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ORIGINAL PAPER

Review of the fossil matamata turtles: earliest well-dated record and hypotheses on the origin of their present geographical distribution

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Abstract The matamata (*Chelus fimbriatus*) is a highly aquatic chelid turtle known exclusively from northern South America. Due to its extremely modified morphology, it is well circumscribed among living taxa, but that is not the case of the two extinct species ascribed to the taxon, *Chelus colombianus* and *Chelus lewisi*. These were originally described for the Miocene of Colombia and Venezuela, respectively, and are known mostly from post-cranial material. Few traits have been considered diagnostic for these fossil taxa, and their shared geographic and temporal distributions raise doubts about their distinctiveness. Here, we describe new turtle remains from the early Miocene Castillo Formation, at Cerro la Cruz, northwestern Venezuela, assigning them to *C. colombianus*. We also review the taxonomy and diagnostic features of the fossil species of *Chelus*, comparing them with the variation recognized within *C. fimbriatus*. All alleged differences between the fossil *Chelus* species were found in our sample of the extant species, and may represent intraspecific variation of a single fossil species. Further, we reviewed the fossil record of *Chelus* spp. and proposed a paleobiogeographic hypothesis to explain its present geographic range.

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Keywords *Chelus* · Chelidae · Miocene · Venezuela · Biogeography

Introduction

The South American chelid turtle genus *Chelus* was erected by Duméril (1806) for the matamata, first described by Schneider (1783) as *Testudo fimbriata*. The modern distribution of *Chelus* includes northern Brazil, Colombia, Ecuador, French Guiana, Guyana, Suriname, Peru, and Venezuela, in both the Orinoco and Amazonas river systems, as well as in Trinidad island (Pritchard 2008) and possibly also in the Maracaibo Basin (Pritchard and Trebbau 1984; Rueda-Almonacid et al. 2007). This species is a highly aquatic turtle, preferably inhabiting "still waters of oxbow lakes and quiet inlets and ponds, and relatively small, slow-moving creeks" (Pritchard 2008), but also found in more energetic and salt-water environments (Pritchard and Trebbau 1984).

Two extinct *Chelus* species are currently recognized, *Chelus colombianus* and *Chelus lewisi*, both described by Wood (1976) based on nearly complete shells (Fig. 1) from the middle Miocene Villa Vieja Formation of Colombia and the late Miocene Urumaco Formation of Venezuela (Linares 2004), respectively. These localities are outside of the current geographic range of the *Chelus* clade (Wood 1976). Shell remains assigned to *C. colombianus* were subsequently reported from the upper Miocene Solimões Formation (Acre, Brazil; Bocquentin 1988; Bocquentin and Rodrigues dos Santos 1989), and further material was reported from the Urumaco (*C. lewisi*, Sánchez-Villagra et al. 1995a) and Solimões (*C. colombianus* and *C. lewisi*; Bocquentin et al. 2001) formations. Cadena et al. (2008) revised the Solimões Formation material first reported by Bocquentin and Rodrigues dos Santos (1989) and concluded that they were

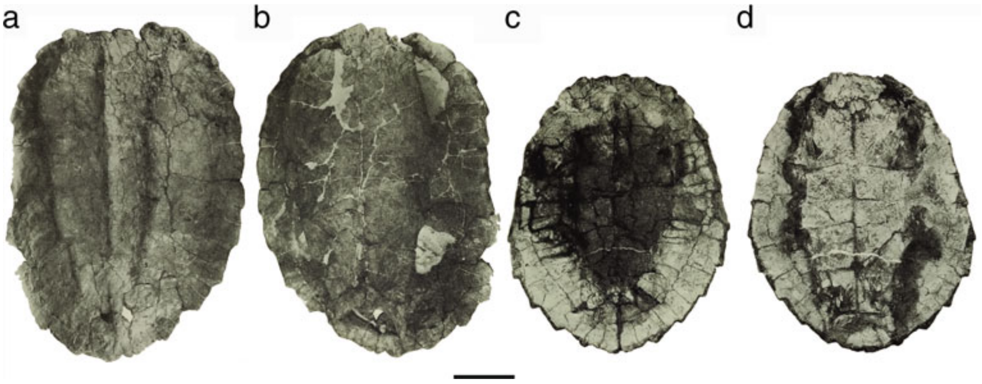


Fig. 1 Holotypes (Wood 1976) of *Chelus colombianus*, UCMP 78762, in dorsal (**a**) and ventral (**b**) views and *C. lewisi*, MCNC 239, in dorsal (**c**) and ventral (**d**) views. *Scale bar* 1 cm

more closely related to *C. lewisi*. Those authors also described new shell elements from the Barzalosa Formation of Colombia. These were assigned to *C. colombianus*, extending the temporal range of that taxon to the early Miocene (Cadena et al. 2008). More recently, shell material assigned to *C. colombianus* and *Chelus* sp. (possibly *C. lewisi*; Cadena and Jaramillo 2015a) and the first partial skull assigned to *C. colombianus* (Cadena and Jaramillo 2015b) were reported from the early Miocene (~16.2 Ma) Castilletes Formation of Colombia.

Here, we describe the first *Chelus* remains found in the early Miocene Castillo Formation, northwestern Venezuela, and review the taxonomy and paleobiogeography of the taxon. Previously reported by Rincón et al. (2014), this material corresponds to the earliest well-dated *Chelus* record.

Geological background

The Castillo Formation was deposited within the Falcón Basin, northwestern Venezuela, which is situated in the state of Falcón and parts of Zulia, Lara, and Yaracuy. Early geological studies suggested that the Castillo Formation was deposited in shallow fresh water to brackish environments, with intermixed local continental episodes (e.g., Wheeler 1960). Its age ranges from late Oligocene in the north to early Miocene in the south of the Falcón Basin (Wheeler 1960; Johnson et al. 2009; Rincón et al. 2014). The diversity of vertebrate remains from the Castillo Formation was recently described for the Cerro La Cruz locality, at the northern part of the Falcón Basin (see Rincón et al. 2014 and Solórzano and Rincón 2016). Cerro La Cruz is near La Mesa village, north of Carora town, Lara, in the southernmost extension of the Sierra de La Baragua (Fig. 2). The lithology of the Cerro La Cruz sequence includes alternating layers of siliciclastic and carbonate sediments, deposited mainly in nearshore marine environments, with apparently short-duration episodes of continental influence (see Rincón et al. 2014 for details). Four $^{87}Sr/^{86}Sr$ radioisotopic ages suggest that the Cerro La Cruz sequences were deposited during the early Miocene (17.21–19.27 Ma; Burdigalian). The *Chelus* material described here comes from the informally named "Cast-40" level which corresponds to the basal beds of "Unit C" sensu Rincón et al. (2014), with a constrained

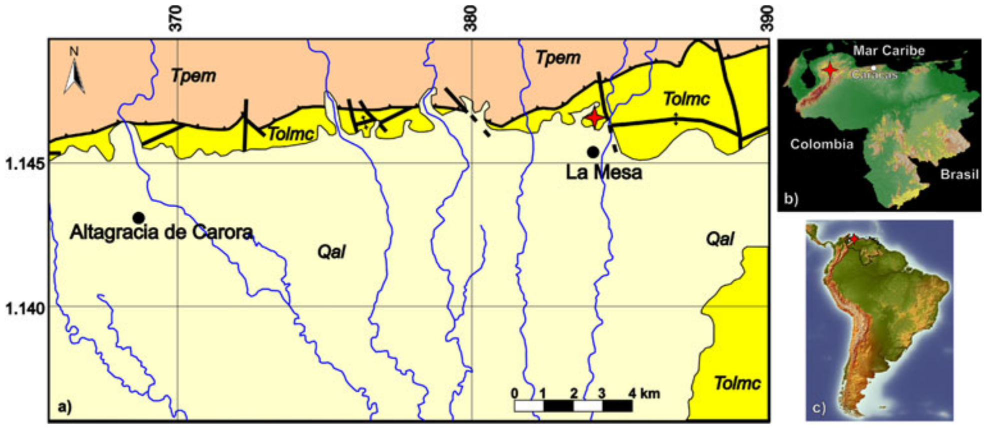


Fig. 2 Location and geological setting of Cerro La Cruz, Castillo Formation, Lara, Venezuela, where the specimens described here were collected. **a** Geological map of Cerro La Cruz, modified from Martínez and Valletta (2008) and Rincón et al. (2014); the *red star* shows the location of the analyzed section. Maps of Venezuela (**b**) and South America (**c**); *red stars* show the location of Cerro La Cruz. *Tpem* Matatere Formation (Eocene), *Tolmc* Castillo Formation (Early Miocene), *Qal* Alluvial (Quaternary)

age between 17.21 and 18.27 Ma (early Miocene, Burdigalian).

The specimens described here are housed at the paleontological collection of Instituto Venezolano de Investigaciones Científicas (IVIC-P) in Caracas, Venezuela.

Materials and methods

The specimen IVIC-P-678 is housed at the Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela. Photographs were taken using a Nikon D300 digital camera, and the figures were prepared on Adobe Photoshop CC and Illustrator CC softwares.

Institutional abbreviations GMB, M1MP and IGEOMINAS, Museo Geológico José Royo y Gómez, paleontological collection INGEOMINAS (Instituto Colombiano de Geología y Mineria), Bogotá, Colombia; IVIC-P, Colección de Paleontología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela; FMNH, Field Museum, Chicago, USA; MCNC, Museo de Ciencias Naturales, Caracas, Venezuela; MCNUSB, Museo de Ciencias Naturales de la Universidad Simón Bolívar, Miranda, Venezuela; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MPEG, Museu Paraense Emílio Goeldi, Belém, Brazil; MPV, Museo Paleontológico de Villavieja, Departamento del Huila, Villavieja, Colombia; MUN, Museo de la Universidad del Norte, Barranquilla, Colombia, -STRI-dbid, Smithsonian Tropical Research Institute, geological sample collection, Balboa, Ancon, Panama; UCMP, University of California Museum of Paleontology, Berkeley, USA; UFAC, Universidade Federal do Acre, Rio Branco, Acre, Brazil; UNEFM, Museo de la Universidad Nacional Experimental Francisco de Miranda, Falcón, Venezuela; USNM, United States National Museum, Washington, DC, USA.

Systematic paleontology

Testudines Batsch, 1788
Pleurodira Cope, 1864
Chelidae Gray, 1825
Chelus Duméril, 1806
(Figs. 3, 4, 5, and 6)

Type of species *Chelus fimbriatus* (Schneider, 1783)

Included species *Chelus fimbriatus* (Schneider, 1783) and *Chelus colombianus* Wood, 1976 (=*Chelus lewisi* Wood, 1976; see "Discussion")

Diagnosis Same as proposed by Cadena and Jaramillo (2015b)

Distribution Early Miocene of Colombia (Barzalosa Formation; referred to as "lower" Miocene) and Venezuela, based on the ^{87}Sr/^{86}Sr 17.21 to 18.27 Ma age of the basal beds of "Unit C" of Cerro La Cruz, Castillo Formation (Rincón et al. 2014), to recent northern South America

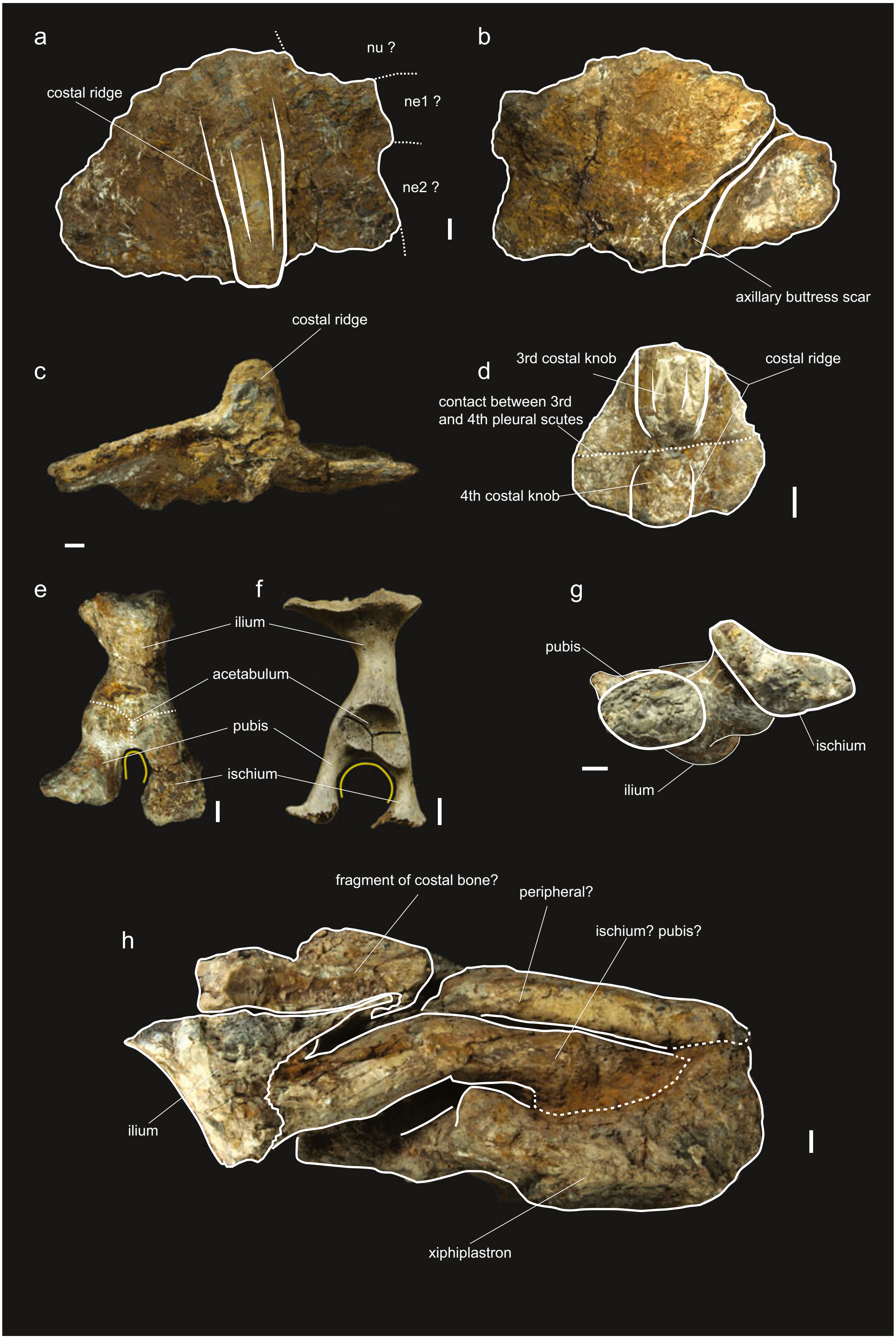
Nomenclatural remarks Two genus names entered the scientific literature in reference to the extant matamata turtle, *Chelus* and *Chelys*, and we agree with Zug (1977) that *Chelus* should be preferred. Cadena et al. (2008) argued that the feminine forms "*colombiana*" and "*fimbriata*" should be used as specific epithets, instead of "*colombianus*" and "*fimbriatus*." This was based on the International Code of Zoological Nomenclature (ICZN 1999; Art. 30.1.2), which states that "a genus-group name that is or ends in a Greek word transliterated into Latin without other changes takes the gender given for that word in standard Greek dictionaries." Indeed, the Greek word *χελύς* is feminine and, if correctly transliterated into Latin as "*chelys*," should maintain its gender, as for several other turtle names, e.g., *Proganochelys* (Gaffney 1990) and *Yaminuechelys* (de la Fuente et al. 2001). Yet, as explained by Zug (1977), Duméril's original description employed the name "*Chelus*," which has priority over "*Chelys*." Thus, the first available genus name for the matamata turtle is not an exact transliteration of the Greek word it is based on, but a Greek word Latinized with a change of the ending (E. Vlachos, pers. comm.). For such cases, the ICZN (1999; Art. 30.1.3) states that "a genus-group name that is a Greek word Latinized with change of ending, or with a Latin or Latinized suffix, takes the gender normally appropriate to the changed ending or the Latin suffix." Accordingly, since the Latin suffix -*us* in *Chelus* suggests a masculine word, the correct spelling of the specific epithets are "*colombianus*" and "*fimbriatus*."

Chelus Colombianus Wood, 1976
(Figs. 1, 3, 4, and 6)

Synonymy *Chelus lewisi* Wood, 1976

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

Referred material New specimen: IVIC-P-678 (Figs. 3 and 4; see "Description"); MCNC 239, complete shell ("*C. lewisi*" holotype; Wood 1976, pls: 4–5); GMB 2045A, incomplete shell lacking part of the right side of the carapace and cranial plastral lobe; GMB 2049, partial disarticulated shell; GMB unnumbered, caudal left quadrant of a carapace (see Wood


a
nu ?
costal ridge
ne1 ?
ne2 ?
b
axillary buttress scar
costal ridge
c
3rd costal knob
d
costal ridge
contact between 3rd
and 4th pleural scutes
4th costal knob
e
f
g
ilium
acetabulum
pubis
ischium
pubis
ischium
ilium
fragment of costal bone?
peripheral?
h
ischium? pubis?
ilium
xiphiplastron

◀ **Fig. 3** IVIC-P-678, *Chelus colombianus*. First left costal bone in **a** dorsal, **b** ventral, and **c** caudal views; fragment of the sixth right costal bone in dorsal view (**d**) and right pelvic girdle in **e** lateral and **g** ventral views; fragments of the left pelvic girdle, costal, peripheral, and xiphiplastral bones (**h**); left pelvic girdle of an uncataloged *Chelus fimbriatus* specimen in lateral view (**f**). *Scale bars* 1 cm. *nu* nuchal bone, *ne1-2* neural bones 1–2. The *yellow curve* represents the curvature between the pubis and the ischium

1976); IGEOMINAS unnumbered, caudal carapace fragment (see Sánchez-Villagra et al. 1995); MCZ 4337 and MCZ 4338, complete shells; MCNC 241, caudal half of carapace and plastron; MCNC 242, crushed vertebra (probably cervical) associated with a right xiphiplastron; MCNUSB-150-85-PB, complete carapace; MCNUSB-07-84-PB, incomplete carapace; MCNUSB-10-87-PB, reconstructed complete plastron, carapace fragments, complete left pelvis, scapular fragment, ulna, fibula, and other long bone fragments; MPV-120, complete carapace; MPV-199, complete carapace; MPV-unnumbered, carapace fragment; MUN-STRI-dbid 38473, partial skull; UFAC PV 4021, carapace caudal portion, right costals 2 and 3; UFAC PV 4345, medial and caudal portions of carapace and plastron; UFAC PV 1002, incomplete carapace and plastron; UNEFM 1371, complete shell. Other smaller fragments (see Wood 1976; Sánchez-Villagra et al. 1995a; Bocquentin et al. 2001; Cadena et al. 2008; Cadena and Jaramillo 2015a, b): GMB 2446; GMB 2042; GMB 2089; GMB 2085; GMB 2242; GMB 1844; GMB 1885; GMB 1891; M1MP60505-41, M1MP60505-44, M1MP60505-46, M1MP60505-61, and M1MP60505-79; MCNC 240; MCNUSB-79-85-PB; MUN-STRI-dbid 37471, MUN-STRI-dbid 37463, MUN-STRI-dbid 37462, MUN-STRI-dbid 37464; MUN-STRI-dbid 37465; MUN-STRI-dbid 37466; MUN-STRI-dbid 37467; MUN-STRI-dbid 37468; MUN-STRI-dbid 37469, MUN-STRI-dbid 37470, MUN-STRI-dbid 37472, MUN-STRI-dbid 37473; UCMP 39014; UCMP 39024; UCMP 38851; UCMP 38838; UFAC PV 755; UFAC PV 944; UFAC PV-1546; UFAC PV 1578; UFAC PV 445; UFAC PV 1578; UFAC PV 1580; UFAC PV 4032; UNEFM 1323; UNEFM 1415; UNEFM 1424; UNEFM 1442.

Taxonomic remarks Two other taxa described by Rodrigues (1892) have been referred to *Chelus* (Campos 1977; Oliveira and Romano 2007): "*Emys*" *quaternaria* and *Colossoemys macrococcygeana*. The former was described based on a left pelvic girdle (Pl. I–II in Rodrigues 1892) and a fragment later identified as a crocodile quadrate (Campos 1977). *Co. macrococcygeana* was based on an alleged pubis fragment later identified as a xenarthran humerus (Huene 1944; Price 1956; Paula-Couto 1960), two vertebrae later referred to Crocodylia (Patterson 1936; Williams 1952; Paula-Couto 1960; Campos 1977), and a hyoplastron fragment (Pl. XI in Rodrigues 1892). Based on the illustrations of Rodrigues (1892), Williams (1952) considered *Co. macrococcygeana* as Testudines incertae sedis. Afterwards, Campos (1977) assigned both "*Emys*" *quaternaria* and *Co. macrococcygeana* to *Chelus*, whereas Lapparent de Broin et al. (1993) considered both referable to Chelidae, but more similar to *Phrynops* than to *Chelus*. We agree with Lapparent de Broin et al. (1993; contra Campos 1977) about the non-*Chelus* chelid affinities of the material, but we are equally unsure about its *Phrynops* affinities. Additionally, no holotype was designated in the original description of both taxa (Rodrigues 1892) and the whereabouts of the referred material are unknown. Thus, we consider both "*E.*" *quaternaria* and *Co. macrococcygeana* as Chelidae insertae sedis, bearing no importance on the nomenclature of the genus *Chelus*.

Diagnosis Differs from *C. fimbriatus* by having the following: (1) the suture of the axillary buttress (on the ventral surface of the carapace) extending onto costal 2 instead of costal 1; (2) the inguinal buttress on costal 5, instead of costal 4; (3) one or more supernumerary scutes preventing the intergular scute from reaching the cranial margin of the plastron.

Results

Description

The Castillo Formation *C. colombianus* specimen IVIC-P-678 (Figs. 3 and 4) includes complete left first (Fig. 3(a–c)) and third (Fig. 3(d)) costal bones; a fragment of the right sixth costal bone (Fig. 4c, d); the suprapygal bone (Fig. 4e, f); either the second, fourth, or sixth neural bone (Fig. 4a, b); the right pelvic girdle (Fig. 3(e, g)); and a very distorted fragment of the shell containing what seems to be the left eight costal bone, the ninth and tenth peripheral bones, the left pelvic girdle, and a fragment of the xiphiplastron (Fig. 3(h)). These were all collected closely associated during several campaigns, thus inferred to represent a single specimen.

Carapace The left first costal bone is entirely preserved and is wider than long, more similar to those ascribed to *C. colombianus* (Wood 1976; Cadena et al. 2008) than to *C. fimbriatus* or *C. lewisi*, which are not as broad. The medial margin of the first costal bone does not seem to be broken, and it is possible to identify the contacts to the nuchal, first neural, and possibly the second neural bones (Fig. 3(a)). This suggests a subquadrangular and very reduced first neural bone, differing from those of other *Chelus* species, including the holotype of *C. lewisi*, which have more rounded first neural bones (Wood 1976). The fragment of the right sixth costal bone shows the contact between the third and fourth pleural scutes (Fig. 3(d)). The sulcus formed by the contact of those scutes strongly constricts the dorsal ridge, defining the costal knobs (Fig. 3(d)). The division of the costal ridges into well-

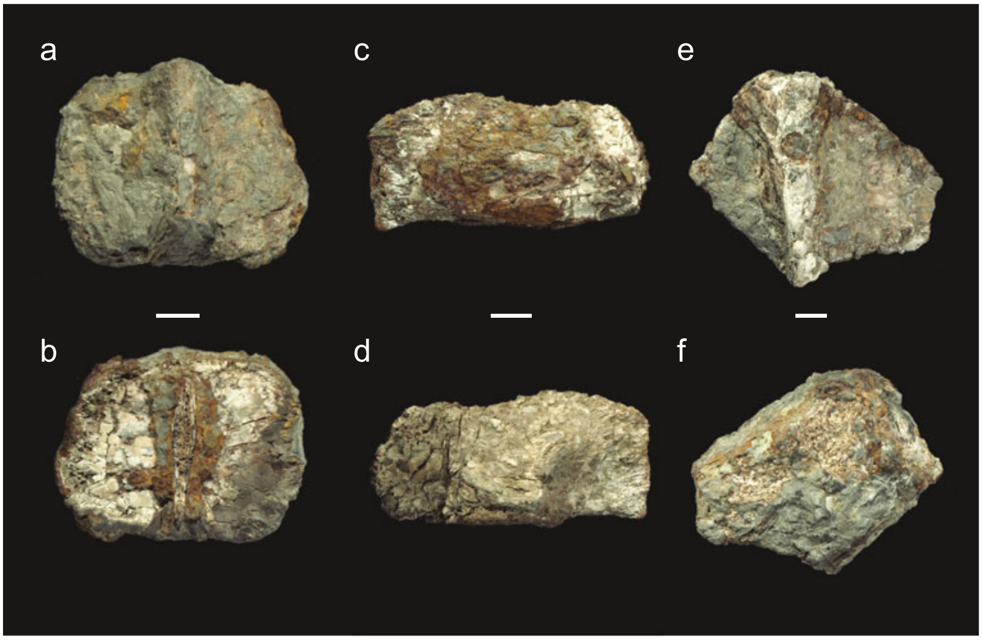


Fig. 4 IVIC-P-678, *Chelus colombianus*. Unidentified neural bone in **a** dorsal and **b** ventral views; fragment of the sixth left costal bone in **c** dorsal and **d** ventral views; fragment of suprapygal bone in **e** dorsal and **f** ventral views. *Scale bars* 1 cm

marked knobs is also seen in *C. colombianus* and *C. fimbriatus* but not in specimens ascribed to *C. lewisi* which have shallower ridges. Other pieces of costal bones in the carapace fragment containing the right pelvic girdle (Fig. 3(h)) are more fragmentary and do not reveal much morphological data. The preserved neural bone may be the second, fourth, or sixth element because its ridge is not constricted by the contact between vertebral scutes (Fig. 4a, b). The central ridge of IVIC-P-678 is not as developed as the costal ridges, a condition found in specimens ascribed to both fossil species, but it is higher than that of *C. lewisi* and closer to that of *C. colombianus* (Sánchez-Villagra et al. 1995a).

Pelvic girdle Unfortunately, pelvic girdle material of *C. colombianus* and *C. lewisi* has not been described, restricting the comparison of IVIC-P-678 to the extant *C. fimbriatus*. In general, the pelvic elements are stouter in IVIC-P-678 with a smaller space between the pubis and ischium in lateral view (Fig. 3(e, f)). Although the sutural surfaces of the pelvis in the xiphiplastra and costal bones are not preserved, their shape can be inferred by the articulation surfaces of the pelvic elements themselves. The ilium lacks the cranial projections on the articular surface seen in *C. fimbriatus* (Fig. 3(e, f)) and is consequently smaller. The pubic articular surface to the plastron is rounded (Fig. 3(g)), more similar to that of UFAC 1578 (*C. lewisi*, Cadena et al. 2008, fig. 2Q; *C. colombianus*, Bocquentin and Rodrigues dos Santos 1989). It differs from the pubic scar of *C. fimbriatus* and of specimens referred to *C. colombianus* which have a concave craniolateral rim (Cadena et al. 2008). The ischium sutural surface is more

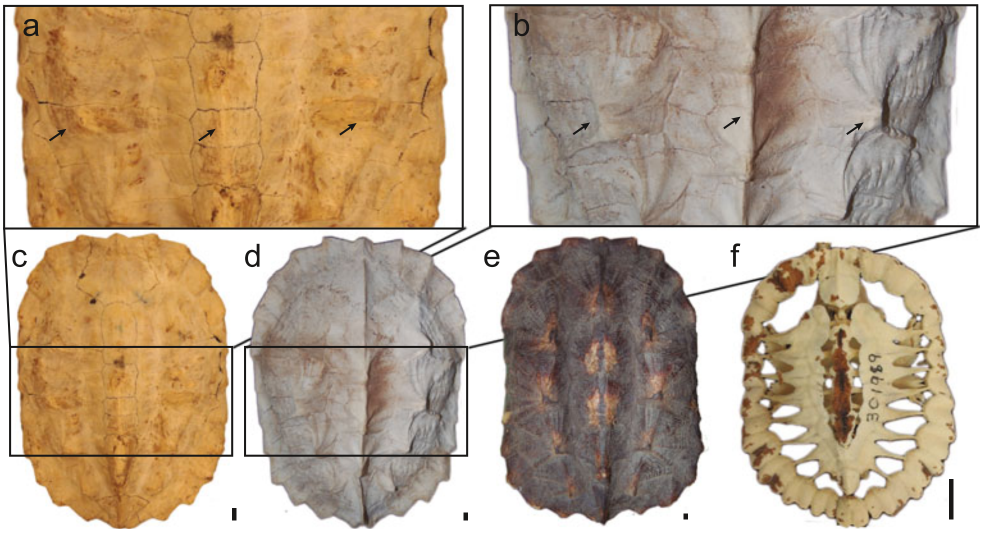


Fig. 5 *Chelus fimbriatus* carapaces in dorsal view, FMNH 22113 (**a**, **c**), MPEG 0407 (**b**, **d**), MPEG 0483 (**e**), and USNM 301989 (**f**). Note the intraspecific variation, with lower (**a**) and higher (**b**) dorsal ridges (pointed by the *black arrows*) and **c**–**f** different carapace outlines. *Scale bars* 1 cm

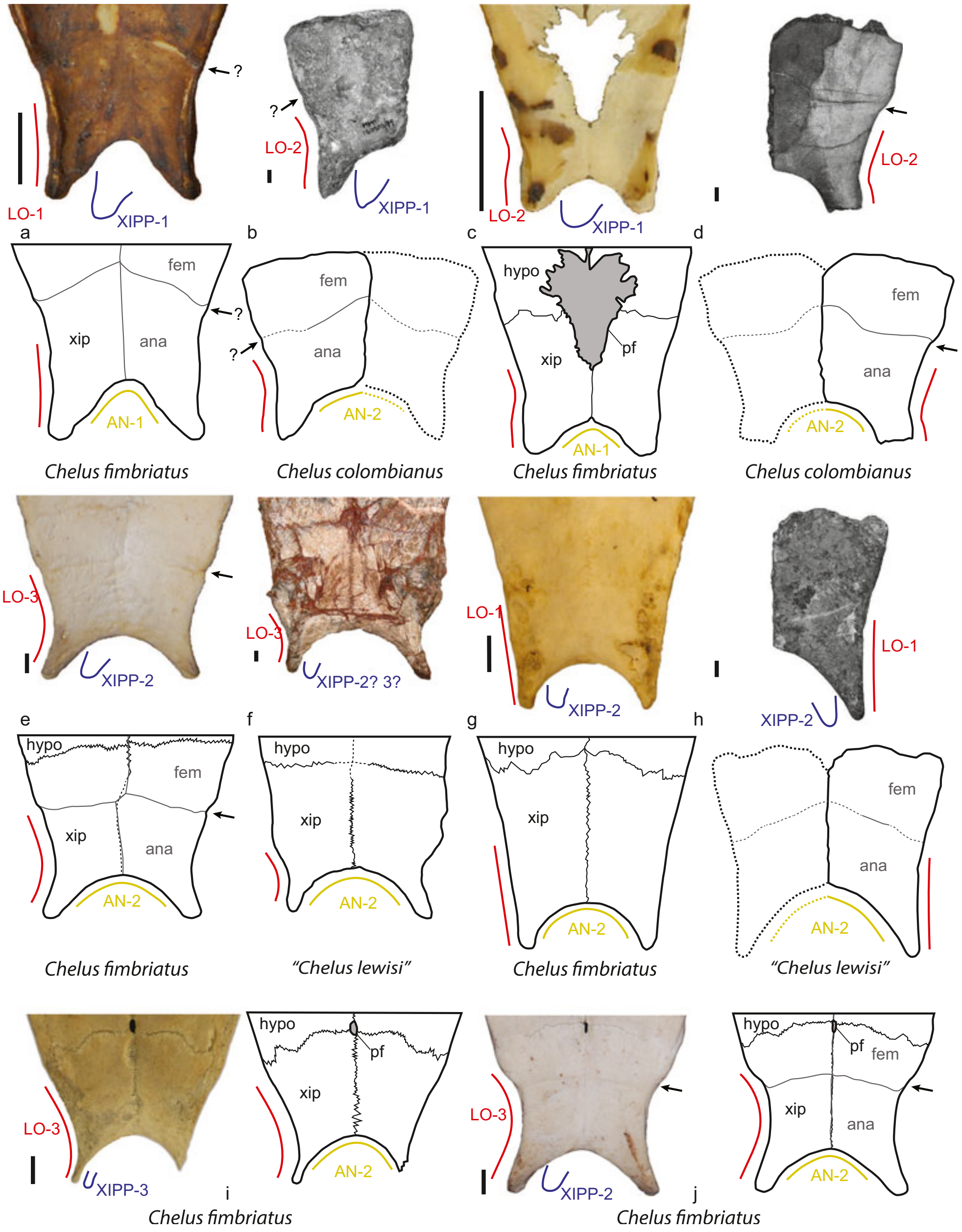


Fig. 6 Xiphiplastra of *Chelus colombianus* (**b**, **d**, **f**, **h**) and *C. fimbriatus* (**a**, **c**, **e**, **g**, **i**, **j**). MNRJ 0024 **a**, M1MP60505-79 **b**, USNM 301989 **c**, GMB 1891 **d**, INPA-H 24196 **e**, MCNC-92-72V **f**, FMNH 22113 **g**, UNEFM 1442 **h**, USNM 117454 **i**, INPA unnumbered **j**. *AN* anal notch, *ana* anal scute, *fem* femoral scute, *hypo* hypoplastron, *LO* lateral outline, *pf* plastral fenestra, *xip* xiphiplastron, *XIPP* xiphiplastral process. The *black arrow* points to the notch between the femoral and anal scutes on the xiphiplastron. *Numbers* following the abbreviations (e.g., AN-1, AN-2) indicate groups of similar morphologies, and the *lines with corresponding colors* (*red* LO, *blue* XIPP, and *yellow* AN) emphasize the outline of the concerned anatomical region. *Scale bars* 1 cm

robust with rounded cranial and caudal margins, and a concave medial rim (Fig. 3(g)). This is more similar to the ischiadic scar of specimens referred to *C. colombianus* and *C. lewisi* than to that of *C. fimbriatus* (Cadena et al. 2008).

Discussion

Taxonomy of the *Chelus* clade

The extant species *C. fimbriatus* is morphologically well defined relative to other chelid turtles (Pritchard 2008), but the same is not true for the other two extinct taxa of the clade, which are not clearly set apart from one another. Sanchez-Villagra et al. (1995b) reviewed the characters that Wood (1976) used to differentiate the three *Chelus* species and concluded that the shape and position of the intergular scute can be used to differentiate *C. fimbriatus* from the fossil taxa, in which the intergular is retracted from the cranial margin of the plastron. Also, *C. lewisi* could be distinguished from *C. colombianus* by its smaller size, less robust dorsal ridge knobs, and a carapace distinctly wider caudally than cranially. More recently, Cadena et al. (2008), based on new specimens assigned to *C. colombianus*, suggested that this fossil species could also be distinguished from *C. lewisi* based on (1) a wider and shorter caudal process of the xiphiplastron and (2) a pubic scar with both a caudally broader oval outline and a concave lateral rim in the cranial edge. Below, we address each of those features in detail, showing that the alleged differences between *C. colombianus* and *C. lewisi* can result from intraspecific variation, as seen among specimens of the extant *C. fimbriatus*.

The carapacial ridges of *C. lewisi* have been described as "rather thin and only moderately undulating" in contrast to those of *C. fimbriatus* and *C. colombianus* (Wood 1976). Yet, some specimens of the extant *C. fimbriatus* have thinner and more continuous ridges on the neurals (Fig. 5(a)), and there are also *C. lewisi* specimens with more robust ridges (e.g., UNEFM-1371; Sanchez-Villagra et al. 1995b, fig. 1b). In addition, several *C. lewisi* specimens, including the holotype, are markedly compressed dorsoventrally (pls. 4–5, Wood 1976), resulting in their dorsal ridges appearing smoother than they actually were in life.

In another paper, based on the specimens known at that time, Sánchez-Villagra et al. (1995a) estimated the shell size range of *C. lewisi* as 410–500 mm (possibly reaching 554 mm) and of *C. colombianus* as 548–720 mm. If MCNUSB-0784PB and MCNUSB-1087PB were correctly assigned to *C. lewisi* by Sánchez-Villagra et al. (1995a) and the specimens described by Bocquentin and Rodrigues dos Santos (1989) as *C. colombianus* (based on their estimated size of 715 mm) were correctly reassigned to *C. lewisi* by Cadena et al. (2008), the size range of both species would overlap. Accordingly, *C. lewisi* specimens could well represent the smaller individuals of a single Miocene taxon. Additionally, those size ranges are known from a very small sample (six to eight specimens of *C. lewisi* and four specimens of *C. colombianus*), which likely underestimates the actual size range of the fossil taxa. Such a bias was identified by Sanchez-Villagra et al. (1995b) for the 19-specimen sample of *C. fimbriatus* provided by Wood (1976), the maximum size of which was surpassed by several specimens studied by the former authors.

The carapace shape has always been regarded as a key feature in the distinction between *C. colombianus* and *C. lewisi.* Wood (1976) stated that it "leaves no doubt about the validity of this taxon [i.e. *C. lewisi*]," and Sánchez-Villagra et al. (1995a) concluded that the carapace shape was among the most important differences between them. The alleged difference is that the carapace of *C. colombianus* resembles one of the two carapace outlines found in *C. fimbriatus*, i.e., subrectangular with nearly parallel lateral edges (Fig. 5(c)), whereas the carapace of *C. lewisi* increases in width from front to rear (Wood 1976). As for the size estimation, the carapace shape differentiation seems also to be biased by restricted sampling. Various specimens of *C. fimbriatus* show a carapace outline similar to that of *C. lewisi* (Fig. 5(e)). Indeed, that shape is more common among juveniles or sub-adults of the living taxon (Fig. 5(f)), suggesting that this feature may change during ontogeny. Given that all more complete shells assigned to *C. lewisi* are smaller than those of *C. colombianus* (Sánchez-Villagra et al. 1995a), the difference in carapace shape can also be explained by ontogenetic variation, i.e., *C. lewisi* could correspond to the less-developed representatives of *C. colombianus*.

More recently, Cadena et al. (2008) proposed that the morphology of the xiphiplastron could be useful to distinguish between the two *Chelus* fossil species. Among the proposed features, they note that *C. colombianus* can be differentiated by a "modest-sized" notch on the lateral xiphiplastral edge near the contact of the femoral and anal scutes (which was considered present in *C. fimbriatus*, but "not nearly as well developed" as in *C. colombianus*) and by a broader and shorter caudal process of the xiphiplastron (Cadena et al. 2008). Once again, all of these features can be found as intraspecific variation of *C. fimbriatus* (Fig. 6). Both xiphiplastral process morphotypes of the fossil taxa have a corresponding morphotype in the extant species: the narrower one of *C. lewisi* (Fig. 6(f, h)) and the wider one of *C. colombianus* (Fig. 6(b)). Similarly, the notch on the lateral edge of the xiphiplastron is absent in some specimens of *C. fimbriatus* (Fig. 6(c, g, i)), but present in others (Fig. 6(e, j)), and sometimes even more strongly developed than in some *C. colombianus* specimens (compare Fig. 6(e–b)). Although Cadena et al. (2008) also proposed that a more medially placed pubic scar, with a concave cranial lateral rim, could be used to distinguish *C. colombianus* from *C. lewisi*, this does not seem to be a reliable feature either. The location of the pubic scar in *C. fimbriatus* is indeed more lateral, but the difference between the specimens figured in Cadena et al. (2008, Fig. 2) is too subtle. Similarly, although the lateral rim of UFAC 1578 (Fig. 2Q of Cadena et al. 2008), referred to *C. lewisi*, is rounded as opposed to concave, the lateral rim of GMB 1891 and UNEFM 1442 (referred to *C. colombianus* and *C. lewisi*, respectively; Figs. 2A,C and I,K of Cadena et al. 2008), are almost indistinguishable.

There are many other variable features found within a small sample of *C. fimbriatus* that could be used to group specimens and taxonomically discriminate fossil taxa. For example, the outlines of the lateral edge and anal notch of the xiphiplastron vary considerably (Fig. 6), with some specimens bearing more rounded (LO-2 and LO-3) or straighter (LO-1) lateral edges and "U"- (AN-2) or "V"-shaped (AN-1) anal notches. Alongside the other mentioned features, these reveal a great shell morphology variation in *C. fimbriatus* that, along with the shared geographic and temporal distributions of *C. colombianus* and *C. lewisi*, precludes their allocation in two different species, in accordance with the most recent phylogenetic analysis to include all *Chelus* taxa (Cadena et al. 2008) which found all of them in a politomy. Thus, we propose that both species are synonymous and consider *C. colombianus* as the senior synonym of *C. lewisi.*

Additionally, several authors (Strauch 1862; Pritchard and Trebbau 1984; Sanchez-Villagra et al. 1995b) identified morphological variation among *C. fimbriatus* specimens that seemed to be geographically structured. From that variation, some inferred the existence of separated Orinoquian and Amazonian populations (e.g., Pritchard and Trebbau 1984; Sanchez-Villagra et al. 1995b). However, studies with a larger sample (Pritchard 2008) and more detailed morphological analysis (Garbin 2014) found that, although there is a great deal of intraspecific morphological variation within *C. fimbriatus*, this variation is not well structured and/or fixed enough in distinct populations to represent two different species.

Paleobiogeography of *Chelus* spp.

Regardless of the relations among proposed species, it is possible to evaluate the historical biogeographic distribution of *Chelus* from the early Miocene onwards, based on its fossil record and the general distribution patterns of the extant *C. fimbriatus*. The matamata is a highly aquatic turtle, living mainly today in lowlands of the Orinoco and Amazon systems (Pritchard 2008). Accordingly, the geographic distribution of this species seems to be constrained by higher altitudes and the disjunction of river systems. Based on their very similar overall morphology, which seems to be related to the ambush predation feeding strategy of the extant species, providing camouflage on leafy river beds (Pritchard 2008), it is possible to assume that the extinct species had the same habitat preferences and dispersion potential.

The earliest unequivocal *Chelus* records come from the early Miocene (~23–16 Ma) of northwestern South America, i.e., Castillo Formation at Cerro La Cruz Venezuela (17.21–19.27 Ma, Rincón et al. 2014) and Castilletes Formation, Colombia (16.7–14.2 Ma; Handy et al. 2015; Moreno et al. 2015). At this time, the northern

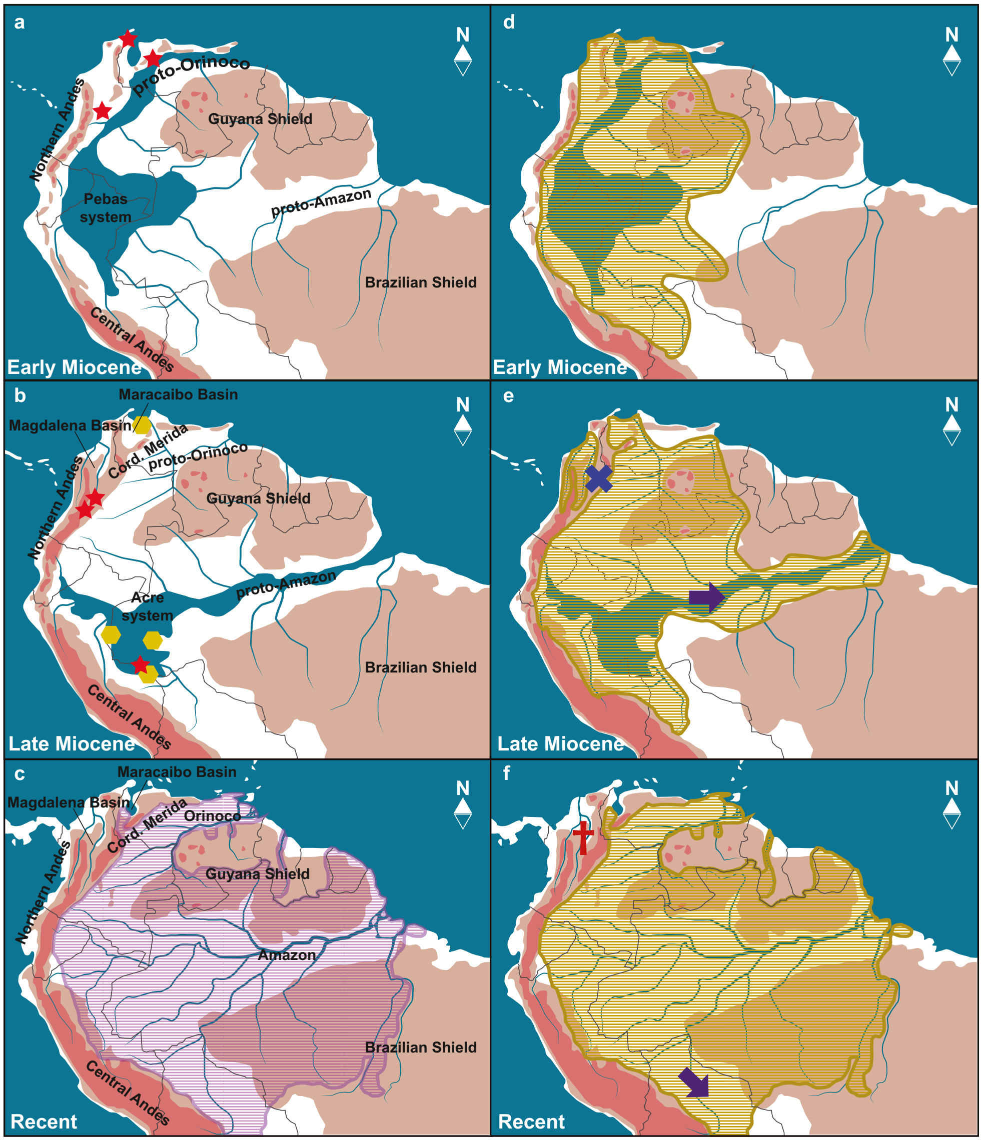


Fig. 7 Northern South America from early Miocene to present, showing records (**a**–**c**) and inferred geographic distribution (**d**–**f**) of *Chelus* spp. Specimens referred to *C. colombianus* are plotted as *red stars* and to "*C. lewisi*" as *yellow hexagons. Hatched areas* represent present and past distributions. The *blue x* denotes geographic isolation events, the *red dagger* local extinctions, and the *purple arrow* dispersal events. The modifications in distribution are inferred based on the modifications on habitat, e.g., uplift and changes of hydrographic basins, considering the constraints affecting the patterns of distribution of the extant *C. fimbriatus*

portion of the Andes did not reach very high altitudes (Rincón et al. 2014), and the present west Amazonian rivers were drained through the Pebas System, a lacustrine environment connected to the sea east of what is today the mouth of the Orinoco River, in Venezuela (Fig. 7a, d; Wesselingh and Macsotay 2006; Hoorn et al. 2010; Rincón et al. 2014). This system connected all rivers between the northern Andes and the Guyana shield, including western Amazonia, possibly allowing *C. colombianus* to occupy the entire basin (Fig. 7d).

C. colombianus fossils were also recovered from the middle to late Miocene (~10–7 Myr) deposits of the Villavieja (Colombia), Urumaco (Venezuela), and Solimões (Brazil) formations (Fig. 7b). During this time, the beginning of the northern Andes uplift isolated the Magdalena River basin (Colombia), which was previously connected to the Pebas System during the early Miocene (Hoorn et al. 2010). This may have caused the isolation of *C. colombianus* populations into this new basin (Fig. 7e). Middle/late Miocene tectonic events also changed water flow direction in the western Amazon, originating the Acre System. This large swamp system was drained through the so-called proto-Amazon River (Hoorn et al. 2010), allowing the dispersion of *C. colombianus* to the eastern areas of the Amazon basin (Fig. 7e). Although waters from the northern parts of the previous Pebas System were mainly drained via the proto-Orinoco River, possible small riparian connections between the proto-Orinoco and the proto-Amazon basins were not unlikely as today found in the Cassiquiare branch of the Orinoco and the Negro rivers. This mechanism might establish temporary or continuous connections between northern and southern *C. colombianus* populations from the middle to the late Miocene (Fig. 7e).

Both the record of *C. colombianus* in the Urumaco Formation (late Miocene, Venezuela) and its present distribution along the Orinoco River have been used as evidence of past direct connections between that area and the proto-Orinoco drainage system (Díaz de Gamero 1996; Aguilera 2004; Sánchez–Villagra and Aguilera 2006). However, Rincón et al. (2014 and references therein) concluded that the sedimentology of the Urumaco Formation seems not to be of deltaic origin (e.g., Díaz de Gamero and Linares 1989; Smith et al. 2010), but was more likely deposited in a complex lagoonal system, with very limited clastic sediment supply. Therefore, the record of *C. colombianus* in the Urumaco Formation would not indicate a connection to the proto-Orinoco, but rather the widespread distribution of that turtle species on the lowlands of northern Venezuela during the early to middle Miocene.

Following the Miocene, the uplift of the northern Andes further extended throughout Venezuela, forming the Cordillera de Merida (Bermúdez et al. 2011) which may have caused the isolation of *Chelus* sp. populations in the Maracaibo Basin (Fig. 7c, f). Some specimens of *C. fimbriatus* were found in Lake Maracaibo (Rueda-Almonacid et al. 2007), but these seem to be much rarer than in other areas (Pritchard 2008). Finally, at some point after their isolation from the Orinoquian-Amazonian basins, the *Chelus* sp. populations of the Magdalena Basin went extinct as no *Chelus* taxa are found in that river system today (Fig. 7c, f; Pritchard 2008).

Lastly, as mentioned above, there are connections between the Orinoco and Amazonian river systems via the Cassiquiare branch of the Orinoco and the Negro River in southern Venezuela. *C. fimbriatus* specimens collected in this area show more morphological variation than in other portions of both basins (Pritchard 2008; Garbin 2014), suggesting some degree of interchange between the Orinoquian and Amazonian matamatas. Population genetics analyses testing gene flow between the different *C. fimbriatus* populations are required to evaluate this hypothesis, which is well supported by morphological data. Thus, a conservative approach is to recognize only one extant and one extinct *Chelus* species. Given that there are no known fossil remains ascribed to *C. fimbriatus*, this hints at the possibility that *C. colombianus* and *C. fimbriatus* are part of an anagenetic lineage, i.e., *C. colombianus* is the direct ancestor of the extant matamata. This would reduce the ghost lineage of *C. fimbriatus* in about 10 Myr, if compared to the assumption that it corresponds to the sister taxon of *C. colombianus* in a strict cladistic sense. We have no means to test this hypothesis since both species have no temporal overlap, but the few autapomorphies that differentiate the species are not enough to disregard it for the moment.

Conclusions

The new specimens of *C. colombianus* described here from Cerro La Cruz, Castillo Formation, extend the early Miocene geographic range of this species to northwestern Venezuela. This reveals a more widespread distribution of *Chelus* spp. during that time interval and also provides an older absolute age for the taxon (17.21 to 18.27 Ma), allowing this age to be used as a fossil calibration datapoint on later divergence time analyses. A review of the diagnostic features of the two fossil *Chelus* species suggests that these most probably represent intraspecific variation, and *C. lewisi* is considered a junior synonym of *C. colombianus*, a species widespread in the Pebas System of northwestern South America, during the early Miocene. The northern Andes uplift changed water flow directions, shaping the matamata geographic distribution. These events allowed the dispersion of the taxon to eastern Amazon during the late Miocene and isolated *Chelus* sp. populations in the Magdalena and Maracaibo basins. Finally, although we cannot test this hypothesis with the current data, due to their disjunct temporal distribution, the similar morphology of the species suggests that *C. colombianus* could be the direct ancestor of *C. fimbriatus*, explaining the lack of *C. fimbriatus* fossils in the Miocene.

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