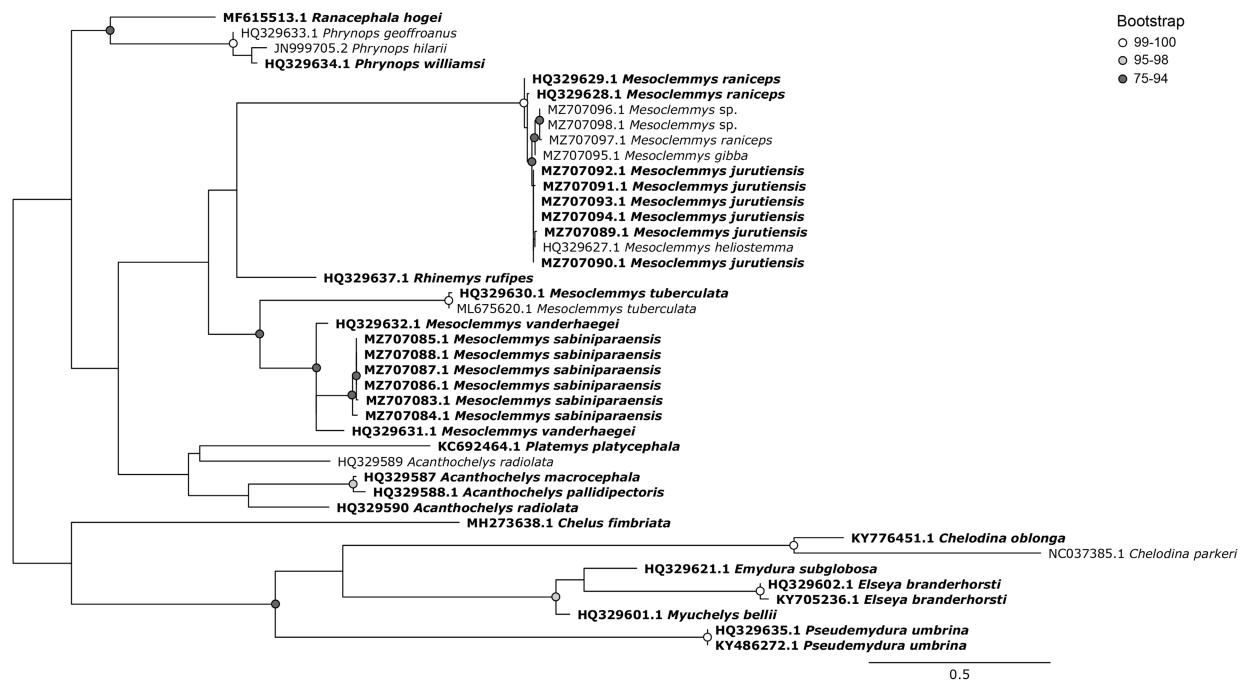
datasets (four adults, three juveniles, and one hatchling of *M. jurutiensis*, and four adults, one subadult, and one juvenile of *M. sabiniparaensis*), which prevented adequate comparisons and quantification of intraspecific variation. Furthermore, Cunha *et al.* (2021, 2022) combined both sexes and juveniles for all morphological analyses, disregarding any potential biases related to age-dependent or sex-dependent variation. Closely related congeneric taxa used in the analysis were also limited in sample size (e.g., *M. perplexa*, n=2) and some other crucial taxa (e.g., *M. wermuthi*) were not compared at all.



**FIGURE 2.** Maximum likelihood trees for the COI (675 bp) and 16S (586 bp) alignments corresponding to the datasets of Cunha *et al.* (2021, 2022). Codes preceding taxon names are GenBank accession numbers. Nomenclature for genera follows TTWG (2021).

Although Cunha *et al.* (2021, 2022) used a thorough battery of morphological measurements relative to carapace length (CL), including many scute measurements, they focused their quantitative analyses mainly on carapace width (CW) and height (CH), head width (HW), and plastron length (PL), which are only gross shape characters. In addition, several of their statistical analyses resulted in incorrect interpretations or findings. For example, Cunha *et al.* (2021, 2022) used ratios to make comparisons across species, but this type of analysis is only sound if the relationship between the numerator and the denominator is a straight line through the origin. If this condition is not met, the ratio will misrepresent the true

relationship between the dependent and independent variables and will render meaningless comparisons between groups (Curran–Everett 2013). Neither study explicitly mentioned if these assumptions were met. They also used an ANCOVA to examine the differences in the ratios (e.g., CW/CL) among species, where they could have used the denominator as the covariate. Finally, they completely disregarded the potential risk of using linear regression models with ratio data, in unequal-sized groups, and with very small sample sizes.



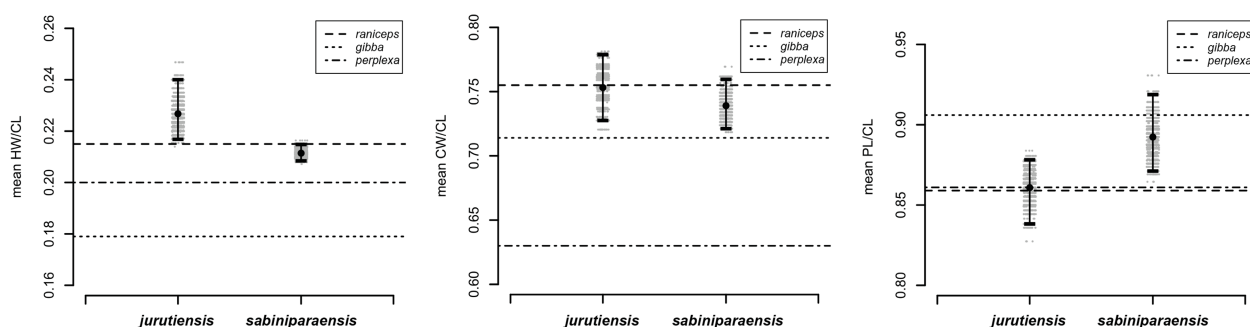
**FIGURE 3.** Maximum likelihood tree using a COI alignment (675 bp) expanding the alignment from Cunha *et al.* (2021, 2022). Sequences used by Cunha *et al.* (2021, 2022) in bold. Codes preceding taxon names are GenBank accession numbers. Nomenclature for genera follows TTWG (2021).

Cunha *et al.* (2021, 2022) also ignored that, beyond the aforementioned methodological shortcomings, their own analyses did not show that *M. jurutiensis* or *M. sabiniparaensis* were distinct from other assessed taxa. For instance, the statistical analyses by Cunha *et al.* (2021) failed to find significant differences between *M. jurutiensis* and either *M. raniceps* or *M. gibba* for CW/CL. For CH/CL and PL/CL, there were no significant differences between *M. jurutiensis* and either *M. raniceps*, *M. perplexa* or *M. vanderhaegei*. For HW/CL, no differences were found between *M. jurutiensis* and either *M. perplexa* or *M. raniceps*. In Cunha *et al.* (2022), the authors reported significant variation across the five included congeneric species, but they did not indicate which taxa were significantly different from which other taxa. In the same way, in their multivariate analysis (Cunha *et al.* 2022), the PCA confidence ellipses of shell measurements of all congeneric species highly overlapped, and their ratio plots showed no morphological distinction whatsoever. Despite this, the authors claimed in both studies that these ratios are diagnostic.

Unlike the genetic analyses, we were unable to replicate their morphological analyses to check their reliability because the data for the outgroups (*M. raniceps*, *M. perplexa*, *M. gibba*, and *M. vanderhaegei*) were not released publicly. However, we used the morphological data (i.e., CW/CL, PL/CL, CH/CL, and HW/CL) of the four sampled adults of *M. jurutiensis* and *M. sabiniparaensis* (tables 4 and 6 of Cunha *et al.* 2021, 2022, respectively) to create 95% confidence intervals around the mean by bootstrapping the observations. We then compared the intervals to the means reported for the congeneric species in Cunha *et al.* (2021, 2022), except that for *M. vanderhaegei*, the putative sister species of *M. sabiniparaensis*, which was unfortunately excluded from their tables. We found that none of these characters were diagnostic, as the confidence intervals overlapped with the mean of one or more of the congeneric species (Fig. 4).

Cunha *et al.* (2021, 2022) provided a thorough description of many other diagnostic features, but these were descriptive traits and lacked statistical analysis and support. For example, Cunha *et al.* (2022) stated that *M. sabiniparaensis* has the largest femoral scute and the smallest abdominal scute of the genus, but they did not demonstrate this quantitatively. They referred to several distinctive features in the skull, such as the tympanic skull width relative to its length (SWT/SL), but they failed to demonstrate that the average in *M. sabiniparaensis* of 83.9% (n=1) was statistically different from that of *M.*

*vanderhaegei* with a range of 84.1–94.2% (n=3). They also introduced a novel morphological trait, a non-ossified bridge, but they did not provide evidence that this is not a juvenile character state and does not vary during ontogenesis.



**FIGURE 4.** Comparison of the mean of the head width (HW), the carapace width (CW), and the plastron length (PL) relative to carapace length (CL) in four adults of *Mesoclemmys jurutiensis* and *M. sabiniparaensis*. The data was retrieved from table 4 in Cunha *et al.* (2021) and table 6 in Cunha *et al.* (2022). The percentile method was used to generate 95% confidence intervals around the mean (black circle) by bootstrapping 1000 times the observations (grey points). The means of the outgroups *M. gibba* (dotted horizontal line), *M. raniceps* (dashed horizontal line), and *M. perplexa* (dot-dashed horizontal line) were retrieved from table 7 in Cunha *et al.* (2022).

In conclusion, we have systematically demonstrated that the assertion by Cunha *et al.* (2021, 2022) of the phylogenetic and morphological distinctiveness of *M. jurutiensis* and *M. sabiniparaensis* was not supported by their own data, which were neither comprehensive nor adequately analyzed or interpreted. We see value in the two studies as a basis for further research, as the beginning of an evidence-collection process, but not as compelling evidence for taxonomic changes. According to the present evidence, *M. jurutiensis* cannot be reliably differentiated from *M. raniceps* and *M. sabiniparaensis* cannot be reliably told apart from *M. vanderhaegei*. Hence, we conclude that *M. jurutiensis* Cunha *et al.*, 2021 should be relegated to the synonymy of *M. raniceps* (Gray, 1856), and that *M. sabiniparaensis* Cunha *et al.*, 2022 should be relegated to the synonymy of *M. vanderhaegei* (Bour, 1973), until adequate data emerge to support their recognition. It should be noted that the type locality of *M. jurutiensis* is situated within the distribution range of *M. raniceps* (TTWG 2021). The type locality of *M. sabiniparaensis* is north of the northernmost record of *M. vanderhaegei* but in the same drainage system (TTWG 2021; Cunha *et al.* 2022).

We must emphasize that it is not our intent to discourage the critical ongoing task of deciphering the diversity of chelids in South America, but we do want to stress that unfounded taxonomic inflation is counterproductive for conservation (Zachos *et al.* 2013; Thomson *et al.* 2018). Thus, systematists must set the taxonomic bar as high as possible to deliver an evidence-based estimate of true species diversity.

## Acknowledgments

Walter Joyce and an anonymous reviewer made helpful comments on the manuscript of this study. F.I. was supported by a Maria Reiche Postdoctoral Fellowship of TU Dresden and the Programme for Women Professors III of the Federal Government and the States (Germany).

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