



# A Review of the Taxonomic Status of the Chelid Turtle *Parahyraspis paranensis* Wieland 1923 from Late Miocene at Parana, Entre Rios Province, Argentina: with Comments on the Paleoenvironmental Settings from the lower Levels of Ituzaingó Formation

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## Research Article

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## Abstract

The panchelid turtles (stem chelid + crown chelid), one of the pleurodiran clades, display a disjunct distribution in Australasia and South America. Panchelids appeared in the fossil record during South America's Early Cretaceous (Aptian-Albian) and Late Cretaceous (Cenomanian) in Australasia. Among the crown Chelidae, the Chelinae include genera such as *Acanthochelys*, *Mesoclemmys*, *Platemys*, *Phrynops*, *Ranacephala*, and *Rhinemys* characterized by a restricted, poor or null fossil record in South America. Among this chelid clade, *Parahyraspis paranensis* is a carapace-based species described by Wieland in 1923 from upper Miocene Ituzaingó Formation outcrops along the Parana river cliffs, Parana city, Entre Rios Province, Argentina. Wieland referred to this new species as a different genus from the extant *Hydraspis* (an old synonymous genus of the genus *Phrynops*), depending upon a misinterpretation of the plastral bridge. Although a recent phylogenetic analysis nested this Miocene species with stem chelid species, in this contribution based on anatomical evidence on the holotype and referred specimens, we consider *Parahyraspis paranensis* as a fully valid species of the *Phrynops* genus. The continental terrestrial and aquatic fauna of the "Conglomerado osifero" lower levels of the Ituzaingó Formation where the holotype and specimens referred to as "*Parahyraspis*" *paranensis* were recovered, indicate a warmer climate and suggest the presence of forested areas along river's shores where these levels were deposited.

**Keywords:** Paleoherpitology; Testudines; Pleurodira; Carapace Anatomy; Neogene; South America

## Introduction

The Testudinata (stem turtles + Testudines) appeared in the fossil record during the Late Triassic (Norian) in Pangea

[1-10]. Testudines rapidly expanded in geographic range and ecological diversity during the Mesozoic [11,12]. The speed with which this diversity built up suggests that turtles may have undergone rapid, early adaptative radiation [13].

However, this early diversification was not sustained, and living turtle diversity is low. Consequently, crown turtles are a relatively species-poor clade of amniotes, with currently 357 recognized living species and 486 taxa relative to other, much younger crown amniote clades such as birds (>10,000 species), mammals (>5,000 species), and squamate reptiles (>10,000 species) [14-18].

According to [19] diversity, time, and diversification analyses indicate that the two major lineages within the clade Cryptodira and Pleurodira, diverged in the Late Triassic, followed by the Early Jurassic divergence between the softshell Trionychia (Carettochelyidae and Trionychidae) and the remaining cryptodires. Most recognized families diverged in the Late Cretaceous or Early Paleogene [20-24].

A specious comparison between these two different clades Cryptodira (hidden-necked turtles) and Pleurodira (side-necked turtles), with extant representatives indicates that the former (261 spp., 379 taxa) is a more specious clade than the latter [14]. Among extant pleurodiran turtles (96 spp, and 107 taxa), crown Chelidae displays the greater species richness (represented by 61 spp., and 67 taxa), in comparison with Pelomedusoidea (35 spp., and 40 taxa) [14].

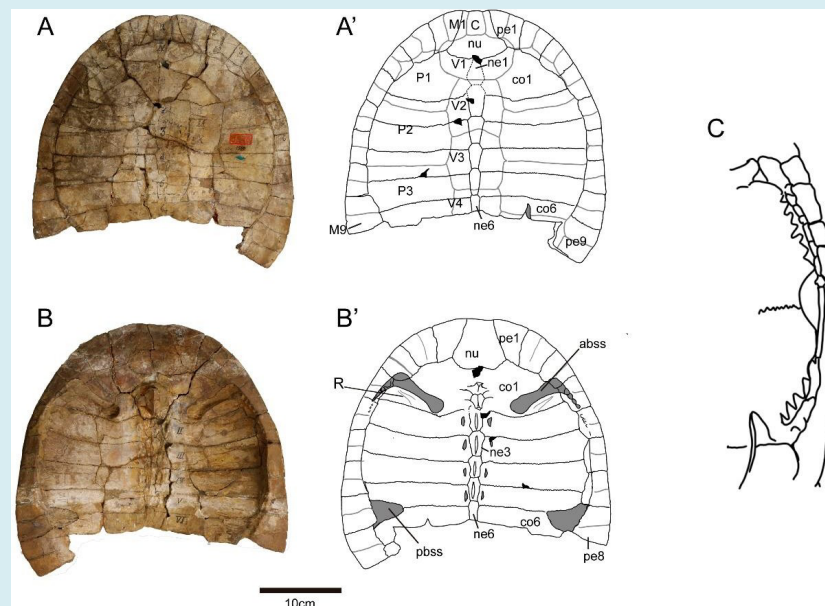
Extinct and extant panchelid (stem + crown) species are aquatic and semiaquatic turtles and display a disjunct distribution across Australasia and South America [14,25,26]. It has 61 extant spp., 67 taxa, and about 26 valid extinct species are known [14,26-28]. The Cretaceous and Paleogene stem chelids are well recorded in Patagonia but

are scarcer in Australia [26,29-44]. In contrast, the Neogene record of valid species is more specious in Australia than in South America [26,29,45-55].

According to [14] among the crown Chelidae, the Chelinae include genera such as *Acanthochelys*, *Chelus*, *Mesoclemmys*, *Phrynops*, *Platemys*, *Ranacephala* and *Rhinemys* [56-59].

Among the Chelinae clade, *Acanthochelys* and *Phrynops* are characterized by a restricted and poor fossil record in southern South America. *Acanthochelys* includes four extant species (*A. macrocephala*, *A. pallidipectoris*, *A. spixii* and *A. radiolata*, but the only extinct species is *A. cosquinensis* from the Pliocene of Cordoba province (Argentina) [48,60-63]. In addition, the genus *Phrynops sensu stricto* (*Phrynops geoffroanus* complex [64] includes three or four extant species (*P. geoffroanus* [65], *P. hilarii* [62] *P. tuberosus* [66], and *P. williamsis* [64], after [14], depending on whether the authors [67, 68] considering *P. tuberosus* as synonymous or as a subspecies of *P. geoffroanus* respectively or recognized it as a whole valid species at first [66,14,59,60,69,70,71].

Among the Chelinae clade *Parhydraspis paranensis* is a carapace-based species described by Wieland in 1923 from upper Miocene Ituzaingó Formation outcrops along the Parana river cliffs, Parana city, Entre Rios Province, Argentina. At this time, Wieland referred to this new species as a different genus from the extant *Hydraspis* (an old synonym of genus *Phrynops*), depending on its particular interpretation of the plastral bridge, which is absent in the holotype (Figures 1A-1C).



**Figure 1:** *Parahydraspis paranensis* holotype (YPM 1565). Photographs and drawings (A) dorsal and (B), visceral views of the carapace, (C) Wieland's interpretation of plastral bridge redrawing from Wieland [46].

Although a recent phylogenetic analysis [28] nested this Miocene species with stem chelid species, most of the current turtle synthesis papers suggest the assignation of *Parahyraspis paranensis* to *Phrynops sensu stricto* or its close relationships with extant species of *Phrynops geoffroanus* complex [48], other authors have proposed its specific validation [26,72]. In this contribution based on anatomical evidence of the holotype and referred specimens, we aim to propose *Parahyraspis paranensis* as a fully valid species of the *Phrynops* genus.

## Materials and Methods

### Materials

The holotype of "*Parahyraspis*" *paranensis* in the study proceeds from "Conglomerado osifero" Ituzaingó Formation (Entre Rios province, Argentina), and it is housed at the Paleontological Vertebrates Collection of the Yale Peabody Museum (YPM 1565), New Haven, USA.

The refereed material to "*Parahyraspis*" *paranensis* belongs to the collection of the Division Paleontología Vertebrados, Museo de La Plata (MLP), Argentina, under the collection numbers: MLP 41-XII-13-782; MLP-41-XII-13-793; MLP-41-XII-13-805; MLP-62-XII-10-9; MLP-79-VIII-12-18; MLP-79-VIII-21-2; MLP-79-VIII-21-5; MLP-79-VIII-21-6; MLP-79-VIII-21-7; MLP-79-VIII-21-8; MLP-79-VIII-21-9; MLP-79-VIII-21-10; MLP-79-VIII-21-1; MLP-79-VIII-21-12; MLP-79-VIII-21-13; MLP-79-VIII-21-14; MLP-79-VIII-21-16; MLP-79-VIII-21-17; MLP-79-VIII-21-18; MLP-79-VIII-21-19; MLP-79-VIII-21-20; MLP-80-IV-9-1 (see below).

The anatomy of the carapace is based on the terminology of [73]. Chronological issues follow the International Chronostratigraphic Chart [74,75].

We used specimens of different extant species of *Phrynops sensu stricto* (e.g., *P. geoffroanus*, *P. hiliarii* and *P. williamsi*) and *Mesoclemmys* (e.g., *M. vanderhaegei*, *M. gibba*) belongs to different institutions for comparisons with the fossil material examined (see institutional abbreviations, description, and discussion).

**Anatomical Abbreviations:** ABSS: Anterior Bridge Strut Scar; C: Cervical Scute; CO: Costal Bone; M: Marginal Scute; Ne: Neural Bones; Nu: Nuchal Bone; PE: Peripheral Bone; P: Pleural Scute; PBSS: Posterior Bridge Strut Scar; R: Rib/Gomphosis; V: Vertebral Scute.

**Institutional Abbreviations:** AMNH: American Museum of Natural History, New York, NY, USA; FCDPV: Colección de Paleontología Vertebrados, Facultad de Ciencias, Universidad de la República, Uruguay; FMNH: Field Museum of Natural History, Chicago, USA; MACN-H, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia,"

Herpetological, collection, Ciudad Autónoma de Buenos Aires, Argentina; MCT, Museu de Ciências da Terra, Serviço Geológico do Brasil, Rio de Janeiro, Brazil; MHNSR-Z, Museo de Historia Natural San Rafael, Zoological collection, San Rafael, Mendoza; Argentina; MNHN, Museum National d'Histoire Naturelle de Paris, France; MLP, Museo de La Plata, Vertebral Paleontological collection, La Plata, Argentina; MZUC, Museo de Zoología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina; MZUSP, Museu de Zoologia Universidade de São Paulo, São Paulo, Brazil; NHMUK, Natural History Museum, London, UK.; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA; YPM, Yale Peabody Museum of Natural History, Yale University, New Haven, USA.

## Results

### Systematic Paleontology

Testudinata [76], sensu [77], Testudines [78], sensu [79], Pleurodira [80], sensu [81], Pan-Chelidae [82], Chelidae [83], sensu [84], Chelinae [85], *Phrynops* [58], *Phrynops paranensis* [46].

### Synonymy

*Parahyraspis paranensis* [46,86,87], *Phrynops geoffroanus* [88], *Phrynops* complex *geoffroanus* [89,48], *Phrynops* s.l. [*Phrynops* s.s.] sp. [29], *Phrynops* cf *Phrynops geoffroanus* complex [90,91], *Phrynops paranensis* [14,26,72].

### Holotype

YPM 1565, most of the carapace except the caudal portion [46] (Figure 1).

### Refereed Material

MLP 41-XII-13-782, medial fragment of the left costal 1; MLP-41-XII-13-793, left hyoplastron; MLP-41-XII-13-805, right hyoplastron; MLP-62-XII-10-9, plastral fragment; MLP-79-VIII-12-18, anterior left portion of the carapace (left nuchal portion, left peripherals 1-4 and left costal 1), visceral carapace surface with an anterior bridge strut scar (= axillary buttress) that extends to the posterior margin of costal one, with a central constriction and a medial expansion, and an acute angle between rib/gomphosis and anterior bridge strut scar about 15 degree (a diagnostic condition of *P. paranensis* as listed below); MLP-79-VIII-21-2, proximal end of the left humerus, fragment of the right hyoplastron; MLP-79-VIII-21-5, left hyoplastron; MLP-79-VIII-21-6, two medial fragments of the costal bones, two fragments of the right epiplastra, four fragments of right and two left

hypoplastra, one left hypoplastron, one fragment of right hyoplastron, one fragment of left xiphoplastron; MLP-79-VIII-21-7, left peripheral bone 8, left peripheral bone 3; MLP-79-VIII-21-8, right peripheral bone 8, a fragment of left costal 1 and a right fragment of costal 8; MLP-79-VIII-21-9, three neural bones; MLP-79-VIII-21-10, left costal 1, two right costal bones; MLP-79-VIII-21-11, four peripheral bones of the posterior carapace, left peripheral 2; MLP-79-VIII-21-12, suprapygal; MLP-79-VIII-21-13, distal end of left xiphoplastron; MLP-79-VIII-21-14, entoplastron; MLP-79-VIII-21-16, left peripheral bones 3-4 and a fragment of the right costal 1; MLP-79-VIII-21-17, lateral extreme of the left costal 8 and a neural bone; MLP-79-VIII-21-18, a left femur, proximal extreme of right humerus, five left pelvic halves, two left ilium, four right ilium, eleven neurals, one lateral fragment of the right costal 1 with an attached axillar pillar of the plastral bridge, a fragment of another costal 1, and one left hypoplastron; MLP-79-VIII-21-19, two right hypoplastra, left peripheral 9; MLP-79-VIII-21-20, left hypoplastron, a costal bone, and a portion of the carapace; MLP-80-IV-9-1, fragment of the carapace.

### Stratigraphic and Geographic Provenance

Lower levels "Conglomerado osifero" from Ituzaingó Formation (late Miocene), see geographic location map and generalized stratigraphic section of the late Cenozoic strata at the left side cliff along the Parana river near the city of Parana, Entre Rios, Argentina [91] (Figures 1 & 2).

### Emended Diagnosis

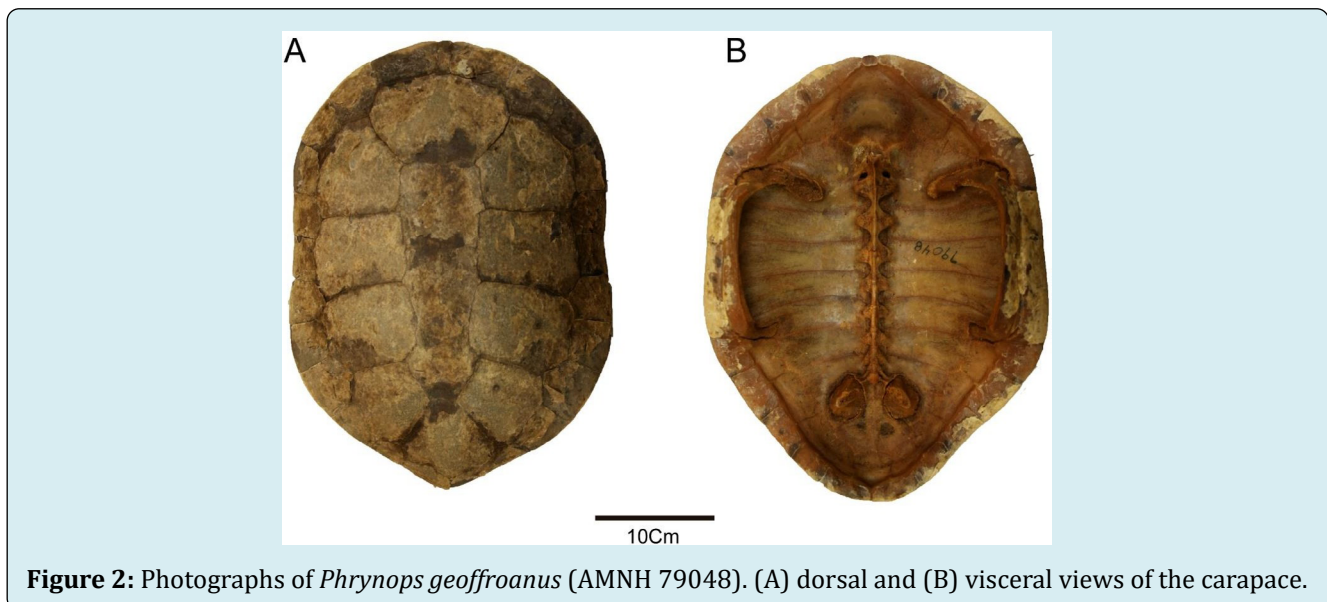
*Parahyraspis paranensis* can be diagnosed as a chelid pleurodiran turtle due to the presence of a cervical scute on the cranial margin of the carapace nuchal bone and the

loose attachment between carapace and plastron. It can be attributed as a representative of *Phrynops sensu stricto* by the presence of a continuous neural series and a likely nuchal neural 1 contact. It differs from the remaining *Phrynops* spp. such as *P. geoffroanus*, *P. tuberosus*, *P. hilarii*, and *P. williamsi* by the presence of a shorter vertebral scute I, a wider cervical scute, and an anterior bridge strut scar (= axillary buttress) that extends to the posterior margin of costal 1, with a central constriction and a medial expansion, and a low acute angle (about 15 degrees) between rib/gomphosis and the strut anterior bridge scar. The posterior bridge strut scar (= inguinal buttress) extends to the most lateral end of costal bones 5 and 6 as other *Phrynops* spp.; but in contrast, reaches the medial ends of the peripheral bones 8-9.

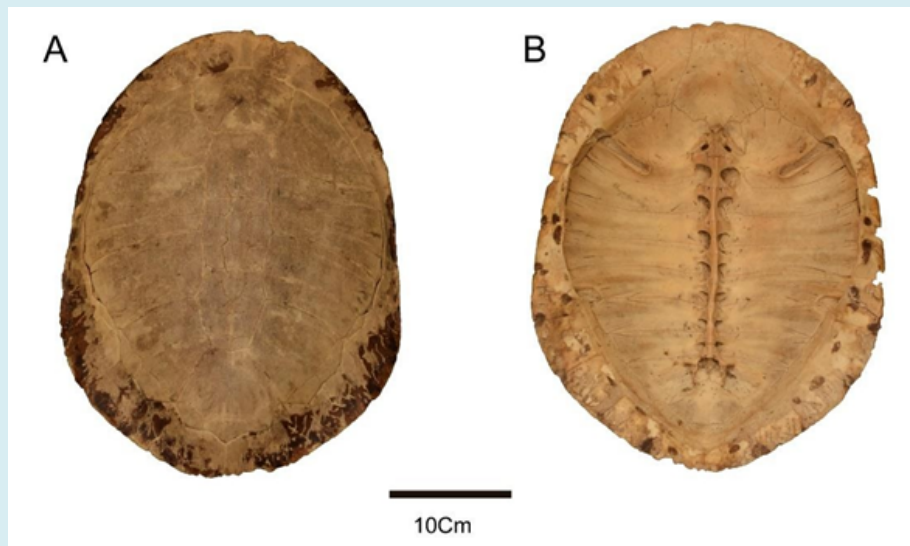
### Redescription of Holotype of *Parahyraspis paranensis*

The carapace in YPM 1565 (Figure 1A) is broadly oval and low-domed as the extant specimens assigned to *Phrynops sensu stricto* such as *Phrynops geoffroanus* (AMNH 79048, MZUSP 2635) (Figure 2), *P. hilarii* (FMNH 22481, MHNSR- Z-1550, NHMUK 86-3-10-1) (Figure 3), or *P. williamsi* (MACN H-38395, USNM 306646) (Figure 4).

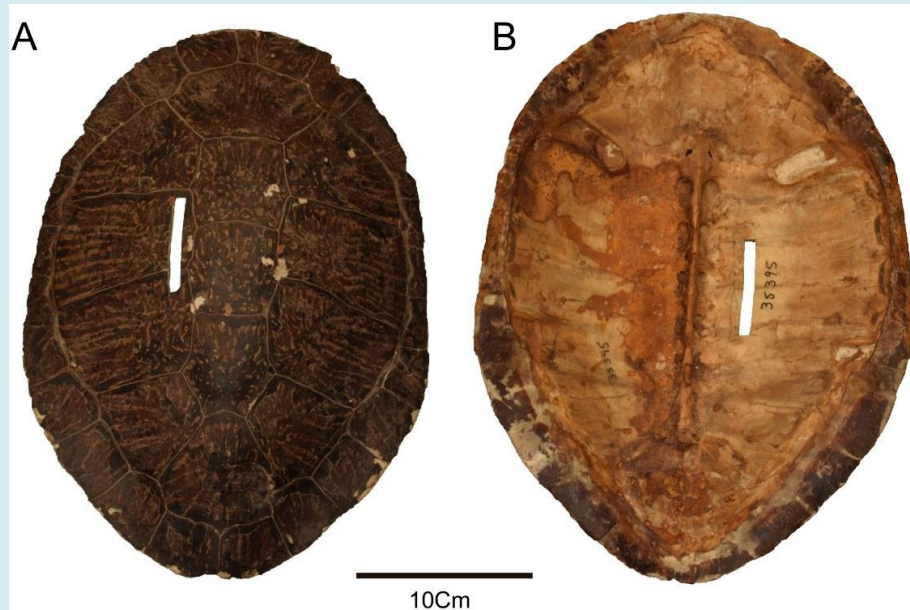
The odd bones series in YPM 1565 starts with a, heptagonal nuchal bone (Figures 1A & 1B). This is in contrast to a typical hexagonal nuchal present in chelid species. The caudal margin width of the nuchal is more than twice the cranial margin. The nuchal is followed by a series of six neural bones in YPM 3536 (Figure 1A). Although the area where the neural 1 is positioned is damaged, the nuchal bone-neural 1 contacts can only be suggested.



**Figure 2:** Photographs of *Phrynops geoffroanus* (AMNH 79048). (A) dorsal and (B) visceral views of the carapace.



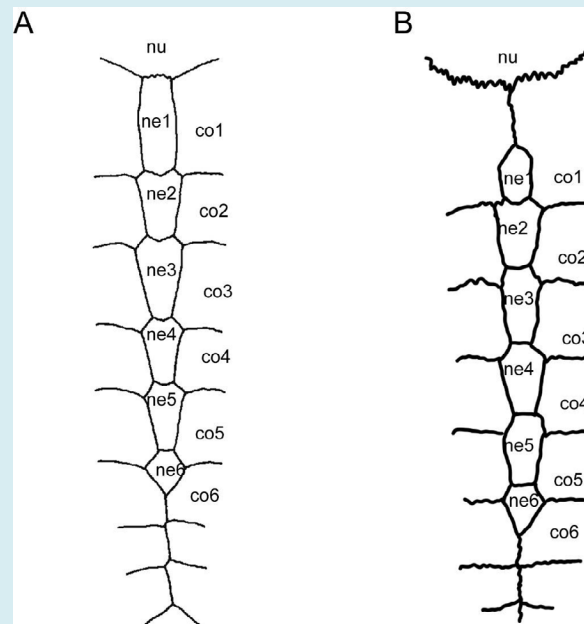
**Figure 3:** Photographs of *Phrynops hilarii* (MHNSR-Z-1550). (A) dorsal and (B) visceral views of the carapace.



**Figure 4:** Photographs of *Phrynops williamsi* (MACN-H-38395). (A) dorsal and (B) visceral views of the carapace.

Although the typical arrange of a continuous series with nuchal-neural 1 contacts are diagnostic characters of *Phrynops sensu stricto*, (Figure 5A) as shown in a specimen (NHMUK 84-2-5-1) assigned to *Phrynops williamsi* [64] (Figure 6). An intraspecific variation is seen in MACN 35395 referred to *P. williamsi* shown [92], where the medial portions of costal bone 1 make contact, preventing contact between the nuchal and neural 1 (Figure 5B). Although the anterior portion of neural 2 is not recognizable in YPM 1565, the neural bones 3 to 6 are hexagonal with short anterolateral margins, displaying a coffin outline appearance. As is typical

in turtles, YPM 1565, the right and left costal bones 1-6 are positioned on both sides of the carapace, with at least 8 pairs of peripheral bones on both sides and only a peripheral 9 on the right. As is typical in chelids, costal 1 is twice longer than the costal 2 and trapezoidal. The remaining costal bones (2-6) are subrectangular and similar in size. Anterior free peripheral bones 1-2 and the lateral portion of peripheral 3 seem slightly shorter than the posterior ones. The peripheral bones 1-3 on both sides are trapezoidal. 4-6 are subrectangular, whereas 7-8, and 9 on the right side are trapezoidal.



**Figure 5:** Schematic drawing of intraspecific variation in nuchal-neural 1 contact in different specimens of *Phrynops williamsi* (NHMUK 84-2-5-1) redrawing from Rhodin, et al. [64] (Figure 6) and (MACN 35395) redrawing from Cabrera [92] (Figure 4).

On the visceral surface, YPM 1565 (Figure 1B), the nuchal bone shows a hexagonal outline in contrast to the heptagonal dorsal shape. The cranial margin of this bone shows the impression of the cervical and a small portion of the marginal scutes 1; the impression of the remaining marginal scutes extends to the anterior peripheral bones. Although the two anterior neural bones are not easily distinguished, they seem to be present, and the posterior portion of the first thoracic vertebra and the posterior part of the second one are preserved. The remaining visceral neural surfaces (3-6) show scars on the upper portion of the neural arch. The anterior bridge strut scar (= axillary buttress) extends from peripherals 3 and 4 to most of the posterior margin of costal 1, almost in contact with the suture with costal 2 on the right side and nearly close to this sutural contact on the left one, with a central constriction and a medial end expansion.

Besides, YPM 1565 shows a 15-degree angle between rib/gomphosis and strut anterior bridge structure scar. In contrast, a subparallel margin of anterior bridge strut scar in *P. geoffroanus* (AMNH 79048, MZUSP 2635), *P. hilarii* (FMNH 22481, MHNSR-Z- 1550), and *P. williamsi* (MACN H-38395, USNM 306646) or some extinct *Phrynops* spp., as some specimens MCT (ex DGM) 302 R, 1472-R, are referred as superspecies (*Phrynops*) (*Phrynops*) (*geoffroanus*) spp. or specimen PVL 3351 from El Morterito Formation, Valle del Cajon (Catamarca province) (Figures 1 & 2) [8,10,12,48,93]. The posterior bridge strut scar (= inguinal buttress) in the holotype (YPM 1565) of *P. paranensis* (Figure 1B) extends on most of the lateral third extremes of posterior costal 5 and anterior costal 6 as other *Phrynops* spp. such as *P. hilarii*

(FMNH 22481, MHNSR-Z-1550) and *P. williamsi* (MACN-H-38395, USNM 306646, see Figures 2B & 3B), but only on costal 5 and peripheral 7-8 in *P. geoffroanus* (AMNH 79048, MZUSP 2635, see Figure 4B); but in contrast to them, the posterior bridge strut scar reaches in *P. paranensis* (YPM 1565) the medial ends of the peripheral bones 8-9.

The cervical scute is slightly longer than wide and covers most of the cranial part of the nuchal bone in YPM 1565 (Figure 1A). In contrast, extant *P. geoffroanus* (AMNH 79048, MZUSP 2635), *P. hilarii* (FMNH 22481, MHNSR-Z- 1550), *P. williamsi* (MACN-H- 35395) show a cervical scute longer than wide (Figures 2A,3A & 4A), as is also in some specimens of extinct species such as PVL 3351 from El Morterito Formation, Valle del Cajon (Catamarca province Argentina) (48, plate 1 Figures 1 & 2), whereas the specimen MCT (ex DGM) 301 R shows a shows a cervical scute significantly wider than long as was illustrated by Kischlat [93], plates 8, from late Oligocene-early Miocene, Tremembe Formation, Tabuate Basin, Sao Paulo, Brazil.

In YPM 1565 (Figure 1A), the intervertebral sulcus V1-V2 seems to cross the caudal portion of neural 1. In contrast, the intervertebral sulcus V2-V3 crosses the neural 3 and the intervertebral sulcus V3-V4 crosses the caudal portion of the neural 5.

The vertebral scute 1 is more expansive than long and shorter than the remaining vertebral scutes 2-3 and probably vertebral 4; a similar pattern is seen in *Phrynops* sp. (PVL

3351) from El Morterito Formation Late Miocene and in the identical specimens of *P. williamsi* (MACN-H-35395) or *P. geoffroanus* (AMNH 79048), but not in other specimens of the same species (USNM 65116) or in *P. hilarii* (MHNSR-Z-1550, MZUC III. 1212) the latter as illustrated by Cabrera [92]. In YPM 1565, vertebral 1 covers the nuchal, a slight portion of caudal of peripheral 1, a possible anterior portion of neural 1 if present, and a medial part of both costal 1. The vertebral 2 covers the caudal portion of neural 1, neural 2, the cranial portion of neural 3, and the medial portion, both costal 1-3. The vertebral 3 covers the caudal portion of neural 3, neural 4, and most of neural 5, as well as medial parts, both costal 3 to 5. The cranial portion of vertebral 4 covers the most caudal portion of neural 5 and neural 6 and a short medial portion of costal bones 5 and 6.

Both pleural scutes 1 are trapezoidal, and the remaining are subrectangular, covering both sides of the carapace. Pleural 1 covers most of costal 1, the cranial portion of costal 2, and the slightly caudal portion of peripheral 2 and 3. Pleural 2 covers the caudal portion of costal 2, costal 3, and cranial portion of costal 4. Finally, pleural 3 covers the caudal portion of costal 4, costal 5, and the cranial portion of costal 6. As is typical in turtles in YPM 1565 (Figure 1A) the marginal scutes cover both sides of lateral extremes of the carapace. The marginal scutes 1-2 are trapezoidal, and marginals 3-7 are subrectangular, whereas the remaining posterior preserved are trapezoidal. The marginal scute 1 covers a lateral portion of the nuchal bone and the same portion of peripheral 1, whereas the remaining marginal scutes cover two alternative successive peripheral bones.

## Discussion

### Taxonomic Comments

The inclusion of the holotype of *Parahyraspis paranensis* plus the refereed specimens to the same taxon [48, plate II] in Pleurodira Chelidae is recognized by having the left half pelvic girdle (pubis, ischium and ilium) attached by suture to the shell as is seen in [48], plate II in specimen MLP 70-VIII-21-18, absence of mesoplastron (MLP-79-VIII-21.20), a cervical scute on the cranial margin of the carapace nuchal bone, and the loose attachment between carapace and plastron in the holotype YPM 1565 (Figures 1A & 2B). When Wieland, a century before, described *Parahyraspis paranensis*, he interpreted several pit bridges present in the peripheral bridge margin (Figures 1B & 1C) for the supposed reception of short plastral digitations and the existence of lateral hyo-hypoplastral fontanella (Figure 1C). However, the plastron is missing in the holotype.

Considering that the *Parahyraspis paranensis* was erected by Wieland based on supposed structures not

present in the preserved plastral bridge of extant *Phrynops* spp., where minor pitting is present in the peripheral border. The validation of the genus *Parahyraspis* is not possible. Besides, the presence of a continuous series of at least the last five neural plates and a possible contact between the nuchal and the neural 1 in YPM 1565 differentiates the material under study from *Platemys*, *Acanthochelys*, and *Mesoclemmys* [26,55]. The holotype and same referred specimen of *P. paranensis*, in turn, differs from *Platemys* by the absence of the well-developed longitudinal ridges of the carapace and from *Acanthochelys* by the absence of a shallow midline depression of the carapace and from both aforementioned short-necked South American general by the presence of neural bones, and mid-size shell in comparison with the small size in *Platemys platycephala* and *Acanthochelys* spp., except for *Acanthochelys macrocephala*. YPM 1565 differs from most species of *Mesoclemmys* by having an uninterrupted neural series and a shell middle size. [55,59,94,95] most species of *Mesoclemmys* [96], *M. dahli* [97], *M. nasuta* [65], *M. raniceps* [98], *M. tuberculata* [99], and some specimens of *M. zuliae* [67] lack neural bones or have a low number of neurals displaying in an interrupted series such as *M. gibba*, (MHNSR-Z -1551), and *M. vanderhaegei* (MZUC Ac-399) as is shown in [92], they do not reach the nuchal, allowing the medial contact between the costal 1 [55]. Only *M. vanderhaegei* is distributed in Argentina [92,100,101]. These extant *Mesoclemmys* species differ from extinct and extant *Phrynops* spp. in the carapace by the presence of three (MZUC- Ac 399) or four (MNHN- P unnumbered) discontinuous neurals as shown [102].

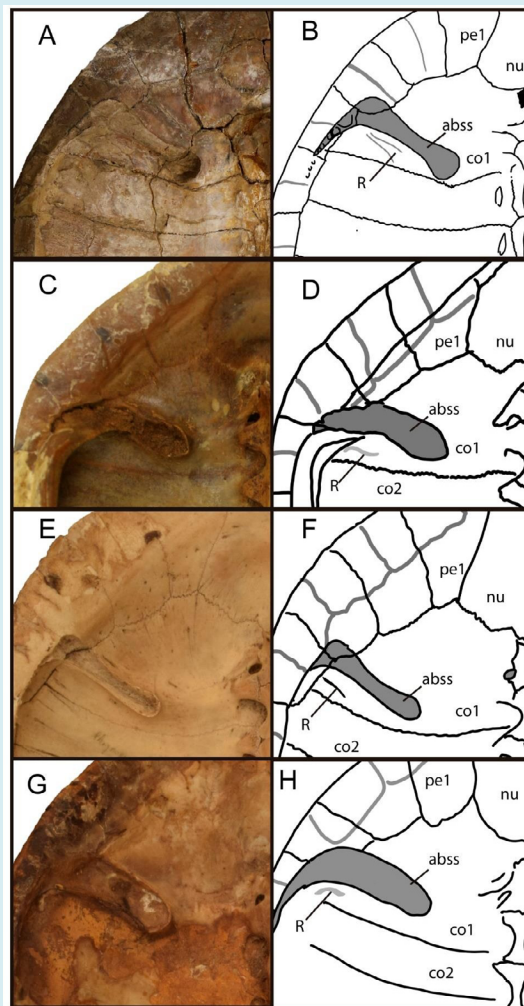
*Acanthochelys* and *Phrynops sensu stricto* is, until now, the only genera of Chelinae recorded from the late Miocene and Pliocene of Argentina. The specimens previously assigned to the latter genus come from outcrops of the El Morterito Fm. (late Miocene); see [103] at Valle del Cajon, Catamarca Province, and from the Andalhuala Fm (late Miocene) at Tio Punco locality, Tucuman Province [48]. As stated above, the genus *Phrynops sensu stricto* is currently comprised of the following extant species: *P. geoffroanus*, *P. hilarii*, *P. tuberosus* and *P. williamsi*, which are part of a supra-specific complex named by [64] as the *P. geoffroanus* complex [14,25,59,92]. In addition, the extinct species *P. paranaensis* from the Late Miocene of Mesopotamia was also referred to in the aforementioned complex by [48]. Posteriorly, Kischlat, in its Magister Thesis, described in 1993 several specimens refereed, as unnamed spp., to the superspecies (*Phrynops*) (*Phrynops*) (*geoffroanus*) from Temembe Formation (late Oligocene-early Miocene), Tabuate Basin, Sao Paulo State, Brazil.

The differences among species of *Phrynops sensu stricto* are mainly observed in characteristics of the scutes of the carapace and the carapace axillary buttress = anterior bridge strut scar; showing differences between the design of this structure and the angle between the rib/gomphosis

and the anterior bridge strut suture scar on the first costal bone as is shown in Australasian chelids such as *Elseya* spp. and other short-necked taxa from Australasia [104-107]. Differences in this structure on the visceral carapace are also distinguished in extant and extinct *Phrynops* spp. (see below).

Considering the similar plates and scute carapace and plastral morphological patterns between the *Phrynops* specimens from late Miocene El Morterito and Andalhuala Formations (PVL 3351, 3152 respectively), but the different morphology of the bridge strut suture scar between the specimen PVL 3351 from El Morterito Formation, Valle del Cajon (Catamarca province), [48, plate 1, figures. 1 & 2], some specimens MCT (ex DGM) 302 R, 1472-R, referred to as superspecies (*Phrynops*) (*Phrynops*) (*geoffroanus*) spp. (plates Figures 2, 4 & 5) than *Phrynops paranensis*

(YPM 1565) [48,93]. These conditions allow us to suggest that different Miocene species seem to be present in South America. *P. paranensis* is characterized by a diagnostic design of the anterior bridge structure with an enlarged medial end in contact with the suture between costal 1-2, and a different angle between rib/gomphosis and the anterior bridge strut scar in the holotype (YPM 1565) from upper Miocene “Conglomerado osifero” from Ituzaingó Formation at Parana (Entre Rios province). In contrast to *P. paranensis* (Figures 6A & 6B), a different design of the anterior bridge strut scar, and the angle between rib/gomphosis and the anterior bridge strut scar is shown in extant *P. geoffroanus* (AMNH 79048, MZUSP 2635) (Figures 6C & 6D), *P. hilarii* (FMNH 22481, MHNSR Z- 1550, NHMUK 86-3-10-1), (Figures 6E & 6F) and *P. williamsi* (MACN-H 38395, USNM 306646) (Figures 6G & 6H).



**Figure 6:** Photographs and drawings of visceral views of the anterior carapace in *Phrynops* spp., showing the anterior bridge carapace scar (abss) design and the angular relationships between it and the rib/ gomphosis (R) (A-B) *Phrynops paranensis* (YPM 1565), (C-D) *P. geoffroanus* (AMNH 79048), (E-F) *P. hilarii* (MHNSR-Z 1550), and (G-H) *P. williamsi* (MACN-H-38395).



Likely, the *Phrynops* sp. (FCVPV-319) described by [108] resembles *P. paranensis*. However, its assignment to *P. paranensis* seems to be possible, as was previously suggested by [108] in the relatively greater width of the cervical scute and the proportions of the last preserved marginals in the holotype of *P. paranensis* (YPM 1565) and FCVPV-319. However, until the visceral surface of the carapace of the Uruguayan specimen is exposed, the diagnostic condition of the anterior bridge strut scar present in the holotype YPM 3536 could not be identified in FCDPV-319, this assessment cannot be supported.

Although a recent total-evidence phylogeny [28] nested *P. paranaensis* inside a stem panchelid node composed of Cretaceous taxa with mesoplastra from Patagonia, this seems to be a spurious result due to the poor preservation of the shell of the holotype of *Phrynops paranaensis*. Whether a mesoplastron is absent in this Miocene taxon, as in post-Paleocene chelids, can only be determined with a preserved plastron in the holotype of *P. paranaensis*. However, from the hyo-hypoplastral contact as is seen in referred specimens (MLP 79-VIII-21-3 and MLP-79-VIII-21-20) recovered at “Conglomerado osifero” lower levels included in Ituzaiingó Formation outcrop along the Parana river at Parana city suggest the absence of mesoplastron in these exemplars that can be referred to *P. paranensis*.

### Paleoenvironment Setting from the “Conglomerado osifero” Ituzaiingó Formation

A panoramic paleoenvironmental scenario from the “Conglomerado osifero” of Ituzaiingó Formation was presented by [91]. According to these authors, the paleogeographic location of Parana, in the subtropical to temperate belts, is confirmed by the absence of crocodylids, podocnemidid turtles, and primates. The taxonomic reptile diversity, particularly, allows these authors to suggest a varied paleoenvironment to these lower levels of the Ituzaiingó lithostratigraphic unit. For instance, the predominance of aquatic birds in these lower levels suggests the presence of woody lowlands and swamps along the riverbanks [91]. In addition, rheas and phorusrhacoids support a savannah-like near the river sides [109,110]. The presence of glyptodonts allows [91] to suggest the existence of gallery forests outside of the pre-Parana River.

Considering tardigrade diversity must have been related to a heterogeneous landscape controlled by the Pre-Parana River and its affluents. The Interatheriidae Interatheriinae and protherotheriids notoungulates also seem related to woody and wet environments. The occurrence of porcupine rodents and procyonids also suggests forested paleoenvironments.

### Conclusion

The re-study of holotype and the referred specimens to “*Parahyraspis*” *paranensis* from “Conglomerado osifero” Ituzaiingó Formation crop out along Parana river at Parana city allows us to propose the validation of *Phrynops paranensis* as a full valid species. The continental terrestrial and aquatic fauna from the “Conglomerado osifero” indicate a warmer climate than the present one and suggest the presence of forested areas along the coasts of the pre-Parana River and its affluents.

This paleoenvironment was inhabited by the chelid turtle *Phrynops paranensis*.

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