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# CONCEALED MORPHOLOGICAL DIVERSITY REVEALED BY NEW FOSSILS OF *CHELUS* (TESTUDINES, CHELIDAE) FROM THE UPPER MIOCENE OF THE ACRE BASIN, BRAZIL.

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Short Description: Osteological analysis of newly discovered fossils of the extinct species *Chelus colombiana* from Miocene deposits in the Solimões Formation, Brazilian Amazon.

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**ABSTRACT**

The Solimões Formation, in the Acre Basin, which outcrops between the states of Acre and Amazonas, northern Brazil, contains the country's most diverse fossil fauna of Neogene amniotes. 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 the clades Chelidae, Podocnemididae, and Testudinidae. The genus *Chelus* (Chelidae) — popularly known as mata-mata —, represented by two extant species, *Chelus fimbriata* and *Chelus orinocensis*, traditionally also includes two extinct species: *Chelus colombiana* and *Chelus lewisi*. In Brazil, fossils attributed to the genus *Chelus* have been reported since the late 19th century. Still, the first valid identifications were made in the 1980s and 1990s, and later in the 2000s, with the proposed presence of *C. colombiana* and *C. lewisi* observed in Miocene strata of the Brazilian Amazon. Here, we describe recently discovered fossils housed at the Laboratório de Pesquisas Paleontológicas at the Universidade Federal do Acre (Campus Rio Branco) and assign them to *Chelus.* Our comparative analyses show that features traditionally and recently used to diagnose the two extinct taxa are present in the same individual. This overlap leads us to question the consistency of these characteristics and consequently the validity of *C. lewisi*.

**Keywords.** *Chelus colombiana*. *Chelus lewisi*. Testudines. Miocene. Brazilian Amazon. Taxonomy

## 1. Introduction

The genus *Chelus* (Chelidae) — popularly known as mata-mata — represented by two living species, *Chelus fimbriata* [1] and *Chelus orinocensis* [2], has traditionally also included two extinct species: *Chelus colombiana* and *Chelus lewisi* [3]. The species of this genus have unique characteristics among the family Chelidae, such as the extremely dorsoventrally flattened skull related to suction-feeding [4] and highly ornamented body that resembles the leaves of aquatic plants [5]. All mata-matas are entirely aquatic, and the extant species inhabit the Amazon and Orinoco rivers drainages in northern South America [6].

Fossil occurrences assigned to *Chelus* have been reported for many localities in northern South America [3,7,8,9,10,11,12,13,14,15,16]. The oldest records of the genus are found in Colombia's early Miocene Castilletes Formation [14] and in the middle to late Miocene many specimens are assigned to *C. colombiana* [3,16]. Fossils assigned to *C. lewisi* were reported from the middle to late Miocene of Venezuela's Socorro and Urumaco formations [13,16]. Additional records assigned to *Chelus* sp. were also reported for the local fauna of Fitzcarrald, middle Miocene of Peru [12,17]. In Brazil, fossils assigned to the genus have been reported since the late XIX century [18], but the first still valid identifications are from the late 1980's. Bocquentin and Rancy [8] described fragmentary shell materials assigned to *C. lewisi* from the Acre river and Bocquentin and Santos [9], reported new carapace and plastron specimens assigned *C. colombiana* collected in the Purus River. New discoveries were only reported 12 years later by Bocquentin et al. [19], which assigned them either to *C. colombiana* or *C. lewisi*. The fossils comprised nearly complete carapaces and isolated shell bones collected from three localities on the banks of the Purus, Acre, and upper Juruá rivers.

The validity of the extinct species has been questioned by Ferreira et al. [15], who reviewed their diagnostic features and proposed that there should be a single extinct species, with *C. lewisi* as a junior synonym of *C. colombiana*. The authors demonstrated that the traits diagnosing the extinct taxa were observed as intraspecific variations in the extant *C. fimbriata*, and should be interpreted similarly in a single extinct species. More recently, though, Cadena et al. [16] described many new well-preserved specimens, including complete carapaces and plastron, and proposed new diagnoses, reaffirming the validity of the species *C. lewisi*. Here, we describe new fossils of *Chelus* from several localities in the Acre State, Brazil, which represent the best-preserved specimens of the genus from the Brazilian fossil record. Our analyses suggest that all *Chelus* specimens from Acre belong to a single species. Moreover, we revised the diagnostic features proposed by Cadena et al. [16] and concluded that they are insufficient to clearly distinguish *C. colombiana* from *C. lewisi*. The presence of a mosaic of characteristics in the new specimens, along with similar intraspecific variation in *C. fimbriata*, supports the hypothesis of a single extinct *Chelus* species in the Miocene of South America.

**Institutional abbreviations. UFAC.** Universidade Federal do Acre, Rio Branco, Brazil. **UNEFM**. Universidad Experimental Francisco Miranda, Coro. **AMU-CURS**. Alcaldía Bolivariana de Urumaco, Museo Paleontológico de Urumaco, Falcón State. **MCNC.** Museo de Ciencias Naturales de Caracas, Caracas.

## 2. Material and Methods

### 2.1. Provenance, geological and paleontological context

The fossils analyzed here comprise 70 new specimens (Table 1) and three materials previously studied and identified as *C. lewisi* [8,9]. All specimens are part of the Paleontology Collection of the Laboratório de Pesquisas Paleontológicas (LPP) at the Universidade Federal do Acre (UFAC, Rio Branco, State of Acre, Brazil) and consist of

almost complete shells, in addition to isolated shell fragments. The specimens were collected during expeditions to the Solimões Formation in the state of Acre and Amazon between 1990 and 2022, in the six different localities: Cachoeira do Bandeira, Patos, Niteroi, Talismã, Aracuã, and Lula (Fig. 1).

### 2.2. Fossiliferous localities

**Cachoeira do Bandeira:** This site is located on the left bank of the Acre river, at coordinates 10°56'21"S and 69°20'37"W. This locality was discovered during expeditions carried out in 1976 [20]. The lithology consists of sedimentary conglomerates and silt-clay. The recorded paleofauna is diverse, including fish [21], turtle [22], crocodiles [23], birds [24] and mammals [25, 26]. Its estimated age is late Miocene [20].

**Patos:** The Patos locality (also known as “Acre 06” or “LACM 4611”) is situated along the upper Acre River at coordinates 10°55'55"S and 69°5'20"W. Most fossils are found in the lower levels, which can only be accessed during the dry season when the water level is low [27,20]. The lithology of the lower levels consists of red to green clay and siltstone, and conglomerates are composed of clay pebbles. The associated paleofauna is diverse and includes invertebrates, fish fragments, turtles [28,10] crocodiles [20], birds [29], and mammals [27,30].

**Niteroi:** Discovered in 1987, the Niteroi locality 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 ± 0.5 million years based on detrital zircon U-Pb ages [31,20]. The lithology consists of a clay conglomerate, varying in layers of gypsum and fossiliferous levels. The associated paleofauna includes fish [32], turtle [19], crocodiles [33], birds [24] and mammals [26,34, 35, 36].

**Talismã:** 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 ± 0.13 million years based on detrital zircon [20,31,37,38,39]. The lithology of this locality consists of white to red clay and siltstone, with gypsum and calcite veins. The associated paleofauna includes anurans [40], turtles [19], crocodilians [41], squamates [42,43,44], birds [24] and mammals [25,34,37,45].

**Aracuã:** Aracuã is less explored than the other localities and is located on the right 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), numerous fossils were collected and are still under study, including many specimens of Testudines.

**Lula:** The Lula outcrop is located on both sides of the road cut for the BR-364 highway at coordinates 09°01'23"S and 68°48'21.00"W [20]. The lithology consists of white to red clay and siltstone. The associated paleofauna includes fish fragments [46], crocodilians [41], and turtles [47].

### 2.3. Comparative material

For osteological comparison, 86 specimens of the extant *C. fimbriata* were examined. Those specimens are part of the collections of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus, Brazil), Museu Paraense Emílio Goeldi (MPEG, Belém, Brazil), Laboratório de Pesquisas Paleontológicas at the Universidade Federal do Acre (LPP/UFAC, Rio Branco, Brazil), the Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil), and the Senckenberg Museum Frankfurt (SMF, Frankfurt am Main, Germany). Straight-line carapace and plastral length and width were measured using a ruler and tape for larger specimens and a digital caliper for smaller specimens. The figures were edited and prepared using CorelDRAW 2020 (version 22.0.0.421) and Corel Photo-Paint 2020 (version 22.0.0.421). Most editing was

performed in CorelDRAW, while Corel Photo-Paint was used to remove the backgrounds.

## 3. RESULTS

### SYSTEMATIC PALEONTOLOGY

Testudines Batsch, 1788.
Pleurodira Cope 1865
Chelidae Gray, 1825
*Chelus* Dumeril, 1806
*Chelus colombiana* Wood, 1976.

**Synonym.** *Chelus lewisi* [3]

**Holotype.** UCMP 78762, a nearly complete shell found in the vicinities of Villavieja, upper Magdalena River Valley, Colombia, late Miocene Villavieja Formation [3]

**Referred material.** UFAC-7344: incomplete carapace; UFAC-6517: almost complete carapace; UFAC-5497: almost complete articulated carapace and pelvic girdle; UFAC-1002: almost complete articulated carapace and pelvic girdle; UFAC-4815: incomplete disarticulated carapace; UFAC-4021: incomplete carapace; UFAC-5805, UFAC-2097: nuchal; 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-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: right femur.

**Revised Diagnosis:** Differs from the extant species *C. fimbriata* and *C. orinocensis* in having the following characteristics: (1) axillary scar extending to the second costal bone rather than restricted to costal I and (2) to the second peripheral bone rather than peripheral III; (3) inguinal scar extending onto costal V, instead of costal IV; (4) broad cervical scute including two small ridges on the nuchal bone instead of a narrow cervical scute with a single ridge on the midline; (5) iliac scar restricted to the suprapygal and costal VIII, rather than extending to costal VII; (6) one or two extra pairs of extragulars usually preventing the gular scute from reaching the anterior margin of the plastron; (7) vertebral scute I almost rectangular, instead of pentagonal; (8) cervicals 7 and 8 having longer and more dorsoventrally projected neural spines instead of shorter, broader, and dorsally projected ones; (9) broader internal scapular angle of 85°, instead of 75°.

**Occurrence.** Miocene of Colombia: Villavieja Formation [3], Barzalosa Formation [48], La Victoria Formation [16]; Venezuela: Castillo Formation [15], Urumaco and Socorro formations [16]; and Brazil: Solimões Formation [19].

## 4. Description.

### Description of the material from Brazil

### 4.1.Carapace

The osteological description of the carapace was based on the most complete specimens, UFAC-5497, UFAC-7344, and UFAC-6517. (Fig 3). They exhibit a carapace with a rectangular shape and three ridges along the dorsal surface of the carapace, two lateral and one on the midline (3). The nuchal bone is hexagonal, with two small anterior ridges

on its dorsal surface (Fig. 4, A-D) that extend posteriorly to half its length. The seven neural bones are arranged sequentially, with no variation in this count among the known specimens from the Solimões Formation. The midline ridge is narrower and lower than the lateral ridges. It is not continuous, being composed of four to five segments distributed along the midline, from the nuchal to the pygal. The height and position of the different segments vary between the specimens (Figs. 2-3). Neural I is the largest in the series and its shape ranges from rectangular, as observed in UFAC-5497 (Fig. 3C, D), to more rounded, as seen in UFAC-4815 (Fig. 5I). Neural VII is pentagonal and is sutured posteriorly to costals VII. The other neurals are similar in shape, being wider than long. Neurals I, III, and V are crossed by dorsal sulci running orthogonally to the midline resulting from the contact between subsequent vertebral scutes. The sulci of the five vertebral scutes can be observed, with vertebrals I and V incomplete in all specimens. Vertebral III is the largest in length and width. Vertebrals II-III have a rectangular shape and are slightly wider anteriorly than posteriorly. Vertebral IV is hexagonal, with the anterior part being nearly twice as wide as the posterior. The costal bones form a sequence of eight, all wider than longer and similarly shaped, except for costal I, which is much longer than the others. The sulci left by the contact between pleural scutes are visible on the dorsal surfaces of costals II, IV, VI, and VIII. Four pleural scutes are present, all displaying a consistent rectangular shape with no variation. Pleural I is incomplete, which makes it challenging to determine the largest scute in the series. However, based on previously published specimens, Pleural I is identified as the largest, while Pleural IV is the smallest, following the sequence I > II > III > IV. On the ventral surface of the costal bones, three scars are present: the axillary scar extending posteromedially from costal I to II (Fig. 6F); the inguinal scar on costal V, extending along the lateromedial axis (Fig. 6H and 7B,D,F); and the iliac scar spamming from costal VIII to the suprapygal (Fig.

4N,O,R,S and 7H). The shape of the suprapygal varies from pentagonal, as in UFAC-6559 (Fig. 4N), to sub-triangular, as seen in UFAC-4469 (Fig. 4R), with the iliac scars positioned laterally on its ventral surface. The pygal bone marks the end of the midline ridge and its posterior edge is W-shaped due to the two posterior knobs (Fig 7I, J). Peripherals I-III are nearly squared with well-developed knobs, as observed in specimen UFAC-4815(Fig. 5A, C). The axillary scar reaches peripheral II ventrally (Fig. 4B), in contrast to the condition in the extant species, in which this scar reaches only until peripheral III. Peripherals IV-VII (UFAC-5497; Fig. 3C, D) are much longer than wide, and peripherals X-XI (UFAC-6417; Fig. 3A, B) are also almost squared. Peripherals IV-XI show less pronounced knobs in comparison to the anterior ones.

### 4.2. Plastron

The plastron is composed of the single entoplastron and paired epi-, hyo-, hypo-, and xiphiplastra. None of the studied specimens shows a completely preserved plastron. Only the anterior lobe (composed of the entoplastron, epiplastra, and hyoplastra) is preserved in the specimen UFAC-1546 (Fig. 8A), which is rounded and relatively wide, while in UFAC-4815 the posterior lobe (composed of the hypoplastra and xiphiplastra) is preserved. There are also many isolated xiphiplastra among the Brazilian material (Fig. 8B-Q). The epiplastron is rectangular, with its length considerably exceeding its width. In the anterior portion, notches are visible, one formed by the contact between the extragular I and extragular II scutes, and another by the contact between the extragular I and humeral scutes. The entoplastron is diamond-shaped, with a wider posterior end compared to the anterior, and it is longer than wide. The hyoplastron is wider than long due to the laterodorsal expansion forming the anterior part of the bridge. Likewise, the hypoplastron also expands laterodorsally, forming the posterior part of the bridge. The xiphiplastron bone is wider in the anterior part and narrows into a tip at its posterior

extremity. 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 be located near the border of the bone (as in UFAC-3143; Fig. 8M), or more medially (as in UFAC-1581; Fig. 8Q). The ischial scar is generally boomerang-shaped but also exhibits considerable shape variation. For example, in UFAC-3143 its ends are thinner compared to those in UFAC-4455 (Fig. 8F), which has rounded ends, in addition to the curvature of the posteromedial edge, which can be more concave, as observed in UFAC-4266, or more straight, as in UFAC-4455 (Fig. 8O and 8F).

In the specimen UFAC-1456, the extragular II are the smallest scutes, triangular in shape, and positioned on the anterior surface of the epiplastron. The extragular I scute is larger than extragular II and is sub-quadrangular. Both pairs of extragulars are restricted to the epiplastra. The gular scute is diamond-shaped and prevents contact between the extragular II scutes by a small projection towards the anterior edge of the plastron. It overlays the epiplastra and the anterior surface of the entoplastron. The humeral scute is quadrangular and overlays the posterior surface of the epiplastron, most of the entoplastron, and the anterior third of the hyoplastron. The pectoral scute is restricted to the hyoplastron, but it is longer than the humeral scute.

### 4.3. Appendicular bones

Currently, only a few appendicular bone specimens are known from extinct *Chelus,* and here we add three new specimens from the state of Acre to this record. UFAC-1559 consists of an incomplete right femur similar to the one described by Cadena et al. [16]. Its head is slim and considerably projected medially from the shaft, and the articular surface is tilted about 20° relative to the shaft axis (Fig. 9A-D). Although the trochanters are not preserved, the intertrochanteric fossa is shallow but relatively wide. The femoral

shaft is thin and slightly curved, like in the extant species. UFAC-1002 (Fig. 9E, F) is an almost complete right pelvic girdle previously described by Bocquentin and Rancy [8], and UFAC-5497 (Fig 9G, H) is a new right pelvic girdle, less complete than the former. The pelvic girdle bones are robust and dorsoventrally compact, the dorsal surface of the ilium that sutures to the costal VIII and suprapygal 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. The contact surface of the pubis that sutures to the xiphiplastron, is oval in both specimens, similar to the condition in the extant species. There is no significant variation between UFAC-1002 and the extant species in relation to the angle formed between the ischium and the pubis.

## 5. DISCUSSION

Our assessment of the three new and mostly complete carapaces (UFAC-5497, UFAC-6517, and UFAC-7344; Fig. 3) together with the previously known articulated and associated carapace and plastral material (e.g., UFAC-1002, UFAC-4815, UFAC-4021 and UFAC-1546) allows us to assess the presence or absence of the recently proposed diagnostic features for both extinct species [16] in the material from Acre. Those include variations in three traits: (1) the shape of the anterior plastral lobe, (2) the shape of the shell outline, and (3) the relative shape of the dorsal ridges. *C. lewisi* would be characterized by having a (1a) very narrow anterior plastral lobe, with a marked lateral notch on the sulcus between extragular I and the humeral scutes, (2a) a posterior widening of the carapace that creates a tapering anterior margin, and (3a) a lower to an almost incipient neural ridge with narrow knobs that is smaller than the costal ridges. *C. colombiana*, on the other hand, could be identified by (1b) a broader anterior margin of

299 the plastron without notches, (2b) an almost rectangular carapace, and (3b) continuous
300 dorsal ridges formed by narrow knobs that do not expand laterally.

301 The Brazilian specimens, though, do not fit neatly either of those sets of
302 characters. Specimens UFAC-1002 (Fig. 2A, B), UFAC-5497, UFAC-6517 and UFAC-
303 7344 (Fig. 3) present non-continuous dorsal ridges with the neural ridge lower than the
304 costal ridges (3a) and could thus be considered *C. lewisi*. Yet, in UFAC-5497 (Fig. 3C,
305 D) and UFAC-7344 (Fig. 3E, F) the dorsal ridges do not "expand laterally" (3b), thus
306 consistent with *C. colombiana*. On the other hand, the plastron UFAC-1546 (Fig. 8A)
307 shows a well-preserved anterior lobe that is broad and not constrained laterally (1b),
308 fitting the diagnosis of *C. colombiana*. Finally, UFAC-6517 (Fig. 3A, B) exhibits a
309 mosaic of diagnostic traits from both species: a rectangular carapace with parallel lateral
310 margins (2b) and costal ridges that do not expand laterally (3b), both diagnostic of *C.*
311 *colombiana*; yet, the neural ridge is almost absent (3a), which characterizes *C. lewisi*.

312 We identified inconsistencies in the set of diagnostic characters also in some
313 specimens from Colombia and Venezuela. The neural ridge is low and much smaller than
314 the costal ridges (3a) in some specimens from Colombia, such as IGMp-002045 [16,49],
315 in MT-22 [16] and even in UCMP-78762, the holotype of *C. colombiana* [3]. At the same
316 time, the specimen UNEFM-1371 assigned to *C. lewisi*, which in Cadena seems to have
317 no preserved ridges, has actually been altered over the years, (compare Fig. 1B of
318 Sánchez-Villagra et al., 1995[49] to Fig. 2E in Cadena et al. [16]). In the old photos it is
319 possible to clearly see the three dorsal ridges similarly developed (3b), and the dorsal
320 ridges are continuous (3b), which are consistent with *C. colombiana* instead. The anterior
321 margin of the plastron in the holotype of *C. lewisi* [3,16] is as broad as that observed in
322 some specimens, such as UFAC-1546, assigned to *C. colombiana*, and a shallow notch
323 between the humeral and extragular-I sulcus (1a) is present in specimen MT-22 assigned

to *C. colombiana* [16]. Additionally, the specimen MCZ-VPRA-4337 from Venezuela (mentioned, but not figured in Cadena et al. [16]) exhibits an oval shape as in some specimens of the extant species. It is important to notice that the shell shape is highly variable in the living species *C. fimbriata* (Fig 10), with some specimens even presenting a posterior expansion (e.g., MPEG-042, Fig. 10D) approaching the proposed shape for *C. lewisi*.

The presence of diagnostic traits from both extinct taxa among the specimens from Acre points to two alternative hypotheses: (i) there were two species of matamata turtles occupying the same environments in the Acre state during the late Miocene (as argued by Bocquentin et al. [19]); or (ii) the observed differences should be considered as intraspecific variation in a single extinct taxon (as previously argued by Ferreira et al. [15]). In favor of the first hypothesis, Bocquentin et al. [19] argued that the different sizes of *C. colombiana* and *C. lewisi* would allow their coexistence by niche separation [15,16,51]. Indeed, UFAC-6517, the specimen that is more safely identified as *C. colombiana* among the Acre specimens (although presenting an incipient neural ridge; Fig. 3A, B) is very large: its carapace length is estimated at 90 cm, making it the largest known extinct *Chelus* specimen. UFAC-5497 is an incomplete carapace with total carapace length estimated in about 70 cm, fitting within the size range of *C. colombiana*. However, according to our assessment, its dorsal ridges point to a *C. lewisi* affinity, suggesting a considerable overlap in the size ranges between the coeval species. Because the ecology of the extant mata-matas is strongly linked to their peculiar morphology [4,5,51], we must assume similar habits for the extinct species. However, if the size differences are not as clear as previously thought, the niche separation by body size argument becomes weak, as does the evidence for two coeval species.

The alternative hypothesis of a single extinct species solves this issue by considering both the character and body size variation as intraspecific variability. In this scenario, Colombia and Venezuela would represent the extremes of the distribution of the extinct species and, as such, the more structured variation observed by Cadena et al. [16] could be explained by more (but not completely) isolated populations. The Acre system, on the other hand, would represent a broader area of this distribution, potentially connected to both northernmost areas [15,52,53,54]. In such a system, intermediate forms, showing combinations of characters that in other areas might be less frequent (like the ones we described here) would be expected. We conclude that the hypothesis of a single extinct taxon of *Chelus* in the Miocene of South America is more successful in explaining both the variation observed in the Tatacoa and Urumaco specimens and the newly described material from Brazil. The Solimões Formation still holds great potential for future discoveries and may further increase our knowledge about the evolution of *Chelus*.

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## REFERENCES

[1] Schneider, J.G. (1783). Allgemeine Naturgeschichte der Schildkröten nebst einem systematischen Verzeichnisse der einzelnen Arten und zwey Kupfern. Müller,Leipzig.

[2] Vargas-Ramírez, M., Caballero, S., Morales-Betancourt, M. A., Lasso, C. A., Amaya, L., Martínez, J. G., Das Neves Silva Viana, M., Vogt, R. C., Farias, I. P., Hrbek, T., Campbell, P. D., and Fritz, U. (2020). Genomic analyses reveal two species of the matamata (Testudines: Chelidae: *Chelus spp.*) and clarify their phylogeography. Mol. Phylogenet. Evol., 148, 106823. https://doi.org/10.1016/j.ympev.2020.106823.

[3] Wood, R. C. (1976). Two new species of *Chelus* (Testudines: Pleurodira) from the late Tertiary of Northern South America. Breviora, 435: 1-26. https://www.biodiversitylibrary.org/page/6590474.

[4] Lemell, P., Lemell, C., Snelderwaard, P., Gumpenberger, M., Wochesländer, R., & Weisgram, J. (2002). Feeding patterns of *Chelus fimbriatus* (Pleurodira, Chelidae). J. Exp. Biol., 205: 1495–1506. https://doi.org/10.1242/jeb.205.10.1495.

[5] Bonin, F., Devaux, B., & Dupré, A. (2006). Turtles of the World. Johns Hopkins University Press, Baltimore, Maryland, 416 pp.

[6] Rhodin, A.G.J., et al. (2021). Turtles of the World: Annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status. 9th ed. Turtle Taxonomy Working Group.

[7] Barbosa-Rodrigues, J. B. (1892). Les reptiles de la vallée de l'Amazone. Vellosia, 2: 41–56.

[8] Bocquentin, J. V., & Rancy, A. (1987). Presença de *Chelus lewisi* Wood, 1976 (Testudinata, Pleurodira) no Neógeno do Estado do Acre, Brasil. In: 4º Congresso Latino-Americano de Paleontologia, Santa Cruz de la Sierra, 1987, edited by Asoc. Bol. Paleontol., pp. 566–573.

[9] Bocquentin, J. V., & Santos, J. C. R. (1989). Ocorrência de *Chelus colombianus* (Chelonii, Chelidae) no Mioceno Superior do Acre, Brasil. Em: Resumos

414 do 11º Congresso Brasileiro de Paleontologia, Curitiba, editado por Soc. Bras. Paleontol.,
415 pp. 104–105.
416
417 [10] Broin, F., Bocquentin, J., & Negri, F. R. (1993). Giant turtles (Pleurodira,
418 Podocnemididae) from the late Miocene-early Pliocene of Southwestern Amazon. Bull.
419 Inst. Fr. Études Andines, 22(3): 657–670.
420
421 [11] Sánchez-Villagra, M. R., Linares, O. J., & Paolillo, A. (1995).
422 Consideraciones sobre la sistemática de las tortugas del género *Chelus* (Pleurodira:
423 Chelidae) y nuevas evidencias fósiles del Mioceno de Colombia y Venezuela.
424 Ameghiniana, 32: 159–167.
425
426 [12] Antoine, P.-O., Salas-Gismondi, R., Baby, P., Benammi, M., Brusset, S., De
427 Franceschi, D., Espurt, N., Goillot, C., Pujos, F., Tejada, J., & Urbina, M. (2007). The
428 middle Miocene (Laventan) Fitzcarrald Fauna, Amazonian Peru. In: Díaz-Martínez, E.,
429 & Rábano, I. (eds.), Proceedings of the 4th EMPSLA, Cuad. Museo Geominero, 8, 355–
430 360.
431
432 [13] Sánchez-Villagra, M. R., & Scheyer, T. M. (2010). Fossil turtles from the
433 northern Neotropics: The Urumaco sequence fauna and finds from other localities in
434 Venezuela and Colombia. In: M. R. Sánchez-Villagra, O. A. Aguilera, & A. A. Carlini
435 (Eds.), Urumaco and Venezuelan Paleontology: The Fossil Record of the Northern
436 Neotropics, Indiana University Press, Bloomington, pp. 173–191.
437
438 [14] Cadena, E. A., & Jaramillo, C. A. (2015). The first fossil skull of *Chelus*
439 (Pleurodira: Chelidae, Matamata turtle) from the Early Miocene of Colombia. Palaeontol.
440 Electron., 18.2.32A: 1–10. https://doi.org/10.26879/545.
441
442 [15] Ferreira, G. S., Rincón, A. D., Solórzano, A., & Langer, M. C. (2016).
443 Review of the fossil matamata turtles: earliest well-dated record and hypotheses on the
444 origin of their present geographical distribution. Sci. Nat., 103(3-4): 1–12.
445 https://doi.org/10.1007/s00114-016-1355-2
446
447 [16] Cadena, E. A., Link-Ospina, A., Vanegas, A., Avellaneda-Otero, C. A.,
448 Perdomo, C., Ureña-Carrillo, D., Sánchez, R., Vanegas, R., Scheyer, T. M., & Carrillo-
449 Briceño, J. D. (2023). New insights into the fossil record of the turtle genus *Chelus*,
450 including new specimens with information on cervicals and limb bones. C. R. Palevol,
451 22(34): 689–709. https://doi.org/10.5852/cr-palevol2023v22a34
452
453 [17] Carrillo-Briceño, J. D., Sánchez, R., Scheyer, T. M., Carrillo, J. D., Delfino,
454 M., Georgalis, G. L., et al. (2021). A Pliocene–Pleistocene continental biota from
455 Venezuela. Swiss J. Palaeontol., 140(9), 1–76. https://doi.org/10.1186/s13358-020-
456 00216-6.
457
458 [18] Oliveira, G.R., & Romano, P.S.R. (2007). Histórico dos achados de
459 tartarugas fósseis do Brasil. Arq. Mus. Nac. Rio de Janeiro, 65(1): 113–133.
460
461 [19] Bocquentin, J. V., Guilherme, E., & Negri, F. R. (2001). Duas espécies do
462 gênero *Chelus* (Pleurodira, Chelidae) no Mioceno Superior-Plioceno da Amazônia Sul-
463 Ocidental. Rev. Univ. Guarulhos, 6(6): 50–55.

[20] Souza-Filho, J., Filho, J., & Guilherme, E. (2015). A paleontologia no Estado do Acre. In: Adamy, A. (Org.), Geodiversidade do Estado do Acre. CPRM, Brasília, pp. 147–158.

[21] Aguilera, O. A., Bocquentin, J., Lundberg, J. G., & Maciente, A. (2008). A new cajaro catfish (Siluriformes: Pimelodidae: Phractocephalus) from the Late Miocene of southwestern Amazonia and its relationship to Phractocephalus nassi of the Urumaco Formation. Paläontol. Z., 82(2): 231–245. https://doi.org/10.1007/BF02988412

[22] Bocquentin-Vilanueva, J., & Guilherme, E. (1997). A cintura pélvica do quelônio *Stupendemys* (Podocnemididae, Podocnemidinae) proveniente do Mioceno Superior-Plioceno do estado do Acre, Brasil. Acta Geol. Leopoldensia, 20: 47–50.

[23] Aureliano, T., Ghilardi, A. M., Guilherme, E., Souza-Filho, J. P., Cavalcanti, M., & Riff, D. (2015). Morphometry, bite-force, and paleobiology of the Late Miocene caiman *Purussaurus brasiliensis*. PLoS One, 10(2), e0117944. https://doi.org/10.1371/journal.pone.0117944.

[24] Alvarenga, H. M. F., & Guilherme, E. (2003). The anhingas (Aves: Anhingidae) from the upper Tertiary (Miocene - Pliocene) of southwestern Amazonia. J. Vert. Paleontol., 23(3): 614–621. https://doi.org/10.1671/1890

[25] Kerber, L., Negri, F., Ribeiro, A., Vucetich, M., & Souza Filho, J. (2016). Late Miocene potamarchine rodents (Caviomorpha: Dinomyidae) from southwestern Amazonia, Brazil (northern South America): with description of new taxa. Acta Geol. Leopoldensia, 61, 191–203. https://doi.org/10.4202/app.00091.2014.

[26] Kerber, L., Negri, F.R., Ribeiro, A.M., Nasif, N., Souza-Filho, J.P., & Ferigolo, J. (2017). Tropical fossil Caviomorph rodents from the southwestern Brazilian Amazonia in the context of the South American faunas: Systematics, biochronology, and paleobio-geography. J. Mammal. Evol., 24, 57–70. https://doi.org/10.1007/s10914-016-9340-2.

[27] Cozzuol, M. A. (2006). The acre vertebrate fauna: age, diversity, and geography. J. South Am. Earth Sci., 21, 185–203. https://doi.org/10.1016/j.jsames.2006.03.005.

[28] Bocquentin, J., & Melo, G. (2006). *Stupendemys souzai sp. nov.* (Pleurodira, Podocnemididae) from the Miocene-Pliocene of the Solimões Formation, Brazil. Rev. Bras. Paleontol., 9(2), 187–192. https://doi.org/10.4072/rbp.2006.2.02.

[29] Guilherme, E., D'Apolito, C., Muniz, F., Lomba, S. O., Aldrin, L., & Hsiou, A. S. (2024). New fossil anhingids from the upper Acre River (Late Miocene of southwestern Amazon). Anat. Rec., 307, 2047–2064. https://doi.org/10.1002/ar.25329.

[30] Kay, R. F., & Cozzuol, M. A. (2006). New platyrrhine monkeys from the Solimoes Formation (late Miocene, Acre State, Brazil). J. Hum. Evol., 50, 673–686. https://doi.org/10.1016/j.jhevol.2006.01.002.

[31] Bissaro-Júnior, M. C., Kerber, L., Crowley, J. L., Ribeiro, A. M., Ghilardi, R. P., Guilherme, E., Negri, F. R., Souza Filho, J. P., & Hsiou, A. S. (2019). Detrital zircon U–Pb geochronology constrains the age of Brazilian Neogene deposits from Western Amazonia. Palaeogeogr. Palaeoclimatol. Palaeoecol., 516, 64–70. https://doi.org/10.1016/j.palaeo.2018.11.032.e

[32] Monsch, K. A. (1998). Miocene fish faunas from the northwestern Amazonia basin (Colombia, Peru, Brazil) with evidence of marine incursions. Palaeogeogr. Palaeoclimatol. Palaeoecol., 143, 31–50. https://doi.org/10.1016/S0031-0182(98)00064-9.

[33] Gasparini, Z. (1985). Un nuevo cocodrilo (Eusuchia) Cenozoico de América del Sur. In: Coletânea de Trabalhos Paleontológicos MME-DNPM, Série Geologia, 1985(27), 51–53. ISSN 0103-1473.

[34] Kerber, L., Bissaro-Júnior, M. C., Negri, F. R., Souza-Filho, J. P., Guilherme, E., & Hsiou, A. S. (2018). A new rodent (Caviomorpha: Dinomyidae) from the upper Miocene of southwestern Brazilian Amazonia. Hist. Biol., 30, 985–993. https://doi.org/10.1080/08912963.2017.1327529.

[35] Bocquentin, J., & Guilherme, E. (1999). As preguiças Mylodontinae (Mammalia, Xenarthra, Mylodontidae) do Neógeno do sítio Niterói, Acre, Brasil. Acta Geol. Leopoldensia, 22, 57–67.

[36] Frailey, C. D. (1986). Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Acre region, western Amazonia. Contrib. Sci., 374, 1–43. https://doi.org/10.5962/p.2081177.

[37] Bergqvist, L., Ribeiro, A. M., & Bocquentin-Villanueva, J. (1998). Primata, roedores e litopternas do Mio/Plioceno da Amazônia Sul-Ocidental (Formação Solimões, Bacia do Acre), Brasil. Geol. Colombiana, 23, 19–29.

[38] Souza-Filho, J. P., & Bocquentin-Villanueva, J. (1991). *Caiman niteroiensis sp. nov.* (Alligatoridae, Crocodylia) do Neógeno do Estado do Acre, Brasil. In: Congr. Bras. Paleontol., 12, 1991, São Paulo, Boletim de Resumos, SBP, p. 126.

[39] Santos, J. C. R., Negri, F. R., & Silva, E. G. (1993). Mamíferos fósseis da Amazônia Sul-Ocidental brasileira – Formação Solimões: considerações bioestratigráficas. In: Bol. Resumos do 13º Congr. Bras. Paleontol. e 1º Simp. Cone Sul, p. 136.

[40] Muniz, F. P., Bissaro-Júnior, M. C., Guilherme, E., Souza-Filho, J. P. D., Negri, F. R., & Hsiou, A. S. (2021). Fossil frogs from the upper Miocene of southwestern Brazilian Amazonia. J. Vert. Paleontol. https://doi.org/10.1080/02724634.2021.2089853.

[41] Fortier, D. C., De Souza-Filho, J. P., Guilherme, E., Maciente, A. A. R., & Schultz, C. L. (2014). A new specimen of *Caiman brevirostris* (Crocodylia, Alligatoridae) from the late Miocene of Brazil. J. Vert. Paleontol., 34, 820–834. https://doi.org/10.1080/02724634.2014.838173.

[42] Hsiou, A. S., & Albino, A. M. (2009). Presence of the genus *Eunectes* (Serpentes, Boidae) in the Neogene of Southwestern Amazonia, Brazil. J. Herpetol., 43, 612–619.

[43] Hsiou, A. S., Albino, A. M., & Ferigolo, J. (2010). Reappraisal of the South American Miocene snakes of the genus *Colombophis*, with description of a new species. Acta Palaeontol. Pol., 55, 365–379.

[44] Hsiou, A., Albino, A., & Ferigolo, J. (2009). First lizard remains (Teiidae) from the Miocene of Brazil (Solimões Formation). Rev. Bras. Paleontol., 12, 225–230.

[45] Negri, F. R. (2004). Os Tardigrada (Mammalia, Xenarthra) do Neógeno, Amazônia Sul-Ocidental, Brasil. Doctoral Thesis, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, 156 pp.

[46] Richter, M. (1989). Dental histology of a characoid fish from the Plio-Pleistocene of Acre, Brazil. Zool. Scripta, 13(1), 69–79.

[47] Souza-Filho, J. P. (1987). *Caiman brevirostres sp. nov.*, um novo Alligatoridae da Formação Solimões (Pleistoceno) do estado do Acre, Brasil. In: Anais do 10º Congr. Brasileiro de Paleontologia, 1987, Rio de Janeiro. SBP, p. 173–180.

[48] Cadena, E. A., Jaramillo, C., & Paramo, M. E. (2008). New material of *Chelus colombiana* (Testudines; Pleurodira) from the lower Miocene of Colombia. J. Vert. Paleontol., 28(4), 1206–1212. https://doi.org/10.1671/0272-4634-28.4.1206.

[49] Sánchez-Villagra, M. R., Linares, O. J., & Paolillo, A. (1995). Consideraciones sobre la sistemática de las tortugas del gênero *Chelus* (Pleurodira: Chelidae) y nuevas evidencias fósiles del Mioceno de Colombia y Venezuela. Ameghiniana, 32, 159–167.

[50] Benson, R. B. J., Frigot, R. A., Goswami, A., Andres, B., & Butler, R. J. (2014). Competition and constraint drove Cope's rule in the evolution of giant flying reptiles. Nat. Commun., 5(1), Article 1. https://doi.org/10.1038/ncomms4567.

[51] Ernst, C. H. & Barbour, R. W. (1989) Turtles of the World (Smithsonian Inst. Press, Washington, DC), p. 313.

[52] Wesselingh, F.P., Macsotay, O. (2006). Pachydon hettneri (Anderson, 1928) as indicator for Caribbean-Amazonian lowland connections during the Early-Middle Miocene. J. S. Am. Earth Sci., 21, 49–53. https://doi.org/10.1016/j.jsames.2005.07.013

[53] Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T., Antonelli, A. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science, 330, 927–931. https://doi.org/10.1126/science.1194585.

[54] Rincón, A.D., Solórzano, A., Benammi, M., Vignaud, P., McDonald, H.G. (2014). Chronology and geology of an Early Miocene mammalian assemblage in North of South America, from Cerro La Cruz (Castillo Formation), Lara State, Venezuela: implications in the changing course of Orinoco River hypothesis. Andean Geol., 41, 507–528.



**FIGURE CAPTIONS**

**Figure 1** – Map of the main fossiliferous localities of *Chelus* in the Solimões Formation, Acre Basin: 1, Patos; 2, Cachoeira do Bandeira; 3, Niterói; 4, Lula; 5, Talismã; 6, Aracuã.

**Figure 2** – Articulated carapaces of *Chelus colombiana*. A, B, UFAC-1002: nearly complete articulated carapace, dorsal view. C, D, UFAC-4021: nearly complete articulated carapace, dorsal view. Abbreviations: co, costal; ne, neural; nu, nuchal; pe, peripheral; Ple, pleural; py, pygal; su, suprapygal; Ver, vertebral scute. Scale bar: 5 cm

**Figure 3** – Articulated carapaces of *Chelus colombiana*. A, B, UFAC-6517: nearly complete articulated carapace, dorsal view. C, D, UFAC-5497: nearly complete articulated carapace, dorsal view. E, F, UFAC-7344: nearly complete articulated

651 carapace, dorsal view. Abbreviations: co, costal; ne, neural; nu, nuchal; pe, peripheral;
652 Ple, pleural; py, pygal; su, suprapygal; Ver, vertebral scute. Scale bar: 10 cm.

653 **Figure 4** – Isolated bones of *Chelus colombiana*. A, B, UFAC-5805: nuchal,
654 dorsal/ventral view; C, D, UFAC-2097: nuchal, dorsal/ventral view; E, F, UFAC-5792:
655 neural three, dorsal/ventral view; G, H, UFAC-5007: neural five, dorsal/ventral view; I,
656 UFAC-1943: neural five, dorsal; J, UFAC-798: neural three, dorsal; K, UFAC-7163:
657 neural five, dorsal; L, UFAC-7021: neural 4 or 6?, dorsal; M, N, UFAC-6559: suprapygal,
658 dorsal/ventral view; O, P, UFAC-2981: suprapygal, dorsal/ventral view; Q, R, UFAC-
659 4469: suprapygal, dorsal/ventral view; S, T, UFAC-5799: suprapygal, dorsal/ventral
660 view. Abbreviations: ilsc, iliac scar; Ver, vertebral scute. Scale bar: 1 cm.

661 **Figure 5** – Bones of the carapace and plastron of *Chelus colombiana*. A, K, UFAC-4815.
662 A, B; first, second, third peripheral, and right first costal, dorsal/ventral view; C; first and
663 second peripheral, and left first costal, dorsal view; D, E; eight costal, dorsal/ventral
664 view; H; five, six, and seven costal bones, dorsal view; F, G; costal third, fourth, and fifth,
665 dorsal/ventral view; I; first neural and fragment of thoracic vertebrae, dorsal view; J, K;
666 xiphiplastron and hypoplastron, dorsal/ventral view. Abbreviations: axs, axillary scar;
667 fas, femoroanal sulcus; ilsc, iliac scar; isc, ischial scar; psc, pubic scar; Ple, pleural scute.
668 Scale bar: 2 cm.

669 **Figure 6** – Isolated bones of *Chelus colombiana*. A, B, UFAC-7349: first costal,
670 dorsal/ventral view; C, D, UFAC-6553: first costal, dorsal/ventral view; E, F, UFAC-
671 7017: second costal, dorsal/ventral view; G, H, UFAC-3168: fifth costal, dorsal/ventral
672 view; I, J, UFAC-6411: fifth costal, dorsal/ventral view. Abbreviations: axs, axillary scar;
673 ing, inguinal scar. Scale bar: 1 cm.

674 **Figure 7** – Isolated bones of *Chelus colombiana*. A, B, UFAC-2970: fifth costal,
675 dorsal/ventral view; C, D, UFAC-7347: fifth costal, dorsal/ventral view; E, F, UFAC-

676 6583: fifth costal, dorsal/ventral view; G, H, UFAC-7348: eighth costal, dorsal/ventral
677 view; I, UFAC-7343: pygal, dorsal view; J, UFAC-2967: pygal, dorsal view.
678 Abbreviations: ilsc, iliac scar; ing, inguinal scar. Scale bar: 1 cm.

679 **Figure 8** – Articulated incomplete plastron and isolated xiphiplastron of *Chelus*
680 *colombiana*. A, UFAC-1546: incomplete plastron, dorsal view; Scale bar: 5 cm. B, C,
681 UFAC-1578: left xiphiplastron, dorsal/ventral view; D, E, UFAC-2075: right
682 xiphiplastron, dorsal/ventral view; F, G, UFAC-4455: right xiphiplastron, dorsal/ventral
683 view; H, I, UFAC-2973: right xiphiplastron, dorsal/ventral view; J, K, UFAC-1047: right
684 xiphiplastron, dorsal/ventral view; L, M, UFAC-3143: left xiphiplastron, dorsal/ventral
685 view; N, O, UFAC-4266: left xiphiplastron, ventral/dorsal view; P, Q, UFAC-1581: left
686 xiphiplastron, ventral/dorsal view. Abbreviations: Abd, abdominal scute; ent,
687 entoplastron; epi, epiplastron; ext, extragular scute; Gul, gular scute; Hum, humeral scute;
688 hyo, hyoplastron; isc, ischial scar; psc, pubic scar. Scale bar: 1 cm.

689 **Figure 9** – Appendicular bones of *Chelus colombiana*. A-D, UFAC-1559: right femur,
690 dorsal/ventral/lateral views; E, F, UFAC-1002: right pelvic girdle, medial/lateral/ventral
691 views; G, H, UFAC-5497: right pelvic girdle, medial/lateral views. Abbreviations: ace,
692 acetabulum; pub, pubis; is, ischium; i, ilium; fia, fibular articulation; tia, tibial
693 articulation; tmi, trochanter minor; tma, trochanter major. Scale bar: 2 cm.

694 **Figure 10** – Articulated carapaces of *Chelus fimbriata*. A, MPEG-0483: carapace, dorsal
695 view; B, MPEG-1249: carapace, dorsal view; C, MPEG-1238: carapace, dorsal view; D,
696 MPEG-042: carapace, dorsal view; E, MPEG-0407: carapace, dorsal view; F, AMH-267:
697 carapace, dorsal view. Scale bar: 2 cm.

698 Table 1– Comparative table of morphological characters used to distinguish *Chelus*
699 *colombiana* and *Chelus lewisi*, showing the conditions observed in the analyzed
700 specimens from Acre (Brazil), Colombia and Venezuela.

| | Specimens (Country) | UFAC-1546 (Brazil) | UFAC-5497 (Brazil) | UFAC-6517 (Brazil) | UFAC-7344 (Brazil) | UFAC-4021 (Brazil) | UFAC-1002 (Brazil) | UCMP-78762 (Colombia) | IGMp-002045 (Colombia) | MT-22 (Colombia) | MCNC-239 (Venezuela) | UNEFM-1371 (Venezuela) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chelus colombiana* | Neural ridge narrow and strongly developed (Cadena et al. 2023) | | | | | X | | | X | | | |
| | Dorsal ridges do not expand laterally (Cadena et al. 2023) | | X | X | X | X | X | | X | | | X |
| | Continuous dorsal ridges (Cadena et al. 2023) | | | | | | | | | | | X |
| | Anterior plastral lobe without lateral notch (Cadena et al. 2023) | X | | | | | | | | | | |
| | Broad anterior plastral lobe (Cadena et al. 2023) | X | | | | | | X | | X | X | X |
| | Rectangular carapace with parallel margins (Wood, 1976) | | | X | | | | X | X | X | | |
| | Carapace length reaching 75.9 cm (Cadena et al. 2023) | | X | X | | | | X | | X | | |
| | Wider and shorter caudal process of the xiphiplastron (Cadena, 2008) | | | | | | | | | | X | X |
| *Chelus lewisi* | Neural ridge with knobs narrower, lower to almost incipient (Cadena et al. 2023) | | | X | | | X | | | | X | |
| | Neural ridge lower and smaller than costal ridges (Cadena et al. 2023) | | X | X | X | X | X | X | X | X | X | |
| | Non-continuous dorsal ridges (Cadena et al. 2023) | | X | X | X | | X | | | | X | |
| | Marked notch in the epiplastron (Cadena et al. 2023) | | | | | | | | | X | X | X |
| | Narrower anterior plastral lobe (Cadena et al. 2023) | | | | | | | | | | | |
| | Oval carapace with posterior widening (Wood, 1976). | | | | | | | | | | X | X |
| | Carapace length reaching up to 55.4 cm (Cadena et al. 2023) | | | | | | X | | X | | X | X |
| | Narrower and longer caudal process of the xiphiplastron (Cadena, 2008) | | | | | | | X | X | X | X | |

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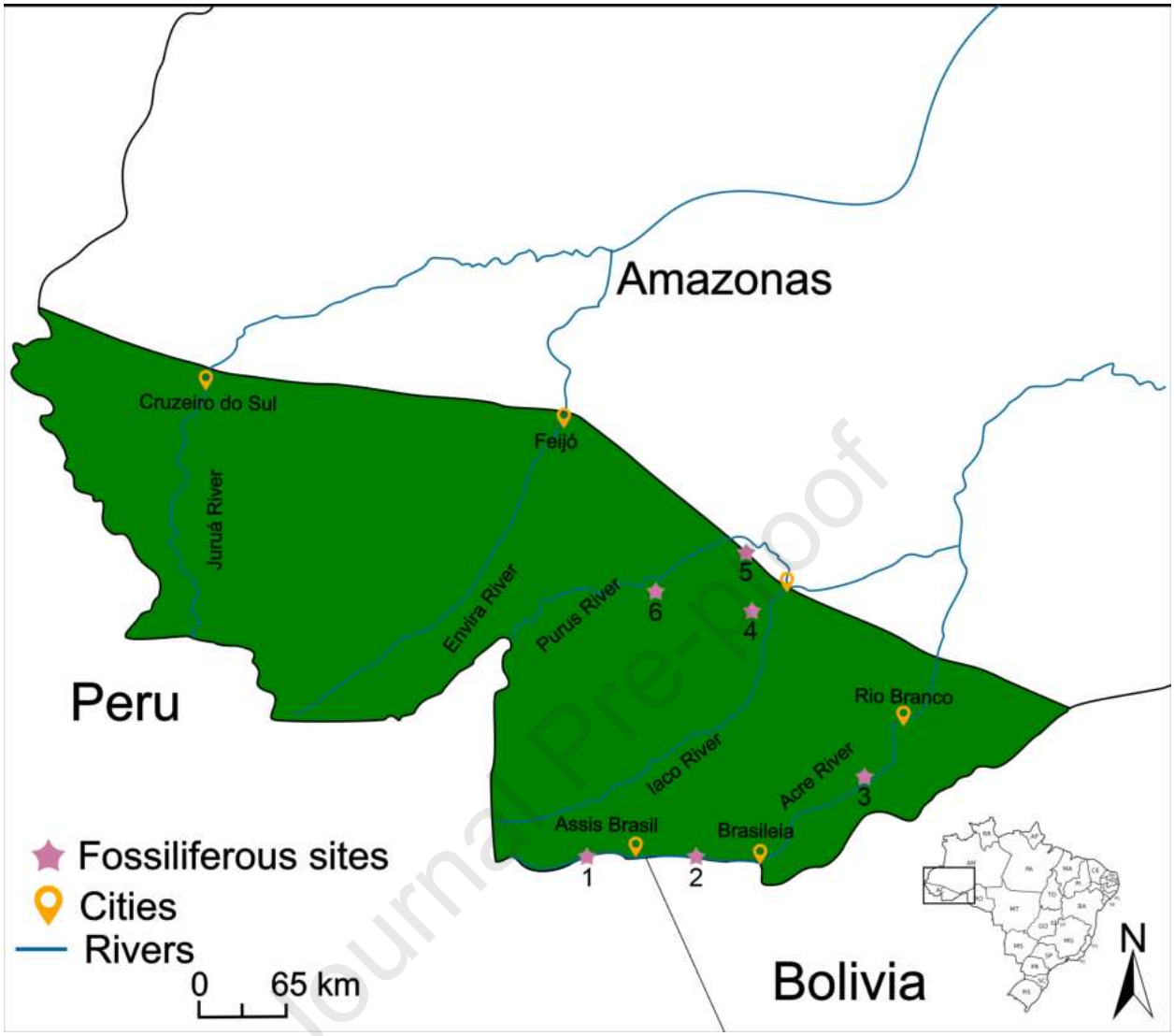

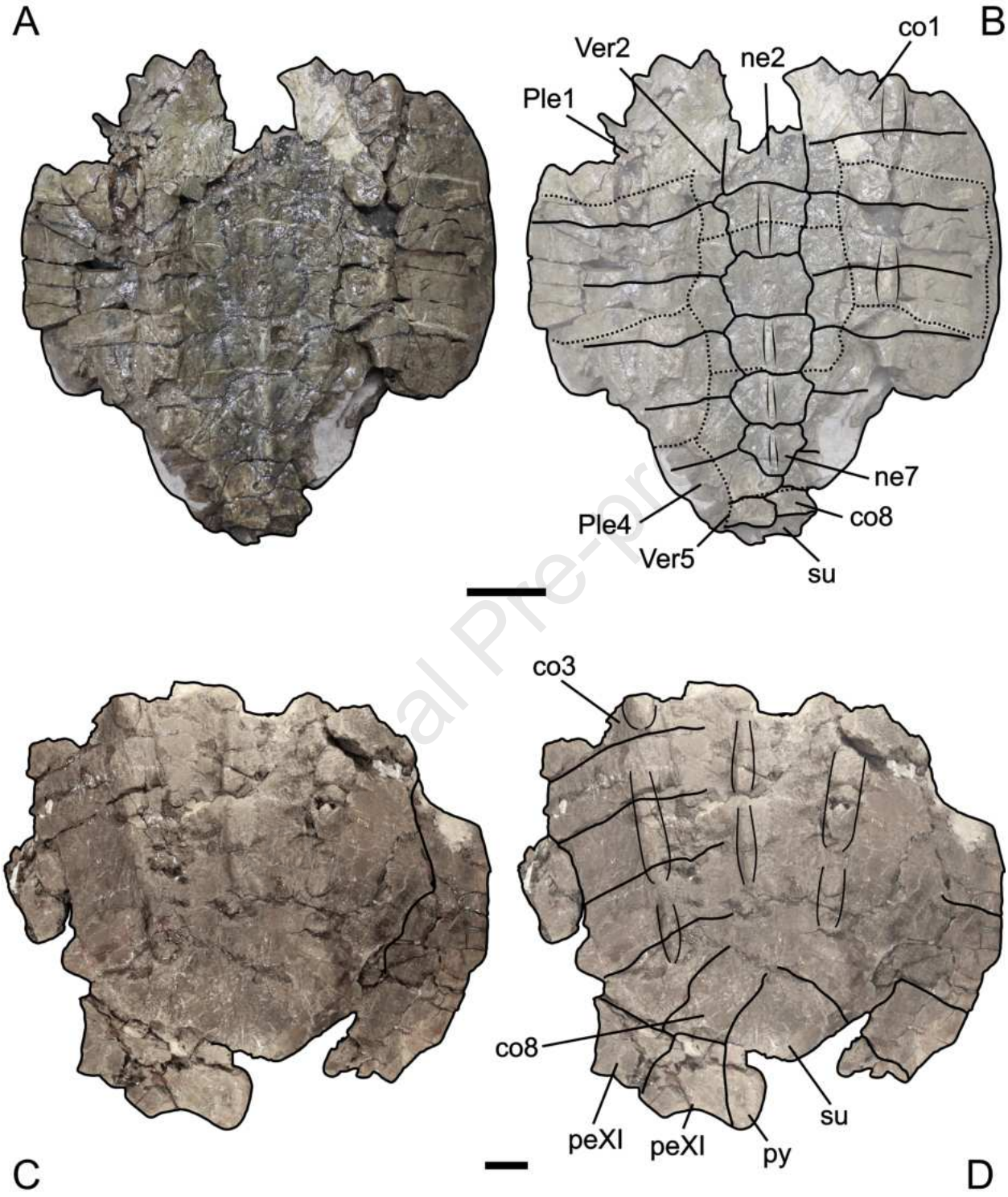

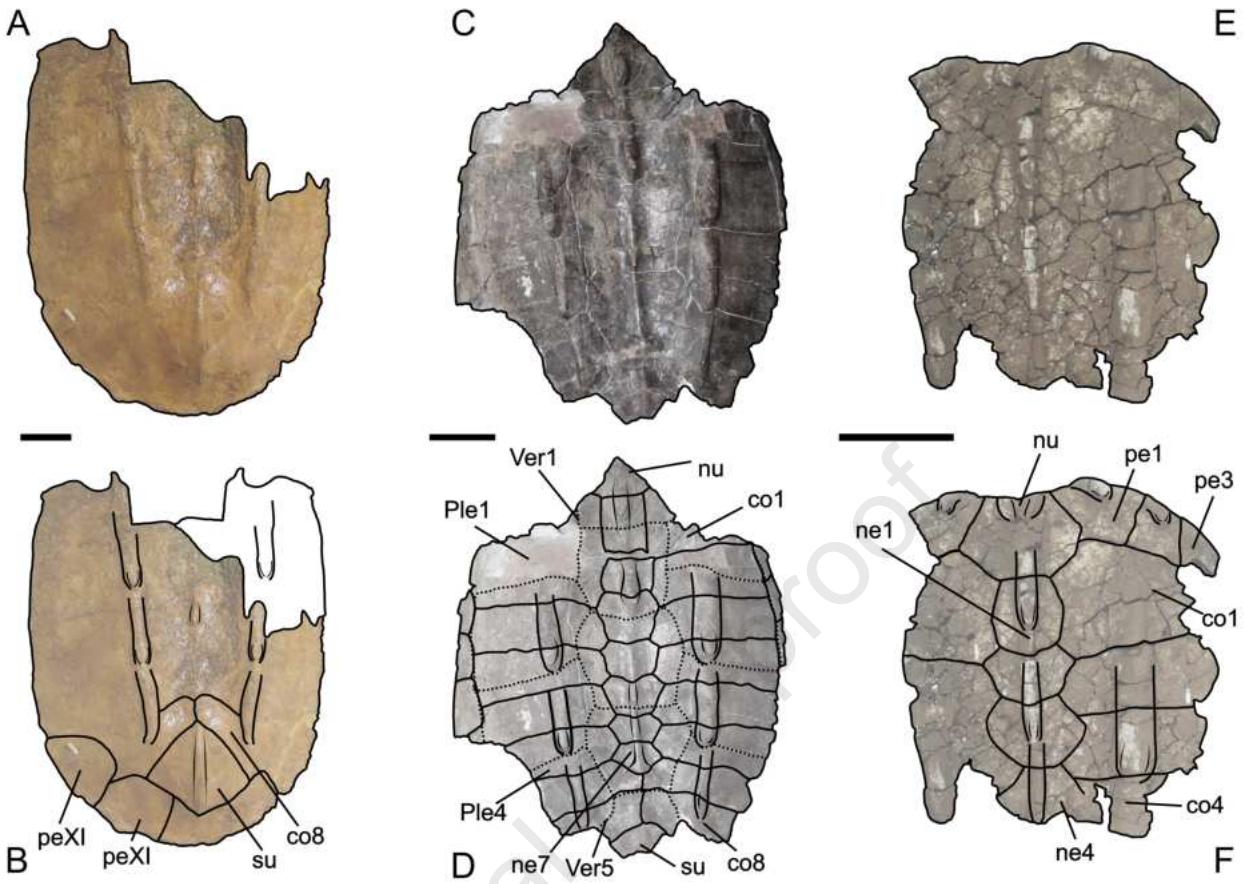

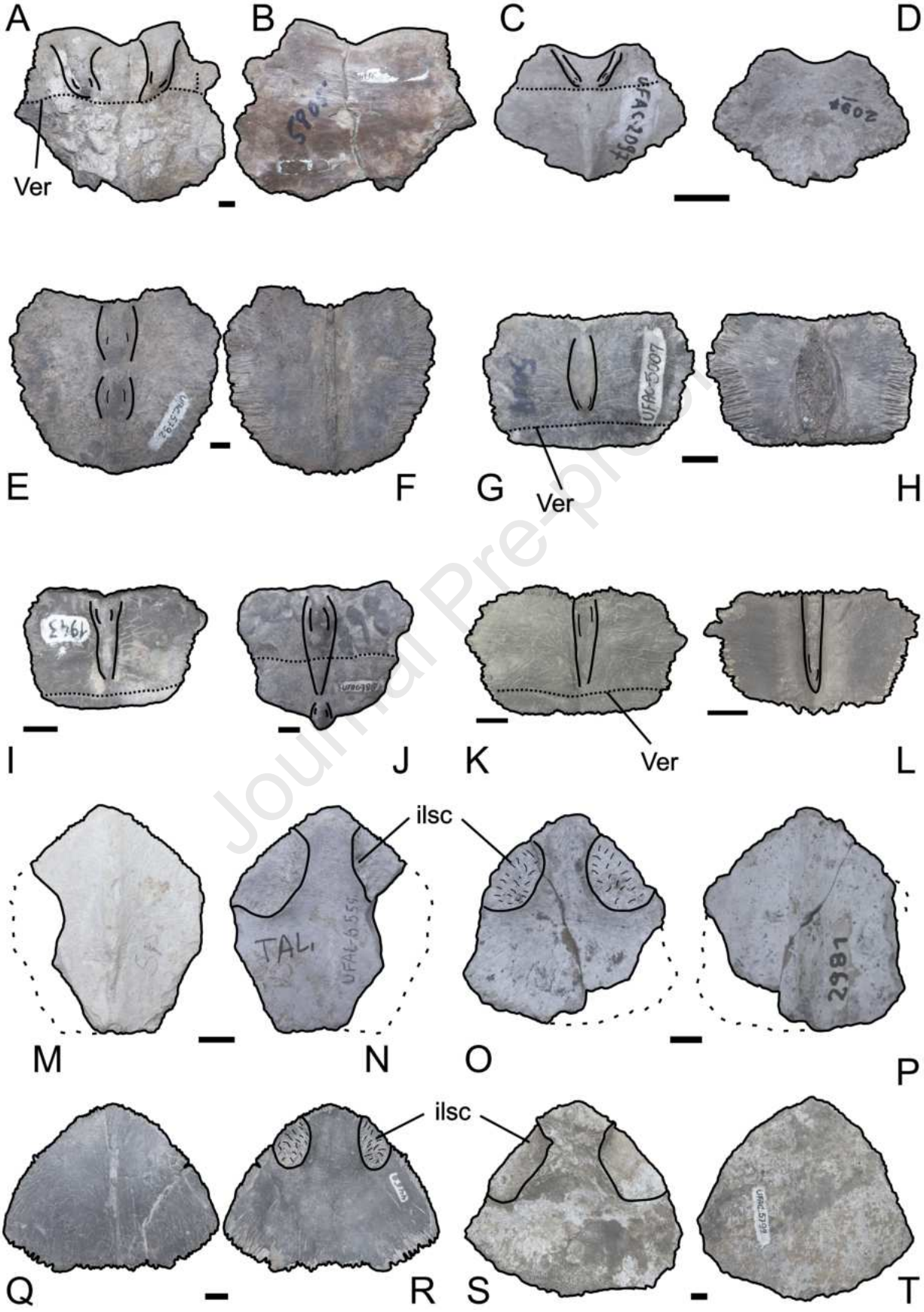

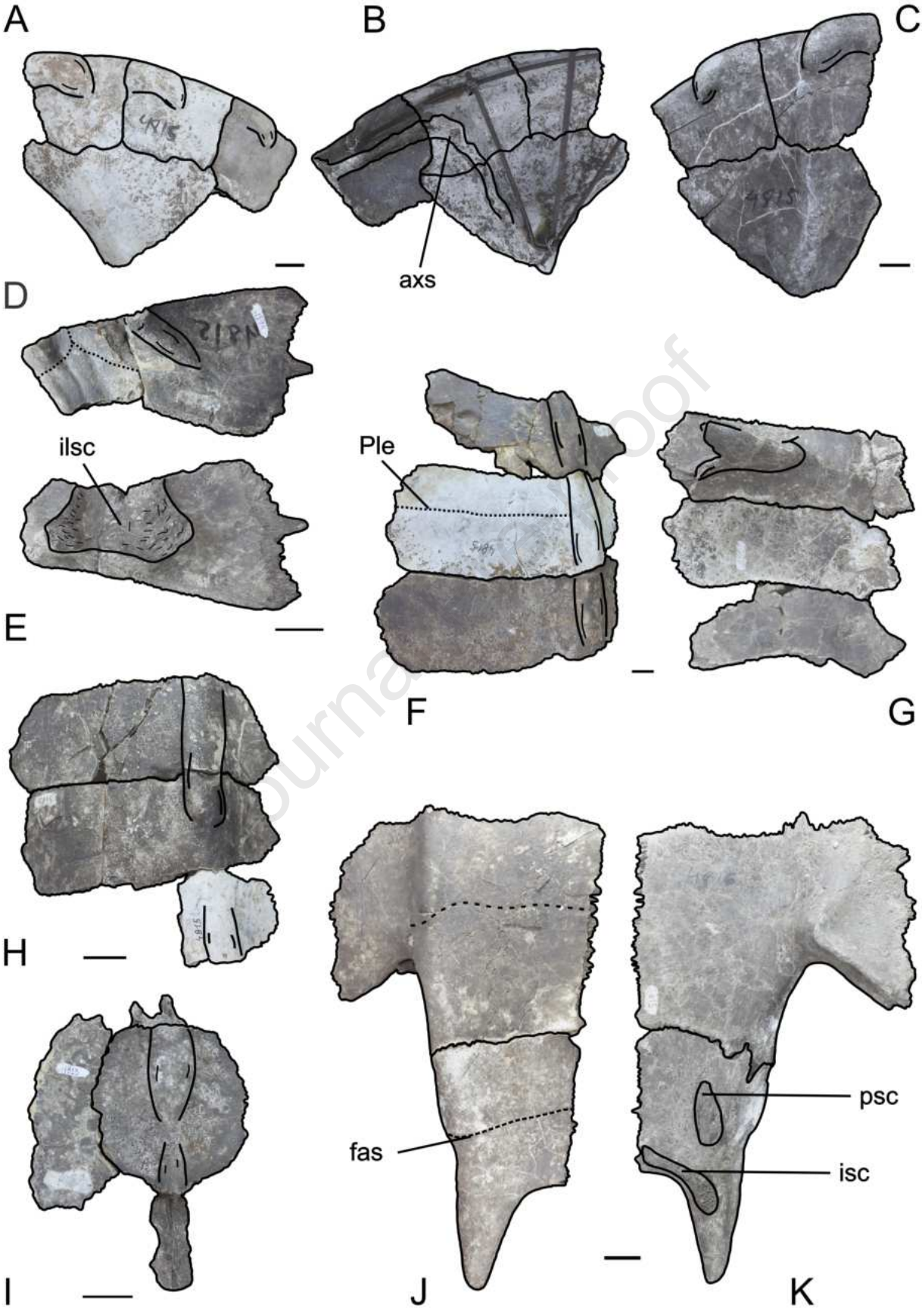

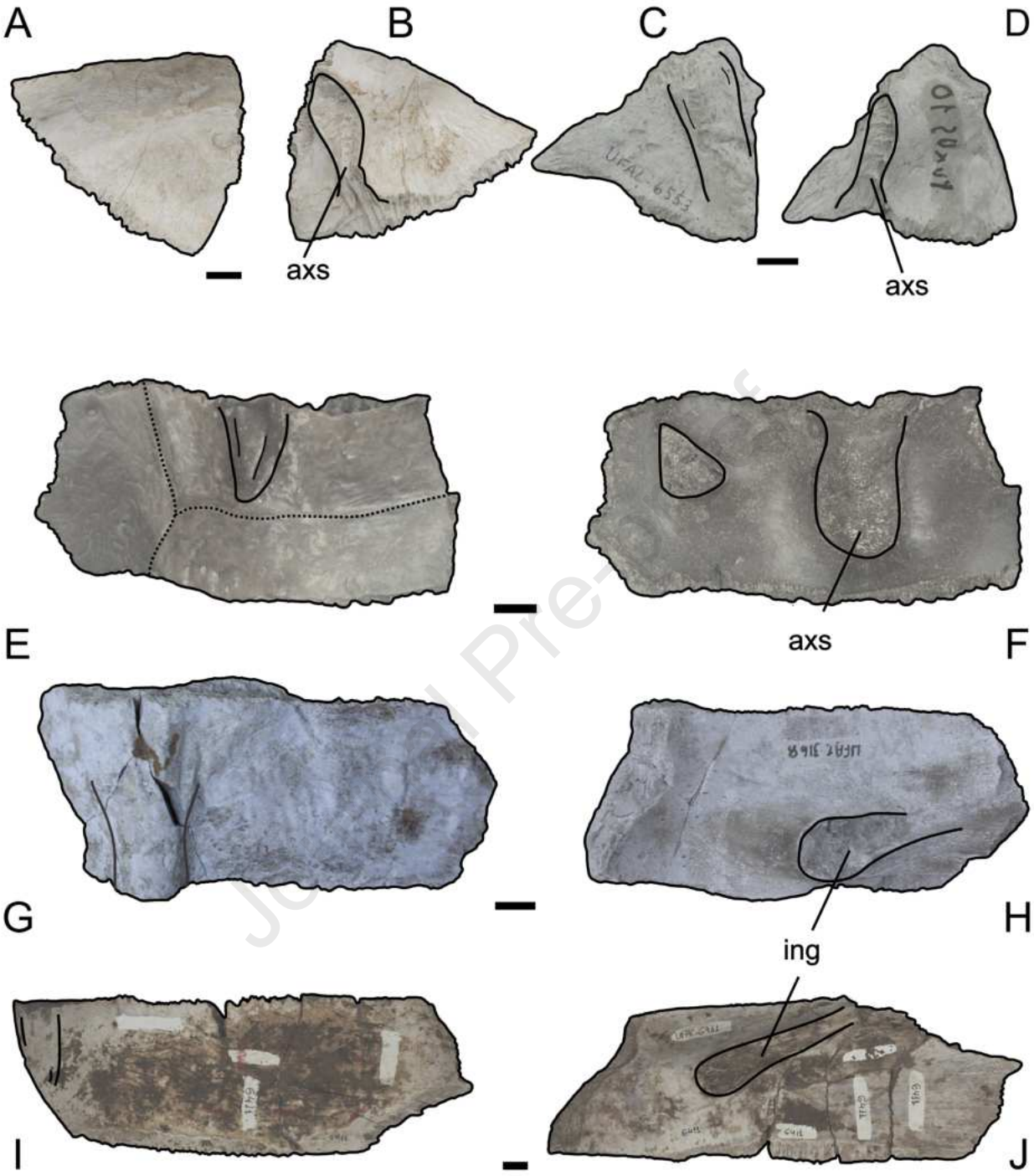
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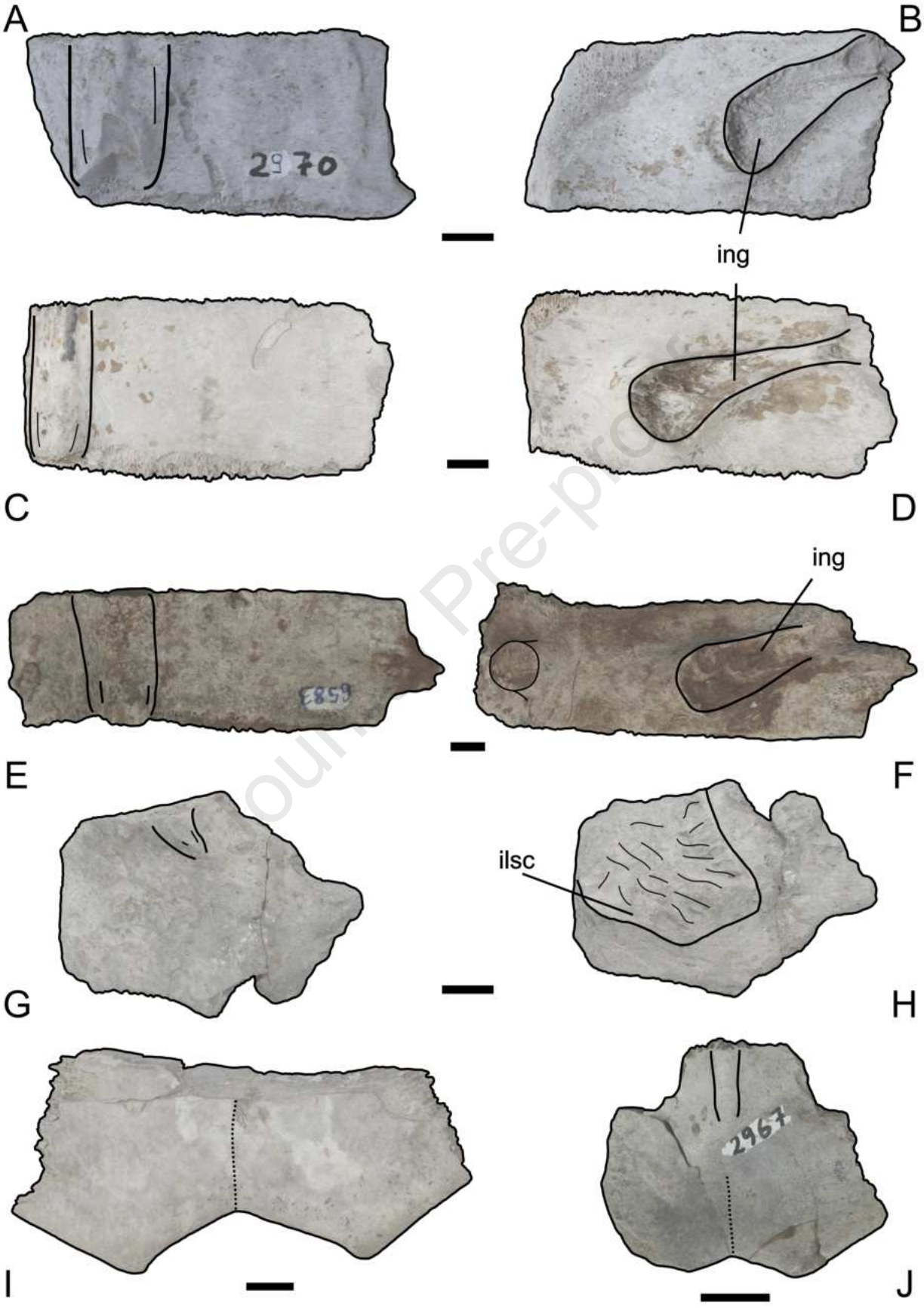

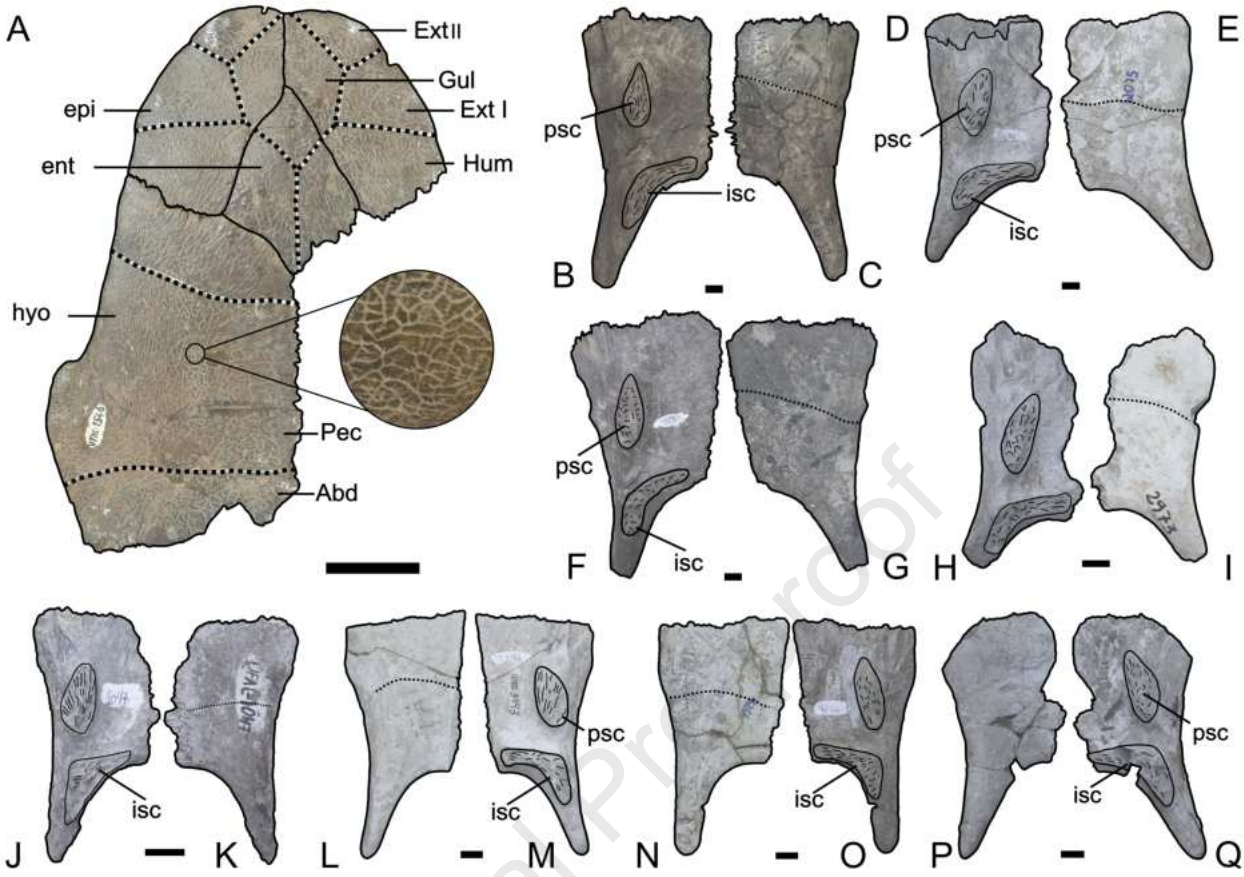

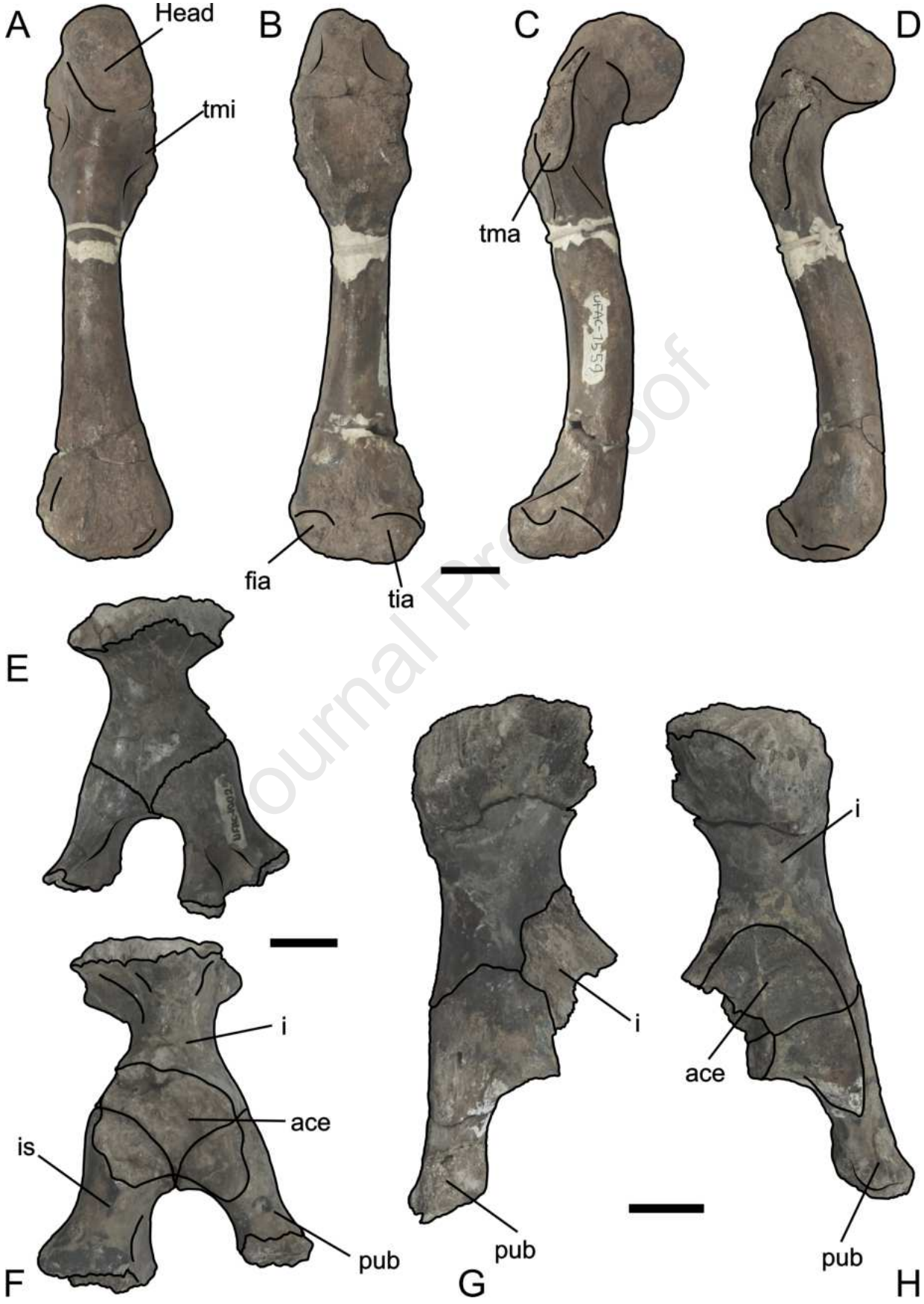

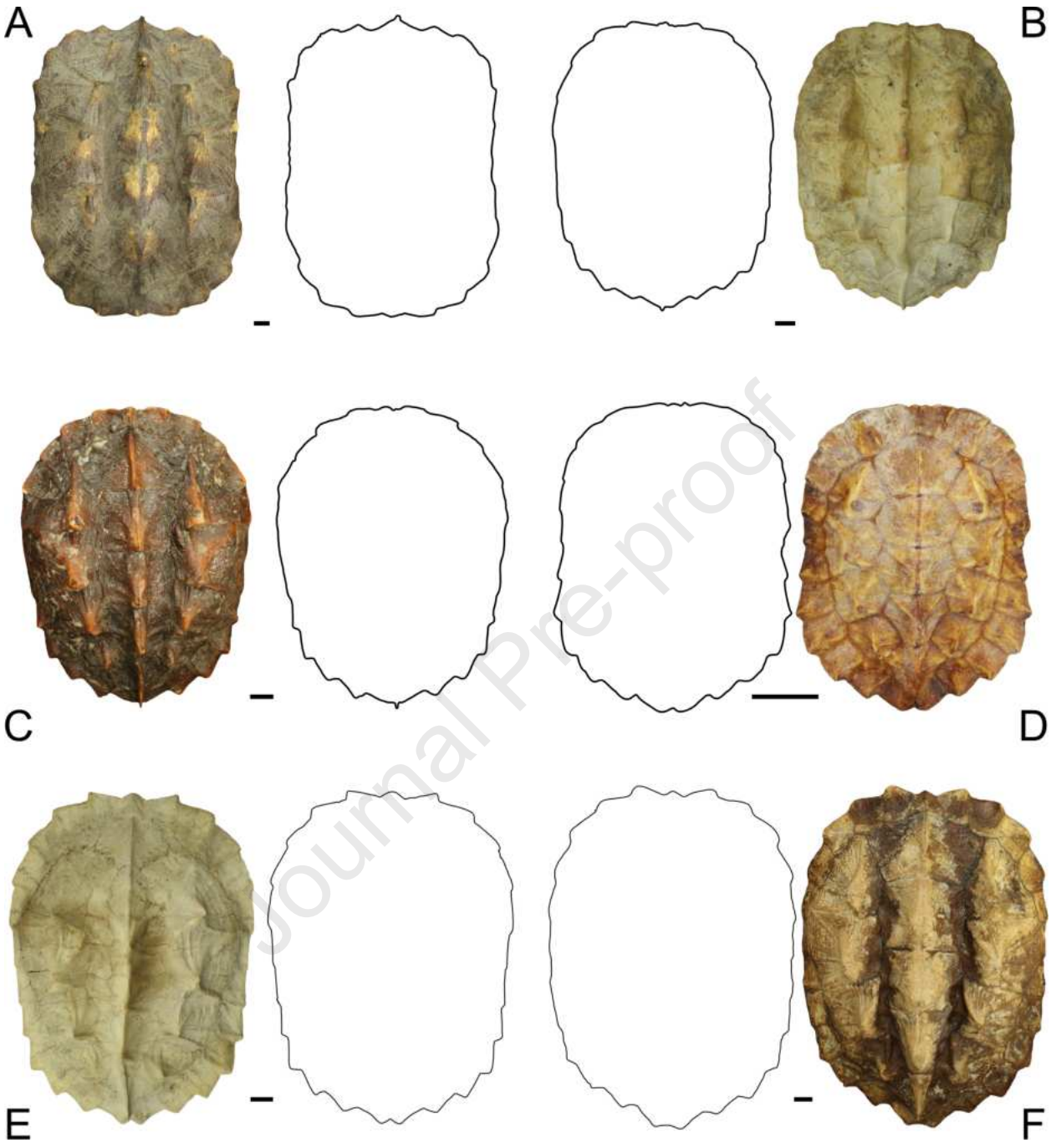

## Highlights

- New fossils present the most complete Miocene record of *Chelus* in Brazil.
- The maximum size of *Chelus* is expanded by a new specimen.
- More complete specimens support a single extinct species of *Chelus* in the Brazilian fossil record.
- Unique trait combinations reveal previously unappreciated morphological diversity
- The Acre Basin was the center of a broader distribution of a single extinct mata-mata species

**Declaration of interests**

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: