

UNIVERSIDADE DE SÃO PAULO  
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO  
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

**Descrição osteológica de *Chelus* (Pleurodira: Chelidae) fósseis e viventes**  
**Osteological description of the fossil and extant *Chelus* (Pleurodira: Chelidae)**

Donato Jesus Martucci Neto

Dissertação apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, como parte das exigências para obtenção do título de Mestre em Ciências, obtido no Programa de Pós-Graduação em Biologia Comparada

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VERSÃO CORRIGIDA

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Orientadora: Profa. Dra. Annie Schmaltz Hsiou  
Co-orientador: Dr. Gabriel de Souza Ferreira

Ribeirão Preto – SP

2024

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## RESUMO

Martucci Neto, D.J. Descrição osteológica de *Chelus* (Pleurodira: Chelidae) fósseis e viventes. Dissertação de Mestrado – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, Ribeirão Preto, 2024.

Testudines é um clado composto por duas linhagens irmãs, Cryptodira e Pleurodira, ambas com representantes viventes e fósseis, que se diferenciam principalmente pela forma de retração do pescoço para dentro do casco: verticalizada e lateralmente, respectivamente. A Formação Solimões, na Bacia do Acre, que aflora entre os estados do Acre e do Amazonas, contém a fauna fóssil mais diversificada de amniotas neógenos do Brasil. Os afloramentos são encontrados principalmente nas margens erosivas dos rios Purus, Acre e Juruá, entre outros, desde o século XIX. Até o momento, assim como registrado em outros depósitos neógenos do norte da América do Sul, a maioria das tartarugas fósseis da Amazônia brasileira é representada principalmente por gêneros atribuídos às famílias Chelidae, Podocnemididae e Testudinidae. O gênero *Chelus* (Chelidae) — popularmente conhecido como mata-mata —, representado por duas espécies recentes, *Chelus fimbriata* e *Chelus orinocensis*, tradicionalmente também inclui duas espécies extintas: *Chelus colombiana* e *Chelus lewisi*. Nesta dissertação, descrevemos e revisamos fósseis do gênero *Chelus* que estão depositados na coleção do Laboratório de Pesquisas Paleontológicas da Universidade Federal do Acre (campus Rio Branco). Além disso, realizamos uma descrição osteológica detalhada da espécie *Chelus orinocensis*, utilizando modelos 3D criados a partir de tomografias realizadas em uma pequena amostra de espécimes. A descrição do material fóssil, utilizando como meio de comparação morfológica espécimes de *Chelus fimbriata*, permitiu-nos observar que certas características que ocorrem como variação intraespecífica nas espécies viventes podem ocorrer da mesma maneira nos fósseis. As comparações morfológicas e análises de variações intraespecíficas permitiram-nos confirmar que apenas a espécie fóssil *Chelus colombiana* é válida para o gênero. A descrição osteológica detalhada da espécie *Chelus orinocensis* permitiu-nos criar um atlas anatômico para a espécie, que esperamos auxiliar em comparações anatômicas futuras.

**Palavras-chave:** Pleurodira, paleontologia, Osteologia, Bacia do Acre, *Chelus*.

Martucci Neto, D.J. Osteological description of the fossil and extant *Chelus* (Pleurodira: Chelidae). Master Dissertation – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, Ribeirão Preto, 2024.

## **ABSTRACT**

Testudines is a clade consisting of two sister lineages, Cryptodira and Pleurodira, both with living and fossil representatives, which differ mainly by the way the neck retracts into the shell: vertically and laterally, respectively. The Solimões Formation, in the Acre Basin, which outcrops between the states of Acre and Amazonas, contains the most diverse fossil fauna of neogene amniotes in Brazil. The outcrops are mainly found on the erosive margins of the Purus, Acre, and Juruá rivers, among others, since the 19th century. So far, as recorded in other neogene deposits in northern South America, most of the fossil turtles of the Brazilian Amazon are represented mainly by genera attributed to the families Chelidae, Podocnemididae, and Testudinidae. The genus *Chelus* (Chelidae) - popularly known as mata-mata represented by two recent species, *Chelus fimbriata* and *Chelus orinocensis*, traditionally also includes two extinct species: *Chelus colombiana* and *Chelus lewisi*. In this dissertation, we describe and review fossils of the genus *Chelus* that are deposited in the collection of the Laboratory of Paleontological Research of the Federal University of Acre (Rio Branco campus). In addition, we performed a detailed osteological description of the species *Chelus orinocensis*, using 3D models created from tomographies performed on a small sample of specimens. The description of the fossil material, using as a means of morphological comparison specimens of *Chelus fimbriata*, allowed us to observe that certain characteristics that occur as intraspecific variation in living species can also occur in fossils. Morphological comparisons and analyses of intraspecific variations allowed us to confirm that only the fossil species *Chelus colombiana* is valid for the genus. The detailed osteological description of the species *Chelus orinocensis* allowed us to create an anatomical atlas for the species, which we hope will assist in anatomical comparisons in future work.

**KEYWORDS:** Pleurodira, Paleontology, Osteology, Acre Basin, *Chelus*.



## INSTITUTIONAL ABBREVIATIONS

**LPP.** Laboratório de Pesquisas Paleontológicas, Rio Branco, Brazil.

**UFAC.** Universidade Federal do Acre, Rio Branco, Brazil.

**FFCLRP-USP.** Faculdade de Filosofia, Ciência e Letras de Ribeirão Preto, Ribeirão Preto, Brazil.

**LPRP.** Laboratório de Paleontologia de Ribeirão Preto, Ribeirão Preto, Brazil.

**IAvH.** Alexander von Humboldt Biological Resources Research Institute

**MPEG.** Museu Paraense Emílio Goeldi, Belém, Brazil.

**INPA.** Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil

**MZUSP.** Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil,

**SMF.** Senckenberg Museum Frankfurt.

## ANATOMICAL ABBREVIATIONS

**Aa** – Anterior articulation

**abd** – Abdominal scute

**Ace** – Acetabulum

**Acp** – Acromial process

**ALW** – Anterior Lobe Width

**An** – Anal notch

**ana** – Anal scute

**as** – Astragalus

**Ax** – Axillary scar

**C** – Centralia

**c** – costal

**c** – medial centrale

**ca** – Coracoid articulation

**ca'** – Calcaneum

**cr** – Crest

**dc** – distal carpal

**distE** – Distal End

**dp** – distal phalange

**dt** – distal tarsals

**En** – Entoplastron

**Ep** – Epiplastron

**ext** – Extragular scute

**Fas** – femoroanal sulcus

**fem** – femoral scar

**Fia** – Fibular articulation

**gle** – glenoid

**gle** – glenoid

**gul** – Gular scute

**hum** – Humeral scute

**Hyo** – Hyoplastron

**Hypo** – Hypoplastron

**i** – intermedium

**ill** – Illium

**Ing** – Inguinal scar

**Int F** – Intertubercular fossa

**Isc** – ischial scar

**Isc** – Ischium

**lc** – lateral centrale

**lp** – lateral process

**lp** – Lateral process

**mc** – medial centrale

**mc** – metacarpal

**Mp** – Medial process

**mt** – metatarsal

**mths** – metatarsal with hooked shape

**n** – neural

**nc** – nuchal

**ns** – neural spine

**p** – peripheral

**p** – pygal

**Pa** – Posterior articulation

**Pec** – Pectoral scute

**pp** – proximal phalange

**proE** – Proximal End

**Ps** – Pleural scute

**Psc** – pubic scar

**ptz** – postzygapophyse

**ptz** – postzygapophyse

**Pub** – Pubis.

**pzf** – prezygapophyse

**pzf** – prezygapophyse

**Scp** – Scapular process

**sp** – suprapygal

**Tf** – trochanteric fossa

**Tia** – Tibial articulation

**Tma** – Trochanter major

**Tmi** – Trochanter minor

**tp** – transverse process

**ul** – ulnare

**un** – unguis

**Vs** – Vertebral scute

**Xiphi** – Xiphiplastron

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## GENERAL BACKGROUND

The present Master's dissertation consists of two chapters. The first chapter focuses on the osteological description of the post-cranium of the species *Chelus orinocensis*, using segmentation and 3D modeling techniques. The second focuses on fossils of *Chelus colombiana* from localities within the Solimões Formation, Acre Basin. In summary, this second chapter identifies and describes fossils of *C. colombiana* collected during paleontological expeditions over time, also comparing the osteology of the fossils with the living species *Chelus fimbriata*.

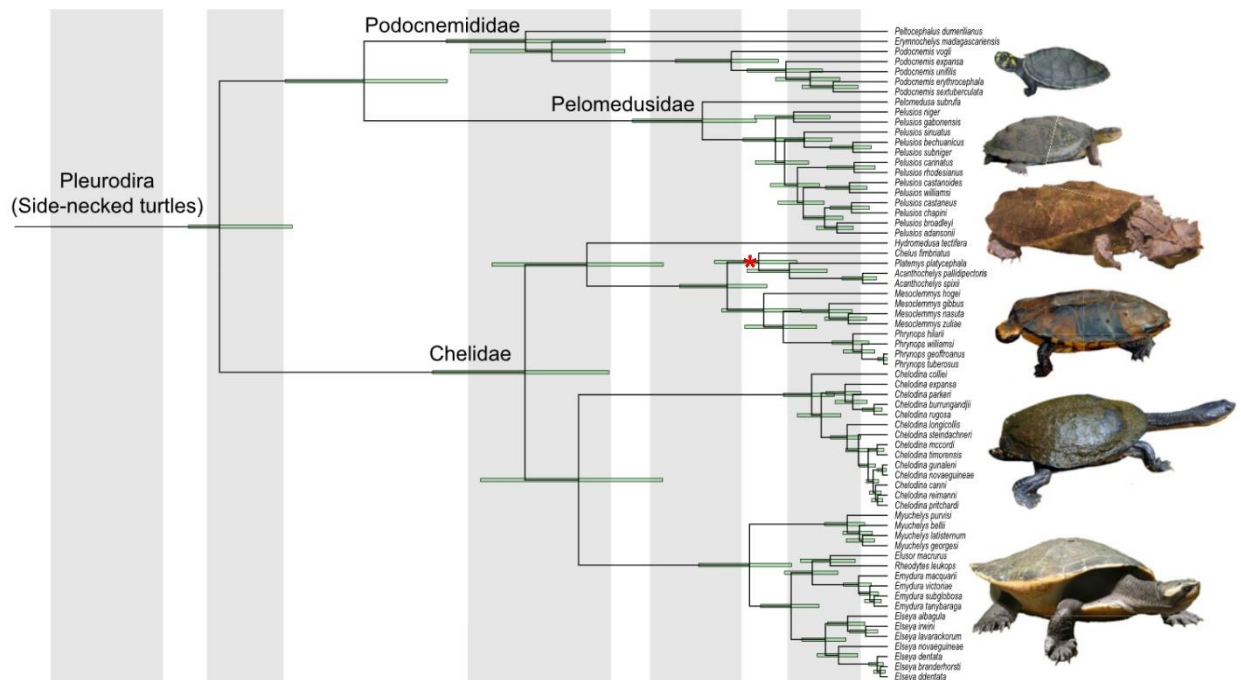
### Testudines

Testudines Batsch, 1788 (turtles and tortoises) is a clade composed of two sister lineages, Cryptodira and Pleurodira, with living and fossil representatives, which differ mainly in the way the neck is retracted into the shell (Herrel et al., 2008). Cryptodira retracts their neck in a vertical plane, while Pleurodira does so in a horizontal plane (Bour, 2007, Herrel et al., 2008). Turtles have unique and distinct morphological characteristics from all other tetrapods, the most striking being the presence of a bone shell divided into a dorsal carapace and a ventral plastron. Although the earliest fossil records indicate the origin of shelled reptiles in the Triassic with the *Proterochersis robusta* being the oldest representative of Testudines (Gaffney and Meylan, 1988; Shaffer et al., 1997; Lapparent de Broin, 2000; Gaffney et al., 2006), more recent phylogenetic analyses suggest the crown-group Testudines' origin around 220 and 200 million years ago (Pereira et al. 2017; Thomson et al., 2021).

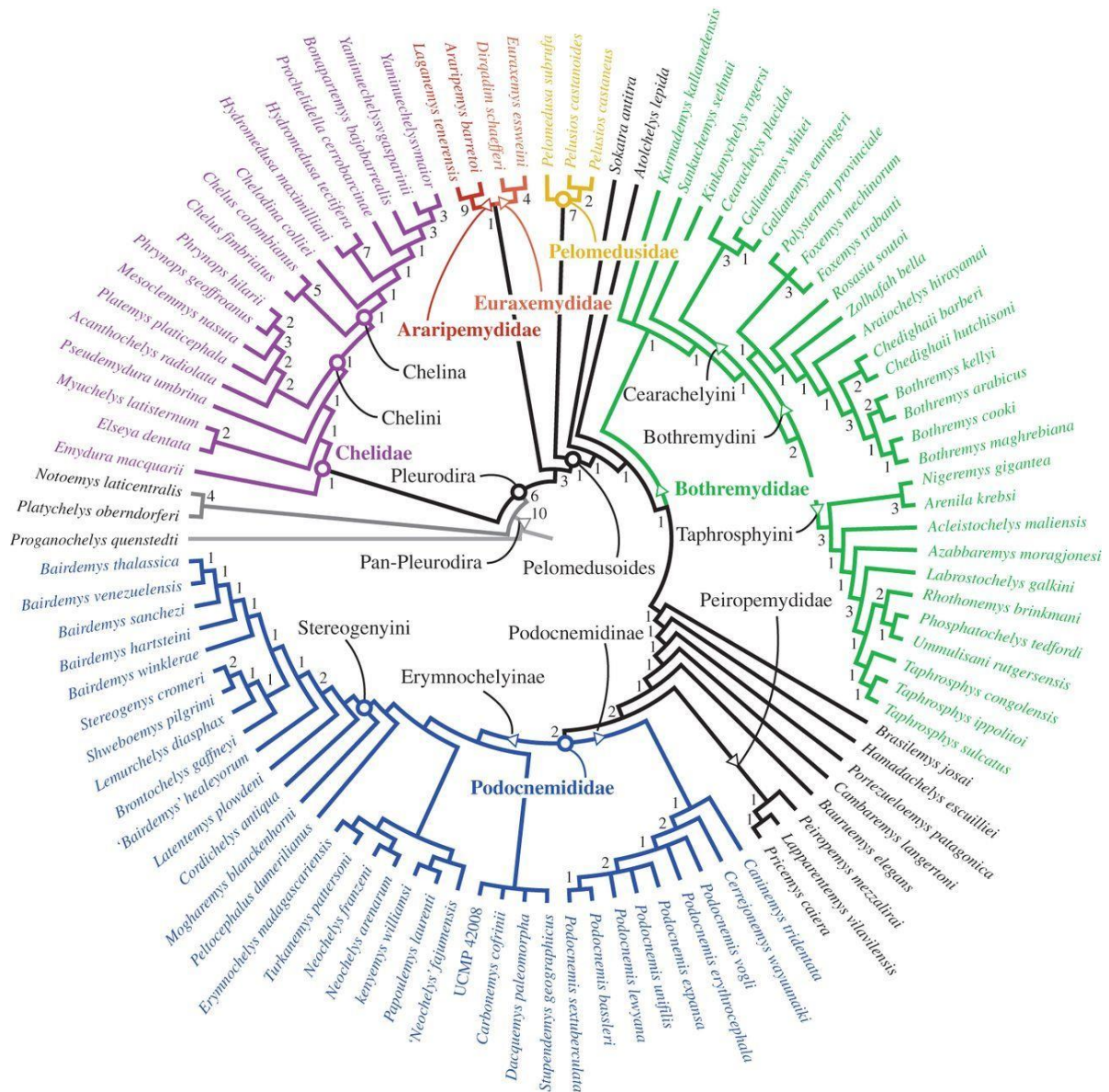
Currently, modern turtles exhibit a low species diversity when compared to other groups of tetrapods, consisting of about 357 known extant species (Rodhin et al., 2021), whereas Squamates comprise 11,302 species (Evans, 2003; Uetz et al., 2022), Anura 7,055, and Rodentia 2,375 (IUCN, 2023). Cryptodira, including 261 extant species; and Pleurodira, with 96 extant species (Rodhin et al., 2021). Cryptodires are globally distributed and include

freshwater, marine, and terrestrial turtles. They are traditionally divided into four lineages with eleven families: Emydidae, Testudinidae, Geoemydidae, Platysternidae, Carretochelyidae, Trionychidae, Chelydridae, Dermatemydidae, Kinosternidae, Cheloniidae, and Dermochelyidae (Bour, 2007).

Pleurodires are divided into three lineages with extant (Chelidae, Podocnemididae, and Pelomedusidae) and fossil representatives (Araripemydidae, Euraxemydidae, and Bothremydidae) (Gaffney et al., 2006, Ferreira et al., 2018). Currently, the extant lineages are restricted to freshwater environments of South America, Africa-Madagascar, and Australasia. In the past, however, they were distributed across the globe, occurring in Eurasia, India, and North America, and they also included marine representatives (Gaffney et al., 2006; Cadena, 2015; Ferreira et al., 2015; Joyce et al., 2016; Ferreira et al., 2018).



**Figure 1.** Cladogram showing phylogenetic relationships in Pleurodira, without fossil representatives. Modified from Thomson et al. (2021).



**Figure 2.** Consensus tree illustrating the relationships among pleurodira, including extant and extinct lineages. Adapted from Ferreira et al., 2018.

### Fossil record in South America

Fossil Testudines, are quite common throughout the South American Cenozoic, as most fossils are represented by complete or isolated elements of the carapace and plastron, which are structures that easily preserve due to the morphology of the shell, composed of resistant materials, making disarticulation difficult after the animal's death and consequently facilitating the preservation of hard parts. In South America, a large portion of fossils found throughout the Cenozoic are from the Paleogene and Neogene deposits of Venezuela,

Colombia, Peru, Argentina, and Brazil, from the middle Paleocene to the upper Miocene. Thus, the fossil content of the South American Cenozoic is rich and relatively diverse, represented by various fossils attributed to Cryptodira (Trionychidae and Testudinidae) and Pleurodira (Chelidae and representatives of the clade Pelomedusoides [Pelomedusoidae + Podocnemididae]).

Overall, the fossil record of cryptodires is less diverse when compared to pleurodires, being found throughout the Miocene of Brazil, Venezuela, Peru, and Colombia. Among the fossils of this group, the Trionychidae (softshell turtles) are currently only present in the upper Miocene/lower Pliocene of Venezuela (see Head et al., 2006; Sánchez-Villagra and Scheyer, 2010), where the extant forms are completely aquatic and found in Asia, Africa, Indo-Australia, and North America. Meanwhile, the Testudinidae are found from the lower and middle Miocene of Colombia and late Miocene of the Brazilian Amazon, represented by the genus *Chelonoidis* (Wood, 1997; Cadena and Jaramillo, 2015; Bocquentin-Villanueva et al., 1991; 1996a e b), as well as for the middle Miocene of Bolivia (Cadena and Jaramillo, 2015), and for the late Pleistocene of Venezuela, fossils attributed to the genus *Chelonoidis* have been described.

The oldest pleurodires in the South American Cenozoic are known from the Paleocene deposits of Colombia, represented by the Bothremydidae and Pelomedusoides, from the Cerrejón, Los Cuervos, and Lisama formations in Colombia (Cadena et al., 2012; Cadena and Schweitzer, 2014; Cadena, 2020). During the Neogene, the localities that stand out in terms of abundance and diversity of pleurodire taxa include geological units from Venezuela, with the genus *Bairdemys* (Podocnemididae) exhibiting at least four known species: *B. winklerae*, *B. sanchezi*, *B. venezuelensis*, and *B. thalassicat* (Wood and Díaz, 1971; Gaffney and Wood, 2002; Riff et al., 2010; Sánchez-Villagra and Scheyer, 2010). Also, for the Miocene of Venezuela, it is from the Urumaco Formation (upper Miocene) the first description of the



giant species *Stupendemys geographicus* (Podocnemididae), (Wood, 1976), being considered the largest freshwater turtle that ever existed (Sánchez-Villagra and Scheyer, 2010; Cadena et al., 2020). Additional records of Podocnemididae have been reported for the Fitzcarrald Local Fauna, middle Miocene of Peru (Antoine et al., 2007), and upper Miocene of the Madre Dios Formation in Bolivia (Riff et al., 2010) and the Miocene of the Brazilian Amazon (Hsiou et al., 2022).

### **Acre Basin and Solimões formation**

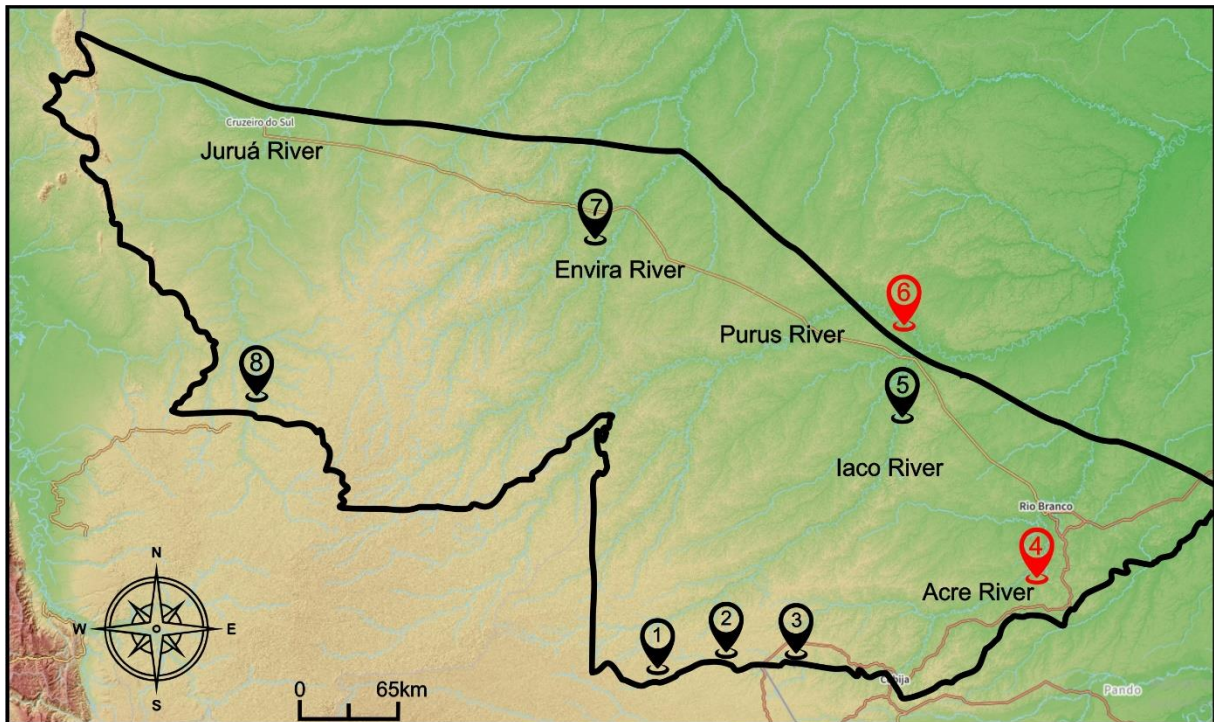
The Acre Sedimentary Basin, with a total area of approximately 150,000 km<sup>2</sup>, is located in the northwest portion of Brazilian territory, between latitudes 6° S and 9° S and longitudes 72° 30' W and 74° W (Cunha 2007). It is a sedimentary basin bordered by the Iquitos Arch to the east (which separates it from the Solimões Basin), extending from the north/northwest and south/southeast to the Ucayali and Madre de Dios basins (Cunha 2007; Wanderley et al. 2010). The chronostratigraphic range of the Acre Basin stands out among Brazilian sedimentary basins for preserving a rich and vast diversity of fossil vertebrates. Among the formations found in the Acre Basin, the Solimões Formation is the youngest, representing a geological unit from the Lower Eocene to the Pliocene (Negri, 2004; Cozzuol, 2006).

In Brazilian territory, the Solimões Formation is widely distributed across much of the state of Acre and a small part of the state of Amazonas. Outside Brazilian territory, outcrops can be found in Peru and Bolivia (Lacerda et al., 2021). Regarding the deposition age of the fossil-bearing layers, studies indicate an age corresponding to the Upper Miocene (Cozzuol, 2006; Latrubesse et al., 2007; Negri et al., 2010). Recent absolute dating studies conducted by Bissaro-Júnior et al. (2019) corroborated the Upper Miocene age. Analyses for dating were performed at five fossiliferous localities in the region, with Seringal Talismã (Purus River) and Niterói (Acre River), and three localities in the Upper Juruá River (PRJ 20, PRJ 26, and PRJ 34) being chosen for dating (Bissaro-Júnior et al., 2019). For the Niteroi locality, an age

of  $8.5 \pm 0.5$  Ma was obtained, while for Talismã, the age was  $10.89 \pm 0.13$  Ma (Bissaro-Júnior et al., 2019). These results confirm an Upper Miocene age for these two localities, refuting previous hypotheses that placed much of the vertebrate biota from these localities between the Miocene/Pliocene (Huayquerian-Montehermosan)

In relation to the paleofauna associated with the Solimões Formation, it is widely recognized for its extensive fossil record, with an emphasis on vertebrates (Cozzuol, 2006; Negri et al., 2010; Ribeiro et al., 2013; Riff et al., 2010; Souza-Filho and Guilherme, 2015; Hsiou et al., 2022). Fossil material from the Solimões Formation is generally collected in fluvial (river) deposits and, in rare cases, along road cuts and riverbanks. Thus, fieldwork mainly focuses on the Juruá River, northwest of Acre, and the Purus, Acre, and Iaco Rivers, between the southern and western Amazonas state. The mammal fossil record has representatives of two major clades, the Metatheria, which are quite rare, and the Eutheria, which constitute the dominant group of mammals. Metatherians (marsupials) are represented only by the clade Didelphimorphia. Eutherians (placental mammals) are the most diversified and abundant taxa of the Solimões Formation, being represented by members of the four major groups that make up the clades: Laurasiatheria, Euarchontoglires, Afrotheria, and Xenarthra (Asher et al., 2009; Hsiou et al., 2022). The vast majority of fossils are of medium to large-sized animals, except for marsupials (Czaplewski, 1996; Cozzuol et al., 2006), small rodents (Kerber et al., 2017a), bats (Czaplewski, 1996), and primates (Kay and Frailey, 1993; Kay and Cozzuol, 2006). Reptiles found in the Solimões Formation are well-known due to the great diversity of extinct forms of crocodyliforms and turtles and their gigantic dimensions, such as the crocodyliform *Purusaurus brasiliensis* and the turtle *Stupendemys* (Riff et al., 2010; Negri et al., 2010), in addition to various fossils of scaled reptiles (lizards and snakes) recognized (see Hsiou, 2010; Hsiou and Albino, 2009, 2010; Hsiou et al., 2009, 2010). A few

recorded bird fossils from the Solimões Formation belong to the Anhingidae family (Macranhinga and Anhinga) (Alvarenga and Guilherme, 2003; Guilherme et al., 2023).



**Figure 3.** Map of the state of Acre, showing rivers with outcrops, and the main outcrops where fossil testudines have been found, with those in red indicating locations with absolute dating. 1. Patos (Acre River); 2. Cavalcante (Acre River); 3. Cachoeira do Bandeira (Acre River); 4. Niterói (Acre River); 5. Lula; 6. Talismã (Purus River); 7. Morro do Carreca; 8. Cantagalo (Upper Juruá River). Locations collected from Annie et al., (2022).

### Testudines in the Acre Basin

Particularly in the Brazilian Amazon, the Solimões Formation (Acre Basin) contains the most diverse fossil fauna of Neogene amniotes in Brazil, with exposure areas in the states of Acre and Amazonas (Cozzuol, 2006). The outcrops are mainly found on the erosive banks of the Purus, Acre, and Juruá rivers, among others, since the 19th century (Cozzuol, 2006; Riff et al., 2010), and have been assigned an upper Miocene age (Bissaro-Júnior et al., 2019). So far, as recorded for other Neogene deposits in northern South America, all fossils from the Brazilian Amazon are mainly represented by genera attributed to Chelidae, Podocnemididae, and Testudinidae (Oliveira and Romano, 2007; Riff et al., 2010; De la Fuente et al. 2014).

Paleontological expeditions have been conducted in various sites of the Solimões Formation since the 1970s. As a result of these countless expeditions, numerous specimens of Testudines have been studied and cataloged. Within the crown group Pleurodira, two major families have fossil representatives in the Solimões Formation: Chelidae and Podocnemidae. The known Podocnemidae include *Caninemys tridentata* (Meylan et al., 2009), *Stupendemys geographicus* (Negri and Bocquentin 1991; Lapparent de Broin et al., 1993, Bocquentin & Guilherme (1997), Negri & Bocquentin (1998), *Stupendemys souzai* (Bocquentin and Melo 2006), *Podocnemis negrii* (Carvalho et al. 2002) and a possible new species of the genus *Podocnemis* (Dumont Júnior, 2013). *C. tridentata* was described based on a skull, however, in Meylan et al. (2009) and Gaffney et al. (2011), the authors emphasize that the skull attributed to *C. tridentata* cannot be distinguished from the shell of *Stupendemys geographicus*. The assignment of *S. souzai* to the referred genus is criticized, Meylan et al. (2009) and Gaffney et al. (2011) considered the presented characteristics as insufficient to designate *S. souzai* as a new species, therefore only *S. geographicus* was considered a valid species for the genus, while *P. negrii* was considered as *incertae sedis* for a long time (Meylan et al., 2009; Gaffney et al., 2011). However, the unpublished phylogenetic analyses conducted by Dumont Júnior (2013) identified *P. negrii* as the sister taxon of *P. sextuberculata*. Among the Chelidae, the genus *Chelus* is the only taxon known from the fossil record of the Solimões Formation, which will be discussed in the next section.

### **The genus *Chelus***

The genus *Chelus* (Chelidae) — popularly known as mata-mata — is represented by two living species: *Chelus fimbriata* Schneider, 1783 and *Chelus orinocensis* Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Farias, Hrbek, Campbell and Fritz, 2020. It has traditionally also included two extinct species: *Chelus colombiana* Wood, 1976 and *Chelus lewisi* Wood, 1976. The species of this genus have

unique characteristics among turtles, such as the extremely dorsoventrally flattened skull and highly ornamented body related to their camouflage and powerful suction-feeding behaviors (Lemell et al. 2002 and references therein). All mata-matas are fully aquatic and the extant species inhabit the Amazon and Orinoco rivers drainages in northeastern South America (Rhodin et al. 2021).

The occurrences of fossil *Chelus* have been reported and discussed in several publications (Barbosa Rodrigues (1892), Wood (1976), Bocquentin-Villanueva and Rancy (1987), Bocquentin-Villanueva and Santos (1989), Broin et al. (1993), Sánchez-Villagra et al. (1995), Antoine et al. (2007), Sánchez-Villagra and Scheyer (2010), Cadena and Jaramillo (2015), Ferreira et al. (2016), Cadena et al. (2023). The oldest records of the genus are found in the early Miocene of the Castilletes Formation in Colombia (Cadena and Jaramillo, 2015). In the middle to late Miocene, many specimens attributed to *C. colombiana* are known from Colombia (Wood, 1976; Cadena et al., 2023). From the same period, fossils assigned to *Chelus lewisi* have been reported for the Socorro and Urumaco formations of Venezuela (Sánchez-Villagra and Scheyer, 2010; Ferreira et al., 2016; Cadena et al., 2023), as well as specimens related to *Chelus* for the Local Fauna of Fitzcarrald, middle Miocene in Peru (Antoine et al., 2007). In Brazil, the presence of *Chelus* fossils has been reported since the late 80s, Bocquentin and Rancy (1987) describe fragmented materials that they attribute to the species *Chelus lewisi*, two years later Bocquentin and Santos (1989) describe new materials of carapace and plastron from the Rio Purus, classify it as *Chelus colombiana*. New materials were only reported 12 years later, with the work of Bocquentin et al., (2001), here the authors describe new materials of *Chelus colombiana* and *Chelus lewisi*, the materials consisted of nearly complete carapaces and isolated bones from the carapace and plastron, the material comes from three locations on the banks of the Purus, Acre and Alto Juruá rivers.

## **OBJECTIVES**

The present dissertation aims to describe and report new fossils of the species *Chelus colombiana* for the Miocene of the Brazilian Amazon, presenting new anatomical features for the carapace that shed light on the systematic issues of the group. Additionally, it seeks to provide a detailed description of the extant species *Chelus orinocensis*, which will play a fundamental role in comparison with extant and fossil species. The Chapter 1 presents a deep and detailed osteological description of the post-cranium of the species *Chelus orinocensis*. Using Micro-Computed Tomography ( $\mu$ CT) allowed us to scan and segment the specimens bone by bone, thus creating 3D models of each bone. Utilizing two ontogenetic stages also allowed the assessment of changes occurring during the species' growth. The Chapter 2 presents the description of the new fossils of the genus *Chelus*. The osteological comparisons demonstrated that *Chelus* has only one valid fossil species, *Chelus colombiana*. Therefore, the characteristics used to define *Chelus lewisi* are intra-specific variations occurring in *Chelus colombiana*.

## **CHAPTER 1 - OSTEOLOGICAL DESCRIPTION OF THE POST-CRANIUM OF *CHELUS ORINOCENSIS* - USING MICRO CT SCANNER TO CREATE 3D MODELS**

### **Abstract**

The crown group of Pleurodira consists of three lineages with extant representatives: Chelidae, Pelomedusidae, and Podocnemididae. These turtles are widely distributed across freshwater environments in Africa, Australia, Madagascar, and South America. Among them, the Chelidae family is exclusively found in South America and Australia, with one of the most iconic representatives of this family in South America being the mata-mata turtles, two extant species: *Chelus fimbriata* Schneider, 1783, and *Chelus orinocensis* Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Farias, Hrbek, Campbell, and Fritz, 2020. These species exhibit a peculiar morphology, particularly their flat skulls, characterized by an extreme flattening of the anterior part, reduced eyes, tube-shaped snout, and an extremely wide mouth, but also an elongated neck with fringes along its length. The carapace displays three crests that extend over its dorsal surface, and the most notable feature of the plastron is the xiphiplastron bone, which presents a horn-shaped structure in the mid-posterior portion. Minimal information is available about the osteology of *C. orinocensis*, as its description was based on molecular analyses; therefore, in this work, we provide a detailed comparative osteological description of the post-cranium of *C. orinocensis* specimens.

**Keywords.** *Chelus fimbriata*. *Chelus orinocensis*. Pleurodira. Osteology. *Chelus*.

## 1. INTRODUCTION

The crown group of Pleurodira consists of three lineages with extant representatives: Chelidae, Pelomedusidae, and Podocnemididae. They have a wide geographic distribution, occurring in freshwater environments in Africa, Australia, Madagascar, and South America (Ferreira et al., 2018). The Chelidae family is exclusively found in South America and Australia, this geographical distribution has sparked debates surrounding the relationships of the long-necked chelids (*Chelodina*, *Hydromedusa*, and *Chelus*). Phylogenetic analyses based on morphological data have shown that the three genera of long-necked chelids, *Chelodina* (Australia), *Hydromedusa*, and *Chelus* (South America), do indeed constitute a monophyletic group (Gaffney, 1977; Bona and De La Fuente, 2005; De La Fuente et al., 2017; Ferreira et al., 2018). On the other hand, phylogenetic analyses based on molecular data suggest that Australasian and South American chelids are monophyletic. Seddon et al. (1997), in their analyses, found that *Chelodina* is more closely related to the short-necked Australasian genera than to *Chelus* or *Hydromedusa*. Subsequently, Georges et al. (1998) conducted a new analysis adding more molecular data, in this work the authors found that *Chelus* + *Hydromedusa* are monophyletic, but exclude *Chelodina*, furthermore, the authors make it clear that the analyses performed were not informative about the monophyly of *Chelodina* and the Australian chelids).

As mentioned above, the Chelidae family is exclusively found in South America and Australia, with 19 genera and over 60 species (Rhodin et al., 2021), and its members are predominantly carnivorous. They differ from other pleurodires by the following osteological characteristics: absence of the mesoplastron and quadratojugal, and the shape of the vertebral centrum along the cervical spine, which is represented as follows: [=)1(, (2(, (3(, (4(, (5),)6),)7(, (8) or biconvex atlas, three opisthocoelous cervicals, two biconvex, one procoelous, one biconcave, and one biconvex (Gaffney, 1977; Broin and De La Fuente,



1993). One of the most iconic representatives of this family in South America are the mata-mata turtles, with two extant species: *Chelus fimbriata* Schneider, 1783 and *Chelus orinocensis* Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Farias, Hrbek, Campbell and Fritz, 2020. These species exhibit a peculiar morphology, particularly their flat skulls, characterized by an extreme flattening of the anterior part, reduced eyes, tube-shaped snout, and an extremely wide mouth, but also an elongated neck with fringes along its length. The carapace displays three crests that extend over its dorsal surface, and the most notable feature of the plastron is the xiphiplastron bone, which presents a horn-shaped structure in the mid-posterior portion. This morphology is thought to be related to their highly specialized predation style, as they remain motionless on the riverbed and suck in approaching prey. This suction is accomplished by the combination of two factors: specialized muscles of the jaw, namely the external adductor and the posterior adductor, and the three muscles of the hyoid apparatus (branchiomandibular and the two geniohyoid muscles), which allow the hyoid to move posteroventrally, instead of anteriorly. The conjunction of these muscles creates a high-speed flow that pulls the prey into the oral cavity. Subsequently, the hyoid apparatus returns to its original position, causing all the water acquired during the suction movement to be expelled (Lemmel et al., 2002).

### 1.1 *Chelus fimbriata* and *Chelus orinocensis*

*Chelus fimbriata* was initially described as *Testudo terrestres major putamine echinato et striato* by Barrère (1741). Twenty years later, Fermin (1765) redescribed a new specimen, changing the name to *Testudo terrestris*. Subsequently, Schneider (1783) described new specimens attributed to the same species, giving it the name *Testudo fimbriata*. The first two names, however, are not valid according to Ceriaco and Bauer (2017), the names were invalidated by the International Commission on Zoological Nomenclature, as they appeared in

a work that did not adhere to the principles of binomial nomenclature (ICZN 1963), and, thus, the first valid name for the mata-mata is *Testudo fimbriata*.

In a review conducted by Dumeril (1805), he revised the taxonomy of the turtles previously described and reallocated them into four distinct genera according to their habits, shell morphology, and locomotor limbs: *Testudo Linnaeus*, 1758; *Emys Duméril*, 1805; *Chelonia Brongniart*, 1800; and *Chelus Duméril*, 1805. Only the species described by Bruguière (1792) was included in the genus *Chelus* (Garbin, 2014).

*Testudo bispinosa* was initially described by Daudin (1802). However, the characteristics used for its description were identical to those proposed by Bruguière (1792), being thus considered a junior synonym of *T. fimbriata* Schneider (1783). Gray also assigned various names to *Chelus* specimens: *Testudo rapara* (Gray, 1831), *Testudo raparara* (Gray, 1844), and *Testudo raxarara* (Gray, 1855). In some regions, "Raparapa" is the common name for *Chelus fimbriatus*, similar to "matamata"

According to the work of Ceríaco and Bauer (2017), the records made by the Portuguese naturalist Alexandre Rodrigues Ferreira during his expeditions to Brazil between 1783 and 1792 were only recently published. A.R. Ferreira conducted studies and described some specimens collected in the state of Pará, assigning them the name '*Testudo torticollis*'. However, of these records, only one watercolor painting was published in 2002, causing the name *Testudo torticollis* to not be a valid name and resulting in the name being infrequently mentioned in the literature (Ceríaco and Bauer, 2017). According to Garbin (2014), the name *Chelus fimbriata* only came to be used in scientific works after the name *Testudo fimbriata* Schneider, 1783, was considered officially valid by Opinion 660 of the International Code of Zoological Nomenclature (ICZN, 1963) and for an extended period, *Chelus fimbriata* remained the sole species within the genus *Chelus*. Despite this, morphological differences have always been noted among individuals from various populations. Schmidt (1966) initially

observed variations in carapace, plastron, and head coloration, as well as differences in the shape of the nuchal scute, cranial structure, and the configuration of the intergular scute (Rhodin et al., 2008). Pritchard and Trebbau (1984) compared the carapace shape of matamata populations from the Orinoco and Amazon basins, they observed that specimens from the Amazon had a rectangular carapace shape, while specimens from the Orinoco had an oval carapace shape. However, Garbin (2014) argued that the observed characters are insufficient to separate individuals from Amazon and Orinoco populations as independent species, pointing out that they do not exhibit character states entirely exclusive to the populations.

Recent analyses based on different populations of mata-mata have provided novel insights into this discussion. Using molecular data collected from specimens in populations from Colombia, Brazil, French Guiana, Guyana, and Peru, Vargas-Ramírez et al., (2020) showed that individuals inhabiting the Orinoco and Rio Negro basins exhibit genetic and morphological differences from those in the Amazon basin and the Essequibo and Mahury drainages, consistent with two separate lineages. Based on these results, a new species, *Chelus orinocensis*, was described as the sister taxon to the previously known *Chelus fimbriata*. Given that the species *C. orinocensis* was described based on molecular data, there is a lack of osteological information for the species. Therefore, in this work we perform the complete osteological description of the post-cranium of *C. orinocensis*.

## **1.2 MATERIAL AND METHODS**

### **1.2.1 Provenance**

In this study, we examined four specimens of *Chelus orinocensis*, collected from different rivers in Colombia during the 1980s and 1990s and currently part of the herpetological collection of the Senckenberg Naturmuseum in Frankfurt, Germany. They are four complete wet specimens preserved in alcohol: SMF-73431 is the smallest, a juvenile,

SMF-73473 is slightly larger than SMF-73431, a juvenile, SMF-73472, a sub-adult, and, SMF-55153 the largest, an adult, however, specimen SMF-55153 was only segmented to the carapace and the plastron.

### 1.2.2 Methods

The specimens were tomographed individually using the Nikon XT H 320 micro-CT scanner of the University of Tübingen, Germany, using a tungsten reflection target, 4476 projections, and a 0.25 mm aluminum filter. The scanning parameters were adjusted to each specimens: SMF-73431 was scanned using voltage = 200 kV, current = 100  $\mu$ A, at 0.0418625 mm (voxel size); SMF-73472 and 73473 were both scanned with the voltage set to 180kV, the current to 85  $\mu$ A, and the voxel size to 0.084529 mm.

The dataset of each specimen was processed individually using Amira v. 2023.2 (Thermo Fisher Scientificfor) segmenting the bones with brush, lasso, magic wand tools and open-source tool Biomedisa, using a frequency of 50 slices. The surface of each skeletal element was exported as STL files, visualized using Meshlab software v. 2022.02.

To anatomical nomenclature, we follow Zangerl (1969) for the shell and Gaffney (1990) and Romer (1956) for the appendicular and axial skeleton, and we used other Chelidae species, such as *Acanthochelys radiolata*, *Chelodina expansa*, *Chelodina longicollis*, *Chelodina parkeri*, *Elseya lavarockorum*, *Elseya novagineae*, *Emydura macquarii*, *Emydura subglobosa*, *Emydura victoriae*, *Hydromedusa maximilliani*, *Hydromedusa tectifera*, *Mesoclemmys tuberculata*, *Myuchelys latisternum*, *Phrynops geoffroanus*, *Platemys platycephala* and *Rheodytes leukops*, as a basis for the morphological comparisons.

## 1.3 RESULTS

### SYSTEMATIC

Testudines Batsch, 1788

Pleurodire Cope 1865

Chelidae Gray, 1825

***Chelus*** Duméril, 1806

**Type species.** *Chelus fimbriata* (Schneider, 1783)

**Included species:** *Chelus fimbriata* (Schneider, 1783), *Chelus orinocensis* Vargas-Ramírez et al, 2020, and *Chelus colombiana* Wood, 1976 (= *Chelus lewisi* Wood, 1976; Ferreira et al., 2016).

***Chelus orinocensis*** Vargas-Ramírez et al, 2020

**Diagnosis** A large-sized chelid turtle, sharing with *Chelus fimbriata* the carapace with three well-defined ridges, the elongated thick neck, the wide triangular flattened head with long tubular proboscis, the small eyes, the extremely wide mouth, and the skin flaps on head and neck, which are unique traits of the genus *Chelus*. In addition to its genetic distinctiveness, *C. orinocensis* is morphologically easy to tell apart from *C. fimbriata* by a lighter coloration of shell and soft parts, in particular an unpigmented pale-yellow plastron instead of a mainly dark plastron in *C. fimbriata* (Modified from Varga-Ramírez et al., 2020)

**Geographic occurrence.** Brazil, Colombia, Ecuador, Bolivia, Peru, French Guiana, Guyana, Suriname, Venezuela, Trinidad.

Figures 4 - 16

**Holotype:** IAvH-R-8755, Colombia.

**Type locality:** Colombia, Vichada, Pto. Carreño, Bitá River

**Referred material.** SMF-73431, SMF-73472, SMF-73473.

**Geographic occurrence.** Brazil, Colombia, Guyana, Venezuela

### 1.3.1 Description

#### 1.3.1.1 Carapace

The four specimens described here display minimal variation in the carapace shape, with SMF-73472 having an oval shape, while SMF-73473, SMF-73431 and SMF-55153 are more quadrangular (Figs 1 and 2). Three ridges extend along the dorsal surface of the

carapace of all specimens, two laterals, over the costal bones, and one on the midline, over the nuchal, neurals, suprapygal and pygal. The carapace is composed of 48 or 49 bones, one nuchal, seven or eight neurals, eight pairs of costals, eleven pairs of peripherals, one suprapygal and one pygal. The nuchal bone has a hexagonal shape and is sutured with the first peripheral posteriorly, with the first costal anteriorly, and with the first neural posteriorly. The neural bones are in sequence and possess troughs on their dorsal surface along the midline, where the vertebral scutes attach. The first neural is the largest in the series in terms of length and is sutured with the nuchal bone posteriorly, and with the first costal laterally. The second neural is smaller in the series of neurals, has a rectangular shape, and is sutured laterally with the second costal. The third neural has an almost square shape, being slightly wider than long, is sutured laterally with the third costal. The fourth neural has a rectangular shape, and is sutured laterally with the fourth costal. The fifth neural has the posterior part rounder than the anterior, and is sutured laterally with the fifth costal. The sixth neural has a rectangular shape, and is sutured lateroanteriorly with the fifth costal, and lateroposteriorly with the sixth costal. The seventh neural does not have a well-defined shape, it is the narrowest of the neurals, being considerably taller than it is wide and is sutured anteriorly with the eighth costal, and laterally with the sixth and seventh costal. None of the specimens showed an eighth neural, however, in *Chelus fimbriatus*, when the eighth costal is present, it has a shape similar to seventh neural. The first costal bone is notably wider than longer and has the first knob of the lateral crest on its dorsal surface. It is sutured with the nuchal bone anteromedially, medially with the first neural, posteriorly with the second costal, and laterally with first, second, third and fourth peripherals. The second through seventh costal bones exhibit the same shape, being longer than they are wide. The second costal exhibits on its dorsal surface the end of the first knob of the lateral ridge and is sutured medially with the second neural, anteriorly with the first costal, posteriorly with the third costal, and laterally with fourth and fifth peripherals.

The third costal exhibits on its dorsal surface the beginning of the second knob of the lateral ridge and is sutured medially with the third neural, anteriorly with the second costal, posteriorly with the fourth costal, and laterally with the fifth and sixth peripherals. The fourth costal has the lateral part wider than the medial part, exhibits on its dorsal surface the end of the second knob, and is sutured medially with the fourth neural, anteriorly with the third costal, posteriorly with the fifth costal, and laterally with sixth and seventh peripherals. The fifth costal exhibits on its dorsal surface the initial part of the third knob and is sutured medially with the fourth and fifth neurals, anteriorly with the fourth costal, posteriorly with the sixth costal, and laterally with the seventh and eighth peripherals. The sixth costal exhibits on its dorsal surface the end of the third knob and is sutured medially with the sixth and seventh neurals, anteriorly with the fifth costal, posteriorly with the seventh costal, and laterally with eighth ninth peripherals. The seventh costal is the smallest in the series of costals, exhibits on its dorsal surface the initial part of the fourth and last knob of the lateral ridge and is sutured medially with the seventh neural, anteriorly with the sixth costal, posteriorly with the eighth costal, and laterally with ninth and tenth peripherals. The eighth costal is longer than wide and is the second widest in the series of costals, with the end of the fourth and last knob of the lateral ridge on its dorsal surface. It is sutured medially with the seventh neural, with the eighth costal on the opposite side, anteriorly with the seventh costal, posteriorly with the suprapygal, and laterally with the tenth and eleventh peripherals. The peripheral bones have slight variations in shape, except for the fourth, fifth, and sixth ones, which are wider than long. The bridge connects to the third, fourth, fifth, and sixth peripherals, and the fourth, fifth, sixth, and seventh peripherals have concave medial parts.

On the ventral surface of the first costal, the axillary scar extends posteromedially. In the specimens described here, it reaches less than half the length of the first costal. In *Hydromedusa tectifera*, this scar is reduced, marking solely the lateral surface of the first

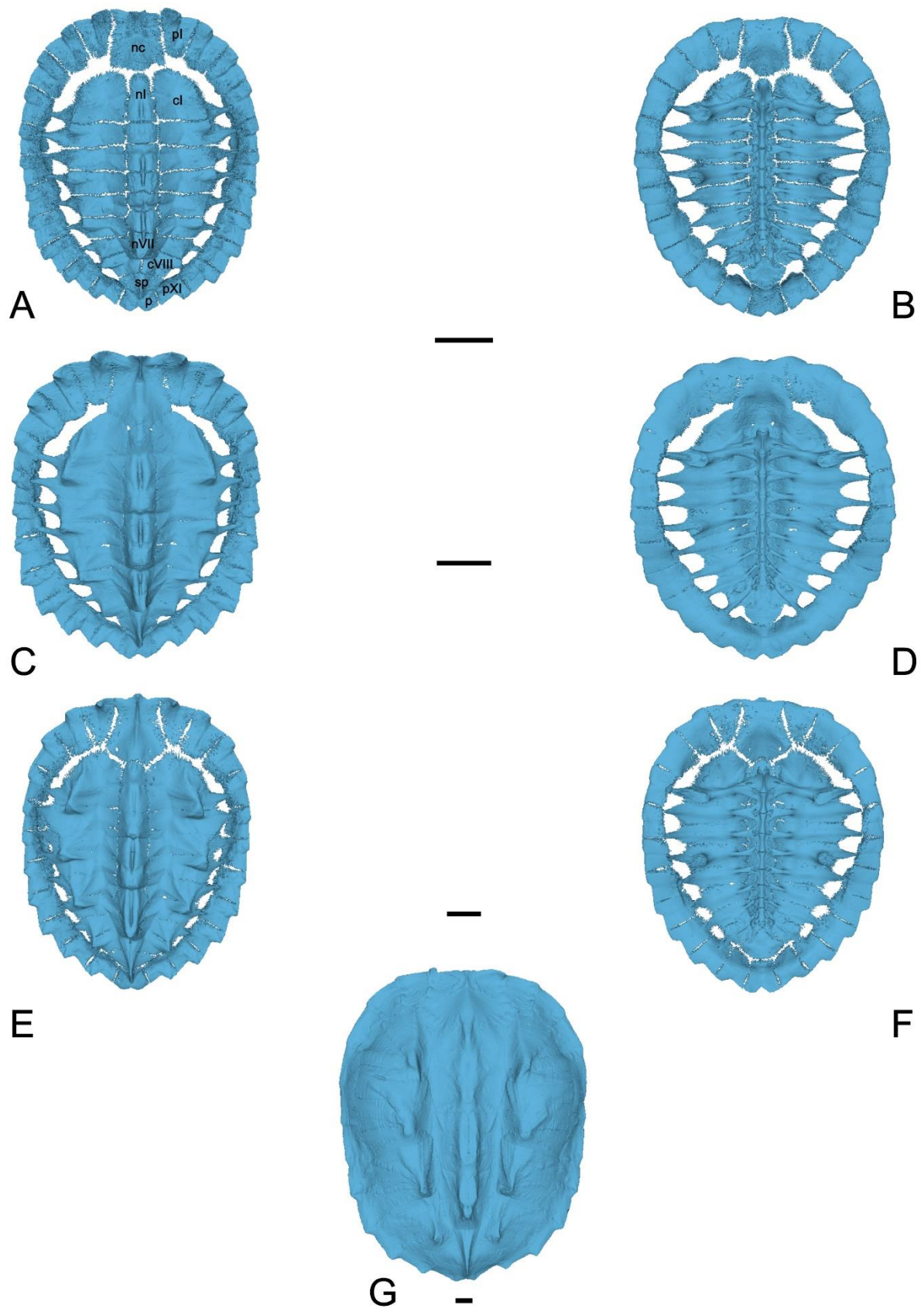
costal. On the other hand, in *Mesoclemmys tuberculata* and *Phrynops geoffroanus*, the axillary scar exceeds half the length of the first costal. On the ventral surface of the fourth costal the inguinal scar extends anterolaterally. In other species of Chelidae, the position and even presence of the inguinal scar varies. In *Chelodina longicollis*, this scar is absent on the costals, being present only on the seventh peripheral, while in *Rheodytes leukops* and *Platemys platycephala*, the scar is present on the fifth costal, and in *Elseya lavarockorum* and *Phrynops geoffroanus*, it is present on the fifth and sixth costals. Regarding the seventh and eighth costal, and suprapygal, the ilium scar is observed, this scar is oval and expands anteroposteriorly. In *Chelodina longicollis*, the scar is also oval, however, it expands mediolaterally. In *Emydura macquarrii* and *Rheodytes leukops*, this scar has a triradiate shape.

On the dorsal surface of the carapace, a total of 38 dermal scutes are present: one cervical, five vertebrals, four pairs of pleurals, and twelve pairs of marginals. The cervical scute has a rectangular shape and is longer than it is wide. It is positioned at the anterior end of the nuchal bone, making contact with the first vertebral scute posteriorly and laterally with the first marginal scute. The vertebral scutes have a slight variation in size, following the formula in relation to length,  $V1 > V2 > V3 > V5 > V4$ , with all of them being wider than long. The first vertebral scute is pentagonal and is positioned over the nuchal bone, first peripheral, and first costal. It makes contact with the cervical scute anteriorly, with the first marginal anterolaterally, and with the first pleural anteriorly. The second vertebral scute is hexagonal and is positioned over first, second and third neurals, and over first, second and third costals. It contacts the first and third vertebral anteriorly and posteriorly, respectively, and laterally it contacts the first and second pleurals. The third vertebral scute is hexagonal and is positioned over neurals 3-5 and costals 3-5. It makes anterior contact with the second vertebral, posterior contact with the fourth vertebral, and lateral contact with the second and third pleurals. The



fourth vertebral scute is hexagonal and has the anterior part twice as wide as the posterior. It is positioned over the sixth, seventh neurals and sixth, seventh and eighth costals, contacting anteriorly the third vertebral, posteriorly the fifth vertebral, and laterally the third and fourth pleurals. The fifth vertebral scute is pentagonal and is positioned over the eighth costal, suprapygal, pygal, and eleventh peripheral. It makes anterior contact with the fourth vertebral, lateral anterior contact with the fourth pleural, lateral contact with the eleventh marginal, and posterior contact with the twelfth peripheral. Of the Pleural scutes, the first has greater width and the second greater length, the first pleural is wider than it is long, while the second, third, and fourth are longer than wide. The first pleural is positioned over the first and second costal bones, and makes contact medially with the first and second vertebral, anteriorly with the second marginal, laterally with the third, fourth, and fifth peripherals, and posteriorly with the second pleural. The second pleural is positioned over the second, third, and fourth costal bones, and makes contact medially with the second and third vertebral, anteriorly with the first pleural, laterally with the fifth, sixth, and seventh peripherals, and posteriorly with the third pleural. The third pleural is positioned over the fourth, fifth, and sixth costal bones, and makes contact medially with the third and fourth vertebral, anteriorly with the second pleural, laterally with the seventh, eighth, and ninth peripherals, and posteriorly with the fourth pleural. The fourth pleural is positioned over the sixth, seventh, and eighth costal bones, and makes contact medially with the fourth and fifth vertebral, anteriorly with the third pleural, laterally with the ninth and tenth peripherals, and posteriorly with the eleventh peripheral and fifth vertebral. The marginal scutes do not present significant variation in shape and are positioned over the peripheral bones, except the first which covers the first peripheral and part of the posterior surface of the nuchal bone, and the twelfth which covers part of the posterior surface of the eleventh peripheral and part of the pygal bone surface.

The costal bones of SMF-73431, SMF-73472, and SMF-73473 are not yet fully developed, showing incomplete contact between the costal and peripheral bones. Full ossification of these bones is expected solely during the adult stage of the species, as observed in SMF-55153.



**Figure 4.** *Chelus orinocensis*. SMF-73431: A, B. carapace, dorsal and ventral view; SMF-73473: C, D. carapace, dorsal and ventral view; SMF-73472: E, F. carapace, dorsal and ventral view; SMF-55153: G carapace, dorsal view. Abbreviations: nc – nuchal; nl – neural; c – costal; p – peripheral; sp – suprapygal; p – pygal. Scale bar: 2cm.

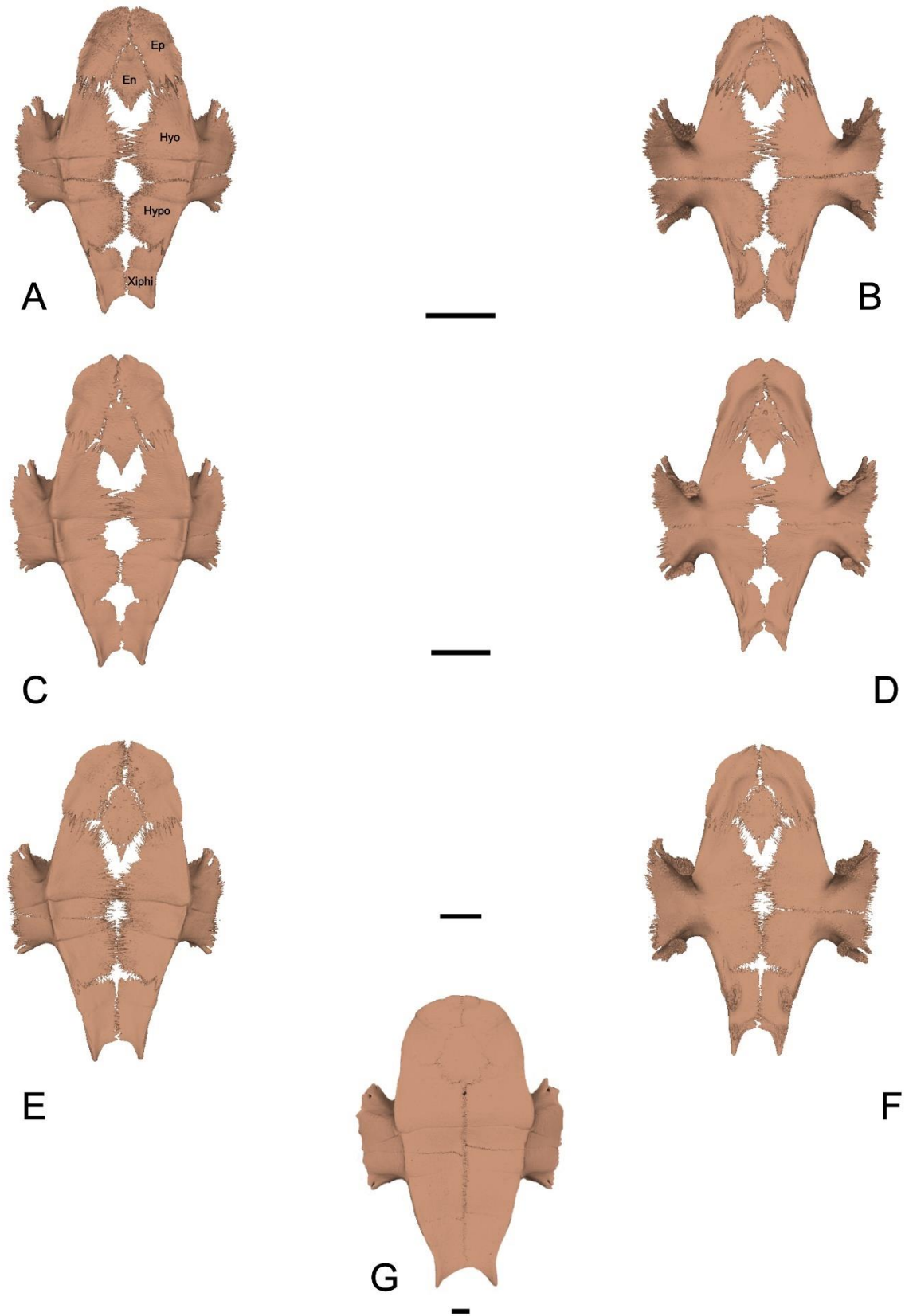
### 1.3.1.2 Plastron

The plastron is composed of eleven bones, including one entoplastron and pairs of epiplastra, hyoplastra, hypoplastra, and xiphiplastra. The relative lengths of the plastral bones varies among specimens observed. In specimens SMF-73472 and SMF-73473, the length sequence is hyoplastron > xiphiplastron > epiplastron > hypoplastron > entoplastron. However, in specimens SMF-73431 and SMF-55153, the xiphiplastron exhibits a shorter anterior process, resulting in its length being shorter than that of the epiplastron and hypoplastron in SMF-73431, and shorter than the epiplastron in SMF-55153. The epiplastron is longer than it is wide and is sutured medially with the entoplastron and posteriorly with the hyoplastron. The entoplastron is diamond-shaped with a rounded anterior end and a triangular posterior end becoming thinner anteroposteriorly. In SMF-73431, SMF-73472, and SMF-73473, the entoplastron is 1.5 times longer than wider, however, in SMF-55153, this difference is almost non-existent, with the length slightly greater than the width. Additionally, the entoplastron is sutured anterolaterally with the epiplastron and posterolaterally with the hyoplastron. The hyoplastron is wider than it is long and is sutured anteriorly with the epiplastron, anteriomedially with the entoplastron, and posteriorly with the hypoplastron. It expands laterodorsally to form part of the bridge, this lateral expansion extends anteriorly along the lateral margin of the carapace as far as the first costal and attaches to the posterior part of the third peripheral. The hypoplastron is wider than it is long, is sutured anteriorly with the hyoplastron and anteriorly with the xiphiplastron. Like the hyoplastron, the hypoplastron expands laterodorsally, thus forming the bridge, which extends posteriorly along the lateral margin of the carapace as far as the fourth costal and attaches to the middle of the seventh peripheral. The xiphiplastron is twice as long as it is wide, ending in a horn-shaped process. Between the right and left processes, a generally U-shaped anal notch is formed, though its shape may vary based on the posterior processes. SMF-73473, SMF-73431, and SMF-55153

have the shortest process, resulting in a wider anal notch in these three specimens compared to SMF-73472, which has long, straight processes, resulting in a deeper but narrower anal notch. Three fontanelles are present in the plastron of the non-adult specimens, one posterior, one central, and one anterior. The first is located between the hyoplastron and entoplastron bones, the second is located between the hyoplastron and hypoplastron, and the third is between the hypoplastron and the xiphoplastron. In the smaller specimens SMF-73431 and SMF-73473, these fontanelles are well open, in SMF-73472 they are still open but more reduced, and in adult SMF-55153 they are completely closed. The presence of these fontanelles in SMF-73431, SMF-73472, and SMF-73473 indicates that bone growth and ossification are not yet complete, and full bone contact only occurs in adults, as observed in SMF-55153.

Thirteen dermal scutes are present on the ventral surface of the plastron, including one gular and pairs of extragulars, humerals, pectorals, abdominals, femorals, and anals, being all longer than wide, except for the pectoral and abdominal, which are wider than long. Regarding their length, the following order is observed: Femoral > Pectoral > Humeral > Anal > Gular > Abdominal > Extragular. The gular has a triangular shape and, in specimens SMF-73431, 73472, and 73472, it makes lateral contact with the extragular and posteriorly with the humeral, positioning itself over the anterior part of the epiplastron and entoplastron. However, in SMF-55153, the gular is not as long, with no posterior contact with the humeral and is restricted to the epiplastron. The extragular makes posterior contact with the gular and anteriorly with the humeral, in specimens SMF-73431, 73472, and 73472, the longer gular prevents contact between the extragulars, whereas in SMF-55153, the extragulars are in medial contact. The extragulars are positioned over the epiplastron and entoplastron. The humeral makes posterior contact with the extragular and posteriorly with the pectoral, positioned over the epiplastron, entoplastron, and the posterior part of the hypoplastron. The

pectoral makes posterior contact with the humeral, anteriorly with the abdominal, and laterally with marginals IV-VI, positioned over the entoplastron and hyoplastron posterior end. The abdominal makes anterior contact with the pectoral, posteriorly with the femoral, and laterally with the sixth, seventh, and eighth marginals, positioned over the posterior part of the hyoplastron and anterior part of the hypoplastron. The femoral makes anterior contact with the abdominal and posteriorly with the anal, positioned over the hypoplastron and xiphiplastron. The anal makes anterior contact with the femoral and is restricted to the xiphiplastron, on the lateral surface of the xiphiplastron, a notch left by the contact of the scutes can be observed. On the ventral surface of the xiphiplastron, the scars of the pubis and ischium are located, having an oval and triangular shape, respectively.



**Figure 5.** *Chelus orinocensis*. SMF-73431: A, B plastron, dorsal and ventral view; SMF-73473: C, D plastron, dorsal and ventral view; SMF-73472: E, F plastron, dorsal and ventral view; SMF-55153: G plastron, dorsal view. Abbreviations: ep – epiplastron; En – Entoplastron; hyo – hyoplastron; hypo – hypoplastron; Xiphi – Xiphiplastron. Scale bar: 2cm.

### 1.3.1.3 Cervical vertebrae

Among the eight cervical vertebrae the cervical 3 has the longest vertebral body, and cervical 8 has the greatest height. All cervical vertebrae in *Chelus orinocensis* are composed of three elements: two neural arches and the centrum. In specimen SMF-73431, the neural arches are not completely fused to the centra yet, while in SMF-73432 all the cervical vertebrae are completely fused, confirming this as an ontogenetic variable character in *Chelus orinocensis*.

The atlas is the smallest among the cervical vertebrae, the posterior articulation is wider than it is high, while the anterior is higher than it is wide, featuring a subtriangular shape. In *Chelus orinocensis* the atlas is relatively large, only slightly smaller than the axis, in contrast to some other chelids, e.g. *Emydura macquariae* and *Myuchelys latisternum*, in which the atlas is extremely reduced. The anterior articulation is formed by the centrum and the neural arches, which can be observed in the unfused atlas of the juvenile specimen (SMF-73431), whereas in all other cervicals all articulations are formed exclusively by their centra. The vertebral centrum is amphicoelous and of the prezygapophyses are absent. On the lateral edge of the posterior articulation, there are lateral processes that extend posterior-anteriorly to half the length of the centrum and at the ventral edge of the anterior articulation, it is possible to observe a process that extends more posteriorly than the articulation. In lateral view, it is possible to observe that these processes, together with the transverse process, form a tube-shaped cavity. The postzygapophyses are not elevated in a single process, but have their own processes separated by a V-shaped notch, and their articulation facets are directed medially. The vertebral formula in *Chelus orinocensis* is  $1(2)(3)(4)(5)6)7(8)$ , the same as in *Chelus fimbriata* and other chelids.

The axis is the second cervical vertebra. It is twice as long as high, being the second longest vertebra in the cervical series. A longer-than-high axis is also observed in other long-



necked chelids, e.g. *Chelodina parkeri*, *Chelodina longicollis*, *Chelodina expansa*, and *Hydromedusa maximilliani*, while in the short-necked chelids, the opposite occurs, with the axis being higher than long, as in *Emydura macquarii*, *Myuchelys latisternum*, and *Rheodytes leukops*. The vertebral centrum is opisthocelous, and just posterior to the anterior articulation, a ventral crest extends to mid-length of the centrum. The transverse process is relatively short, but longer than that of the atlas. The prezygapophyses are elevated in a single peduncle that projects anteriorly fitting into the posterior notch of the postzygapophyses of the atlas. The articulation facets of the prezygapophyses are laterally directed, whereas in *Myuchelys latisternum* and species of the genus *Chelodina* the facets are directed dorsally. The postzygapophyses are elevated in a single posterior peduncle, with the articulation surfaces directed laterally and separated by a small U-shaped notch.

The third cervical vertebra is opisthocelous and the longest in the series, being longer than higher, whereas in *Emydura macquarii*, *Myuchelys latisternum* and *Rheodytes leukops* it is higher than long. The ventral crest of the centrum initiates posterior to the anterior articulation and extends to the middle of the vertebra. The transverse process is located at mid-length, formed by the neural arch and vertebral centrum. The prezygapophyses are separated and their articulation surfaces are directed dorsomedially. The postzygapophyses are elevated in the neural spine, which projects posteriorly but is short, with minimal height increase. The articulation surfaces of the postzygapophyses face laterally and are divided by a small notch.

The fourth cervical vertebra is opisthocelous with a short ventral crest that initiates posteriorly to the anterior articulation and extends until mid-length. The transverse process is formed by the neural arch and vertebral body, positioned in the posterior half. The prezygapophyses are widely separated and have articulation surfaces directed mediodorsally. The neural spine is higher and wider than in the anterior cervicals. The postzygapophyses are

large and elevated in the neural spine, with the articulation surfaces facing lateroventrally and separated only by a small notch.

The fifth cervical vertebra features a biconvex vertebral centrum, with the posterior articulation wider ventrally than the anterior, which is higher than wide. The ventral crest is similar to those of the cervical 4. The transverse process is wide, covering the entire length of the neural arch and showing a slight curvature posteriorly. The prezygapophyses have articulation surfaces facing mediodorsally. The neural spine is short, displaying a slight depression along its entire length. The postzygapophyses are large, with articular facets facing laterally and divided by a small notch, similar to the cervical 4.

The sixth cervical vertebra is procoelous with transverse processes located at mid-length of the vertebra. The ventral crest is reduced, but it projects more anteriorly than the anterior articulation. The articulation surfaces of the prezygapophyses face medially, and the neural spine exhibits a slight curvature as it approaches the postzygapophyses. Laterally just ventral to the postzygapophyses, the neural spine shows two small lateral pits. The articulation surfaces of the postzygapophyses are turned lateroventrally.

The seventh cervical vertebra is amphicoelous. The anterior articulation is sub-triangular, while the posterior articulation has a more rounded shape, but is higher than wide. As in the cervical 6, the ventral crest is short and projects anteriorly. The transverse process is located more posteriorly, displaying a slight posterior curvature. The prezygapophyses have articulation surfaces directed mediodorsally. The neural spine is the longest in the cervical series and becomes broader anteroposteriorly as it approaches the postzygapophyses. The postzygapophyses are anteroposteriorly elongated and elevated in the neural spine, with articulation facets oriented ventrally. In the genus *Chelodina*, the neural spine of the seventh cervical is considerably lower than in *Chelus*, and in *Emydura*, the spine has a more pronounced curvature, with the postzygapophyses oriented laterally.

The eighth cervical, the last in the cervical sequence, has the highest vertebral center and neural spine. It has a biconvex vertebral centrum (as cervical 5) with the anterior articulation dorsoventrally elongated, whereas the posterior one is rounded. The ventral crest runs along the entire length of the vertebra, but does not project anteriorly beyond the anterior articulation. The transverse process is long and positioned at mid-length in the vertebra. The articulation surfaces of the prezygapophyses are directed dorsally. Unlike in the other cervicals, the neural spine becomes thinner as it approaches its posterior end. The neural arch has a dorsal projection, separated from the postzygapophyses. The postzygapophyses are extremely reduced and positioned very closely, with the articulation surfaces directed laterally. In *Chelodina*, the postzygapophyses, have the facets positioned ventrally, while in *Elseya novagineae*, they are positioned laterally, without contacting each other.

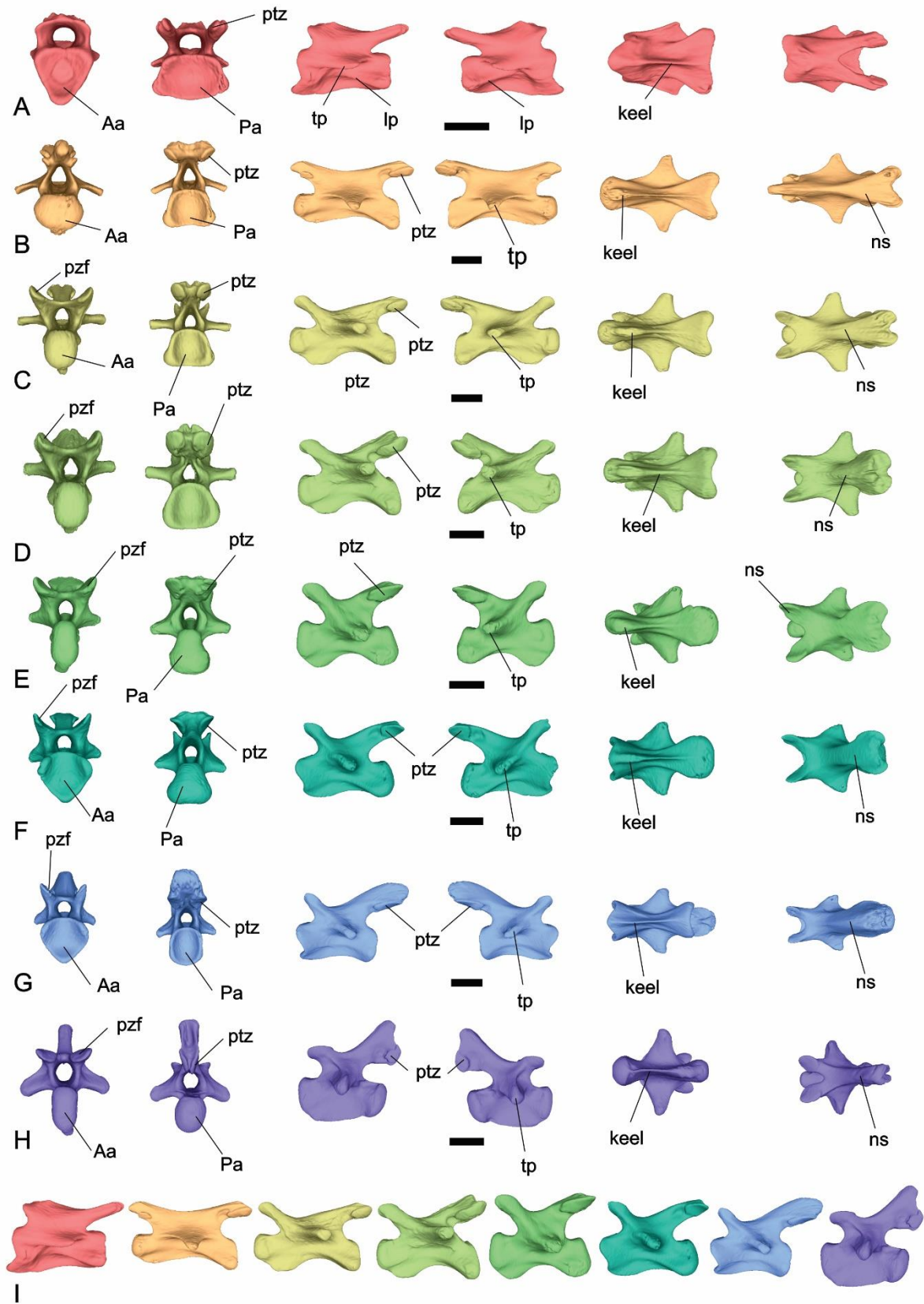
#### **1.3.1.4 Thoracic, Sacral and Caudal vertebrae**

There are 8 thoracic, 3 sacrals and 17 caudal vertebrae in all three specimens of *Chelus orinocensis* analyzed, with minimal morphological variation. In the youngest specimen, SMF-73431, the neural arches are not yet fused to the centra in caudal vertebrae 1-5, while in the posterior vertebrae they are already fused, suggesting a posterior-to-anterior ontogenetic pattern in this species.

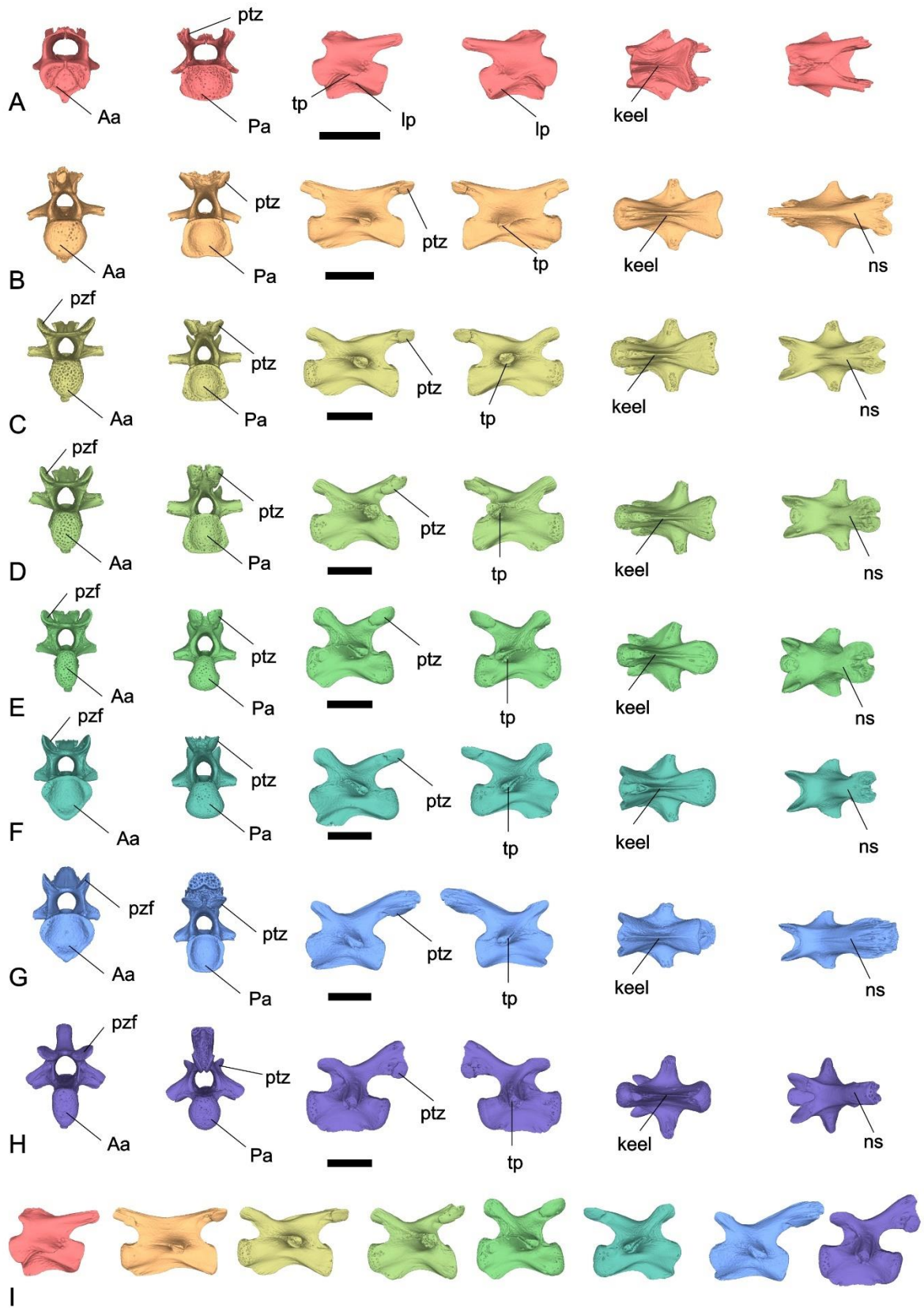
The first thoracic vertebra is the only that has prezygapophyses, being these are very close to each other and with the articular facets positioned medially. In the series, the first thoracic vertebra is the largest, and the ninth is the smallest. The keel on the ventral side is considerably thinner in the first and is absent in the seventh and eighth. On the lateral side of all thoracic vertebrae, the ribs are articulated. The first rib articulates solely with the 1st thoracic vertebra, the second rib is articulated with the 1st and 2nd thoracic vertebrae, the third rib is articulated with the 2nd and 3rd vertebrae, the fourth rib is articulated with the 3rd and 4th vertebrae, the fifth rib is articulated with the 4th and 5th vertebrae, the sixth rib is

articulated with the 5th and 6th vertebrae, the seventh rib is articulated with the 6th and 7th vertebrae, and the eighth rib is articulated with the 6th and 7th vertebrae. Between the articulation of the ribs with the thoracic vertebrae and the neural bones lies the costovertebral tunnel. Notably, the diameter of this tunnel in *Chelus* is considerably larger than in other members of the Chelidae family. The three sacral vertebrae are articulated with the last three ribs, the first being laterally articulated with the ninth rib, the second with the tenth rib, and the third with the eleventh rib. In terms of size, the first is the largest, the second is the smaller. The third vertebra stands out for having a well-developed neural spine with the postzygapophyses elevated in their own peduncle, which displays a marked similarity to the morphology of the first caudal vertebrae.

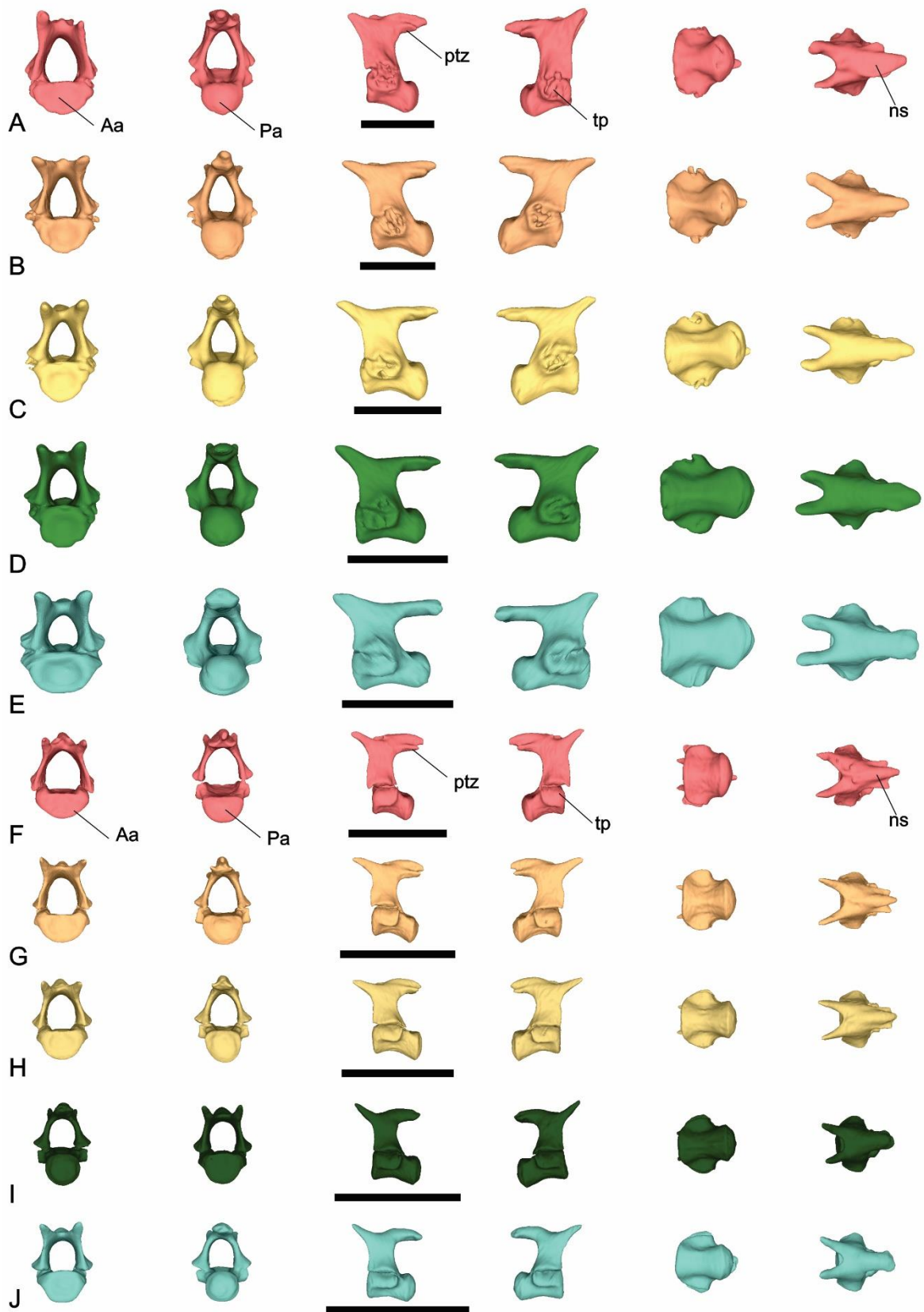
All caudal vertebrae are procoelous in *Chelus orinocensis*. The caudals become smaller antero-posteriorly, with the first being the largest and the 17th being the smallest, the same occurs with the neural canal also, marking the closure of the neural tube canal at the 17th caudal vertebra. The articulation facets of the prezygapophyses are directed ventrally and are separated, elevated in their own peduncle. The neural spine becomes progressively smaller in an anterior to posterior direction from the sixth vertebra, being absent from twelfth onward. The postzygapophyses are positioned in the neural spine and their articular facets face ventrally. In all caudals, the neural spine projects posteriorly beyond the level of the postzygapophyses, a projection that fits between the two peduncles of the subsequent prezygapophyses.



**Figure 6.** *Chelus orinocensis*. SMF-73472 – Set of cervical vertebrae in anterior, posterior, medial, lateral, ventral and dorsal views. A. atlas; B. axis; C. cervical 3; D. cervical 4; E. cervical 5; F. cervical 6; G. cervical 7; H. cervical 8; I. axis to cervical 8 in sequence. Abbreviations: Aa – Anterior articulation; Pa – Posterior articulation; ptz – postzygapophyses; tp – transverse process; lp – lateral process; pzf – prezygapophyses; ns – neural spine: Scale 5 mm.



**Figure 7.** *Chelus orinocensis*. SMF-73431 – Set of cervical vertebrae in anterior, posterior, medial, lateral, ventral and dorsal views. A. atlas; B. axis; C. cervical 3; D. cervical 4; E. cervical 5; F. cervical 6; G. cervical 7; H. cervical 8; I. axis to cervical 8 in sequence. Abbreviations: Aa – Anterior articulation; Pa – Posterior articulation; ptz – postzygapophyses; tp – transverse process; lp – lateral process; pzf – prezygapophyses; ns – neural spine; Scale 5 mm.

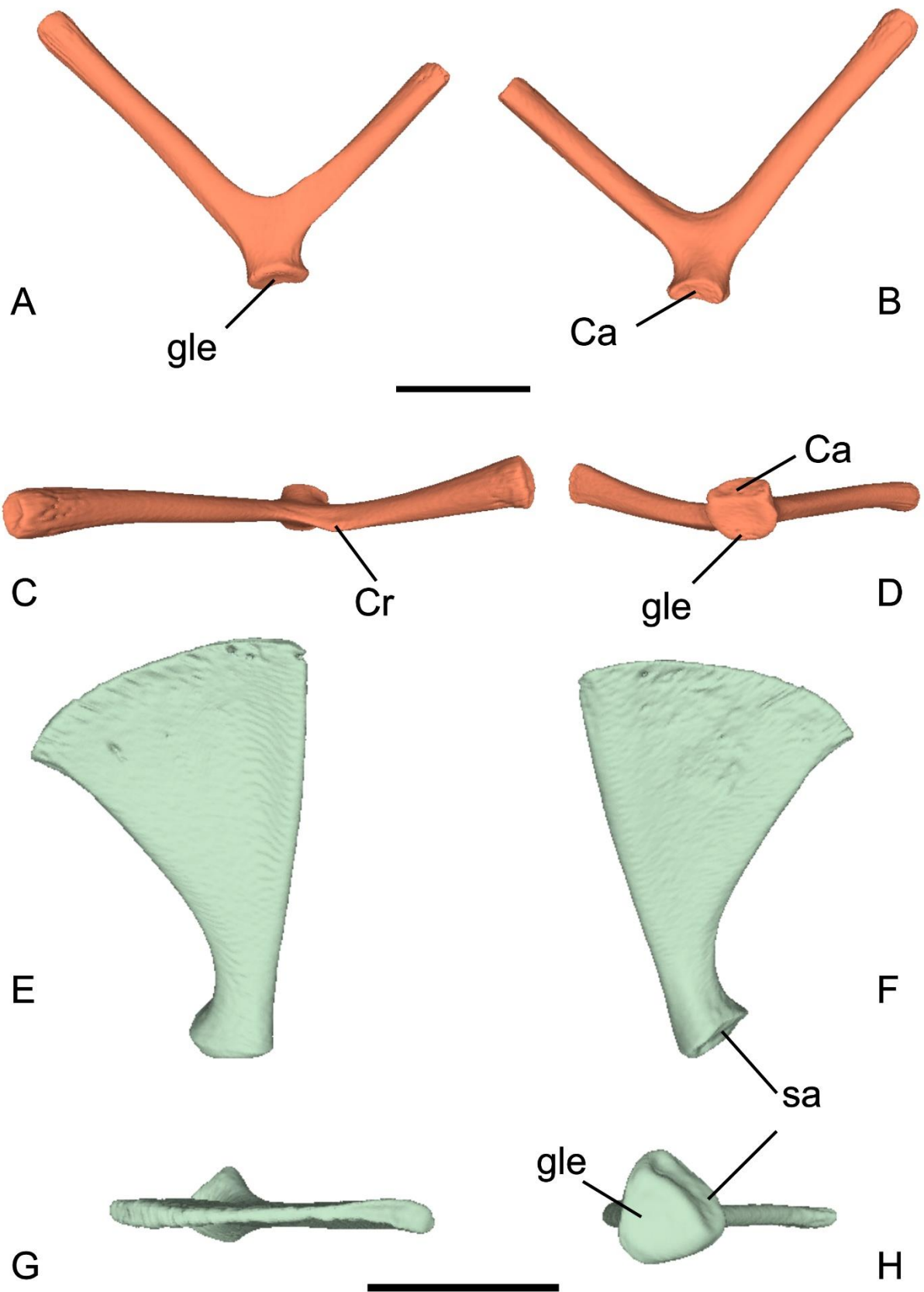


**Figure 8.** *Chelus orinocensis*. A, B, C, D, and E = SMF-73472; F, G, H, I and J = SMF-73431 – Set of cervical vertebrae in anterior, posterior, ventral, lateral, ventral and dorsal view. A, F. 1st caudal; B, G. 2th caudal; C, H. 3th caudal; D, I. 4th caudal; E, J. 5th caudal. Abbreviations: Aa – Anterior articulation; Pa – Posterior articulation; ptz – postzygapophyses; tp – transverse process; pzf – prezygapophyses; ns – neural spine: Scale 5 mm. Scale 5 mm.

### 1.3.1.5 Shoulder Girdle

The scapula has the characteristic L shape of turtles, consisting of the scapular and acromial processes, and the glenoid articular surface. The scapular process is 25% larger than the acromial one, and they contact each other at their bases, forming the broadest and flattest section of the scapula. The acromion is oriented at about  $97^\circ$  relative to the scapular process, which differs slightly from the conditions of *H. tectifera* and *H. maximiliani*, which have angles between  $78^\circ$  and  $86^\circ$ . On the other hand, it is very similar to the  $98^\circ$  angle found in *Yaminuechelys maior* (Maniel et al., 2018; Bona & de la Fuente 2005). A short crest is observed on the medial edge of the acromial process, which extends only about 20% the length of the process. The dorsal end of the scapular process is rounded, while the medial tip of the acromial process has a more oval shape. The process of the glenoid projects laterally and develops two articular surfaces, one for the coracoid and one for the humerus. The coracoid articulates with the scapula on the ventral surface of its lateral end, forming together the glenoid fossa. The lateral end of the coracoid is rounded and also has two articular surfaces, an anterodorsal one for the scapula, and a posteroventral one for the humerus which is part of the glenoid fossa. The coracoid becomes wider and flatter as it approaches the medial end, resembling a lamina. The anterior edge of the bone is considerably curved and concave, while the posterior edge is almost straight. The coracoid of *Chelus orinocensis* resembles *Hydromedusa tectifera* in terms of the curvature of the anterior edge and the width of the medial end, and differs from that of *Podocnemis expansa*, as in this species, the medial end is only slightly expanded and the anterior edge not as curved.





**Figure 9.** *Chelus orinocensis*. SMF-73472: A-D. scapula in anterior, posterior, medial and lateral views; E- F. coracoid in dorsal, ventral, medial and lateral views. Abbreviations: scp – scapular process; acp – acromial process; gle – glenoid; Ca – coracoid articulation; Cr – crest; sa – scapular articulation. Scale bar: 1cm

### 1.3.1.6 Forelimbs

#### **Humerus**

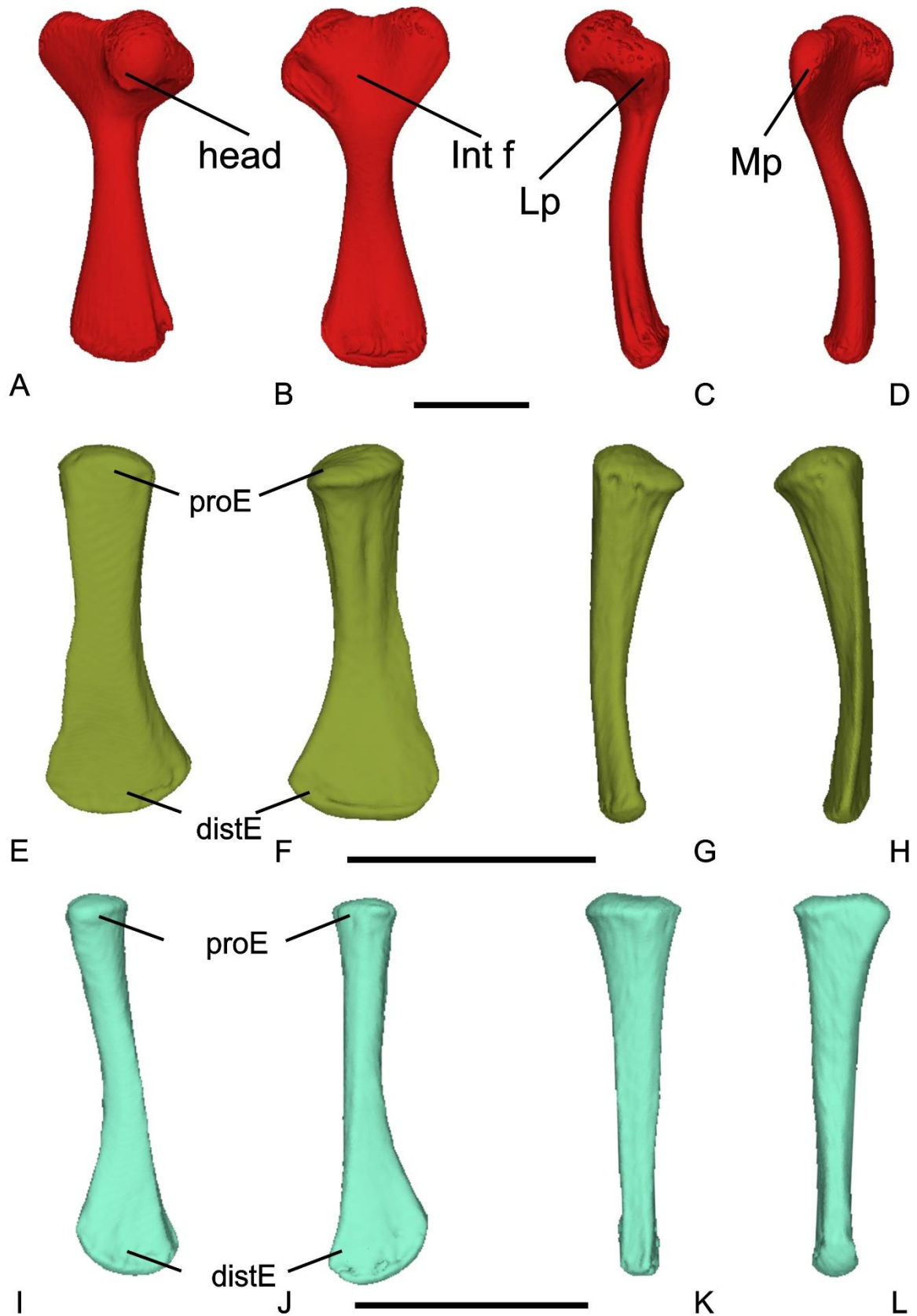
The head, ventral and lateral processes, and the intertubercular fossa for the proximal part of the humerus. The head is rounded and slightly curved relative to the axis of the shaft. The ventral process is more developed than the lateral one, being twice its size, and they are positioned in line, resulting in a relatively shallow intertubercular fossa. The tip of the medial process does not exceed the plane of the proximal end of the humeral head; however, in some pleurodires such as *Hydromedusa tectifera*, *Stupendemys geographicus*, and *Peltocephalus dumerilianus*, the tip of the medial process extends beyond this plane. The shaft has a rounded cross-section on the dorsal side and becomes flattened distally. The distal end is ellipsoid and serves as the articulation point for the radius and the ulna, but radial and ulnar joints cannot be clearly distinguished. The ectepicondylar foramen is developed within a long groove near the distal articular facet.

#### **Ulna**

The proximal end of the ulna is rounded and is where it articulates with the ulnar process of the humerus, the shaft has a slight curvature in the opposite direction of the radius (Figure 9). As it approaches the distal end, the shaft becomes wider and flatter, almost like a lamina, where it articulates with the ulnare and intermedium.

#### **Radius**

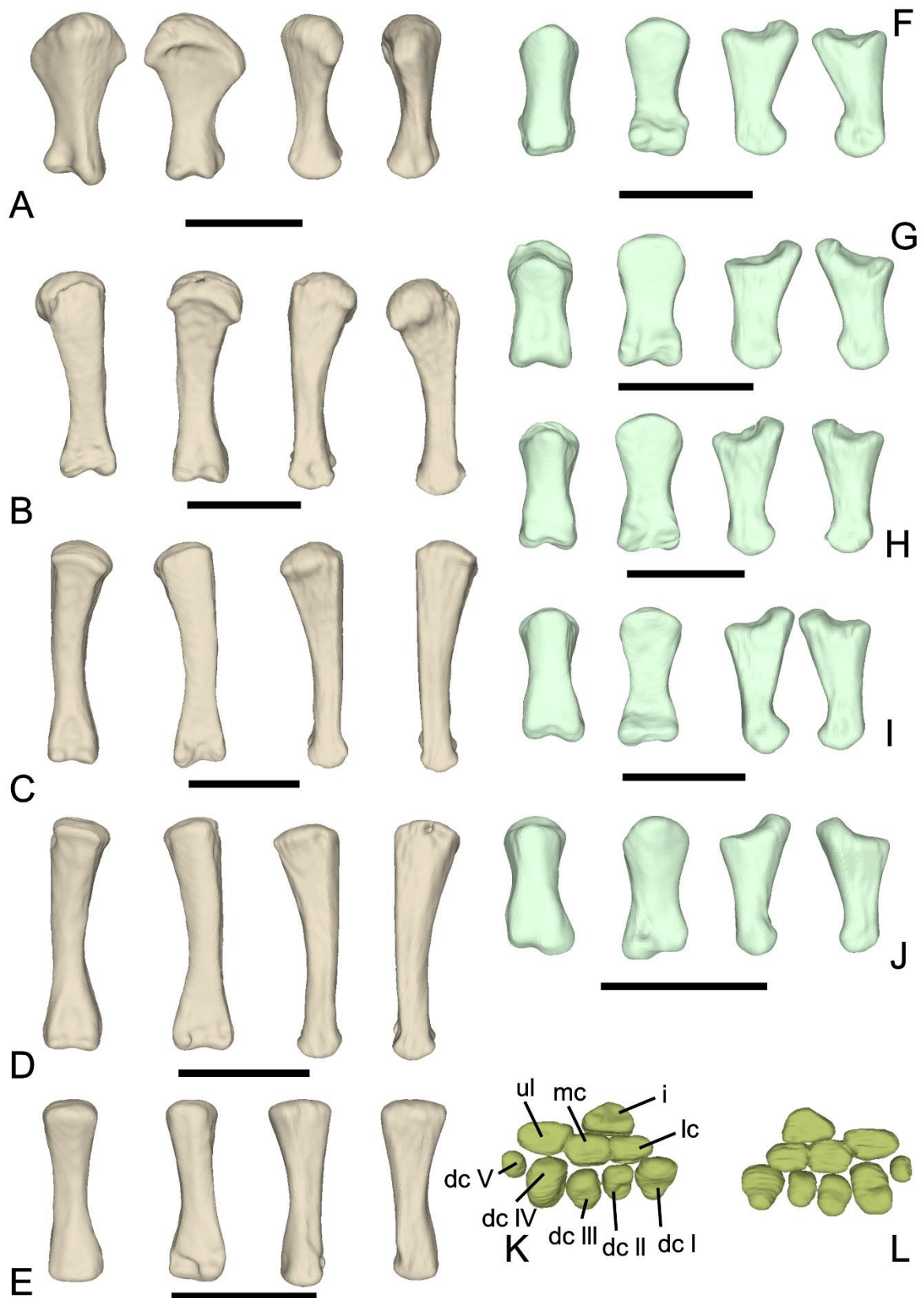
The radius is thinner and longer compared to the ulna and is positioned medially. The proximal end has a semicircular shape, articulating with the radial articulation in the laterodistal region of the humerus. The shaft is cylindrical near the proximal end, becoming wider and flatter near the distal end, however, the mediodistal region is more elongated than the laterodistal region. The radius articulates with the intermedium and lateral centrale in the medial region of the distal end.



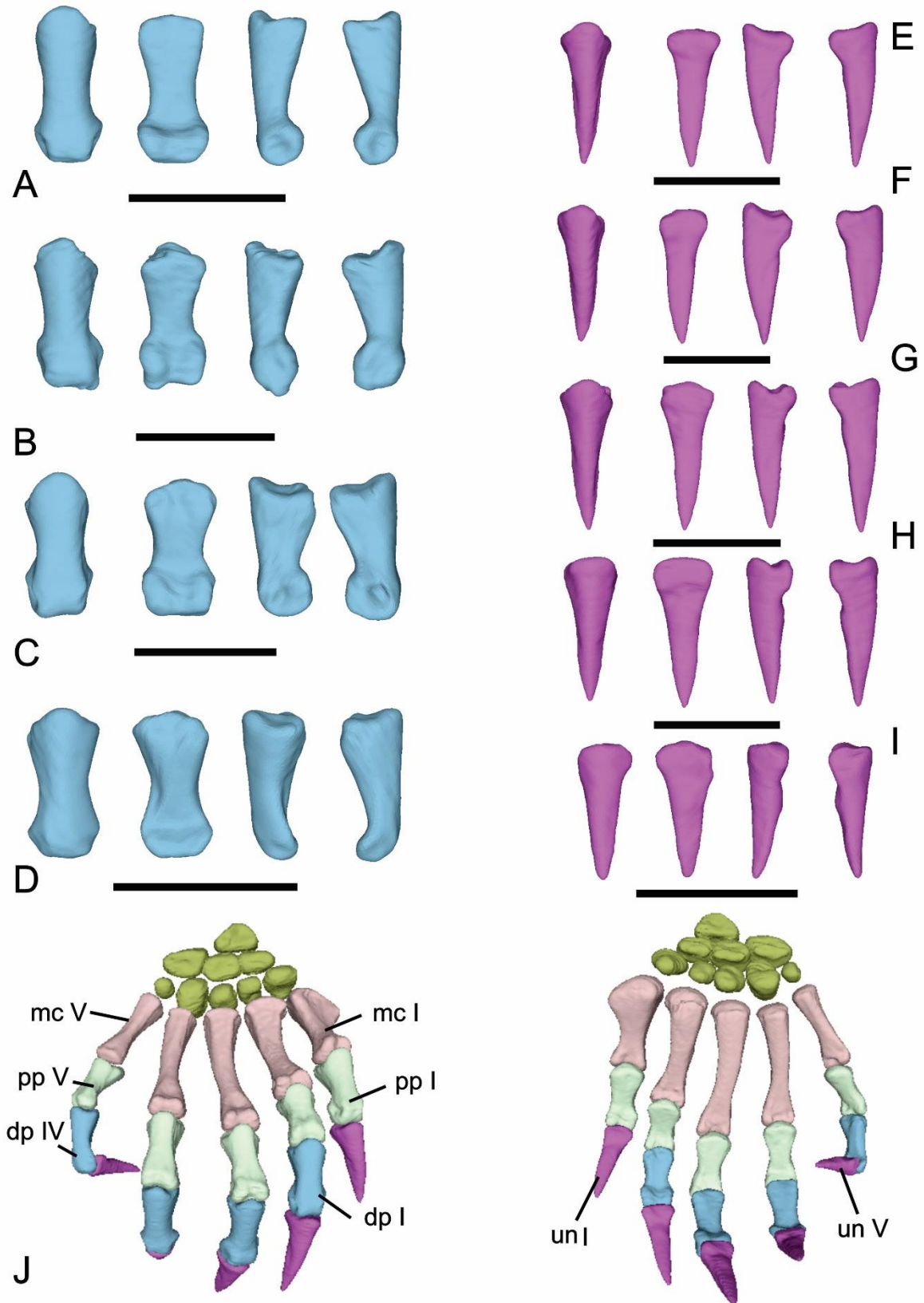
**Figure 10.** *Chelus orinocensis*. SMF-73472: A – D. Right humerus in dorsal, ventral, medial and distal views; E- F. Right ulna in dorsal, ventral medial and lateral views; I – L. Right radius in dorsal, ventral, medial and distal views. Abbreviations: Int f – Intertubercular fossa; Lp – Lateral process; Mp – Medial process; ProE – Proximal End; DistE – Distal End. Scale Bar: 1cm.

### **Carpus and Manus.**

The manus consist of 28 bones, comprising, from proximal to distal, four carpal bones, five distal carpals, five metacarpals, and five digits with the formula 2-3-3-3-3. The intermedium articulates with the radius and ulna proximally and with the lateral and medial centrale distally. While the ulnare is slightly larger than the intermedium in *Chelus orinocensis* and *Chelus fimbriata* (Sánchez-Villagra et al. 2007), in other species of the Chelidae family, such as *Chelodina expansa* and *Emydura victoriae*, the intermedium is the largest carpal bone. Additionally, in *Phrynops Geoffroanus*, *Chelodina longicollis*, *Chelodina expansa*, *Emydura victoriae*, and *Hydromedusa tectifera*, the pisiform bone is present, articulating laterally with the ulnare, but this bone is absent in *Chelus*. The distal carpals (dc1-5) are all separated and spherical and nearly uniform in size, except for the dc 5, which is considerably smaller. In *Phrynops Geoffroanus* and *Chelodina longicollis*, distal carpals 3-5 are fused, while in *Emydura subglobosa*, fusion occurs between dc 2-3 and dc 4-5 (Sánchez-Villagra et al., 2007). Among the metacarpals, the third is the longest, and the fifth is the shortest. Metacarpal I has a proximal end considerably wider than the distal end, with a medial expansion on the proximal end. Metacarpals II-V share similar morphology, with proximal and distal ends of comparable size, and the proximal more flattened while the distal end has a rounded trochlear articulation. The shaft is almost square and has a slight curvature projecting ventrally. The proximal and distal phalanges also display similar morphology, with the proximal end featuring a slightly depressed articulation, and the rounded trochlea at the distal end, along with small pits on both the lateral and medial sides. The unguals are claw-shaped tapering towards the distal end. The third ungual is the longest, and the fifth is the shortest.



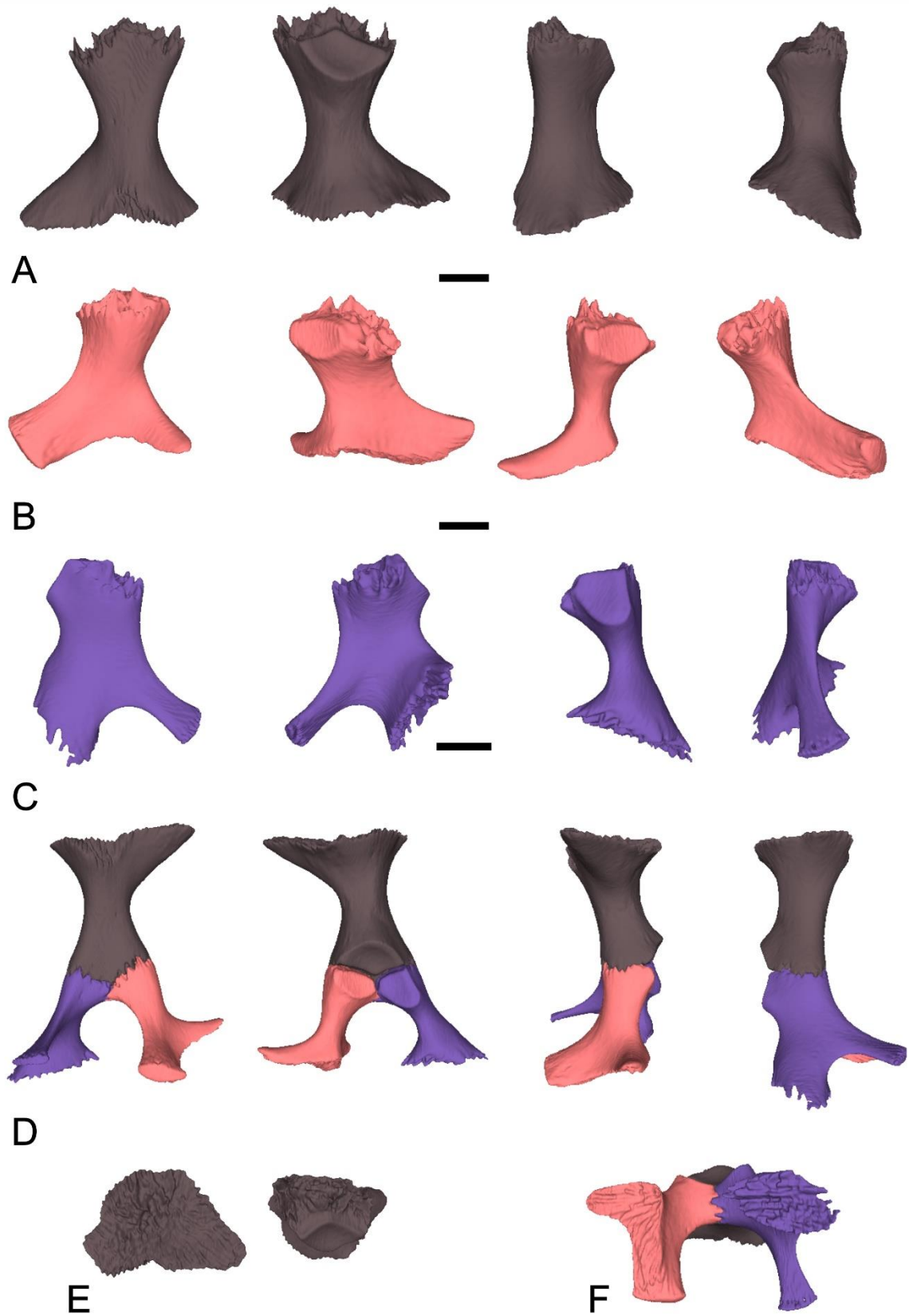
**Figure 11.** *Chelus orinocensis*. SMF-73472: A – E. right metatarsals in ventral, dorsal, medial and lateral views; F – J. right proximal phalanges in dorsal, ventral, lateral and medial views, K, L. right carpals in dorsal and ventral views. A. metatarsal 1; B. metatarsal 2; C. metatarsal 3; D. metatarsal 4; E. metatarsal 5; F. proximal phalange 1; G. proximal phalange 2; H. proximal phalange 3; I. proximal phalange 4; J. proximal phalange 5; K, L. carpals. Abbreviations: ul – ulnare; mc – medial centrale; i – intermedium; lc – lateral centrale; dc – distal carpals. Scale bar: 5mm.



**Figure 12.** *Chelus orinocensis*. SMF-73472: A – E. right distal phalanges in dorsal, ventral, lateral and medial views, E – I right unguis in dorsal, ventral, lateral and medial views, J. right complete forelimb including carpals, metatarsals, proximal and distal phalanges na unguis in dorsal and ventral views. A. distal phalange I; B. distal phalange II; C. distal phalange III; D. distal phalange IV; E. unguis I; F. unguis II; G. unguis III; H. unguis IV; I. unguis V. Abbreviations: mc – metacarpal; pp – proximal phalange; dp – distal phalange; un – unguis. Scale bar: 5mm.

### 1.3.1.7 Pelvic Girdle

The pelvic girdle is formed by the ilium dorsally, and the pubis and ischium bones ventrally. Among them, the ilium stands out for its greater length and robustness. On the dorsal surface, there is an almost rounded area that is sutured to the carapace, more precisely with the 7th and 8th costal bones, and the suprapygal. The posterior ilial process reaches the suprapygal. Some species of Chelidae present variations in the shape of this sutural surface, *Emydura macquarii* exhibits a triradiate form, while in *Acanthochelys radiolata*, the form is rounded, lacking the posterior ilial process, and contacting only the 8<sup>th</sup> costal and suprapygal. The anterior, posterior, and lateral surfaces of the shaft present a slight curvature, while the medial surface is flat. Lateroventrally, the ilium forms the dorsal half of the acetabulum, where it contacts the ischium and pubis. The pubis, the anterior element of the pelvic girdle, articulates with the ischium posterodorsally and with the ilium dorsally. Ventrally, the pubis is divided into lateral and epipubic processes. The distal part of the lateral process has an oval shape and is sutured to the xiphiplastron. The epipubic process extends medially, having a more flattened shape. The ischium articulates with the ilium dorsally and with the pubis anterodorsally. The distal part of the ischium has a triangular shape where it is sutured to the xiphiplastron. The ischium and pubis develop a curvature where the contact angle measures 84 degrees. The acetabulum has a rounded shape with an elongation on the pubic part.



**Figure 13.** *Chelus orinocensis*. SMF-73472: A, E. right ilium in medial, lateral, posterior, anterior, dorsal and ventral views; B. right ischium in medial, lateral, posterior and anterior; C. right pubis in anterior, posterior, lateral and medial views; D. complete right pelvic girdle in medial, lateral, posterior and anterior views; F. púbis and ischium in distal view. Scale 5mm.



### **1.3.1.8 Hindlimbs**

#### **Femur**

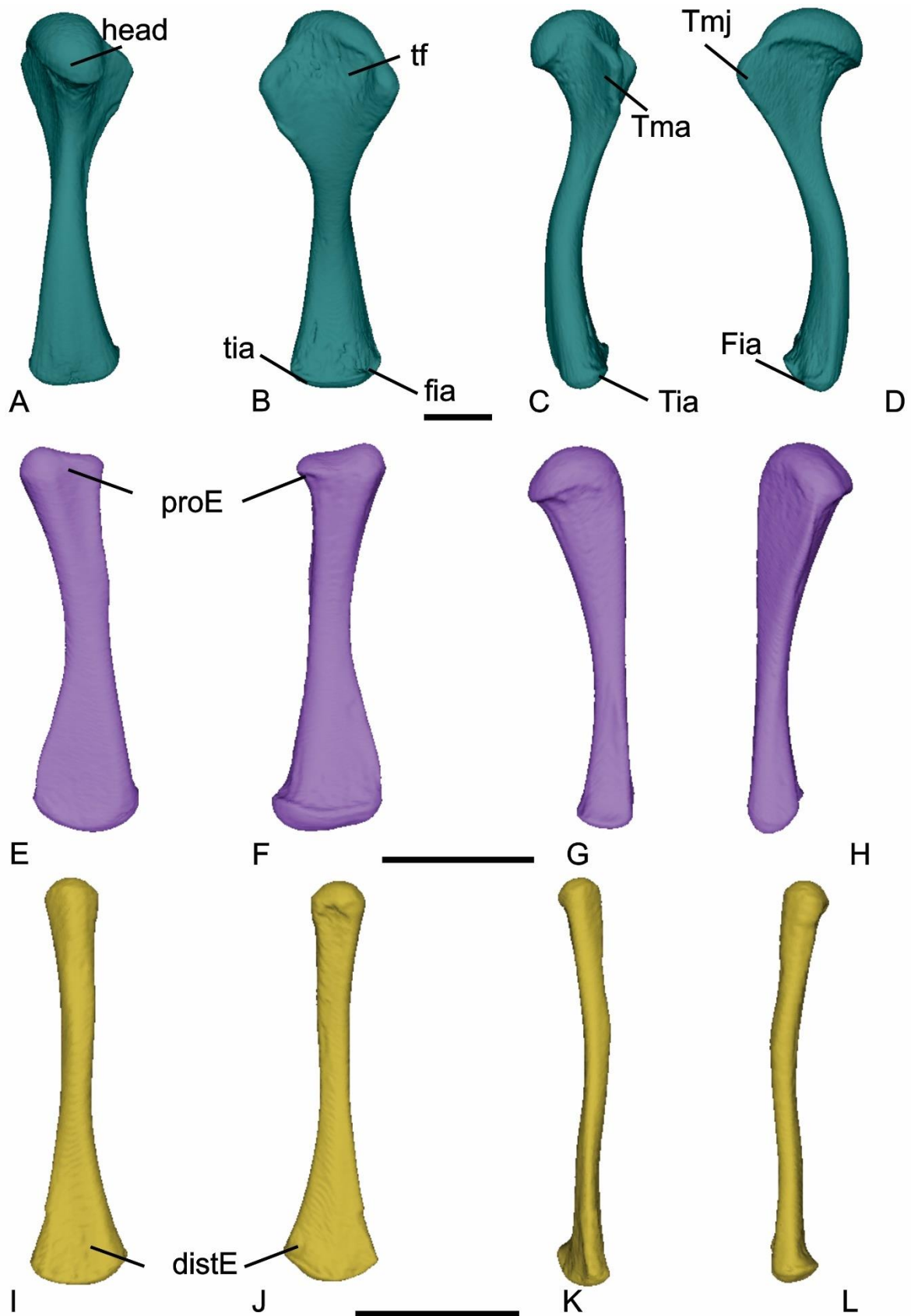
The head of the femur is slim and projected slightly from the shaft, with the articular surface tilted about 20° in relation to the shaft axis. This angle in *Acanthochelys radiolata* is about 25° and in *Chelodina expansa* is 27°. The trochanters major and minor do not project considerably, making the trochanteric fossa shallow and wide. The femoral shaft is thin and only slightly curved. The distal end of the femur consists of two not well distinguishable condyles, an anterior one that articulates with the tibia and a posterior one that articulates with the fibula. Between the articulation surfaces with the tibia and fibula, there is a small elevation of the bone, creating separation between the articulations, and the intercondylar fossa is absent.

#### **Tibia**

The shaft of the tibia has a slight curvature opposite to the fibula. The proximal end of the fibula is wide, nearly twice as wide as the distal end. At the distal end, there is a slight concavity where it articulates with the astragalus.

#### **Fibula**

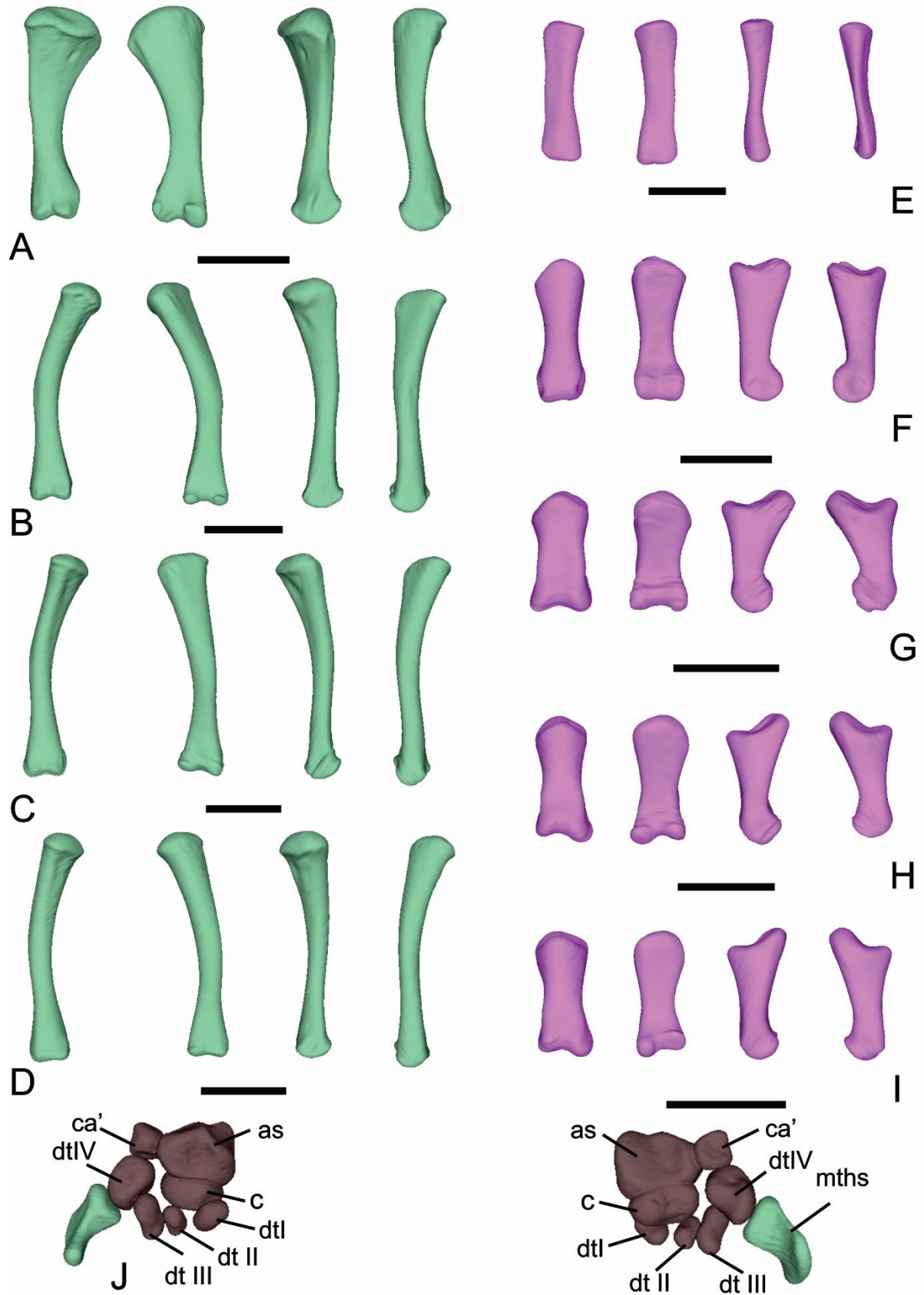
The proximal end of the fibula is rounded and almost as thin as the shaft. The shaft is slightly curved in the opposite direction of the tibia and widens as it approaches the distal end. The distal end is broad and flattened, with the lateral surface being wider due to its articulation with the astragalus and calcaneum.



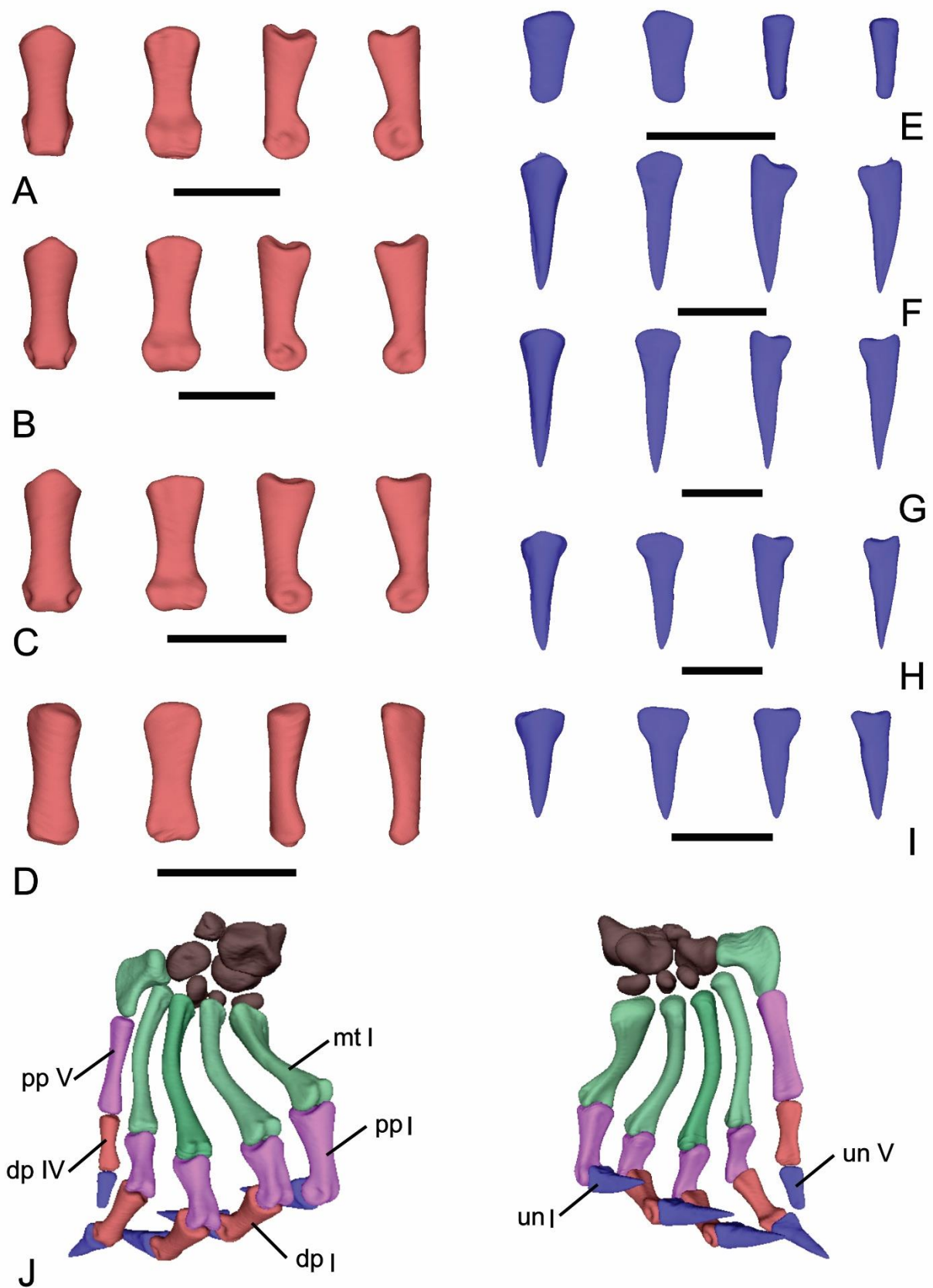
**Figure 14.** *Chelus orinocensis*. SMF-73472. A – D. Right femur in dorsal, ventral, anterior and posterior views; E – F. Right tibia in dorsal, ventral, anterior and posterior views; I – L. Right fibula in dorsal, ventral, anterior and posterior views. Abbreviations: tf – trochanteric fossa; mit – minor trochanter; mjt – major trochanter; fia – fibular articulation; tia – tibial articulation; ProE – Proximal End; DistE – Distal End. Scale bar: 1cm.

## **Tarsus and Pes**

The pes consists of 26 bones: astragalus, calcaneum, centralia, four tarsal bones, five metatarsals, five digits with the formula 3-3-3-3-2. The astragalus, the largest element of the tarsalia, has a rounded shape. It develops two articular surfaces, one medial for the fibula and one lateral for the tibia. Distally it articulates with the centrale and laterally to the astragalus. The astragalus is reduced, cubic-shaped, and it has a concave ventral surface. It articulates with the tibia proximally. The metatarsal V is hooked, as in other turtles (Joyce et al. 2013) and is the shortest of the metatarsals. The metatarsal I is the second shortest, with a rounded proximal end that is about twice as wide as metatarsals II, III, and IV. The shaft is slightly curved, and the distal end is concave, articulating with the proximal phalanges. The metatarsals II, III, and IV have similar morphology, with rounded proximal ends, slightly curved shafts, and concave distal ends with articulation surfaces for the phalanges. Among the proximal phalanges, the V is the longest, with a rounded proximal surface and a flattened distal surface, it also has the flattest shaft. The proximal phalange I is the second longest, while the II is shorter. The distal phalange IV is poorly developed, with a flattened shaft. Digit I lacks a distal phalanx. The unguis I-V are rounded dorsally and flattened ventrally, with the proximal surface considerably wider than the distal, tapering toward the distal end; II and III are the longest among the unguis, the unguis V does not have the characteristic claw shape of the unguis, being more flattened and with a rounded distal edge.



**Figure 15.** *Chelus orinocensis*. SMF-73472. A – D. metatarsal 1 – 4 in dorsal, ventral, anterior and posterior view; E – I. proximal tarsals 1 – 5 in dorsal, ventral, anterior and posterior view; J. tarsals bones in dorsal, ventral, posterior and proximal views. Abbreviations: as – astragalus; ca' – calcaneum; mths – metatarsal with hooked shape; C – centralia; dt – distal tarsals. Scale 5mm.



**Figure 16.** *Chelus orinocensis*. SMF-73472: A – D. right distal tarsals 1 – 4 in dorsal, ventral, anterior and posterior view; E – I. right unguis 1 – 5 in dorsal, ventral, anterior and posterior view; J. right complete hindlimb. Abbreviations: pp – proximal phalange; dp – distal phalange; mt – metatarsal; un – unguis. Scale: 5mm.

## 1.4 DISCUSSION

The  $\mu$ CT scans performed on specimens SMF-73431, SMF-73472, and SMF-73473 allowed us to segment all post-cranial bones and create 3D models for each bone individually to provide a thorough description of their morphology. In addition to providing the first osteological characterization for *Chelus orinocensis*, we analyzed possible ontogenetic and intraspecific variations. Among the observed features, the carapace with three well-defined ridges is the most distinctive in relation to other Chelidae species. We also identified similarities and differences between the cervical vertebrae of *Chelus orinocensis* and other long-necked chelids. The first four cervical vertebrae - atlas, axis, 2nd cervical, and 3rd cervical - are considerably elongated, a trait also observed in *Chelodina* and *Hydromedusa*. However, the neural spines of the 7th and 8th cervical vertebrae of the specimens described here rise significantly anteroposteriorly, this characteristic is not observed in the other genera. Regarding the observed characteristics in the post-cranial skeleton, *Chelus orinocensis* showed more similarities with *Hydromedusa* and *Chelodina* than to other species of the family Chelidae, in accordance to morphology based phylogenetic studies, (e.g. Ferreira et al., 2018; Holley et al., 2020, Maniel et al., 2020; Selvatti et al., 2023), which show a closer phylogenetically between those taxa.

We did not identify many postnatal ontogenetic changes among the specimens observed. However, the complete development of the shell bones happens only in the adult form. For example, in SMF-73431, SMF-73472, and SMF-73473 the costal bones are not yet fully ossified, leaving gaps between them and the peripheral bones, but in SMF-55153 the ossification is complete. A similar pattern is observed in the plastron, where the bones are not fully ossified. As a result, in younger specimens, it is possible to observe 3 fontanelles. The first, positioned more posteriorly, occurs due to the incomplete growth of the entoplastron and hyoplastron. The second, located in the central part of the plastron, occurs due to the

incomplete growth of the hyoplastron and hypoplastron and the third, located posteriorly, is due to the incomplete development of the hypoplastron and xiphiplastron. In SMF-55153, the three fontanelles are fully closed due to full ossification and complete contact of the bones. Additionally, we observed variations in the length and shape of the bones and scutes of the plastron. The first is about the length of the posterior processes of the xiphiplastron, which is smaller in SMF-73431, SMF-73473, and SMF-55153 and larger in SMF-73472. This does not appear to be an ontogenetic variation, as the smaller specimens and the largest present the same shape, differing only in the subadult specimen. Ferreira et al.,(2016) has already documented similar traits occurring in *Chelus fimbriata* as intraspecific variations. Given the degree of similarity, we consider that this variation occurs in the same way in *Chelus orinocensis*. A second characteristic that varied was the shape of the gular scute, which has a reduced length in SMF-55153 and does not prevent the contact of the extragular scutes in the medial part, this is also a characteristic observed in *C. fimbriata*, and therefore we also consider it as an intraspecific variable trait in *C. orinocensis*.

We also observed the development of cervical and caudal vertebrae, which follows a posterior-to-anterior pattern. In SMF-73431, the centrum and neural arch of the cervical vertebrae are not yet fused, and in the caudals, the more posterior vertebrae show complete development, while the more anterior ones remain sutured. In SMF-73472, all vertebrae are fully fused, indicating that vertebral development begins in a posterior-to-anterior sequence.

## 1.5 CONCLUSION

Despite the limited sample size, the  $\mu$ CT data presented here allowed us to delineate patterns of osteological growth in three ontogenetic stages. Additionally, we were able to provide a comprehensive and comparative description of the anatomical characteristics of all postcranial bones for *Chelus orinocensis*. In general, the post-cranium of turtles is neglected

in anatomical studies, and the majority of characters used in phylogenetic matrices are related to the skull. Therefore, we hope our work inspire future studies, serving as a comparative reference for new anatomical descriptions and analyses.



## **CHAPTER 2 - NEW FOSSILS OF THE GENUS *CHELUS* (TESTUDINES, CHELIDAE) FROM THE MIOCENE OF THE BRAZILIAN AMAZON, ACRE BASIN, BRAZIL.**

### **Abstract**

The Solimões Formation, located in the Acre Basin, which outcrops in the states of Acre and Amazonas, contains the most diverse fossil fauna of Neogene amniotes in Brazil. The outcrops are mainly found along the erosive banks of the Purus, Acre, and Juruá rivers, as well as road cuts such as those along BR-364, among others, since the 19th century. So far, as recorded for other Neogene deposits in northern South America, most of the fossil turtles from the Brazilian Amazon are primarily represented by genera attributed to the families Chelidae, Podocnemididae, and Testudinidae. The present chapter aims to review materials previously classified as *Chelus lewisi* and provide an osteological description of new *Chelus* fossils. The description of the fossil material, using as a means of morphological comparison specimens of *Chelus fimbriata*, allowed us to observe that certain characteristics that occur as intraspecific variation in living species can also occur in fossils. Morphological comparisons and analyses of intraspecific variations allowed us to confirm that only the fossil species *Chelus colombiana* is valid for the genus.

**Keywords.** *Chelus colombiana*. *Chelus lewisi*. Testudines. Miocene. *Chelus*.

## 2. INTRODUCTION

The genus *Chelus* (Chelidae) — popularly known as mata-mata — represented by two living species, *Chelus fimbriata* Schneider, 1783 and *Chelus orinocensis* Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Farias, Hrbek, Campbell & Fritz, 2020, has also included two extinct species: *Chelus colombiana* and *Chelus lewisi* (Wood, 1976). The species of this genus have unique characteristics among turtles, such as the extremely dorsoventrally flattened skull and highly ornamented body related to their camouflage and powerful suction-feeding behaviors (Lemell et al. 2002 and references therein). All mata-matas are fully aquatic, and the extant species inhabit the Amazon and Orinoco River drainages in northeastern South America (Rhodin et al. 2021).

Occurrences of fossil *Chelus* have been reported and discussed in several publications (Barbosa Rodrigues (1892), Wood (1976), Bocquentin-Villanueva & Rancy (1987), Bocquentin-Villanueva & Santos (1989), Lapparent de Broin et al. (1993), Sánchez-Villagra et al. (1995), Antoine et al. (2007), Sánchez-Villagra & Scheyer (2010), Cadena & Jaramillo, (2015), Ferreira et al. (2016), Cadena et al. 2023). The oldest genus records are in Colombia's early Miocene of the Castilletes Formation (Cadena & Jaramillo, 2015). In the middle to late Miocene of Colombia, many specimens assigned to *C. colombiana* are known (Wood, 1976; Cadena et al., 2023). Fossils assigned to *Chelus lewisi* were also reported from the middle to late Miocene Socorro and Urumaco formations of Venezuela (Sánchez-Villagra & Scheyer, 2010; Cadena et al., 2023). Additional genus records were also reported for the Local Fauna of Fitzcarrald, middle Miocene Peru (Antoine et al., 2007), and early Pleistocene from San Gregorio formation (Carillo-Briceño et al., 2021). For Brazil, few studies involving the genus *Chelus* have been conducted. In the early 2000s, new materials of *Chelus* were described by Bocquentin et al. (2001). The material described was collected by the Paleontology Laboratory of the Federal University of Acre (UFAC) from several localities of the Solimões

Formation located along the Acre, Iaco, Juruá, and Purus rivers in the state of Acre, Brazil. The materials found in Brazil consist of complete or nearly complete shells and isolated whole or fragmented bones of the shell and plastron.

Discussions about the validity of two species within the genus *Chelus* have persisted since Wood's (1976) description of the holotypes of *Chelus colombiana* and *Chelus lewisi*. Studies have attempted to clarify whether both species are indeed valid. Ferreira et al. (2016) reviewed the species within the genus and proposed the synonymization of the species *Chelus lewisi*. In this study, the author demonstrated that diagnostic features between the species could be interpreted as intraspecific variations in extant species, leaving only *Chelus colombiana* as a valid species. Recently, Cadena et al. (2023) described new materials and identified new morphological characteristics, reaffirming the validity of the species *Chelus lewisi*. Herein are described new fossils of *Chelus* from several localities in Acre, Brazil. Those represent the best-preserved specimens of *Chelus* from the Brazilian fossil record.

## **2.1 MATERIAL AND METHODS**

### **2.1.1 Provenance, geological and paleontological contextthods**

The fossil *Chelus* of this study comprised 69 new specimens, and three specimens previously classified as *Chelus lewisi* were reviewed. All the materials are deposited in the paleontology collection of the Laboratório de Pesquisas Paleontológicas (LPP) at the Universidade Federal do Acre (UFAC, Rio Branco, State of Acre) and consist of almost complete shells as well as isolated carapace and plastron fragments. The material studied here was collected during expeditions to fossiliferous localities of the Solimões Formation in the state of Acre between 1990 and 2022: Niteroi, Talismã, Lula, Cachoeira do Bandeira, Aracuã and Patos (Fig. 1)

On the fossil localities, one of the several sites of Acre River is the Cachoeira do Bandeira site is located on the left bank of the river, at coordinates 10°56'21"S and

69°20'37"W. This locality was discovered in the 1970s during expeditions carried out in 1976 (Souza-Filho & Guilherme, 2015). The lithology found in this Formation consists of sedimentary conglomerates and silt-clay. The paleofauna found is diverse, with records of turtles (Bocquentin-Villanueva & Guilherme, 2007), crocodiles (Aureliano et al., 2015), birds (Alvarenga & Guilherme, 2003), and mammals (Kerber et al., 2014, 2017). The estimated age for this locality is the Late Miocene (Souza-Filho & Guilherme, 2015).

The Patos locality (Acre 06 or LACM 4611) is situated along the upper Acre River at coordinates 10°55'55"S and 69°5'20"W. In this locality, most fossils are found in the lower levels, which can only be accessed during the dry season when the river level is low (Cozzuol et al., 2006; Souza-Filho & Guilherme, 2015). The lithology of the lower levels consists of red to green clay and siltstone and conglomerates composed of clay pebbles. The associated paleofauna is diverse and includes invertebrates, fish fragments, turtles (Bocquentin, 2006; Broin et al., 1993), crocodiles (Kay & Cozzuol, 2006), birds (Guilherme et al., 2023), and mammals (Cozzuol et al., 2006; Kay & Cozzuol, 2006).

The Niteroi locality was discovered back in 1987 and is situated on the right bank of the Acre River, at coordinates 10°14'00 "S and 67°82'00"W, with an assigned age of  $8.5 \pm 0.5$  million years (Bissaro-Júnior et al., 2019; Souza-Filho and Guilherme, 2015). The lithology of this locality consists of a conglomerate of clay, varying in layers of gypsum and fossiliferous levels. The associated paleofauna includes fish (Monsch, 1998), mammals (Kerber et al., 2017, 2018; Bocquentin and Guilherme, 1999; Frailey, 1986) crocodiles (Gasparini, 1985; Souza-Filho and Bocquentin-Villanueva, 1991), birds (Alvarenga and Guilherme, 2003) and turtle (Bocquentin et al., 2001).

The Talismã locality is situated on the right bank of the Purus River, with its discovery dating back to 1980, at coordinates 08°48'22 "S and 68°48'12"W, with an assigned age of  $10.89 \pm 0.13$  million years (Bissaro-Júnior et al., 2019; Souza-Filho and Guilherme, 2015;

Bergqvist et al., 1998; Bocquentin-Villanueva and Negri, 1993; Santos et al., 1993). The lithology of this locality consists of white to red clay and siltstone, with gypsum and calcite veins. The associated paleofauna includes crocodylians (Fortier et al., 2014), Turtles (Bocquentin et al., 2001), squamates (Hsiou et al., 2009, 2010; Hsiou and Albino, 2009), Mammals (Bergqvist et al., 1998; Kerber et al., 2016, 2018; Negri, 2004), birds (Alvarenga and Guilherme, 2003), and amphibians (Muniz et al., 2021).

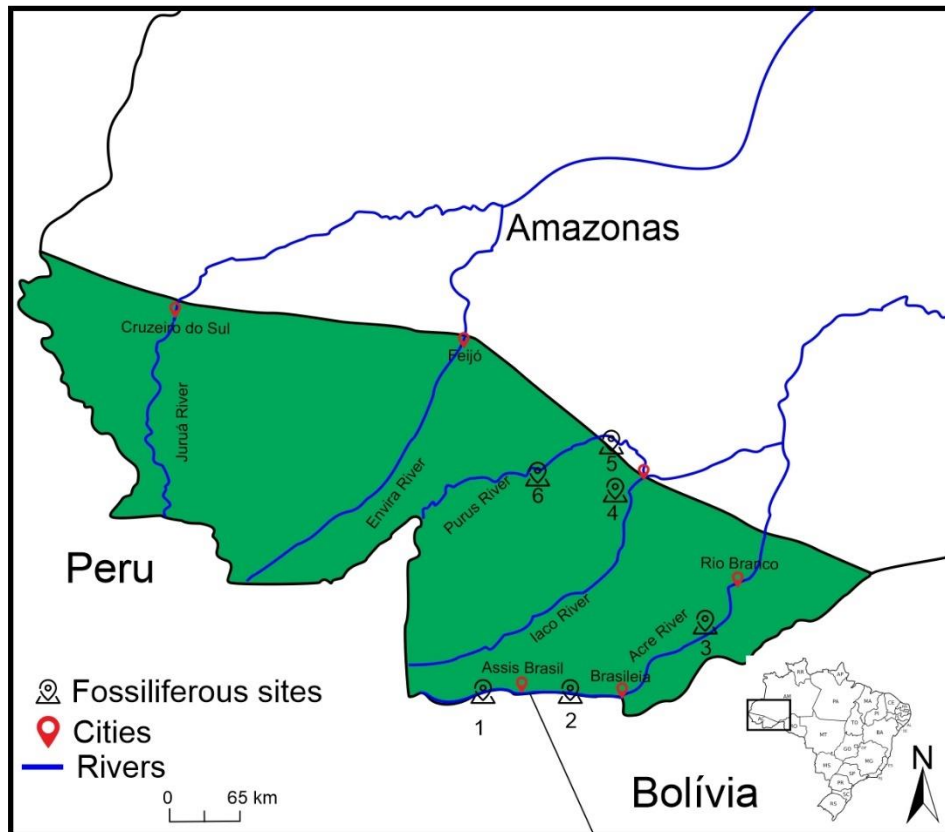
The Aracuã locality is a little-explored area and is located on the left bank of the Purus River, at coordinates 09°01'03.1"S and 69°25'35.7"W. During expeditions conducted in 2013 in collaboration with researchers from the Universidade de São Paulo (USP), Universidade Federal do Acre (UFAC) and Universidade Estadual Paulista (UNESP), many materials were collected but not yet published, including variety of Testudines.

Unlike the previous localities, the Lula outcrop is not situated along waterways. It is located on both sides of the BR-364 highway along a road cut at coordinates 09°01'23 "S and 68°48'21.00"W ( Souza-Filho and Guilherme, 2015). The lithology of this locality consists of white to red clay and siltstone. The associated paleofauna includes fish fragments (Richter, 1984), and reptiles (Souza-Filho, 1987).

**Table 1: Described Specimens with Collection Locations**

Number	Material	Locality
UFAC-5805	Nucal	Acre River
UFAC-2097	Nucal	Solimões Formation
UFAC-5792	Neural 3	Acre River
UFAC-1943	Neural 5	Acre River
UFAC-5007	Neural 5	Patos
UFAC-997	Neural 5	Solimões Formation
UFAC-7163	Neural 5	Patos
UFAC-7021	Neural 4 or 6	Patos
UFAC-807	Costal 1	Cachoeira do Bandeira
UFAC-6553	Costal 1	Talismã
UFAC-5509	Costal 1	Lula
UFAC-4758	Costal 1	Envira River
UFAC-7379	Costal 1	Talismã
UFAC-7350	Costal 1	Talismã
UFAC-755	Costal 2	Solimões Formation
UFAC-2713	Costal 2	Talismã
UFAC-2205	Costal 2	Niterói

UFAC-944	Costal 2	Solimões Formation
UFAC-6720	Costal 2	Cachoeira do Bandeira
UFAC-556	Costal 2	Solimões Formation
UFAC-4753	Costal 2	Solimões Formation
UFAC-7017	Costal 2	Patos
UFAC-4887	Costal 2 and 3	Niterói
UFAC-7362	Costal 3 or 6	Talisma
UFAC-3574	Costal 4	Solimões Formation
UFAC-2712	Costal 5	Purus River
UFAC-2970	Costal 5	Talismã
UFAC-6541	Costal 5	Talismã
UFAC-3168	Costal 5	Purus River
UFAC-5803	Costal 5	Acre River
UFAC-6583	Costal 5	BR-364
UFAC-6411	Costal 5	Purus River
UFAC-S/N	Costal 5	Solimões Formation
UFAC-3240	Costal 5	Lula
UFAC-7347	Costal 5	Talismã
UFAC-2714	Costal 8	Purus River
UFAC-7348	Costal 8	Talismã
UFAC-3003	Costal 8	Talismã
UFAC-6490	Costal 8	Cachoeira do Bandeira
UFAC-3288	Costal 7,8 and Suprapygal	Acre River
UFAC-4469	Suprapygal	Patos
UFAC-2981	Suprapygal	Talismã
UFAC-5799	Suprapygal	Acre River
UFAC-6893	Suprapygal	Patos
UFAC-2967	Pygal	Talismã
UFAC-2438	Pygal	Iaco River
UFAC-7353	Pygal	Talismã
UFAC-945	Peripheral	Solimões Formation
UFAC-7354	Peripheral	Talismã
UFAC-7344	Incomplete Carapace	Aracuã
UFAC-6517	Almost complete carapace	Solimões Formation
UFAC-5497	Almost complete carapace	Acre River
UFAC-4815	Disarticulated carapace	Acre River
UFAC-953	Left Xiphiplastron	Talismã
UFAC-1006	Left Xiphiplastron	Solimões Formation
UFAC-2075	Left Xiphiplastron	Purus River
UFAC-2597	Left Xiphiplastron	Acre River
UFAC-4267	Left Xiphiplastron	Talismã
UFAC-2973	Left Xiphiplastron	Talismã
UFAC-4262	Left Xiphiplastron	Talismã
UFAC-4455	Left Xiphiplastron	Patos
UFAC-4266	Right Xiphiplastron	Talismã
UFAC-3143	Right Xiphiplastron	Talismã
UFAC-3145	Right Xiphiplastron	Talismã
UFAC-3144	Right Xiphiplastron	Talismã
UFAC-1047	Right Xiphiplastron	Solimões Formation
UFAC-6548	Right Xiphiplastron	Talismã
UFAC-1581	Right Xiphiplastron	Solimões Formation
UFAC-1559	Femur	Purus River



**Figure 17.** Location map of fossiliferous localities of *Chelus* from the Solimões Formation, Acre Basin: 1. Patos, 2. Cachoeira do Bandeira, 3. Niterói, 4. Lula, 5. Talismã, 6. Aracuã.

### 2.1.2 Methods

Nearly 86 specimens of the extant *Chelus fimbriata* were used for comparative anatomy. Most *C. fimbriata* specimens are available in the Brazilian collections of Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus, Amazonas State), Museu Paraense Emílio Goeldi (MPEG, Belém, Pará State), Laboratório de Pesquisas Paleontológicas of Universidade Federal do Acre (LPP/UFAC, Rio Branco, Acre State), Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, São Paulo State), and from the German institution Senckenberg Museum Frankfurt (Frankfurt, Germany). All specimens had the measurements of the total length and width of the carapace and plastron collected, using a ruler and tape for larger specimens, and digital calipers for smaller specimens. The figures were edited and prepared using CorelDraw and Corel Photo Paint.

## 2.2 RESULTS

### SYSTEMATIC PALEONTOLOGY

Testudines Batsch, 1788.

Pleurodira Cope 1865

Chelidae Gray, 1825

*Chelus* Duméril, 1806

#### *Chelus colombiana* Wood, 1976

**Synonymy:** *Chelus lewisi* Wood, 1976

**Holotype:** UCMP 78762, a nearly complete shell found in the vicinities of Villavieja, upper Magdalena River Valley, Colombia, late Miocene Villavieja Formation (Wood 1976, pls. 1–2).

**Referred material:** UFAC-5805, UFAC-2097: nucal; UFAC-5792: neural 3; UFAC-1943, UFAC-5007, UFAC-997, UFAC-7163: neural 5; UFAC-7021: neural 4 or 6; UFAC-807, UFAC-6553, UFAC-5509, UFAC-4758, UFAC-7379, UFAC-7350: costal 1; UFAC-755, UFAC-2713, UFAC-2205, UFAC-944, UFAC-6720, UFAC-556, UFAC-4753, UFAC-7017: costal 2; UFAC-4887: costal 2 and 3 articulated; UFAC-7362: costal 3 or 6; UFAC-3574: costal 4; UFAC-2712, UFAC-2970, UFAC-6541, UFAC-3168, UFAC-5803, UFAC-6583, UFAC-6411, UFAC-S/N, UFAC-3240, UFAC-7347: costal 5; UFAC-2714, UFAC-7348, UFAC-3003, UFAC-6490: costal 8; UFAC-3288: costal 7, 8, and suprapygal articulated; UFAC-4469, UFAC-2981, UFAC-5799, UFAC-6893: suprapygal; UFAC-2967, UFAC-2438, UFAC-7353: pygal; UFAC-945, UFAC-7354: peripheral; UFAC-7344: incomplete carapace; UFAC-6517: almost complete carapace; UFAC-5497: almost complete articulated carapace and pelvic girdle; UFAC-4815: incomplete disarticulated carapace; UFAC-953, UFAC-1006, UFAC-2075, UFAC-2597, UFAC-4267, UFAC-2973, UFAC-4262, UFAC-4455: left



xiphiplastron; UFAC-4266, UFAC-3143, UFAC-3145, UFAC-3144, UFAC-1047, UFAC-6548, UFAC-1581: right xiphiplastron; UFAC-1559: femur.

**Revised Diagnosis:** Differs from the extant species *Chelus fimbriata* and *Chelus orinocensis* in having the following characteristics: (1) axillary scar extending to the second costal bone, rather than restricted to the first costal bone (extant taxa); (2) inguinal buttress onto costal 5, instead of costal 4 (extant taxa); (3) a broader cervical scute including two small ridges on the nuchal bone instead of a narrow cervical scute with one ridge on the midline; (4) ilium scar on the suprapygal and eighth costal bones, rather than extending to seventh costal (extant taxa); (5) one or two extra pairs of extragular scutes usually prevents the gular scute from reaching the anterior margin of the plastron; (6) vertebral scute 1 almost rectangular, instead of pentagonal (extant); (7) cervicals 7 and 8 having longer and more dorsoventrally projected neural spines, and broader internal scapular angle of 85°." (Modified from Cadena et al., 2023).

**Geographic occurrence.** Miocene of Colombia (Villavieja formation, Wood, 1976; Barzalosa Formation, Cadena, 2008; La Victoria Formation, Cadena et al., 2023), Venezuela (Castillo Formation, Ferreira, 2016; Urumaco and Socorro formations Cadena et al., 2023) and Brazil (Solimões formation, Bocquentin et al., 2001).

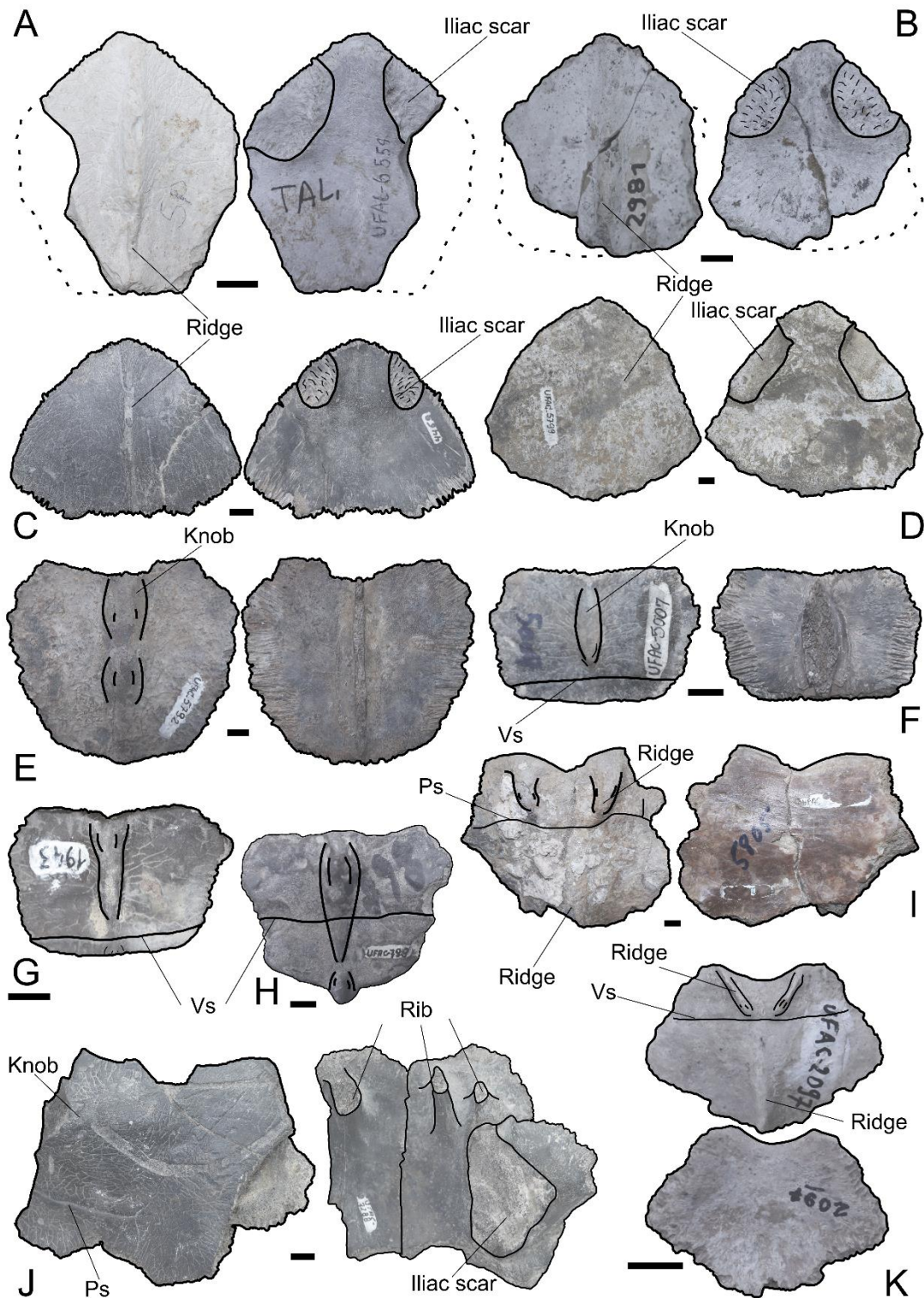
## 2.2.1 Description

### 2.2.1.1 Carapace

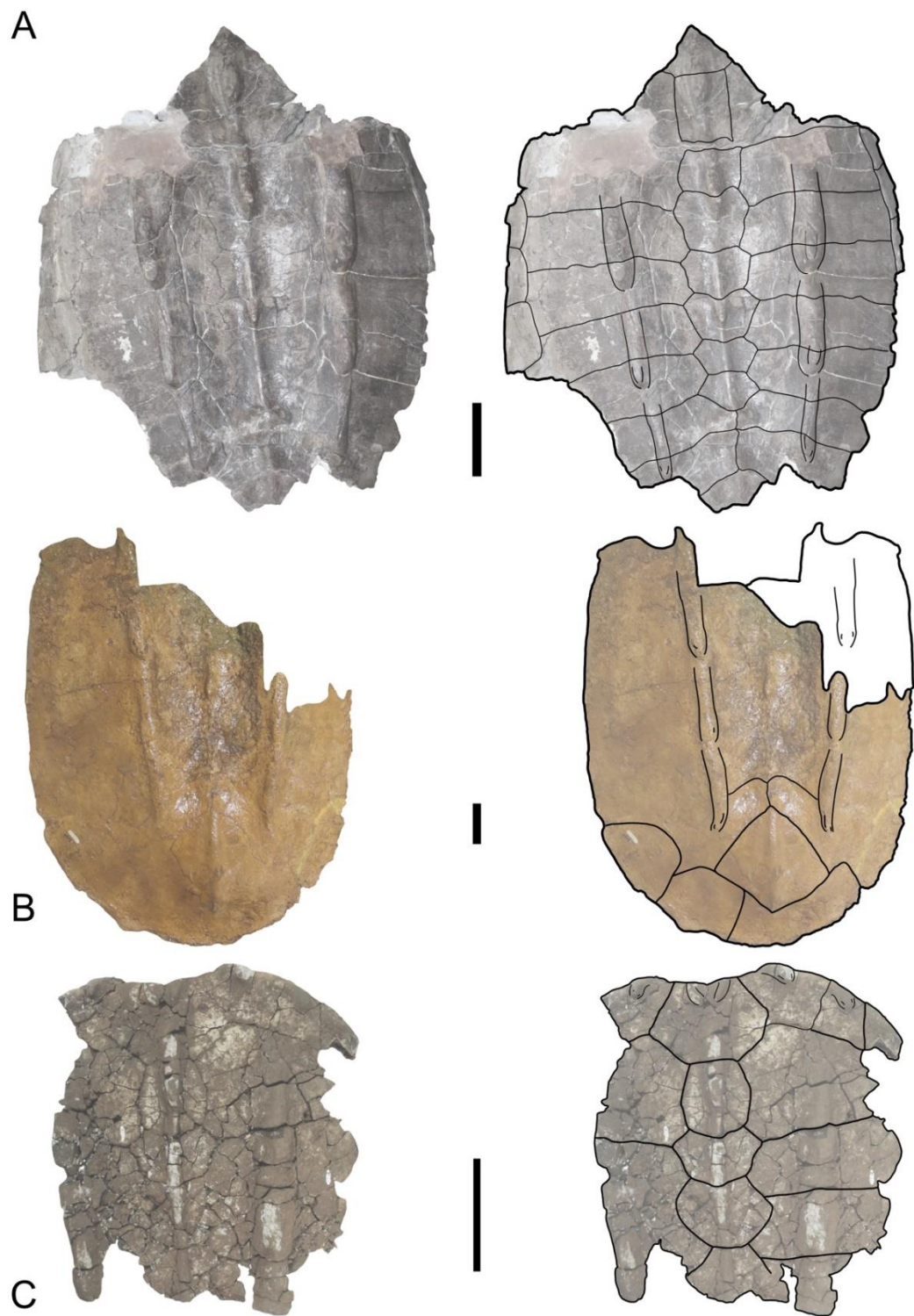
The osteological description of the carapace was based on the most complete specimens, UFAC-5497, UFAC-7344, and UFAC-6517. The three more complete specimens from Acre exhibit a carapace with a rectangular shape and three ridges along the dorsal surface of the carapace, two lateral and one on the midline. The nuchal bone assumes a hexagonal configuration, with small ridges identified on the anterior edge of its dorsal surface (Fig. 18, K), extending posteriorly to half its length. The seven neural bones are arranged

sequentially, with no variation in this count among the specimens analyzed. The first neural bone is the largest in the series, and its shape ranges from rectangular, as observed in UFAC-5497 (Fig. 19A), to more rounded, as seen in UFAC-4815 (Fig. 20I). A midline ridge runs along the entire neural series and extends posteriorly until the pygal. The first, third, and fifth neural bones also display dorsal sulci resulting from the contact between subsequent vertebral scutes. The costal bones form a sequence of eight, with the first exhibiting the most significant shape variation in the series, notably wider than longer. The sulci created by the adjacent scutes are visible on their dorsal surfaces on the second, fourth, sixth, and eighth costal bones. On the ventral surface, three scars are present: the axillary scar extending lateromedially from the 1st to the end of the second costal (Fig. 21A and 22G); the inguinal scar on the fifth costal, extending anteroposteriorly with a slight curvature (Fig. 23F and 24E); and the ilium scar spanning from the eighth costal to the suprapygal bone (Fig. 21I and 22J). The shape of the suprapygal varies from pentagonal, as in UFAC-6559 (Fig. 18A, B), to triangular, as seen in UFAC-4469 (Fig. 18C, D), with ilium scars positioned laterally on its ventral surface. The pygal bone marks the end of the midline ridge and has a W-shaped form (Fig. 21H and 23G). The first three peripheral bones have a nearly quadrate shape with well-developed knobs, as observed in specimen UFAC-4815 (Fig. 20D). On the ventral surface of second and third peripherals, it is possible to observe the axillary scar (Fig. 20G) in contrast to what occurs in the living species, where the scar is restricted to the fourth peripheral (Fig. 20H). The medial and posterior peripherals have a more quadrate shape, with less developed and lower crests, as in UFAC-5497, which preserves the peripherals fourth, fifth, sixth, and seventh, and UFAC-6517, in which peripherals tenth and eleventh can be seen (Fig. 18B). On the ventral surface of second and third peripherals, it is possible to observe the axillary scar (Fig. 20G) in contrast to what occurs in the living species, where the scar is restricted to the fourth peripheral (Fig. 20H). The medial and posterior peripherals have a more quadrate

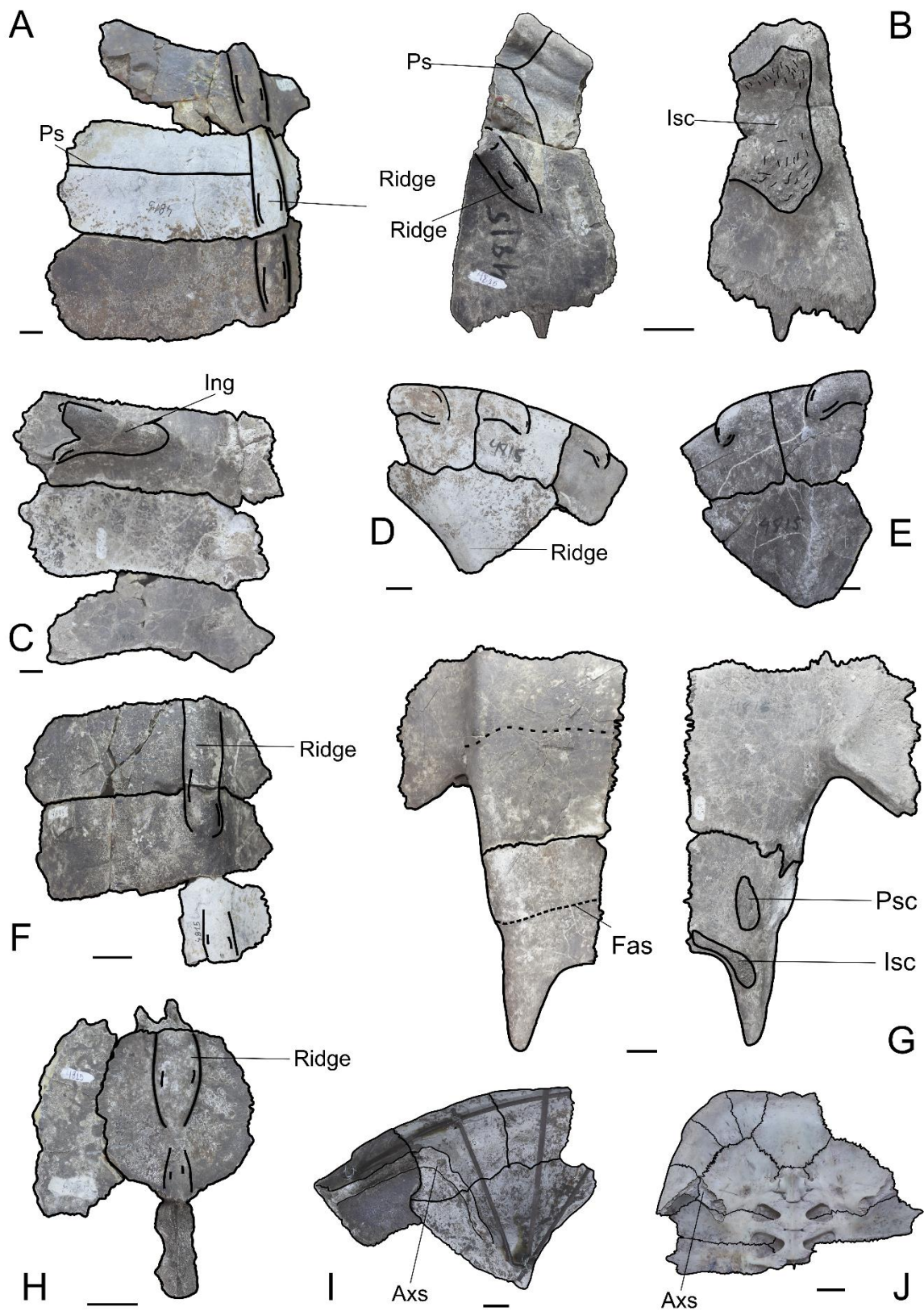
shape, with less developed and lower crests, as in UFAC-5497, which preserves the peripherals fourth, fifth, sixth, and seventh, and UFAC-6517, in which tenth and eleventh peripherals can be seen (Fig. 18B).



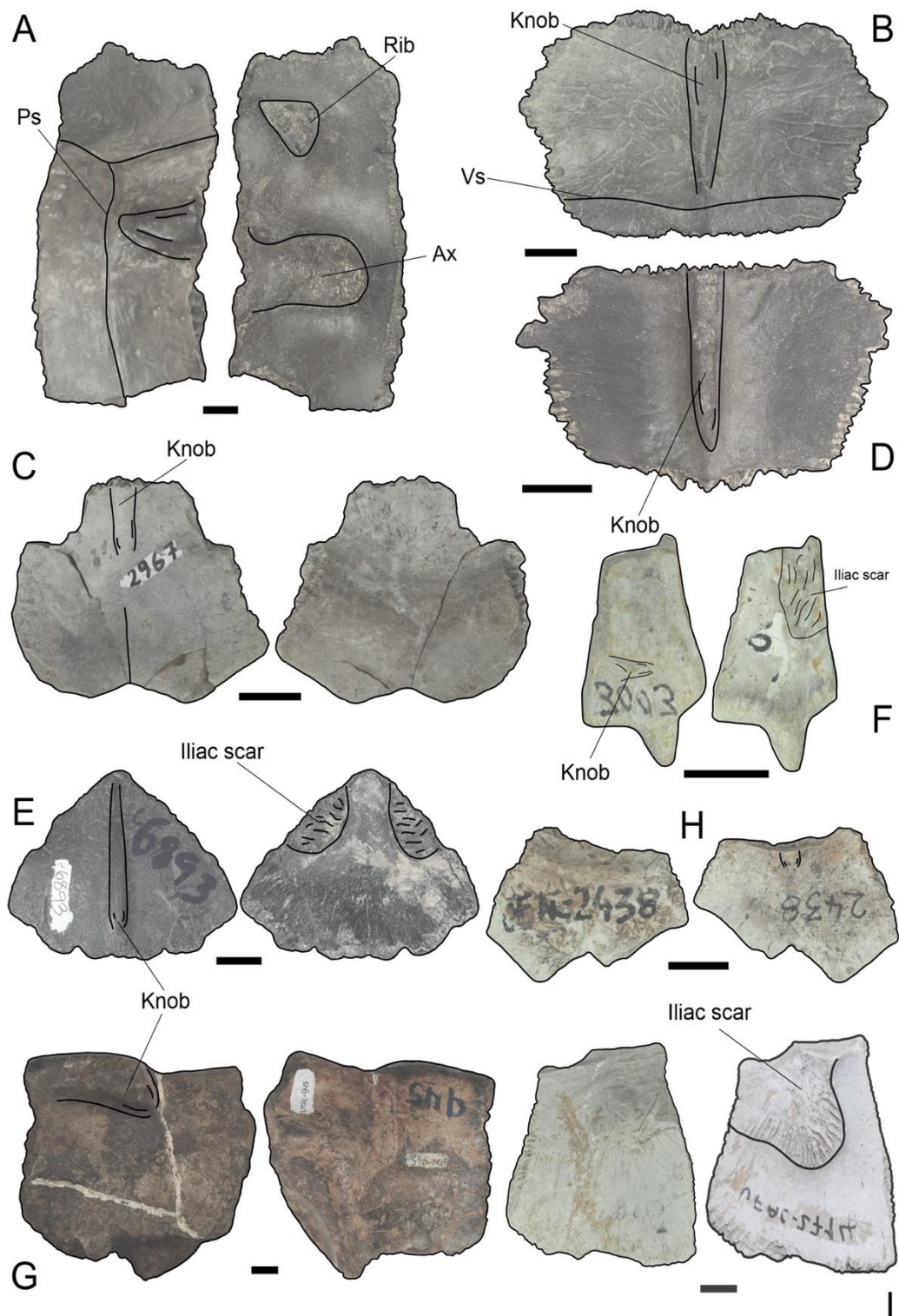
**Figure 18.** *Chelus colombiana*. A. UFAC-6559: suprapygal, dorsal/ventral view; B. UFAC-2981: suprapygal, dorsal/ventral view; C. UFAC-4469: suprapygal, dorsal/ventral view; D. UFAC-5799, suprapygal, dorsal/ventral view; E. UFAC-5792, neural three, dorsal/ventral view; F. UFAC-5007, neural five, dorsal/ventral view; G. UFAC-1953, neural five, dorsal/ventral view; H. UFAC-798, neural three?, dorsal/ventral view; I. UFAC-5805, nucal, dorsal/ventral view; J. UFAC-3288, costal seven and eight, dorsal/ventral view; K. UFAC-2097, nucal, dorsal/ventral view. Scale: 1cm. Abbreviations: Ax – Axillary Scar; Ing – Inguinal Scar; Ps – Pleural Scute; Vs – Vertebral Scute. Scale Bar 1 cm.



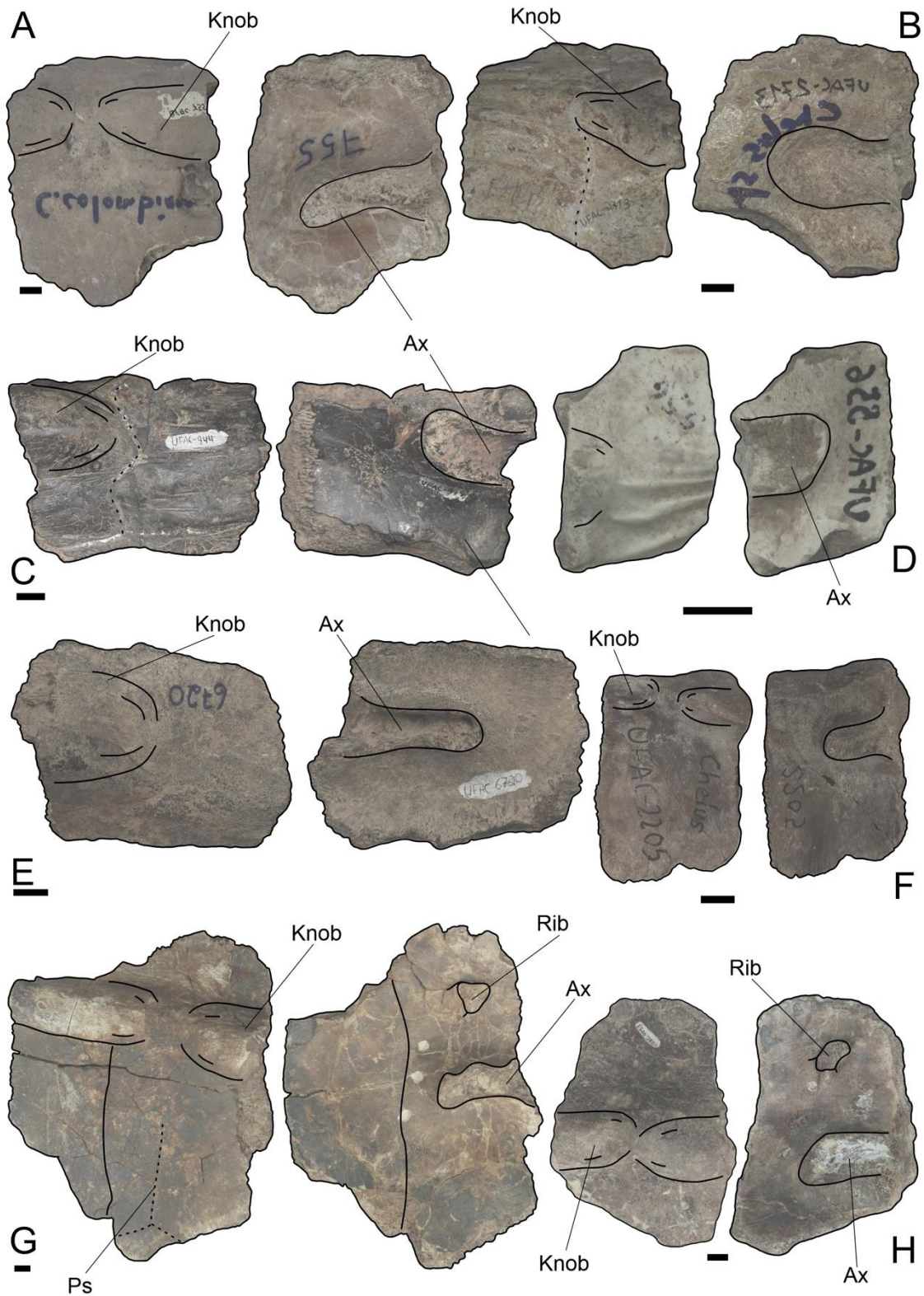
**Figure 19.** *Chelus colombiana*. A. UFAC-5497: nearly complete articulated carapace, dorsal view; B. UFAC-6517: nearly complete articulated carapace, dorsal view; C. UFAC-7344: fragmented articulated carapace, dorsal/ventral view. Scale bar: 10 cm



**Figure 20.** *Chelus colombiana*. A-I. UFAC-4815 - A,C: costal five, six, and seven, dorsal/ventral view; B: left costal eighth, dorsal/ventral view; D,G: first and second peripheral, and left costal first, dorsal/ventral view; E: first, second, third peripheral, and right first costal; F: costal third, fourth, and fifth, dorsal view; I: neural first and fragment of costal first; J: xiphiplastron and hypoplastron; J. UFAC-R550: incomplete anterior portion of the carapace. Scale: 3 cm. Abbreviations: An – Anal notch; Fas – Femoroanal sulcus; Psc – Pubic scar; Axs – Axillary scar; Isc – Ischial scar; Ps – Pleural scute. Scale bar: 2cm

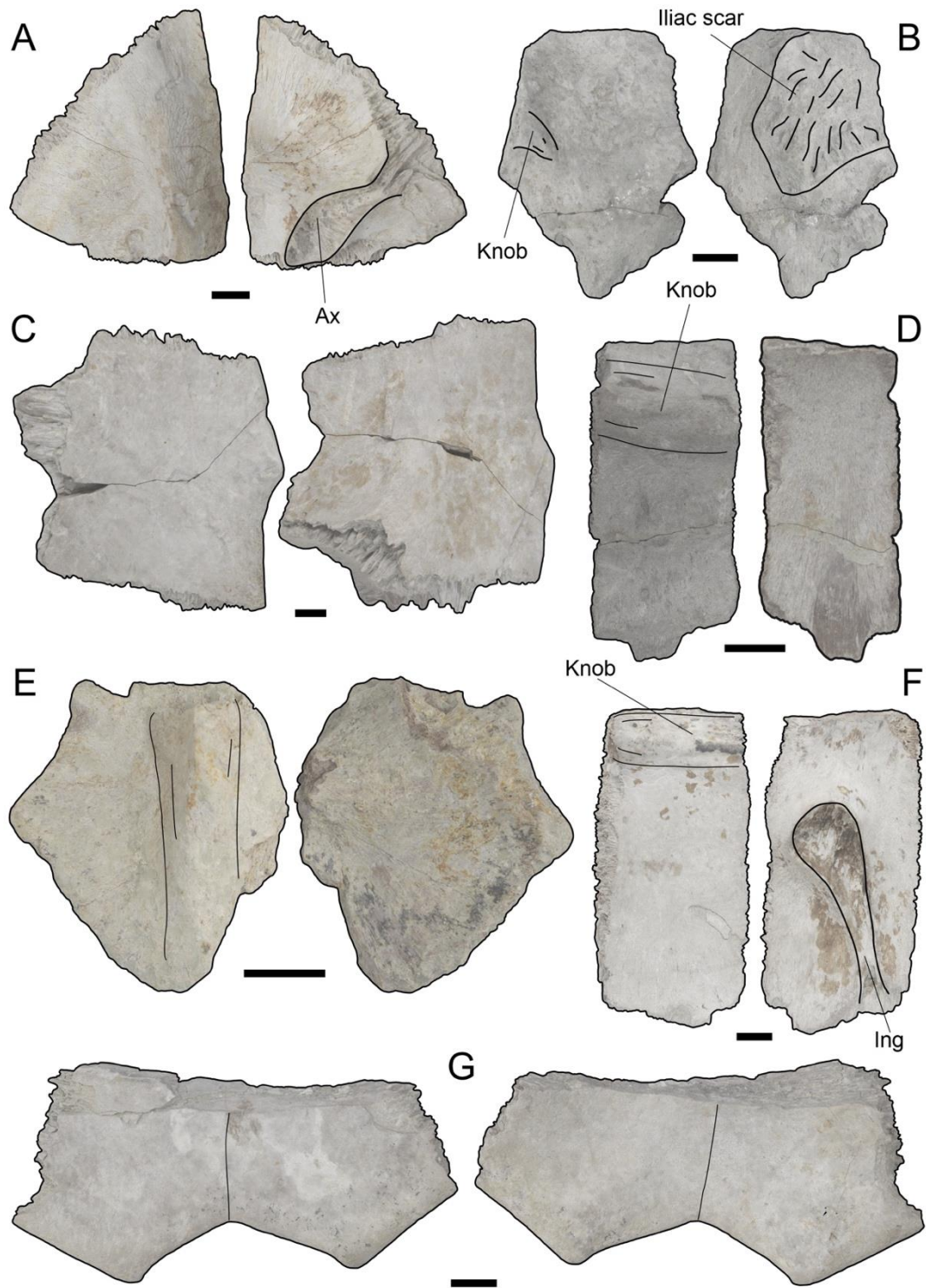


**Figure 21.** *Chelus colombiana*. A. UFAC-7017: right costal 2, dorsal/ventral view; B. UFAC-7163: neural 5, dorsal view; C. UFAC-2967: pygal, dorsal/ventral view; D. UFAC-7021, neural 4 or 6, dorsal view; E. UFAC-6893, suprapygal, dorsal/ventral view; F. UFAC-3003, costal 8, dorsal/ventral view; G. UFAC-945, right peripheral, dorsal/ventral view; H. UFAC-2438, pygal, dorsal/ventral view; I. UFAC-2714, costal 8, dorsal/ventral view. Abbreviations: Ps – Pleural Scute; Ax – Axillary Scar; Vs – Vertebral Scute. Scale bar: 1cm

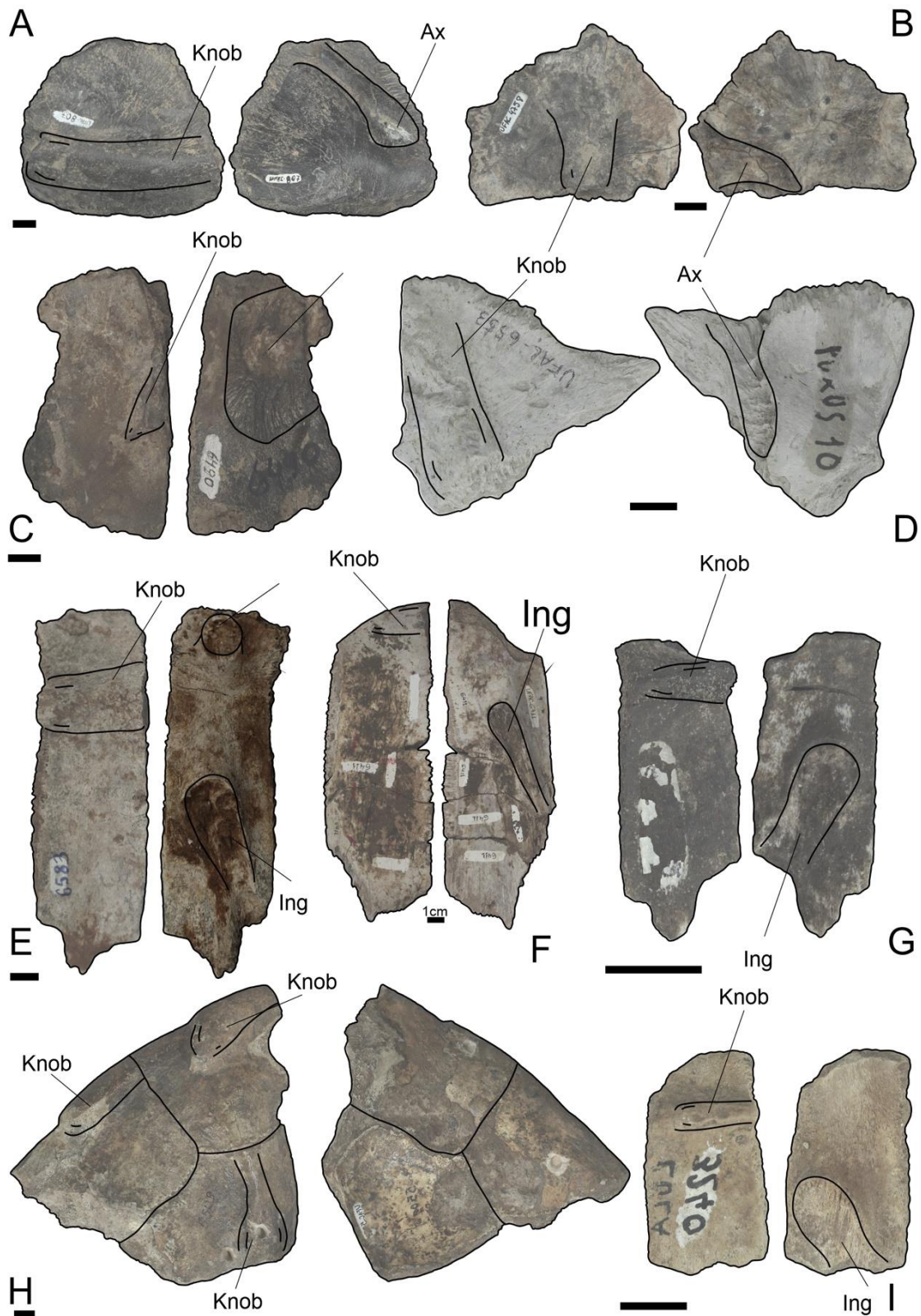


**Figure 22.** *Chelus colombiana*. A. UFAC-755: left costal two, dorsal/ventral view; B. UFAC-2713: left costal two, dorsal/ventral view; C. UFAC-944: left costal two, dorsal/ventral view; D. UFAC-556, right costal two, dorsal/ventral view; E. UFAC-6720, right costal two, dorsal/ventral view; F. UFAC-2205, left Costal two, dorsal/ventral view; G. UFAC-4887, left costal two and three, dorsal/ventral view; H. UFAC-4753, left costal two, dorsal/ventral view. Abbreviations: Ax – Axillary Scar; Ing – Inguinal Scar; Scute – Scute. Scale bar: 1cm





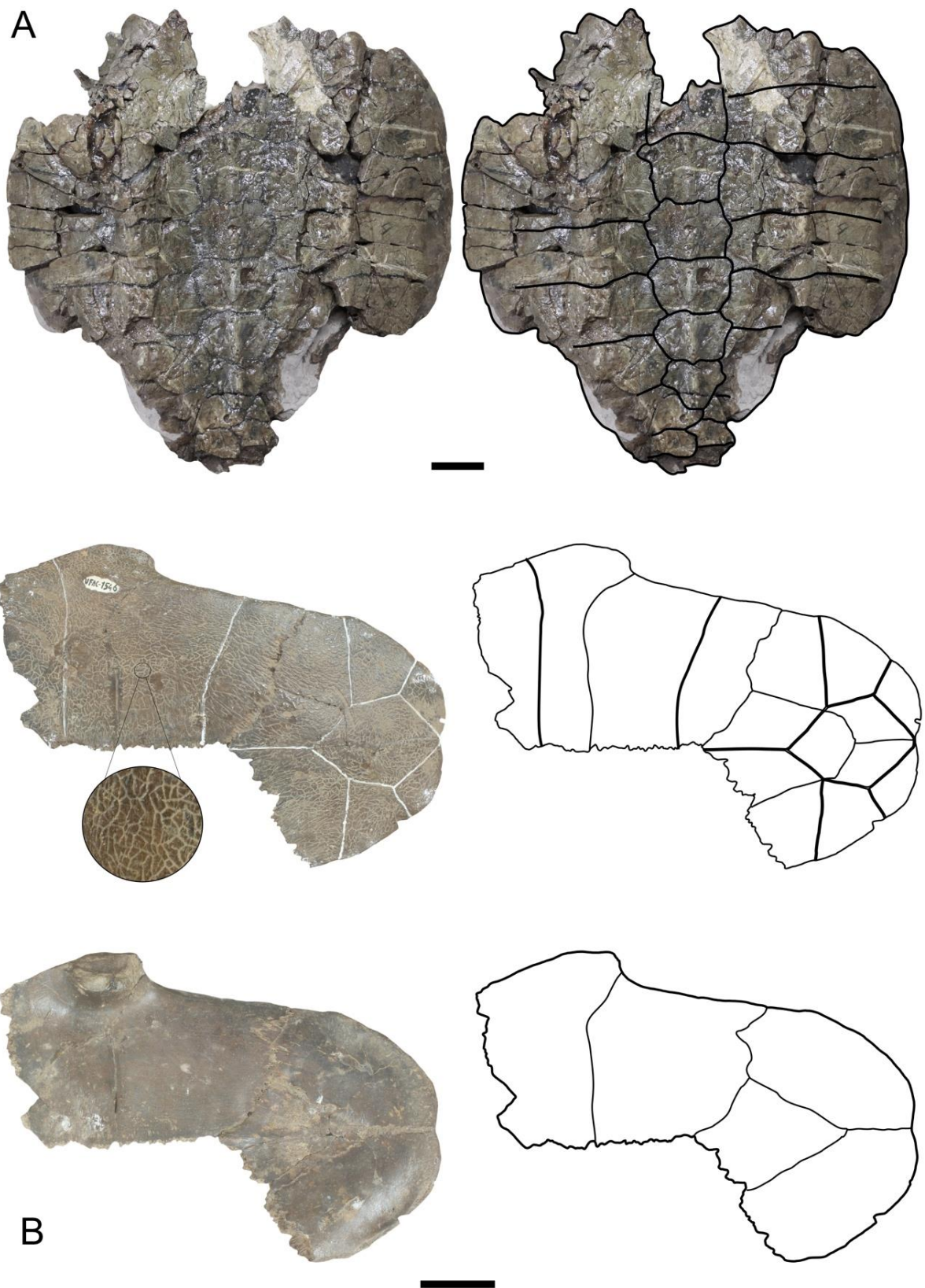
**Figure 23.** *Chelus colombiana*. A. UFAC-7349: costal 1, dorsal/ventral view; B. UFAC-7348: costal 8, dorsal view; C. UFAC-7354: peripheral, dorsal/ventral view; D. UFAC-7362, costal 3 or 6, dorsal/ventral view; E. UFAC-7350, costal 1, dorsal/ventral view; F. UFAC-7347, right Costal 5, dorsal/ventral view; G. UFAC-7353, pygal, dorsal/ventral view. Abbreviations: Ax – Axillary Scar; Ing – Inguinal Scar. Scale bar: 1cm



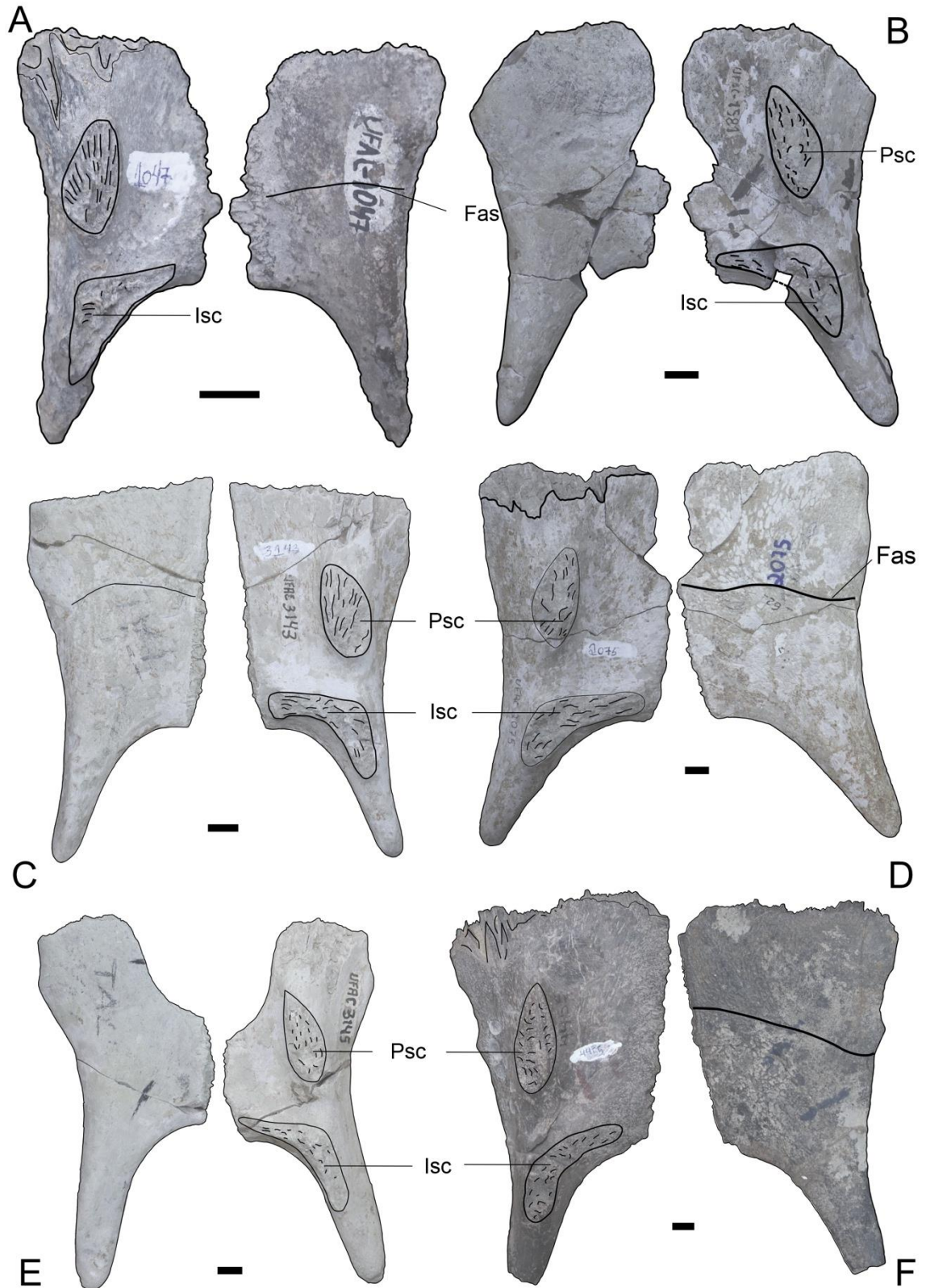
**Figure 24.** *Chelus colombiana*. A. UFAC-807: costal 1, dorsal/ventral view; B. UFAC-4758: costal 1, dorsal/ventral view; C. UFAC-6490: costal 8, dorsal/ventral view; D. UFAC-6553, costal 1, dorsal/ventral view; E. UFAC-6583, left costal 5, dorsal/ventral view; F. UFAC-6411, right Costal 5, dorsal/ventral view; G. UFAC-S/N, left costal 5, dorsal/ventral view; H. UFAC-5509, peripheral and right costal 1, dorsal/ventral view; I. UFAC-3240, right costal 5, dorsal/ventral view. Abbreviations: Ax – Axillary Scar; Ing – Inguinal Scar. Scale bar 1cm.

### 2.2.1.2 Plastron

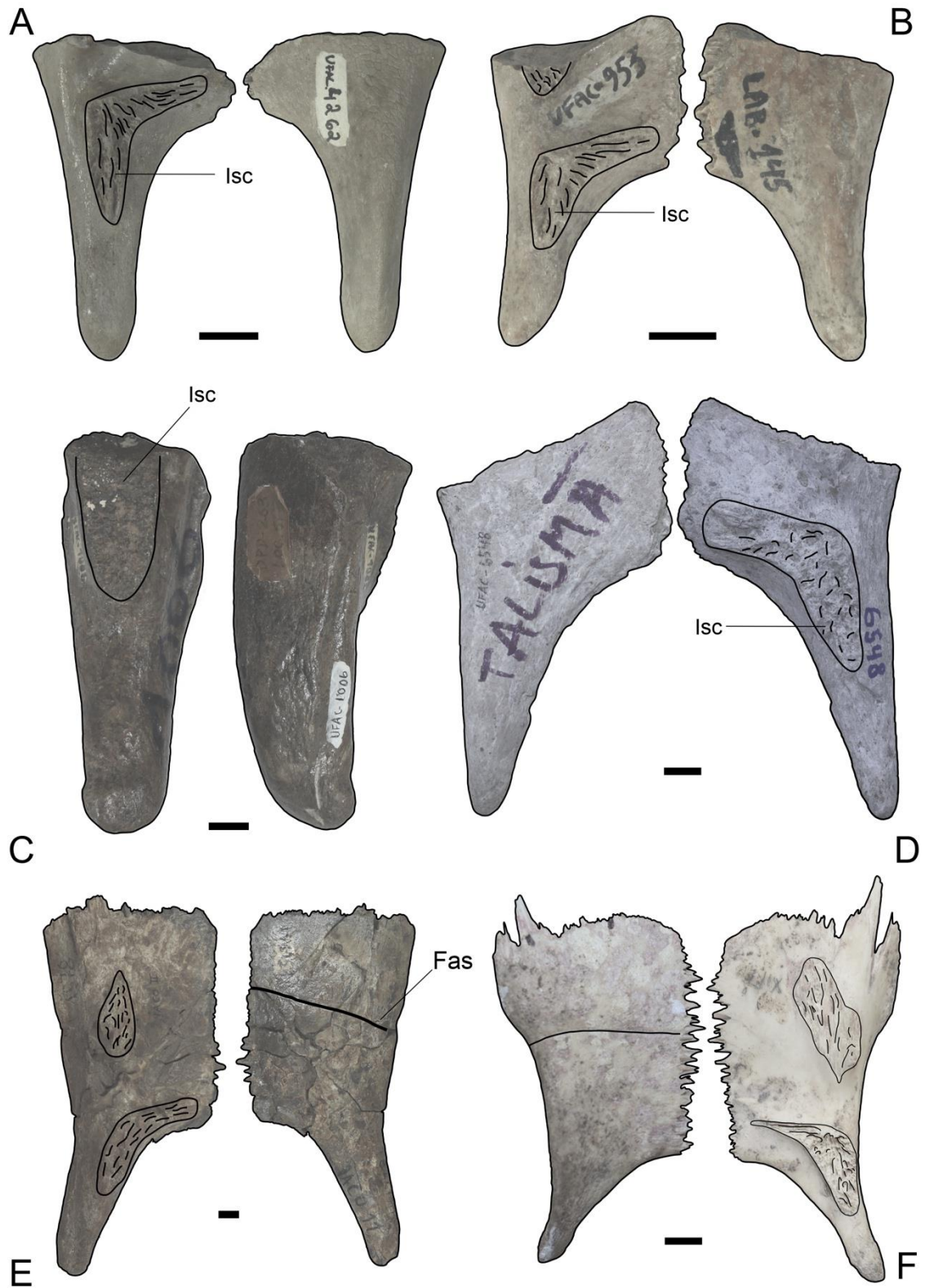
On the ventral surface of the anterior lobe of the plastron, the extra pair of extragular scutes hinders the gular from reaching the anterior edge of the plastron, a trait exclusively present in the extinct species (Wood, 1976). However, in the specimen UFAC-1546, although the extra pair of extragulars is present, it does not prevent the gular scute from stretching to the anterior margin of the plastron (Fig. 25B). The xiphiplastron bone is wider in the anterior part. It narrows into a horn-shaped process in the posterior portion. On the ventral surface, the femoroanal sulcus forms a notch laterally at the edge of the bone. On the dorsal surface, the pubic and ischiadic scars exhibit a slight variation in shape and position. The pubic scar is generally oval but can vary in position and form, as observed in UFAC-3143 (Fig. 26C), where the scar is near the border of the bone, while in UFAC-1581 (Fig. 26B), the scar is more medially located. The oval shape can vary from being narrower with a thin anterior edge, as observed in UFAC-3145 (Fig. 26E), to broader with a rounded anterior edge, as seen in UFAC-3143. The ischiadic scar has a boomerang shape but also exhibits considerable shape variation. For example, in UFAC-3143 its ends are thin compared to those in UFAC-4455 (Fig. 26F), which has rounded ends, in addition to the curvature of the posteromedial edge, which can be more concave, as observed in UFAC-4262, or without concavity, as in UFAC-4455 (Fig. 27A and 26F).



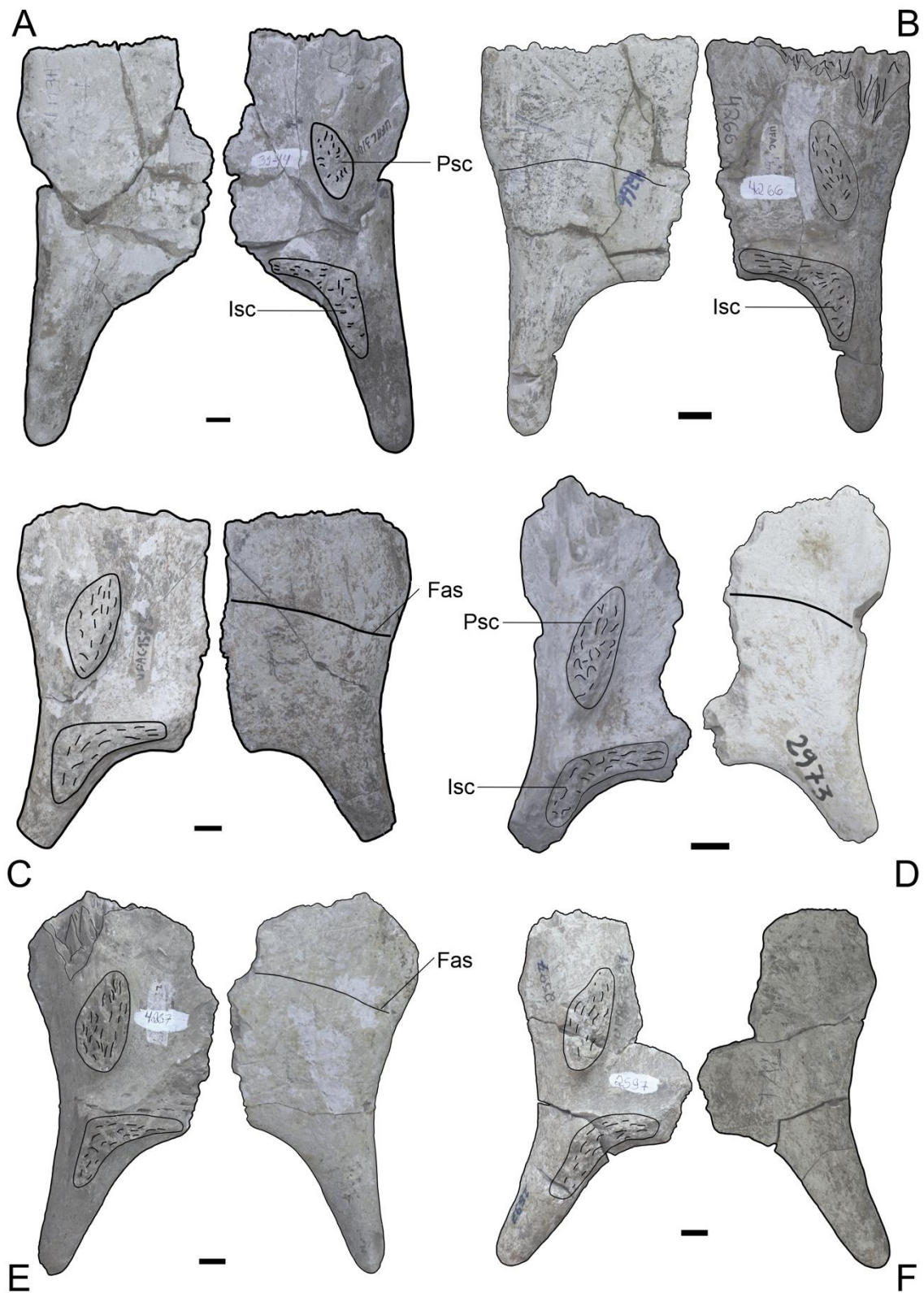
**Figure 25.** *Chelus colombiana*. A. UFAC-1002: nearly complete articulated carapace, dorsal view; B. UFAC-1546: incomplete articulated plastron, dorsal/ventral view. In zoom, ornamentations can be observed, which occur on the carapace and plastron. Scale: 5 cm.



**Figure 26.** *Chelus colombiana*. A. UFAC-1047: left xiphiplastron, dorsal/ventral view; B. UFAC-1581: right xiphiplastron, dorsal/ventral view; C. UFAC-3143: right xiphiplastron, dorsal/ventral view; D. UFAC-2075, left xiphiplastron, dorsal/ventral view; E. UFAC-3145, right xiphiplastron; F. UFAC-4455: left xiphiplastron, dorsal/ventral view. Abbreviations: Fas – Femoroanal sulcus; Isc – Ischial scar; Psc – Pubic scar. Scale bar: 1cm



**Figure 27.** *Chelus colombiana*. A. UFAC-4262: left xiphiplastron, dorsal/ventral view; B. UFAC-953: left xiphiplastron, dorsal/ventral view; C. UFAC-1006: left xiphiplastron, dorsal/ventral view; D. UFAC-6548: right xiphiplastron, dorsal/ventral view; E. UFAC-1578: left xiphiplastron; *Chelus fimbriata*. F. UFAC-R550: xiphiplastron. Abbreviations: Fas – Femoroanal sulcus; Isc – Ischial scar. Scale bar: 1cm



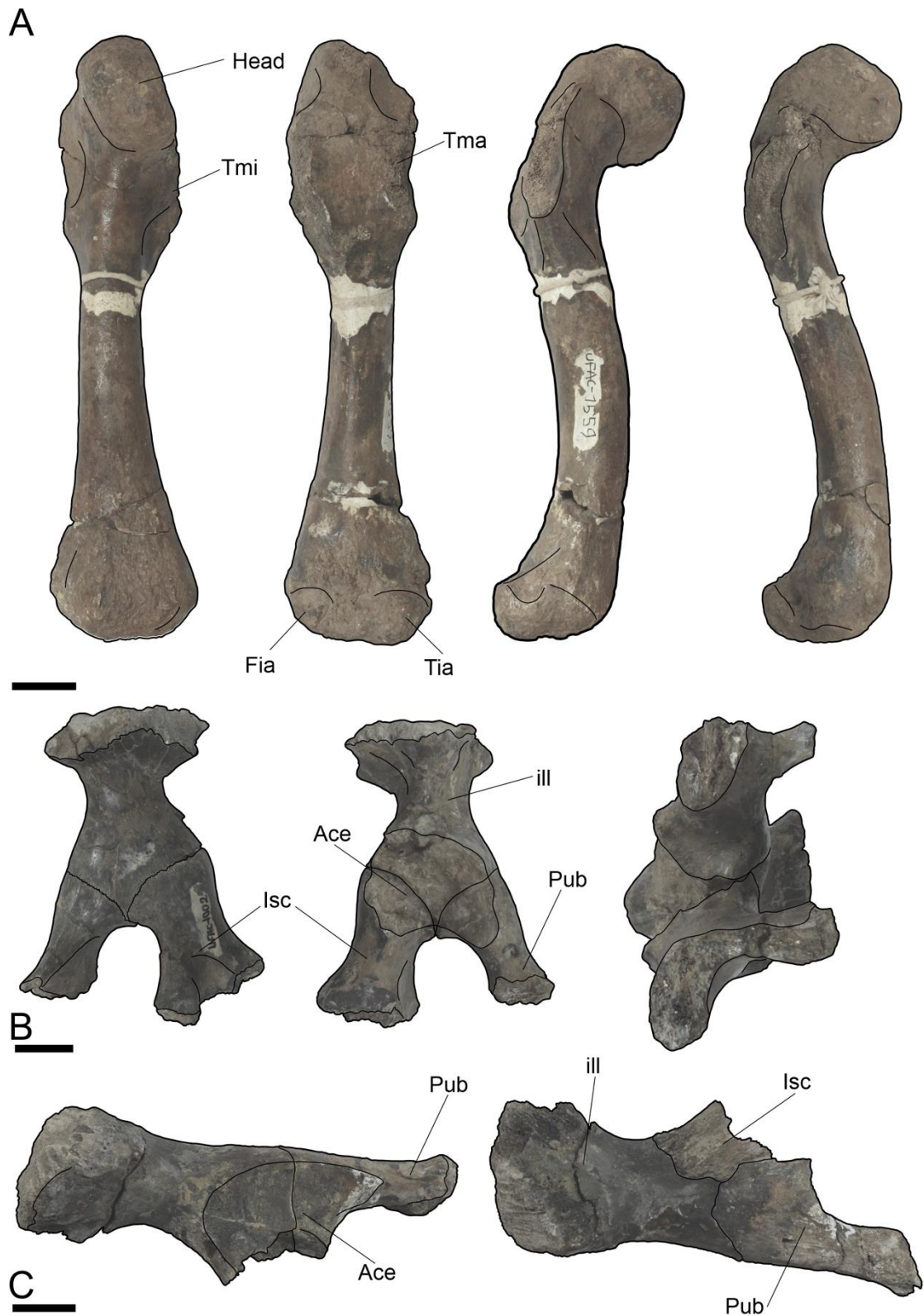
**Figure 28.** *Chelus colombiana*. A. UFAC-3144: right xiphiplastron, dorsal/ventral view; B. UFAC-4266: right xiphiplastron, dorsal/ventral view; C. UFAC-1575: left xiphiplastron, dorsal/ventral view; D. UFAC-2973: left xiphiplastron, dorsal/ventral view; E. UFAC-4267: left xiphiplastron; F. UFAC-2597: left xiphiplastron, dorsal/ventral view. Abbreviations: Fas – Femoroanal sulcus; Isc – Ischial scar; Psc – Pubic scar. Scale bar: 1 cm

### 2.2.1.3 Appendicular bones

Currently, only a few fossil materials related to the appendicular bones are known for the genus *Chelus*, and here we add three new specimens from the state of Acre to its fossil record. UFAC-1559 consists of an incomplete right femur similar to the one described by Cadena et al. (2023). Its head is slim and considerably projected medially from the shaft, and the articular surface is tilted about 20° concerning the shaft axis (Fig. 29A). Although the trochanters are not preserved, the intertrochanteric fossa is shallow but relatively wide. Like the living species, the femoral shaft is thin and slightly curved.

UFAC-1002 is an almost complete right pelvic girdle, and UFAC-5497 is a second right pelvic girdle, less complete than the former (Fig. 29B-C). The pelvic girdle bones are robust and dorsoventrally compact, the sutural surface of the ilium with the costal bones is reduced in comparison to the extant species, and the acetabulum is not entirely round, having an anteroventral elongation in the pubis. In UFAC-1002, the contact surface of the ischium to the xiphiplastron has rounded extremities (Fig 29B). The contact surface of the pubis, connecting it to the xiphiplastron, is oval in both specimens, similar to what is observed in extant species. There is no significant variation between UFAC-1002 and the extant species concerning the angle formed between the ischium and the pubis: this angle is 66° in UFAC-1002 versus 64° in the extant species. However, the scar caused by the contact of the pubis with the plastron can vary in its position, either closer to the lateral edge of the xiphiplastron bone, as seen in living species, or more centralized as in UFAC-1578 and UFAC-3144 (Fig. 27A and 28E).

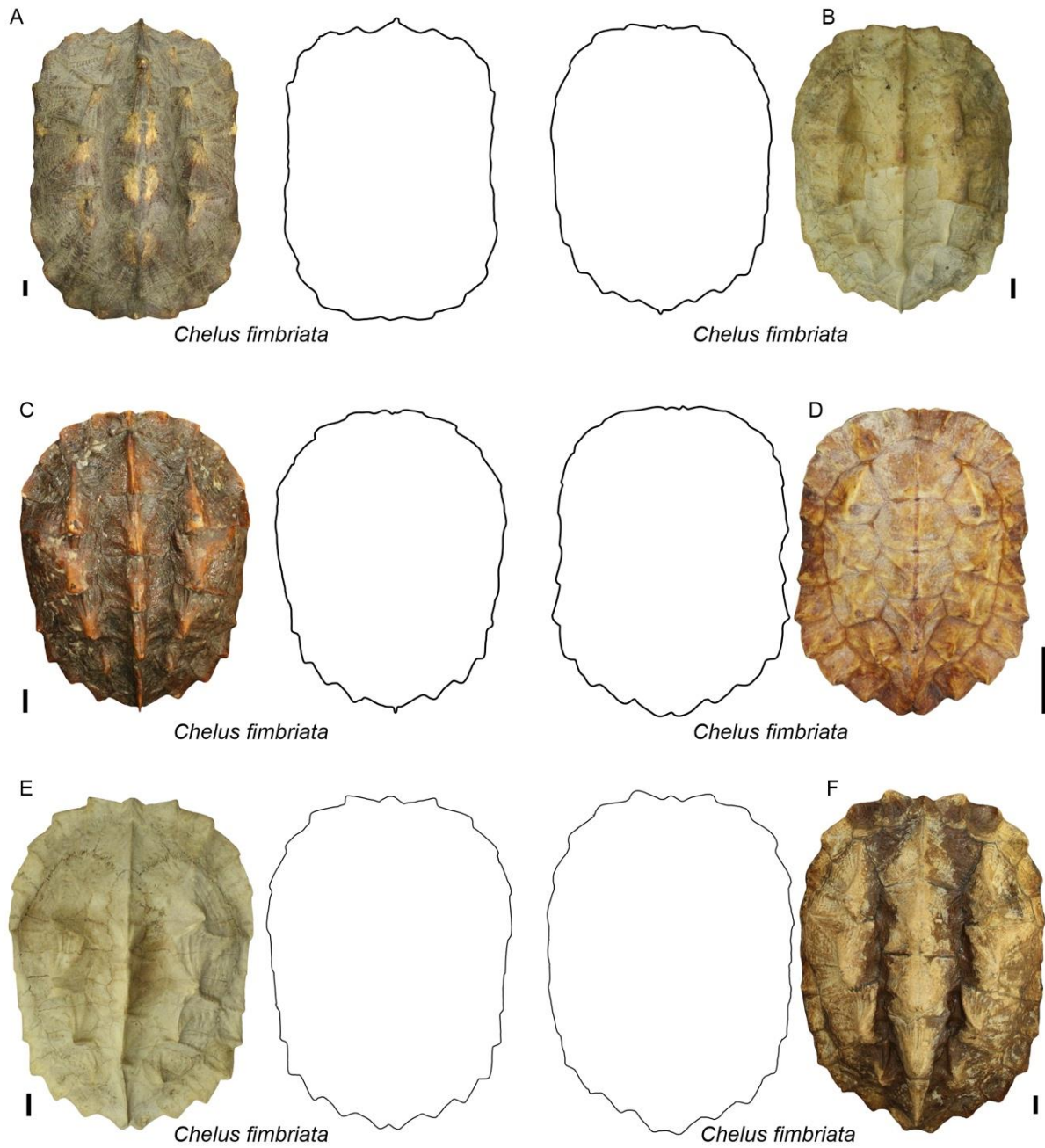




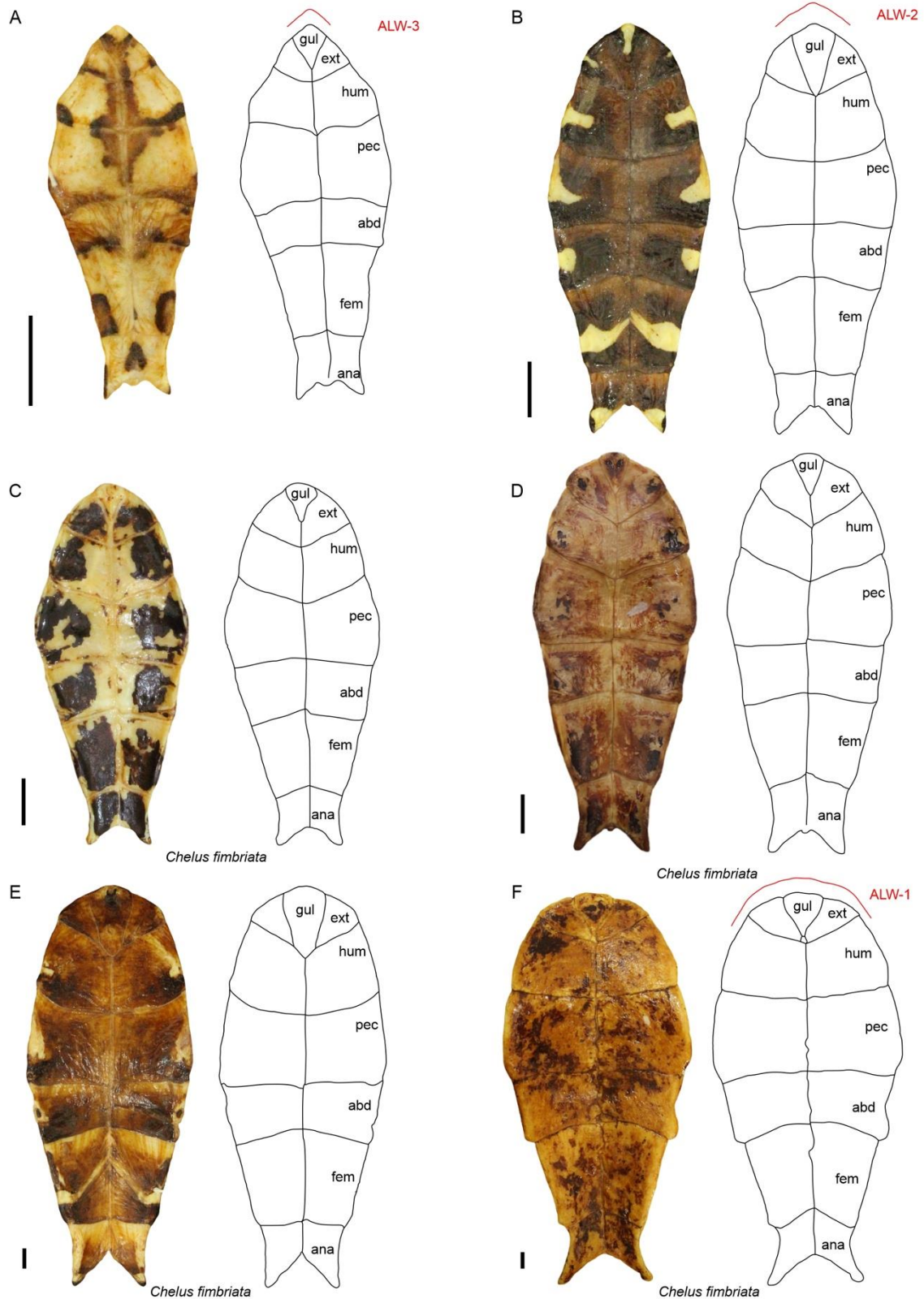
**Figure 29.** *Chelus colombiana*. A. UFAC-1559: Right Femur, dorsal/ventral/lateral views; B. UFAC-1002: right pelvic girdle, medial/lateral/ventral views; C. UFAC-5497: right pelvic girdle, medial/lateral views. Abbreviations: Ace – Acetabulum; Pub – Pubis; Isc – Ischium; ill – Ilium; Fia – Fibular articulation; Tia – tibial articulation; Tmi – trochanter minor; Tma – trochanter major. Scale bar: 2cm

### 2.2.1 Intraspecific variation in *Chelus fimbriata*

There are a significant number of intraspecific morphological variations both in the carapace and in the plastron of the extant *Chelus fimbriata*. On the carapace, the overall shape exhibited the most variation. We observed the following shape variations: rectangular with parallel edges (Fig. 30A), rectangular with a broader posterior half (Fig. 30D), oval with a wider anterior part (Fig. 30E), oval with the posterior part slightly wider (Fig. 30 B, F.) We also identified three states of variation in the shape and thickness of the midline ridge concerning the lateral ridges. The first is a thinner midline ridge compared to the lateral ridges (Fig. 30E, B). The second is a midline ridge of equivalent thickness to the lateral ridges (Fig. 30C). The third is a more robust medial ridge, with the knobs being almost indistinguishable, making it thicker than the lateral ridges (Fig. 30F). In the plastron, we observed two variations: (1) the width of the anterior lobe, narrow in MPEG-1238 (Fig. 30B) and significantly wider in MPEG-042 (Fig. 31F); (2) the length and shape of the gular scute, reduced size and triangular shape as in MZUSP-2048 (Fig. 31D), larger size and triangular shape as in MPEG-36 (Fig. 31B), or larger size and triangular shape with the posterior portion wider than the previous ones (Fig. 31E).



**Figure 30.** *Chelus fimbriata*. A. MPEG-0483: carapace, dorsal view; B. MPEG-1249: carapace, dorsal view; C. MPEG-1238: carapace, dorsal view; D. MPEG-042: carapace, dorsal view; E. MPEG-0407: carapace, dorsal view; F. AMH-267: carapace, dorsal view. Scale bar: 2 cm.



**Figure 31.** *Chelus fimbriata*. A. MPEG-1238: plastron, ventral view; B. MPEG-36: plastron, ventral view; C. MPEG-0510: plastron, ventral view; D. MZUSP-2048: plastron, ventral view; E. MPEG-1240: plastron, ventral view; F. MPEG-042: plastron, ventral view. Abbreviations: ALW – anterior Lobe width; ext – extragular scute; gul – gular scute; hum – humeral scute; Pec – pectoral scute; abd – abdominal scute; fem – femoral scar; ana – Anal scute. Scale bar: 1 cm

### 2.3 DISCUSSION

The species *Chelus colombiana* and *Chelus lewisi* were initially described by Wood (1976). The author emphasized that the differences between *C. colombiana* and *C. lewisi* primarily revolved around size and carapace shape. Subsequently, Cadena (2008) proposed that the length and width of the xiphiplastron process, the presence or absence of an anal notch on the xiphiplastron bone, and differences in the shape of the scars of the pubis and ischium on the dorsal surface of the xiphiplastron together with Wood (1976)'s diagnostic traits also distinguish the two extinct taxa. Following these works, Ferreira et al. (2016) reviewed fossil *Chelus* and analyzed intraspecific variation in the extant *C. fimbriata*. The authors have shown that the new characteristics presented by Cadena (2008) occur as intraspecific variations in the extant species, arguing that *C. lewisi* should be considered a synonym of *C. colombiana*. More recently, Cadena et al. (2023) presented new specimens of *Chelus* from Colombia and Venezuela and proposed new diagnostic characters to distinguish the fossil taxa, thus revalidating *C. lewisi*. According to the authors, *C. lewisi* exhibits a narrower anterior plastral region, with a marked notch in the epiplastron, an oval shell outline, and a medial ridge smaller than the two costal ridges. *C. colombiana*, on the other hand, displays a wider anterior plastron, narrow knobs on the medial crest, making it continuous and not extending laterally, and a more rectangular carapace shape. The authors also suggested that more fragmentary and incomplete material that does not preserve all three diagnostic traits, such as those known from Brazil, should not be assigned to any of the extinct species but instead should be better identified as *Chelus* sp.

The presence of fossil specimens of *Chelus* in the Miocene of Acre has been reported since the last century. Barbosa Rodrigues (1892) described two fragmentary specimens from the Purus River, which he attributed to *Chelus* due to their resemblance with the extant species *C. fimbriata*. Subsequently, Bocquentin & Rancy (1987) described an incomplete

carapace and a pelvic girdle, assigning them to *C. lewisi*, mainly based on the specimen's size and the oval shape. Two years later, Bocquentin & Santos (1989) described new specimens assigned to *C. colombiana* collected during expeditions to the Acre, Purus, Iaco, and Jurua rivers. Among these materials, the most noteworthy are the more complete specimens, UFAC-1546, an almost complete plastron, and UFAC-1578, a complete xipiplastron. Subsequently, Bocquentin et al. (2001) described new material collected in various localities of the Solimões Formation and reinterpreted the specimen UFAC-1578 as *C. lewisi*. Cadena (2008) reinterpreted the materials described by Bocquentin & Santos (1989), concluding that UFAC-1578 and UFAC-1546 exhibit characteristics more related to *C. lewisi*.

After analyzing three new and mostly complete fossils (UFAC-5497, UFAC-6517, and UFAC-7344), as well as numerous fragmentary and old specimens (such as the almost complete plastron UFAC-1546), we conclude that all of the *Chelus* material from Brazil belong to a single taxon. This conclusion is based on the nearly complete lack of variation (see below) and the consistency of many traits in the more complete and fragmentary specimens. These characteristics include the two costal ridges higher and thicker than the midline/neural ridge, an inguinal scar restricted to the fifth costal, an axillary scar on the first and second costals and reaching the second and third peripherals, two ridges present on the nuchal bone, and two pairs of extragular scutes on the plastron. We also understand that UFAC-1002, UFAC-1578, and UFAC-1546 belong to the same taxon, as they do not deviate from the morphological features described for new specimens described here. We also observed possible intraspecific variations occurring in the characteristics of the carapace and plastron of the fossil specimens. The xipiplastron bone in UFAC-3145 exhibits a thin and elongated final process, whereas, in UFAC-4815, the process is broader and shorter.

Additionally, we observed variations in the extragular scutes; in specimen UFAC-1546, the extragular scutes do not prevent the gular scute from touching the anterior edge of the

plastron (Fig 25). In the holotype described by Wood (1976), the extra pair of extragulars prevents the gular scute from touching the anterior edge of the plastron. In light of this, we consider that all the *Chelus* specimens from Acre, Brazil, belong to a single species.

Finally, after examining a broad sample of individuals belonging to the extant *Chelus fimbriata*, we found that the same features used by Cadena et al. (2023) to distinguish between the fossil species occur as intraspecific variation, with nearly identical patterns in the extant species. Three characters were proposed to distinguish *Chelus colombiana* from *C. lewisi* (Cadena et al. 2023): (1) the width of the anterior plastral lobe, (2) the relative size of the three carapace ridges, and (3) the overall outline of the carapace. The shape of the carapace varies from rectangular to oval and different proportions between the anterior and posterior halves in individuals of the extant species, the thickness of the midline/neural ridge can be thinner, similar or thicker than the costal ridges; and the edge of the anterior plastral can be triangular or rounded, and the rounded state can be broader or narrower. Moreover, the specimens from Acre do not fit the diagnostic characters of either *C. colombiana* or *C. lewisi* completely: although the anterior plastral is wide without epiplastral notches (traits of *C. colombiana*), the neural ridge is narrower than the costal ridges, which also show well-defined knobs (traits of *C. lewisi*). Although those characters appear to be consistent among the specimens from Tatacoa and Urumaco (Cadena et al. 2023), the occurrence of such traits as intraspecific variation in the extant species, as well as the existence of specimens with a "mosaic" of both diagnoses in Brazil, lead us to question the validity of their distinction. We thus agree with the previous hypothesis (Ferreira et al. 2018) of a single extinct taxon of *Chelus* in the Miocene of South America and conclude that the specimens from Brazil, as well as those from Tatacoa and Urumaco, are all *Chelus colombiana*.

## 2.4 CONCLUSIONS

The fossils from the Solimões Formation described here represent one of the most complete records of the genus *Chelus* from the Miocene of the Brazilian Amazon, demonstrating the extensive paleodistribution that this genus exhibited in the past. The *Chelus* fossils from the Solimões Formation housed at LPP/UFAC belong to the same species, *C. colombiana*. Therefore, specimens UFAC-1002, UFAC-1578, and UFAC-1546, previously classified as *Chelus lewisi*, are now considered *C. colombiana*. The Solimões Formation holds significant potential for further discoveries, as fossiliferous areas are challenging to access, and few expeditions are carried out. Future findings may further illuminate the characteristics and phylogenetic relationships of this unique South American genus.

## GENERAL CONCLUSIONS

The first chapter provides a thorough osteological analysis of the post-cranium of *Chelus orinocensis*. Utilizing Micro-Computed Tomography ( $\mu$ CT) allowed for precise scanning and segmentation of each bone, culminating in detailed 3D models. The examination across three ontogenetic stages provided valuable insights into developmental changes within the species.

In the second chapter, we analyzed fossils of *Chelus colombiana* and *Chelus lewisi*. The fossils deposited in the paleontological collection of the Federal University of Acre are the result of years of expeditions carried out in various fossiliferous sites. The description of these specimens is of great importance for a better understanding of the distribution of *C. colombiana* during the Miocene in Acre. Furthermore, the availability of nearly complete specimens and a considerable diversity of isolated bones allowed us to perform osteological comparisons with the extant species *C. fimbriata*. The result of these comparisons showed that the characteristics used to differentiate *C. colombiana* and *C. lewisi* are, in fact, intraspecific variations that occur in *C. colombiana*, therefore, the only valid fossil species is *C. colombiana*.



The genus *Chelus* indisputably exhibits a unique morphology, easily distinguishable from other pleurodiras. Few studies addressing post-cranial osteology have been conducted since *C. fimbriata* and *C. orinocensis* were described. Therefore, the second chapter of this dissertation aimed to enhance the knowledge of the osteology of *Chelus orinocensis*, initially conducting a descriptive osteological work for each post-cranial bone.

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