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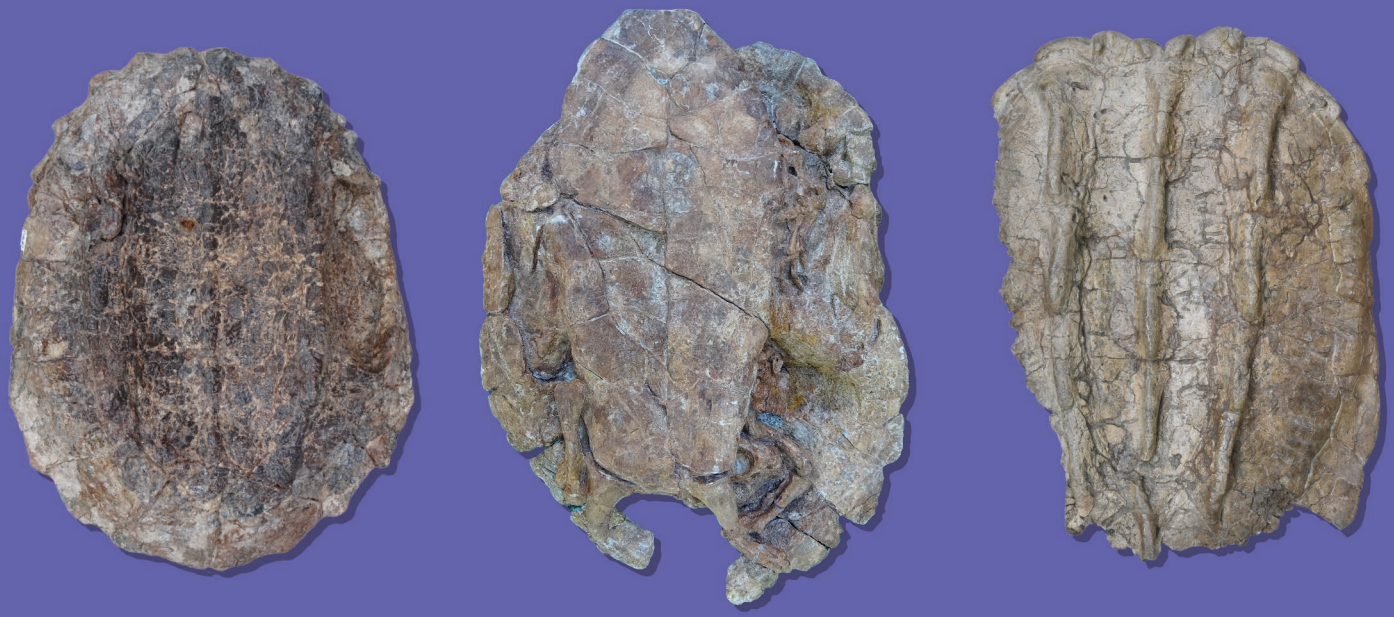

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New insights into the fossil record of the turtle genus *Chelus* Duméril, 1806 including new specimens with information on cervicals and limb bones

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ABSTRACT
Matamata turtles (*Chelus* Duméril, 1806) are composed of two extant species, *Chelus fimbriata* Schneider, 1783 and *Chelus orinocensis* Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Farias, Hrbek, Campbell & Fritz, 2020, inhabitants of the main freshwater drainages of northern South America. The systematics and palaeobiogeography of *Chelus* is still unresolved. Here, we describe several new fossil specimens from the Late Miocene of Urumaco (Venezuela) and Tatacoa (Colombia). The fossils are mostly complete, articulated shells that allow reestablishing validity of two extinct taxa, *Chelus colombiana* Wood, 1976 and *Chelus lewisi* Wood, 1976. One of the specimens of *C. lewisi* from Urumaco represents the first record within the genus for which autopodial bones (a left manus) and additional limb bones are preserved together with ashell, demonstrating evolutionary conservatism in limb anatomy for the genus. The specimen comes from the Socorro Formation, representing the earliest so far known record of *Chelus* for the Urumaco sequence. Additionally, one specimen from Tatacoa is the first fossil for which cervical and pectoral girdle elements are preserved. Phylogenetic analysis supports the existence of two separate clades inside of *Chelus*, one formed by the extinct species and the other by the extant ones.

KEY WORDS
Testudines,
South America,
Chelidae,
Matamata,
Miocene fossils.

RÉSUMÉ
De nouvelles informations sur les archives fossiles du genre de tortue Chelus *Duméril, 1806, y compris de nouveaux spécimens avec des informations sur les os cervicaux et les os des membres.*
Les tortues Matamata (*Chelus* Duméril, 1806) sont composées de deux espèces actuelles, *Chelus fimbriata* Schneider, 1783 et *Chelus orinocensis* Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Farias, Hrbek, Campbell, Fritz, 2020, habitants des principaux bassins versants d'eau douce du nord de l'Amérique du Sud. La systématique et la paléobiogéographie de *Chelus* ne sont toujours pas résolues. Nous décrivons ici plusieurs nouveaux spécimens fossiles du Miocène supérieur d'Urumaco (Venezuela) et de Tatacoa (Colombie). Les fossiles correspondent, pour la plupart, à des coquilles complètes et articulées, qui permettent de rétablir la validité de deux taxons éteints, *Chelus colombiana* Wood, 1976 et *Chelus lewisi* Wood, 1976. L'un des spécimens d'Urumaco représente la première occurrence au sein du genre pour lequel les os autopodiaux (manus gauche) et certains os des membres supplémentaires sont conservés avec une coquille, démontrant le conservatisme évolutif dans l'anatomie des membres du genre. Ce nouveau spécimen de *Chelus lewisi* provient de la formation de Socorro, représentant le plus ancien fossile connu de *Chelus* pour la séquence d'Urumaco. De plus, l'un des nouveaux spécimens de Tatacoa est le premier du genre pour lequel les éléments de la ceinture cervicale et pectorale sont conservés. L'analyse phylogénétique soutient l'existence de deux clades distincts à l'intérieur de *Chelus*, l'un formé par les espèces éteintes et l'autre par les espèces actuelles.

MOTS CLÉS
Testudines,
Amérique du Sud,
Chelidae,
Matamata,
fossiles du Miocène.

INTRODUCTION

With an extremely flat head and a highly decorated shell (dorsal ridges on the carapace) and limbs (integumentary fringes), the extant representatives of the genus *Chelus* Duméril, 1806, commonly known as matamata turtles, are iconic inhabitants of tropical South America. Besides its distinctive look, *Chelus* has been subject of debate in terms of whether the extant representatives constitute a monotypic taxon (a single species), or whether the morphological differences between the populations of the Amazon and the Orinoco basins represent two separate taxa (Sánchez-Villagra *et al.* 1995a, b; Pritchard 2008). Recently, a molecular study provided evidence for the existence of two genetically distinct lineages, *Chelus fimbriata* Schneider, 1783 (*fimbriatus* for some authors) and *Chelus orinocensis* Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Farias, Hrbek, Campbell & Fritz, 2020, which were estimated to have been geographically separated since at least the Late Miocene (*c.* 12.7 Ma) (Vargas-Ramírez *et al.* 2020).

The two extinct taxa that were considered as valid by several authors for decades are *Chelus colombiana* Wood, 1976 (*colombianus* for some authors) and *Chelus lewisi* Wood, 1976 (Wood 1976; Bocquentin 1988; Sánchez-Villagra *et al.* 1995a; Cadena *et al.* 2008; Cadena & Jaramillo 2015a). Ferreira *et al.* (2016) more recently proposed that morphological differences between the two extinct taxa could be explained as intraspecific variation and, thus, synonymized both taxa as *C. colombiana* (Ferreira *et al.* 2016).

Two decades of palaeontological expeditions to two of the most remarkable Miocene fossiliferous regions of northern South America, Urumaco, Falcón State, Venezuela and La Tatacoa, Huila Department, Colombia have yielded exceptionally rich remains of fossil vertebrates (Kay *et al.* 1997; Sánchez-Villagra *et al.* 2003; Carrillo *et al.* 2018; Carrillo-Briceño *et al.* 2018; Scheyer *et al.* 2013; Cadena *et al.* 2020a, b, 2021; and references therein). Here we present several new articulated fossil shells (carapace and plastron) and other remains referrable to *Chelus*. This includes a specimen from the Middle Miocene Socorro Formation (Quiroz & Jaramillo 2010), which represents the oldest record of the genus in the Urumaco area and for the first time preserves limbs bones. The new material provides evidence for reestablishing two extinct taxa, as initially suggested by Wood (1976), instead of a single one (Ferreira *et al.* 2016). Finally, we performed a phylogenetic analysis to further explore the evolutionary history of matamata turtles.

MATERIAL AND METHODS

Fossil specimens

The new specimens of *Chelus* described herein were prepared using air scribes and dental picks at the laboratory of the Museo Paleontológico de Urumaco (AMU-CURS) and the Museo de Historia Natural La Tatacoa (VPPLT) where they are housed. Measurements were taken using a caliper or obtained based on images with scales in Image J (1.52q). Figures were produced using Adobe Illustrator and Photoshop.

Comparisons

We compared the new fossil specimens with the holotypes and other specimens as follow: direct examination of the *Chelus lewisi* holotype; high-resolution images shared by Dr Patricia Holroyd, Museum of Paleontology University of California for *Chelus colombiana*; images available from the literature for *Chelus orinocensis* (Vargas-Ramírez *et al.* 2020); direct examination for other specimens of *Chelus orinocensis* and *Chelus fimbriata* (Table 1). Determination of sexual dimorphism (male or female) of some of the fossil specimens was established following Pritchard (2007). For plastral and shell scutes nomenclature, we follow Hutchison & Bramble (1981).

Phylogenetic analysis

We modified one of the most recent character-taxon matrices of chelids (Cadena *et al.* 2020b), by adding four characters from Cadena *et al.* (2008) for a total of 88 characters (Appendix 1). We also added three taxa to the matrix (*Chelus colombiana*, *C. lewisi*, and *C. orinocensis*) for a total of 35 taxa (Appendix 2). We performed a phylogenetic analysis in TNT 1.6 (Goloboff & Catalano 2016; and references therein) in order to establish the relationships between the four taxa of *Chelus*. *Chelydra serpentina* (Linnaeus, 1758), *Notoemys laticentralis* Cattoi & Freiberg, 1961, and *Platychelys oberndorferi* Wagner, 1853 were selected as the outgroups. We used the following settings for the analysis: traditional search; 20 trees saved per replicate, other parameters by default; memory increased to max. trees 10000; collapse of zero-length branches according to rule 1; and 1000 replicates of random addition sequences and other parameters by default. All characters were equally weighted and characters 2, 4, 9,13, 16, 25, 26, 44, 45, 56, 57, 58, 62, 70, 71, and 73 were treated as ordered, because they represent a morphocline, following Oriozabala *et al.* (2019). A strict consensus tree was generated and statistics obtained, included consistency (CI) and retention (RI) indexes and Bremer support, calculated using implemented scripts in TNT.

GEOLOGICAL FRAMEWORK

Urumaco, Venezuela

Fossils of *Chelus* are abundant in the Urumaco region, where we collected nearly complete shells from at least ten localities, corresponding to different stratigraphic horizons of the Socorro and Urumaco formations (Fig. 1). The earliest occurrence of *Chelus* in the Urumaco region is described herein. AMU-CURS-1244 was discovered at the Raspiñito (Sector Quebrada Honda, Llano Largo) locality (11°11'23.20"N, 70°6'36.30"W), located approximately 16 km east of the town of Urumaco, in the vicinity of Paují Creek, Falcón State (Fig. 1A). The outcrops of this locality correspond to the middle Miocene Socorro Formation (Fig. 1B). This geological unit was informally divided by Hambalek *et al.* (1994) into three members (Lower, Middle and Upper), with a total estimated thickness of 2300 m (Quiroz & Jaramillo 2010).

The Raspiñito locality is located at the base of the Middle Member (Fig. 1B). This member has an estimate thickness of 880 m and is characterized by complex interbeddings of medium to fined-grained sandstones, organic mudstones, coal, shales, and coquinoidal limestones (Quiroz & Jaramillo 2010). The Raspiñito locality itself is characterized by dark to light brown, organic-rich mudstones of approximately 1.5 meters thickness, in which we found abundant vertebrate remains, including indeterminate turtles (possible podocnemidids), crocodiles, and terrestrial mammals. According to Quiroz & Jaramillo (2010), the Middle Member of the Socorro Fm. was deposited in a palaeoenvironment within a deltaic system, with heterolithic intervals of organic-rich sediments associated with interdistributary bays and crevasse splays. Other *Chelus* (sp.) records in the Urumaco sequence originate from the Cocuiza Member (Early Pleistocene) of the San Gregorio Formation (Carrillo-Briceño *et al.* 2021).

La Tatacoa, Colombia

Together with podocnemidids, fossils of *Chelus* are the most abundant fossil turtles in the Tatacoa Desert region (Fig. 1C). They are found throughout the rock sequences of the La Victoria and Villavieja formations. They are particularly abundant in the Cerro Gordo, Chunchullo, and Tatacoa beds of the La Victoria Formation (Fig. 1D), a segment of the formation dominated by overbank deposits, palaeosols, and sandstone channels with a middle Miocene age range of 13.77 to 12.76 Ma (Mora-Rojas *et al.* 2023; and references therein). Fossil remains of *Chelus* are also abundant in the Cerbatana and La Venta beds of the Villavieja Formation, corresponding to overbank deposits, palaeosols, and swamp to lake deposits ranging between 12.58 to 11.12 Ma, Middle Miocene (Mora-Rojas *et al.* 2023; and references therein). The new fossil specimens described herein were collected in the following localities and horizons: VPPLT-1748 originates from the Los Guayabos locality (3°21'59.04"N, 75°8'31.89"W), Cerro Gordo beds, La Victoria Formation; VPPLT-380 from La Cuarenta 1 locality (3°20'15.43"N, 75°10'42.60"W); VPPLT-968 from Tres Pasos Sur 1 (3°19'14.40"N, 75°9'38.73"W); and MT-22 from the Paraseco locality (3°16'10.45"N, 75°5'9.28"W). These three localities are located within the Chunchullo beds, La Victoria Formation. VPPLT-1756 originates from the Cañadas locality (3°17'24.9"N, 75°6'26.76"W) from a horizon between the Chunchullo and Tatacoa beds.

Abbreviations

Institutions

AMU-CURS Alcaldía Bolivariana de Urumaco, Museo Paleontológico de Urumaco, Falcón State;
IAvH Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá;
ICN Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá;
IGMp (synonym of GMB) Museo Geológico Nacional José Royo y Gómez, Servicio Geológico Colombia, Bogotá;
LET Leticia specimens referred in Vargas-Ramírez *et al.* (2020);
MCNC Museo de Ciencias Naturales de Caracas, Caracas;
MCZ-VPRA Museum of Comparative Zoology, Harvard University, Cambridge;
MNHN Muséum national d'Histoire naturelle, Paris;
MT Museo de Paleontología La Tormenta, Villavieja;
NMW Naturhistorisches Museum Wien, Vienna;
UNEFM Universidad Experimental Francisco Miranda, Coro;
USNM Smithsonian National History Museum, Maryland;
VPPLT Museo de Historia Natural de La Tatacoa, La Victoria.

Others

Abd abdominal scute;
Ana anal scute;
CI consistency index;
Ext II extragular scute II;
Fem femoral scute;
Gul gular scute;
Hum humeral scute;
Pec pectoral scute;
RI retention index.

SYSTEMATIC PALAEONTOLOGY

Order TESTUDINES Batsch, 1788
Sudorder PLEURODIRA Cope, 1865
Family Chelidae Lindholm, 1929
Genus *Chelus* Duméril, 1806

Chelus lewisi Wood, 1976
(Figs 2-4)

Chelus lewisi Wood, 1976: 7.

Type specimen. — MCNC-239, an articulated shell (Wood 1976) (Fig. 2A, B).

Referred material. — Specimens referred by Wood (1976): MCZ-VPRA-4338, a complete shell (Fig. 2C, D); MCZ-VPRA-4337, a complete shell; MCNC-240, a costal bone; MCNC-241, posterior half of a carapace and plastron; MCNC-242, a crushed vertebra (probably a cervical) associated with a right xiphiplastron. Specimens referred by Bocquentin (1998): UNEFM-1323, a plastron and an isolated bone from the anterior half of the carapace; UNEFM-1371, a complete, articulated shell (Sánchez-Villagra *et al.* 1995a: fig. 1B, Fig. 2E, F); UNEFM-1415, anterior half of a plastron. Specimen described by Sánchez-Villagra *et al.* 1995a): MCNUSB-150-85-PB, a complete shell. This study: AMU-CURS-600, an articulated shell (Fig. 2G, H), AMU-CURS-119, an articulated shell (Fig. 2I, J), AMU-CURS-207, an articulated shell (Fig. 2K, L), and AMU-CURS-1244, an articulated shell preserving most of the left forelimb bones, some bones of the left hindlimb and the right femur (Figs 3; 4).

Occurrences and age. — Socorro and Urumaco formations, Falcón State, Venezuela, Middle to Late Miocene (Quiroz & Jaramillo 2010).

Revised diagnosis. — *Chelus lewisi* differs from all other extant and extinct *Chelus* by a marked posterior widening of the carapace that creates a tapering anterior margin and by a neural ridge that is smaller than the two costal ridges (left and right). *Chelus lewisi* differs from *C. colombiana* by having a very narrow anterior region of the anterior plastral lobe, with a marked notch in the epiplastron at the lateral contact between the extragular I and the humeral scute. *Chelus lewisi* and *Chelus colombiana* share and differ from the extant taxa by the presence an axillary buttress that extends onto costal 2, instead of being restricted to costal 1 (extant taxa); inguinal buttress that extend onto costal 5, instead of costal 4 (extant taxa); two or

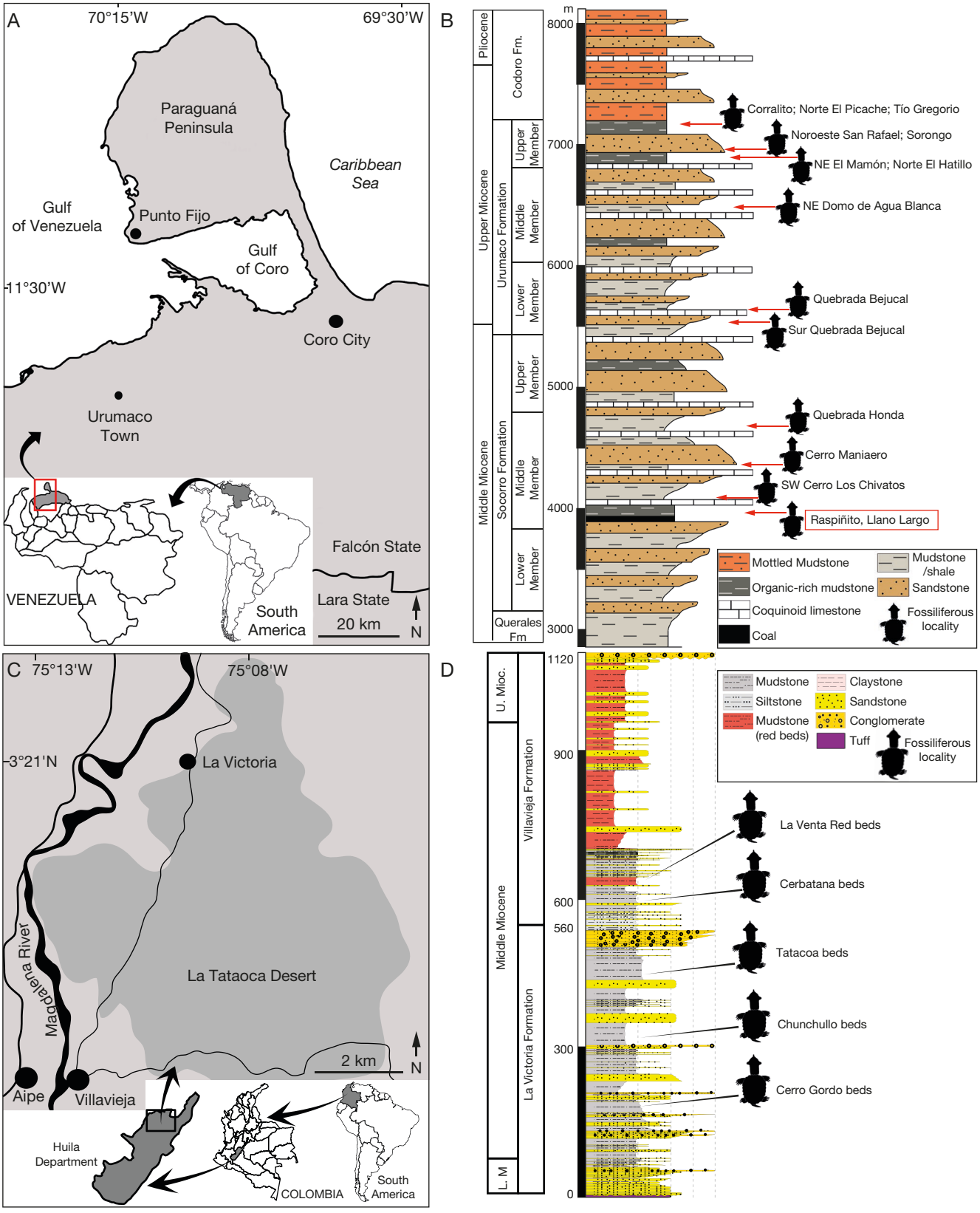

FIG. 1. — Location of Urumaco and Tatacoa localities, and stratigraphic occurrence of fossils: **A**, map of the Urumaco region, Falcón State, northwestern of Venezuela; **B**, general stratigraphic column for the Urumaco rock sequence indicating the occurrence of *Chelus* Duméril, 1806; **C**, map of the Tatacoa region, Huila Department, southwestern of Colombia; **D**, general stratigraphic column for the La Victoria and Villavieja formations indicating the occurrence of *Chelus,* taken and modified from Mora-Rojas *et al.* (2023). Abbreviations: **Fm**, Formation; **L.M.**, Early Miocene; **U**, Upper.

TABLE 1. — Measurements of the new fossil specimens of *Chelus colombiana* Wood, 1976 and *C. lewisi* Wood, 1976 describe here, as well as some extant individuals of *C. fimbriata* (Schneider, 1783) and *C. orinocensis* Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martînez, Silva-Viana, Vogt, Pires-Farias, Hrbek, Campbell & Fritz, 2020 figured in Figure 9, in millimeters (mm). Abbreviations: **CL**, carapace length at midline as preserved; **CML**, carapace maximum length as preserved; **CW**, carapace width at midline as preserved; **PL**, plastron length at midline as preserved; **PW**, plastron width at midline as preserved.

Species	Specimen	CL	CW	CML	PL	PW
Chelus colombiana Wood, 1976	VPPLT-380	–	–	–	659	339
	VPPLT-968	272	373	340	272	185
	VPPLT-1748	581	440	596	–	–
	VPPLT-1756	759	486	759	663	397
	MT-22	682	477	776	635	321
	IGMp-002045	596	468	598	295	198
Chelus lewisi Wood, 1975	AMU- CURS-1244	554	456	672	552	361
	MCNC-239	456	358	460	396	230
	MCV-VPRA-4338	513	428	514	459	318
	UNEFM-1371	436	394	458	362	304
	AMU-CURS-600	552	435	557	–	–
	AMU-CURS-119	506	356	506	–	–
	AMU-CURS-207	423	353	423	395	208
Chelus fimbriata (Schneider, 1783)	USNM-117455	409	305	411	374	265
	MNHN-9406	268	183	270	263	159
	NWW-1859	410	315	414	395	286
	LET-65	140	125	140	–	–
Chelus orinocensis Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martînez, Silva-Viana, Vogt, Pires-Farias, Hrbek, Campbell & Fritz, 2020	IAvH-R8755	270	–	270	–	–
	MNHN-D40	230	168	230	–	–
	MNHN-A5200	265	198	230	252	160
	ICN-1776	474	362	474	470	303

three pairs of extragular scutes that encapsulate the gular, instead of gular reaching the anterior margin of the plastron and a single pair of extragular scutes (extant taxa); vertebral scute 1 almost rectangular, instead of pentagonal (extant); and vertebral scute 1 almost same width of vertebral scute 2, instead vertebral 1 wider than 2 (extant).

DESCRIPTIONS

Measurements for the new and all other previously described specimens are provided in Table 1.

AMU-CURS-600 is a complete, articulated shell. The carapace is oval in shape, having three dorsal ridges of knobs, one on the left costals, one along midline of the neurals, and one on the right costals. It is much wider posteriorly, with anterior and posterior peripherals having indentations at the contact between marginal scutes (Fig. 2G). The bone surface of the carapace is highly eroded, making bone sutural contacts and sulci poorly recognizable. Only some of the sutural contacts between the posterior peripherals are visible. The plastron is slightly shorter than the carapace, with its posterior lobe longer than the anterior. The margins of the anterior lobe taper anteriorly, ending in a narrow straight anteriormost edge and exhibiting marked lateral indentations on the epiplastra where the contact between extragular I and humeral scutes potentially were located (Fig. 2H, O). The bone surface of the carapace is badly preserved, making any sulci impression unrecognizable, but the sutural contacts between the bones are visible.

AMU-CURS-119 is a complete, articulated shell. The left side of the carapace and the plastron are affected by crushing. The bone surface of both carapace and plastron is covered with a layer of gypsum that makes it difficult to discern sutural contacts and sulci. The more intact right margin suggests that the carapace was originally oval in shape, being wider posteriorly than anteriorly, and exhibited three knobby dorsal ridges (Fig. 2I). The anterior plastral lobe (Fig. 2J, P) exhibits the same shape and pattern described for AMU-CURS-600.

AMU-CURS-207 is a complete, though highly crushed articulated shell. The bone surface of both carapace and plastron is covered with a hard, black layer of rock matrix mixed with gypsum that rendered any sutural contacts and sulci unrecognizable (Fig. 2K, L).

AMU-CURS-1244 is a nearly complete, articulated shell that is considerably affected by crushing and missing the posteromedial region of the carapace (Fig. 3A-E). The bone surface of the carapace is badly preserved allowing only the identification of sutural contacts between some of the bones. The plastron, by contrast, is complete and its bone surface is better preserved.

The carapace of AMU-CURS-1244 exhibits three knobby ridges on its dorsal side (Fig. 3A, B). The nuchal has a pentagonal shape, being wider than long (Fig. 3). The neural series is composed of at least six bones. Neural 1 is almost rectangular and positioned between costals 1. Neurals 2 to 5 are almost hexagonal in shape. Neural 6 is slightly deformed by crushing into a trapezoidal shape. Six pairs of costals are well defined by their sutures. Costals 2 and 4 exhibit almost the same width, while costals 3 and 5 are slightly anteroposteriorly narrower than the others. The shape of the carapacial scutes is not possible to establish due to the eroded bone surface that erased the sulci. However, it is possible to outline the sulci between the cervical and marginals 1.

The plastron of AMU-CURS-1244 is complete, exhibiting a bit of crushing at its central region and at the beginning of the xiphiplastral tips (Fig. 3C, D). The anterior plastral lobe exhibits the same shape and pattern described above for AMU-CURS-600 and other specimens of *C. lewisi*

Fig. 2. — Articulated shells of *Chelus lewisi* Wood, 1976 from Venezuela: **A**, **B**, MCNC-239 holotype: **A**, shell in dorsal view; **B**, shell in ventral view; **C**, **D**, MCZ-VPRA-4338: **C**, shell in dorsal view; **D**, shell in ventral view; **E**, **F**, UNEFM-1371: **E**, shell in dorsal view; **F**, shell in ventral view; **G**, **H**, AMU-CURS-600: **G**, shell in dorsal view; **H**, shell in ventral view; **I**, **J**, AMU-CURS-119: **I**, shell in dorsal view; **J**, shell in ventral view; **K**, **L**, AMU-CURS-207: **K**, shell in dorsal view; **L**, shell in ventral view; **M**-**P**, anterior plastral lobe for several specimens of *C. lewisi* tapering anteriorly ending in a narrow straight anterior edge, and exhibiting marked lateral indentations on the epiplastra where the contact between extra and humeral scutes potentially were located: **M**, MCNC-239 holotype in ventral view; **N**, MCZ-VPRA-4338 in ventral view; **O**, AMU-CURS-600 in ventral view; **P**, AMU-CURS-119 in ventral view. Abbreviations: **ent**, entoplastron; **epi**, epiplastron; **hyo**, hyoplastron. Scale bar: 10 cm.

(Figs 2M-P; 3C, D). It is slightly shorter than the posterior lobe. The epiplastra have a long median contact between each other and a straight anterior edge. The entoplastron has a diamond shape. The hyoplastra are longer and larger than the hypoplastra and the xiphiplastra exhibit narrow and long posterior process (tips). The sulci indicate that the gular scute had a diamond shape and was located between the two pairs of extragulars (I and II), and the humerals (Fig. 3D).

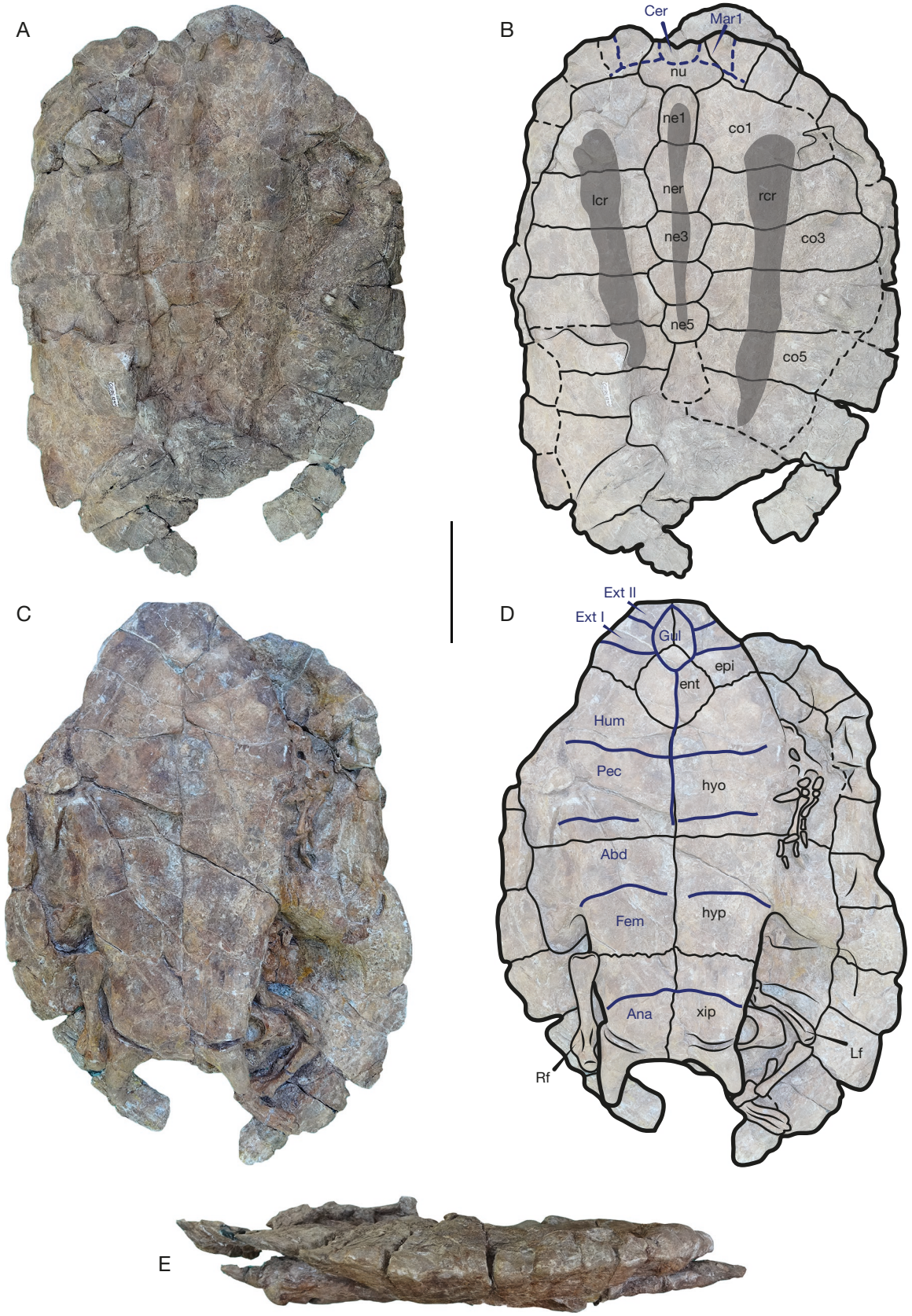

Fig. 3. — Articulated shell of *Chelus lewisi* Wood, 1976 AMU-CURS-1244 specimen from the Socorro Formation of Venezuela: **A**, **B**, shell in dorsal view; **C**, **D**, shell in ventral view; **E**, shell in right lateral view. Abbreviations: **Abd**, abdominal scute; **Ana**, anal scute; **Cer**, cervical scute; **co**, costal bone; **ent**, entoplastron; **epi**, epiplastron; **Ext I**, extragular scute I; **Ext II**, extragular scute II; **Fem**, femoral scute; **Gul**, gular scute; **Hum**, humeral scute; **hyo**, hyoplastron; **hyp**, hypoplastron; **lcr**, left costal ridge; **Lf**, left femur; **Mar**, marginal scute; **ne**, neural bone; **ner**, neural ridge; **nu**, nuchal bone; **Pec**, pectoral scute; **rcr**, right costal ridge; **Rf**, right femur; **xip**, xiphiplastron. Scale bar: 10 cm.

FIG. 4. — Left manus and other limb bones of *Chelus lewisi* Wood, 1976 AMU-CURS-1244 specimen from the Socorro Formation of Venezuela: **A**, **B**, left manus in dorsal view; **C**, left manus of *Chelus fimbriata* Schneider, 1783 NMW-1859 specimen in dorsal view; **D**, **E**, left hindlimb bones in dorsolateral view and left ilium in dorsal view; **F**, left posterolateral view of the shell, indicating the femora; **G**, **H**, left femur in lateral view, **red square** in **F**; **I**, **J**, right femur in ventral view, **red rectangle** in **F**; **K**, close-up of the left metatarsals. Abbreviations: **c**, central; **dc**: distal carpal; **di**, digit; **dt**, distal tarsal; **f**, femur; **fi**, fibula; **h**, humerus; **i**, intermedium; **il**, ilium; **mc**, metacarpal; **mcV**, metacarpal V; **mt**, metatarsal; **r**, radius; **ph**, phalange; **tia**, tibia articulation; **tmin**, trochanter minor; **u**, ulna; **ul**, ulnare; **r**, radius. Scale bars: 10 cm.

The extragulars I were almost rectangular in shape and the extragulars II were triangular, barely touching each other medially. The humerals and femorals almost had almost the same length medially and are both longer than the pectorals, the abdominals, and the anals, for a plastral formula of Fem = Hum > Ana > Abd > Pec > Gul > ExtII.

Most of the bones of the left forelimb of AMU-CURS-1244 are preserved, including the humerus, the ulna, radius, and the manus, including the ulnare, two centralia, the distal carpals, intermedium, metacarpals, some phalanges, and some distal phalanges (Fig. 4A, B). These resemble the forelimb of *Chelus fimbriata* (NMW-1859, Fig. 4C; Sánchez-Villagra *et al.* 2007: figs 1H, 2E) both in number of elements and their shape, except for the missing (not preserved) phalanges and distal phalanges. From the hindlimbs, both femora are preserved (Fig. 4D-J). The right femur exhibits a robust, oval-shaped head and a relatively narrow trochanter minor that is located close to the femoral head, as well as a dorsally arched shaft (Fig. 4G-J). The left fibula, three metatarsals, and three distal tarsals are also preserved (Fig. 4E, K).

Most of the left ilium of AMU-CURS-1244 is preserved showing the concave surface that contributed to the acetabulum (Fig. 4D, E).

Chelus colombiana Wood, 1976
(Figs 5-8)

Chelus colombiana Wood, 1976: 3.

Type specimen. — UCMP-78762, an articulated shell (Wood 1976) (Fig. 5A, B)

Referred material. — Specimens referred by Wood (1976): IGMp-002045, incomplete shell lacking part of the right side of the carapace and anterior plastral lobe, possibly a male (Sánchez-Villagra *et al.* 1995a: fig. 1A; Fig. 6); IGMp-002049, a partially disarticulated shell; IGMp-002085, a left epiplastron. This study: VPPLT-1748, nearly complete carapace (Fig. 5C-G), VPPLT-380, complete plastron and MT-22, complete shell (Fig. 5H-J).

Occurrences and age. — Villavieja and La Victoria formations, Huila Department, Colombia. Middle to Late Miocene 16 to 10.52 Ma (Mora-Rojas *et al.* 2023).

Revised diagnosis. — *Chelus colombiana* differs from all other extant and fossil *Chelus* by having narrow knobs that form continuous dorsal ridges on the carapace that do not expand laterally, a feature that is present independently of size. It shares with *C. fimbriata* an almost rectangular carapace, with parallel lateral margins. *Chelus colombiana* and *Chelus lewisi* share and differ from the extant taxa by the presence of an axillary buttress that extends onto costal 2, instead of being restricted to costal 1 (extant taxa); inguinal buttress onto costal 5, instead of costal 4 (extant taxa); two or three pairs of extragular scutes that encapsulate the gular, instead of gular reaching the anterior margin of the plastron and a single pair of extragular scutes (extant taxa); vertebral scute 1 almost rectangular, instead of pentagonal (extant); and vertebral scute 1 almost same width of vertebral scute 2, instead vertebral 1 wider than 2 (extant). It shares with the two extant taxa a wider anterior plastral lobe than *C. lewisi*. It differs from *C. fimbriata* by cervicals 7 and 8 having longer and more dorsoventrally projected neural spines, and broader internal scapular angle of 85°.

Descriptions

Measurements for the new and all other previously described specimens are provided in Table 1.

VPPLT-1748 is a nearly complete carapace, missing most of its left and posterior margins (Fig. 5C, D). The carapace is almost rectangular in shape, exhibits three dorsal ridges formed by knobs, one on the left costals, one along midline of the neurals, and one on the right costals. The knobs are narrow and do not extend radially or laterally. The surface of the bone is well preserved, allowing clear identification of sutural contacts between the bones and the sulci left by the scutes. The nuchal bone is hexagonal in shape. The neural series is composed of six bones, most of which are wider than long (except neural 4) and have a hexagonal shape. VPPLT-1748 has eight pairs of costal bones. The peripherals have a marked lateral indentation at the contact between the marginals. The sulci indicate that the cervical scute was almost rectangular in shape. Five vertebral scutes were present, of which vertebrals 1 to 4 were wider than long and rectangular to slightly hexagonal in shape, while vertebral 5 was trapezoidal. Pleural scute 1 was large, covering most of costals 1 and 2, and peripherals 1 to 3. The other pleurals were slightly smaller than pleural 1 and rectangular to trapezoidal in shape, with pleural 3 being the smallest of the four pairs. Some of the sulci between the marginals are preserved. Marginals 1 to 3 were restricted to the anterior peripherals and marginals 8 to 10 were potentially restricted to the posterior peripherals, without reaching the costals. On the ventral surface of the carapace (Fig. 5E, F), most of both axillary buttresses are preserved reaching costals 2. The inguinal buttress scar left is restricted to costal 5, while the iliac scar covered most of costal 8 and potentially the suprapygal. In right lateral view (Fig. 5G), the carapace exhibits a low dome shape showing the left and right costal series of knobs forming the ridges, which are narrow without extending radially or laterally.

MT-22 is an almost complete shell (Fig. 5H-J). It has a rectangular shape, with the left and right lateral margins almost parallel to each other. The three ridges of knobs are narrow without expanding radially or laterally on the dorsal surface of the carapace. Some of the sutural contacts between contacts are visible. The nuchal bone is hexagonal, slightly wider than long, and its anterior margin a bit eroded. Bioerosion marks are well preserved on one of the left peripherals and some costals (Fig. 5I). In left lateral view (Fig. 5J), the carapace shows a low dome shape and the narrow and low knobs without developing peaks or extending laterally.

IGMp-002045 is an articulated shell (Fig. 6), preserving most of the left half of the carapace and a portion of the medial region of the right half. Most of the anterior plastral lobe and right bridge with the carapace region are missing. The missing parts of the carapace and right bridge region were reconstructed with plaster originally during the preparation of the specimen in the 1970s.

The carapace of IGMp-002045 (Fig. 6A, B) exhibits on its dorsal surface three ridges of narrow knobs, without developing lateral or radial expansion. The sutural contacts between bones are poorly identifiable. However, the sulci left by the

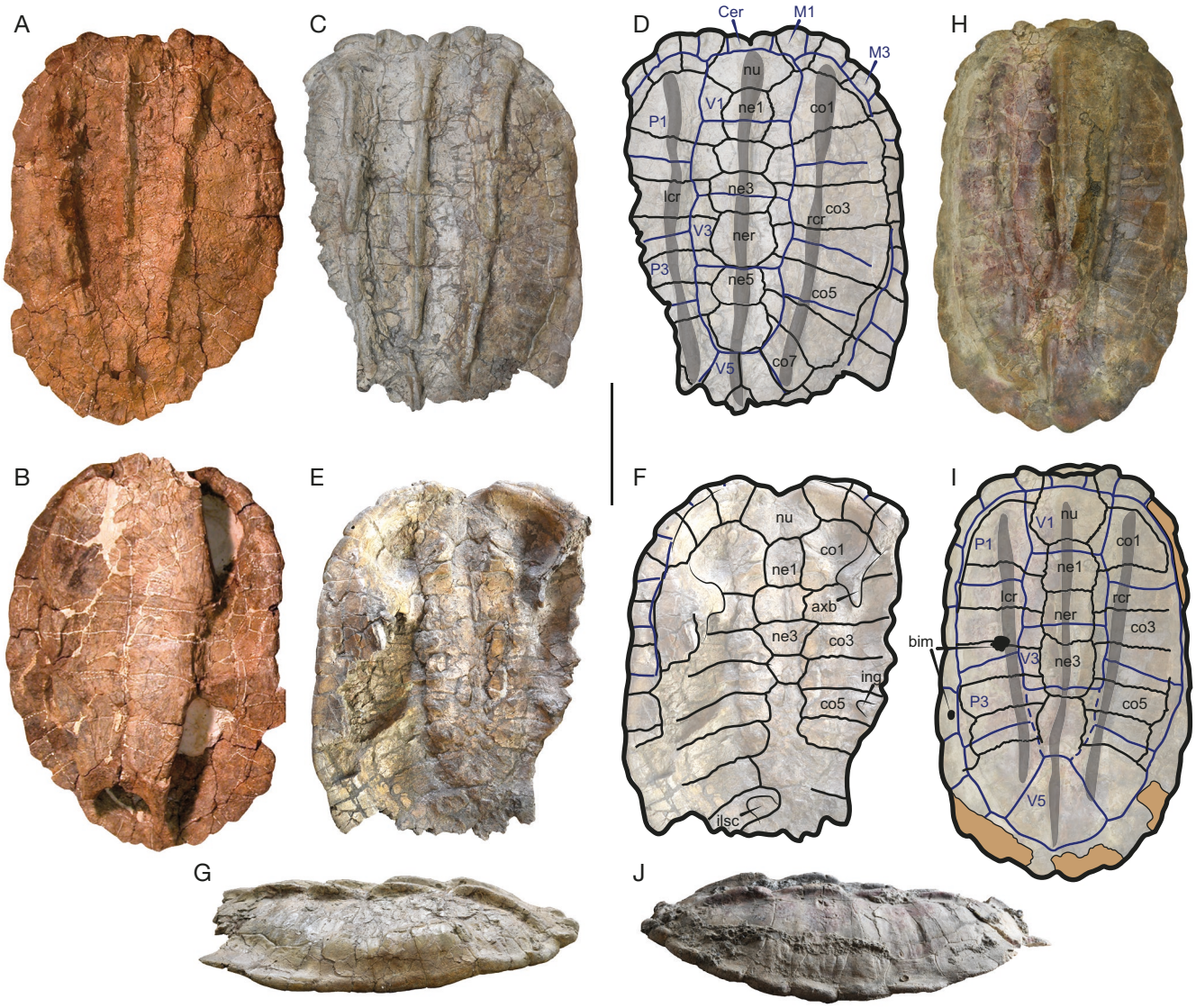

Fig. 5. — Shell and carapaces of *Chelus colombiana* Wood, 1976 from the Tatacoa of Colombia: **A**, **B**, UCMP-78762 holotype, articulated shell: **A**, shell in dorsal view; **B**, shell in ventral view; **C**-**G**, VPPLT-1748: **C**, **D**, carapace in dorsal view; **E**, **F**, carapace in ventral view; **G**, carapace in right lateral view; **H**-**J**, MT-22: **H**, **I**, carapace in dorsal view; **J**, carapace in left lateral view. Abbreviations: **axb**, axillary buttress; **bim**, bioerosion marks; **Cer**, cervical scute; **co**, costal bone; **ilsc**, iliac scar; **ing**, inguinal scar; **lcr**, left costal ridge; **M**, marginal scute; **ne**, neural bone; **ner**, neural ridge; **P**, pleural scute; **rcr**, right costal ridge; **V**, vertebral scute. Scale bar: 20 cm.

scutes are well-preserved. There were five vertebral scutes. Vertebral 1 was almost rectangular in shape and vertebrals 2 and 3 hexagonal and wider than long. Vertebral scute 4 was almost equally wide than long and vertebral scute 5 trapezoidal in shape. There were eleven marginal scutes and four pleural scutes, of which pleural 1 was the largest. On its ventral surface, the carapace of IGMp-002045 exhibits an axillary buttress that reaches costal 2, and a very large costovertebral tunnel (Fig. 6C). The plastron is complete and articulated with the carapace (Fig. 7E). The sutures between bones, as well as the sulci left by the scutes are clearly identifiable. The preserved sulci indicate that the femoral was longer than the abdominal and pectoral, and the anal was the shortest one of these scutes (Fig. 7F). The xiphiplastra exhibit a large and deep U-shaped anal notch and long and narrow posterior tips, as well as they are characterized by a deep medial concavity. The anterior plastral lobe is wide and has evidence of two pairs of extragulars and an elongated gular scute.

The plastron of IGMp-002045 is well-preserved, without any evidence of crushing, only some minor cracks, and missing most of the anterior plastral lobe (Fig. 6D, E). The sutures between the bones, as well as the sulci left by the scutes are clearly identifiable. The preserved sulci indicate that the femoral was longer than the abdominal, and the anal was the shortest one of these three scutes. The xiphiplastra exhibit a large and deep U-shaped anal notch and long and narrow posterior tips. The plastron is characterized by a deep. medial concavity (Fig. 6E-H). These features suggest that the specimen potentially represents a male. Even though most of the anterior plastral lobe is missing, its left margin is preserved enough to indicate that this lobe was wider than the posterior.

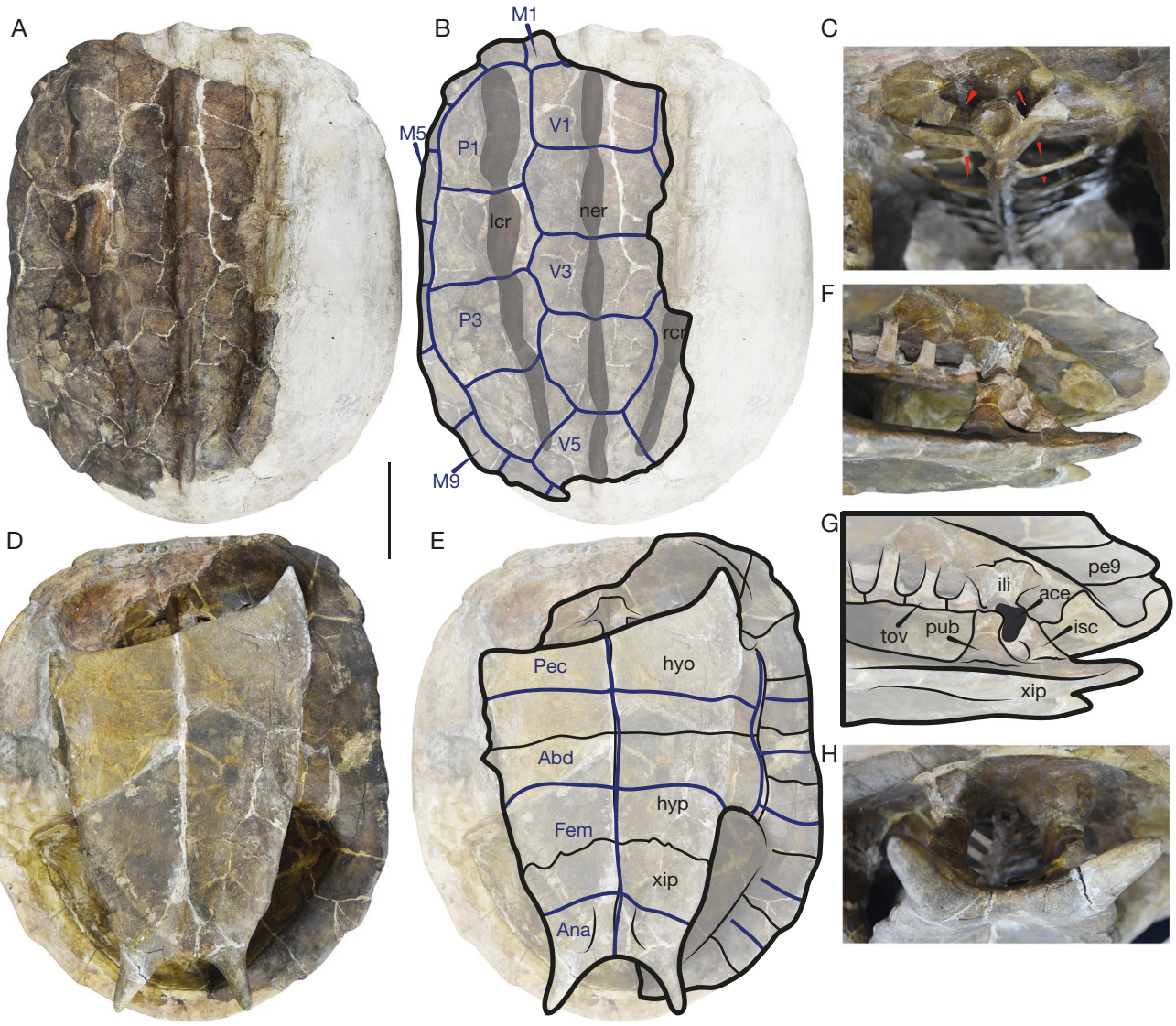

Fig. 6. — Articulated shell of *Chelus colombiana* Wood, 1976 IGMp-002045 from the Tatacoa of Colombia: **A**, **B**, shell in dorsal view; **C**, view of the most antero-visceral view of the shell showing the large costovertebral tunnel (**red arrows**); **D**, **E**, shell in ventral view; **F**, **G**, left posterolateral view of the shell showing the left pelvic girdle and the posterior end of the costovertebral tunnel; **H**, posterior view of the shell showing both pelvic girdles and the xiphiplastral notch. Abbreviations: **Abd**, abdominal scute; **ace**, acetabulum; **Ana**, anal scute; **Fem**, femoral scute; **hyo**, hyoplastron; **hyp**, hypoplastron; **ili**, ilium; **isc**, ischium; **lcr**, left costal ridge; **M**, marginal scute; **ner**, neural ridge; **pe**, peripheral bone; **P**, pleural scute; **Pec**, pectoral scute; **pub**, pubis; **rcr**, right costal ridge; **tov**, thoracic vertebra; **V**, vertebral scute; **xip**, xiphiplastron. Scale bar: 10 cm.

The pelvic girdle of IGMp-002045 is well preserved, showing a strong sutural contact between the ilia and the carapace and the ischia and pubes with the plastron (Fig. 6F-H). In left lateral view (Fig. 6F, G), the acetabulum is well defined, only slightly dislocated from its original anatomical orientation due to some fractures present in the left ischium. The ilia are robust at their contact with costals 8, suprapygal and possibly reaching a portion of the pygal (Fig. 6H).

VPPLT-380 consists of a nearly complete plastron, only missing the most lateral portions of the left hyoplastron and hypoplastron (Fig. 7). In visceral view (Fig. 7A, B), the pubic scars are oval in shape and the ischia scars are nearly trapezoidal in shape indicating that the ischia almost touch each other medially. In ventral view (Fig. 7C, D), the sutures between the bones and the sulci left by scutes are well-preserved. The anterior plastral lobe is wider than the posterior, having a large entoplastron and a relatively long medial contact between both epiplastra. The hyoplastra are slightly larger than the hypoplastra. There were two pairs of extragular scutes (I and II), enclosing together with the humerals the gular scute, which had a hexagonal shape and barely reached the anteromedial margin of the plastral lobe. The plastral formula was Abd > Fem > Pec = Hum = Gul > Ana > ExtII. The xiphiplastra exhibit a large and deep U-opened anal notch, long and narrow posterior tips and a medial concavity at the medial sutural contact between each other, indicating that the specimen was potentially a male.

VPPLT-1756. It is an articulated shell, preserving most of the plastron (missing the anterior regions of epiplastra and entoplastron), most of the peripherals and the pygal

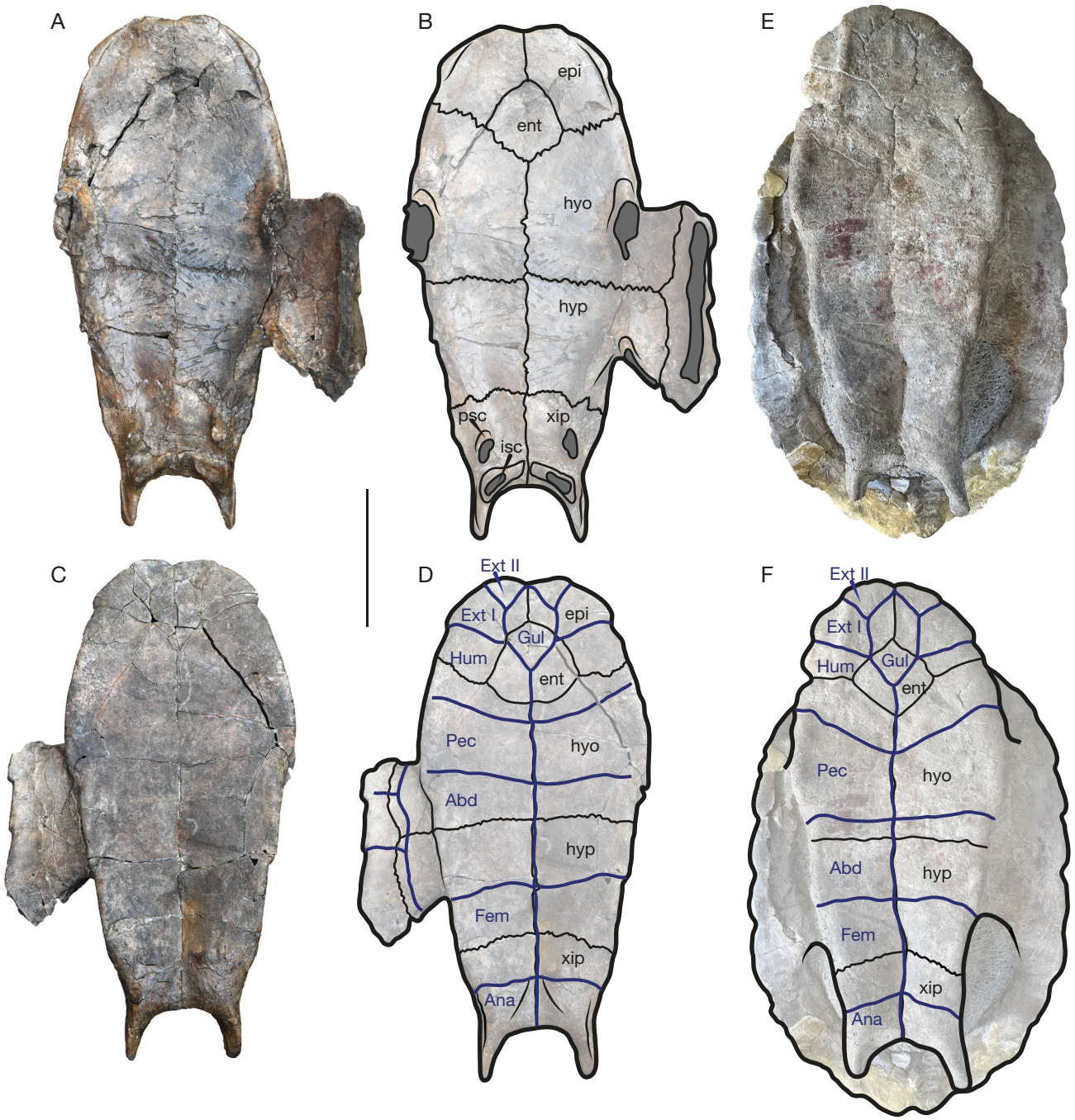

FIG. 7. — Complete plastra of *Chelus colombiana* Wood, 1976 VPPLT-380 and MT-22 from the Tatacoa of Colombia: **A**, **B**, VPPLT-380 specimen in dorsal view; **C**, **D**, VPPLT-380 specimen in ventral view; **E**, **F**, MT-22 specimen, plastron articulated with carapace in ventral view. Abbreviations: **Abd**, abdominal scute; **Ana**, anal scute; **ent**, entoplastron; **epi**, epiplastron; **Ext I**, extragular scute I; **Ext II**, extragular scute II; **Fem**, femoral scute; **Gul**, gular scute; **isc**, ischium scar; **Hum**, humeral scute; **hyo**, hyoplastron; **hyp**, hypoplastron; **Pec**, pectoral scute; **psc**, pubis scar; **xip**, xiphiplastron. Scale bar: 20 cm.

(missing portions of peripherals 1 and the nuchal), and most of costals 1 and lateral portions of costals 5 (Fig. 8). It also preserves the right femur, most of the right scapula, the right coracoid, cervical vertebrae 7 and 8, and remains of some thoracic vertebrae.

Carapace

The shape of the carapace is rectangular, slightly curved at its anterior and posterior margins. Both costals 1 are preserved; including ventrally the long axillary buttress that likely reached costals 2. Other preserved regions of the carapace are the lateral portions of costals 5, most of the peripherals and the pygal. However, peripherals 1 and the nuchal are missing (Fig. 8A).

Plastron

The plastron is almost completely preserved, missing only the most anterior portions of both epiplastra and the most anterior corner of the entoplastron (Fig. 8B, C). The sutures

between bones, as well as the sulci left by the scutes are clearly identifiable. The femoral scute was the longest of the scutes, resulting in a plastral formula Fem > Abd > Pec > Ana = Hum. The xiphiplastra exhibit a large and deep U-shaped anal notch and long and narrow posterior tips. Portions of both pelvic girdles are still attached to the plastron via the ischia and pubis. The plastron lacks of deep concavity at the medial region of xiphiplastral, suggesting that it was possibly a female individual.

The right femur is preserved, missing most of the major and minor trochanters (Fig. 8D-F). The femoral shaft is arched and exhibits an oval-shaped outline. The femoral head is oval in shape, eroded at its more proximal region and slightly projected laterally. In all aspects, the femur of VPPLT-1756 resembles the femur of the extant specimens of *C. fimbriata* and *C. lewisi*.

VPPLT-1756 preserved the right scapula and coracoid (Fig. 8G, H, J). The anterodorsal process of the scapula has an oval-shaped when seen in cross section, and it is broken, missing most of its distal end. There is a moderate notch in proximity to the glenoid fossa. The ventromedial prong (acromial process) is flatter than the anterodorsal and exhibits a dorsomedial ridge. The internal angle between the two processes is 85° (Fig. 8H). In *C. fimbriata* this angle is 75° (Fig. 8I). The coracoid has a flat distal blade which, although broken, is preserved enough to indicate that this region formed a broad surface, similarly to the coracoid of *C. fimbriata* (Fig. 8K).

Cervicals

Cervicals 7 and 8 are preserved slightly crushed (Fig. 8L-U). Cervical 7 has a biconcave centrum, exhibiting a long and robust dorsoventrally projected neural spine, with postzygapophyses facing ventrally and meeting medially, and a long ventral keel (Fig. 8L-P). Cervical 8 has a biconvex centrum, exhibiting also a long dorsoventrally projected neural spine that ends at the postzygapophyses as cervical 7, which face ventrolaterally and meet medially. It is shorter than cervical 7, and it has a very long ventral keel that ends in a drop-shape anterior tip (Fig. 8Q-U). VPPLT-1756 cervicals 7 and 8 resemble the centra of the same vertebrae in *C. fimbriata* (ICN-1781; Fig. 8V). In the extant taxon, however, the neural spines of these vertebrae are shorter, broader and more dorsally projected.

Chelus cf. *colombiana*
(Appendices 3; 4)

Referred material. — Carapace: VPPLT-783, neural bone (Appendix 3A, B); VPPLT-1747, nuchal bone (Appendix 3C, D); VPPLT-898, suprapygal bone (Appendix 3E, F); MT-28, neural 3? bone (Appendix 3G, H); MT-48, neural 3? bone (Appendix 3I, J); MT-26, right costal 5 bone (Appendix 3K, L); VPPLT-790, left costal 3 bone (Appendix 3M, N); MT-25, right costal 6? bone (Appendix 3O, P); MT-27, left costal 2 bone (Appendix 3Q, R); MT-47, left costal 2 bone (Appendix 3S, T); MT-49, left costal 8 bone (Appendix 3U, V); MT-24, left costal 2 bone (Appendix 3W, X). Plastron: VPPLT-987, left xiphiplastron (Appendix 4A, B); MT-41, right xiphiplastron (Appendix 4C, D); MT-42, left xiphiplastron (Appendix 4E, F); MT-43, left xiphiplastron (Appendix 4G, H); MT-50, left xiphiplastron (Appendix 4I, J); MT-51, right xiphiplastron (Appendix 4K, L); MT-52, right xiphiplastron (Appendix 4M, N); MT-53, right xiphiplastron (Appendix 4O, P); MT-30, right xiphiplastron (Appendix 4Q, R); VPPLT-350, left xiphiplastron (Appendix 4S, T); VPPLT-1746, right xiphiplastron (Appendix 4U, V); VPPLT-1745, entoplastron (Appendix 4W, X); VPPLT-968, partial plastron preserving both xipiplastra, both hypoplastra and portions of both hyoplastra (Appendix 4Y-BB).

Occurrences and age. — Villavieja and La Victoria formations, Huila Department, Colombia. Middle to Late Miocene 16 to 10.52 Ma (Mora-Rojas *et al.* 2023).

Chelus sp.

Referred material. — All fossil specimens described in Bocquetin (1988); Bocquentin & Rodrigues Do Santos (1989); Bocquentin *et al.* (2001); Cadena *et al.* (2008); Cadena & Jaramillo (2015a, b); Carrillo-Briceño *et al.* (2021); Ferreira *et al.* (2016).

Occurrences and age. — Early Miocene, Castillo Formation, Venezuela (Ferreira *et al.* 2016); Early Miocene, Barzalosa Formation, Colombia (Cadena *et al.* 2008); Early Miocene, Castilletes Formation, Colombia (Cadena & Jaramillo 2015a, b); Late Miocene, Solimões Formation, Brazil (Bocquetin 1988; Bocquentin & Rodrigues Do Santos 1989; Bocquentin *et al.* 2001); and Late Pliocene, San Gregorio Formation, Vergel Member, Venezuela (Carrillo-Briceño *et al.* 2021)

RESULTS

Phylogenetic analysis

The phylogenetic analysis produced 21 most parsimonious trees, from which a strict consensus was obtained (tree length = 297, CI = 0.765, RI = 0.821; Fig. 9N). The four *Chelus* taxa form a monophyletic clade inside Chelidae supported by characters: 48 (large costovertebral tunnel); 49 (nuchal bone width greater than length but less than two times); 58 (inguinal buttress extending onto peripherals 6 and 7); and 85 (carapace with three longitudinal ridges of knobs). *Chelus colombiana* and *C. lewisi* form a clade separate from the two extant taxa by the following characters: 52 (axillary buttress that extends onto costal 2); 62 (vertebral scute 1 almost rectangular); 63 (vertebral scute 1 almost same width of vertebral scute 2); 86 (inguinal buttress onto costal 5); and 87 (two or three pairs of extragular scutes). Future studies should include the skull characters for *C. orinocensis*.

DISCUSSION

Two extinct species instead of one

The new fossil specimens of *Chelus* described herein from Urumaco (Venezuela) and Tatacoa (Colombia) show strong differences in the shape of the carapace, with a rectangular shape in *C. colombiana* (Fig. 9L) and an oval shape in *C. lewisi* (Fig. 9F). This supports the initial hypothesis of Wood (1976) and is further reinforced by the larger number of specimens.

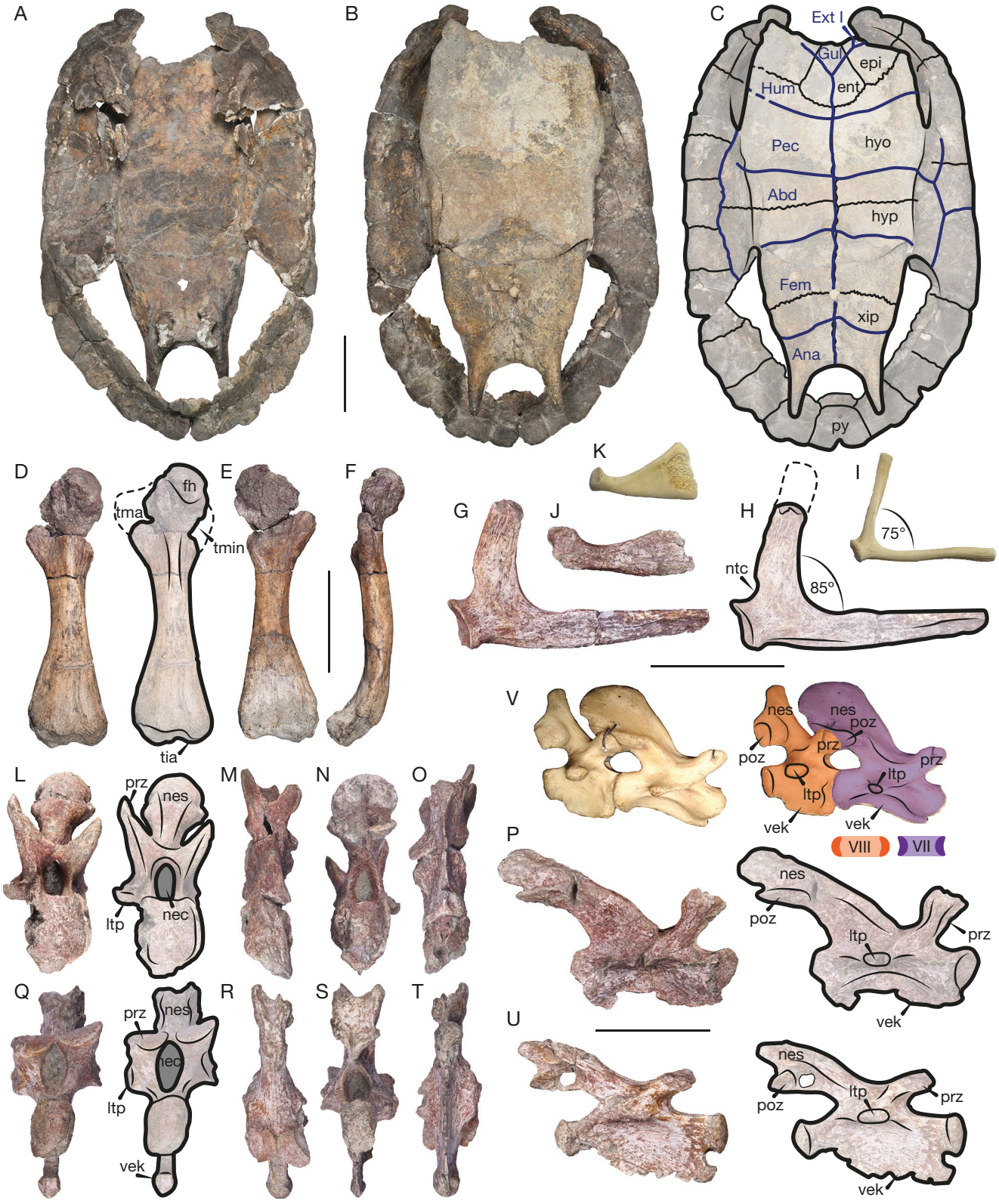

FIG. 8. — *Chelus colombiana* Wood, 1976 VPPLT-1756 specimen from the Tatacoa of Colombia: **A**, shell in dorsal view; **B**, **C**, plastron in ventral view; **D**-**F**, right femur in: **D**, dorsal view; **E**, ventral view; **F**, anterior view; **G**, **H**, right scapula in anterior view; **I**, right scapula *Chelus fimbriata* Schneider, 1783 UR-uncatalogued specimen in ventral view; **J**, right coracoid in ventral view; **K**, right coracoid *C. fimbriata* UR-uncatalogued specimen in ventral view; **L**-**P**, cervical vertebra 7 in: **L**, anterior view; **M**, dorsal view; **N**, posterior view; **O**, ventral view; **P**, right lateral view; **Q**-**U**, cervical vertebra 8 in: **Q**, anterior view; **R**, dorsal view; **S**, posterior view; **T**, ventral view; **U**, right lateral view; **V**, cervicals 7 and 8 of *C. fimbriata* ICN-1781 specimen in right lateral view, with schematic centra articulation below. Abbreviations: **Abd**, abdominal scute; **Ana**, anal scute; **ent**, entoplastron; **epi**, epiplastron; **Ext I**, extragular scute I; **Fem**, femoral scute; **fh**, femoral head; **Gul**, gular scute; **Hum**, humeral scute; **hyo**, hyoplastron; **hyp**, hypoplastron; **ltp**, lateral process; **nec**, neural canal; **nes**, neural spine; **ntc**, notch; **Pec**, pectoral scute; **poz**, postzygapophysis; **prz**, prezygapophysis; **tia**, tibial articulation; **tma**, trochanter major; **tmin**, trochanter min; **vek**, ventral keel; **xip**, xiphiplastron. Scale bars: A-C, 10 cm; D-V, 5 cm.

The differences in the carapace shape between the two taxa are consistent even in specimens of similar size (Table 1), disproving the hypothesis of Ferreira *et al.* (2016) that the oval shape of *C. lewisi* may be due to it representing an early ontogenetic stage. Furthermore, we present here a robust number of specimens of *C. lewisi*, all of which exhibit the same carapace outline shape, regardless of their size. Comparing the maximum carapace length between the two taxa, it is evident that *C. colombiana* developed larger size, as VPPLT-1758 reached 75.9 cm in carapace length, represents the largest specimen known for this taxon so far. In contrast, the largest specimen so far known for *C. lewisi* (AMU-CURS-1244) reached 55.4 cm. Another feature that helps differentiate *C. colombiana* from *C. lewisi* is the shape of the anterior plastral lobe. *Chelus lewisi* has a narrower anterior plastral lobe, with a marked notch in the epiplastron at lateral contact between the extragular I and the humeral scute, in contrast to *C. colombiana* has a wider anterior plastral lobe. There are also differences in the neural ridge of knobs, which in *C. colombiana* is narrow and strongly developed, forming a continuous dorsal ridge that does not expand laterally. In contrast, in *C. lewisi*, the neural ridge of knobs is narrower, lower to almost incipient in many specimens (Fig. 2). These differences are consistent with the holotypes of *C. colombiana* and *C. lewisi* described originally by Wood (1976) and have been also discussed by previous works based on a smaller number of specimens (Wood 1976; Pritchard 2008; Ferreira *et al.* 2016), supporting the reestablishment and validity of the two taxa, instead of a hypothesis that combines them into a single taxon, *C. colombiana*, and suggests that *C. lewisi* is the juvenile form of *C. colombiana* (Ferreira *et al.* 2016). The two morphological and geographically separated extinct taxa share similarities with the two extant taxa *C. fimbriata* and *C. orinocensis*, which were recently differentiated based on genomic analyses by Vargas-Ramírez *et al.* (2020). *Chelus orinocensis* shares with *C. lewisi* a more oval in shape carapace, with the width of the carapace increasing markedly from anterior to posterior region (Fig. 9A-F), on the other hand, *C. fimbriata* shares with *C. colombiana* an almost rectangular shape of the carapace with parallel-sides (Fig. 9G-L). The available evidence suggests that *C. colombiana* inhabited the western and southern regions of the Pebas system wetland during the Early to Middle Miocene and the Acre system/proto-Amazon during the Late Miocene. On the other hand, *C. lewisi* lived in the proto-Orinoco and the Maracaibo Basin during the Miocene, but went locally extinct in the Maracaibo Basin. Despite extensive fossil collection of numerous *Chelus* specimens at both Urumaco and Tatacoa over several decades, there is no current evidence to support the coexistence of the two extinct species in the exact same part of the Pebas or Acre systems (Fig. 9M).

There are distinct morphological differences between fossil (*C. colombiana* and *C. lewisi*) and extant *Chelus* (*C. fimbriata* and *C. orinocensis*). These synapomorphic differences include: an axillary buttress that extends onto costal 2, instead of being restricted to costal 1 (extant taxa); inguinal buttress onto costal 5, instead of costal 4 (extant taxa); two or three pairs of extragular scutes that encapsulate the gular, instead of gular reaching the anterior margin of the plastron and a single pair of extragular scutes (extant taxa); vertebral scute 1 almost rectangular, instead of pentagonal (extant); and vertebral scute 1 almost same width of vertebral scute 2, instead vertebral 1 wider than 2 (extant). Taking all these major differences into account, it is also plausible that the extinct taxa might not necessarily represent the direct ancestors of each of the extant taxa, but instead members of a single lineage that existed for most of the Miocene as supported by the phylogenetic analysis (Fig. 9N). Molecular analysis suggests that the split that gave origin to the extant taxa took place during the Late Miocene at 12.71 mya (Vargas-Ramírez *et al.* 2020). Finding complete Pliocene to Holocene specimens of *Chelus* will be crucial to better understand the evolution and palaeobiogeography history of the genus and the extant taxa, fossils that could probably document the morphological transitions leading to the anatomy of extant taxa.

Fossils with uncertain affinity

We suggest that isolated bones or partial shells that do not correspond to diagnostic parts, but that nevertheless are found in the same stratigraphic horizons or localities than the holotype or referred specimens should be only considered as "confer (cf)" to that particular taxon. Until now each of the two known extinct species have been found in very distant regions and there is not so far evidence that they coexisted. In the case of localities or regions for which only fragmentary specimens of the genus have been found (i.e., Castilletes, La Guajira Peninsula, Colombia, Cadena & Jaramillo 2015a, eastern Falcón in Tortonian rocks of the Caujarao Formation, Carrillo-Briceño *et al.* 2018, and the Solimões Formation of the Acre region, Bocquentin *et al.* 2001), they should be considered as *Chelus* sp., meaning that the specimen has not been identified down to the species level, nor it has been related to any known species following Sigovini *et al.* (2016).

Autopodia and limb anatomy

AMU-CURS-1244, which is referrable to *Chelus lewisi*, is the only fossil specimen within *Chelus* for which associated shell and postcranial bones are preserved together, allowing a glimpse at the autopodial evolution in this group of chelid turtles. The left manus of AMU-CURS-1244 shows the identical number of bones, size and shape than some extant specimens of *C. fimbriata*. According to Sánchez-Villagra *et al.* (2007), *C. frimbriata* exhibits two different conditions for the centralia: fused, or separated as in *C. lewisi* AMU-CURS-1244. As preserved, it seems that the pisiform bone was absent in *C. lewisi* AMU-CURS-1244, which by contrast is present in the extant *C. fimbriata* (Sánchez-Villagra *et al.* 2007), however, this could be a taphonomical artifact considering that the pisiform is one of smallest bones of the manus making it easy to be lost during pre-burial events. All other limb bones preserved in *C. lewisi* AMU-CURS-1244 and *C. colombiana* VPPLT-1756 are almost identical in shape and proportions to the corresponding ones of specimens of the extant *C. fimbriata*.

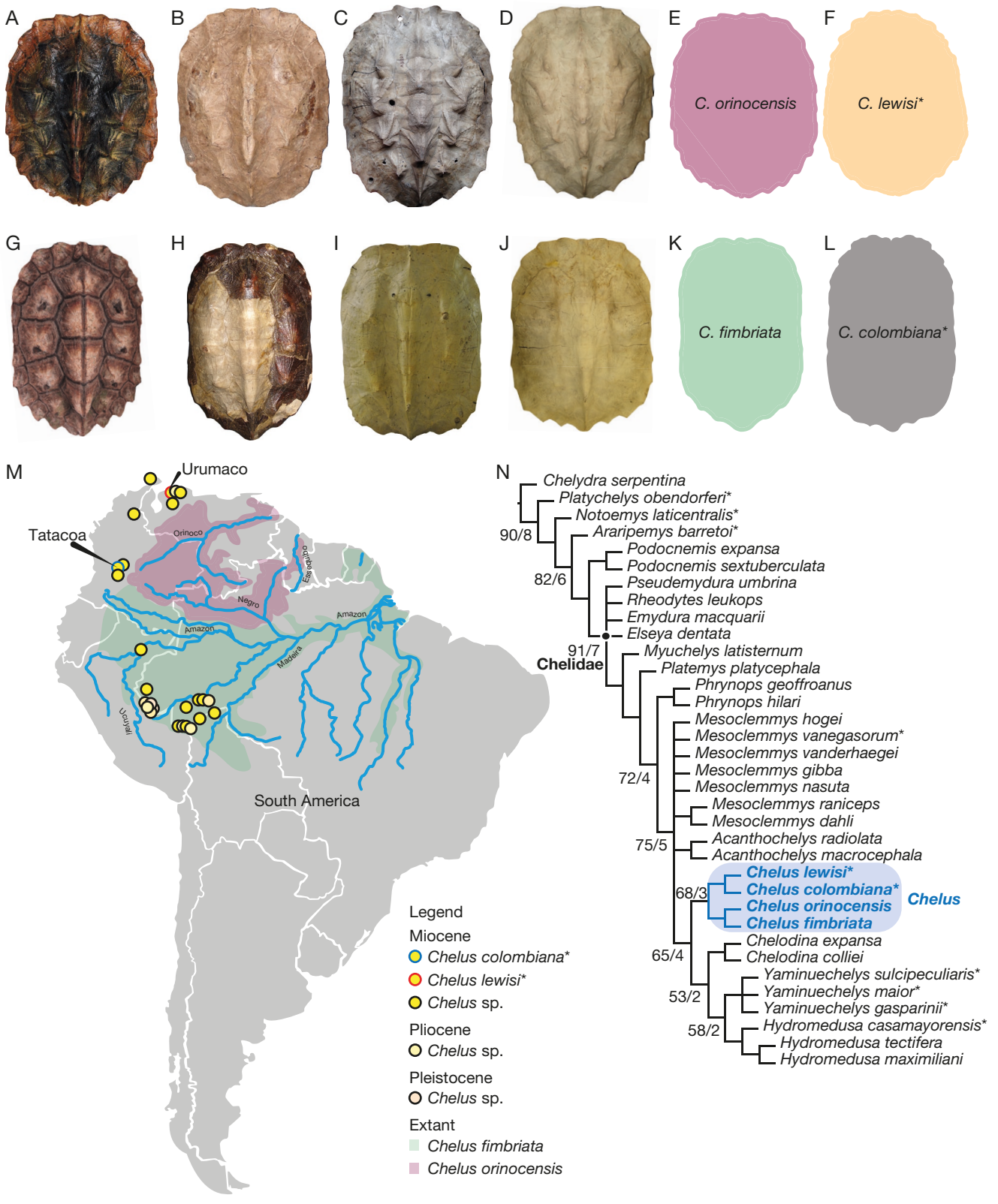

Fig. 9. — Comparisons between carapaces of *Chelus* Duméril, 1806 taxa, their biogeography and phylogenetic hypothesis: **A**-**D**, carapaces of *Chelus orinocensis* Vargas-Ramírez, Caballero, Morales-Betancourt, Lasso, Amaya, Martínez, Silva-Viana, Vogt, Farias, Hrbek, Campbell & Fritz, 2020 in dorsal view: **A**, IAvH-R8755 holotype; **B**, MNHN-D40 specimen; **C**, MNHN-A5200 specimen; **D**, ICN-1776 specimen; **E**, carapace outline of *Chelus orinocensis*; **F**, carapace outline of *Chelus lewisi* Wood, 1976; **G**-**J**, carapaces of *Chelus fimbriata* Schneider, 1783 in dorsal view: **G**, LET-65 specimen; **H**, MNHN-9406 specimen; **I**, NMW-1859 specimen; **J**, USNM-117455 specimen; **K**, carapace outline of *Chelus fimbriata*; **L**, carapace outline of *Chelus colombiana* Wood, 1976; **M**, biogeography distribution of extant *C. fimbriata* and *C. orinocensis* based on Turtle Taxonomy Working Group (2021), and fossil record occurrences of *Chelus* spp. based on PaleoBioDB (2023), indicating sites for which *C. colombiana* (Tatacoa, Colombia) and *C. lewisi* (Urumaco, Venezuela) have been documented; **N**, strict consensus tree of 5 MPT for Chelidae, showing the two separate clades (extant and extinct taxa) inside *Chelus*.

Earliest record in the Urumaco sequence

AMU-CURS-1244, referrable to *Chelus lewisi*, represents the earliest record of this taxon in the Urumaco sequence (Fig. 1B), considering that it was found at the base of the lower segment of the Socorro Formation, which is Middle Miocene in age (Quiroz & Jaramillo 2010; and references therein). The oldest record of *Chelus* for Venezuela corresponds to Early Miocene fossil remains from the Castillo Formation (18.27 to 17.21 Ma) (Ferreira *et al.* 2016), which should be considered as *Chelus* sp.

CONCLUSIONS

The new fossil specimens of *Chelus lewisi* from Urumaco (Venezuela) and *Chelus colombiana* from Tatacoa (Colombia) described herein show morphological differences that are unique to each of them, including the shape of the carapace and anterior plastral lobe supporting the reestablishment and validity of the two taxa, instead of representing intraspecific variations of a single taxon. AMU-CURS-1244, referrable to *Chelus lewisi*, not only represents the earliest record of *Chelus* for the Urumaco sequence, being from the Middle Miocene Socorro Formation, but also the only fossil *Chelus* for which associated shell and postcranial bones are preserved together. The preserved left manus bones, femora, left humerus, ulna and radius of *C. lewisi* show no major variation in terms of their size, shape and number compared with the same bones of the extant *C. fimbriata*, indicating a conservative anatomy of the manus inside the genus for the last 13 Ma.

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APPENDICES

APPENDIX 1. — Characters added or modified to the Cadena *et al.* (2020a). Chelidae matrix. Data for this study (Appendices 1-4) are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.34tmpg4q7

Modified

Character 56. Axillary buttresses extending over costal 1: (0) until lateral edge; (1) until medial portion; (2) until medial edge; (3) until medial portion of costal 2. *Modification*: State 3 added.

Added from Cadena et al. (2008).

Character 85. Carapace with three longitudinal ridges of knobs: (0) absent; (1) present. *Modification*: Only two states considered. *Modified from character 1*.

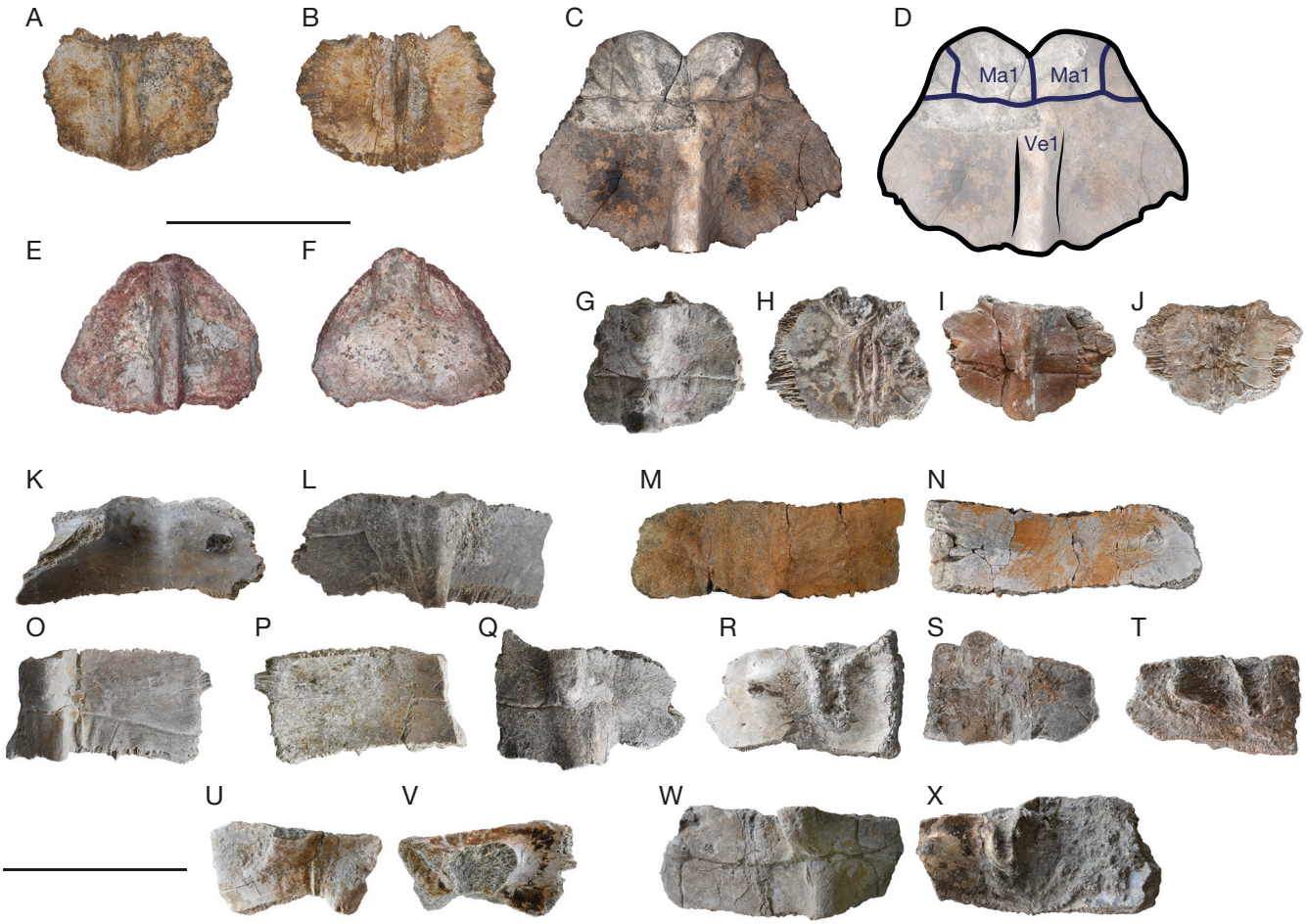
Character 86. Position of inguinal scar on ventral surface of carapace: (0) onto costal 5 or sutural contact between costals 5 and 6; (1) restricted to costal 4. *Modified from character 2.*

Character 87. Number of extragular scutes pairs: (0) one pair; (1) two or three pairs encapsulating the gular scute. *Modified from character 3.*

Character 88. Dorsal outline of carapace: (0) almost pentagonal tapering posteriorly; (1) rectangular, with lateral sides approximately parallel; (2) oval to semioval. *Modified from character 5.*

APPENDIX 2. — Character-taxon matrix for Chelidae including *Chelus* taxa in Nexus format. Available at the following address: https://doi.org/10.5852/cr-palevol2023v22a34_s1

APPENDIX 3. — Isolated carapacial bones of *Chelus* cf. *colombiana* from Tatacoa, Colombia: **A**, **B**, VPPLT-783 neural bone; **C**, **D**, VPPLT-1747 nuchal bone; **E**, **F**, VPPLT-898 suprapygal bone; **G**, **H**, MT-28 neural 3? bone; **I**, **J**, MT-48, neural 3? bone; **K**, **L**, MT-26 right costal 5 bone; **M**, **N**, VPPLT-790 left costal 3 bone; **O**, **P**, MT-25 right costal 6? bone; **Q**, **R**, MT-27 left costal 2 bone; **S**, **T**, MT-47 left costal 2 bone; **U**, **V**, MT-49 left costal 8 bone; **W**, **X**, MT-24 left costal 2 bone. Abbreviations: **Ma**, marginal scute; **Ve**, vertebral scute. Scale bars: A-J, 5 cm; K-X, 10 cm.



APPENDIX 4. — Isolated platral bones of *Chelus* cf. *colombiana* from Tatacoa, Colombia: **A**, **B**, VPPLT-987 left xiphiplastron; **C**, **D**, MT-41 right xiphiplastron; **E**, **F**, MT-42 left xiphiplastron; **G**, **H**, MT-43 left xiphiplastron; **I**, **J**, MT-50 left xiphiplastron; **K**, **L**, MT-51 right xiphiplastron; **M**, **N**, MT-52 right xiphiplastron; **O**, **P**, MT-53 right xiphiplastron; **Q**, **R**, MT-30 right xiphiplastron; **S**, **T**, VPPLT-350 left xiphiplastron; **U**, **V**, VPPLT-1746 right xiphiplastron; **W**, **X**, VPPLT-1745 entoplastron; **Y**-**BB**, VPPLT-968 partial plastron preserving both xiphiplastra, both hypoplastra and portions of both hyoplastra. Abbreviations: **Abd**, abdominal scute; **Ana**, anal scute; **Fem**, femoral scute; **Gul**, gular scute; **Hum**, humeral scute; **hyo**, hyoplastron; **hyp**, hypoplastron; **isc**, ischial scar; **pgl**, left pelvic girdle; **psc**, pubis scar; **xip**, xiphiplastron. Scale bar: 10 cm.