UNIVERSIDADE FEDERAL DE VIÇOSA

REASSESSMENT OF THE SPECIES “PODOCNEMIS” BRASILIENSIS STAESCHE, 1937 (TESTUDINES, PLEURODIRA, PELOMEDUSOIDES)

Joaquin Pedro Bogado Diniz
Magister Scientiae

VIÇOSA - MINAS GERAIS
2024

JOAQUIN PEDRO BOGADO DINIZ

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Assent:

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While in Viçosa, most of my time was spent at the university campus, more specifically at the *Laboratório de Paleontologia e Osteologia Comparada* (LAPOC), Pedro Romano’s lab. My lab was an integral part of my Master’s studies, partly due to the infrastructure it provided, but mostly thanks to the people who shared that space with me. The people at the LAPOC were receptive towards me even before I had formally joined their team, and their companionship was really important during my time in Viçosa. My previous experience with a research lab in Rio was negative, but my new labmates helped me recover from the ills of the past, proving how much a constructive, respectful and inclusive working space can contribute to a person's academic and personal well-being. I am very thankful towards Pedro Seyferth Ribeiro Romano, Thiago Fiorillo Mariani, Natália Benevenuto Lopes, Monique Póvoa de Oliveira, Isabella Vasconcellos Goulart, Dias Campos de Andrade, Juliana Moreira da Silva, Enzo Raggio del Cima, Laio Sebastião Rodrigues Silva, Miriam Ferreira do Lago, Thaíz Martins Andrade, Thaís Ribeiro de Miranda and Daniela Patrícia Werneck Silva for their continued amity, support and intellectual exchange. Their contribution was fundamental in the completion of this dissertation, whether through direct input into my research or through the support and friendship they manifested during the two and a half years I stayed in Viçosa.

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During my Master's studies I visited several scientific institutions, accessing fossil and recent material which aided me in my research. These were the *Museu de Ciências da Terra* (MCTer), *Museu Nacional* (MN), Geology Department of the Federal University of Rio de Janeiro (UFRJ-DG), *Museu de Zoologia da Universidade de São Paulo* (MZSP), *Instituto de Pesquisas Ambientais* (IPA), *Laboratório de Paleontologia Sistemática* (LPS) of the Institute of Geosciences of the University of São Paulo, *Museu de Ciências e Tecnologia da PUCRS* (MCP), *Museu de Ciências Naturais* (MCN), *Museu de Paleontologia "Prof. Antonio Celso de Arruda Campos"* (MPMA), *Museu de Paleontologia Pedro Candolo* (MPPC), *Centro de Pesquisas Paleontológicas Llewellyn Ivor Price* (CPPLIP), *Muséum national d'Histoire naturelle* (MNHN) and *Muséum Cantonal des Sciences Naturelles* (*Naturéum*). Acknowledgments are due to all the people who hosted me in these facilities, receiving me with great willingness and putting up with all sorts of demands I came up with, from lighting equipment and spirit levels to taxonomic redeterminations and curatorial enquiries. I would have liked to name all the people who aided me, as I did with the institutions. But unfortunately this will not be possible, owing to the limit of characters in the Acknowledgment section of dissertations submitted at the Federal University of Viçosa.

Over the course of my Master's studies I had the opportunity to present data pertaining to this dissertation in two scientific meetings: the *XII Simpósio Brasileiro de Paleontologia de Vertebrados* in Santa Maria, Brazil (2023), and the Turtle Evolution Symposium 2024 in Fribourg, Switzerland (2024). A third abstract was submitted to the *XXVIII Congresso Brasileiro de Paleontologia* in Maceió, Brazil (2024). I am thankful to the organizing committees behind these meetings for giving me the opportunity to participate in them, and also for the reviewers who revised my abstracts for taking the time to revise and contribute to my work. I extend my thanks to those attendees who watched my talks and gave me feedback on my research, as well as those who accompanied me in the "merriment and diversion" that went on during the leisure hours of the meetings.

As a closing statement, I would like to thank friends, family and research colleagues for their support and friendship. I feel the last two and a half years have been a time of great development for me, not only in my academic carreer, but also in my personal life. One of the greatest lessons obtained during this time was discovering how important it is to have a respectable, healthy work environment, and how much social relations affect an individual's academic output and mental health. Thus, I find it important to acknowledge here all the people who accompanied me during my Master's studies, and who in so doing have aided me in completing this dissertation. Naming individuals would be impractical and leave me in the risk of forgetting names that should have been included in the list. Thus, I use this paragraph as a general "thank you" to all those who accompanied me during this two year period. Without them, this work would not have been possible.

“*Ainda bem, ainda bem que os homens concentravam sua atenção em várias coisas,*
de acordo com as inclinações, inclusive em jabutis”.
(Antonio Carlos Callado)

ABSTRACT

DINIZ, Joaquin Pedro Bogado, M.Sc., Universidade Federal de Viçosa, August, 2024. **Reassessment of the species “Podocnemis” brasiliensis Staesche, 1937 (Testudines, Pleurodira, Pelomedusoides)**. Adviser: Pedro Seyferth Ribeiro Romano. Co-adviser: André Eduardo Piacentini Pinheiro.

The Bauru Group is a sedimentary sequence of the Paraná Basin, dated to the Late Cretaceous. Its palaeofaunistical assemblage includes a rich record of turtles of the lineage Podocnemidoidae, but many of the taxa that have been described from this geologic unit have an uncertain taxonomy. An example is the species “*Podocnemis*” *brasiliensis*, known from a single fragmentary plastron and regarded by many authors as a *nomen dubium*. The discovery of specimen FFP PG 218, comparable to “*Podocnemis*” *brasiliensis*, permitted the attribution of this specimen to this taxon, adding to its hypodigm. The new fossil preserves anatomical parts that are lacking in the type specimen of “*P.*” *brasiliensis*, permitting an amendment to the species’ diagnosis, with the addition of new diagnostic characteristics. With the new diagnosis, it was possible to revisit specimens that had been attributed to the species “*P.*” *brasiliensis* in the past, and assess whether they could really be attributed to this taxon. The revision showed that none of the past attributions can be confirmed. However, there are two occurrences of specimens similar to “*P.*” *brasiliensis* that were compared to this species through the use of open taxonomy modifiers, indicating the uncertainty behind these associations. A geometric morphometric analysis was performed using the epiplastra of the turtles of the Bauru Group, with the aim of evaluating the shape variation of this structure. The analysis recovered considerable variation described by three principal components, linked mainly to changes in the width of the intergular scute and the length of the epiplastron as a whole. The morphometric analysis also corroborated the current taxonomy of Bauru Group forms, organizing the sampled individuals in a way similar to the previously proposed taxonomic groupings, with “*P.*” *brasiliensis* appearing as a distinct taxon. To assess the relevance of shell thickness as a diagnostic characteristic in alpha-taxonomy, correlation tests and linear regressions were run using a sample of living and extinct Podocnemidoidae, as well as subsets for three taxa of the Bauru Group. It was not possible to make a subset out of “*P.*” *brasiliensis* due to the small number of available specimens. The analysis indicated that the shell of *Roxochelys wanderleyi* is proportionally thicker than that of other Podocnemidoidae. Still, the results show that the proportional thickness of the shell exhibits considerable intra-specific variation, and that the allometric effect of the regressions recovered from the whole sample and the subsets is rather subtle, not very different from isometry.

Keywords: podocnemidoidae; bauru group; geometric morphometric analysis; epiplastron; shell thickness; alpha-taxonomy

RESUMO

DINIZ, Joaquin Pedro Bogado, M.Sc., Universidade Federal de Viçosa, agosto de 2024. **Reavaliação da espécie "Podocnemis" brasiliensis Staesche, 1937 (Testudines, Pleurodira, Pelomedusoides)**. Orientador: Pedro Seyferth Ribeiro Romano. Coorientador: André Eduardo Piacentini Pinheiro.

O Grupo Bauru é uma sequência sedimentar da Bacia do Paraná, datada do Cretáceo Tardio. Sua assembleia paleofaunística inclui um rico registro de tartarugas da linhagem Podocnemidoidae, mas muitos dos táxons descritos para essa unidade geológica têm a taxonomia incerta. Um exemplo é a espécie "*Podocnemis*" *brasiliensis*, conhecida a partir de um único plastrão fragmentário e tida por muitos autores como um *nomen dubium*. A descoberta do espécime FFP PG 218, comparável a "*Podocnemis*" *brasiliensis*, permitiu uma atribuição do exemplar a esse táxon, aumentando o hipodigma da espécie. O novo fóssil preserva partes anatômicas que faltavam ao espécime-tipo de "*P.*" *brasiliensis*, o que permitiu uma emenda à diagnose da espécie, com a adição de novas características diagnósticas. A partir dessa nova diagnose foi possível revisitar espécimes que haviam sido outrora atribuídos à espécie "*P.*" *brasiliensis*, e avaliar se eles poderiam realmente ser atribuídos a esse táxon. A revisão mostrou que nenhuma das atribuições passadas pode ser confirmada. Contudo, existem duas ocorrências de espécimes similares a "*P.*" *brasiliensis* que foram comparados a essa espécie através do uso de modificadores de taxonomia aberta, demonstrando a incerteza dessas associações. Foi realizada uma análise de morfometria geométrica usando epiplastrões de tartarugas do Grupo Bauru, com o intuito de avaliar a variação na forma dessa estrutura. A análise recuperou uma variação considerável descrita por três componentes principais, ligados principalmente a mudanças na largura do escudo intergular e no comprimento do epiplastrão como um todo. A análise morfométrica também corroborou a taxonomia atual das formas do Grupo Bauru, organizando os indivíduos amostrados de forma similar aos agrupamentos taxonômicos previamente propostos, com "*P.*" *brasiliensis* aparecendo como um táxon distinto. Para avaliar a pertinência do uso da espessura do casco como uma característica diagnóstica na taxonomia alfa, testes de correlação e regressões lineares foram realizados usando uma amostra com Podocnemidoidae extintos e viventes, assim como *subsets* com três táxons do Grupo Bauru. Não foi possível fazer um *subset* de “*P*.” *brasiliensis* devido ao número reduzido de espécimes disponíveis. A análise indicou que o casco de *Roxochelys wanderleyi* é proporcionalmente mais espesso que o de outros Podocnemidoidae. Contudo, os resultados mostram que a espessura proporcional do casco exibe variação intra-específica considerável, e que o efeito alométrico das regressões recuperadas a partir da amostra inteira e dos *subsets* é relativamente sutil, não muito diferente da isometria.

Palavras-chave: podocnemidoidae; grupo bauru; análise de morfometria geométrica; epiplastrão; espessura do casco; taxonomia alfa

LIST OF ACRONYMS AND ABBREVIATIONS

CCMFC	Calenturitas Coal Mine, fossil collection.
CPPLIP	Centro de Pesquisas Paleontológicas Llewellyn Ivor Price.
FFP PG	Faculdade de Formação de Professores da Universidade do Estado do Rio de Janeiro.
GP	Departamento de Geologia e Paleontologia, Faculdade de Filosofia, Ciências e Letras de São José do Rio Preto
GP/2E	Systematic Paleontology Lab, Geosciences Institute, Universidade de São Paulo.
IG	Instituto Geológico do estado de São Paulo.
MAS	Museo de los Andes de Socha.
MCT.R	Museu de Ciências da Terra, Fossil Reptiles Collection.
MCT.RR	Museu de Ciências da Terra, Recent Reptiles Collection.
MHNC	Museo de História Nacional de Cochabamba.
MNHN	Muséum national d‘Histoire naturelle.
MPCA	Museo Paleontológico Carlos Ameghino.
MZSP-PV	Museu de Zoologia da USP, Vertebrate Palaeontology Collection.
MZUFV-P	Museu de Zoologia João Moojen, Palaeontology Collection.
PUC RCL	Pontifical Catholic University of Minas Gerais, Reptile paleontology collection.
RM	Redpath Museum.
UF/IGM	Florida Museum of Natural History Vertebrate Paleontology Collections / Museo Geológico José Royo y Gómez.
UFRJ-DG	Universidade Federal do Rio de Janeiro, Departamento de Geologia.
URP RT	Universidade Estadual Paulista, Campus São José do Rio Preto.
WUS	School of International Liberal Studies, Waseda University.

SUMMARY

1 INTRODUCTION

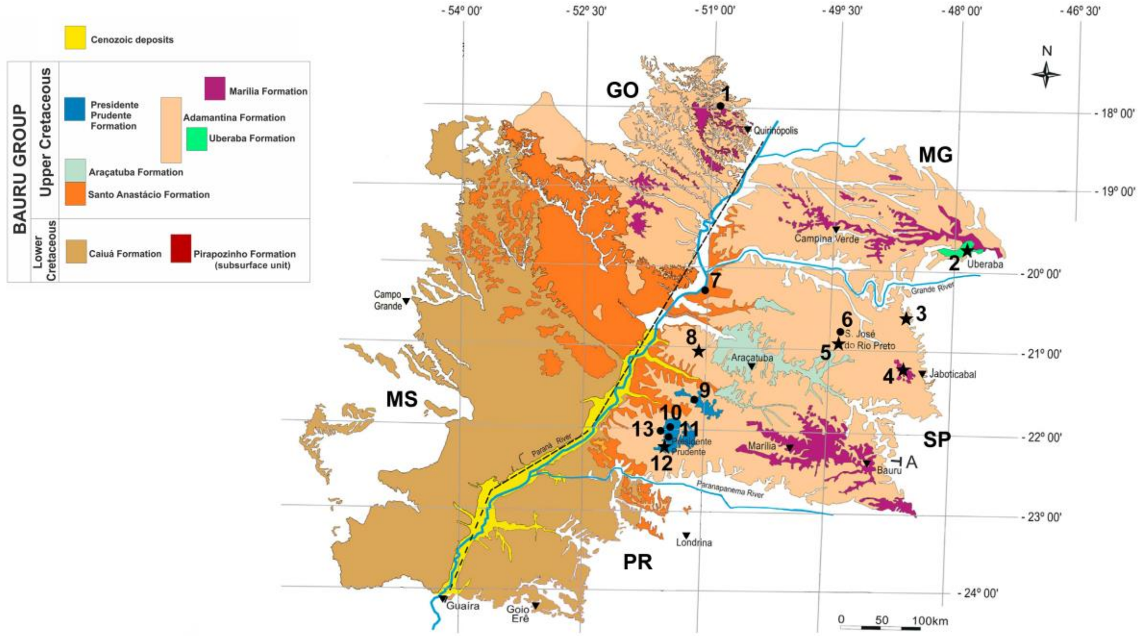
The Bauru Group serves as the main window into the Late Cretaceous ecosystems of continental Brazil (Bertini *et al.*, 1993). This sedimentary sequence is part of the Paraná Basin, and spans an area covering the Brazilian states of Minas Gerais, São Paulo, Paraná, Mato Grosso do Sul and Goiás, as well as a small area of neighbouring Paraguay (Soares *et al.*, 1980). Its consists mostly of siliciclastic sedimentary strata, deposited during the Early to Late Cretaceous (Soares *et al.*, 1980; Dias-Brito *et al.*, 2001; Pinheiro *et al.*, 2018). Several conflicting lithostratigraphic schemes for the Bauru Group have been proposed, which contradict themselves in several important aspects (see Menegazzo *et al.*, 2016 and Arai & Dias-Brito, 2023 for two such schemes and extensive literature surveys). In this contribution, I follow the proposal of Pinheiro *et al.* (2018, 2021), according to which the Bauru Group is divided into eight formations, namely the Caiuá (Aptian), Pirapozinho (Aptian), Santo Anastácio (Cenomanian), Araçatuba (Turonian), Adamantina (Turonian – early Maastrichtian), Uberaba (Coniacian – Campanian), Presidente Prudente (Campanian – late Maastrichtian) and Marília (Maastrichtian) Formations (Figure 1).

Since the publishing of the first reports of fossil remains from the Bauru Group, over a century ago, a rich fossil assemblage has been recovered from these strata, including micro- and macroremains, as well as trace fossils (Ihering, 1911; Pacheco, 1913; Price, 1955; Mezzalira, 1974; Bertini *et al.*, 1993). Vegetable remains are scarce, and consist mostly of palynomorphs and charophyte oogonia (Mezzalira, 1974; Dias-Brito *et al.*, 2001; Arai & Fernandes, 2023). Invertebrates are represented by “conchostracans”, ostracods, freshwater bivalves and land snails (Mezzalira, 1974; Dias-Brito *et al.*, 2001; Carbonaro *et al.*, 2014), and the vertebrate record includes remains of fishes, anurans, mammals, squamates, crocodylomorphs, pterosaurs, dinosaurs (non-avian and avian) and turtles (Ihering, 1911; Pacheco, 1913; Price, 1955; Cunha *et al.*, 1987; Bertini *et al.*, 1993; Bandeira *et al.*, 2018).

Turtles are among the first taxa reported from the Bauru Group, with fragmentary shell material being mentioned in the earliest records of fossil finds in the unit (Ihering, 1911; Pacheco, 1913; Roxo, 1929). Nine taxa – all belonging to the side-necked lineage Podocnemidoidae (*sensu* França & Langer, 2006) – have been formally named. These are “*Podocnemis*” *harrisi* Pacheco, 1913, “*Podocnemis*” *brasiliensis* Staesche, 1937, *Roxochelys wanderleyi* Price, 1953, *Bauruemys elegans*

(Suárez, 1969), *Cambaremys langertoni* França & Langer, 2005, *Peiropemys mezzalirai* Gaffney *et al.*, 2011, *Pricemys caiera* Gaffney *et al.*, 2011, *Yuraramirim montealtensis* Ferreira *et al.*, 2018 and *Amabilis uchoensis* Hermanson *et al.*, 2020. Two informal shell morphotypes – “Peirópolis A” and “Peirópolis B” – have also been proposed (Gaffney *et al.*, 2011), and there are several fragmentary postcranial remains that cannot be confidently identified to specific or generic level (Arid & Vizotto, 1966; Cunha *et al.*, 1987; Menegazzo *et al.*, 2015; Ferreira *et al.*, 2018; Bogado *et al.*, 2023). The main fossil sites from where turtles have been recovered in the Bauru Group are presented in Figure 1.

Figure 1 – Main fossil sites in the Bauru Group from where turtle remains have been recovered, plotted over a geological map of the unit, following the proposal of Pinheiro *et al.* (2018).



Municipalities with published reports of turtle fossils:

State of Goiás	State of São Paulo			Symbols:
1. Rio Verde	3. Colina	7. Rubineia	10. Alfredo Marcondes	★ Type locality
State of Minas Gerais	4. Monte Alto	8. Mirandópolis	11. Presidente Prudente	● Fossil site
	5. Ibirá	9. Flórida Paulista	12. Pirapozinho	▼ Urban centre
2. Uberaba	6. São José do Rio Preto		13. Álvares Machado	

Source: Original image by the author, taken from Bogado *et al.* (2023).

Despite the abundance of fossil material and apparent taxonomic diversity, there are still many gaps and uncertainties in our understanding of the Testudines of the Bauru Group (see Bogado *et al.*, 2023). One of the foremost problems in this regard is taxonomic instability (Romano *et al.*, 2013). Of the nine nominal species that have been proposed for this unit, four are known exclusively from shells, namely "*Podocnemis*" *harrisi*, "*Podocnemis*" *brasiliensis*, *Roxochelys wanderleyi* and *Cambaremys langertoni*. Though pleurodire taxonomy was historically reliant on shell morphology (e.g., Hay, 1908; Zangerl, 1948, 1969), it became increasingly clear from the second half of the XXth Century onwards that the shell morphology of side-necked turtles was mostly unfit for taxonomic use (Gaffney *et al.*, 2006, 2011). The pleurodire shell consists of a mosaic of traits that are either highly conserved along phyletic lineages or highly variable, even among individuals of a single species (Wood & Díaz de Gamero, 1971; Guerrero & Pérez-García, 2021a). This mix of conservative anatomy and frequent individual variation makes it hard to make reliable taxonomic inferences based on shell material alone, severely hampering the identification of postcranial remains of Pelomedusoides (Gaffney *et al.*, 2006, 2011).

To further complicate this issue, the majority of the Bauru taxa are known from only a few, fragmentary fossils. "*Podocnemis*" *harrisi*, "*Podocnemis*" *brasiliensis* and *Cambaremys langertoni* are known only through their holotypes, which consist of fragmentary shells, and *Roxochelys wanderleyi* is known only from five published shell specimens (Pacheco, 1913; Staesche, 1944; França & Langer, 2005; Romano *et al.*, 2013; Bogado *et al.*, 2023). The skull-based taxa show a similar situation, with *Peiropemys mezzalirai*, *Yuraramirim montealtensis* and *Amabilis uchoensis* being based solely on isolated type skulls and *Pricemys caiera* being known from the fragmentary type skull and one referred, isolated quadrate (Gaffney *et al.*, 2011; Rogério *et al.*, 2013; Ferreira *et al.*, 2018; Hermanson *et al.*, 2020). The scarcity and bad preservation of the available fossils makes it hard to identify diagnostic characteristics in the type material and to attribute new fragments to pre-existing taxa. Only *Bauruemys elegans*, known from a site preserving an accumulation of hundreds of articulated fossils, is known from a large sample of individuals (Suárez, 1969, 2002; Henriques, 2006; Bertini *et al.*, 2006). This has permitted a solid definition of this taxon, as well as the development of studies about the degree of morphological variation within this species (Kischlat, 1995; Figueira & Bertini, 2002b; Romano & Azevedo, 2007; Mariani & Romano, 2017).

The species “*Podocnemis*” *brasiliensis* is a good example of the problematic taxonomy of the Bauru Group turtles. The type material of this taxon was collected along with other turtle remains from railway cuts along the Araçatuba – Jupiá branch of the Noroeste do Brasil railway, in the present day municipality of Mirandópolis in the state of São Paulo (Wanderley, 1936). Alberto Lavenère Wanderley – a technician of the *Departamento Nacional da Produção Mineral* (DNPM) – collected these fossils in 1935 and took them to the collections of the institution (now housed in the *Museu de Ciências da Terra*, MCTer). The fossils were preliminarily examined by the staff of the Palaeontology Section of the DNPM, who variously identified them as belonging to *Naiadochelys? harrisi* (Oliveira, 1936), the genus *Podocnemis* (Duarte, 1936) or to the family “Bothremyidae” [sic], “possibly belonging to one of two genera, *Bothremys* Leidy or *Naiadchelys* Hay [sic]” (Roxo, 1936). Though generic attributions varied widely, all agreed on the pelomedusoid affinities of the material. The technician Axel Löfgren prepared some of the fossils from Mirandópolis and supposedly wrote a preliminary report about them (Löfgren, 1936; Roxo, 1936), but this work was never published.

DNPM technician Paulo de Araújo Alvim produced five photographs of three of the Mirandópolis turtle fossils, namely an incomplete plastron (then identified as specimen n. 2980 of the “*Collecção Padrão*” (Standard Collection) of the DNPM, now MCT.R.214), an anterior carapace fragment (then n. 2981, now MCT.R.216) and a middle carapace fragment (then unnumbered, now MCT.R.233) (Alvim, 1936). These photographs were given to palaeontologist Friedrich von Huene from Tübingen, who forwarded them to his research associate, Karl von Staesche. Staesche believed the fragments represented a single individual, and proposed that the photographed material belonged to a new species, for which he erected the name *Podocnemis brasiliensis*. Staesche’s article was later translated into Portuguese by DNPM mining engineer Gerson de Faria Alvim (Alvim, 1939; Staesche, 1944).

When he consulted the Mirandópolis turtle sample in the 1950’s, DNPM palaeontologist Llewellyn Ivor Price noticed a curatorial and nomenclatural mistake: the three fragments that Staesche used to erect *Podocnemis brasiliensis* did not belong to a single animal, but rather to different individuals belonging to distinct taxa (Price, 1953a). Price (1953b) maintained the name *Podocnemis brasiliensis* for the plastron (MCT.R.214), but erected a new taxon – *Roxochelys wanderleyi* – for the anterior carapace fragment (MCT.R.216), which was associated with a previously unpublished anterior plastral lobe that was also considered part of specimen

MCT.R.216 (Price, 1953b). The other carapace fragment that had been included in Staesche's *Podocnemis brasiliensis* (MCT.R.233) was excluded from the definition of both taxa, as Price believed it was not originally associated with either of the other fragments (Price, 1953b, p. 11-12).

Following Price's revision, the type plastron of "*Podocnemis*" *brasiliensis* remained the sole specimen confidently assigned to this species. Arid & Vizotto (1966) tentatively attributed an incomplete carapace of a juvenile pelomedusoid to "*P.*" *brasiliensis*, based on its perceived difference from *Roxochelys*, but most subsequent authors have disregarded this attribution (Broin, 1971, 1991; Campos, 1977; Gaffney *et al.*, 2011, but see Bertini, 1993; Langer, 1994 and Menegazzo *et al.*, 2015 for exceptions). Muizon *et al.* (1983) and Marshall & Muizon (1988) cited the presence of "*P.*" *brasiliensis* in the site of Tiupampa, Bolivia, but presented no evidence to back this claim. França & Langer (2005) and Menegazzo *et al.* (2015) suggested that the type of *Cambaremys langertoni* and an incomplete shell from the Santo Anastácio Formation could belong to "*P.*" *brasiliensis*, but did not take a definite stance.

The type of "*Podocnemis*" *brasiliensis* only preserves so much anatomical information, so its diagnosis was based on few characteristics. Price (1953b) differentiated this species from *Roxochelys wanderleyi* in that the latter had a thicker shell, and provided the following diagnosis for "*P.*" *brasiliensis*:

> Plastron long and narrow. Anterior lobe only slightly narrower than posterior lobe. Anal notch deep. Entoplastron quadrangular [sic] not rounded posteriorly, and very large in relation to the anterior lobe. Mesoplastron extending to a line drawn between the axillary and inguinal notches, and terminating in an obtuse angle. Ischial suture semi-triangular, terminating posteriorly above the level of the apex of the anal notch. Gular shields separated by an intergular. Femoral shields very long; the sulcus between them being nearly as long as the sum of that sulcus of the inter-abdominal and inter-pectoral shields [sic]. Sculpture of fine scattered sulci which normally present dichotomic division. (Price, 1953b, p. 31).

This diagnosis – almost identical to the one provided by Staesche (1937, 1944) – is rather poor. The unsatisfactory nature of the species' diagnosis and the fragmentary state of its type specimen prompted subsequent authors to question the validity of "*Podocnemis*" *brasiliensis*. Simpson (1943) expressed his opinion that "*P.*" *brasiliensis* was possibly synonymous with the sympatric "*Podocnemis*" *harrisi*, and Wood & Díaz de Gamero (1971) and Wood (1984) believed that until better material referable to the species became available, "*P.*" *brasiliensis* was best recognized as an indeterminate pelomedusoid. Broin (1971, 1977) was more confident in the validity of the taxon, considering it a valid species more akin to the genus *Podocnemis* than to representatives of her "*Roxochelys* group" – *Roxochelys wanderleyi*, "*Podocnemis" elegans* Suárez, 1969 (currently *Bauruemys elegans*) and ? *Roxochelys vilavilensis* Broin, 1971 (currently *Lapparentemys vilavilensis* (Broin, 1971)). The same author later produced a new diagnosis for "*P.*" *brasiliensis* (Broin, 1991), and argued that the species might be represented not only by the type plastron, but also by fragmentary remains from the states of Mato Grosso, São Paulo and Minas Gerais, including a fragmentary skull that would later be designated as the holotype of *Pricemys caiera* (Broin, 1991; Lapparent de Broin, 2000).

Kischlat (1994a) assigned the species "*Podocnemis*" *brasiliensis* to the genus *Bauruemys* "provisionally" (Kischlat, 1994a, p. 345), but placed it back in *Podocnemis* in Kischlat (1995), and finally considered it a *nomen dubium* in Kischlat (1996a, 1996b). Langer (1994) and Langer & Bertini (1995) recovered "*P.*" *brasiliensis* (including both the type plastron and the carapace of Arid & Vizotto, 1966) as the sister taxon of *Roxochelys* in a fenetic analysis of South American podocnemidoids, suggesting a new genus should be erected to house this species.

When describing *Cambaremys langertoni*, França & Langer (2005) considered the possibility that the holotype of this taxon was a juvenile individual of "*Podocnemis*" *brasiliensis*. Romano & Azevedo (2006) stated that "*P.*" *brasiliensis* could represent a species of the genus *Bauruemys* or the senior synonym of *C. langertoni*, but pondered that, given the state of knowledge at the time, no definite conclusion about these issues could be reached. Romano (2006, 2008) and Oliveira & Romano (2007) considered the synonymy between "*P.*" *brasiliensis* and *C. langertoni* was plausible, and furthermore stated that "*P.*" *brasiliensis* should be considered as a species *incertae sedis*, perhaps referable to the genus *Roxochelys* (not *Bauruemys*). These authors adopted a slightly different position in a later abstract, submitted to the Gaffney Turtle Symposium held in 2009 (Brinkman *et al.*, 2013). In this abstract, they stated that:

> (1) *Bauruemys brasiliensis* and *Bauruemys elegans* might represent the same species; (2) *Cambaremys langertoni* is clearly based on a young individual and probably is a junior synonym of *Roxochelys wanderleyi* (and not *B. brasiliensis* as presumed by França & Langer 2005); (3) it is impossible to distinguish adequately *Roxochelys harrisi* from the other Bauru Basin species and, due to the Principle of Priority, this species is potentially the senior synonym of *Roxochelys wanderleyi* or *Bauruemys brasiliensis* […] (Romano *et al.*, 2009, pp. 143-144).

The taxonomic fortunes of "*Podocnemis*" *brasiliensis* would suffer a strong blow after the Gaffney Turtle Symposium, when Pedro S. R. Romano and Gustavo R. Oliveira met with Eugene Gaffney at the American Museum of Natural History, after having all attended the event (Pedro S. R. Romano, 2024, personal communication). In this occasion, these three specialists discussed the taxonomy of the Testudines of the Bauru Group, and agreed that "*P.*" *brasiliensis* was best regarded as a *nomen dubium* (Pedro S. R. Romano, 2024, personal communication). Following this discussion, the authors went on to publish papers that incorporated this conclusion. In his landmark treatise on the Podocnemidoidae, Gaffney addressed the validity of "*P.*" *brasiliensis* with a straightforward one-liner, stating that "the type is inadequate for an objective diagnosis, and Oliveira and Romano (2007) correctly considered it a *nomen dubium*" (Gaffney *et al*., 2011, p. 69). In Romano *et al*. (2013), a work derived from the abstracts that Pedro Romano and Gustavo Oliveira submitted to the Gaffney Turtle Symposium (Oliveira *et al*., 2009; Romano *et al*., 2009), the authors argued that "*P.*" *brasiliensis* should be considered a *nomen dubium* (Romano *et al*., 2013, p. 273), a claim that had not been explicitly stated in any of their previous work.

Following these two papers, the consensus has been that "*Podocnemis*" *brasiliensis* is a nomen *dubium*. Though Menegazzo *et al*. (2015) have considered this species as being valid and synonymous with *Cambaremys langertoni*, the Arid & Vizotto (1966) carapace and an incomplete shell from the Santo Anastácio Formation (Menegazzo, 2009; Menegazzo *et al*., 2015), subsequent authors have not followed this interpretation. de la Fuente *et al*. (2014) regarded "*P.*" *brasiliensis* as a *nomen dubium* (de la Fuente *et al*., 2014, p. 113), and Ferreira *et al*. (2018) and Hermanson *et al*. (2017, 2020) referred to this species as being "dubious". Bogado *et al*. (2023) stated that "*P.*" *brasiliensis* was "shrouded by significant taxonomic uncertainty, being considered by many authors a *nomen dubium*" (Bogado *et al*., 2023, p. 13).

In this contribution I present a fragmentary plastron from the Adamantina Formation of the Bauru Group, showing remarkable similarities with the type plastron of "*Podocnemis*" *brasiliensis*. I reassess this taxon based on both the holotype and the new referred specimen, and explore the topic of its taxonomic validity.

2 OBJECTIVES

2.1 GENERAL OBJECTIVES

To describe and identify specimen FFP PG 218, and to revise the taxonomy of the problematic taxon "*Podocnemis*" *brasiliensis*.

2.2 SPECIFIC OBJECTIVES

- To describe shape variation in the epiplastra of Bauru Group turtles, aiming at a better understanding of the plastral morphology of these taxa.
- To test if shell thickness is a useful trait for distinguishing Bauru Group shell taxa, or if allometric effects make it unsuitable for this purpose.
- To emend the diagnosis of the species "*Podocnemis*" *brasiliensis*.
- To revisit specimens that have been tentatively assigned to "*P.*" *brasiliensis* in the past, reassessing their attribution to this species.

3 MATERIALS AND METHODS

3.1 MATERIALS

Specimen FFP PG 218 was collected by Felipe Medeiros Simbras, Kamila Luisa Nogueira Bandeira and Paulo Victor Luiz Gomes da Costa Pereira during a field campaign in the municipality of Ibirá, São Paulo, Brazil (locality 5 in Figure 1). The collecting site was a hillside outcrop exposing intercalated layers of sandstone and conglomerate, located to the north of the Irmãos Garcia site, from where the sauropod *Ibirania parva* Navarro *et al*. 2022 was collected (Kamila Bandeira, 2022, personal communication). The fossil is now deposited in the collections of the Faculdade de Formação de Professores, Universidade Estadual do Rio de Janeiro, in São Gonçalo, Rio de Janeiro, Brazil.

3.2 METHODS

3.2.1 ANATOMIC AND TAXONOMIC TERMINOLOGY

I follow Hutchison & Bramble (1981) for anatomical terminology of the shell. The usage of the open nomenclature modifiers *affinis* (aff.) and *confer* (cf.) follows the work of Sigovini *et al*. (2016). Most supra-generic taxa cited in this work follow the definition of Joyce *et al*. (2021), based on the PhyloCode. Podocnemidoidae, a taxon that was not included in the taxonomic scheme of Joyce *et al*. (2021), is used here following the definition of França & Langer (2006). Podocnemidoidae is synonymous with the Podocnemidinura of Gaffney et al. (2006), but the former name was chosen over the latter because it has priority and is of more frequent usage in the literature. A more detailed reasoning behind this decision is given in Bogado *et al*. (2023).

In this work, I refer to some shell morphotypes that, though more or less clearly defined and distinguishable from other fossil turtles found in continental strata from the Upper Cretaceous and Palaeogene of South America, have not been formally named. These are the shell morphotypes identified as “Peirópolis A” and “Peirópolis B” by Gaffney et al. (2011), originating from the Maastrichtian Serra da Galga Member of the Marília Formation, and another shell morphotype identified by Cadena *et al*. (2012a) as “Pelomedusoides shell taxon B”, hailing from the Palaeocene Cerrejón Formation of Colombia. For consistency with the names of the morphotypes identified by Gaffney et al. (2011) and clarity about geographic and stratigraphic provenance, I chose to identify this latter shell taxon as “Cerrejón B”.

Throughout this work, I also mention published specimens that, while not identified to a specific level, do appear to represent distinct taxa. These are the shell described by de la Fuente (1993) from the Upper Cretaceous Río Colorado Subgroup in Planicie Banderita, Argentina (MPCA 7049); the plastron described by Cadena & Schweitzer (2014) from the upper Palaeocene – lower Eocene Los Cuervos Formation in La Jagua de Ibirico, Colombia (CCMFC01); and the shell described by Menegazzo et al., (2015) from the lower Upper Cretaceous Santo Anastácio Formation in Rubineia, Brazil (URP RT-1). For the sake of concision and convenience, these are henceforth identified in the text as the “Río Colorado form”, “Los Cuervos form” and “Santo Anastácio form”, respectively.

3.2.2 MECHANICAL PREPARATION

I mechanically prepared specimen FFP PG 218 in the facilities of the *Laboratório de Paleontologia e Osteologia Comparada* (LAPOC) of the *Departamento de Biologia Animal*, *Universidade Federal de Viçosa*. A PaleoTools® Micro Jack 3 tool was used for most of the rock-clearing process, and an assortment of dental picks of varying shapes and sizes were used for more delicate work, such as excavating small fragile fragments and clearing matrix that directly adhered onto fossil bones.

A Canon EOS 850D digital camera with an attached EF-S 18-55mm f/3.5-5.6 IS STM lens was used to take detailed photographs of the block containing FFP PG 218 prior to preparation, so as to record the original spatial configuration of the bones in the matrix. The same camera was used to produce time-lapse videos recording the preparation process.

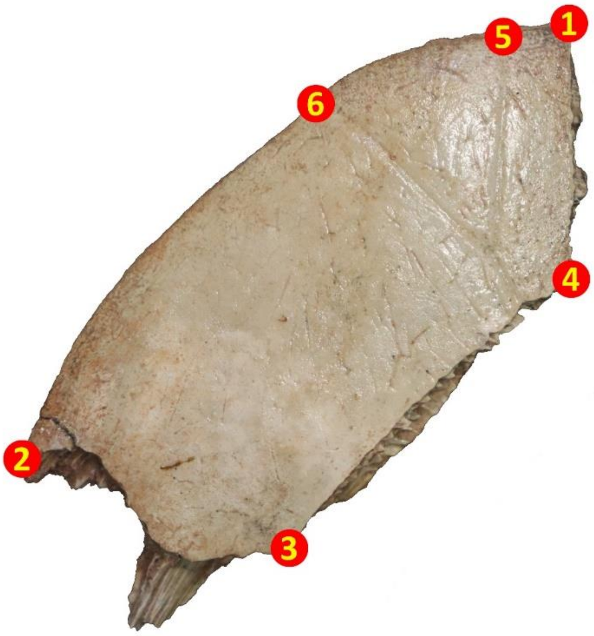
3.2.3 IMAGE ACQUISITION

For the morphometric analyses conducted in this research, strict image acquisition protocols were followed, as indicated for this type of study (e.g., Viscosi & Cardini, 2011; Zelditch *et al.*, 2012). Photos were taken with a Canon EOS 850D digital camera with an attached EF-S 18-55mm f/3.5-5.6 IS STM lens. When preparing a shot, the camera lens was positioned with its long axis perpendicular to the surface, and the zoom set to 55mm. Tripods and photographic stations were used to hold the camera in place, and spirit levels were used, when available, to check the camera angulation. I refrained from using photographs taken by other researchers, but opted to include some images taken by my adviser Pedro Seyferth Ribeiro Romano in my sample, because he follows photography protocols similar to the ones I employed and had access to specimens that I could not personally assess.

3.2.4 GEOMETRIC MORPHOMETRY OF EPIPLASTRA

The analysis was employed in a sample of right epiplastra belonging to fossil podocnemidoids from the Bauru Group. In specimens where the right epiplastra were missing, incomplete or distorted, I opted to use mirrored images of the left epiplastra, assuming eventual asymmetries to be irrelevant for the purposes of this study. Six anatomical landmarks were identified for usage in the analyses. They are described in Figure 2 and Table 1. The list of specimens used in the analysis (*n* = 28) can be found in the Appendix (Table 2).

Figure 2 – Anatomical landmarks used in this study, plotted onto specimen FFP PG 218.



Source: Original image by the author.

Table 1 – Anatomical landmarks used to study the morphology of the epiplastra in pelomedusoid turtles from the Bauru Group.

Landmark	Description	Type (Bookstein, 1991)
1	Anterior extremity of the inter-epiplastral suture	2
2	Lateral extremity of the epi-hyoplastral suture	2
3	Meeting of the epi-, ento- and hyoplastron	1
4	Meeting of the epiplastra and the entoplastron	1
5	Anterior extremity of the gular-extragular sulcus	2
6	Anterior extremity of the extragular-humeral sulcus	2

Source: Original table by the author.

Initial steps of data processing were conducted using the tps series of softwares, (Rohlf, 2015). tpsUtil (Version 1.82) was used to combine the images in the sample into a single stack in TPS format, and tpsDig2 (Version 2.31) was used to add a scale factor and digitize the landmarks in each image. The data was then subjected to Procrustes operations (generalized least squares superimposition (GLS), Rohlf & Slice, 1990; Zelditch et al., 2012) using the software PAST (Version 4.11; Hammer *et al.*, 2001). Principal Component Analysis (PCA) was performed in PAST using the Procrustes residuals matrix, and the same software was used to visualize and interpret biplots of the sampled individuals based on their PC scores and deformation grids. PCs were considered significant following the Broken-Stick Model (Jackson, 1993).

In order to investigate the presence of an evolutionary allometric effect (*sensu* Gould, 1966), linear regressions were carried out to test whether changes in the scores of the significant PCs were correlated to changes in size of the specimens. Log-transformed centroid size values – used as a size proxy – were plotted as the abscissa (independent variable), while PC scores were plotted as the ordinate (dependent variable). Regression models were calculated with the Robust approach in PAST (Hammer, 2024) assuming uncorrelation between the two variables as the null hypothesis for the linear correlation test (i.e. Pearson's r; Zar, 2010).

3.2.5 LINEAR REGRESSION OF SHELL SIZE VS SHELL THICKNESS

A correlation test (Pearson's r) of two variables – shell thickness and shell size – was carried out to evaluate if shell thickness is a useful trait for distinguishing Bauru Group shell taxa, and also if an increase in shell thickness is correlated with a proportional increase in shell size among representatives of the Podocnemidoidae. The sample for this test consisted of adult and sub-adult individuals of South American podocnemidoids, both living and extinct, with 61 specimens in total (see Table 3 in the Appendix for the full list). For the linear correlation test, the null hypothesis was the uncorrelation between the two variables.

To sample shell thickness, measurements were taken along the axis of the ventral epi-hyoplastral suture, using an Absolute AOS Digimatic 200mm Mitutoyo calliper. For shell size, the width of the epi-hyoplastral suture in ventral view was used as a proxy, because total plastron length could not be determined in most of the fossil material, owing to its fragmentary nature. The software ImageJ (Version 1.54g; Schneider *et al.*, 2012) was used for digitally measuring suture widths.

Measurements were taken three times using the same parametres, and the mean between the three raw results was used as the definite value for the analyses. Most measurements were taken personally, but for the shell thickness of specimens MCT.R.933 and both variables of MCT.R.1787 I relied on data provided by Rafael Costa da Silva and Romano *et al.* (2013), respectively, as I was not able to measure these specimens personally. The measurements taken by third parties were all made with callipers.

Robust bivariate regressions (Hammer, 2024) of log-transformed values of the two studied variables were recovered with the software PAST (Version 4.11; Hammer *et al.*, 2001), plotting the shell size proxy as the abscissa (independent variable) and shell thickness as the ordinate (dependent variable). I recovered one regression for the entire sample, as well as a separate regression from each of the three Bauru Group shell taxa with a sufficiently large sample (*Bauruemys*, *Roxochelys* and “Peirópolis A”). For each regression, correlation (r) and and goodness-of-fit (R^2) values were inspected for assessing the degree of relationship between the variables and the amount of variation explained by each variable (Zar, 2010). Slope values were used to identify the type of allometry present in each case, following the nomenclature by Huxley & Teissier (1936). In order to determine whether isometry was present, I inspected the confidence intervals for each slope value, considering isometry could not be discarded if the confidence intervals contained number 1. Confidence intervals (CI) for the slope values were obtained through bootstrap resampling (95% out of an N of 1999).

4 RESULTS

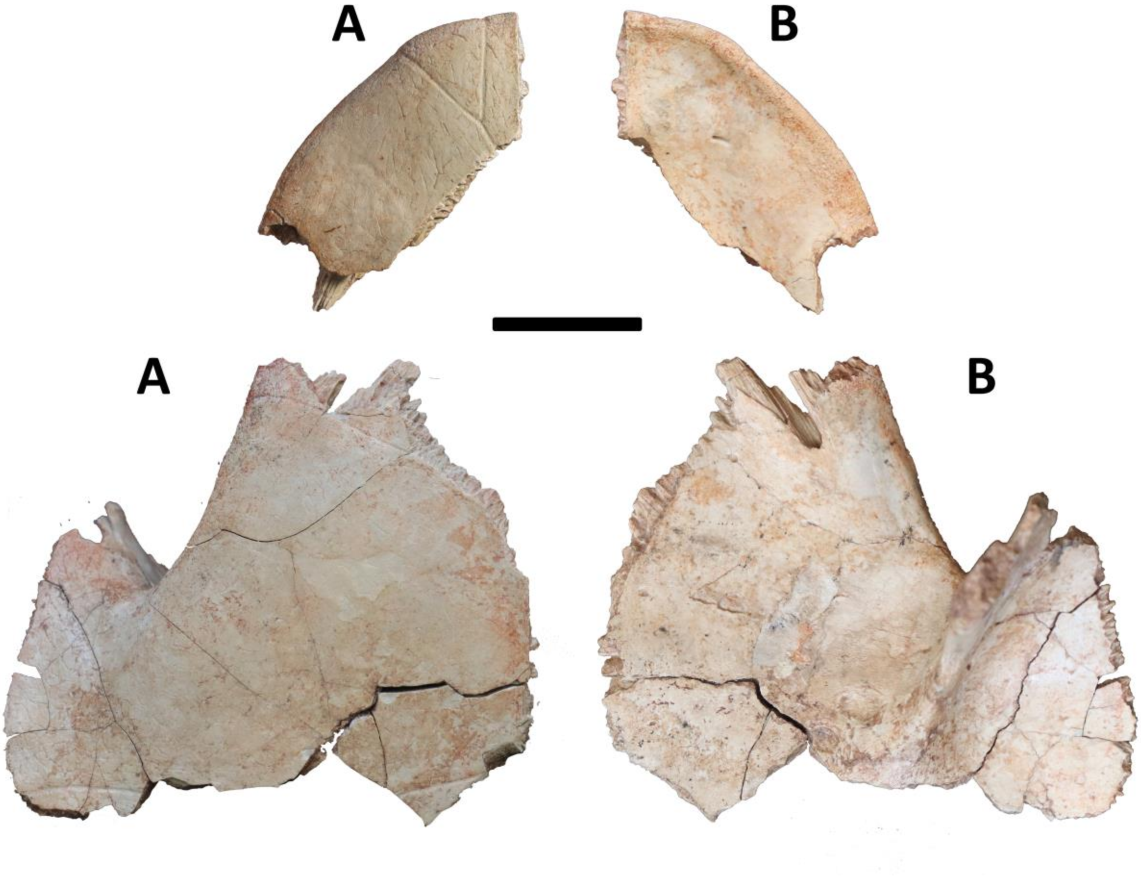
4.1 FOSSIL DESCRIPTION

FFP PG 218 (Fig. 3) consists of a right epiplastron and hyoplastron, found very closely associated. Both bones are in a good state of conservation, preserving the original shell texture, serrated sutural surfaces between adjacent plates and delicate anatomical structures, such as the posterior epiplastral projection.

The outer rim of the epiplastron forms a very feeble rounded lip, grading into a more angular border in the hyoplastron. The suture between the epiplastron and the entoplastron has a simple, slightly concave outline in ventral view (Fig. 3), but in dorsal view has a more complex outline. Its anterior extremity bears a conspicuous angular recess, which in life would accommodate a matching dorsal process of the entoplastron. Postero-laterally to this embayment the suture becomes convex, until it reaches a wedge-shaped, concave recess, which articulates with a short antero-medial process of the hyoplastron (Fig. 3). The epiplastron has a well-developed postero-lateral projection of triangular shape (Fig. 3), which fits into a matching slot in the hyoplastron. In ventral view, the epi-hyoplastral suture has a simple, sinuous shape (Fig. 3). The midline sutures of the hyoplastron indicate the posterior half of the entoplastron would have been longer than the anterior half, tapering at a shallower angle relative to the midline (Fig. 3). The posterior extremity of the hyoplastron is not preserved, but this plate still preserves part of the contacts with the left hyoplastron, the right bridge peripherals and the right mesoplastron, which would have occupied a lateral position (Fig. 3). The axillary process is well-developed and clearly verticalized (Fig. 3), suggesting the shell would have been relatively high for a pelomedusoid.

The external surfaces of both the epi- and hyoplastron are covered in small, dichotomously branching ornamental grooves, which in most of the preserved parts do not form a mosaic of anastomosed grooves, instead being clearly separated from one another (Fig. 3). Only in the lateralmost portion of the bridge are the grooves more well-developed, forming a closed network (Fig. 3). The gular scute is narrow, being slightly narrower at its anterior end than at the triple junction between the gular, extragular and humeral (Fig. 3). The extragular does not reach the entoplastron and has a triangular shape with almost straight sides (Fig. 3). The anterior end of each extragular would have been wider than the anterior end of the entire gular (counting the area on the unpreserved left epiplastron). The humero-pectoral sulcus runs anterolaterally at an angle of roughly 65° relative to the plastral midline. It does not reach the epiplastron, running just posterior to the posteriormost part of the epi-hyoplastral suture (Fig. 3). The pectoro-abdominal sulcus is only partially preserved, but apparently ran along a slightly sinuous course. It does not cross over onto the mesoplastron (Fig. 3).

Figure 3 – Specimen FFP PG 218. **A**-**B**, right epiplastron in ventral (**A**) and dorsal (**B**) views; **C**-**D**, right hyoplastron in ventral (**C**) and dorsal (**D**) views.



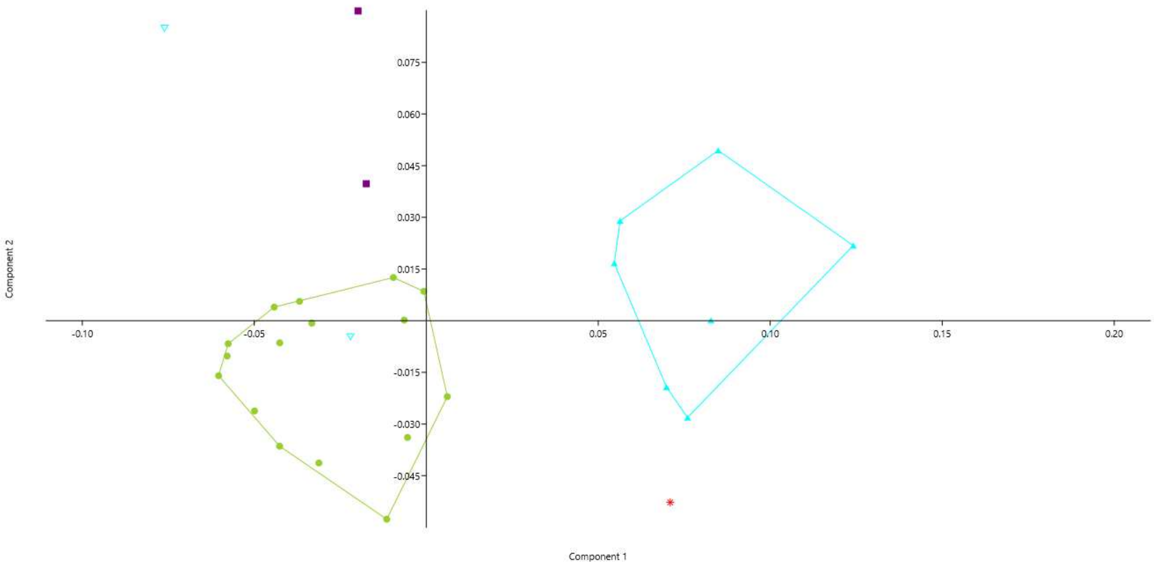
Source: Original image by the author.

4.2 GEOMETRIC MORPHOMETRY OF EPIPLASTRA

The PCA recovered PCs 1, 2 and 3 as significant according to the Broken-Stick Model, and accounting for 47.981%, 20.44% and 14.41% of variance within the sample, respectively. FFP PG 218 and “Peirópolis A” have positive PC1 scores, while *Bauruemys*, *Roxochelys* and two indeterminate epiplastra from the Serra da Galga Member (CPPLIP-593 and MCT.R.2092) have negative scores. FFP PG 218 has the second greatest negative PC2 score (-0.052737). Most *Bauruemys* (10 out of 16 specimens) show PC2 scores close to zero, with some few attaining greater negative values (scores between -0.057629 and 0.012538). Most “Peirópolis A” epiplastra (5 out of 7 specimens) have positive PC2 scores, but two specimens have negative scores. The two *Roxochelys* specimens and specimen CPPLIP-593 have high positive PC2 scores. *Bauruemys* and “Peirópolis A” specimens have PC3 scores averaging around zero, with individuals varying between positive and negative scores. The two *Roxochelys* have strong positive scores, while FFP PG 218 and the two indeterminate epiplastra from the Serra da Galga Member have negative scores.

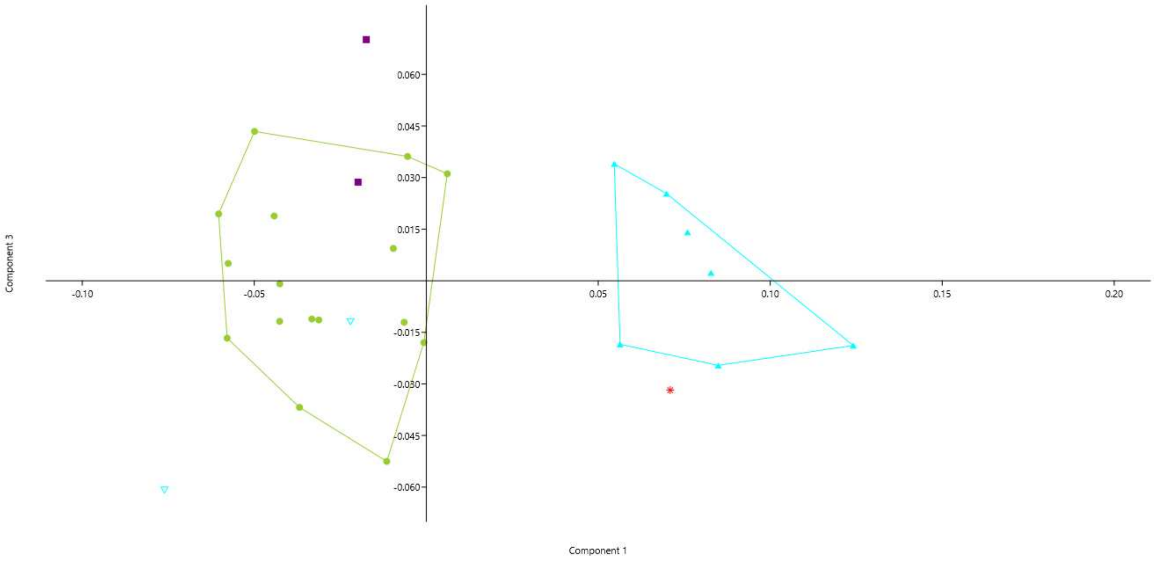
The morphospace decomposed by the projection of the sampled individuals onto a graph showing PC1 values as the abscissa and the PC2 values as the ordinate (PC1 vs PC2) reveals a clear pattern (Fig. 4). The PC1 axis clearly describes the differences between “Peirópolis A” and FFP PG 218, with positive scores, and *Bauruemys*, *Roxochelys* and both indeterminate epiplastra from the Serra da Galga Member, with negative scores. The PC2, on the other hand, is useful to differentiate *Bauruemys* and FFP PG 218 from “Peirópolis A” and *Roxochelys*. Specimen MCT.R.2092 has a PC2 score similar to those of “Peirópolis A”, while CPPLIP-593 has a score compatible with *Roxochelys* (Fig. 4). The PC1 vs PC3 biplot shows basically the same structure as the PC1 vs PC2 biplot, with only a few differences. The clearest divergence between the two is the projection of CPPLIP-593, one of the indeterminate epiplastra from the Serra da Galga Member. While this specimen has high positive PC2 scores similar to those of the two *Roxochelys* specimens, it has the greatest negative PC3 score (-0.018827), differing from the positive scores of *Roxochelys*.

Figure 4 – PC1 vs PC2 graph, showing specimen clusters largely coincident with current taxonomy. PC1 values plotted along the abscissa and PC2 values plotted along the ordinate. Red asterisk represents FFP PG 218, green circles represent specimens of *Bauruemys*, purple squares represent *Roxochelys*, filled blue triangles represent *bona fide* "Peirópolis A" and inverted hollow triangles represent indeterminate epiplastra from the Serra da Galga Member.



Source: Original image by the author.

Figure 5 – PC1 vs PC3 graph, showing taxonomic clusters similar to those of the PC1 vs PC2 graph, but not as clear. Note the considerable displacement of specimen CPPLIP-593 along the ordinate axis. PC1 values plotted along the abscissa and PC3 values plotted along the ordinate. Symbols as in Fig. 4.



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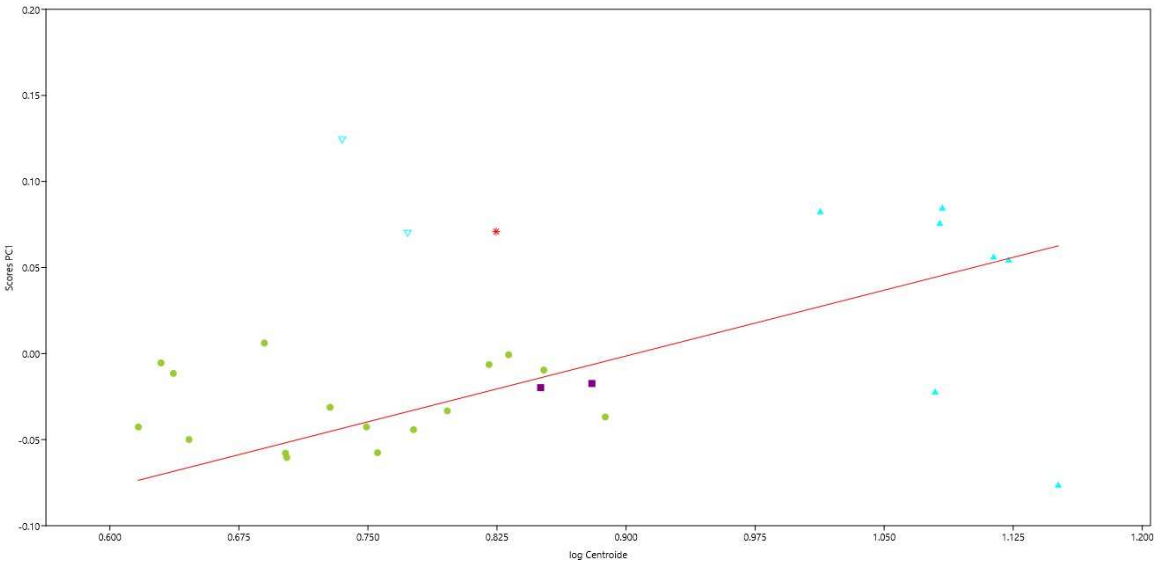
The deformation grid of the PC1 reveals that a change from negative to positive scores is associated with a narrowing of the region of the epiplastron covered by the gular scute, associated with an expansion in the remaining postero-lateral region of the plate. In the PC2, the change from negative to positive values is associated with a reduction in the width of the gular and an expansion in the lateralmost tip of the epiplastron. The PC3 shows an overall shortening of the epiplastron, particularly clear in the shortening of the interepiplastral suture and the posterior displacement of the anterior border of the plate.

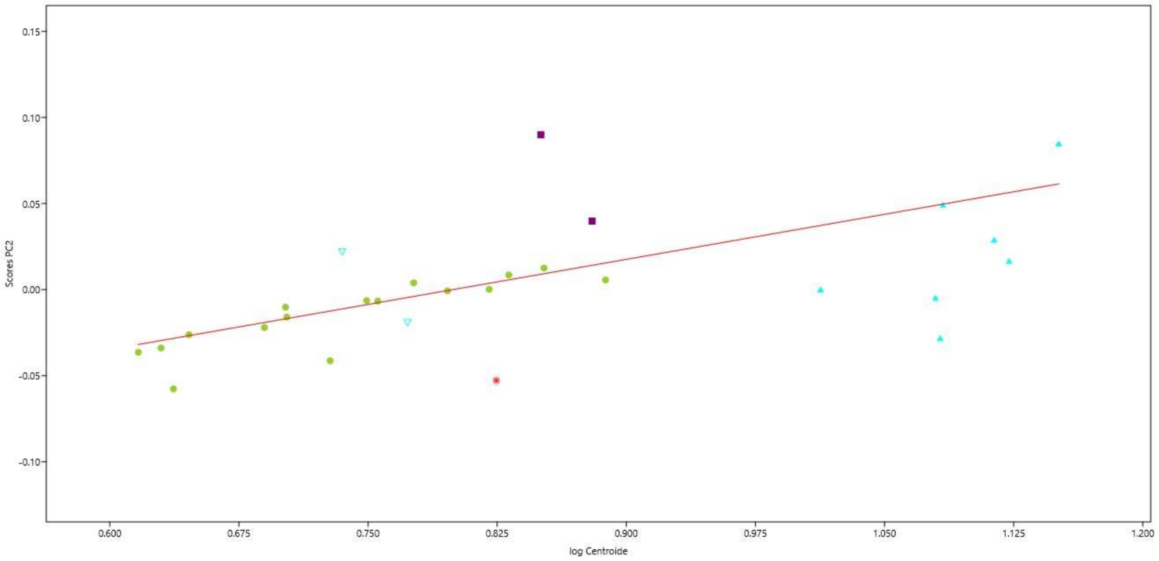
No correlation between size (centroid size log) and the PC1 and PC3 scores was found (PC1 – r = 0.36109, p = 0.0616; PC3 – r = -0.18156, p = 0.3653). On the other hand, the PC2 was found to be correlated with size (PC2 – r = 0.56595, p = 0.0011), evincing that the changes in shape described by the PC2 possess an allometric effect. The regression traced in the centroid size vs PC2 score biplot had a slope of 0.17437 (CI: 0.094 – 0.316).

Figure 6 – Centroid size (log) vs PC1 scores graph. Centroid size (log) values plotted along the abscissa and PC1 score values plotted along the ordinate. Symbols as in Fig. 4.



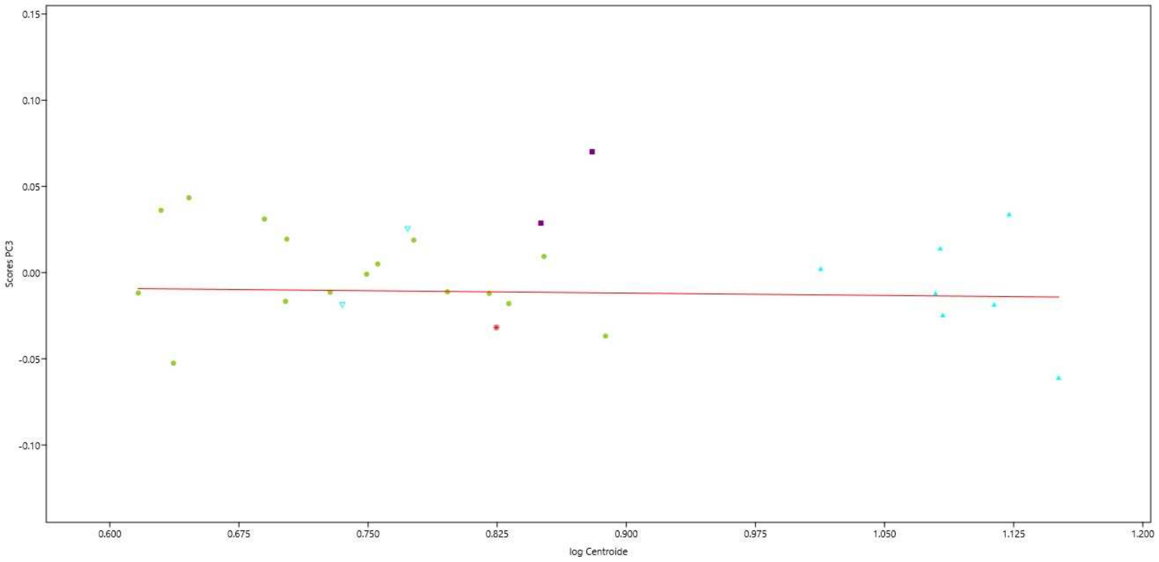
Source: Original image by the author.

Figure 7 – Centroid size (log) vs PC2 scores graph. Centroid size (log) values plotted along the abscissa and PC2 score values plotted along the ordinate. Symbols as in Fig. 4.



Source: Original image by the author.

Figure 8 – Centroid size (log) vs PC3 scores graph. Centroid size (log) values plotted along the abscissa and PC3 score values plotted along the ordinate. Symbols as in Fig. 4.



Source: Original image by the author.

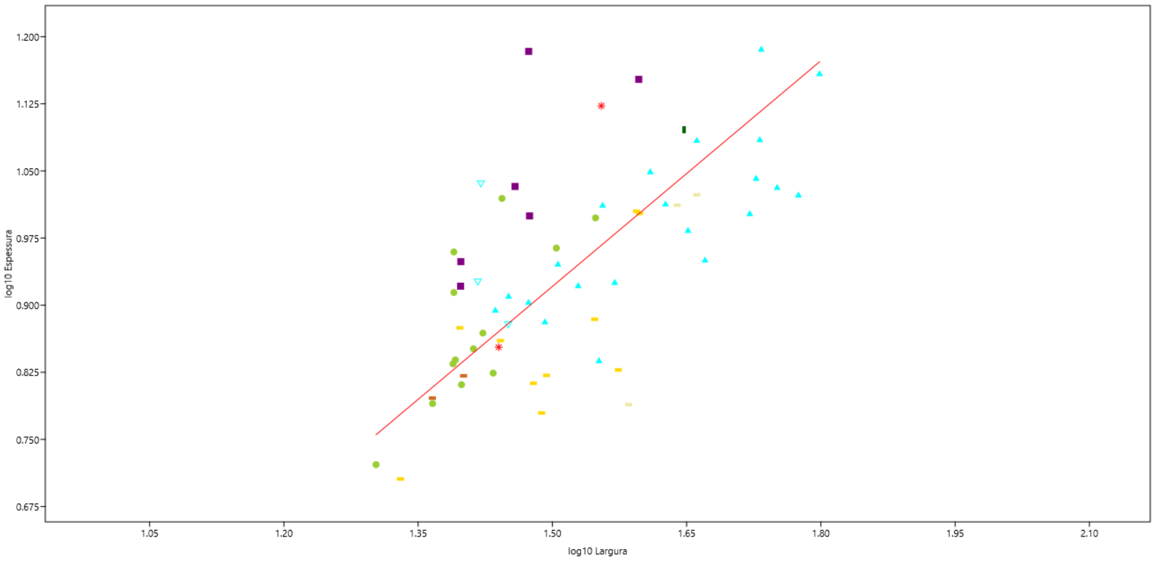
4.3 LINEAR REGRESSION

In the analysis including all sampled Podocnemidoidae (r = 0.66475; R^2 = 0.44189), permutation *p* for the correlation test had a value 0.0001 and was considered to be significant, falsifying the null hypothesis of uncorrelation between the two studied variables. The Robust regression obtained in this analysis had a slope of 0.84099 (CI: 0.602 – 1.368), characterizing a case of negative allometry (1 > slope > 0).

The correlation tests of the subsets with the Bauru shell taxa had the following results: *Bauruemys*: r = 0.75351, R^2 = 0.56777, permutation *p* = 0.0025; *Roxochelys*: r = 0.76419, R^2 = 0.58398, permutation *p* = 0.0601; “Peirópolis A”: r = 0.78781, R^2 = 0.62064, permutation *p* = 0.0001. While *Bauruemys* and “Peirópolis A” fall within the $p < 0.05$ threshold used to identify statistically significant results, *Roxochelys* falls short of this limit. This allows me to falsify the null hypothesis of uncorrelation only for the former two taxa, but not for *Roxochelys*. Still, it should be noted that the permutation p value of *Roxochelys* is quite close to 0.05, and that the low sample size for this taxon is expected to lower the statistical significance of tests run using this data subset.

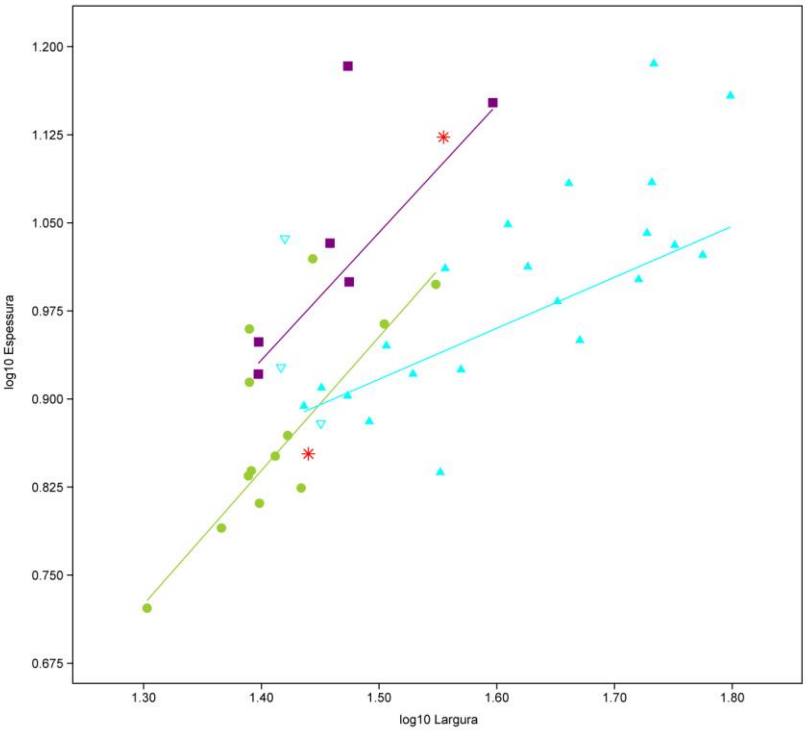
The regressions obtained from each taxon differed from the one recovered for the entire sample. *Bauruemys* and *Roxochelys* display slope values larger than 1 (*Bauruemys* = 1.1394 (CI: -0.058 – 4.428); *Roxochelys* = 1.0869 (CI: -122.29 – 183.97)), characterizing positive allometries. The regression for “Peirópolis A” had a slope value of 0.43428 (CI: -0.227 – 0.666). Though this demonstrates a case of negative allometry, like in the regression obtained from the entire sample, the slope value is considerably lower.

Figure 9 – Negative allometric tendency of increase in shell thickness relative to increase in shell size, as demonstrated by a Robust linear regression obtained from the coordination of these two variables, in a sample of living and fossil podocnemidoids. Shell size values plotted in the abscissa and shell thickness plotted in the ordinate. Red asterisks represent specimens of "*Podocnemis*" *brasiliensis*, green circles represent *Bauruemys*, purple squares represent *Roxochelys*, filled blue triangles represent *bona fide* "Peirópolis A" and inverted hollow triangles represent indeterminate epiplastra from the Serra da Galga Member. Dashes represent recent species of *Podocnemis* (brown = *P. sextuberculata*; pale = *P. expansa*; yellow = *P. unifilis*), and the dark green column represents a specimen of *Peltocephalus*.



Source: Original image by the author.

Figure 10 – Different taxa of turtles from the Bauru Group showing different allometric tendencies of change in shell thickness relative to changes in shell size. Robust linear regressions obtained for each taxon group through the coordination of shell thickness and shell size variables. Shell size values plotted in the abscissa and shell thickness plotted in the ordinate. Symbols as in Figure 7.



Source: Original image by the author.

5 DISCUSSION

5.1 GEOMETRIC MORPHOMETRY OF EPIPLASTRA

The PCA resulted in a scheme that mostly reflects the current taxonomy of Bauru Group turtles, as clearly discernible in the biplot of the scores of the PC1 vs PC2 (Fig. 4). The PC1 shows a clear distinction between FFP PG 218 and “Peirópolis A”, with positive scorings, and *Bauruemys*, *Roxochelys* and the indeterminate epiplastra from the Serra da Galga Member, displaying negative values. The PC2 was effective at differentiating taxa that had negative scores in the PC1. *Bauruemys* and specimen MCT.R.2092 had negative or low positive scores, while *Roxochelys* and specimen CPPLIP-593 had high positive scores. The PC3 scores show a considerable overlap between specimens of different groups, but recover specimen CPPLIP-593 with a disparate value (-0.018827, the largest negative PC3 score in the sample), completely different from those of *Roxochelys* (0.070096 for MCT.R.1787 and for 0.028658 UFRJ-DG 404-R), with which it shares similar PC1 and PC2 scores.

As evidenced by the geometric morphometric analysis (Fig. 4 and 5), CPPLIP-593 and MCT.R.2092 are morphologically distinct from other epiplastra found in the Serra da Galga Member, which fit into the morphology of “Peirópolis A”, as outlined by Gaffney *et al.* (2011). CPPLIP-593 has a very wide gular and a posterior epiplastral projection, reminiscent of *Roxochelys*, while MCT.R.2092 has a narrow gular flanked by a long and narrow extragular that contacts the entoplastron, reminiscent of *Bauruemys*. Unsurprisingly, CPPLIP-593 had a PC2 score within the variation range for the scores of *Roxochelys*, and the scores of all three significant PCs of MCT.R.2092 fell within the range of *Bauruemys* specimens. Still, the indeterminate epiplastra from the Serra da Galga Member are not identical to these taxa. CPPLIP-593 has a smooth shell, different from the ornamented shell of *Roxochelys* (Price, 1953b), while MCT.R.2092 differs from *Bauruemys* in lacking a posterior epiplastral projection and an overlap between the epiplastron and the humeral scute (Suárez, 1969).

These two epiplastral morphotypes from the Serra da Galga Member differ clearly from other epiplastra found in the same beds, and though superficially similar to other taxa from the Bauru Group, they also differ from these forms. The origin and meaning of this morphological variation is presently unclear. It could be the result of a taxonomic distinction, but also of intra-specific variation. It is striking that both CPPLIP-

593 and MCT.R.2092 are medium-sized individuals, while the epiplastra of *bona fide* “Peirópolis A” are all remarkably large, close in size to or larger than the largest known individuals of *Bauruemys* and *Roxochelys*. This size distinction suggests that maybe there is some ontogenetic trend at play, and that the smaller and larger epiplastral morphotypes might represent individuals of different ages. However, discussions about the alpha-taxonomy and intra-specific variation of the Serra da Galga Member turtles fall outside the scope of the present work, and I will not delve into this matter here.

The deformation grids of the PCA analysis show that the two PCs that account for most of the variance within the sample both have an effect that is linked to changes in the width of the gular. Gular width has long been deemed a useful characteristic in pelomedusoid systematics (e.g., Broin, 1991; de la Fuente, 2003; Gaffney *et al.*, 2006, 2011), and is of particular interest for the alpha-taxonomy of the turtles of the Bauru Group. The type of *Roxochelys* has a remarkably wide gular (Price, 1953b), differing from the gulars of other pelomedusoids, which are usually narrower (Kischlat, 1995; Gaffney *et al.*, 2011). Kischlat (1995), working only with the type specimen of *Roxochelys*, suggested that the abnormal width of its gular could be an individual abnormality, rather than a diagnostic trait for the taxon. However, specimens that were later referred to *Roxochelys* also have wide gulars (Romano *et al.*, 2013; Bogado *et al.*, 2023), indicating that this trait is autapomorphic for this taxon (Gaffney *et al.*, 2011), and not the result of individual variation. The prominent effect of gular width in our analysis supports the usage of this characteristic in alpha-taxonomy.

5.2 LINEAR REGRESSION

Shell thickness has long been recognized as a trait of systematic importance in the alpha-taxonomy of South American pelomedusoids. Price (1953b) argued that the shell of *Roxochelys wanderleyi* was “very thick” (Price, 1953b, p. 32), and that this likened it to “*Podocnemis*” *harrisi* and the Argentinean species of “*Naiadochelys*” described by Staesche (1929) (currently recognised as chelids, see Broin, 1987 and Bona & de la Fuente, 2005). Price (1954) remarked that *Apodichelys lucianoi* Price, 1954 had a thick plastron, and Wood (1976) stated that the disproportionally thick shell of *Stupendemys geographicus* Wood, 1976 was possibly a diagnostic feature of this taxon. Arid & Vizotto (1966) assigned specimen GP-1350 to “*Podocnemis*” *brasiliensis* based on its thin shell, setting it apart from *Roxochelys* and *Apodichelys*.

In her description of ? *Roxochelys vilavilensis* (now *Lapparentemys vilavilensis*), Broin (1971) identified the species as a thick-shelled form, and listed *Apodichelys lucianoi*, "*Podocnemis*" *harrisi*, *Naiadochelys ingravata* Hay, 1908, Staesche's Patagonian "*Naiadochelys*" and *Roxochelys wanderleyi* as other thick-shelled pelomedusoids from the New World that were possibly related to the newly erected species. "*Podocnemis*" *brasiliensis* was identified as a thin-shelled form (Broin, 1971, p. 449-450). Broin (1991) again explored shell thickness in a taxonomic context, and considered it to be a diagnostic trait of her "*Roxochelys* group", containing (from thickest to thinnest) ? *Roxochelys vilavilensis* (now *Lapparentemys vilavilensis*), ? *Roxochelys elegans* (now *Bauruemys elegans*) and *Roxochelys wanderleyi*. "*Podocnemis*" *brasiliensis* and "*Podocnemis*" *argentinensis* were considered unthickened forms, closer to recent *Podocnemis*. de la Fuente (1993) followed the proposal by Broin (1991), and furthermore stated that the "Río Colorado form" had a thin shell, closer to that of "*P.*" *brasiliensis* and "*P.*" *argentinensis*.

Kischlat (1994a) and Kischlat et al. (1994) also explored shell thickness in a taxonomic context, but reached conclusions different to those of Broin (1971, 1991). This author stated that the genus *Roxochelys* (including *Roxochelys wanderleyi* and an undescribed species) had a thick shell, while the genus *Bauruemys* (including the species *Bauruemys elegans* and *Bauruemys brasiliensis*) had a thinner shell, comparable to that of recent *Podocnemis* (Kischlat, 1994a; Kischlat et al. 1994). Kischlat (1995) made a similar statement, but remarked that only small specimens of *Bauruemys elegans* had thin shells, while large individuals had thick shells similar to those of *Roxochelys*. Kischlat (2015) again used shell thickness as a basis for taxonomic decisions, claiming that an expressively thickened plastron was a diagnostic feature for a new genus uniting "*Podocnemis*" *harrisi* and a supposed new species of Podocnemididae from the Bauru Group.

After the works of Broin (1971, 1991) and Kischlat (1994a), the usage of shell thickness in taxonomic studies of fossil Pelomedusoides from South America decreased. Menegazzo (2009) used shell thickness as a diagnostic characteristic in her Master's degree dissertation, but this feature was dropped in the published version of her work (Menegazzo *et al.*, 2015). Gaffney *et al.* (2011) mostly avoided the topic of shell thickness, but did diagnose *Lapparentemys vilavilensis* as a species with a "relatively thick, elongate shell" (Gaffney *et al.*, 2011, p. 24). Romano *et al.* (2009, 2013) were apparently the first to criticize the usage of shell-thickness as a diagnostic feature for identifying the Bauru Group turtles, noting that thickness increased proportionally to shell length, and that differences in shell thickness were more likely explained by ontogenetic changes and taphonomic processes than by taxonomy (Romano *et al*., 2009, p. 143, Romano *et al*., 2013, p. 272-273).

It was not possible to test whether "*Podocnemis*" *brasiliensis* is a thin-shelled form in this study, as the limited amount of available specimens (*n* = 2) makes it impossible to calculate a separate regression of shell size vs shell thickness for this species. Therefore, it was not possible to compare the proportional thickness of the shell of "*P.*" *brasiliensis* to that of other Bauru Group turtles, or to the regression obtained from all sampled Podocnemidoidae. A visual inspection of the placement of the two specimens of "*P.*" *brasiliensis* in the size vs thickness biplot did not help with this issue either. Specimen FFP PG 218 has a similar width to specimens of *Bauruemys* with a similar size, being plotted very close to the regression line for this genus (Fig. 10). Yet, MCT.R.214 – the type of *P. brasiliensis* – is proportionally thicker, being plotted very near to the *Roxochelys* regression instead (Fig. 10). These results are consistent with the observations of previous authors, which have reported the existence of smaller specimens with relatively thinner shells and larger ones with thicker shells (Kischlat, 1995; Romano *et al*., 2013).

Though results concerning "*Podocnemis*" *brasiliensis* were not conclusive, the regression demonstrated that *Roxochelys* is generally thicker than other podocnemidoids of similar size, especially *Bauruemys* (Figs. 9 and 10). The regression obtained from *Roxochelys* has a similar slope (1.0869) to that of *Bauruemys* (1.1394), yet the shell thickness values of the former are considerably higher than those of the latter (Fig. 10). This can be interpreted as evidence that *Roxochelys* has a thicker shell in relation to *Bauruemys*, confronting the suggestion of Broin (1991) and supporting that of Kischlat (1994a).

Still, it should be noted that some specimens of *Bauruemys* (LPRP USP 0457, LPRP 0730 and MCT.R.2101) are proportionally thicker than expected from the regression obtained from this taxon, being plotted closer to the regression line for *Roxochelys* (Fig. 10). Similarly, the type specimen of Roxochelys (MCT.R.216) is exceedingly thick, standing out from other individuals of this taxon (Fig. 10). Thus, it is possible to conclude that, even though proportional shell thickness can be used as a diagnostic characteristic in alpha-taxonomy, it is subject to significant intra-specific variation, and should be used with caution. It would be prudent to consider this feature in a diagnosis only when combined with other, more informative morphological characteristics, and never as a “standalone” diagnostic trait.

All regressions obtained in this study had slope values close to 1, and the confidence intervals for all regressions except that of the “Peirópolis A” subset included number 1 in them, so that isometry could not be ruled out. This indicates that, though the increase in shell thickness relative to shell size in pelomedusoids is allometric, this allometry is relatively subtle, and not much different from isometric growth.

5.3 IDENTITY OF FFP PG 218

The outer rim of the epiplastron in FFP PG 218 forms a subtle rounded lip. In the type of “*Podocnemis*” *brasiliensis*, as well as in *Roxochelys*, *Lapparentemys* and “Peirópolis A” this lip tends to be more pronounced, more so in the latter two taxa (Gaffney *et al*., 2011). In *Bauruemys*, as well as in recent representatives of the genus *Podocnemis*, the outer rim of the anterior lobe ends in an angular edge rather than a rounded lip (Gaffney *et al*., 2011). Though the lip in FFP PG 218 is rather feeble, it does compare more closely to taxa with thicker lips than with those that have an angular plastral border.

FFP PG 218 shows a strongly developed process in the postero-lateral extremity of its epiplastron, with a pointed triangular shape. A comparable projection, visible in dorsal view, can be seen in *Bauruemys*, *Roxochelys* and the type of “*Podocnemis*” *brasiliensis*, though in the latter this structure is not as developed as in the two former taxa (Gaffney *et al*., 2011). In MHNC 6904, a shell from Tiupampa attributed by Broin (1991) to *Lapparentemys* but interpreted by Gaffney *et al*. (2011) as an indeterminate Podocnemidoidae, there are projections as developed as those of FFP PG 218, *Bauruemys* and *Roxochelys*. In other specimens of *Lapparentemys* (MNHN VIL-3 and RM 20.5155), as well as in *Puentemys mushaisaensis* Cadena *et al*., 2012b and the “Los Cuervos form”, a faint projection is visible, but it is very subtle, way more than in any of the aforementioned taxa (Broin, 1971, 1991; Cadena & Schweitzer, 2014; Cadena *et al*., 2012b; Gaffney *et al*., 2011). In all but one of the epiplastra from the Serra da Galga Member that I have seen, as well as in *Gestemys powelli* de la Fuente *et al*., 2022 and “Cerrejón B”, these processes are absent, and the sutures between the epi- and hyoplastra are straight and/or sinuous in both dorsal and ventral views (Cadena *et al*., 2012a; de la Fuente *et al*., 2022; Rogério *et al*., 2013).

FFP PG 218 does not have a preserved entoplastron. However, the left sutural contacts of this bone are discernible in the preserved epi- and hyoplastron, and evince that the anteriormost tip of the entoplastron had a sub-rectangular projection in dorsal view. A comparative assessment of different specimens from distinct taxa demonstrates that the morphology of this region of the entoplastron varies greatly in podocnemidoids from the Late Cretaceous and Palaeogene of South America. A sub-rectangular or trapezoidal projection, like the one in FFP PG 218, may be present (*Bauruemys* – LPRP USP 0730-B/C, MCT.R.1981-C, MZSP-PV 137; *Roxochelys* – MCT.R.216, UFRJ-DG 404-R; *Lapparentemys* – MHNC 6904) or absent (*Bauruemys* – LPRP USP 0457, MCT.R. 1981-E, MZSP-PV 136; *Roxochelys* – MCT.R.1722, MCT.R.1787; *Lapparentemys* – MNHN VIL-3, RM 20.5155) in different specimens of a same species (Price, 1953b; Broin, 1971, 1991; Matiazzi, 2007; Bogado *et al.*, 2023; personal observation). Given the expressive intraspecific variation exhibited by this feature, it appears to be of little interest for taxonomic discussions.

The posterior part of the entoplastron also varies greatly in shape. In dorsal view, the posterior moiety of the entoplastron in FFP PG 218 is longer and more pointed than the anterior half. In all specimens of *Bauruemys* that I have seen, the dorsal face of the entoplastron has this same morphology, while *Roxochelys*, the type of "*Podocnemis*" *brasiliensis* and "Peirópolis A" have entoplastra that are divided in two roughly equidimensional moyeties (Price, 1953b; Suárez, 1969; Matiazzi, 2007; Ferreira, 2011; personal observation). Despite this apparently clear separation among the Bauru taxa, specimens of *Lapparentemys* figured in the literature showcase both morphologies (longer posterior half – MHNC 6904, MNHN VIL-3; equidimensional halves – RM 20.5155), indicating that this difference may not be as clear-cut as it may seem at first glance (Broin, 1971, 1991). Gaffney *et al.* (2009) also presented expressive variation in the entoplastra of Bothremydini from the Late Cretaceous of North America (Gaffney & Zangerl, 1968; Gaffney *et al.*, 2009), and I have observed an expressive degree of variability in the entoplastra of recent *Podocnemis* (personal observation). This leads me to consider this variation in the shape of the dorsal surface of the entoplastron as uninformative for the purposes of taxonomy.

In ventral view, the entoplastron of FFP PG 218 does not reach the level of the axillary notch of the bridge. In this, it agrees morphologicaly with *Bauruemys*, *Roxochelys*, the type of "*Podocnemis*" *brasiliensis*, the "Santo Anastácio form", the "Río Colorado form", *Portezueloemys patagonica* de la Fuente, 2003, "*Podocnemis*" *argentinensis* Cattoi & Freiberg, 1958 and “Cerrejón B” (Cattoi & Freiberg, 1958; de la Fuente, 1993, 2003; Cadena *et al.*, 2012a; Romano *et al.*, 2013; Menegazzo *et al.*, 2015), but differs from *Lapparentemys*, *Puentemys*, *Gestemys* and “Peirópolis A”, where the entoplastron extends past the axillary notch posteriorly (Broin, 1971, 1991; Cadena *et al.*, 2012b; Rogério *et al.*, 2013; de la Fuente *et al.*, 2022).

The hyoplastron of FFP PG 218 preserves a small postero-lateral sutural contact for articulation with a small, lateralized mesoplastron, excluded from the midline. The presence of small and rounded mesoplastra that do not meet in the midline is a diagnostic feature of the Pelomedusoides, being present in nearly all representatives of the group, to the exception of the African genus *Pelusios*, where these plates become secondarily reunited at the midline (Gaffney *et al.*, 2006). FFP PG 218 also preserves a strongly developed and verticalized axillary process, showing that the shell bridge would have been dorso-ventrally high and antero-posteriorly long. This is a common feature among representatives of the clade Pan-Podocnemididae, formed by the lineages Bothremydidae and Podocnemidoidae (Lapparent de Broin, 2000). Though the actual height of the shell may vary within the group, the bridge maintains its relatively large size even in forms with flattened shells, such as the Bothremydini (Gaffney *et al.*, 2006).

The extragular in FFP PG 218 is short, and does not reach the entoplastron posteriorly. This is also the case in most continental pelomedusoids from the Late Cretaceous and Palaeogene of South America, to the exception of *Bauruemys* and *Lapparentemys*, where the extragulars tend to extend into the entoplastron (though in the former taxon this might vary) (Gaffney *et al.*, 2011).

FFP PG-218 has a narrow gular, like *Bauruemys, Lapparentemys*, *Portezueloemys* and the “Río Colorado form” (de la Fuente, 1993, 2003; Gaffney *et al.*, 2011). *Roxochelys*, *Gestemys*, “*Podocnemis*” *argentinensis*, *Puentemys* and “Cerrejón B” have a wider gular (Cattoi & Freiberg, 1958; Cadena *et al.*, 2012a, 2012b; de la Fuente *et al.*, 2022; Bogado *et al.*, 2023). In most epiplastra from the Serra da Galga Member, interpreted as representing “Peirópolis A”, the gular is rather wide at mid-length, but becomes narrower anteriorly due to a medial inflection of the gulo-extragular sulcus (Rogério *et al.*, 2013). This makes the anterior width of the gular in “Peirópolis A” narrower than or subequal to that of the extragulars, as stated by Gaffney *et al.* (2011, p. 203). The width of the gular in the type of “*Podocnemis*” *brasiliensis* is unkown, as the epiplastra of this specimen are mostly missing (Staesche, 1944).

Judging from the angulation of the gulo-humeral sulcus in the epiplastron of FFP PG 218, the gular would only have occupied a small area at the anterior tip of the entoplastron. In *Roxochelys*, the type of "*Podocnemis*" *brasiliensis*, the "Santo Anastácio form", *Portezueloemys*, the "Río Colorado form", "*Podocnemis*" *argentinensis*, *Puentemys* and all entoplastra from the Serra da Galga Member that I have seen, the gular is also restricted to the anterior portion of the entoplastron (Staesche, 1944; Cattoi & Freiberg, 1958; de la Fuente, 1993, 2003; Cadena *et al.*, 2012b; Rogério, 2013; Menegazzo *et al.*, 2015; Bogado *et al.*, 2023; personal observation). Meanwhile, in *Gestemys* and "Cerrejón B" the enlarged gular occupies all the anterior half of the entoplastron (Cadena *et al.*, 2012a; de la Fuente *et al.*, 2022).

In *Lapparentemys* and *Bauruemys*, the posterior extent of the gular is variable. Most figured specimens of *Lapparentemys* have a gular that is restricted to the anteriormost part of the entoplastron, as in most continental pelomedusoids from the Late Cretaceous and Palaeogene of South America (Broin, 1971, 1991). However, in MHNC 6902 – a small shell categorized by Broin (1991, p. 511) as "a nearly hatchling specimen" – the gular is elongated, extending onto the middle of the entoplastron (Broin, 1991). In *Bauruemys*, the posterior end of the gular tends to be acutely tapered, elongating the scute so it reaches the middle of the entoplastron (e.g., LPRP USP 402, MCT.R.1492; MCT.R.1891-E, PUC RCL 101). However, some specimens have a shorter gular, that does not occupy the entire anterior half of the plate (e.g., IG 317-V; LPRP USP 730A, MCT.R.1891-B, MZSP-PV 136) (Suárez, 1969; Matiazzi, 2007; personal observation). This variation suggests the length of the gular-entoplastron overlap might not be taxonomically informative among the Podocnemidoidae.

The pectoral scute only overlaps the ento- and hyoplastra in FFP PG 218, but its humero-pectoral sulcus is antero-laterally deflected, nearly reaching the epiplastron. In this it resembles the type of "*Podocnemis*" *brasiliensis* and the "Santo Anastácio form", whose humero-pectoral sulci either come very close to touching the epi-hyoplastral suture or actually do have a punctual contact with the epiplastra. This morphology seems to be intermediate between taxa with posteriorly located sulci, like *Roxochelys*, "Peirópolis A", *Portezueloemys*, the "Río Colorado form" and *Puentemys* (Cadena *et al.*, 2012b; de la Fuente, 1993, 2003; Gaffney *et al.*, 2011; Price, 1953b), and those with anteriorly displaced sulci, such as *Bauruemys*, "*Podocnemis*" *argentinensis*, *Gestemys*, *Lapparentemys* and "Cerrejón B" (Broin, 1971; Cadena *et al.*, 2012a; Cattoi & Freiberg, 1958; de la Fuente *et al.*, 2022; Suárez, 1969).

Since the gular appears to have occupied only the anterior tip of the entoplastron in FFP PG 218, and the humero-pectoral sulcus crosses into the entoplastron at a rather posteriorly displaced position, it can be inferred that the humerals would have had a long midline contact in this specimen. A long interhumeral sulcus is present in *Roxochelys*, the type of "*Podocnemis*" *brasiliensis*, the "Santo Anastácio form", *Portezueloemys*, the "Río Colorado form", "*Podocnemis*" *argentinensis*, *Puentemys* and all entoplastra from the Serra da Galga Member that I have seen (Staesche, 1944; Cattoi & Freiberg, 1958; de la Fuente, 1993, 2003; Cadena *et al.*, 2012b; Rogério *et al.*, 2013; Menegazzo *et al.*, 2015; Bogado *et al.*, 2023; personal observation). The anterior displacement of the pectorals and, to a lesser extent, the lengthening of the gular led to a considerable shortening of the interhumeral sulcus in *Bauruemys* and *Lapparentemys* (Suárez, 1969; Broin, 1971, 1991; Gaffney *et al.*, 2011). In *Gestemys* and "Cerrejón B" this sulcus is altogether absent, and the enlarged gular completely separates the humerals (Cadena *et al.*, 2012a; de la Fuente *et al.*, 2022).

The pectoro-abdominal sulcus in FFP PG 218 does not reach the mesoplastron posteriorly. The same condition is observed in *Roxochelys*, the "Santo Anastácio form", *Portezueloemys*, "*Podocnemis*" *argentinensis*, *Gestemys* and "Cerrejón B" (Cattoi & Freiberg, 1958; Cadena *et al.*, 2012a; de la Fuente, 2003; Menegazzo *et al.*, 2015; de la Fuente *et al.*, 2022; Bogado *et al.*, 2023). *Bauruemys*, *Elkanemys pritchardi* Maniel *et al.* 2021, *Lapparentemys* and *Puentemys* also tend to have an anteriorly displaced pectoro-abdominal sulcus, but in a few specimens there may be a punctual contact (*Bauruemys* – MCT.R.2103; *Elkanemys* - MMCH-Pv 73; *Puentemys* – UF/IGM 55, UF/IGM 60) or even a small overlap (*Lapparentemys* – WUS 2160; *Puentemys* – MAS-002) between the pectoral scute and the mesoplastron (Gaffney *et al.*, 2011; Cadena *et al.*, 2012b; Maniel *et al.*, 2021; personal observation). In "Peirópolis A" (MCT.R.321, MCT.R.1499 and MCT.R.1890), the pectoro-abdominal sulcus takes a strongly inflexed posterior turn, crossing onto the mesoplastron and occupying a considerable part of the antero-lateral extremity of the plate (Gaffney *et al.*, 2011; personal observation). However, in many isolated mesoplastra from the Serra da Galga Member (CPPLIP 498, CPPLIP-513, MCT.R.2104, MCT.R.2105 and MCT.R.2106), as well as in the type of *Cambaremys*, there is no trace of the pectoro-abdominal sulcus, indicating this sulcus must have occupied a more anterior position in these specimens (França & Langer, 2005; personal observation).

FFP PG 218 bears a conspicuous surface ornamentation, matching the pelomedusoid ornamentation identified by Broin (1977). This morphology – widespread among the Pelomedusoides and also observed in some Chelidae – is present in several fossil forms from the Upper Cretaceous and Palaeogene of South America, including the type of “*Podocnemis*” *brasiliensis*, “Peirópolis A”, the “Río Colorado form”, “*Podocnemis*” *argentinensis*, *Lapparentemys* and the “Los Cuervos form” (Price, 1953b; Cattoi & Freiberg, 1958; Broin, 1971; de la Fuente, 1993; Gaffney *et al.*, 2011; Cadena & Schweitzer, 2014). The type of *Cambaremys*, though identified by França & Langer (2005) as lacking ornamentation (França & Langer, 2005, p. 396), is actually covered in conspicuous grooves that match the pelomedusoid ornamentation. Though this decoration is not visible in the published photos of the specimen, they are plainly visible to the naked eye, as I could see during my personal assessment of the specimen (personal observation). *Puentemys*, also originally described as unornamented (Cadena et al., 2012b, p. 692), has been recently shown to bear the typical pelomedusoid ornamentation (Cadena *et al.*, 2024, p. 160, Fig. 3).

Roxochelys has a characteristic pattern of ornamentation, which appears to be a more accentuated version of the widespread pelomedusoid pattern (Broin, 1991; Gaffney *et al.*, 2011). In this taxon the ornamental grooves are deeper and wider than in other ornamented pelomedusoids, anastomosing throughout the entire shell, rather than in only a few isolated areas (Price, 1953b). *Bauruemys*, *Elkanemys* and *Gestemys*, to the contrary, are truly smooth-shelled forms, with a plain, featureless surface texture (Gaffney *et al.*, 2011; Maniel *et al.*, 2021; de la Fuente *et al.*, 2022). In a few *Bauruemys*, such as GP/2E – 341, GP/2E – 344 and MZUFV-P 23, it is possible to see sparse and very small grooves, rarely branching, that resemble the ornamental grooves of other pelomedusoids (personal observation). This could indicate that, at least in *Bauruemys*, the smoothness of the shell is a secondary modification of the original pelomedusoid pattern.

FFP PG 218 can be differentiated from nearly all fossil pelomedusoids known from continental Upper Cretaceous and Palaeogene strata of South America, to the exception of “*Podocnemis*” *brasiliensis*. The new specimen is virtually indistinguishable from the type of “*P.*” *brasiliensis* – MCT.R.214. The two plastra agree in nearly all morphological details that are preserved in both, the only differences being the shape of the epi-hyoplastral suture in ventral view (strongly sinuous in FFP PG 218; straighter in MCT.R.214) and the posterior end of the entoplastron (long and narrow in FFP PG

218; shorter and wider in MCT.R.214). However, these anatomical differences are subtle, and after my personal exhamination of several recent and fossil podocnemidoid specimens, I have observed that they fall within the range of intra-specific variation that is known to occur in representatives of this lineage. As FFP PG 218 and MCT.R.214 cannot be convincingly differentiated, it is reasonable to attribute the new specimen to "*Podocnemis*" *brasiliensis*. This assignment expands our knowledge about the anatomy of this taxon, allowing an amendment of its specific diagnosis.

5.4 SYSTEMATIC PALAEONTOLOGY

Testudines Batsch, 1788
Pleurodira Cope, 1864
Pelomedusoides Broin, 1988
Pan-Podocnemididae Joyce et al., 2004
Podocnemis Wagler, 1830
"*Podocnemis*" *brasiliensis* Staesche, 1937

Synonymy: *Podocnemis brasiliensis* Staesche, 1937
Podocnemis brasiliensis Staesche, 1937 (*sensu* Price, 1953b)
Bauruemys brasiliensis (Staesche, 1937) (*sensu* Kischlat, 1994a)

Type specimen: MCT.R.214, a partial plastron preserving parts of the epi-, hyo- hypo- and xiphiplastra, with missing parts filled in with plaster.

Type locality: Railway cut between kilometres 101 and 104 of the Araçatuba-Jupiá branch of the Noroeste do Brasil Railway. Municipality of Mirandópolis, state of São Paulo, Brazil. Not municipality of Araçatuba, as in Bertini *et al*. (1993), Romano (2006), Oliveira & Romano (2007), Romano *et al*. (2009), Ferreira (2011) and Rogério *et al*. (2013).

Horizon and age: Adamantina Formation, Bauru Group, Paraná Basin. Late Cretaceous (late Campanian – early Maastrichtian *sensu* Pinheiro *et al*., 2018). Not Araçatuba Formation, as in Menegazzo (2009) and Menegazzo *et al*. (2015).

Referred material: FFP PG 218, a fragmentary plastron consisting of a right epiplastron and a right hyoplastron, found in close association.

Distribution: Late Cretaceous of the state of São Paulo, Brazil.

Emmended diagnosis: "*Podocnemis*" *brasiliensis* can be diagnosed as a member of ther Pleurodira because of the fusion between its pelvic girdle and shell, and as a member of the Pelomedusoides due to the presence of paired mesoplastra that do not meet in the midline, instead occupying a lateral position in the plastron. It is recognized as a representative of the Pan-Podocnemididae owing to its elongated and high plastral bridge.

"*Podocnemis*" *brasiliensis* can be distinguished from other Pan-Podocnemididae due to the combination of the following characteristics: (1) shell surface with ornamentation composed of dichotomously branching shallow grooves, which may locally anastomose into an interconnected network ("pelomedusoid ornamentation" *sensu* Broin, 1977); (2) extragular scutes restricted to the epiplastra; (3) gular scute relatively narrow; (4) long midline contact between humeral scutes; (5) humero-pectoral sulcus departs from the midline at a posterior position, but progresses antero-laterally so as to nearly contact or slightly overlap the epiplastra; (6) pectorals reach entoplastra but not mesoplastra.

Discussion: As previous authors have often noted, the type plastron of "*Podocnemis*" *brasiliensis* is, by itself, inadequate for the definition of a valid taxon (Wood & Díaz de Gamero, 1971; Gaffney *et al.*, 2011; Romano *et al.*, 2013). Though it does feature a few characteristics that help differentiate it from other Bauru Group shell taxa, it shows no autapomorphies, and its unique combination of features could be interpreted as individual variation in an aberrant specimen. However, the finding of a second individual – identical to the type in their shared morphology, but preserving novel anatomical information – adds strength to the idea that the type of "*P.*" *brasiliensis* is truly the representative of a distinct, objectively identifiable taxon, and not some fragmented anatomical oddball.

Some of the anatomical characteristics that were originally used to identify "*Podocnemis*" *brasiliensis* are indeed unfit to diagnose a species. Some of these, such as the shape of the entoplastron and of the anal notch, are subject to such intra-specific variation that they are rendered useless for alpha-taxonomy (Wood & Díaz de Gamero, 1971; Wood, 1995; Gaffney et al., 2009; Guerrero & Pérez-García, 2021a). Others, such as the presence of small extragulars separated by a larger gular, are plesiomorphic traits, widespread among the pelomedusoids (Gaffney et al., 2006). Still, the type plastron of "*P.*" *brasiliensis* does preserve a few characteristics that help in its diagnosis, such as its classic "pelomedusoid ornamentation", extragulars restricted to epiplastra and long interhumeral sulcus. When combined with the new characteristics preserved in FFP PG 218 (a narrow gular, pectoral scutes that do not contact the mesoplastra), these traits can be used to make a differential diagnosis that sets "*P.*" *brasiliensis* apart from other, well-defined pelomedusoid taxa, especially those from the Bauru Group.

While the species *brasiliensis* appears to be valid, the issues of its generic assignment and phylogenetic position are still unresolved. As demonstrated by Wood & Díaz de Gamero (1971) and Kischlat (1994a), this species is clearly not a representative of the genus *Podocnemis*, agreeing with the argumentation by Wood (1984) that *Podocnemis* originated in the Cenozoic, and that the assignment of Cretaceous species to this genus is invalid. The large entoplastron, long interhumeral contact and pectoral scute with a feeble or absent overlap onto the epiplastron all preclude the inclusion of "*Podocnemis*" *brasiliensis* in *Podocnemis*. The inclusion of this species in the genus *Bauruemys* is not well founded either. The species *brasiliensis* differs from *Bauruemys elegans* – the type and only confidently assigned species of the genus *Bauruemys* – in nearly all of its diagnostic characteristics, and a preliminary phylogenetic analysis does not recover the two as being particularly close. A third possibility, implied (but not formally proposed) by both França & Langer (2005) and Menegazzo *et al.* (2015), is that the species *brasiliensis* belongs in the genus *Cambaremys*, through synonymy with its type species, *Cambaremys langertoni*. While less unlikely than the two former generic assignments, this taxonomic decision is also problematic, as discussed in the following sub-chapter.

Given that the species *brasiliensis* seems to fit into none of the genera to which it has been assigned in the past, proposing a new generic attribution would be adequate. Moving it into a pre-existing genus seems unfit, as preliminary phylogenetic analyses have been unable to confidently ascertain its phylogenetic position. This leaves the possibility of creating a new genus for housing this species, but I am hesitant with this alternative. As Romano et al. (2009, 2013) have previously remarked, the taxonomy of the Testudines of the Bauru Group is unnecessarily inflated, with several taxa based on fragmentary and undiagnostic shell remains. Recent years have seen this scenario grow more complex with the proposal of four new taxa based on isolated skulls (Gaffney *et al.*, 2011; Ferreira *et al.*, 2018; Hermanson *et al.*, 2020), which could potentially be synonymous with some of the previously defined shell-only taxa. While the erection of a new generic name is entirely possible, I believe that creating a new genus for *brasiliensis* would only bring further confusion to the already confusing taxonomic history of Bauru Group turtles.

Considering these issues, I prefer not to propose a new generic attribution for the species *brasiliensis* until better material is known. Instead, I opt to refer to this taxon as "*Podocnemis*" *brasiliensis*, with the generic name between quotation marks. This retains the original combination used by Staesche (1937) and Price (1953b), without supporting any of the subsequent generic assignments. Still, the quotation marks make it clear that the attribution of this species to *Podocnemis* is problematic, and that "*P.*" *brasiliensis* should not be understood as a true member of this genus.

5.5 DUBIOUS RECORDS OF "*Podocnemis*" *brasiliensis*

5.5.1 MCT.R.233 (Staesche, 1937)

The original type material of "*Podocnemis*" *brasiliensis* contained three fragmentary specimens – an incomplete plastron (MCT.R.214), an anterior carapace fragment (MCT.R.216) and a fragment from the middle-left portion of a carapace (MCT.R.233). In his revision of this sample, Price (1953b) maintained MCT.R.214 as the type of "*P.*" *brasiliensis*, but used specimen MCT.R.216 to erect a new taxon – *Roxochelys wanderleyi*. MCT.R.233 was briefly treated by Price, who identified it as a possible pleurodiran that was not confidently associated with either of the other specimens (Price, 1953b). Even though MCT.R.233 was explicitly removed from the hypodigm of "*P.*" *brasiliensis* by Price (1953b, p. 11-12), some subsequent authors seem to have ignored this. Wood & Díaz de Gamero (1971) included this specimen in their definition of "*P.*" *brasiliensis*, and Kischlat (1994a) stated that Price (1953b) had "ignored" MCT.R.233, and that this specimen should be regarded as the paralectotype of "*P.*" *brasiliensis* (Kischlat, 1994a, p. 348).

The possibility that MCT.R.233 and the type plastron of "*Podocnemis*" *brasiliensis* (MCT.R.214) represent the same taxon (or even the same individual) arises from their possible association in the field, as both were found in a 4 km stretch of railroad in the municipality of Mirandópolis, during the same field campaign (Price, 1953b). Two main sources inform us about the provenance of these fossils: a technical report written by the geologist who collected them (Wanderley, 1936) and the collection records at the MCTer. In the report, Wanderley (1936) identifies four main railroad cuts from which fossil material was collected in Mirandópolis. While the text is rather vague about the fossil finds, it makes reference to an articulated set of three costal plates from the posterior left side of the shell, found in a railroad cut at Km 104 (Wanderley, 1936, p. 107, 109-110). While Wanderley (1936) gives no collection number for these plates, his description fits MCT.R.233, and I believe he is referring to this specimen.

To pinpoint the provenance of MCT.R.214, it is necessary to look at the records of the MCTer. Both the catalog of the old "*Collecção Padrão*", in which the specimen was originally deposited, and the catalog of the Fossil Reptile collection, in which it is currently included, state that MCT.R.214 comes from a railroad cut at Km 102.5 of the Araçatuba-Jupiá railroad branch – a site different from that of MCT.R.233. Thus, we can discard the idea that these two specimens were found associated in the field. It is worth mentioning that there is an old identification tag for specimen 214 that had the number "214 crossed in pencil and the number "233" written over. This tag, now stored with MCT.R.233, has Km 102.5 as the collection site. Though the data on this tag is seemingly contradictory, it seems clear that the information refers to specimen MCT.R.214 – the type plastron, and not MCT.R.233 – the posterior carapace fragment.

Direct morphological comparison between the carapace of MCT.R.233 and "*Podocnemis*" *brasiliensis* is impossible, because this species is known only from plastral remains. The only characteristic the two share is the ornamentation of the shell surface, as MCT.R.233 is covered in the same shell texture as "*P.*" *brasiliensis* and "Peirópolis A" – the pelomedusoid ornamentation of dichotomously branching grooves that rarely anastomose (Broin, 1977; Gaffney *et al.*, 2011). This differs from *Bauruemys*, which has an unornamented shell (Gaffney *et al.*, 2011), and *Roxochelys*, whose ornamentation is far more developed (Bogado *et al.*, 2023; Gaffney *et al.*, 2011; Price, 1953b). MCT.R.233 further differs from *Roxochelys* is that the former has a relatively small, medio-laterally narrow inguinal scar, while in the latter this scar reaches much farther laterally (Bogado *et al.*, 2023; Gaffney *et al.*, 2011).

Though the anatomy of MCT.R.233 does not preclude an attribution to "*Podocnemis*" *brasiliensis*, I believe the available evidence does not allow a confident taxonomic assignment. The purported association of this specimen with the type plastron is not supported, and the only characteristic shared by the two fragments – the pelomedusoid ornamentation – is a widespread trait among the Pelomedusoides, insufficient to establish a species level identification. Thus, I believe MCT.R.233 is best regarded as an indeterminate turtle, as previously suggested by Price (1953b).

5.5.2 GP-1350 (Arid & Vizotto, 1966)

Another carapace that has been attributed to "*Podocnemis*" *brasiliensis* is GP-1350, a juvenile individual collected in the municipality of São José do Rio Preto. Like in the case of MCT.R.233, direct comparison with "*P.*" *brasiliensis* is limited to shell ornamentation, as only the carapace is preserved in GP-1350. According to the original description, GP-1350 has an ornamentation composed of "very fine sulci that branch out, sometimes anastomosing" (Arid & Vizotto, 1966, p. 424), which would be in agreement with the morphology of "*P.*" *brasiliensis*, *Cambaremys* and "Peirópolis A". The seventh costal appears to be antero-posteriorly short and to have contacted only the 9th peripheral, showing further similarities with *Cambaremys* and "Peirópolis A". GP-1350 can be clearly differentiated from *Bauruemys* owing to its sub-rectangular first neural and ornamented shell (Suárez, 1969; Gaffney *et al.*, 2011). Judging from the figures in Arid & Vizotto (1966), it appears that the inguinal scars of GP-1350 would not have been projected far medially onto costals 5. This, together with the feeble ornamentation, differentiates this carapace from *Roxochelys* (Gaffney *et al.*, 2011).

While GP-1350 can be differentiated from *Bauruemys* and *Roxochelys*, and apparently had the same shell ornamentation pattern as "*Podocnemis*" *brasiliensis*, this does not justify an attribution to the latter species. As stated previously, the pelomedusoid ornamentation is widespread among the Pelomedusoides, and is also present in *Cambaremys* and specimens of the informal morphotype "Peirópolis A", both from the Serra da Galga Member of the Marília Formation (Gaffney *et al.*, 2011). Interestingly, GP-1350 also resembles "Peirópolis A" and *Cambaremys* in having a notably short costal 7. While I believe that an attribution to either of these taxa is as unfounded as an attribution to "*P.*" *brasiliensis*, the similarities are noteworthy. Still, for the time being, I believe GP-1350 is best regarded as an indeterminate pelomedusoid.

5.5.3 Peirópolis material (Broin, 1991)

Broin (1991) and Lapparent de Broin (2000), followed by de la Fuente (1993), have suggested that some of the material from the locality of Peirópolis could belong to "*Podocnemis*" *brasiliensis*, namely some "very large pieces of shell" (Broin, 1991, p. 515), "large vertebrae with linked postzygapophyses" and a "large posterior skull" collected in 1958 (Lapparent de Broin, 2000, p. 72). This latter skull corresponds to

MCT.R.1498, the type of *Pricemys caiera*, a species known only from cranial remains (Gaffney *et al.*, 2011; Rogério *et al.*, 2013). The “large vertebrae” could be a reference to a cervical sequence belonging to MCT.R.321 – material which has unfortunately been lost in the 2018 fire of the Museu Nacional (Thiago Fiorillo Mariani, 2023, personal communication). Due to the lack of overlapping anatomical parts, no comparison can be made between these fossils and the hypodigm of “*P.*” *brasiliensis*.

The “large pieces of shell” represent a different problem, and it is appropriate to explain the situation of the Peirópolis shell material before discussing this issue. Since the middle of the XXth Century, thousands of fossils have been retrieved from the municipality of Uberaba, in the state of Minas Gerais (Price, 1951, 1955; Bertini *et al.*, 1993; Ribeiro & Carvalho, 2009). Most of these hail from quarries in the district of Peirópolis, where strata of the Maastricthian Serra da Galga Member of the Marília Formation crop out. Additional material, also belonging to the Serra da Galga Member, has been recovered from the Serra da Galga range, located to the Northwest of Peirópolis, as well as other sites in neighbouring areas (Bertini *et al.*, 1993; Ribeiro & Carvalho, 2009). These localities have yielded a rich fossil assemblage, in which turtles are particularly abundant (Price, 1951, 1955; França & Langer, 2005; Gaffney *et al.*, 2011; Rogério *et al.*, 2013; Hermanson *et al.*, 2017). However, to the exception of a few specimens (namely MCT.R.321, MCT.R.1499, MCT.R.1890, MCT.R.2100 and CPPLIP-252), all of these remains are isolated and disarticulated fossils, mostly shell plates. The fragmentary nature of the sample makes studying the Testudines of the Serra da Galga Member a challenging task.

To my knowledge, only four scientific collections contain turtle fossils from the Serra da Galga Member. The first specimens collected in the Serra da Galga Member outcrops in Uberaba are now deposited in the collections of the former *Instituto Geográfico e Geológico de São Paulo* (IGG) (now *Instituto de Pesquisas Ambientais* (IPA)) (personal observation), and Menegazzo (2009) mentions material in the *Museu de Paleontologia e Estratigrafia “Prof. Dr. Paulo Milton Barbosa Landim”* (MPE). However, these collections have only a few, fragmentary specimens, and none of these remains have been described or figured in published palaeontological studies, as far as I am aware. Thus, most of our knowledge about the Serra da Galga Member turtles comes from material deposited in just two institutions, each holding an impressive collection – the *Centro de Pesquisas Paleontológicas Llewellyn Ivor Price* (CPPLIP) in Uberaba and the *Museu de Ciências da Terra* (MCTer) in Rio de Janeiro.

The CPPLIP was created in 1991, and houses fossils that have been collected since then in Uberaba and neighbouring areas. The collections include around three hundred catalogued turtle remains, mostly isolated fragments (personal observation). Though the collections are not as extensive as those in the MCTer, they have been visited by several researchers, enabling the development of many studies in the last few decades (Langer, 1994; Figueira & Bertini, 2002a; França & Langer, 2005; Rogério *et al.*, 2013; Hermanson *et al.*, 2017; this study). Though much of what we know about the Serra da Galga Member turtles today derives from this material, the works of Broin (1991), Lapparent de Broin (2000) and Gaffney *et al.* (2011) ignored this sample. Gaffney *et al.* (2011) did discuss *Cambaremys*, whose type is deposited in the CPPLIP, but the senior author of the paper did not have personal access to the specimen, and instead based his conclusions on descriptions and figures available in the literature.

The MCTer houses the vast historical collections of the former *Departamento Nacional da Produção Mineral* (DNPM), accumulated over the course of the XX Century. The turtle material from the Serra da Galga Member housed in this institution includes a single peripheral collected at the site of Mangabeira in 1945 (MCT.R.312, Price, 1951; Bertini, 1993; Melo & Schwanke, 2006; Menegazzo, 2009) and hundreds of fossils from the sites of Peirópolis and Serra da Galga, collected between 1948 and 1974 (Price, 1955; Ribeiro & Carvalho, 2009). It was this collection that France de Lapparent de Broin and Eugene Gaffney had access to during their trips to Brazil, and it was based on this sample that they developed their work on the turtles of the Serra da Galga Member (Broin, 1991; Lapparent de Broin, 2000; Gaffney *et al.*, 2011).

With the exception of the peripheral from Mangabeira (MCT.R.312) and eleven fragmentary specimens collected during the first fossil collecting efforts in 1948 (specimens MCT.R.321 through MCT.R.331, Bertini, 1993; Melo & Schwanke, 2006; Menegazzo, 2009), none of the fossils from the MCTer collection were originally catalogued. Three better preserved specimens were catalogued for Eugene Gaffney during his trip to Brazil (MCT.R.1497 though MCT.R.1499, Gaffney *et al.*, 2011), and a few dozens of fragments have more recently been catalogued upon the request of myself and my colleague, Mariana Leite Ambrosim (personal observation). Still, most of the Serra da Galga sample in the MCTer remains uncatalogued to this day (personal observation). This makes working with this material a great challenge, as it is very hard to objectively identify and reference the uncatalogued fragments, and nearly impossible to recover precise collecting and curatorial data for each fossil specimen.

Based on the MCTer collection, Broin (1991) suggested that "three to four species are possibly in the Uberaba area at Peiropolis and Galga" (Broin 1991, p. 512), and that one of these was either synonymous with "*Podocnemis*" *brasiliensis* or a new species altogether. However, she did not describe or diagnose any of these supposed taxa, nor did she identify the specimens on which they were based. Thus, it is impossible to know precisely what material in the MCTer she believed was comparable to "*P.*" *brasiliensis*. Gaffney *et al.* (2011) later recognized two skull-based and three shell-based species in the Serra da Galga Member. The shell forms comprised the species *Cambaremys langertoni*, previously described by França & Langer (2005) and known only from the type held in the CPPLIP, and two informal morphotypes based on the MCTer sample – "Peirópolis A" and "Peirópolis B". "Peirópolis A" was characterized as a large form, defined based on a few articulated specimens containing carapace, plastron and cervical remains (MCT.R.321, MCT.R.1499 and a third uncatalogued specimen), as well as several uncatalogued fragments. "Peirópolis B" was defined as a smaller turtle, known from a series of uncatalogued and disarticulated shell plates in the MCTer collections, different from those of the larger "Peirópolis A" (Gaffney *et al.*, 2011). Isolated and uncatalogued scapulae were also attributed tentatively to each morphotype, on the basis of size (Gaffney *et al.*, 2011, p. 205).

While most authors (Rogério *et al.*, 2013; Hermanson *et al.*, 2017; Bogado *et al.*, 2023) have accepted the three shell taxa which Gaffney *et al.* (2011) recognized in the Serra da Galga Member, I have since come to question their validity as distinct, identifiable taxa. As Gaffney *et al.* (2011) and Rogério *et al.* (2013) have stated, most of the material attributable to "Peirópolis A" belongs to very large individuals, while all known specimens of "Peirópolis B" are small to medium-sized isolated plates. This distinction in size hints at the possibility that some differences between the two shell morphotypes might be the result of ontogeny, and not taxonomy. After examining the large collections of turtles from the Serra da Galga Member at the MCTer and CPPLIP collections, I have noticed that some of the characteristics that purportedly distinguish Gaffney's two morphotypes (e.g., nuchal shape, iliac scar shape and position, pleuro-marginal scute incision, internal gutter of posterior peripherals…) appear to represent the extremes in a continuum of morphological variation. Smaller shell fragments usually show the typical "Peirópolis B" morphology, but as size increases, specimens tend to grade into the morphology of "Peirópolis A", with mid-sized individuals having an intermediate morphology. This lends support to the idea that "Peirópolis A" and

"Peirópolis B" are ill-defined taxa, and that at least part of their defining characteristics may be the result of ontogenetic variation. The current definition of *Cambaremys* is also problematic, but given that this species has been properly described as a formal taxon, I will discuss it separately in the following section.

To make the taxonomic situation of the Serra da Galga Member shells more complicated, there is some morphological variation in this sample that appears to be systematically informative, but has not been previously recognized as being so. Gaffney *et al.* (2011) stated that the first neural in "Peirópolis A" could be either four- or six- sided, and that this trait was not systematically informative (Gaffney *et al.*, 2011, p. 199). Still, many authors believe the shape of the first and second neurals to be highly informative for the alpha-taxonomy of the Pan-Podocnemididae (Suárez, 1969; Broin, 1991; Kischlat, 1994a; Maniel *et al.*, 2021), and this feature has been used as a phylogenetic character in many cladistics studies, including those by Eugene Gaffney himself (e.g., Lapparent de Broin, 2000; Gaffney *et al.*, 2006, 2011; de la Fuente, 2022). I think the presence of two different states for this character in the Serra da Galga shells, together with the fact that skulls belonging to two different species are known in the same beds, is an indication that perhaps two distinct taxa, not necessarily synonymous with "Peirópolis A" and "Peirópolis B", might be present in the Serra da Galga Member. CPPLIP-593 and MCT.R.2092, the indeterminate epiplastra presented in the subsection about geometric morphometrics, are another example of potentially taxonomically significant morphological variation in the Serra da Galga Member assemblage that had so far remained undetected, encouraging further study.

In sum, I consider the taxonomy of the Serra da Galga Member shell remains to be currently unsatisfactory. Only with a thorough revision of the available material – both in the CPPLIP and MCT collections – will it be possible to identify reliable diagnostic traits and discern valid shell-based taxa among the few complete shells and the countless fragments that these deposits have yielded. While I believe this revision is necessary, it falls outside the scope of this dissertation. For my purposes, it suffices to say that the complete (or nearly complete) shells from the Serra da Galga Member cannot be assigned to "*Podocnemis*" *brasiliensis*, owing to the absence of a posterior epiplastral projection (absent in all Serra da Galga Member epiplastra except CPPLIP-593; present in "*P.*" *brasiliensis*), as well as the overlap between the abdominal scute and the mesoplastron (present in MCT.R.321, MCT.R.1499 and MCT.R.2100; absent in "*P.*" *brasiliensis*). *Cambaremys* is discussed separately in the following subsection.

5.5.4 *Cambaremys langertoni* (França & Langer, 2005)

In the original description of *Cambaremys langertoni*, França & Langer (2005) remarked that this taxon was similar to "*Podocnemis*" *brasiliensis*, and could potentially represent a junior synonym. The type and only known specimen of *C. langertoni* consists of an incomplete shell, including parts of the carapace and plastron, together with axial and appendicular elements. The plastron of *C. langertoni* – the only anatomical part that can be compared with "*P.*" *brasiliensis* – is extremely fragmentary, being represented only by a right mesoplastron, a complete right xiphiplastron and fragments of the left xiphiplastron (França & Langer, 2005). In my personal reassessment of the type of *C. langertoni* I was only able to access the right xiphiplastron, as the mesoplastron was on loan during my visit to the CPPLIP and the left xiphiplastron, which was neither figured nor described in the original description (França, 2004, p. 27), is apparently lost (personal observation).

Before I begin to discuss the synonymy between *Cambaremys langertoni* and "*Podocnemis*" *brasiliensis*, I must note that, during my personal reassessment of the type material, I was able to determine that a series of characteristics that were presented in the original description by França & Langer (2005) and the reassessment by Gaffney *et al.* (2011) are mistaken or ambiguous. Most relevant to the taxonomic discussion at hand is the fact that the shell is not unornamented (França & Langer, 2005, p. 396), but instead bears the typical pelomedusoid ornamentation. Besides, several characteristics of the carapace have also been incorrectly identified. The anterior limit of the axillary buttress is not peripheral 2 (França & Langer, 2005, p. 400), but peripheral 3. The shape of the axillary buttress scar cannot be determined (*contra* Gaffney *et al.*, 2011), because this scar is entirely covered by sedimentary matrix. The caudal peripherals have been misidentified – the adjacent plates identified as the left peripherals 9, 10 and 11 are truly right peripherals 9, 10 and 11, while the plates identified as the right peripherals 10 and 11 are left peripherals 9 and 10 (*contra* França & Langer, 2005, Figs. 3-5). The isolated and damaged plate identified as the 8th right peripheral (França & Langer, 2005, Figs. 3-5) appears to be the pygal.

When these corrections are taken into account, the definition of *Cambaremys langertoni* becomes virtually indistinguishable from that of the morphotype "Peirópolis A". The few traits that could warrant distinction between these two shell-taxa (see Gaffney *et al.*, 2011, table 4) have either been incorrectly described (shell ornamentation and anterior limit of the axillary buttress) or could be interpreted as ontogenetic variation (degree of incision of the pleuro-marginal sulci, iliac scar shape and internal guttering of the posterior peripherals). The only remaining feature that could distinguish these taxa would be the overlap between the pectoral scute and the mesoplastron (absent in *C. langertoni*, present in *bona fide* "Peirópolis A") (França & Langer, 2005; Gaffney *et al.*, 2011). These similarities add strength to the argument that the alpha-taxonomy of the Serra da Galga Member shell-based taxa is currently unsatisfactory, and that current taxonomic distinctions are probably artificial. Though I will here refer to *C. langertoni* based only on its type material, I stress that a future taxonomic revision is likely to alter the definition of this taxon, or even deem it invalid.

As has been remarked by previous authors, "The differentiation of *Cambaremys langertoni* [...] from '*Podocnemis*' *brasiliensis* is not so straightforward, due to the small overlapping of elements preserved in both taxa" (França & Langer, 2005, p. 408). França & Langer (2005) state that the pectoro-abdominal sulcus of *C. langertoni* does not contact the mesoplastron, just like in "*P.*" *brasiliensis*. The right xiphiplastron of *C. langertoni* is covered by the pelomedusoid ornamentation (personal observation), also like in "*P.*" *brasiliensis*. Yet, the right xiphiplastron of *C. langertoni* differs from the type of "*P.*" *brasiliensis* in having a shallower, V-shaped anal notch, as well as pelvic scars of a different shape (França & Langer, 2005). While the xiphiplastra of these two taxa do differ in a few details, this bone is known to exhibit considerable intra-specific variation among turtles (Guerrero & Pérez-García, 2021a, 2021b; Wood, 1995, 2003; Wood & Díaz de Gamero, 1971), and these differences are of little taxonomic value (as acknowledged by França & Langer, 2005, p. 401, 408).

Cambaremys langertoni may not be confidently differentiated from "*Podocnemis*" *brasiliensis*, and could be seen as its junior synonym, as previously suggested by França & Langer (2005) and Menegazzo *et al.* (2015). If future work comes to corroborate this idea, then the species *brasiliensis* might come to be included in the genus *Cambaremys*, under the combination *Cambaremys brasiliensis*. While this synonymy is certainly plausible and is not at present falsifiable, the plastron of *C. langertoni* is too incomplete to warrant a definite statement regarding its affinities with "*P.*" *brasiliensis*. Furthermore, I believe the type of *C. langertoni* and the remaining Serra da Galga Member shell material are currently in need of taxonomic revision, as stated previously. Future investigation is required to elucidate the alpha-taxonomy of the Serra da Galga Member turtles and their possible affinities with "*P.*" *brasiliensis*.

5.5.5 “Santo Anastácio form” (Menegazzo *et al.*, 2015)

The “Santo Anastácio form” has been suggested to be a synonym of both *“Podocnemis*” *brasiliensis* and *Cambaremys langertoni* (Menegazzo, 2009; Menegazzo *et al*., 2015). The main difference between the “Santo Anastácio form” and these two species is its supposedly unornamented shell, marked only by faint, radiating striations (mentioned in Menegazzo, 2009, p. 51, visible in Menegazzo *et al.*, 2015, Fig. 3), probably linked to the growth of the epidermal scutes (see Broin, 1977, p. 10-11). Another distinguishing trait of the “Santo Anastácio form” is its remarkably broad and rounded plastron (Menegazzo *et al.*, 2015, Fig. 3), which differs clearly from the elongated and narrower plastron of the type of “*P.*” *brasiliensis* (Staesche, 1944).

While ornamentation and plastron shape set the “Santo Anastácio form” apart from “*P.*” *brasiliensis*, some caution is advised before using these characteristics to inform taxonomic decisions. Differences in plastron shape could be the result of ontogenetic variation, since the “Santo Anastácio form” is a rather small individual, and shell shape is known to change with age (Broin, 1971). As for shell ornamentation, even though it is a useful characteristic in pelomedusoid alpha taxonomy, it is not always visible in figures, and may be mistakenly identified or ambiguously referred to in textual descriptions. As stated previously, *Cambaremys* and *Puentemys* were both originally described as unornamented (França & Langer, 2005, p. 396; Cadena *et al.*, 2012b, p. 692), even though they have the pelomedusoid ornamentation (Cadena *et al.*, 2024; personal observation). Menegazzo *et al.* (2015) states “There is no distinctive ornamentation on shell external” (Menegazzo *et al.*, 2015, p. 23) of the “Santo Anastácio form”, but I believe this would only be objectively demonstrated with high quality photos of the specimen or a personal reassessment, none of which were available to me.

If a future reappraisal of the “Santo Anastácio form” were to demonstrate its shell is not unornamented, being covered in the pelomedusoid ornamentation instead, then an attribution to “*P.*” *brasiliensis* would be entirely seemly. Still, I regard the apparent differences in the surface texture of the shell to be sufficient for taxonomic differentiation – for the time being, at least. I classify the “Santo Anastácio form” as “*Podocnemis*” aff. *brasiliensis* – a representative of a taxon close to the species *brasiliensis*, but not necessarily belonging to it.

5.5.6 Alfredo Marcondes entoplastra (Bogado *et al.*, 2023)

In a previous contribution, I have described and figured three fragmentary entoplastra recovered from the Presidente Prudente Formation of the Bauru Group – UFRJ-DG 713-R, UFRJ-DG 720-R and UFRJ-DG 721-R (Bogado *et al.*, 2023). These specimens are characterized by a long interhumeral contact and the typical pelomedusoid ornamentation of sparse and lightly inscribed ornamental furrows – traits that are also present in "*Podocnemis*" *brasiliensis*. While I recognized the similarity between these entoplastra and "*P.*" *brasiliensis*, I preferred not to assign them to this species, given the dubious taxonomic standing of "*P.*" *brasiliensis* and the fragmentary state of the new fossils (Bogado *et al.*, 2023, p. 13). These entoplastra resemble "*P.*" *brasiliensis* not only in their ornamentation and interhumeral sulci, but also in the absence of extragular-entoplastron contact and the small area of the entoplastron occupied by the gular. Still, they are far too fragmentary to make a confident taxonomic assignment, and I prefer to leave them in open nomenclature, identifying them as "*Podocnemis*" cf. *brasiliensis*.

5.5.7 Álvares Machado material (Broin, 1991)

Broin (1991) proposed that "large pieces of shell" from the municipality of Álvares Machado in the state of São Paulo could belong to "*Podocnemis*" *brasiliensis*. This material is part of a sample of turtle fossils extracted from the "Myzobuchi Farm", the type locality of the sauropod *Gondwanatitan faustoi* Kellner & Azevedo, 1999. The remains were preliminarily described and figured by Cunha et al. (1987), and were briefly explored in several subsequent abstracts (Kischlat, 1994b, 1995, 1996a, 1996b, 2015; Kischlat *et al.*, 1994). In these abstracts, the Álvares Machado turtles have been alternatively identified as members of the genus *Roxochelys* (Kischlat, 1994b; Kischlat *et al.*, 1994), a new genus and species akin to the Eurafrican Podocnemididae (Kischlat, 1996a, b) and a new species congeneric with "*Podocnemis*" *harrisi*, with both these species belonging to a new genus within the "*Bairdemys-Stereogenys* lineage" (Kischlat, 2015). The available descriptions and figures give a very limited picture of the material, and until a high quality figures and a full description are available, nothing certain may be said regarding the taxonomic standing of these remains.

5.5.8 Mato Grosso material (Broin, 1991)

Broin (1991) stated that some shell fragments from Cretaceous outcrops in Cambambe Hill, located in the state of Mato Grosso, Brazil, could possibly be attributed to "*P.*" *brasiliensis*. The shell material from Cambambe Hill reported by Broin (1991) corresponds to specimens MCT.R.413, MCT.R.414 and MCT.R.2102, each consisting of samples of isolated shell fragments collected by DNPM staff in 1936, 1941 and 1958, respectively (Roxo, 1937, 1946; Price, 1958). I have examined these fossils, and I believe they cannot be confidently assigned to "*P.*" *brasiliensis* (or any other species). While most fragments bear the typical pelomedusoid ornamentation, and some few preserve diagnostic features of the Pelomedusoides, such as a nuchal without a cervical scute and a left hyoplastron contacting a small, lateralized mesoplastron – both included in number MCT.R.414 – the fossils are far too fragmentary to permit a confident specific assignment.

5.5.9 Tiupampa material (Muizon *et al.*, 1993)

Muizon *et al.* (1983) and Marshall & Muizon (1988) have indicated the presence of "*Podocnemis*" *brasiliensis* in the Bolivian site of Tiupampa, dated to the Palaeocene Epoch. Muizon et al. (1983) cited personal communication with France de Broin to back this identification, but no more information was given on the reasoning behind this taxonomic assignment or the material it was based upon.

Interestingly, Broin (1991) did not mention any remains of "*P.*" *brasiliensis* from Bolivia in her revision of Bolivian fossil turtles, instead identifying the Tiupampa turtles as belonging solely to ? *Roxochelys vilavilensis* (now *Lapparentemys vilavilensis*). Furthermore, when I had the opportunity of personally meeting France, she informed me that she did not remember ever having told Muizon that "*P.*" *brasiliensis* was present in Tiupampa, and that she believed *Lapparentemys vilavilensis* to be the only turtle known from the Palaeocene of Bolivia, as previously stated in her 1991 paper. Thus, I regard the purported occurrence of "*Podocnemis*" *brasiliensis* in Bolivia as a spurious record.

6 CONCLUSION

FFP PG 218 could be identified as an individual of "*Podocnemis*" *brasiliensis*, a taxon with a convoluted taxonomic history that was previously known only through its type, an incomplete plastron (MCT.R.214). An examination of the anatomy of these two specimens allowed me to revise "*P.*" *brasiliensis*, considering it a valid taxon and proposing an emended diagnosis for it. Though clearly not a representative of the genus *Podocnemis*, the generic attribution of this species remains uncertain, giving it the status of an *incertae sedis*. I revisited specimens that were tentatively referred to "*P.*" *brasiliensis* in the past, and concluded that none except the type plastron could be confidently identified as belonging to this species. A morphometric geometric analysis of epiplastra from turtles of the Bauru Group corroborates the idea that "*P.*" *brasiliensis*, as here redefined, represents a species of its own, distinct from other taxa known in the unit. A linear regression demonstrated that shell thickness cannot be used to distinguish "*P.*" *brasiliensis* from other Podocnemidoidae. However, this analysis revealed that *Roxochelys* has a proportionally thicker shell relative to its podocnemidoid relatives, as had been previously suggested in the literature.

As concerns our specific objectives, we have demonstrated that:

- Geometric morphometric analysis of the epiplastra of Bauru Group turtles recovered three significant PCs. Variation in the PC1 and PC2 was linked to the widening of the gular scute, while changes in the PC3 captured the proportional shortening of the anterior region of the epiplastron.

- Changes in shell thickness reflect changes in shell size, following an allometric regime. For Bauru turtles, differences in thickness appear to be taxonomically significant, as *Roxochelys* has a generally thicker shell than *Bauruemys*. Still, this trait exhibits much intra-specific variation, and should be used with caution.

- "*Podocnemis*" *brasiliensis* can be distinguished from other pelomedusoids by the following differential diagnosis, based on the type plastron and the new referred specimen: (1) shell with pelomedusoid ornamentation); (2) extragulars restricted to epiplastra; (3) narrow gular; (4) long interhumeral contact; (5) humero-pectoral sulcus nearly contacts or slightly overlaps epiplastra; and (6) pectoral scutes reach the entoplastron but not the mesoplastra.

- Previous records of “*P.*” *brasiliensis* in the published literature – to the exception of the type plastron – are unjustified. Still, two occurrences are compared to this taxon using open nomenclature modifiers – with the “Santo Anastácio form” (URP RT-1) identified as “*Podocnemis*” aff. *brasiliensis* and three fragmentary entoplastra from the Presidente Prudente Formation at Alfredo Marcondes (UFRJ-DG 713-R, UFRJ-DG 720-R and UFRJ-DG 721-R) identified as “*Podocnemis*” cf. *brasiliensis*).

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APPENDIX

Table 2 – Specimens used in the Geometric Morphometric Analysis.

Specimen	**Taxon**
FFP GP 218	“*Podocnemis*” *brasiliensis*
MCT.R.1787	*Roxochelys wanderleyi*
UFRJ-DG 404-R	*Roxochelys wanderleyi*
LPRP USP 0201	*Bauruemys elegans*
LPRP USP 0202	*Bauruemys elegans*
LPRP USP 0730	*Bauruemys elegans*
MCT.R.1492	*Bauruemys elegans*
MCT.R.1891-D	*Bauruemys elegans*
MCT.R.1894	*Bauruemys elegans*
MCT.R.1895	*Bauruemys elegans*
MCT.R.2103	*Bauruemys elegans*
MN 6772	*Bauruemys elegans*
MN 6795	*Bauruemys elegans*
MN 6800	*Bauruemys elegans*
MN 6807	*Bauruemys elegans*
MPMA 40-0002/01	*Bauruemys elegans*
MZSP-PV 136	*Bauruemys elegans*
PUC RCL 101	*Bauruemys elegans*
PUC RCL 102	*Bauruemys elegans*
CPPLIP-734	“Peirópolis A”
MCT.R.321	“Peirópolis A”
MCT.R.1499	“Peirópolis A”
MCT.R.1888	“Peirópolis A”
MCT.R.1889-A	“Peirópolis A”
MCT.R.1889-C	“Peirópolis A”
MCT.R.2100	“Peirópolis A”
CPPLIP-593	Indeterminate epiplastra from the Serra da Galga Member
MCT.R.2092	Indeterminate epiplastra from the Serra da Galga Member

Source: Original table by the author.

Table 3 – Specimens used in the Linear Regressions. (continues)

Specimen	**Taxon**
FFP GP 218	“*Podocnemis*” *brasiliensis*
MCT.R.214	“*Podocnemis*” *brasiliensis*
MCT.R.216	*Roxochelys wanderleyi*
MCT.R.933	*Roxochelys wanderleyi*
MCT.R.1722	*Roxochelys wanderleyi*
MCT.R.1787	*Roxochelys wanderleyi*
UFRJ-DG 404-R	*Roxochelys wanderleyi*
UFRJ-DG 423-R	*Roxochelys wanderleyi*
LPRP USP 0201	*Bauruemys elegans*
LPRP USP 0202	*Bauruemys elegans*
LPRP USP 0455	*Bauruemys elegans*
LPRP USP 0457	*Bauruemys elegans*
LPRP USP 0730	*Bauruemys elegans*
MCT.R.1492	*Bauruemys elegans*
MCT.R.1891-B	*Bauruemys elegans*
MCT.R.1891-D	*Bauruemys elegans*
MCT.R.2101	*Bauruemys elegans*
MZSP-PV 136	*Bauruemys elegans*
MZSP-PV 137	*Bauruemys elegans*
MZSP-PV sem nº	*Bauruemys elegans*
MZUFV-P 0023	*Bauruemys elegans*
CPPLIP-293	“Peirópolis A”
CPPLIP-294	“Peirópolis A”
CPPLIP-495	“Peirópolis A”
CPPLIP-524	“Peirópolis A”
CPPLIP-646	“Peirópolis A”
CPPLIP-730	“Peirópolis A”
CPPLIP-734	“Peirópolis A”
CPPLIP-780	“Peirópolis A”
CPPLIP-784	“Peirópolis A”
MCT.R.321	“Peirópolis A”
MCT.R.1499	“Peirópolis A”

Table 4 – Specimens used in the Linear Regressions. (conclusion)

MCT.R.1888	“Peirópolis A”
MCT.R.1889-A	“Peirópolis A”
MCT.R.1889-C	“Peirópolis A”
MCT.R.1889-F	“Peirópolis A”
MCT.R.1890	“Peirópolis A”
MCT.R.2093	“Peirópolis A”
MCT.R.2094	“Peirópolis A”
MCT.R.2095	“Peirópolis A”
MCT.R.2096	“Peirópolis A”
MCT.R.2100	“Peirópolis A”
CPPLIP-593	Indeterminate epiplastra from the Serra da Galga Member
CPPLIP-843	Indeterminate epiplastra from the Serra da Galga Member
MCT.R.2092	Indeterminate epiplastra from the Serra da Galga Member
MCT.RR.276	*Podocnemis expansa*
MCT.RR.277	*Podocnemis expansa*
MCT.RR.366	*Podocnemis expansa*
MCT.RR.188	*Podocnemis sextuberculata*
MCT.RR.280	*Podocnemis sextuberculata*
MCT.RR.222	*Podocnemis unifilis*
MCT.RR.224	*Podocnemis unifilis*
MCT.RR.229	*Podocnemis unifilis*
MCT.RR.281	*Podocnemis unifilis*
MCT.RR.284	*Podocnemis unifilis*
MCT.RR.363	*Podocnemis unifilis*
MCT.RR.364	*Podocnemis unifilis*
MCT.RR.373	*Podocnemis unifilis*
MNRJ 3780	*Podocnemis unifilis*
MNRJ 25207	*Podocnemis unifilis*
MCT.RR.360	*Peltocephalus dumerilianus*

Source: Original table by the author.